DARWINISM THROUGH HUNDRED YEARS

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IT was an uncommon coincidence in the history of science that two tireless naturalists, Darwin and Wallace, should have been writnig up their views on the problem of the origin of varieties and species in nature at the same time in different places unknown to each other, and should have come to nearly identical conclusions. Wallace was then in the Malay Archipelago. His essay "on the Tendency of Varieties to Depart Indefinitely from the Original Type", was sent to Darwin for perusal and subsequent communication to Lyell for publication if found fit. Darwin, on the other hand, at the persistent insistence of Lyell and Hooker was writing up his theory of Natural Selection which he had conceived clearly even in 1839, on the basis of his laborious collections and studies particularly during his 5-year voyage in the Beagle. This was early in the summer of 1858. The receipt of Wallace's essay created a crisis in Darwin's life. But true to his character and generosity his first reaction was to hold back his own work and allow Wallace's to be published. Lyell and Hooker had to use all their powers of persuasion to make Darwin consent to have an abstract of his own manuscript published along with Wallace's essay in *The Journal of the Proceedings of the Linnean Society*. This was the epoch-making Darwin-Wallace essays of 1858, of which the centenary is now being celebrated. Lyell and Hooker did not stop at that. They pressed Darwin to prepare a volume on his theory. At the end of more than a year of hard work, the volume was published in 1859 under the title, "On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life". (The "Origin of Species" or "The Origin", for short.)

It is implied in the title itself that Natural Selection is not Evolution. The two are different facts of nature. According to Darwin, and it is generally accepted, the former is the means by which the latter is brought about. This causational relation between the two is the essence of the theory of Darwin, what has come to be known as Darwinism. Though the credit for putting the concept of evolution on a scientific basis of facts of nature is mainly Darwin's, the concept is much older than Darwin. Even the Greeks had realized that change was the essence of existence.

Darwin's achievement was not the collection of the enormous data to support his theory. Anybody with patience and industry could have done that. Nor was the principle of Natural Selection altogether his own. His inspiration for it was from Malthus's Essay on Population. His real achievement was, as Carter says (1957), that from such simple and common premises he "produced the fundamental and, to his contemporaries, novel results of his proof of the truth of evolution and his theory of its causation". To those who accepted it, it provided a unifying concept in the light of which organisms ceased to be isolated entities, and came to be understood as part of the single flux of life continually changing with the changing world. Darwin gave Biology an intelligible background and made it logically comprehensible.

The early reaction to Darwinism was from two sources, from the general public and the biologists. There was fierce sentimental opposition from a section of the public to evolution and its method as expounded in Darwinism. So, it is no wonder that the simple forthright interpretation of evolution by Darwin in terms of fortuitous events leading to order and seeming purpose through Natural Selection was unpalatable to them as it conflicted with their ideas of the Creator and Design. The climax of this was reached at the Oxford Meeting in 1860 at which Bishop Wilberforce deliberately attempted to "smash Darwin" and ended up in being smashed by Huxley.

The more important point was the reaction of the biologists to Darwin. Generally, the biologists of the day reacted favourably, but it should not be imagined that all the biologists acknowledged the theory without adverse criticism. There were many points of criticism which were valid and real weaknesses of Darwinism. The following few among many are noteworthy.

1. Though Darwin had observed variations and realized their basic importance to evolution, he was fully ignorant of their causes or nature. He himself admitted and deplored it and considered the so-called acquired variations also as important to evolution. He even went to the extent of suggesting a mechanism of inheritance in the form of his theory of pangenesis which however never deserved and

got any acceptance. It was exactly this gap in Darwinism that was filled by modern genetics.

2. Evolutionary change involves co-ordinated changes. For example, an increase in the size of the body will need many correlated changes if the animal is to be efficient. Darwin almost overlooked this fact in his thesis. Perhaps he did not consider it as a serious difficulty to his view of evolution by accumulation of small variations. However, such correlated changes are not now difficult to understand in terms of polygenes and pleiotropism (Dobzhansky, 1951), and allometric changes (Huxley, 1932).

3. Those whose biology was based on *Naturphilosophie* did not easily accept Darwinism, as it was not an answer to their quest for the Absolute idea or the Divine plan of Nature or the conception of the archetype. To them law was something immutable, to Darwin it was a deduction from known facts.

