

British Association for the Advancement of Science.

[Reference No. 1]



AUSTRALIA, 1914.

ADDRESS

BY

PROFESSOR WILLIAM BATESON, M.A., F.R.S.,
PRESIDENT.

PART I.—MELBOURNE. August 14

THE outstanding feature of this Meeting must be the fact that we are here—in Australia. It is the function of a President to tell the Association of advances in science, to speak of the universal rather than of the particular or the temporary. There will be other opportunities of expressing the thoughts which this event must excite in the dullest heart, but it is right that my first words should take account of those achievements of organisation and those acts of national generosity by which it has come to pass that we are assembled in this country. Let us, too, on this occasion, remember that all the effort, and all the goodwill, that binds Australia to Britain would have been powerless to bring about such a result had it not been for those advances in science which have given man a control of the forces of Nature. For we are here by virtue of the feats of genius of individual men of science, giant-variations from the common level of our species; and since I am going soon to speak of the significance of individual variation, I cannot introduce that subject better than by calling to remembrance the line of pioneers in chemistry, in physics, and in engineering, by the working of whose rare—or, if you will, abnormal—intellects a meeting of the British Association on this side of the globe has been made physically possible.

I have next to refer to the loss within the year of Sir David Gill, a former President of this Association, himself one of the outstanding great. His greatness lay in the power of making big foundations. He built up the Cape Observatory; he organised international geodesy; he conceived and carried through the plans for the photography of the whole sky, a work in which Australia is bearing a conspicuous part.

Astronomical observation is now organised on an international scale, and of this great scheme Gill was the heart and soul. His labours have ensured a base from which others will proceed to discovery otherwise impossible. His name will be long remembered with veneration and gratitude.

As the subject of the Addresses which I am to deliver here and in Sydney I take *Heredity*. I shall attempt to give the essence of the discoveries made by Mendelian or analytical methods of study, and I shall ask you to contemplate the deductions which these physiological facts suggest in application both to evolutionary theory at large and to the special case of the natural history of human society.

Recognition of the significance of heredity is modern. The term itself in its scientific sense is no older than Herbert Spencer. Animals and plants are formed as pieces of living material split from the body of the parent organisms. Their powers and faculties are fixed in their physiological origin. They are the consequence of a genetic process, and yet it is only lately that this genetic process has become the subject of systematic research and experiment. The curiosity of naturalists has of course always been attracted to such problems; but that accurate knowledge of genetics is of paramount importance in any attempt to understand the nature of living things has only been realised quite lately even by naturalists, and with casual exceptions the laity still know nothing of the matter. Historians debate the past of the human species, and statesmen order its present or profess to guide its future as if the animal Man, the unit of their calculations, with his vast diversity of powers, were a homogeneous material, which can be multiplied like shot.

The reason for this neglect lies in ignorance and misunderstanding of the nature of Variation; for not until the fact of congenital diversity is grasped, with all that it imports, does knowledge of the system of hereditary transmission stand out as a primary necessity in the construction of any theory of Evolution, or any scheme of human polity.

The first full perception of the significance of variation we owe to Darwin. The present generation of evolutionists realises perhaps more fully than did the scientific world in the last century that the theory of Evolution had occupied the thoughts of many and found acceptance with not a few before ever the 'Origin' appeared. We have come also to the conviction that the principle of Natural Selection cannot have been the chief factor in delimiting the species of animals and plants, such as we now with fuller knowledge see them actually to be. We are even more sceptical as to the validity of that appeal to changes in the conditions of life as direct causes of modification, upon which latterly at all events Darwin laid much emphasis. But that he was the

first to provide a body of fact demonstrating the variability of living things, whatever be its causation, can never be questioned.

There are some older collections of evidence, chiefly the work of the French school, especially of Godron¹—and I would mention also the almost forgotten essay of Wollaston²—these however are only fragments in comparison. Darwin regarded variability as a property inherent in living things, and eventually we must consider whether this conception is well founded; but postponing that inquiry for the present, we may declare that with him began a general recognition of variation as a phenomenon widely occurring in Nature.

If a population consists of members which are not alike but differentiated, how will their characteristics be distributed among their offspring? This is the problem which the modern student of heredity sets out to investigate. Formerly it was hoped that by the simple inspection of embryological processes the modes of heredity might be ascertained, the actual mechanism by which the offspring is formed from the body of the parent. In that endeavour a noble pile of evidence has been accumulated. All that can be made visible by existing methods has been seen, but we come little if at all nearer to the central mystery. We see nothing that we can analyse further—nothing that can be translated into terms less inscrutable than the physiological events themselves. Not only does embryology give no direct aid, but the failure of cytology is, so far as I can judge, equally complete. The chromosomes of nearly related creatures may be utterly different both in number, size, and form. Only one piece of evidence encourages the old hope that a connection might be traceable between the visible characteristics of the body and those of the chromosomes. I refer of course to the accessory chromosome, which in many animals distinguishes the spermatozoon about to form a female in fertilisation. Even it however cannot be claimed as the cause of sexual differentiation, for it may be paired in forms closely allied to those in which it is unpaired or accessory. The distinction may be present or wanting, like any other secondary sexual character. Indeed, so long as no one can show consistent distinctions between the cytological characters of somatic tissues in the same individual we can scarcely expect to perceive such distinctions between the chromosomes of the various types.

