

Evolution: The Modern Synthesis, 1942

THE THEORY OF NATURAL SELECTION

Evolution may lay claim to be considered the most central and the most important of the problems of biology. For an attack upon it we need facts and methods from every branch of the science—ecology, genetics, paleontology, geographical distribution, embryology, systematics, comparative anatomy—not to mention reinforcements from other disciplines such as geology, geography, and mathematics.

Biology at the present time is embarking upon a phase of synthesis after a period in which new disciplines were taken up in turn and worked out in comparative isolation. Nowhere is this movement towards unification more likely to be valuable than in this many-sided topic of evolution; and already we are seeing the first-fruits in the re-animation of Darwinism.

By Darwinism I imply that blend of **induction and deduction** which Darwin was the first to apply to the study of evolution. He was concerned both to establish the fact of evolution and to discover the mechanism by which it operated; and it was precisely, because he attacked both aspects of the problem simultaneously, that he was so successful. On the one hand he amassed enormous quantities of facts from which inductions concerning the evolutionary process could be drawn; and on the other, starting from a few general principles, he deduced the further principle of natural selection.

It is as well to remember the strong deductive element in Darwinism. Darwin based his theory of natural selection on three observable facts of nature and two deductions from them. The first fact is the

tendency of all organisms to increase in a geometrical ratio. The tendency of all organisms to increase is due to the fact that offspring, in the early stages of their existence, are always more numerous than their parents; this holds good whether reproduction is sexual or asexual, by fission or by budding, by means of seeds, spores, or eggs.¹ The second fact is that, in spite of this tendency to progressive increase, the numbers of a given species actually remain more or less constant.

The first deduction follows. From these two facts he deduced the struggle for existence. For since more young are produced than can survive, there must be competition for survival. In amplifying his theory, he extended the concept of the struggle for existence to cover reproduction. The struggle is in point of fact for survival of the stock; if its survival is aided by greater fertility, an earlier breeding season, or other reproductive function, these should be included under the same head.

Darwin's third fact of nature was variation: all organisms vary appreciably. And the second and final deduction, which he deduced from the first deduction and third fact, was Natural Selection. Since there is a struggle for existence among individuals, and since these individuals are not all alike, some of the variations among them will be advantageous in the struggle for survival, others unfavourable. Consequently, a higher proportion of individuals with favourable variations will on the average survive, a higher proportion of those with unfavourable variations will die or fail to reproduce themselves. And since a great deal of variation is transmitted by heredity, these effects of differential survival will in

Pages 13–28 from *Evolution: The Modern Synthesis* by Julian Huxley. Copyright © 1942 by Julian S. Huxley, renewed © 1970 by Julian S. Huxley. Reprinted by permission of HarperCollins Publishers, Inc.

¹The only exception, so far as I am aware, is to be found in certain human populations which fall far short of replacing themselves.

large measure accumulate from generation to generation. Thus natural selection will act constantly to improve and to maintain the adjustment of animals and plants to their surroundings and their way of life.

A few comments on these points in the light of the historical development of biology since Darwin's day will clarify both his statement of the theory and the modern position in regard to it.

His first fact has remained unquestioned. All organisms possess the potentiality of geometric increase. We had better perhaps say *increase of geometric type*, since the ratio of offspring to parents may vary considerably from place to place, and from season to season. In all cases, however, the tendency or potentiality is not merely to a progressive increase, but to a multiplicative and not to an additive increase.

Equally unquestioned is his second fact, the actual constancy of numbers of any species. As he himself was careful to point out, the constancy is only approximate. At any one time, there will always be some species that are increasing in their numbers, others that are decreasing. But even when a species is increasing, the actual increase is never as great as the potential: some young will fail to survive. Again, with our much greater knowledge of ecology, we know to-day that many species undergo cyclical and often remarkably regular fluctuations, frequently of very large extent, in their numbers (see Elton, 1927). But this fact, although it has certain interesting evolutionary consequences does not invalidate the general principle.

The first two facts being accepted, the deduction from them also holds: a struggle for existence, or better, a struggle for survival, must occur.

The difficulties of the further bases of the theory are greater, and it is here that the major criticisms have fallen. In the first place, Darwin assumed that the bulk of variations were inheritable. He expressly stated that any which were not inheritable would be irrelevant to the discussion; but he continued in the assumption that those which are inheritable provide an adequate reservoir of potential improvement.²

As Haldane (1938, p. 107) has pointed out, the decreased interest in England in plant-breeding, caused by the repeal of the Corn Laws, led Darwin to take most of his evidence from animal-breeders.

