SCIENCE

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*VARIATION AND SOME PHENOMENA CONNECTED WITH REPRODUCTION AND SEX.**

I.

IN the following address an attempt is made to treat the facts of variation and heredity without any theoretical preconceptions. The ground covered has already been made familiar to us by the writings of Darwin, Spencer, Galton, Weismann, Romanes, and others. I have not thought it advisable to discuss the theories of my predecessors, not from a want of appreciation of their value, but because I was anxious to look at the facts themselves and to submit them to an examination which should be as free as possible from all theoretical bias.

Zoology is the science which deals with animals. Knowledge regarding animals is, for convenience of study, classified into several main branches, amongst the most important of which may be mentioned; (1) the study of structure; (2) the study of the functions of the parts or organs; (3) the arrangement of animals in a system of classification; (4) the past history of animals; (5) the relations of animals to their environment; (6) the distribution of animals on the earth's surface. That part of the Science of Zoology which deals

* Address of the president to the Zoological Section of the British Association for the Advancement of Science, Dover, 1899.

with the functions of organs, particularly of the organs of the higher animals, is frequently spoken of as Physiology, and separated more or less sharply from the rest of Zoology under that heading. So strong is the line of cleavage between the work of the Physiologist and that of other Zoologists, that this Association has thought it advisable to establish a special Section for the discussion of physiological subjects, leaving the rest of Zoology to the consideration of the old-established Section, D. In calling attention to this fact, I do not for one moment wish to question the advisability of the course of action which the Association has taken. The Science of Physiology in its modern aspects includes a vast body of facts of great importance and great interest which no doubt require separate treatment. But what I do wish to point out is that it is quite impossible for us here to abrogate all our functions as physiologists. Some of the most important problems of the physiological side of Zoology still remain within the purview of this Section.

For instance, the important and far-reaching problems connected with reproduction and variation are very largely left to this Section, and that large group of intricate and almost entirely physiological phenomena connected with the adaptations of organisms to their environment are dealt with almost exclusively here. Indeed, we may go further, and say that apart altogether from practical questions of convenience, which make it desirable to separate a part of physiological work from the Zoological Section, it is, as a matter of fact, impossible to divorce the intelligent study of structure from that of function. The two are indissolubly connected together. The differentiation of structure involves the differentiation of function, and the differentiation of function that of structure. The conceptions of structure and function are as closely associated as those of matter and force. A zoologist who confined himself to the study of the structure of organisms, and paid no attention to the functions of the parts, would be as absurd a person as a philologist who studied the structure of words and took no account of their meaning. In the early part of this century, when the subject matter of zoology was not so vast as it is at present, this aspect of the case was fully recognized, and one of the greatest zoologists of the century, whether considered from the point of view of modern anatomy, or of modern physiology, was Professor of Anatomy and Physiology at the University of Berlin.

Having said that much as to the various aspects of living Nature, of natural history, if you like, which it falls within the province of this Section to deal with, I may now proceed to the subject of my address. And when I mention to you what that subject is, you will be able to make some allowance for the somewhat commonplace remarks with which I have treated you. For that subject, though it has its important morphological aspects, is in the main a physiological one; at any rate, no study which does not take account of the physiological aspect of it can ever hope to satisfy the intellect of man.

The subject, then, to which I wish to draw your attention at the outset of our proceedings, is the great subject of Variation of Organisms.

As everyone knows, there is a vast number of different kinds of organisms. Each kind constitutes a species, and consists of an assemblage of individuals which resemble one another more closely than they do other animals, which transmit their characteristics in reproduction and which habitually live and breed together. But the members of a species, though resembling one another more closely than they resemble the members of other species, are not absolutely alike. They present differences, differences which make themselves apparent even in members of the same family, *i. e.*, in the offspring of the same parents. It is these differences to which we apply the term *variation.* The immense importance of the study of variations may be judged from the fact that, according to the generally received evolution theory of Darwin, it is to them that the whole of the variety of living and extinct organisms is due. Without variation there could have been no progress, no evolution in the structure of organisms. If offspring had always exactly resembled their parents and presented no points of difference, each succeeding generation would have resembled those previously existing, and no change, whether backwards or forwards, could have occurred. This phenomenon of genetic variation forms the bedrock upon which all theories of evolution must rest, and it is only by a study of variations, of their nature and cause, that we can ever hope to obtain any real insight into the actual way in which evolution has taken place. Notwithstaading its importance, the subject is one which has scarcely received from zoologists the attention which it merits.