For these methods of attack we now substitute another, less ambitious, perhaps, because less comprehensive, but not less direct. If we cannot see how a fowl by its egg and its sperm gives rise to

¹ *De l'Espèce et des Races dans les Êtres Organisés*, 1859.

² *On the Variation of Species*, 1856.

a chicken or how a Sweet Pea from its ovule and its pollen grain produces another Sweet Pea, we at least can watch the system by which the differences between the various kinds of fowls or between the various kinds of Sweet Peas are distributed among the offspring. By thus breaking the main problem up into its parts we give ourselves fresh chances. This analytical study we call Mendelian because Mendel was the first to apply it. To be sure, he did not approach the problem by any such line of reasoning as I have sketched. His object was to determine the genetic definiteness of species; but though in his writings he makes no mention of inheritance it is clear that he had the extension in view. By cross-breeding he combined the characters of varieties in mongrel individuals and set himself to see how these characters would be distributed among the individuals of subsequent generations. Until he began this analysis nothing but the vaguest answers to such a question had been attempted. The existence of any orderly system of descent was never even suspected. In their manifold complexity human characteristics seemed to follow no obvious system, and the fact was taken as a fair sample of the working of heredity.

Misconception was especially brought in by describing descent in terms of 'blood.' The common speech uses expressions such as consanguinity, pure-blooded, half-blood, and the like, which call up a misleading picture to the mind. Blood is in some respects a fluid, and thus it is supposed that this fluid can be both quantitatively and qualitatively diluted with other bloods, just as treacle can be diluted with water. Blood in primitive physiology being the peculiar vehicle of life, at once its essence and its corporeal abode, these ideas of dilution and compounding of characters in the commingling of bloods inevitably suggest that the ingredients of the mixture once combined are inseparable, that they can be brought together in any relative amounts, and in short that in heredity we are concerned mainly with a quantitative problem. Truer notions of genetic physiology are given by the Hebrew expression 'seed.' If we speak of a man as 'of the blood-royal' we think at once of plebeian dilution, and we wonder how much of the royal fluid is likely to be 'in his veins'; but if we say he is 'of the seed of Abraham' we feel something of the permanence and indestructibility of that germ which can be divided and scattered among all nations, but remains recognisable in type and characteristics after 4,000 years.

I knew a breeder who had a chest containing bottles of coloured liquids by which he used to illustrate the relationships of his dogs, pouring from one to another and titrating them quantitatively to illustrate their pedigrees. Galton was beset by the same kind of mistake when he promulgated his 'Law of Ancestral Heredity.' With modern

research all this has been cleared away. The allotment of characteristics among offspring is not accomplished by the exudation of drops of a tincture representing the sum of the characteristics of the parent organism, but by a process of *cell-division*, in which numbers of these characters, or rather the elements upon which they depend, are sorted out among the resulting germ-cells in an orderly fashion. What these elements, or *factors* as we call them, are we do not know. That they are in some way directly transmitted by the material of the ovum and of the spermatozoon is obvious, but it seems to me unlikely that they are in any simple or literal sense material particles. I suspect rather that their properties depend on some phenomenon of arrangement. However that may be, analytical breeding proves that it is according to the distribution of these genetic factors, to use a non-committal term, that the characters of the offspring are decided. The first business of experimental genetics is to determine their number and interactions, and then to make an analysis of the various types of life.

Now the ordinary genealogical trees, such as those which the stud-books provide in the case of the domestic animals, or the *Heralds' College* provides in the case of man, tell nothing of all this. Such methods of depicting descent cannot even show the one thing they are devised to show—purity of 'blood.' For at last we know the physiological meaning of that expression. An organism is pure-bred when it has been formed by the union in fertilisation of two germ-cells which are alike in the factors they bear; and since the factors for the several characteristics are independent of each other, this question of purity must be separately considered for each of them. A man, for example, may be pure-bred in respect of his musical ability and cross-bred in respect of the colour of his eyes or the shape of his mouth. Though we know nothing of the essential nature of these factors, we know a good deal of their powers. They may confer height, colour, shape, instincts, powers both of mind and body; indeed, so many of the attributes which animals and plants possess that we feel justified in the expectation that with continued analysis they will be proved to be responsible for most if not all of the differences by which the varying individuals of any species are distinguished from each other. I will not assert that the greater differences which characterise distinct Species are due generally to such independent factors, but that is the conclusion to which the available evidence points. All this is now so well understood, and has been so often demonstrated and expounded, that details of evidence are now superfluous.

