II.

ON HEREDITY.

1883.

ON HEREDITY.

PREFACE.

THE following essay was my inaugural lecture as Pro-Rector of the University of Freiburg, and was delivered publicly in the hall of the University, on June 21, 1883; it first appeared in print in the following August. Only a few copies of the first edition were available for the public, and it is therefore now reprinted as a second edition, which only differs from the first in a few not unimportant improvements and additions.

The title which I have chosen requires some explanation. I do not propose to treat of the whole problem of heredity, but only of a certain aspect of it—the transmission of acquired characters which has been hitherto assumed to occur. In taking this course I may say that it was impossible to avoid going back to the foundation of all the phenomena of heredity, and to determine the substance with which they must be connected. In my opinion this can only be the substance of the germ-cells; and this substance transfers its hereditary tendencies from generation to generation, at first unchanged, and always uninfluenced in any corresponding manner, by that which happens during the life of the individual which bears it. If these views, which are indicated rather than elaborated in this paper, be correct, all our ideas upon the transformation of species require thorough modification, for the whole principle of evolution by means of exercise (use and disuse), as proposed by Lamarck, and accepted in some cases by Darwin, entirely collapses.

The nature of the present paper—which is a lecture and not an elaborate treatise—necessitates that only suggestions and not an exhaustive treatment of the subject could be given. I have also abstained from giving further details in the form of an appendix, chiefly because I could hardly have attempted to complete a treatment of the whole range of the subject, and I hope to refer again to these questions in the future, when new experiments and observations have been made.

I am very glad to see that such an important authority as Pflüger[1] has in the meantime come to the same opinion, from an entirely different direction—an opinion which forms the foundation of the views here brought forward, namely, that heredity depends upon the continuity of the molecular substance of the germ from generation to generation.

A. W.

[1] Pflüger, 'Ueber den Einfluss der Schwerkraft auf die Theilung der Zellen und auf die Entwicklung des Embryo,' Arch. f. Physiol. Bd. XXXII. p. 68, 1883.

II.

ON HEREDITY.

WITH your permission I wish to bring before you to-day my views on a problem of general biological interest—the problem of heredity.

Heredity is the process which renders possible that persistence of organic beings throughout successive generations, which is generally thought to be so well understood and to need no special explanation. Nevertheless our minds cannot fail to be much perplexed by the multiplicity of its manifestations, and to be greatly puzzled as to its real nature. A celebrated German physiologist says[1], 'Although many hands have at all times endeavoured to break the seal which hides the theory of heredity from our view, the results achieved have been but small; and we are in a certain degree justified in looking with little hope upon new efforts undertaken in this direction. We must nevertheless endeavour from time to time to ascertain how far we have advanced towards a complete explanation.'

Such a course is in every way advisable, for we are not dealing with phenomena which from their very nature are incomprehensible by man. The great complexity of the subject has alone rendered it hitherto insuperable, but in the province of heredity we certainly have not reached the limits of attainable knowledge.

From this point of view heredity bears some resemblance to certain anatomical and physiological problems, e. g. the structure and function of the human brain. Its structure—with so many millions of nerve-fibres and nerve-cells—is of such extraordinary complexity that we might well despair of ever completely understanding it. Each fibre is nevertheless distinct in itself, while its connection with the nearest nerve-cell can be frequently traced, and the function of many groups of cell elements is already known. But it would seem to be impossible to unravel the excessively complex network

[1] Victor Hensen in his 'Physiologie der Zeugung,' Leipzig, 1881, p. 216.

into which the cells and fibres are knit together; and hence to arrive at the function of each single element appears to be also beyond our reach. We have not however commenced to untie this Gordian knot without some hope of success, for who can say how far human perseverance may be able to penetrate into the mechanism of the brain, and to reveal a connected structure and a common principle in its countless elements? But surely this work will be most materially assisted by the simultaneous investigation of the structure and function of the nervous system in the lower forms of life—in the polypes and jelly-fish, worms and Crustacea. In the same way we should not abandon the hope of arriving at a satisfactory knowledge of the processes of heredity, if we consider the simplest processes of the lower animals as well as the more complex processes met with in the higher forms.