Though much has been written on the causes of variation, too little attention has of late years been paid to the phenomenon. Since the publication of Darwin's great work on the 'Variation of Animals and Plants under Domestication,' there have been but few books of first-rate importance dealing with the subject. The most important of these is Mr. William Bateson's work, entitled 'Materials for the Study of Variation.' I have no hesitation in saying that I regard this work as a most important contribution to the literature of the Evolution theory. In it attention is called, with that emphasis which the subject demands, to the supreme importance of the actual study of variation to the evolutionist, and a systematic attempt is made to classify variations as they occur in Nature. In preparing this book Mr. Bateson has performed a very real service to zoology, not the least part of which is that he has made a most effective protest against that looseness of speculative reasoning which, since the publication of the 'Origin of Species,' has marred the pages of so many zoological writers.

The Variations of Organisms may be grouped under two heads, according to their nature and source: (1) There are those variations which appear to have no relation to the external conditions, for they take place when these remain unchanged, *e. g.*, in members of the same litter; they are inherent in the constitution of the individual. These we shall call constitutional variations, or as their appearance seems nearly always to be connected with reproduction, they may be called *genetic* (congenital, blastogenic) *variations.* (2) The second kind of variations are those which are caused by the direct action of external conditions. These variations constitute the so-called *acquired characters.*

My first object is to consider these two kinds of variations, their nature, their causes and their results on subsequent generations and to inquire whether there are any fundamental differences between them. In this connection it is of particular importance that we should inquire whether acquired modifications are transmitted in reproduction. As is well known, there are two schools of thought holding directly opposite views as to this matter. The one of these schools—the so-called Lamarckian school—holds that they may be transmitted as such in reproduction; the other school, on the other hand, maintains that acquired modifications affect only the individual concerned, and are not handed on as such in reproduction. That the decision of the matter is not only theoretically important, but also practically, is evident, for upon it depends the answer to the question whether mental or other facilities acquired by the laborious exercise of the individual are ever transmitted to the offspring—whether the facility which the individual acquires in resisting temptation makes it any easier for the offspring to do the same, whether the effects of education are cumulative in successive generations. To put the matter as Francis Galton has put it, is nature stronger than nurture, or nurture than nature?

We have then two kinds of variation to consider: (1) genetic variation, (2) acquired modification. It is the former of these—namely, genetic variation—with which I wish primarily to deal. Let us examine more fully the mode of its occurrence.

GENETIC VARIATION.

Organized beings present, as you are aware, two main kinds of reproduction, the sexual and the asexual. These two kinds of reproduction present certain differences, of which the most important, and the only one which concerns us now, is the fact that genetic variation is essentially associated with sexual reproduction, and is rarely, if ever, found in asexual reproduction. In other words, whereas the offspring resulting from asexual reproduction as a rule exactly resemble the parent, they are always different from the parents in sexual reproduction. I am aware that I am treading on disputed ground. You will observe that I do not make the assertion that asexually produced offspring *always* exactly resemble the parent, and never present genetic variations. To say that would be going too far in the present state of our knowledge. Therefore I have put the matter less strongly, and merely assert that whereas asexual reproduction is on the whole characterized by identity between the offspring and the parent, sexual reproduction is always characterized by differences more or less marked between the two; and I reserve the question as to whether genetic variations are ever found in asexual reproduction for later consideration.

This modified form of the statement will, I think, be admitted on all hands, but before going on I will illustrate my meaning by reference to actual examples.

Asexual reproduction is a phenomenon comparatively rare in the animal kingdom, and when it does occur it is exceedingly difficult to investigate from this particular point of view. In the vegetable kingdom, on the other hand, it is quite common. All, or almost all, plants possess this power, and in a very great many of them the result of its exercise can be fully followed out, and contrasted with that of sexual reproduction. Let us follow it out in the potato-plant. The potato can and does normally propagate itself asexually by means of its underground tubers. As you will know, if you take one of these and plant it, it gives rise to a plant exactly resembling the parent. If the tuber (seed as it is sometimes erroneously called) be that of the Magnum Bonum, it gives rise to a plant with foliage, flowers and tubers of the Magnum Bonum variety; if it be the Snowdrop, the foliage, flowers, habit and tubers are totally different from the Magnum Bonum, and are easily identified as Snowdrops. In this way a favorable variety of potato can be reproduced to almost any extent with all its peculiarities of earliness or lateness, pastiness or mealiness, power of resisting disease and so forth. By asexual reproduction the exact fac-simile of the parent may always be obtained, provided the conditions remain the same.