But for the benefit of those who are unfamiliar with such work let me briefly epitomise its main features and consequences. Since genetic factors are definite things, either present in or absent from any germ-cell, the individual may be either 'pure-bred' for any particular factor,

or its absence, if he is constituted by the union of two germ-cells both possessing or both destitute of that factor. If the individual is thus pure, all his germ-cells will in that respect be identical, for they are simply bits of the similar germ-cells which united in fertilisation to produce the parent organism. We thus reach the essential principle, that an organism cannot pass on to offspring a factor which it did not itself receive in fertilisation. Parents, therefore, which are both destitute of a given factor can only produce offspring equally destitute of it; and, on the contrary, parents both pure-bred for the presence of a factor produce offspring equally pure-bred for its presence. Whereas the germ-cells of the pure-bred are all alike, those of the cross-bred, which results from the union of dissimilar germ-cells, are mixed in character. Each positive factor segregates from its negative opposite, so that some germ-cells carry the factor and some do not. Once the factors have been identified by their effects, the average composition of the several kinds of families formed from the various matings can be predicted.

Only those who have themselves witnessed the fixed operations of these simple rules can feel their full significance. We come to look behind the simulacrum of the individual body and we endeavour to disintegrate its features into the genetic elements by whose union the body was formed. Set out in cold general phrases such discoveries may seem remote from ordinary life. Become familiar with them and you will find your outlook on the world has changed. Watch the effects of segregation among the living things with which you have to do—plants, fowls, dogs, horses, that mixed concourse of humanity we call the English race, your friends' children, your own children, yourself—and however firmly imagination be restrained to the bounds of the known and the proved, you will feel something of that range of insight into Nature which Mendelism has begun to give. The question is often asked whether there are not also in operation systems of descent quite other than those contemplated by the Mendelian rules. I myself have expected such discoveries, but hitherto none have been plainly demonstrated. It is true we are often puzzled by the failure of a parental type to reappear in its completeness after a cross—the merino sheep or the fantail pigeon, for example. These exceptions may still be plausibly ascribed to the interference of a multitude of factors, a suggestion not easy to disprove; though it seems to me equally likely that segregation has been in reality imperfect. Of the descent of quantitative characters we still know practically nothing. These and hosts of difficult cases remain almost untouched. In particular the discovery of E. Baur, and the evidence of Winkler in regard to his 'graft hybrids,' both showing that the sub-epidermal layer of a plant—the layer from which the germ-cells are derived—may bear exclusively the characters

of a part only of the soma, give hints* of curious complications, and suggest that in plants at least the interrelations between soma and gamete may be far less simple than we have supposed. Nevertheless, speaking generally, we see nothing to indicate that qualitative characters descend, whether in plants or animals, according to systems which are incapable of factorial representation.

The body of evidence accumulated by this method of analysis is now very large, and is still growing fast by the labours of many workers. Progress is also beginning along many novel and curious lines. The details are too technical for inclusion here. Suffice it to say that not only have we proof that segregation affects a vast range of characteristics, but in the course of our analysis phenomena of most unexpected kinds have been encountered. Some of these things twenty years ago must have seemed inconceivable. For example, the two sets of sex organs, male and female, of the same plant may not be carrying the same characteristics; in some animals characteristics, quite independent of sex, may be distributed solely or predominantly to one sex; in certain species the male may be breeding true to its own type, while the female is permanently mongrel, throwing off eggs of a distinct variety in addition to those of its own type; characteristics, essentially independent, may be associated in special combinations which are largely retained in the next generation, so that among the grandchildren there is numerical preponderance of those combinations which existed in the grandparents—a discovery which introduces us to a new phenomenon of polarity in the organism.

We are accustomed to the fact that the fertilised egg has a polarity, a front and hind end for example; but we have now to recognise that it, or the primitive germinal cells formed from it, may have another polarity shown in the groupings of the parental elements. I am entirely sceptical as to the occurrence of segregation solely in the maturation of the germ-cells,³ preferring at present to regard it as a special case of that patch-work condition we see in so many plants. These mosaics may break up, emitting bud-sports at various cell-divisions, and I suspect that the great regularity seen in the F_2 ratios of the cereals, for example, is a consequence of very late segregation, whereas the excessive irregularity found in other cases may be taken to indicate that segregation can happen at earlier stages of differentiation.

The paradoxical descent of colour-blindness and other sex-limited conditions—formerly regarded as an inscrutable caprice of nature—has been represented with approximate correctness, and we already know something as to the way, or, perhaps, I should say ways, in which the

* The fact that in certain plants the male and female organs respectively carry distinct factors may be quoted as almost decisively negating the suggestion that segregation is confined to the reduction division.

determination of sex is accomplished in some of the forms of life—though, I hasten to add, we have no inkling as to any method by which that determination may be influenced or directed. It is obvious that such discoveries have bearings on most of the problems, whether theoretical or practical, in which animals and plants are concerned. Permanence or change of type, perfection of type, purity or mixture of race, 'racial development,' the succession of forms, from being vague phrases expressing matters of degree, are now seen to be capable of acquiring physiological meanings, already to some extent assigned with precision. For the naturalist—and it is to him that I am especially addressing myself to-day—these things are chiefly significant as relating to the history of organic beings—the theory of Evolution, to use our modern name. They have, as I shall endeavour to show in my second address to be given in Sydney, an immediate reference to the conduct of human society.