This was much more obscure than what the plant-breeders in France had obtained: in fact Vilmorin, before Darwin wrote, had fully established the roles of heritable and non-heritable variation in wheat.

Thus in Darwin's time, and still more in England than in France, the subject of inheritance was still very obscure. In any case the basic laws of heredity, or, as we should now say, the principles of genetics, had not yet emerged. In a full formulation of the theory of Natural Selection, we should have to add a further fact and a further deduction. We should begin, as he did, with the fact of variation, and deduce from it and our previous deduction of the struggle for existence that there must be a *differential survival* of different types of offspring in each generation. We should then proceed to the fact of inheritance. *Some* variation is inherited: and that fraction will be available for transmission to later generations. Thus our final deduction is that the result will be a differential transmission of inherited variation. The term Natural Selection is thus seen to have two rather different meanings. In a broad sense it covers all cases of differential survival: but from the evolutionary point of view it covers only the differential transmission of inheritable variations.

Mendelian analysis has revealed the further fact, unsuspected by Darwin, that recombination of existing genetic units may both produce and modify new inheritable variations. And this, as we shall see later, has important evolutionary consequences.

Although both the principle of differential survival and that of its evolutionary accumulation by Natural Selection were for Darwin essentially deductions, it is important to realize that, if true, they are also facts of nature capable of verification by observation and experiment. And in point of fact differential mortality, differential survival, and differential multiplication among variants of the same species are now known in numerous cases.

The criticism, however, was early made that a great deal of the mortality found in nature appeared to be accidental and nonselective. This would hold for the destruction of the great majority of eggs and larvae of prolific marine animals, or the death of seeds which fell on stony ground or other unsuitable habitats. It remains true that we require many more quantitative experiments on the subject before we can know accurately the extent of non-selective elimination. Even a very large percentage of such eliminations, however, in no way invalidates the selection principle from holding for the remaining fraction (see p. 467). The very fact that it is accidental and non-selective ensures that the residue shall be a random sample, and will therefore contain any variation of selective value in the same proportions as the whole population. It is, I think,

²*Origin of Species* (6th ed., one vol. ed., p. 9): ". . . any variation which is not inherited is unimportant for us. But the number and diversity of inheritable deviations of structure, both those of slight and those of considerable physiological importance, are endless. No breeder doubts how strong is the tendency to inheritance: that like produces like is his fundamental belief." And so on.

fair to say that the fact of differential survival of different variations is generally accepted, although it still requires much clarification, especially on the quantitative side. In other words, natural selection within the bounds of the single generation is an active factor in biology.

THE NATURE OF VARIATION

The really important criticisms have fallen upon Natural Selection as an evolutionary principle, and have centred round the nature of inheritable variation.

Darwin, though his views on the subject did not remain constant, was always inclined to allow some weight to Lamarckian principles, according to which the effects of use and disuse and of environmental influences were supposed to be in some degree inherited. However, later work has steadily reduced the scope that can be allowed to such agencies: Weismann drew a sharp distinction between soma and germplasm, between the individual body which was not concerned in reproduction, and the hereditary constitution contained in the germ-cells, which alone was transmitted in heredity. Purely somatic effects, according to him, could not be passed on: the sole inheritable variations were variations in the hereditary constitution.

Although the distinction between soma and germplasm is not always so sharp as Weismann supposed, and although the principle of Baldwin and Lloyd Morgan, usually called Organic Selection, shows how Lamarckism may be simulated by the later replacement of adaptive modifications by adaptive mutations, Weismann's conceptions resulted in a great clarification of the position. It is owing to him that we to-day classify variations into two fundamentally distinct categories—modifications and mutations (together with new arrangements of mutations, or recombinations; see below, p. 20). Modifications are produced by alterations in the environment (including modifications of the internal environment such as are brought about by use and disuse), mutations by alterations in the substance of the hereditary constitution. The distinction may be put in a rather different but perhaps more illuminating way. Variation is a study of the differences between organisms. On analysis, these differences may turn out to be due to differences in environment (as with an etiolated plant growing in a cellar as against a green one in light; or a sun-tanned sailor as against a pale slum-dweller); or they may turn out to be due to differences in hereditary constitution (as between an albino and a green seedling in the same plot, or a negro and a white man in the same city); or of course to a simultaneous difference both in environment

and in constitution (as with the difference in stature between an undernourished pigmy and a well-nourished negro). Furthermore, only the latter are inherited. We speak of them as genetic differences: at their first origin they appear to be due to mutations in the hereditary constitution. The former we call modifications, and are not inheritable.