The word heredity in its common acceptation, means that property of an organism by which its peculiar nature is transmitted to its descendants. From an eagle's egg an eagle of the same species developes; and not only are the characteristics of the species *transmitted to the following generation, but even the individual* peculiarities. The offspring resemble their parents among animals as well as among men.

On what does this common property of all organisms depend?

Häckel was probably the first to describe reproduction as 'an overgrowth of the individual,' and he attempted to explain heredity as a simple continuity of growth. This definition might be considered as a play upon words, but it is more than this; and such an interpretation rightly applied, points to the only path which, in my opinion, can lead to the comprehension of heredity.

Unicellular organisms, such as Rhizopoda and Infusoria, increase by means of *fission. Each individual grows to a certain size, and* then divides into two parts, which are exactly alike in size and structure, so that it is impossible to decide whether one of them is younger or older than the other. Hence in a certain sense these organisms possess immortality: they can, it is true, be destroyed, but, if protected from a violent death, they would live on indefinitely, and would only from time to time reduce the size of their overgrown bodies by division. Each individual of any such unicellular species living on the earth to-day is far older than mankind, and is almost as old as life itself.

From these unicellular organisms we can to a certain extent understand why the offspring, being in fact a part of its parents, must therefore resemble the latter. The question as to why the part should resemble the whole leads us to a new problem, that of assimilation, which also awaits solution. It is, at any rate, an undoubted fact that the organism possesses the power of taking up certain foreign substances, viz. food, and of converting them into the substance of its own body.

Among these unicellular organisms, heredity depends upon the continuity of the individual during the continual increase of its body by means of assimilation.

But how is it with the multicellular organisms which do not reproduce by means of simple division, and in which the whole body of the parent does not pass over into the offspring?

In such animals sexual reproduction is the chief means of multiplication. In no case has it always been completely wanting, and in the majority of cases it is the only kind of reproduction.

In these animals the power of reproduction is connected with certain cells which, as germ-cells, may be contrasted with those which form the rest of the body; for the former have a totally different rôle to play; they are without significance for the life of the individual [1], and yet they alone possess the power of preserving the species. Each of them can, under certain conditions, develope into a complete organism of the same species as the parent, with every individual peculiarity of the latter reproduced more or less completely. How can such hereditary transmission of the characters of the parent take place? how can a single reproductive cell reproduce the whole body in all its details?

Such a question could be easily answered if we were only concerned with the continuity of the substance of the reproductive cells from one generation to another; for this can be demonstrated in some cases, and is very probable in all. In certain insects the development of the egg into the embryo, that is the segmentation of the egg, begins with the separation of a few small cells from the main body of the egg. These are the reproductive cells, and at a later period they are taken into the interior of the animal and form its reproductive organs. Again, in certain small freshwater Crustacea (*Daphnidae*) the future reproductive

[1] That is for the preservation of its life.

cells become distinct at a very early period, although not quite at the beginning of segmentation, i. e. when the egg has divided into not more than thirty segments. Here also the cells which are separated early form the reproductive organs of the animal. The separation of the reproductive cells from those of the body takes place at a still later period, viz. at the close of segmentation, in *Sagitta*—a pelagic free-swimming form. In Vertebrata they do not become distinct from the other cells of the body until the embryo is completely formed. Thus, as their development shows, a marked antithesis exists between the substance of the undying reproductive cells and that of the perishable body-cells. We cannot explain this fact except by the supposition that each reproductive cell potentially contains two kinds of substance, which at a variable time after the commencement of embryonic development, separate from one another, and finally produce two sharply contrasted groups of cells.