I suppose that everyone is familiar in outline with the theory of the Origin of Species which Darwin promulgated. Through the last fifty years this theme of the Natural Selection of favoured races has been developed and expounded in writings innumerable. Favoured races certainly can replace others. The argument is sound, but we are doubtful of its value. For us that debate stands adjourned. We go to Darwin for his incomparable collection of facts. We would fain emulate his scholarship, his width and his power of exposition, but to us he speaks no more with philosophical authority. We read his scheme of Evolution as we would those of Lucretius or of Lamarck, delighting in their simplicity and their courage. The practical and experimental study of Variation and Heredity has not merely opened a new field; it has given a new point of view and new standards of criticism. Naturalists may still be found expounding teleological systems⁴ which would have delighted Dr. Pangloss himself, but at the present time few are misled. The student of genetics knows that

⁴ I take the following from the Abstract of a recent Croonian Lecture 'On the Origin of Mammals' delivered to the Royal Society:—'In Upper Triassic times the larger Cynodonts preyed upon the large Anomodont, *Kannemeyeria*, and carried on their existence so long as these Anomodonts survived, but died out with them about the end of the Trias or in Rhætic times. The small Cynodonts, having neither small Anomodonts nor small Cotylosaurs to feed on, were forced to hunt the very active long-limbed Thecodonts. The greatly increased activity brought about that series of changes which formed the mammals—the flexible skin with hair, the four-chambered heart and warm blood, the loose jaw with teeth for mastication, an increased development of tactile sensation and a great increase of cerebrum. Not improbably the attacks of the newly-evolved Cynodont or mammalian type brought about a corresponding evolution in the Pseudosuchian Thecodonts which ultimately resulted in the formation of Dinosaurs and Birds.' Broom, R., *Proc. Roy. Soc. B.*, 87, p. 88.

the time for the development of theory is not yet. He would rather stick to the seed-pan and the incubator.

In face of what we now know of the distribution of variability in nature the scope claimed for Natural Selection in determining the fixity of Species must be greatly reduced. The doctrine of the survival of the fittest is undeniable so long as it is applied to the organism as a whole, but to attempt by this principle to find value in all definiteness of parts and functions, and in the name of Science to see fitness everywhere is mere eighteenth-century optimism. Yet it was in application to the parts, to the details of specific difference, to the spots on the peacock's tail, to the colouring of an Orchid flower, and hosts of such examples, that the potency of Natural Selection was urged with the strongest emphasis. Shorn of these pretensions the doctrine of the survival of favoured races is a truism, helping scarcely at all to account for the diversity of species. Tolerance plays almost as considerable a part. By these admissions almost the last shred of that teleological fustian with which Victorian philosophy loved to clothe the theory of Evolution is destroyed. Those who would proclaim that whatever is is right will be wise henceforth to base this faith frankly on the impregnable rock of superstition and to abstain from direct appeals to natural fact.

My predecessor said last year that in physics the age is one of rapid progress and profound scepticism. In at least as high a degree this is true of Biology, and as a chief characteristic of modern evolutionary thought we must confess also to a deep but irksome humility in presence of great vital problems. Every theory of Evolution must be such as to accord with the facts of physics and chemistry, a primary necessity to which our predecessors paid small heed. For them the unknown was a rich mine of possibilities on which they could freely draw. For us it is rather an impenetrable mountain out of which the truth can be chipped in rare and isolated fragments. Of the physics and chemistry of life we know next to nothing. Somehow the characters of living things are bound up in properties of colloids, and are largely determined by the chemical powers of enzymes, but the study of these classes of matter have only just begun. Living things are found by a simple experiment to have powers undreamt of, and who knows what may be behind?

Naturally we turn aside from generalities. It is no time to discuss the origin of the Mollusca or of Dicotyledons, while we are not even sure how it came to pass that *Primula obconica* has in twenty-five years produced its abundant new forms almost under our eyes. Knowledge of heredity has so reacted on our conceptions of variation that very competent men are even denying that variation in the old sense is a genuine occurrence at all. Variation is postulated as the basis of all evolutionary change. Do we then as a matter of fact find in the world

about us variations occurring of such a kind as to warrant faith in a contemporary progressive Evolution? Till lately most of us would have said 'yes' without misgiving. We should have pointed, as Darwin did, to the immense range of diversity seen in many wild species, so commonly that the difficulty is to define the types themselves. Still more conclusive seemed the profusion of forms in the various domesticated animals and plants, most of them incapable of existing even for a generation in the wild state, and therefore fixed unquestionably by human selection. These, at least, for certain, are new forms, often distinct enough to pass for species, which have arisen by variation. But when analysis is applied to this mass of variation the matter wears a different aspect. Closely examined, what is the 'variability' of wild species? What is the natural fact which is denoted by the statement that a given species exhibits much variation? Generally one of two things: either that the individuals collected in one locality differ among themselves; or perhaps more often that samples from separate localities differ from each other. As direct evidence of variation it is clearly to the first of these phenomena that we must have recourse—the heterogeneity of a population breeding together in one area. This heterogeneity may be in any degree, ranging from slight differences that systematists would disregard, to a complex variability such as we find in some moths, where there is an abundance of varieties so distinct that many would be classified as specific forms but for the fact that all are freely breeding together. Naturalists formerly supposed that any of these varieties might be bred from any of the others. Just as the reader of novels is prepared to find that any kind of parents might have any kind of children in the course of the story, so was the evolutionist ready to believe that any pair of moths might produce any of the varieties included in the species. Genetic analysis has disposed of all these mistakes. We have no longer the smallest doubt that in all these examples the varieties stand in a regular descending order, and that they are simply terms in a series of combinations of factors separately transmitted, of which each may be present or absent.

