The Theory of Evolution since Darwin.[1]

By Prof. E. W. MacBride, F.R.S.

NO event in the intellectual world has had such a profound influence on the mental outlook of mankind in general as the publication of the "Origin of Species" by Charles Darwin in 1859. A distorted version of the theory embodied in it figured largely in the propaganda that led to the Russian revolution. Nothing could be more interesting to the student of the history of thought than to analyse the ideas and assumptions involved in this theory and to trace their fate in the subsequent course of scientific criticism.

The outlines of Darwin's theory are familiar to all, and the technical terms which he introduced—"natural selection," "the struggle for existence," "the survival of the fittest"—have passed into everyday language. It is to be noted that he termed his theory "Descent with modification," and that the name "evolution" was first applied to it by Herbert Spencer. This is significant, because in Herbert Spencer's mouth, evolution denoted a general theory of everything that was going on in the universe, of which the development of animals and plants formed only a small part. We must emphasise, therefore, the fact that Darwin takes life and the fundamental properties of living things for granted; he does not strive, like Spencer, to explain them in terms of matter and motion.

Founding on what he could observe of the nature of life as he saw it, Darwin strove to argue back to what was the condition of the living world in past times and what are the influences at work in modifying it at the present time. He assumed that animals and plants are continually giving rise to small variations in all directions and that these variations are inheritable. This is the positive idea which is embedded in what is generally called the theory of "natural selection." For "natural selection," the death of the many and the survival of the few, is only the pruning knife and can of itself originate nothing new. These random variations Darwin attributed not to chance but to the environment, which, as Darwin imagined, produced an instability in the hereditary qualities of organisms which are exposed to new conditions. But besides this effect, Darwin asserted that the results of increase in size of organ by use and its diminution in size by disuse were inheritable. He was driven to this assumption by the endeavour to account for the disappearance of unused organs in such cases as that of cave-animals which had lost their eyes. He could not conceive how small decreases in size in organs which were no longer used could give their possessors the victory in the struggle for existence. Darwin imagined, further, that the struggle for a bare existence was in many species accompanied by a struggle to find a mate, a struggle which was undertaken by the male; and he attributed the varied peculiarities of colour, shape, ornaments, and voice which distinguished males from females, to the preference of the female for the most attractive male. The results of this supplementary struggle were termed by Darwin "sexual selection." This part of the theory has not met with general acceptance, and we can therefore leave it out of account.

The difficulties in his theory which Darwin felt most acutely were the beginnings of useful organs from small useless rudiments and the origin of the sterility which usually exists between allied species. The first difficulty has been largely removed by the progress of embryological research, for it has been shown that new organs do not originate from useless rudiments but by the modification of older and simpler organs, but the second difficulty has not been fully solved even to-day. Believing as he did that allied species were only more sharply differentiated local races of the same species, Darwin yet had to admit that local races were mutually fertile, and that allied species when crossed were sterile. He pointed out that sterility could arise between members of the same species as it has done in the case of the primrose, and he imagined that sterility was, so to speak, a by-product of increasing divergence of constitution.

Of course, as Darwin himself pointed out, many naturalists before him had interpreted the likenesses of allied species as evidence of blood relationship, and had even put forward speculations as to the course of evolution; but the weak point in all these theories had been that they did not point to causes now in existence by which evolution could have been brought about. The first effect of Darwin's theory was to convince scientific men, especially naturalists, that evolution really had occurred and that it was in fact still going on. The feature in the theory which secured their assent was "natural selection." It seemed to his contemporaries that Darwin had laid hold of a fact which, when once attention was directed towards it, no one could deny, namely, the death of the many and the survival of the few. It is true that Lamarck had previously relied on natural causes, such as the effects of use and disuse and the production of new habits as the agents in evolution, and I myself believe that he was in great measure right, but the changes of habits in animals which he postulates are phenomena which are slow in their effects and do not constantly occur, and they are not easily observable within the limits of a human life. Moreover, the facts which now give support to Lamarck's views were not known when he wrote, nor even when Darwin wrote, and hence Lamarck failed to produce an effect on contemporary thought at all comparable to that which was effected by Darwin.