It is evidently unimportant, as regards the question of heredity, whether this separation takes place early or late, inasmuch as the molecular constitution of the reproductive substance is determined before the beginning of development. In order to understand the growth and multiplication of cells, it must be conceded that all protoplasmic molecules possess the power of growing, that is of assimilating food, and of increasing by means of division. In the same manner the molecules of the reproductive protoplasm, when well nourished, grow and increase without altering their peculiar nature, and without modifying the hereditary tendencies derived from the parents. It is therefore quite conceivable that the reproductive cells might separate from the somatic cells much later than in the examples mentioned above, without changing the hereditary tendencies of which they are the bearers. There may be in fact cases in which such separation does not take place until after the animal is completely formed, and others, as I believe that I have shown [1], in which it first arises one or more generations later, viz. in the buds produced by the parent. Here also there is no ground for the belief that the hereditary tendencies of the reproductive molecules are in any way changed by the length of time which elapses before their separation from the somatic molecules.

[1] Compare Weismann, 'Die Entstehung der Sexualzellen bei den Hydromedusen,' Jena, 1883.

And this theoretical deduction is confirmed by observation, for from the egg of a Medusa, produced by the budding of a Polype, a Polype, in the first instance, and not a Medusa arises. Here the molecules of the reproductive substance first formed part of the Polype, and later, part of the Medusa bud, and, although they separated from the somatic cells in the bud, they nevertheless always retain the tendency to develope into a Polype.

We thus find that the reproduction of multicellular organisms is essentially similar to the corresponding process in unicellular forms; for it consists in the continual division of the reproductive cell; the only difference being that in the former case the reproductive cell does not form the whole individual, for the latter is composed of the millions of somatic cells by which the reproductive cell is surrounded. The question, 'How can a single reproductive cell contain the germ of a complete and highly complex individual?' must therefore be re-stated more precisely in the following form, 'How can the substance of the reproductive cells potentially contain the somatic substance with all its characteristic properties?'

The problem which this question suggests, becomes clearer when we employ it for the explanation of a definite instance, such as the origin of multicellular from unicellular animals. There can be no doubt that the former have originated from the latter, and that the physiological principle upon which such an origin depended, is the principle of division of labour. In the course of the phyletic development of the organized world, it must have happened that certain unicellular individuals did not separate from one another immediately after division, but lived together, at first as equivalent elements, each of which retained all the animal functions, including that of reproduction. The *Magosphaera planula* of Häckel proves that such perfectly homogeneous cell-colonies exist [1], even at the present day. Division of labour would produce a differentiation of the single cells in such a colony: thus certain cells would be set apart for obtaining food and for locomotion, while certain other cells would be exclusively reproductive. In this way colonies consisting of somatic and of reproductive cells must have arisen, and among these for

[1] It is doubtful whether *Magosphaera* should be looked upon as a mature form; but nothing hinders us from believing that species have lived, and are still living, in which the ciliated sphere has held together until the encystment, that is the reproduction, of the constituent single cells.

the first time death appeared. For in each case the somatic cells must have perished after a certain time, while the reproductive cells alone retained the immortality inherited from the Protozoa. We must now ask how it becomes possible that one kind of cell in such a colony can produce the other kind by division? Before the differentiation of the colony each cell always produced others similar to itself. How can the cells, after the nature of one part of the colony is changed, have undergone such changes in *their* nature that they can now produce more than one kind of cell?

Two theories can be brought forward to solve this problem. We may turn to the old and long since abandoned *nisus formativus*, or adapting the name to modern times, to a phyletic force of development which causes the organism to change from time to time. This *vis a tergo* or teleological force compels the organism to undergo new transformations without any reference to the external conditions of life. This theory throws no light upon the numerous adaptations which are met with in every organism; and it possesses no value as a scientific explanation.

Another supposition is that the primary reproductive cells are influenced by the secondary cells of the colony, which, by their adaptability to the external conditions of life, have become somatic cells: that the latter give off minute particles which entering into the former, cause such changes in their nature that at the next succeeding cell-division they are compelled to break up into dissimilar parts.