The important fact is that only experiment can decide between the two. Both in nature and in the laboratory, one of two indistinguishable variants may turn out to be due to environment, the other to genetic peculiarity. A particular shade of human complexion may be due to genetic constitution making for fair complexion plus considerable exposure to the sun, or to a genetically dark complexion plus very little tanning; and similarly for stature, intelligence, and many other characters.

This leads to a further important conclusion: characters as such are not and cannot be inherited. For a character is always the joint product of a particular genetic composition and a particular set of environmental circumstances. Some characters are much more stable in regard to the normal range of environmental variation than are others—for instance, human eye-colour or hair-form as against skin-colour or weight. But these too are in principle similar. Alter the environment of the embryo sufficiently, and eyeless monsters with markedly changed brain-development are produced.

In the early days of Mendelian research, phrases such as "in fowls, the character rose-comb is inherited as a Mendelian dominant" were current. So long as such phrases are recognized as mere convenient shorthand, they are harmless; but when they are taken to imply the actual genetic transmission of the characters, they are wholly incorrect.

Even as shorthand, they may mislead. To say that rose-comb is inherited as a dominant, even if we know that we mean the genetic factor for rose-comb, is likely to lead to what I may call the one-to-one or billiard-ball view of genetics. There are assumed to be a large number of characters in the organism, each one represented in a more or less invariable way by a particular factor or gene, or a combination of a few factors. This crude particulate view is a mere restatement of the preformation theory of development: granted the rose-comb factor, the rose-comb character, nice and clear-cut, will always appear. The rose-comb factor, it is true, is not regarded as a sub-microscopic replica of the actual rose-comb, but is taken to represent it by some form of unanalysed but inevitable correspondence.

The fallacy in this view is again revealed by the use of the difference method. In asserting that rose-comb is a dominant character, we are merely stating in a too abbreviated form the results of experiments

to determine what constitutes the difference between fowls with rose-combs and fowls with single combs. In reality, what is inherited as a Mendelian dominant is the gene in the rose-combed stock which differentiates it from the single-combed stock: we have no right to assert anything more as a result of our experiments than the existence of such a differential factor.

Actually, every character is dependent on a very large number (possibly all) of the genes in the hereditary constitution: but some of these genes exert marked differential effects upon the visible appearance. Both rose- and single-comb fowls contain all the genes needed to build up a full-sized comb: but "rose" genes build it up according to one growth-pattern, "single" genes according to another.

This principle is of great importance. For instance, up till very recently the chief data in human genetics have been pedigrees of abnormalities of diseases collected by medical men. And in collecting these data, medical men have usually been obsessed with the implications of the ideas of "character-inheritance". When the character has not appeared in orthodox and classical Mendelian fashion they have tended to dismiss it with some such phrase as "inheritance irregular", whereas further analysis might have shown a perfectly normal *inheritance* of the gene concerned, but an irregular *expression* of the character, dependent on the other genes with which it was associated and upon differences in environment (see discussion in Hogben, 1933).

This leads on to a further and very vital fact, namely, the existence of a type of genetic process undreamt of until the Mendelian epoch. In Darwin's day biological inheritance meant the reappearance of similar characters in offspring and parent, and implied the physical transmission of some material basis for the characters. What would Darwin or any nineteenth-century biologist say to facts such as the following, which now form part of any elementary course in genetics? A black and an albino mouse are mated. All their offspring are grey, like wild mice: but in the second generation greys, blacks, and albinos appear in the ratio 9:3:4. Or again, fowls with rose-comb and pea-comb mated together produce nothing but so-called walnut combs: but in the next generation, in addition to walnut, rose, and pea, some single combs are produced.

To the biologist of the Darwinian period the production of the grey mice would have been not inheritance, but "reversion" to the wild type, and the reappearance of the blacks and whites in the next generation would have been "atavism" or "skipping a generation". Similarly the appearance of single

combs in the fowl cross would have been described as reversion, while the production of walnut combs would have been regarded as some form of "sport."

In reality, the results are in both cases immediately explicable on the assumption of two pairs of genes, each transmitted from parent to offspring by the same fundamental genetic mechanism. The "reversions", "atavisms", and "sports" are all due to new combinations of old genes. Thus, although all the facts are in one sense phenomena of inheritance, it is legitimate and in some ways desirable to distinguish those in which the same characters reappear generation after generation from those in which new characters are generated. As Haldane has put it, modern genetics deals not only with inheritance, but with recombination.