The appearance of contemporary variability proves to be an illusion. Variation from step to step in the series must occur either by the addition or by the loss of a factor. Now, of the origin of new forms *by loss* there seems to me to be fairly clear evidence, but of the *contemporary acquisition* of any new factor I see no satisfactory proof, though I admit there are rare examples which may be so interpreted. We are left with a picture of variation utterly different from that which we saw at first. Variation now stands out as a definite physiological event. We have done with the notion that Darwin came latterly to favour, that large differences can arise by accumulation of small

differences. Such small differences are often mere ephemeral effects of conditions of life, and as such are not transmissible; but even small differences, when truly genetic, are factorial like the larger ones, and there is not the slightest reason for supposing that they are capable of summation. As to the origin or source of these positive separable factors, we are without any indication or surmise. By their effects we know them to be definite, as definite, say, as the organisms which produce diseases; but how they arise and how they come to take part in the composition of the living creature so that when present they are treated in cell-division as constituents of the germs, we cannot conjecture.

It was a commonplace of evolutionary theory that at least the domestic animals have been developed from a few wild types. Their origin was supposed to present no difficulty. The various races of fowl, for instance, all came from *Gallus bankiva*, the Indian jungle-fowl. So we are taught; but try to reconstruct the steps in their evolution and you realise your hopeless ignorance. To be sure there are breeds, such as Black-red Game and Brown Leghorns, which have the colours of the jungle-fowl, though they differ in shape and other respects. As we know so little as yet of the genetics of shape, let us assume that those transitions could be got over. Suppose, further, as is probable, that the absence of the maternal instinct in the Leghorn is due to loss of one factor which the jungle-fowl possesses. So far we are on fairly safe ground. But how about White Leghorns? Their origin may seem easy to imagine, since white varieties have often arisen in well-authenticated cases. But the white of White Leghorns is not, as white in nature often is, due to the loss of the colour-elements, but to the action of something which inhibits their expression. Whence did that something come? The same question may be asked respecting the heavy breeds, such as Malays or Indian Game. Each of these is a separate introduction from the East. To suppose that these, with their peculiar combs and close feathering, could have been developed from pre-existing European breeds is very difficult. On the other hand, there is no wild species now living any more like them. We may, of course, postulate that there was once such a species, now lost. That is quite conceivable, though the suggestion is purely speculative. I might thus go through the list of domesticated animals and plants of ancient origin and again and again we should be driven to this suggestion, that many of their distinctive characters must have been derived from some wild original now lost. Indeed, to this unsatisfying conclusion almost every careful writer on such subjects is now reduced. If we turn to modern evidence the case looks even worse. The new breeds of domestic animals made in recent times are the carefully selected products of recombination of pre-existing breeds. Most of the

new varieties of cultivated plants are the outcome of deliberate crossing. There is generally no doubt in the matter. We have pretty full histories of these crosses in *Gladiolus*, *Orchids*, *Cineraria*, *Begonia*, *Calceolaria*, *Pelargonium*, &c. A very few certainly arise from a single origin. The Sweet Pea is the clearest case, and there are others which I should name with hesitation. The *Cyclamen* is one of them, but we know that efforts to cross *Cyclamens* were made early in the cultural history of the plant, and they may very well have been successful. Several plants for which single origins are alleged, such as the Chinese Primrose, the Dahlia, and Tobacco, came to us in an already domesticated state, and their origins remain altogether mysterious. Formerly single origins were generally presumed, but at the present time numbers of the chief products of domestication, dogs, horses, cattle, sheep, poultry, wheat, oats, rice, plums, cherries, have in turn been accepted as 'polyphyletic' or, in other words, derived from several distinct forms. The reason that has led to these judgments is that the distinctions between the chief varieties can be traced as far back as the evidence reaches, and that these distinctions are so great, so far transcending anything that we actually know variation capable of effecting, that it seems pleasanter to postpone the difficulty, relegating the critical differentiation to some misty antiquity into which we shall not be asked to penetrate. For it need scarcely be said that this is mere procrastination. If the origin of a form under domestication is hard to imagine, it becomes no easier to conceive of such enormous deviations from type coming to pass in the wild state. Examine any two thoroughly distinct species which meet each other in their distribution, as, for instance, *Lychnis diurna* and *vespertina* do. In areas of overlap are many intermediate forms. These used to be taken to be transitional steps, and the specific distinctness of *vespertina* and *diurna* was on that account questioned. Once it is known that these supposed intergrades are merely mongrels between the two species the transition from one to the other is practically beyond our powers of imagination to conceive. If both these can survive, why has their common parent perished? Why when they cross do they not reconstruct it instead of producing partially sterile hybrids? I take this example to show how entirely the facts were formerly misinterpreted.