Huxley in England and Haeckel in Germany were the great champions of the evolutionary principle against theological opponents. Haeckel[2] made to the theory one great addition which is of far-reaching consequence: it had been dimly perceived by Darwin and is hinted at in the "Origin of Species," but it was first clearly enunciated by Haeckel. In his "General Morphology," first published in 1866, he stated that "Ontogenesis, or the development of the individual, is a short and quick repetition (recapitulation) of phylo-

[1] From a lecture delivered at King's College, University of London, on November 28, for the Board of Studies on the History, Principles, and Methods of Science.

[2] My friend Prof. Dendy has pointed out to me that Haeckel derived his "Law of Biogenetics" from Meckel, who wrote in 1827, but as Meckel was opposed by von Baer, the great comparative embryologist of the day, his views were ignored.

genesis, or the development of the tribe to which it belongs determined by the laws of inheritance and adaptation." This in shortened form, "Ontogeny is a recapitulation of Phylogeny," was called the "Fundamental Law of Biogenetics."

The validity of this law Haeckel sought to establish by numerous examples, and he has been accused, apparently with justice, with misrepresenting some of the facts in order to bring them into conformity with it. He is said to have made four separate drawings of the same embryo and to have labelled them with different names so as to show the identity of the early embryonic form in four different groups. This was detected, and together with the wildness of much of Haeckel's speculation tended, especially in Germany, to produce a strong reaction against most of Haeckel's teaching. But in spite of Haeckel's unscrupulous action he was in many respects a far-reaching genius. Though some naturalists have affected to disbelieve in the biogenetic law, in practice, in their morphological reasoning all assume its validity. Even Haeckel's special theory, namely, the derivation of the higher animals from a single hypothetical hydra-like ancestor, which he called the "gastræa," has received more and more confirmation as embryological research has proceeded.

Haeckel never thought that variations could be due to chance; on the contrary, he attributes them all to differences in nutrition. Some which we call "directly adaptive," like the effects of use and disuse, which alter the flow of blood to an organ and so change its nutrition, show their effects in a single generation, whilst others which he calls "indirectly adaptive" only make themselves felt in the next or succeeding generations. He says that the "superiority of Englishmen is due to their being fed on excellent beef; but the beef results from the cattle being grazed on rich clover pasture. Clover is fertilised by wild bees, but wild bees are decimated by field-mice, which are kept in check by cats. Cats are usually kept by old maids, and therefore this peculiarity of unmarried females is the original cause of British pre-eminence."

Huxley, though he contributed immensely to the building up of a scientific zoology on the basis of Darwin's theory, added nothing to the theory itself, but one of his sayings may be quoted as showing his insight into the matter at stake. "We have got our theory of evolution; what we want now is a good theory of evolution." We shall find that practically all subsequent criticisms of what for brevity's sake we may term Darwinism turn on these two questions, namely: (1) What is the nature and cause of variation? (2) Why are species usually mutually sterile?

We have already directed attention to the fact that the development of animals and plants from simpler ancestors was included by Herbert Spencer in his theory of evolution, a theory intended to explain everything that was going on in the universe on the basis of the laws of mass and motion. But Spencer laboured under all the disadvantages which beset those who write treatises on subjects with which they have only a second-hand or superficial acquaintance. It is true that in his "Principles of Biology" he sees clearly that the vital point at issue in Darwinism is the origin of variations, and he throws his whole weight on the side of the inheritability of the effects of use and disuse. But his arguments are not convincing, since they always involve a "petitio principii"; he never seems to see that a thorough experimental examination of the subject is necessary, but considers that his point is proved by vague plausible suggestions. He suggests that animals are made up of "physiological units," and that these units become modified in response to changed conditions and are then passed into the germ-cells and make their effect felt in the next generation. This conception resulted from his comparison of the regeneration of the limb with the self-completion of a broken crystal in its mother liquor, a conception which we now know to be utterly futile and misleading. No doubt Spencer did much to popularise the idea of evolution with the general public, but it is impossible to point to one addition of any scientific importance which he made to the theory of evolution.