Thus the raw material available for evolution by natural selection falls into two categories—mutation and recombination. Mutation is the only begetter of intrinsic change in the separate units of the hereditary constitution: it alters the nature of genes.³

Recombination, on the other hand, though it may produce quite new combinations with quite new effects on characters, only juggles with existing genes. It is, however, almost as important for evolution. It cannot occur without sexual reproduction: and its importance in providing the possibility of speedily combining several favourable mutations doubtless accounts for the all-but-universal presence of the sexual process in the life-cycle of organisms. We shall in later chapters see its importance for adjusting mutations to the needs of the organism.

Darwinism to-day thus still contains an element of deduction, and is none the worse for that as a scientific theory. But the facts available in relation to it are both more precise and more numerous, with the result that we are able to check our deductions and to make quantitative prophecies with much greater fullness than was possible to Darwin. This has been especially notable as regards the mathematical treatment of the problem, which we owe to R. A. Fisher, J. B. S. Haldane, Sewall Wright, and others. We can now take mutation-rates and degrees of advantage of one mutation or combination over another, which are within the limits actually found in genetic experiments, and can calculate the rates of evolution which will then occur.

³Strictly speaking, this applies only to gene-mutation. Chromosome-mutation, whether it adds or subtracts chromosome-sets, whole chromosomes, or parts of chromosomes, or inverts sections of chromosomes, merely provides new quantitative or positional combinations of old genes. However, chromosome-mutation may alter the *effects* of genes. Thus we are covered if we say that mutation alters either the qualitative nature or the effective action of the hereditary constitution.

If mutation had a rate that was very high it would neutralize or over-ride selective effects: if one that was very low, it would not provide sufficient raw material for change; if it were not more or less at random in many directions, evolution would run in orthogenetic grooves. But mutation being in point of fact chiefly at random, and the mutation-rate being always moderately low, we can deduce that the struggle for existence should be effective in producing differential survival and evolutionary change.

THE ECLIPSE OF DARWINISM

The death of Darwinism has been proclaimed not only from the pulpit, but from the biological laboratory; but, as in the case of Mark Twain, the reports seem to have been greatly exaggerated, since to-day Darwinism is very much alive.

The reaction against Darwinism set in during the nineties of last century. The youngest zoologists of that time were discontented with the trends of their science. The major school still seemed to think that the sole aim of zoology was to elucidate the relationship of the later groups. Had not Kovalevsky demonstrated the vertebrate affinities of the sea-squirts, and did not comparative embryology prove the common ancestry of groups so unlike as worms and molluscs? Intoxicated with such earlier successes of evolutionary phylogeny, they proceeded (like some Forestry Commission of science) to plant wildernesses of family trees over the beauty-spots of biology.

A related school, a little less prone to speculation, concentrated on the pursuit of comparative morphology within groups. This provides one of the most admirable of intellectual trainings for the student, and has yielded extremely important results for science. But if pursued too exclusively for its own sake, it leads, as Radl has pithily put it in his *History of Biological Theories*, to spending one's time comparing one thing with another without ever troubling about what either of them really is. In other words, zoology, becoming morphological, suffered divorce from physiology. And finally Darwinism itself grew more and more theoretical. The paper demonstration that such and such a character was or might be adaptive was regarded by many writers as sufficient proof that it must owe its origin to Natural Selection. Evolutionary studies became more and more merely case-books of real or supposed adaptations. Late nineteenth-century Darwinism came to resemble the early nineteenth-century school of Natural Theology. Paléy *redivivus*, one might say, but philosophically upside down, with Natural Selection instead of

a Divine Artificer as the *Deus ex machina*. There was little contact of evolutionary speculation with the concrete facts of cytology and heredity, or with actual experimentation.

A major symptom of revolt was the publication of William Bateson's *Materials for the Study of Variation* in 1894. Bateson had done valuable work on the embryology of *Balanoglossus*; but his sceptical and concrete mind found it distasteful to spend itself on speculations on the ancestry of the vertebrates, which was then regarded as the outstanding topic of evolution, and he turned to a task which, however different it might seem, he rightly regarded as piercing nearer to the heart of the evolutionary problems. Deliberately he gathered evidence of variation which was discontinuous, as opposed to the continuous variation postulated by Darwin and Weismann. The resultant volume of material, though its gathering might fairly be called biassed, was impressive in quantity and range, and deeply impressed the more active spirits in biology. It was the first symptom of what we may call the period of mutation theory, which postulated that large mutations, and not small "continuous variations", were the raw material of evolution, and actually determined most of its course, selection being relegated to a wholly subordinate position.