Now let us turn to the results of sexual reproduction—the seeds, *i. e.*, the real seeds, which as you know are produced in the flowers, are the means by which sexual reproduction is effected. They are produced in great quantity by most plants, and when placed in the ground under the proper conditions they germinate and produce plants. But these plants do not resemble the parent. Try the seed of the Magnum Bonum potato and raise plants from it. Do you think that any of them will be the Magnum Bonum with all its properties of keeping, resisting disease and so forth? Not a bit of it. The probability is, that not one of your seedling plants will exactly reproduce the parents; they will all be different. Again, take the apple; if you sow the seed of a Blenheim Orange and raise young apple-trees, you will not get a Blenheim Orange. All your plants will be different, and probably not one will give you apples with the peculiar excellence of the parent. If you want to propagate your Blenheim Orange and increase the number of your trees, you must proceed by grafting or by striking cuttings, which are the methods by which such a tree may be asexually reproduced. And so on. Examples might be multiplied indefinitely. Every horticulturist knows that variety characterizes seedlings, *i. e.*, sexual offspring, whereas identity is found in slips, grafts and offsets, *i. e.*, in asexual offspring; and that if you want to get a new plant you must sow seeds, while if you want to increase your stock of an old one you must strike cuttings, plant tubers or proceed in some analogous manner.

An apparent exception to this rule is afforded by so-called bud variation, but it is not certain that this is really an exception. In so far as these bud variations are not of the nature of acquired variations produced by a change of external conditions, and disappearing as soon as the old conditions are renewed, they are probably stages in the growth and development of the organism. That is to say, they are of the same nature as those peculiarities in animals which appear at a particular time of life, such as a single lock of hair of a different color from the rest of the hair,* the change in color of hair with growth,† the appearance of insanity or of epilepsy at a particular age. There is nothing more remarkable in a single bud on a tree departing from the usual character at a particular time of life, than in a particular hair of a mammal doing the same thing.

* Darwin, *Variation*, Vol. I., p. 449.

† As an example I may refer to the Himalayan rabbit; Darwin, *Variation*, Vol. I., p. 114.

We have seen that, speaking broadly, genetic variation is connected with sexual reproduction, and it becomes necessary to examine this mode of reproduction a little more fully. What is the essence of sexual reproduction, and how does it differ from asexual? What I am now going to say applies generally to the phenomenon whether it occurs in plants or animals. Sexual reproduction is generally carried on by the co-operation of two distinct individuals—these are called the male and female respectively. They produce, by a process of unequal fission which takes place at a part of their body, called the reproductive gland, a small living organism called the reproductive cell. The reproductive cell produced by the male is called in animals the spermatazoon, and is different in form from the corresponding cell produced by the female, and called in animals the ovum. The object with which these two organisms are produced is to fuse with one another and give rise to one resultant uninucleated organism or cell, which we may call the *zygote*. This process of fusion between the two kinds of reproductive cells, which are termed *gametes*, is called conjugation. The difference in structure between the male and female gamete is a matter of secondary importance only, and is connected with the primary function of coming into contact and fusing. The same may be said with regard to the so-called sexual differences of the parents of the two kinds of gametes, and to the powerful instincts which regulate their action. The conjugation of the male and female gamete, or the fertilization of the ovum, as it is sometimes called, consists in the fusion of two distinct masses of protoplasm which are nearly always produced by different individuals. In the case of hermaphrodites, the term applied to organisms which produce both male and female gametes in the same individual, there is generally some arrangement which tends to prevent the male gamete from conjugating with the female gamete of the same parent; but this phenomenon is not absolutely excluded, and takes place as a normal phenomenon in many plants and possibly in some animals.

This fusion of the protoplasm of the two gametes gives us a uninucleated organism —for the fusion of the nuclei of the two gametes seems to be an essential part of the process—in which the potencies of the two gametes are blended. The *zygote*, as the mass formed of the fused gametes is called, is formed by the combination of two individualities, and is therefore essentially a new individuality, the characters of which will be different from the characters of both of the parents. This fact, which is not apparent in the zygote when first established, because the parts are hardly distinguishable by our senses, becomes obvious as soon as organs, with the appearance of which we are familiar, are formed. As a general rule this cannot be said to have occurred until what we call maturity has been nearly reached, because we are not familiar enough with the features of immature organisms to detect individual differences. But you may rest assured that such differences exist at all stages of growth from that of the uninucleated zygote till death. How the characters of the two parents will combine in the zygote it is impossible to predict, and the result is never the same even though the conjugations have been between gametes of identical origin. There may be an almost perfect mixture, the blending extending to even quite minute details; or the characters of the one parent may predominate—be prepotent, as we call it—over those of the other; or they may blend in such a way that the zygote offers characters found in neither parent. Or, finally, the features of one parent may come out at one stage of growth, those of the other at another stage. But, however the characters may blend, the product never exactly resembles the parents. The extent to which it differs from them is the measure of the variation.

