Heredity—I*

New Theories and Facts Relating to the History of Organic Beings

By Prof. William Bateson

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 realized 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, wore a homogenous 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 realizes 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 skeptical 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 endeavor 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 analyze 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 fertilization. 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 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 recognizable in type and characteristics after 4,000 years.

I knew a breeder who had a chest containing bottles of colored 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 fertilization 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 color 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, color, 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 characterize 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 epitomize 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 fertilization 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 fertilization. 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 endeavor 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 course 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 inter-

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

² "On the Variation of Species," 1859.

relations 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 labors 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 fertilized egg has a polarity, a front and hind end for example; but we have now to recognize 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 color-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 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 endeavor 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 favored races has been developed and expounded in writings innumerable. Favored 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 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 coloring 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 favored 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 has 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 the 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

⁴I 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 Rhaetic 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.

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 favor, 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.

(To be continued.)

Combined Effect of Electric and Magnetic Fields on Spectrum Lines

By J. Stark

THE helium line $\lambda 4471.646$ was found by Lohmann [Abstract No. 617 (1908)] to yield a normal Zeeman triplet in the transverse effect; but when subject to an electric field of from 20,000 to 30,000 volts/centimeters the line gives a quartet with two components oscillating parallel to the field and two perpendicular to it. Two cases of the transverse effect occur with superimposed electric and magnetic fields: (1) Electric and magnetic fields parallel to one another. The question then arises as to whether in this case the two electric components of the line oscillating perpendicular to the electric field are each separated into a doublet by the magnetic field, while the two components oscillating parallel to the electric field remain unaffected, or does another kind of electromagnetic separation take place. (2) Electric and magnetic fields perpendicular to one another. Do the two electric components oscillating parallel to the electric field each split up into a doublet under the action of the magnetic field, the two perpendicular components remaining unaffected, or does another type of separation occur here? Experiments are being undertaken with a view to elucidating these problems. It was found that by the admission of a certain amount of hydrogen to the helium in the discharge tube the light emission of the canal rays in the mixture is more intense than in pure He. A description is given, with diagrams, of the apparatus to be used for investigating the combined effect of the electric and magnetic fields. The results of the experiments will be published later.—*Deutsches Phys. Gesellschaft.*

Influence of Occluded Gases of the Selective Photoelectric Effect

By R. Pohl and P. Pringsheim

POTASSIUM which had been boiled continuously for in one case 180 hours and in another 430 hours in an extremely good vacuum, whereby its yield of occluded hydrogen changed from 2 cubic centimeters to 4×10^{-4} cubic centimeters per hour per cubic centimeter of potassium, was found to give the same selective photoelectric effect to within the limits of experimental error as potassium not so treated. The presence of hydrogen in the metal does not therefore appear to be of prime importance. This result is in direct opposition to that obtained by Wiedemann and Hallwachs [see Abstract No. 722 (1914)], the cause of which the authors are unable to explain. A general discussion on the causes of the emission of electrons by short electromagnetic waves, by chemical action, and by heat and the possibility of connecting them is included.—*Deutsches Phys. Gesellschaft.*

³The 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.