When once the idea of a true-breeding—or, as we say, homozygous—type is grasped, the problem of variation becomes an insistent oppression. What can make such a type vary? We know, of course, one way by which novelty can be introduced—by crossing. Cross two well-marked varieties—for instance, of Chinese Primula—each breeding true, and in the second generation by mere recombination of the various factors which the two parental types severally introduced, there will be a profusion of forms, utterly unlike each other, distinct also from

the original parents. Many of these can be bred true, and if found wild would certainly be described as good species. Confronted by the difficulty I have put before you, and contemplating such amazing polymorphism in the second generation from a cross in *Antirrhinum*, Lotsy has lately with great courage suggested to us that all variation may be due to such crossing. I do not disguise my sympathy with this effort. After the blind complacency of conventional evolutionists it is refreshing to meet so frank an acknowledgment of the hardness of the problem. Lotsy's utterance will at least do something to expose the artificiality of systematic zoology and botany. Whatever might or might not be revealed by experimental breeding, it is certain that without such tests we are merely guessing when we profess to distinguish specific limits and to declare that this is a species and that a variety. The only definable unit in classification is the homozygous form which breeds true. When we presume to say that such and such differences are trivial and such others valid, we are commonly embarking on a course for which there is no physiological warrant. Who could have foreseen that the Apple and the Pear—so like each other that their botanical differences are evasive—could not be crossed together, though species of *Antirrhinum* so totally unlike each other as *majus* and *molle* can be hybridized, as Baur has shown, without a sign of impaired fertility? Jordan was perfectly right. The true-breeding forms which he distinguished in such multitudes are real entities, though the great systematists, dispensing with such laborious analysis, have pooled them into arbitrary Linnean species, for the convenience of collectors and for the simplification of catalogues. Such pragmatical considerations may mean much in the museum, but with them the student of the physiology of variation has nothing to do. These 'little species,' finely cut, true-breeding, and innumerable mongrels between them, are what he finds when he examines any so-called variable type. On analysis the semblance of variability disappears, and the illusion is shown to be due to segregation and recombination of series of factors on pre-determined lines. As soon as the 'little species' are separated out they are found to be fixed. In face of such a result we may well ask with Lotsy, is there such a thing as spontaneous variation anywhere? His answer is that there is not.

Abandoning the attempt to show that positive factors can be added to the original stock, we have further to confess that we cannot often actually prove variation by loss of factor to be a real phenomenon. Lotsy doubts whether even this phenomenon occurs. The sole source of variation, in his view, is crossing. But here I think he is on unsafe ground. When a well-established variety like 'Crimson King' *Primula*, bred by Messrs. Sutton in thousands of individuals, gives off, as it did a few years since, a salmon-coloured

variety, 'Coral King,' we might claim this as a genuine example of variation by loss. The new variety is a simple recessive. It differs from 'Crimson King' only in one respect, the loss of a single colour-factor, and, of course, bred true from its origin. To account for the appearance of such a new form by any process of crossing is exceedingly difficult. From the nature of the case there can have been no cross since 'Crimson King' was established, and hence the salmon must have been concealed as a recessive from the first origin of that variety, even when it was represented by very few individuals, probably only by a single one. Surely, if any of these had been heterozygous for salmon this recessive could hardly have failed to appear during the process of self-fertilisation by which the stock would be multiplied, even though that selfing may not have been strictly carried out. Examples like this seem to me practically conclusive.⁵ They can be challenged, but not, I think, successfully. Then again in regard to those variations in number and division of parts which we call meristic, the reference of these to original cross-breeding is surely barred by the circumstances in which they often occur. There remain also the rare examples mentioned already in which a single wild origin may with much confidence be assumed. In spite of repeated trials, no one has yet succeeded in crossing the Sweet Pea with any other leguminous species. We know that early in its cultivated history it produced at least two marked varieties which I can only conceive of as spontaneously arising, though, no doubt, the profusion of forms we now have was made by the crossing of those original varieties. I mention the Sweet Pea thus prominently for another reason, that it introduces us to another though subsidiary form of variation, which may be described as a *fractionation* of factors. Some of my Mendelian colleagues have spoken of genetic factors as permanent and indestructible. Relative permanence in a sense they have, for they commonly come out unchanged after segregation. But I am satisfied that they may occasionally undergo a quantitative disintegration, with the consequence that varieties are produced intermediate between the integral varieties from which they were derived. These disintegrated conditions I have spoken of as subtraction—or reduction—stages. For example, the Picotee Sweet Pea, with its purple edges, can surely be nothing but a condition produced by the factor which ordinarily makes the fully purple flower, quantitatively diminished. The pied animal, such as the Dutch rabbit, must similarly be regarded as the result of partial defect of the chromogen from which the pigment is formed, or conceivably of the factor which effects its oxidation. On such lines I think we may with great confidence

⁵ The numerous and most interesting 'mutations' recorded by Professor T. H. Morgan and his colleagues in the fly, *Drosophila*, may also be cited as unexceptionable cases.

interpret all those intergrading forms which breed true and are not produced by factorial interference.