To resume, it will be observed that in the method of reproduction sometimes called sexual, two distinct processes occur. One of these is the real reproductive act, which consists in the production by fission of uninuclear individuals called gametes; the second is the fusion of the gametes to form the zygote. The gametes are of two kinds, and the reason of there being two kinds is intelligible when we consider the parts they have to play. The male gamete is nearly always endowed with locomotive power, and the female gamete is stored with food material to be used by the zygote in the first stages of growth. The destiny of these two uninucleated organisms is to fuse with one another, and so to give rise to a zygote which ultimately assumes the typical form of the species. As a general rule the gametes have but a limited duration * of life unless they conjugate, and this is quite intelligible when we remember that they have no organs, *e. g.*, digestive organs, suitable for the maintenance of life. It is rarely found that they have the power of assuming the form of their parent, unless they conjugate. This never happens in the case of the male gamete (at any rate in animals), and only rarely in that of the female. When it occurs—that is to say, when the ovum develops without conjugation—we call the phenomenon parthenogenesis. Parthenogenesis is found more

*Under favorable conditions they may live a considerable time—*e. g.*, the spermatozoon of certain ants, which are stated by Sir John Lubbock to live in some cases for seven years.

commonly in Arthropods than in other groups, but it may be more common than is supposed.*

In sexual reproduction then, in addition to the real reproductive act, which is the division by fission of the parent into two unequal parts, the one of which continues to be called the parent, while the other is the gamete, there is the subsequent conjugation process. It is to this conjugation process that that important concomitant of sexual reproduction must be attributed, namely genetic variation. We have thus traced genetic variation to its lair. We have seen that it is due to the formation of a new individuality by the fusion of two distinct individualities. We have also seen that in the higher animals it is always associated with the reproductive act.

Let us now take a wider survey and endeavor to ascertain whether this most important process, a process upon which depends the improvement as well as the degradation of races, ever takes place independently of the reproductive act. In the Metazoa, to which for our present purpose I allude under the term higher animals, conjugation never takes place except in connection with reproduction. It is impossible from the nature of the process that it should do so, as I hope to explain later on. But among the Protozoa, the simplest of all animals, it is conceivable that conjugation might take place apart from reproduction, and as a matter of fact it does do so. Let us now examine a case in which this occurs. Amongst the free-swimming ciliated Infusoria it frequently happens that two individuals become applied together, and that the protoplasm of their bodies becomes continuous. They remain in this condition of fusion for some days, retaining however their external form and not undergoing complete fusion. While the continuity lasts there is an exchange of living substance between the two bodies, in which exchange a bit of the nucleus of each participates. It thus happens that at the end of conjugation, when the two animals separate, they are both different from what they were at the commencement; each has received protoplasm and a nucleus from its fellow, and the introduced nucleus fuses, as we know, with the nucleus which has not moved. It would therefore appear that all the essential features of the conjugation process, as we learned them in the case of the conjugation of the gametes in the Metazoa are present, and it is impossible to doubt that we have here an essentially similar phenomenon. The phenomenon differs, however, from the conjugation first described in this interesting and important respect, that the two animals separate and resume their ordinary life. It is true that their constitution must have been profoundly changed, but they retain their general form. I say that the constitution of the exconjugates, as we may call them after they are separated, must be different from what it was before conjugation, but so far as I know no difference in structure corresponding with this difference in constitution has been recorded. I feel no sort of doubt, however, that structural differences, *i. e.*, variations, will be detected when the exconjugates are closely scrutinized and compared with the animals before conjugation, and I would suggest that definite observations be made with a view to testing the point. Here, then, we have a case of conjugation entirely dissociated from reproduction. Other cases of a similar character are known among the Protozoa, though as a general rule the fusion between the conjugating organisms is complete and permanent. Among plants, conjugation is generally associated with repro-

*It may be mentioned as a curious fact that parthenogenesis is rarely found in the higher plants, and, as I have said, is not known for the male gamete among animals.

duction, but not always, for in certain fungi* fusion of hyphæ and consequent intermingling of protoplasm occurs, and is not followed by any form of reproduction. Among bacteria alone, so far as I know, has the phenomenon of conjugation never been observed.

To sum up, we have seen that the phenomenon of conjugation is very widely distributed. Excluding the bacteria, there is reason to believe that it forms a part of the vital phenomena of all organisms. Its essential features are a mixture and fusion of the protoplasm of two different organisms, accompanied by a fusion of their nuclei. It results in the formation of a new individuality, which differs from the individualities of both the conjugating organisms. This difference manifests itself in differences in habit, constitution, form and structure; such differences constituting what we have called genetic variations.