4. Many other criticisms, which then looked like real difficulties have lost their point in the light of the new knowledge. One such related to complex structures like the vertebrate eye. The question was, could they have been of any use in the initial stages when they could have hardly functioned? If not, how could they have been selected? A study of the light-perceiving organs in the animal world makes it readily clear that even the simplest of them like the eye-spots of the green flagellates have been functionally efficient at their level. So evolution has not only been in structure but also in function. This removes the seemingly insuperable difficulty to accept the complex organs as the products of Natural Selection.

During the forty-one years of the 19th century after the publication of the "Origin", evolution came to be almost fully accepted, thanks partly to the championship of Thomas Huxley in England and of Haeckel in Germany. Huxley was a competent biologist himself and had no difficulty in winning the battle for Darwin. Haeckel too had accepted Darwinism, but his version of the theory was tinged with *Naturphilosophie*. His chief contribution was the theory of Recapitulation which was almost *Naturphilosophie* with the commonness of descent instead of the archetype. It was quite contrary to Von Baer's laws of ontogenesis. In the later years of the 19th century, Darwinism remained practically unchanged except for the rejection of the Lamarckian part of it along with Lamarckism in general, as a consequence of the Weismannian theory of the isolatedness of the gonad from the soma, so as to leave the former unaffected by the changes of the latter. In this period there was little progress in evolutionary biology, but there was an enormous output of morphological work in the several branches of biology. Much of it was by way of attempting to prove evolution and Natural Selection. It was only towards the end of the century that experimental embryology began to change the outlook of biologists a little.

The present century began with evolution well established as a fact, except for those who did not want to accept it. The almost total acceptance of evolution restricted the field of discussion and controversy to the means by which evolution took place. By the close of the 19th century, Darwinism too had been accepted as the means of evolutionary change. The idea had penetrated all aspects of human thought.

The history of Darwinism from the beginning of this century is a good example of how a comprehensive scientific concept undergoes change and refinement by impact of growing and more precise knowledge. The most important factor that affected Darwinism in the last 58 years was the rapid growth of the science of heredity, *i.e.*, genetics. "This supplied the missing parts of the structure first erected by Darwin" (Fisher, 1930). The basis of modern genetics was the laws of Mendel published in the latter half of the 19th century. They were far ahead of the times and remained unknown till they were rediscovered in the beginning of this century. The particulate nature of inheritance discovered by Mendel had revolutionary effects on the understanding of evolutionary problems.

Darwin had imagined the hereditary characters of the parents to blend in the progeny like water and milk. That would result in a levelling off of variations to uniformity in the members of a population, and would defeat selection. This was the most serious difficulty in Darwinism and it was obviated by Mendelian particulate inheritance. As shown by Fisher (1930), if inheritance had not been particulate evolution as we know it would not have been possible. Mendelian heredity provided a mechanism for both inheritance and variation, the conservative and the progressive aspects of evolution.

At this stage it may look strange that the first result of the Mendelian studies was to create a degree of disbelief in Natural Selection. De Vries's work on the evening primrose was published in 1901. He had noticed that many new forms suddenly appeared among his plants and bred true. He called such changes "mutations" and contended that evolution took place at least partly through such abrupt changes without involving the Natural Selection of small variations. Natural selection acted in such cases only after the origin of the new form, conserving or eliminating it. Bateson also held similar views. This gave a new importance to the distinction between the continuous and the discontinuous variations in regard to the process of evolutionary change. Darwin had attached little importance to the discontinuous variations. That accounts for the temporary loss of faith in Natural Selection. Mendelism seemed to conform to the views of these doubters of Natural Selection because of the apparent possibility of the large changes of De Vries and Bateson being inherited as Mendelian units. It was soon found, however, that many kinds of characters of organisms were inherited in the Mendelian manner. Meanwhile Morgan and others discovered the cytological basis of Mendelian inheritance in terms of chromosomes and genes, and their behaviour in reproduction. It will be going too far from the topic to consider the progress of genetics in the last fifty years. Suffice it to say that in this period, genetics became in itself an exact body of science and illumined many dark corners in biological knowledge, particularly in evolutionary studies. The understanding of genetic variations, mutations in the wide sense, their nature and frequency and even some of their causes (Muller, 1927), the problems of population genetics, the conceptions of the genotype and the phenotype, clarified and strengthened Natural Selection steadily and surely. But as mentioned earlier, the first impact of genetical knowledge on Darwinism had the unexpected result of many giving up the theory. It is not difficult to understand either. Darwinism involved the gradual accumulation by Natural Selection of small-graded changes. This was the indication of palæontological studies too. On the other hand, the early genetics dealt with changes that could be readily and easily noticed and so were of the discontinuous type. It seemed impossible to the leading biologists of the day that the observed evolutionary changes could be the result of selection of such genetic changes. This led to violent clashes in the biological world in the first two decades of this century. Bateson took an extreme view and declared that the Darwinian theory had collapsed. He went to the extent of reverting to a sort of preformationism in evolution, involving the progressive expression in organisms of the potentialities that had existed from the beginning of evolution. Many took up similar though less extreme views.