At first sight this hypothesis seems to be quite reasonable. It is not only conceivable that particles might proceed from the somatic to the reproductive cells, but the very nutrition of the latter at the expense of the former is a demonstration that such a passage actually takes place. But a closer examination reveals immense difficulties. In the first place, the molecules of the body devoured are never simply added to those of the feeding individual without undergoing any change, but as far as we know, they are really assimilated [1], that is, converted into the molecules of the latter. We cannot therefore gain much by assuming that a number of molecules can pass from the growing somatic cells into the growing reproductive cells, and can be deposited unchanged in the latter, so

[1] Or is an exception perhaps afforded by the nutritive cells of the egg, which occur in many animals?

that, at their next division, the molecules are separated to become the somatic cells of the following generation. How can such a process be conceivable, when the colony becomes more complex, when the number of somatic cells becomes so large that they surround the reproductive cells with many layers, and when at the same time by an increasing division of labour a great number of different tissues and cells are produced, all of which must originate *de novo* from a single reproductive cell? Each of these various elements must, *ex hypothesi*, give up certain molecules to the reproductive cells; hence those which are in immediate contact with the latter would obviously possess an advantage over those which are more remote. If then any somatic cell must send the same number of molecules to each reproductive cell[1], we are compelled to suspend all known physical and physiological conceptions, and must make the entirely gratuitous assumption of an affinity on the part of the molecules for the reproductive cells. Even if we admit the existence of this affinity, its origin and means of control remain perfectly unintelligible if we suppose that it has arisen from differentiation of the complete colony. An unknown controlling force must be added to this mysterious arrangement, in order to marshal the molecules which enter the reproductive cell in such a manner that their arrangement corresponds with the order in which they must emerge as cells at a later period. In short, we become lost in unfounded hypotheses.

It is well known that Darwin has attempted to explain the phenomena of heredity by means of a hypothesis which corresponds to a considerable extent with that just described. If we substitute gemmules for molecules we have the fundamental idea of Darwin's provisional hypothesis of pangenesis. Particles of an excessively minute size are continually given off from all the cells of the body; these particles collect in the reproductive cells, and hence any change arising in the organism, at any time during its life, is represented in the reproductive cell[2]. Darwin believed that he had by this means rendered the transmission of acquired characters intelligible, a conception which he held to be necessary in order to

[1] Or more precisely, they must give up as many molecules as would correspond to the number of the kind of cell in question found in the mature organism.

[2] See Darwin, 'The Variation of Animals and Plants under Domestication,' 1875, vol. ii. chapter xxvii. pp. 349-399.

explain the development of species. He himself pointed out that the hypothesis was merely provisional, and that it was only an expression of immediate, and by no means satisfactory knowledge of these phenomena.

It is always dangerous to invoke some entirely new force in order to understand phenomena which cannot be readily explained by the forces which are already known.

I believe that an explanation can in this case be reached by an appeal to known forces, if we suppose that characters acquired (in the true sense of the term) by the parent cannot appear in the course of the development of the offspring, but that all the characters exhibited by the latter are due to primary changes in the germ.

This supposition can obviously be made with regard to the above-mentioned colony with its constituent elements differentiated into somatic and reproductive cells. It is conceivable that the differentiation of the somatic cells was not primarily caused by a change in their own structure, but that it was prepared for by changes in the molecular structure of the reproductive cell from which the colony arose.

The generally received idea assumes that changes in the external conditions can, in connection with natural selection, call forth persistent changes in an organism; and if this view be accepted it must be as true of all Metazoa as it is of unicellular or of homogeneous multicellular organisms. Supposing that the hypothetical colonies, which were at first entirely made up of similar cells, were to gain some advantages, if in the course of development, the molecules of the reproductive cells, from which each colony arose became distributed irregularly in the resulting organism, there would be a tendency towards the perpetuation of such a change, wherever it appeared as the result of individual variability. As a result of this change the colony would no longer remain homogeneous, and its cells would become *dissimilar from the first*, because of the altered arrangement of the molecules in the reproductive cells. Nothing prevents us from assuming that, at the same time, the nature of a part of the molecule may undergo still further change, for the molecules are by nature complex, and may split up or combine together.