The conjugation of the ovum and spermatozoon in the higher animals, and the corresponding process in the higher plants, are special cases of this conjugation, in which special conjugating individuals are produced, the ordinary individuals being physically incapable of the process. The phenomenon of sex, with all its associated complications, which is so characteristic of the higher animals and plants, is merely a device to ensure the coming together of the two gametes. In the lower animals it is possible for the ordinary organism to conjugate; consequently the phenomenon does not form the precursor of developmental change, and is in no way associated with reproduction. Indeed, in such cases it is often the opposite of reproduction, inasmuch as it brings about a reduction in the number of individuals two separate individuals fusing to form one.

* It must be mentioned, however, that in the case of these fungi the fusion of nuclei has not been observed, nor has it been noticed whether the habit, structure, or constitution of the conjugating plants are altered after the fusion.

ACQUIRED CHARACTERS.

We now come to the consideration of the second kind of variations—namely, those which owe their origin to the direct action of external agencies upon the particular organism which shows the variation; or, as Darwin puts it, to the definite action of external conditions. These are the variations which I have called acquired variations or acquired characters. This is not a good name for them, but at the present moment, when I am about to submit them to a critical examination, I do not know of any other which could be suitably applied. Later on, when I sum up the various effects of the direct action of external agencies upon the organism, I may be able to use a more suitable term.

The main peculiarities of acquired variations are two in number: (*a*) they make their appearance as soon as the organism is submitted to the changed conditions; (*b*) speaking generally they are more or less the same in all the individuals of the species acted upon. As examples of this kind of variations, I may mention the effect of the sun upon the skin of the white man; the Porto Santo rabbit, an individual of which recovered the proper color of its fur in four years under the English climate;* the change of *Artemia salina* to *Artemia milhausenii*; the increase in size of muscles as the result of exercise; and the development of any special facility in the central nervous system. Among plants, variations of this kind are very easily acquired, by altering the soil and climate to which the individuals are submitted. So common are they, that it is quite possible that a large number of species are really based upon characters of this kind; characters which are produced solely by the external conditions and which

* Darwin, *Variation*, ed. 2, Vol. I., p. 119.

frequently disappear when the old conditions are reverted to.

With regard to these variations, we want to ask the following question: Do they ever last after the producing cause of them is removed, and are they transmitted in reproduction? In a great number of cases they either cease when the cause which has produced them is removed, or if they last the life of the individual they are not transmitted in reproduction. But is this always the case? That is the important question we now have to consider.

But before doing so let us inquire what acquired characters really are. The so-called adults of all animals have, as part of their birthright, a certain plasticity in their capacity of reacting to external influences; they all have a certain power of acquiring bodily and mental characters under the influence of appropriate stimuli. This power varies in degree and in quality in different species. In plants, for instance, it is mainly displayed in habit of growth, form of foliage, etc.; in man in mental acquirements, and so on. But however it is displayed, it is this property of organisms which permits of the acquisition of those modifications of structure which have been so widely discussed as *acquired* characters. Now this power, when closely considered, is in reality only a portion of that capacity for development which all organisms possess, and with which they become endowed at the act of conjugation. A newly formed zygote possesses a certain number of hidden properties which are not able to manifest themselves unless it is submitted to certain external stimuli. It is these stimuli which constitute the external conditions of existence, and the properties of the organism which are only displayed under their influence are what we call acquired characters. They are acquired in response to the external stimuli.

It would appear, then, that every feature which successively appears in an organism in the march from the uninucleated zygote to death is an acquired character. At first the stimuli which are necessary are quite simple, being little more than appropriate heat and moisture; later on they become more complicated, until finally, when the developmental period is over and the mature life begins, the necessary conditions attain their greatest complexity, and their fulfilment constitutes what we call in the higher animals education. Education is nothing more than the response of the nearly mature organism to external stimuli, the penultimate response of the zygote to external stimuli, the ultimate being those of senile decay, which end in natural death. Acquired properties, it will be seen, are really stages in the developmental history. They differ in the complexity of the stimulus required to bring them out. For instance, the segmentation of the egg requires little more than heat and moisture, the walking of the chick the stimulus of light and sound and gravity, the evolutions of an acrobat the same in greater complexity, and lastly the action of a statesman requires the stimulation of almost every sense in the greatest complexity. Moreover, not only are there differences in the complexity of the stimulus required, but also in the rapidity with which the organism reacts to it. The chick undergoes its whole embryonic development in three weeks, a man in nine months; the chick develops its walking mechanism in a few minutes, while a man requires twelve months or more to effect the same end. Chickens are much cleverer than human beings in this respect. There is the same kind of difference between them that there is between the power of learning displayed by a Macaulay and that displayed by a stupid child.