It is to be inferred that these fractional degradations are the consequence of irregularities in segregation. We constantly see irregularities in the ordinary meristic processes, and in the distribution of somatic differentiation. We are familiar with half segments, with imperfect twinning, with leaves partially petaloid, with petals partially sepaloid. All these are evidences of departures from the normal regularity in the rhythms of repetition, or in those waves of differentiation by which the qualities are sorted out among the parts of the body. Similarly, when in segregation the qualities are sorted out among the germ-cells in certain critical cell-divisions, we cannot expect these differentiating divisions to be exempt from the imperfections and irregularities which are found in all the grosser divisions that we can observe. If I am right, we shall find evidence of these irregularities in the association of unconformable numbers with the appearance of the novelties which I have called fractional. In passing let us note how the history of the Sweet Pea belies those ideas of a continuous evolution with which we had formerly to contend. The big varieties came first. The little ones have arisen later, as I suggest by fractionation. Presented with a collection of modern Sweet Peas how prettily would the devotees of Continuity have arranged them in a graduated series, showing how every intergrade could be found, passing from the full colour of the wild Sicilian species in one direction to white, in the other to the deep purple of 'Black Prince,' though happily we know these two to be among the earliest to have appeared.

Having in view these and other considerations which might be developed, I feel no reasonable doubt that though we may have to forgo a claim to variations by addition of factors, yet variation both by loss of factors and by fractionation of factors is a genuine phenomenon of contemporary nature. If then we have to dispense, as seems likely, with any addition from without we must begin seriously to consider whether the course of Evolution can at all reasonably be represented as an unpacking of an original complex which contained within itself the whole range of diversity which living things present. I do not suggest that we should come to a judgment as to what is or is not probable in these respects. As I have said already, this is no time for devising theories of Evolution, and I propound none. But as we have got to recognise that there has been an Evolution, that somehow or other the forms of life have arisen from fewer forms, we may as well see whether we are limited to the old view that evolutionary progress is from the simple to the complex, and whether after all it is conceivable that the process was the other way about. When the facts of genetic discovery become familiarly known to biologists, and cease to be the preoccupa-

tion of a few, as they still are, many and long discussions must inevitably arise on the question, and I offer these remarks to prepare the ground. I ask you simply to open your minds to this possibility. It involves a certain effort. We have to reverse our habitual modes of thought. At first it may seem rank absurdity to suppose that the primordial form or forms of protoplasm could have contained complexity enough to produce the divers types of life. But is it easier to imagine that these powers could have been conveyed by extrinsic additions? Of what nature could these additions be? Additions of material cannot surely be in question. We are told that salts of iron in the soil may turn a pink hydrangea blue. The iron cannot be passed on to the next generation. How can the iron multiply itself? The power to assimilate the iron is all that can be transmitted. A disease-producing organism like the pebrine of silkworms can in a very few cases be passed on through the germ-cells. Such an organism can multiply and can produce its characteristic effects in the next generation. But it does not become part of the invaded host, and we cannot conceive it taking part in the geometrically ordered processes of segregation. These illustrations may seem too gross; but what refinement will meet the requirements of the problem, that the thing introduced must be, as the living organism itself is, capable of multiplication and of subordinating itself in a definite system of segregation? That which is conferred in variation must rather itself be a change, not of material, but of arrangement, or of motion. The invocation of additions extrinsic to the organism does not seriously help us to imagine how the power to change can be conferred, and if it proves that hope in that direction must be abandoned, I think we lose very little. By the re-arrangement of a very moderate number of things we soon reach a number of possibilities practically infinite.

That primordial life may have been of small dimensions need not disturb us. Quantity is of no account in these considerations. Shakespeare once existed as a speck of protoplasm not so big as a small pin's head. To this nothing was added that would not equally well have served to build up a baboon or a rat. Let us consider how far we can get by the process of removal of what we call 'epistatic' factors, in other words those that control, mask, or suppress underlying powers and faculties. I have spoken of the vast range of colours exhibited by modern Sweet Peas. There is no question that these have been derived from the one wild bi-colour form by a process of successive removals. When the vast range of form, size, and flavour to be found among the cultivated apples is considered it seems difficult to suppose that all this variety is hidden in the wild crab-apple. I cannot positively assert that this is so, but I think all familiar with Mendelian analysis would agree with me that it is probable, and that the wild crab contains presumably