If then the reproductive cells have undergone such changes that they can produce a heterogeneous colony as the result of continual division, it follows that succeeding generations must behave in exactly the same manner, for each of them is developed from a portion of the reproductive cell from which the previous generation arose, and consists of the same reproductive substance as the latter.

From this point of view the exact manner in which we imagine the subsequent differentiation of the colony to be potentially present in the reproductive cell, becomes a matter of comparatively small importance. It may consist in a different molecular arrangement, or in some change of chemical constitution, or it may be due to both these causes combined. The essential point is that the differentiation was originally due to some change in the reproductive cells, just as this change itself produces all the differentiations which appear in the ontogeny of all species at the present day. No one doubts that the reason why this or that form of segmentation takes place, or why this or that species finally appears, is to be found in the ultimate structure of the reproductive cells. And, as a matter of fact, molecular differentiation and grouping, whether present from the beginning or first appearing in the course of development, plays a rôle which can be almost directly observed in certain species. The first segmentation furrow divides the egg of such species into an opaque and a clear half, or, as is often the case among Medusae, into a granular outer layer and a clear central part, corresponding respectively with the ectoderm and endoderm which are formed at a later period. Such early differentiations are only the visible proofs of certain highly complex molecular rearrangements in the cells, and the fact appears to indicate that we cannot be far wrong in maintaining that differentiations which appear in the course of ontogeny depend upon the chemical and physical constitution of the molecules in the reproductive cell.

At the first appearance of the earliest Metazoa alluded to above, only two kinds of cells, somatic and reproductive, arose from the segmentation of the reproductive cell. The reproductive cells thus formed must have possessed exactly the same molecular structure as the mother reproductive cell, and would therefore pass through precisely the same developmental changes. We can easily imagine that all the succeeding stages in the development of the Metazoa have been due to the same causes which were efficient at the earliest period. Variations in the molecular structure of the reproductive cells would continue to appear, and these would be increased and rendered permanent by means of natural selection, when their results, in the alteration of certain cells in the body, were advantageous to the species. The only condition necessary for the transmission of such changes is that a part of the reproductive substance (the germ-plasm) should always remain unchanged during segmentation and the subsequent building up of the body, or in other words, that such unchanged substance should pass into the organism, and after the lapse of a variable period, should reappear as the reproductive cells. Only in this way can we render to some extent intelligible the transmission of those changes which have arisen in the phylogeny of the species; only thus can we imagine the manner in which the first somatic cells gradually developed in numbers and in complexity.

It is only by supposing that these changes arose from molecular alterations in the reproductive cell that we can understand how the reproductive cells of the next generation can originate the same changes in the cells which are developed from them; and it is impossible to imagine any way in which the transmission of changes, produced by the direct action of external forces upon the somatic cells, can be brought about [1].

The difficulty or the impossibility of rendering the transmission of acquired characters intelligible by an appeal to any known force has been often felt, but no one has hitherto attempted to cast doubts upon the very existence of such a form of heredity.

There are two reasons for this: first, observations have been recorded which appear to prove the existence of such transmission; and secondly, it has seemed impossible to do without the supposition of the transmission of acquired characters, because it has always played such an important part in the explanation of the transformation of species.