An instinct is nothing more than an internal mechanism which is developed with great rapidity in response to an appropriate stimulus. It is difficult for us to understand instincts, because with us almost all developmental processes are extremely slow and gradual. This particularly applies to the development of those nervous mechanisms, the working of which we call reason.

Within certain limits the external conditions may vary without harming the organism, but such variations are generally accompanied by variations in the form in which the properties of the zygote are displayed. If the variations of the conditions are too great, their action upon the organism is injurious, and results in abortions or death. And in no case can the external conditions call out properties with which the zygote was not endowed at the act of conjugation.

It would thus appear that acquired characters are merely phases of development; they are the manifestations of the properties of the zygote, and are called forth only under appropriate stimulation; moreover, they are capable of varying within certain limits, according to the nature of the stimulus, and it is to these variations that the term acquired character has been ordinarily applied.

A genetic character, on the other hand, is the possibility of acquiring a certain feature under the influence of a certain stimulus; it is not the feature itself—that is an acquired character— but it is the possibility of producing the feature. Now as the possibility of producing the feature can only be proved to exist by actually producing it, the term genetic character is frequently applied to the feature itself, which is, as we have seen, an acquired character. In consequence of this fact, that we can only determine genetic characters by examining acquired characters, a certain amount of confusion may easily arise, and has indeed often arisen, in dealing with this subject. This can be avoided by remembering that in describing genetic characters account must always be taken of the conditions. For example, the white fur of the Arctic hare is an acquired character, acquired in response to a certain stimulus; while the power of so responding to the particular stimulus when applied at the correct time is a genetic character. Thus a genetic character is a character which depends upon the nature of the organism, while an acquired character depends on the nature of the stimulus.

If we imagine a zygote to be a machine capable of working out certain results on material supplied to it, then we should properly apply the term genetic character to the features of the machinery itself, and the words acquired character to the results achieved by its working. These clearly will depend primarily on the structure of the machinery, and secondarily upon the material and energy supplied to it—that is to say, upon the way in which it is worked.

Variations in genetic characters are variations in the machinery of different zygotes that is to say, in the constitution—while variations in acquired characters are variations in the results of the working of one zygote according to the conditions under which it is worked.

For instance, let us take the case of those twins which arise by the division of one zygote, and are consequently identical in genetic characters, *i. e.*, in constitution. If they are submitted to different conditions, they will develop differences which will depend entirely upon the conditions and the time of life when the differentiation in the conditions occurred. These differences then will be a function of the external conditions, *i. e.*, of the manner in which the machinery is worked, and constitute what we call variation in acquired characters.

ARE ACQUIRED CHARACTERS TRANSMISSIBLE AS SUCH IN REPRODUCTION?

To return to our question, are the so-called acquired characters ever transmitted in reproduction? Let us consider what this question means in the light of the preceding discussion. Acquired characters are features which arise in the zygote in response to external stimuli. Now the zygote at its first establishment has none of the characters which are subsequently acquired. All it has is the power of acquiring them. Clearly, then, acquired characters are not transmitted. The power of producing them is all that can be transmitted; and this power resides in the reproductive organs and in the gametes to which the reproductive organs give rise, so that the question must be put in another form. Is it possible by submitting an organism to a certain set of conditions, and thus causing it to acquire certain characters, so to modify its reproductive organs that the same characters will appear in its offspring as the result of the application of a different and simpler stimulus?

For instance, the power of reading conferred by education, the hardness of the hands and increased size of the muscles produced by manual labor: is it possible that these characters, now produced by complex external stimuli applied at a particular period of life, should ever in future ages be produced by the simpler stimuli found within the uterus, so that a man may be born able to read or write, or with hands horny and hard like those of a navvy?

In trying to find an answer to this question let us first of all look into the probabilities of the case, to see if we can relate the question to any other class of phenomena about which we have, or think we have, definite knowledge.