It is true that Darwin in a later and far too imperfectly known book, "The Variation of Animals and Plants under Domestication," put forward a suggestion somewhat similar to that of the "physiological units" to explain the origin of variation. This is the theory of "pangenesis." According to this hypothesis, every part of the body of animal or plant is continually throwing off "gemmules" which are endowed with the power of multiplication and with the capacity, in suitable circumstances, of growing into the likeness of the part from which they came. These gemmules are carried from part to part by the circulation, and they accumulate in the germ-cells. They become altered in character in accordance with the alteration of the part from which they come, and when sufficient of the altered gemmules have accumulated in the germ-cells, the alteration becomes hereditary. Darwin's gemmules, however, are living units endowed with the characteristic vital properties of growth and reproduction, whereas Spencer's physiological units are merely large organic molecules.

The next important event in the history of the theory of evolution is the advent of Weismann, who in 1885 published his "Essays on Heredity," which were later consolidated into a book termed "The Germ-Plasm." Until his time it had been tacitly assumed that the effects of use and disuse could be inherited; and the only reason for refusing to assign to them the exclusive importance attributed to them by Lamarck was the difficulty which many naturalists felt in explaining some evolutionary changes by the accumulation of the results of efforts on the part of the animals or plants which exhibited them. But Weismann challenged the validity of the whole of the Lamarckian doctrine, and this he did on two grounds: first, that the evidence in favour of acquired characters was not sound, and secondly, that on account of the structure of what he calls the "germ-plasm," acquired qualities could not be transmitted. He therefore sought to explain the origin of variations by what I can only term the accidents besetting the ripening of the egg. Since all the father's potencies in heredity are contained in the sperm-head, which is a condensed mass of chromosomes equal in number to those in the ripe and unfertilised egg, the real bearers of hereditary powers must be the chromosomes.

If now we suppose that a single chromosome, which Weismann terms an "idant," nay, even a portion of a chromosome which he calls an "id," is theoretically capable of carrying out the entire development of the species, but that different "ids" would give rise to slightly different types of development and that the actual development of the egg is a compromise between the potencies of the various "ids," we arrive at the Weismannian explanation of variations. If it is mere chance which group of "ids" are thrown out of the nucleus when the number of chromosomes is halved at ripening, then obviously all sorts of different groups may be left in the make-up of the various eggs and various sperm-cells; and these different groups will give rise to different inheritable variations of which natural selection will preserve those best adapted to the circumstances of the animal.

But why should the various "ids" differ from one another? To this question an extraordinary answer was given by Weismann. When a cell divides, the nucleus divides first and each chromosome gives rise to daughter chromosomes by longitudinal splitting, which then by nourishing themselves at the expense of the protoplasm grow as big as their parent. During this growth, variations in nutrition of the daughters are the causes of variations in their structure which are handed on to their posterity at the next division! So that the very principle which Weismann rejects at the beginning of his hypothesis, he reintroduces in dealing with the chromosomes, namely, external circumstances giving rise to inheritable variation. Let us now glance for a moment at the way in which the theory is worked out in detail. The fertilised egg begins its development with a selected group of "ids" derived in equal proportions from the father and the mother; each of these "ids" contains within it the entire potency to bring about the development of the adult form. When the egg-cell divides, the division, though apparently an equal one, is in reality unequal—one daughter retains the "ids" undisturbed, but in another the "ids" have already undergone decomposition and are now represented only by "determinants," each of which has only the potency of causing the development of that part of the body to which this daughter-cell will give rise. As development continues, the determinants suffer further decomposition until at length they are resolved into "biophores," which have only the capacity of conferring on the cell in which they lie the power to become a muscle-cell, a nerve-cell, a gland-cell, etc. The descendants of the other daughter-cell of the original two, however, receive unbroken "ids" and eventually give rise to the germ-cells of the next generation. Their lineage is called the "germ-track."