It is perfectly right to defer an explanation, and to hesitate

[1] To this class of phenomena of course belong those acts of will which call forth the functional activity of certain groups of cells. It is quite clear that such impulses do not originate in the constitution of the tissue in question, but are due to the operation of external causes. The activity does not arise directly from any natural disposition of the germ, but is the result of accidental external impressions. A domesticated duck uses its legs in a different manner from, and more frequently than a wild duck, but such functional changes are the consequence of changed external conditions, and are not due to the constitution of the germ.

before we declare a supposed phenomenon to be impossible, because we are unable to refer it to any of the known forces. No one can believe that we are acquainted with all the forces of nature. But, on the other hand, we must use the greatest caution in dealing with unknown forces; and clear and indubitable facts must be brought forward to prove that the supposed phenomena have a real existence, and that their acceptance is unavoidable.

It has never been proved that acquired characters are transmitted, and it has never been demonstrated that, without the aid of such transmission, the evolution of the organic world becomes unintelligible.

The inheritance of acquired characters has never been proved, either by means of direct observation or by experiment[1]. It must be admitted that there are in existence numerous descriptions of cases which tend to prove that such mutilations as the loss of fingers, the scars of wounds, etc., are inherited by the offspring, but in these descriptions the previous history is invariably obscure, and hence the evidence loses all scientific value.

As a typical example of the scientific value of such cases I may mention the frequently quoted instance of the cow, which lost its left horn from suppuration, induced by some 'unknown cause,' and which afterwards produced two calves with a rudimentary left horn in each case. But as Hensen[2] has rightly remarked, the loss of the cow's horn may have arisen from a congenital malformation, which would certainly be transmitted, but which was not an acquired character.

The only cases worthy of scientific discussion are the well-known experiments upon guinea-pigs, conducted by the French physiologist Brown-Séquard. But the explanation of his results is, in my opinion, open to discussion. In these cases we have to do with the apparent transmission of artificially produced malformations. The division of important nerves, or of the spinal cord, or the

[1] Upon this subject Pflüger states—'I have made myself accurately acquainted with all facts which are supposed to prove the inheritance of acquired characters,—that is of characters which are not due to the peculiar organization of the ovum and spermatozoon from which the individual is formed, but which follow from the incidence of accidental external influences upon the organism at any time in its life. Not one of these facts can be accepted as a proof of the transmission of acquired characters.' *l. c.* p. 68.

[2] 'Physiologie der Zeugung.'

removal of parts of the brain, produced certain symptoms which reappeared in the descendants of the mutilated animals. Epilepsy was produced by dividing the great sciatic nerve; the ear became deformed when the sympathetic nerve was severed in the throat; and prolapsus of the eye-ball followed the removal of a certain part of the brain—the corpora restiformia. All these effects were said to be transmitted to the descendants as far as the fifth or sixth generation.

But we must inquire whether these cases are really due to heredity and not to simple infection. In the case of epilepsy, at any rate, it is easy to imagine that the passage of some specific organism through the reproductive cells may take place, as in the case of syphilis. We are, however, entirely ignorant of the nature of the former disease. This suggested explanation may not perhaps apply to the other cases: but we must remember that animals which have been subjected to such severe operations upon the nervous system have sustained a great shock, and if they are capable of breeding, it is only probable that they will produce weak descendants, and such as are easily affected by disease. Such a result does not however explain why the offspring should suffer from the same disease as that which was artificially induced in the parents. But this does not appear to have been by any means invariably the case. Brown-Séquard himself says, 'The changes in the eye of the offspring were of a very variable nature, and were only occasionally exactly similar to those observed in the parents.'

There is no doubt, however, that these experiments demand careful consideration, but before they can claim scientific recognition, they must be subjected to rigid criticism as to the precautions taken, the number and nature of the control experiments, etc.

Up to the present time such necessary conditions have not been sufficiently observed. The recent experiments themselves are only described in short preliminary notices, which, as regards their accuracy, the possibility of mistake, the precautions taken, and the exact succession of individuals affected, afford no data upon which a scientific opinion can be founded. Until the publication of a complete series of experiments, we must say with Du Bois Reymond [1], 'The hereditary transmission of acquired characters remains an

[1] See 'Ueber die Uebung,' Berlin, 1881.

unintelligible hypothesis, which is only deduced from the facts which it attempts to explain.'