The real point at that time was whether the small variations on which Natural Selection was said to act were also Mendelian. This was not discussed then, as probably it could not have been in that state of genetical knowledge. The discussion was concentrated on whether the continuous or the discontinuous variations were the raw materials of evolution. This was a wrong question to ask and largely accounts for the biological stalemate of the time. This was resolved by further genetical studies in the recent decades. Two important advances in the field of genetics contributed to this. One was the new outlook on the genotype, and the other the new approach to studies of natural populations and their genetics. These also threw revealing light on the operations of Natural Selection.

In the earlier decades of the century a genotype was considered more or less as an aggregate of genes, each with a degree of independence of action. Recent decades brought the realization that the genes of a genotype constitute an intricately interacting system and that the phenotype is the product of such combined action of the genotype and the environment. A mutation in such a system will have its effect much modified by the other genes present and also by other mutations. Since individuals in a population vary in their genotype the effect of a mutation also will vary correspondingly. Further, when many genes may influence a character and any one gene may influence many characters the phenotypic expressions of the individuals may show the gradation observed in the palæontological studies of evolutionary changes, and envisaged by the theory of Natural Selection. It is true that a mutation is inherited as a unit, all or none. But its expression in the individual depends on the genotype and the environment. That explains the varying effect of mutation on individuals. However, it should not be forgotten that there are many known instances of mutations with phenotypic effects very distinctive and inherited like the characters of Mendel's peas. The pigmentation in what is known as "industrial melanism" is one such. They are comparatively rare. Normally in nature the differences are those based on many genes and varying in degree. This understanding brought about a reconciliation between the geneticists and the selectionists and the objection of Bateson and others thus disappeared. It also became clear that selection was not directly of the genotype but through the phenotype. Selection of a particular phenotype meant the selection of the genotype that produced it. It is largely a case of selection of the favourable recombinations of genes and allows for a margin of phenotypic adjustment to environmental variations. In the course of generations the more suitable gene combinations become more numerous in the population. In this process the favourable mutations that may arise may be incorporated into the genotype. The first effect of any mutation is usually a discordance as it is something new in a harmonious system. But subsequent selection will integrate it into the genotype if useful, or eliminate it if harmful. Either way, the harmony is restored which implies that a mutation has to undergo a probation before it is accepted as a full member of the genotype with suitable modification of its action by the rest of the genotype (Huxley, 1942). Natural Selection in this sense is the differential survival of the favourable genetic variants.

The slowness of selection makes observation of changes very difficult, if not impossible, but something like it has been observed in recent times. Germs are known to develop resistance to antibiotics rather quickly and this is obviously a case of selection of the favourable genotype at the expense of the others, in the presence of a new factor in the growth medium, the antibiotics (Demerec, 1950). Varieties of Drosophila kept in equal numbers in set environments have been found to undergo selective survival in relation to the environment. Green *Mantis* was found to survive largely when tied on green grass but mostly eaten by birds on brown grass. On the other hand, brown *Mantis* survived on brown grass but got decimated on green grass. The selective advantage of harmonising colour is thus demonstrated. These may not be true pictures of selection in nature. But their value is significant.

The new knowledge of selection in genetical terms has in its turn clarified the nature of the changes within a species and between species. That brings us to population studies, another sphere of advance in recent times. The world of biology owes tremendously in this connection to the brilliant mathematical analyses of the genetics of population and selection by R. A. Fisher (1930), J. B. S. Haldane (1932) and Sewall Wright (1942). To this must be added the names of Dobzhansky, E. B. Ford and E. Mayr. Their expositions of the interactions of selection, mutation and the other factors of evolution in populations have made possible the synthesis of varied observations and experimental results into a coherent thesis (Simpson, 1942).