This was first formally promulgated by de Vries (1901, 1905) as a result of his work with the evening primroses, *Oenothera*, and was later adopted by various other workers, notably T. H. Morgan, in his first genetical phase. The views of the early twentieth-century geneticists, moreover, were coloured by the rediscovery of Mendel's laws by Correns, de Vries, and Tschermak in the spring of 1900, and the rapid generalization of them, notably by Bateson.

Naturally, the early Mendelians worked with clear-cut differences of large extent. As it became clearer that Mendelian inheritance was universal, it was natural to suppose that all Mendelian factors produced large effects, that therefore mutation was sharp and discontinuous, and that the continuous variation which is obviously widespread in nature is not heritable.

Bateson did not hesitate to draw the most devastating conclusions from his reading of the Mendelian facts. In his Presidential Address to the British Association in 1914, assuming first that change in the germplasm is always by large mutation and secondly that all mutation is loss, from a dominant something to a recessive nothing, he concluded that the whole of evolution is merely an unpacking. The hypothetical ancestral amoeba contained—actually and not just potentially—the entire complex of life's hereditary factors. The jetti-

soning of different portions of this complex released the potentialities of this, that, and the other group and form of life. Selection and adaptation were relegated to an unconsidered background.

Meanwhile the true-blue Darwinian stream, leaving Weismannism behind, had reached its biometric phase. Tracing its origin to Galton, biometry blossomed under the guidance of Karl Pearson and Weldon. Unfortunately this, the first thorough application of mathematics to evolution, though productive of many important results and leading to still more important advances in method, was for a considerable time rendered sterile by its refusal to acknowledge the genetic facts discovered by the Mendelians. Both sides, indeed, were to blame. The biometricians stuck to hypothetical modes of inheritance and genetic variation on which to exercise their mathematical skill; the Mendelians refused to acknowledge that continuous variation could be genetic, or at any rate dependent on genes, or that a mathematical theory of selection could be of any real service to the evolutionary biologist.

It was in this period, immediately prior to the war, that the legend of the death of Darwinism acquired currency. The facts of Mendelism appeared to contradict the facts of paleontology, the theories of the mutationists would not square with the Weismannian views of adaptation, the discoveries of experimental embryology seemed to contradict the classical recapitulatory theories of development. Zoologists who clung to Darwinian views were looked down on by the devotees of the newer disciplines, whether cytology or genetics, *Entwicklungs-mechanik* or comparative physiology, as old-fashioned theorizers; and the theological and philosophical antipathy to Darwin's great mechanistic generalization could once more raise its head without fearing too violent a knock.

But the old-fashioned selectionists were guided by a sound instinct. The opposing factions became reconciled as the younger branches of biology achieved a synthesis with each other and with the classical disciplines: and the reconciliation converged upon a Darwinian centre.

It speedily became apparent that Mendelism applied to the heredity of all many-celled and many single-celled organisms, both animals and plants. The Mendelian laws received a simple and general interpretation: they were due in the first place to inheritance being particulate, and in the second place to the particles being borne on the chromosomes, whose behaviour could be observed under the microscope. Many apparent exceptions to Mendelian rules turned out to be due to aberrations of chromosome-behaviour. Segregation and recombination, the fundamental Mendelian facts, are all

but universal, being co-extensive with sexual reproduction; and mutation, the further corollary of the particulate theory of heredity, was found to occur even more widely, in somatic tissues and in parthenogenetic and sexually-reproducing strains as well as in the germtrack of bisexual species. Blending inheritance as originally conceived was shown not to occur, and cytoplasmic inheritance to play an extremely subsidiary role.

The Mendelians also found that mutations could be of any extent, and accordingly that apparently continuous as well as obviously discontinuous variation had to be taken into account in discussing heredity and evolution. The mathematicians found that biometric methods could be applied to neo-Mendelian postulates, and then become doubly fruitful. Cytology became intimately linked with genetics. Experimental embryology and the study of growth illuminated heredity, recapitulation, and palcontology. Ecology and systematics provided new data and new methods of approach to the evolutionary problem. Selection, both in nature and in the laboratory, was studied quantitatively and experimentally. Mathematical analysis showed that only particulate inheritance would permit evolutionary change: blending inheritance, as postulated by Darwin, was shown by R. A. Fisher (1930a) to demand mutation-rates enormously higher than those actually found to occur. Thus, though it may still be true in a formal sense that, as such an eminent geneticist as Miss E. R. Saunders said at the British Association meeting in 1920, "Mendelism is a theory of heredity: it is not a theory of evolution", yet the assertion is purely formal. Mendelism is now seen as an essential part of the theory of evolution. Mendelian analysis does not merely explain the distributive hereditary mechanism: it also, together with selection, explains the progressive mechanism of evolution.