When an organism is affected by external agents the action may apply to the whole organization or principally to one organ. Let us take a case in which one organ only appears to be affected, *e. g.*, the enlargement by exercise of the right arm of a man. Now, although in this case it is only the muscles of the arm which appear at first sight to be affected, we must not forget that the organs of the body are correlated with one another, and an alteration of one will produce an alteration in others. By exercise of the right arm the muscles of that arm are obviously enlarged, but other changes not so obvious must also have taken place. The bones to which the muscles are attached will be altered; the blood-vessels supplying the muscles will be enlarged, and the nerves which act upon the muscles, and probably the part of the central nervous system from which they proceed, will also be altered. These are some of the more obvious correlated changes which will have occurred; no doubt there will have been others—indeed it is not perhaps too much to say that all the organs of the body will have reacted to the enlargement of the arm —but the effect on organs not in functional correlation with the muscles of the right arm will be imperceptible, and may be neglected. Thus the color of the hair, the length and character of the alimentary canal, size of the leg muscles, the renal organs, etc., will not show appreciable alteration. Above all, the other arm will not be affected, or if it is affected the alteration will be so slight as not to be noticeable. Now, we know that homologous parts, whether symmetrically homologous or serially so, are in some kind of close connection. For instance, when one member of an homologous series varies, it is commonly found that other members of the same series will also vary. Yet in spite of this connection which exists between the right and left arms and between the right arm and right leg there is no similar alteration either in the left arm or in the right leg. Now, if parts which from these facts we may suppose to be in some connection are not affected, how can we expect the reproductive organs not only to be modified, but also to be so modified that the germs which are about to be budded off from them will be so affected as to produce exactly the same character—in this case enlarged muscle, etc.—without the application of the same stimulus, viz, exercise? Thus, while I freely admit that every alteration of an organ in response to external agents will react through the whole organization, affecting each organ in functional correlation with the affected organ in a way which will depend upon the function of the correlated organ, and possibly other organs not in functional correlation in an indefinite way and to a slight extent, yet I maintain that it is very hard to believe that it will have such a sharp and precise effect upon every spermatozoon and ovum subsequently produced that not merely will these products be altered generally in all their properties, but that one particular part of them—and that part of them always the same—will be so altered that the organisms which develop from them will be able to present the same modification on the application of a different stimulus. It is inconceivable; unless, indeed, we suppose that the very molecules of the incipient organs in the germ are more closely correlated with corresponding parts of the parent body than are the homologous parts of the parent body with one another.

Now, to prove the existence of such a remarkable and intimate correlation would surely require the very strongest and most conclusive evidence. Is there any such strong evidence? I think I may fairly answer this question in the negative. The evidence which has been brought forward in favor of the so-called inheritance of acquired characters is far from conclusive. That such evidence* exists I do not deny, but it is all, or almost all, capable of receiving other interpretations.

* For a good statement and discussion of the evidence in favor of this view, see Romanes' *Darwin and after Darwin*, Vol. II. chaps., 3 and 3.

EFFECT OF CHANGED CONDITIONS UPON THE REPRODUCTIVE ORGANS.

On the other hand, all the certain evidence we have concerning what happens when the reproductive organs are affected, either directly or by correlation, by a change of conditions—and, as we have seen above, they must be affected if there is to be any change in the offspring—tends to show that there is not any relation between the effect produced on the parent and that appearing in the offspring.

The only means of judging whether the reproductive organs are affected by external conditions is by observing any change which may occur in their function. Now, only two such physiological effects of a change of conditions are certainly known; these are (1) the production of sterility or of partial sterility; (2) the production of an increased but indefinite variability in the offspring. With regard to the first of these effects: One of the most common, or at any rate one of the most noticeable alterations in an organism, effected by change in the external conditions, is an alteration of the reproductive system, an alteration of such a kind that organisms which had previously freely interbred with one another are no longer able to do so. One of the most common results of removing organisms from their natural surroundings is to induce sterility or partial sterility. There is no reason to doubt that this sterility or tendency to sterility is, broadly speaking, due to an affection of the reproductive system. In the case of the higher animals, it may in some cases be due to an action upon the instincts, but in the lower animals and in plants we can hardly doubt that it is due to a direct action upon the reproductive organs. Indeed in plants these organs are often visibly affected. Among animals, however, there does not appear to be any satisfactory evidence on the point, and it is not known what organs are affected, whether it is the actual gametes, or the reproductive glands, or some of the other organs concerned.*

The other result of changed conditions which is certainly known is to induce an increased amount of variability of the genetic kind, though not immediately, often indeed not until after the lapse of some generations. On this point Darwin says: "Universal experience shows us that when new flowers are first introduced into our gardens they do not vary; but ultimately all, with the rarest exceptions, vary to a greater or less extent" ('Variation,' 2, p. 249).† With regard to the variability thus induced, it is to be noticed that it is not confined to any particular organ, nor does it show itself in any particular way. On the contrary, the whole organization is affected, and the variations are quite indefinite.