On the Weismannian hypothesis, then, the germ-cells are separated from the body at the very beginning of development and are not afterwards influenced by what happens to the body during its growth; and Weismann, with true Teutonic thoroughness, having formed this conception of the structure of animals, declares it be *a priori* impossible that acquired characters, *i.e.* new habits, could affect the germ-cells, since, as he states, he can form no conception of how the change in structure resulting from a changed habit can be represented in the nucleus of the germ-cell. The experiments alleged to prove the inheritance of acquired qualities which were available to Weismann were supposed examples of the hereditary transmission of mutilations; these he sought to explain away, and he cut off the tails of mice and bred from these maimed animals, and showed that the offspring did possess well-developed tails.

Weismann's doctrines obtained wide acceptance, and were regarded as finally disproving the environmental origin of variations, and the position remained practically unchanged until the beginning of the twentieth century.

We may now pause for a moment to take up the question of the sterility between species. In 1897, Romanes, a Cambridge man who had migrated to Oxford, published a book entitled "Darwin, and after Darwin." In this book he considers the question of how two divergent species could have arisen from one, and he points out that it is inconceivable that this could have happened by the natural selection of accidental variations, unless two portions of the original species had become isolated from one another so that cross-breeding was prevented. Romanes puts forward the idea that owing to accident (*i.e.* unknown causes) physiological variations occurred, so that two portions of the same stock became mutually sterile. He thinks that geographical isolation is insufficient to account for the appearance of sterility, because species occupying adjacent territories are often mutually sterile, and he cannot conceive how what seem to him slight differences in climate can effect so great a change as sterility, but as to the causes of the appearances of this "physiological isolation" he gives no hint whatever. No further light was thrown on this subject until the last year or two, when Goldschmidt took up the question of the mutual fertility of local races of the same species when crossed. He showed in the case of the gipsy moth that when two races from widely separated localities are crossed, sterile intersexes are often produced which render the continued propagation of the mixed race difficult. His results therefore support Darwin's hypotheses of sterility as a by-product of increasing divergence of constitution.

The twentieth century began with two events of decisive importance for the theory of evolution; namely, the rediscovery of Mendel's researches by Correns in 1900 and the publication by Johannsen in 1903 of a paper entitled "The Bearing of Pure Lines on the Theory of Inheritance." Mendel's researches, which were carried out at the same time as Darwin's work and published soon after the publication of the "Origin of Species," appeared in local journals of too limited circulation, and attracted no notice from the general scientific world. They had in Mendel's mind no relevancy to the formation of species whatsoever, but were concerned only in discovering the laws governing the distribution of paternal and maternal characters amongst hybrid offspring. Mendel in his experiments always chose varieties sharply separated from one another by definite clearly-cut characters. The rediscovery of Mendel's work gave a great impetus to the carrying out of experiments in crossing all kinds of variants from the normal with the type. In these experiments Bateson in England and Morgan in the United States took leading parts, and it was soon discovered that those sudden deviations from the normal which turn up without assignable cause in most breeds of domestic animals and varieties of cultivated plants obey the Mendelian rules when crossed with the types. Johannsen's results proved the non-inheritability in the case of beans of those small random deviations from the normal in all directions on which Darwin had laid such stress, and these results were independently confirmed by Jennings, who worked on Protozoa, and by Agar, who studied small Crustacea (1912).