Biology in the last twenty years, after a period in which new disciplines were taken up in turn and worked out in comparative isolation, has become a more unified science. It has embarked upon a period of synthesis, until to-day it no longer presents the spectacle of a number of semi-independent and largely contradictory sub-sciences, but is coming to rival the unity of older sciences like physics, in which advance in any one branch leads almost at once to advance in all other fields, and theory and experiment march hand-in-hand. As one chief result, there has been a rebirth of Darwinism. The historical facts concerning this trend are summarized by Shull in a recent book (1936). It is noteworthy that T. H. Morgan, after having been one of the most extreme critics of selectionist doctrine, has recently, as a result of modern work in genetics (to

which he has himself so largely contributed), again become an upholder of the Darwinian point of view (T. H. Morgan, 1925, and later writings); while his younger colleagues, notably Muller and Sturtevant, are strongly selectionist in their evolutionary views.

The Darwinism thus reborn is a modified Darwinism, since it must operate with facts unknown to Darwin; but it is still Darwinism in the sense that it aims at giving a naturalistic interpretation of evolution, and that its upholders, while constantly striving for more facts and more experimental results, do not, like some cautious spirits, reject the method of deduction.

Hogben (1931, p. 145 seq.) disagrees with this conclusion. He accepts the findings of neo-Mendelism and the mathematical conclusions to be drawn from them; but, to use his own words, "the essential difference between the theory of natural selection expounded by such contemporary writers as J. B. S. Haldane, Sewall Wright, and R. A. Fisher, as contrasted with that of Darwin, resides in the fact that Darwin interpreted the process of artificial selection in terms of a theory of 'blending inheritance' universally accepted by his own generation, whereas the modern view is based on the Theory of Particulate Inheritance. The consequences of the two views are very different. According to the Darwinian doctrine, evolution is an essentially continuous process, and selection is essentially creative in the sense that no change would occur if selection were removed. According to the modern doctrine, evolution is discontinuous. The differentiation of varieties or species may suffer periods of stagnation. Selection is a destructive agency."

Accordingly, Hogben would entirely repudiate the title of Darwinism for the modern outlook, and would prefer to see the term Natural Selection replaced by another to mark the new connotations it has acquired, although on this latter point he is prepared to admit the convenience of retention.

These objections, coming from a biologist of Hogben's calibre, must carry weight. On the other hand we shall see reason in later chapters for finding them ungrounded. In the first place, evolution, as revealed in fossil trends, is "an essentially contin-

uous process". The building-blocks of evolution, in the shape of mutations, are, to be sure, discrete quanta of change. But firstly, the majority of them (and the very great majority of those which survive to become incorporated in the genetic constitution of living things) appear to be of small extent; secondly, the effect of a given mutation will be different according to the combinations of modifying genes present (pp. 68 seq.); and thirdly, its effect may be masked or modified by environmental modification. The net result will be that, for all practical purposes, most of the variability of a species at any given moment will be continuous, however accurate are the measurements made; and that most evolutionary change will be gradual, to be detected by a progressive shifting of a mean value from generation to generation.

In the second place, the statement that selection is a destructive agency is not true, if it is meant to imply that it is *merely* destructive. It is also directive, and because it is directive, it has a share in evolutionary creation. Neither mutation nor selection alone is creative of anything important in evolution; but the two in conjunction are creative.

Hogben is perfectly right in stressing the fact of the important differences in content and implication between the Darwinism of Darwin or Weismann and that of Fisher or Haldane. We may, however, reflect that the term *atom* is still in current use and the atomic theory not yet rejected by physicists, in spite of the supposedly indivisible units having been divided. This is because modern physicists still find that the particles called atoms by their predecessors do play an important role, even if they are compound and do occasionally lose or gain particles and even change their nature. If this is so, biologists may with a good heart continue to be Darwinians and to employ the term Natural Selection, even if Darwin knew nothing of mendelizing mutations, and if selection is by itself incapable of changing the constitution of a species or a line.

It is with this reborn Darwinism, this mutated phoenix risen from the ashes of the pyre kindled by men so unlike as Bateson and Bergson, that I propose to deal in succeeding chapters of this book.