inhibiting elements which the cultivated kinds have lost. The legend that the seedlings of cultivated apples become crabs is often repeated. After many inquiries among the raisers of apple seedlings I have never found an authentic case—once only even an alleged case, and this on inquiry proved to be unfounded. I have confidence that the artistic gifts of mankind will prove to be due not to something added to the make-up of an ordinary man, but to the absence of factors which in the normal person inhibit the development of these gifts. They are almost beyond doubt to be looked upon as *releases* of powers normally suppressed. The instrument is there, but it is 'stopped down.' The scents of flowers or fruits, the finely repeated divisions that give its quality to the wool of the Merino, or in an analogous case the multiplicity of quills to the tail of the fantail pigeon, are in all probability other examples of such releases. You may ask what guides us in the discrimination of the positive factors and how we can satisfy ourselves that the appearance of a quality is due to loss. It must be conceded that in these determinations we have as yet recourse only to the effects of dominance. When the tall pea is crossed with the dwarf, since the offspring is tall we say that the tall parent passed a factor into the cross-bred which makes it tall. The pure tall parent had two doses of this factor; the dwarf had none; and since the cross-bred is tall we say that one dose of the dominant tallness is enough to give the full height. The reasoning seems unanswerable. But the commoner result of crossing is the production of a form intermediate between the two pure parental types. In such examples we see clearly enough that the full parental characteristics can only appear when they are homozygous—formed from similar germ-cells, and that one dose is insufficient to produce either effect fully. When this is so we can never be sure which side is positive and which negative. Since, then, when dominance is incomplete we find ourselves in this difficulty, we perceive that the amount of the effect is our only criterion in distinguishing the positive from the negative, and when we return even to the example of the tall and dwarf peas the matter is not so certain as it seemed. Professor Cockerell lately found among thousands of yellow sunflowers one which was partly red. By breeding he raised from this a form wholly red. Evidently the yellow and the wholly red are the pure forms, and the partially red is the heterozygote. We may then say that the yellow is YY with two doses of a positive factor which inhibits the development of pigment; the red is yy , with no dose of the inhibitor; and the partially red are Yy , with only one dose of it. But we might be tempted to think the red was a positive characteristic, and invert the expressions, representing the red as RR , the partly red as Rr , and the yellow as rr . According as we adopt the one or the other system of expression we shall interpret the evolutionary change as one of loss or as one of

addition. May we not interpret the other apparent new dominants in the same way? The white dominant in the fowl or in the Chinese Primula can inhibit colour. But may it not be that the original coloured fowl or Primula had two doses of a factor which inhibited this inhibitor? The Pepper Moth, *Amphidasys betularia*, produced in England about 1840 a black variety, then a novelty, now common in certain areas, which behaves as a full dominant. The pure blacks are no blacker than the cross-bred. Though at first sight it seems that the black *must* have been something added, we can without absurdity suggest that the normal is the term in which two doses of inhibitor are present, and that in the absence of one of them the black appears.

In spite of seeming perversity, therefore, we have to admit that there is no evolutionary change which in the present state of our knowledge we can positively declare to be not due to loss. When this has been conceded it is natural to ask whether the removal of inhibiting factors may not be invoked in alleviation of the necessity which has driven students of the domestic breeds to refer their diversities to multiple origins. Something, no doubt, is to be hoped for in that direction, but not until much better and more extensive knowledge of what variation by loss may effect in the living body can we have any real assurance that this difficulty has been obviated. We should be greatly helped by some indication as to whether the origin of life has been single or multiple. Modern opinion is, perhaps, inclining to the multiple theory, but we have no real evidence. Indeed, the problem still stands outside the range of scientific investigation, and when we hear the spontaneous formation of formaldehyde mentioned as a possible first step in the origin of life, we think of Harry Lauder in the character of a Glasgow schoolboy pulling out his treasures from his pocket—'That's a wassher—for makkin' motor cars'!

As the evidence stands at present all that can be safely added in amplification of the evolutionary creed may be summed up in the statement that variation occurs as a definite event often producing a sensibly discontinuous result; that the succession of varieties comes to pass by the elevation and establishment of sporadic groups of individuals owing their origin to such isolated events; and that the change which we see as a nascent variation is often, perhaps always, one of loss. Modern research lends not the smallest encouragement or sanction to the view that gradual evolution occurs by the transformation of masses of individuals, though that fancy has fixed itself on popular imagination. The isolated events to which variation is due are evidently changes in the germinal tissues, probably in the manner in which they divide. It is likely that the occurrence of these variations is wholly irregular, and as to their causation we are absolutely without surmise or even plausible speculation. Distinct types once arisen, no

doubt a profusion of the forms called species have been derived from them by simple crossing and subsequent recombination. New species may be now in course of creation by this means, but the limits of the process are obviously narrow. On the other hand, we see no changes in progress around us in the contemporary world which we can imagine likely to culminate in the evolution of forms distinct in the larger sense. By intercrossing dogs, jackals, and wolves new forms of these types can be made, some of which may be species, but I see no reason to think that from such material a fox could be bred in indefinite time, or that dogs could be bred from foxes.

Whether Science will hereafter discover that certain groups can by peculiarities in their genetic physiology be declared to have a prerogative quality justifying their recognition as species in the old sense, and that the differences of others are of such a subordinate degree that they may in contrast be termed varieties, further genetic research alone can show. I myself anticipate that such a discovery will be made, but I cannot defend the opinion with positive conviction.

Somewhat reluctantly, and rather from a sense of duty, I have devoted most of this Address to the evolutionary aspects of genetic research. We cannot keep these things out of our heads, though sometimes we wish we could. The outcome, as you will have seen, is negative, destroying much that till lately passed for gospel. Destruction may be useful, but it is a low kind of work. We are just about where Boyle was in the seventeenth century. We can dispose of Alchemy, but we cannot make more than a quasi-chemistry. We are awaiting our Priestley and our Mendeléeff. In truth it is not these wider aspects of genetics that are at present our chief concern. They will come in their time. The great advances of science are made like those of evolution, not by imperceptible mass-improvement, but by the sporadic birth of penetrative genius. The journeymen follow after him, widening and clearing up, as we are doing along the track that Mendel found.



PRINTED BY
SPOTTISWOODE AND CO. LTD., LONDON
COLCHESTER AND ETON