To sum up the argument as it at present stands: (1) a change in conditions cannot affect the next generation unless the reproductive organs are affected; (2) from a consideration of the facts of the case, it is almost inconceivable that the effect produced upon any organ of a given organism by a change of conditions should so modify the reproductive organs of that organism as to lead to a corresponding modification in the offspring without the latter being exposed to the same conditions; (3) the only effects, which are certainly known, of changed conditions upon the reproductive organs are (*a*) the production of sterility; (*b*) an increase in genetic variability.

* The exact cause of this sterility in the higher animals is a point which specially needs investigation.

† The phenomenon of increased variability following upon change of conditions has most often been observed when the change has been from a state of nature to a state of cultivation. Hence the conclusion has been drawn that the kind of change involved in domestication alone induces variation. But there is no evidence in favor of this view. The evidence shows that change of conditions in itself may induce greater variability.

As far then as our certain knowledge goes, it would appear that a change of conditions may have one or both of the following effects:

(1) A definite change, of the same character or nearly so, in all the individuals acted upon. Such changes may be adaptive or non-adaptive, but they are not permanent, lasting only so long as the change of conditions, or at most during the life of the individual acted upon. They are not transmitted in reproduction, and do not appear in the offspring unless it is submitted to the same conditions. These variations are the direct result of the action of the environment upon the individual, with the exception of the reproductive organs.

(2) Increase in the variations of the genetic kind. These are seen not in the generation* first submitted to the changed condition, but in the next or some subsequent generations. The effect is produced through the reproductive organs. These variations are non-adaptive, and different in each individual.

If the reproductive organs are affected we get an increase in the variations of the genetic kind. These, we have seen, are usually of an indefinite character; they are different in every case, and their nature cannot be predicted from experience. But we still have to ask: Is this a universal rule? Does it never happen that a change of conditions so affects the reproductive organs as to produce a definite non-adaptive change of the same character or nearly so in all the descendants of the individual acted upon? This is the most obscure question connected with the study of variations. If such changes occur, they might

* No doubt the individuals of the generation first submitted to the changed conditions would be affected as regards their reproductive organs, which would be altered in structure, but this has not been made out, though there are indications of such an effect in certain plants.

be cumulative, being increased in amount by the continued action of the conditions. They would be non-adaptive, their nature depending on the constitution of the reproductive cells and having no functional relation to the original stimulus.

As possible examples of such variation, I may recall those variations referred to by Darwin as 'fluctuating variations which sooner or later become constant through the nature of the organism and of the surrounding conditions, but not through natural selection' ('Origin,' ed. 6, p. 176); to the variations in turkeys and ducks which take place as the result of domestication ('Variation,' 2, p. 250); to those variations which Darwin had in his mind when he wrote the following sentence ('Origin,' p. 72): "There can be little doubt that the tendency to vary in the same manner has often been so strong that all the individuals of the same species have been similarly modified without the aid of selection."

It is, however, as I have said, extremely doubtful if variations of this kind really occur. The appearance of them may be caused by the combination of the two other kinds of variation. In all cases which might be cited in support of their occurrence, there are the following doubtful elements: (1) no clear statement as to whether the variations showed themselves in the individuals first acted upon; (2) no history of the organisms when transported back to the old conditions.

Moreover, a general consideration of the facts of the case renders it improbable that such similar and definite genetic variations should often occur at any rate in sexual reproduction. For although the effect upon the reproductive organs may possibly be almost the same in nearly all the individuals acted upon, it must not be forgotten that the reproductive elements have to combine in the act of conjugation, and that it is the essence of this act to produce products which differ in every case.

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(*To be Concluded.*)

THE LANGUAGE OF HAWAII.

II.

V.—SPECIAL PECULIARITIES.

Volubility.—The language of Hawaii is extremely voluble. The comparative ease with which the same ideas may be repeatedly expressed in a different form, and apparently as new material, is shown by the following incident which happened during my visit.

Owing to the mixed composition of the Hawaiian legislature, it is necessary to employ continually two languages. All speeches in English are immediately translated into Kanaka, and *vice versa.* On this occasion the interpreter innocently exposed a fundamental characteristic of the native tongue in replying to a member. An Hawaiian had spoken possibly ten minutes since his last words were translated. A friend, anxious that nothing of importance should be lost, asked why the interpreter did not perform his duty and give the English-speaking members the benefit of the words just uttered. The reply was: "He has said nothing fresh yet." The speaker had simply repeated in new phraseology the substance of his previous remarks, and so skillfully was it done that the friend, although somewhat conversant with the tongue, was misled by Kanaka volubility.

Here we have a distinguished feature in Polynesian methods of thought. By its very simplicity, its lack of generic terms, and its flexibility, the Hawaiian tongue is capable of almost endless expression of the simplest ideas. As we trace the growth of the language, influenced by the peculiar environment and temperament of the peo-