We therefore naturally ask whether the hypothesis is really necessary for the explanation of known facts.

At the first sight it certainly seems to be necessary, and it appears rash to attempt to dispense with its aid. Many phenomena only appear to be intelligible if we assume the hereditary transmission of such acquired characters as the changes which we ascribe to the use or disuse of particular organs, or to the direct influence of climate. Furthermore, how can we explain instinct as hereditary habit unless it has gradually arisen by the accumulation, through heredity, of habits which were practised in succeeding generations?

I will now attempt to prove that even these cases, so far as they depend upon clear and indubitable facts, do not force us to accept the supposition of the transmission of acquired characters.

It seems difficult and well nigh impossible to deny the transmission of acquired characters when we remember the influence which use and disuse have exercised upon certain special organs. It is well known that Lamarck attempted to explain the structure of the organism as almost entirely due to this principle alone. According to his theory the long neck of the giraffe arose by constant stretching after the leaves of trees, and the web between the toes of a water-bird's foot by the extension of the toes, in an attempt to oppose as large a surface of water as possible in swimming. There can be no doubt that those muscles which are frequently used increase in size and strength, and that glands which often enter into activity become larger and not smaller, and that their functional powers increase. Indeed, the whole effect which exercise produces upon the single parts of the body is dependent upon the fact that frequently used organs increase in strength. This conclusion also refers to the nervous system, for a pianist who performs with lightning rapidity certain pre-arranged, highly complex, and combined movements of the muscles of his hands and fingers has, as Du Bois Reymond pointed out, not only exercised the muscles, but also those ganglionic centres of the brain which determine the combination of muscular movement. Other functions of the brain, such as memory, can be similarly increased and strengthened by exercise, and the question to be settled is whether characters acquired in this way by exercise and practice can be transmitted to the following generations. Lamarck's theory assumes that such transmission takes place, for without it no accumulation or increase of the characters in question would be possible, as a result of their exercise during any number of successive generations.

Against this we may urge that whenever, in the course of nature, an organ becomes stronger by exercise, it must possess a certain degree of importance for the life of the individual, and when this is the case it becomes subject to improvement by natural selection, for only those individuals which possess the organ in its most perfect form will be able to reproduce them. The perfection of form of an organ does not however depend upon the amount of exercise undergone by it during the life of the organism, but primarily and principally upon the fact that the germ from which the individual arose was predisposed to produce a perfect organ. The increase to which any organ can attain by exercise during a single life is bounded by certain limits, which are themselves fixed by the primary tendencies of the organ in question. We cannot by excessive feeding make a giant out of the germ destined to form a dwarf; we cannot, by means of exercise, transform the muscles of an individual destined to be feeble into those of a Hercules, or the brain of a predestined fool into that of a Leibnitz or a Kant, by means of much thinking. With the same amount of exercise the organ which is destined to be strong, will attain a higher degree of functional activity than one that is destined to be weak. Hence natural selection, in destroying the least fitted individuals, destroys those which from the germ were feebly disposed. Thus the result of exercise during the individual life does not acquire so much importance, for, as compared with differences in predisposition, the amount of exercise undergone by all the individuals of a species becomes relatively uniform. The increase of an organ in the course of generations does not depend upon the summation of the exercise taken during single lives, but upon the summation of more favourable predispositions in the germs.

In criticizing these arguments, it may be questioned whether the single individuals of a species which is undergoing modification do, as a matter of fact, exercise themselves in the same manner and to the same extent. But the consideration of a definite example clearly shows that this must be the case. When the wild duck became domesticated, and lived in a farm-yard, all the individuals were compelled to walk and stand more than they had done previously, and the muscles of the legs were used to a correspondingly greater degree. The same thing happens in the wild state, when any change in the conditions of life compels an organ to be more largely used. No individual will be able to entirely avoid this extra use, and each will endeavour to accommodate itself to the new conditions according to its power. The amount of this power depends upon the predisposition of the germ; and natural selection, while it apparently decides between individuals of various degrees of strength, is in truth operating upon the stronger and weaker germs.