The subtle ways of the operation of Natural Selection, and evolution by selection are now satisfactorily understood. The obvious fact that some individuals in a population leave more progeny than the others makes Natural Selection inevitable. This ability to leave more progeny than others in a particular environmental setting is the real fitness in the Darwinian sense. The well-known expressions "struggle for existence" and "the survival of the fittest" were used by Darwin in a metaphorical sense. "I should premise," said Darwin in the 'Origin', "that I use this term in a large and metaphorical sense including....success in leaving progeny." The convenient literal interpretation of the expressions by some persons is quite unwarranted. Reproductive success based on advantageous genotype is therefore the essence of evolutionary change. A population will gradually change in the direction of the genotype which continues to leave more progeny in successive generations. This is how Natural Selection directs evolution using the 'random' genetical variations as the raw material. This is the most significant contribution of the present century to the understanding of Darwinism.

This article is an attempt to trace the history of the theory of evolution by Natural Selection, during the hundred years since Darwin and Wallace propounded it. In the period the theory has been knocked into a cocked hat. But the core of it has stood the test of time. Generally it is adequate to explain the process of evolution, but there are still many problems of evolution, particularly in regard to the large evolutionary changes, which it is not adequate to explain. Most of the biologists agree with Darwin that varieties are incipient species and that species differ from varieties only in the greater degree of divergence making their natural interbreeding difficult or impossible. Some authorities like Goldschmidt (1940) do not agree with this view. He postulates radical mutations which he calls 'systemic mutations' to produce species differences. How such radical changes in individuals with integrated genotype can leave them viable is difficult to see.

There are others who are not convinced of the effectiveness of selection in regard to all the known evolutionary changes. Many bring in the Lamarckian factor in some sort of way. One of the latest is C. H. Waddington (1957). In terms of "genetic assimilation", "epigenetic landscape" and "canalized development" he suggests a causal relationship between an effect caused by the environment and the production and the selection of appropriate mutations. A phenotypic alteration within the normal range of expression of the genotype is understandable. There is no difficulty to see how such a change may help an organism to tide over a reasonable period during which the genotype may be harmonized to the new conditions by selection of appropriate mutations. The difficulty is to understand how enough of the suitable mutations arise at the right time. One possibility is to suppose that mutations are so common and varied as to supply the needed ones. To Waddington this is probably too much to suppose and so he postulates a developmental mechanism.

Fisher (1930) summed up the position as follows:

"The sole surviving theory is that of Natural Selection, and it is impossible to avoid the conclusion that if any evolutionary problem appears to be inexplicable on the theory, it must be accepted at present merely as one of the facts which in the present state of knowledge seems inexplicable." Since this was written many more problems have been explained. But many still remain and the words are still true. It is also implied that with the continued progress of knowledge the area of the inexplicable problems will progressively diminish.

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FISCHER-TROPSCH PROCESS

THE traditional form of fixed catalyst bed in the early Fischer-Tropsch process was a very inefficient arrangement, both as regards aerodynamics and heat transfer and this, in part, accounted for the very wide range of synthetic products produced. The fluid bed has been one device adopted to minimise these variations between different parts of the solid bed. The use of a genuine liquid bed for catalysis is a stage further. In this case the catalyst is suspended in a liquid through which the gaseous mixture rises in a constant stream of bubbles. The finely divided catalyst, with an average grain size of approximately 5 μ, collects at the surface of the rising bubbles and is constantly renewed there. The temperature can be kept remarkably constant, variations being not more than about 1° C. At temperatures of 250-300° C. and at pressures of 8-15 atmospheres, the synthesis gas is converted into hydrocarbons to the extent of over 90% in a single passage through the bubble column. The heat of reaction is removed by a cooling coil suspended in the bubble column and is converted into steam. Whereas by the traditional method the conversion of 1,000 m^3 of synthesis gas per hour required a cooling surface of 3,000 square meters, in a bubble column type of catalyser less than 50 square meters surface is required and the capacity of a single reactor has been raised from approximately 2·5 tons of hydrocarbon per day to 50 tons per day. The method has been used not merely for the hydrogenation of carbon monoxide but for the direct creation of carbon monoxide with water, according to the equation $3\,CO + H_2O = -CH_2 + 2\,CO_2$.