In consequence of these discoveries, biological opinion veered round in favour of regarding the conspicuous aberrations commonly known as sports as the raw material on which natural selection had worked. Darwin, it is true, had considered the question of whether sports might not be the starting-point of new species, and had decided that they could not be so on account of the rarity of their occurrence. He thought that the chance of such a sport mating with its like, even if highly successful in the struggle for existence, was infinitesimal, and that if it did not mate with its like its characters would be "swamped by intercrossing." But if the deviation were in a direction favoured by natural selection, it might be assumed that it would make itself felt in lesser degree even when its orginal possessor crossed with the type, and the first generation descendants might still survive on account of its lessened manifestation. Many have claimed that this argument is strongly reinforced by the discovery of the laws of Mendelism. For if the deviation behaved as a dominant when crossed with the type, all the first generation of the descendants of such a cross would show it in as strong a manner as its orginal possessor; and even if it were recessive it would appear in undiminished strength amongst one-fourth of the second filial generation. The real objection to regarding sports as the initiators of new species lies deeper. An animal does not survive on account of one organ. In its growth from the egg to the adult, it runs the gauntlet of many dangers, and a strong development of some one organ might determine its survival at one period of its existence, but if the deviation occurs very rarely the chances against that particular animal reaching the critical stage at all are enormous.

De Vries, the director of the botanical gardens at Amsterdam, carried out between the years 1886 and 1899 a series of cultures of the garden plant *Œnothera Lamarckiana*, commonly known as the evening primrose. He showed that every year a number of sports turned up, usually about half a dozen in 10,000 specimens, sometimes as many as three in a hundred, and that this sports usually, though not always, bred true when crossed with their like. De Vries called these sports "mutations," and imagined that he had surprised a species in a "fit of mutation," and that new species were not produced by a slow process of differentiation but by sudden jumps, so that they began their existence complete in all their details, as Minerva sprang from the head of Jove. The De Vriesian doctrine joined with Mendelism, and became the dominant doctrine of evolution and heredity for most of the first quarter of the twentieth century, and probably counts amongst its adherents a larger number of biologists than any other doctrine at the present time. It was first seriously put forward by Bateson in 1894 in a book entitled "Materials for the Study of Variation," in which he figured and recorded a large number of examples of monstrous deviations from the normal, and laid down two doctrines, one of which is undeniably true, whilst the second is really the De Vriesian theory. The first was "variation is evolution"; the second, the "discontinuity of species is due to the discontinuity of variation."

The De Vriesian view has reached its climax in a book termed "Age and Area" by Dr. Willis, a distinguished botanist. This book was published two years ago; in it Dr. Willis supports the idea that species originate in sudden inexplicable jumps which occur only rarely. This idea is difficult to distinguish from the pre-Darwinian doctrine of special creation. No wonder that Haeckel, who lived long enough to encounter this view in its early presentation by Bateson, said: "If views like this are to be accepted, it would be better to return to Moses at once."

(*To be continued.*)

Biographical Byways.

By Sir ARTHUR SCHUSTER, F.R.S.

INTRODUCTION.

THERE are things seldom referred to in obituary notices and sometimes omitted even in more ambitious biographies. They tell the tale of peculiarities or weaknesses, which the writer fears may detract from the merits of the man he has set out to praise. The biographer believes, with some show of justice, that his main object is to give a record of work accomplished and not a psychological analysis of character. But eccentricities, or even decided failings, form part of a man's personality. The extent to which his teaching carries conviction and affects the scientific outlook of his time, depend as much on his personal attributes as on the merits of his researches. We destroy the balance of a just valuation, if we ignore those shades of character or temperament which act as handicaps to the full fruition of his work.

It has been my good fortune to be acquainted personally with many of the men who laid the foundations of the science of the nineteenth century, and I have retained a vivid memory of such intercourse as I had with them. In writing down some of my recollections I have tried to outline personalities in a sympathetic spirit. If human frailties are sometimes exposed, I hope that the limits of allowable candour have never been transgressed, and that, apart from the personal factor, the incidents related may be found to contain some substantial contributions to the history of science during the middle period of last century.

1. URBAIN JEAN JOSEPH LEVERRIER (1811–1877).

Towards the end of December 1874, or nearly in the year 1875, I received an invitation from the Royal Society to take part in an expedition which was being