But the very conclusions which have been drawn from the increase of activity which has arisen from exercise, must also be drawn from the instances of atrophy or degeneration following from the disuse of organs.

Darwin long ago called attention to the fact that the degeneration of an organ may, under certain circumstances, be beneficial to the species. For example, he first proved in the instance of Madeira, that the loss of wings may be of advantage to many beetles inhabiting oceanic islands. The individuals with imperfectly developed or atrophied wings have an advantage, because they are not carried out to sea by the frequent winds. The small eyes, buried in fur, possessed by moles and other subterranean mammals, can be similarly explained by means of natural selection. So also, the complete disappearance of the limbs of snakes is evidently a real advantage to animals which creep through narrow holes and clefts; and the degeneration of the wings in the ostrich and penguin is, in part, explicable as a favourable modification of the organ of flight into an organ for striking air or water respectively.

But when the degeneration of disused organs confers no benefits upon the individual, the explanation becomes less simple. Thus we find that the eyes of animals which inhabit dark caves (such as insects, crabs, fish, Amphibia, etc.) have undergone degeneration; yet this can hardly be of direct advantage to the animals, for they could live quite as well in the dark with well-developed eyes. But we are here brought into contact with a very important aspect of natural selection, viz. the power of conservation exerted by it. Not only does the survival of the fittest select the best, but it also maintains it [1]. The struggle for existence does not cease with the foundation of a new specific type, or with some perfect adaptation to the external or internal conditions of life, but it becomes, on the contrary, even more severe, so that the most minute differences of structure determine the issue between life and death.

The sharpest sight possessed by birds is found in birds of prey, but if one of them entered the world with eyes rather below the average in this respect, it could not, in the long run, escape death from hunger, because it would always be at a disadvantage as compared with others.

Hence the sharp sight of these birds is maintained by means of the continued operation of natural selection, by which the individuals with the weakest sight are being continually exterminated. But all this would be changed at once, if a bird of prey of a certain species were compelled to live in absolute darkness. The quality of the eyes would then be immaterial, for it could make no difference to the existence of the individual, or the maintenance of the species. The sharp sight might, perhaps, be transmitted through numerous generations; but when weaker eyes arose from time to time, these would also be transmitted, for even very short-sighted or imperfect eyes would bring no disadvantage to their owner. Hence, by continual crossing between individuals with the most varied degrees of perfection in this respect, the average of perfection would gradually decline from the point attained before the species lived in the dark.

We do not at present know of any bird living in perfect darkness, and it is improbable that such a bird will ever be found; but we are acquainted with blind fish and Amphibia, and among these the eyes are present it is true, but they are small and hidden under the skin. I think it is difficult to reconcile the facts of the case with the ordinary theory that the eyes of these animals have simply degenerated through disuse. If disuse were able to bring about the complete atrophy of an organ, it follows that every trace of it would be effaced. We know that, as a matter of fact, the olfactory organ of the frog completely degenerates when the olfactory

[1] This principle was, I believe, first pointed out by Seidlitz. Compare Seidlitz, 'Die Darwin'sche Theorie,' Leipzig, 1875, p. 198.

nerve is divided; and that great degeneration of the eye may be brought about by the artificial destruction of the optic centre in the brain. Since, therefore, *the effects of disuse are so striking in a single life*, we should certainly expect, if such effects can be transmitted, that all traces of an eye would soon disappear from a species which lives in the dark.

The caverns in Carniola and Carinthia, in which the blind *Proteus* and so many other blind animals live, belong geologically to the Jurassic formation; and although we do not exactly know when for example the *Proteus* first entered them, the low organization of this amphibian certainly indicates that it has been sheltered there for a very long period of time, and that thousands of generations of this species have succeeded one another in the caves.

Hence there is no reason to wonder at the extent to which the degeneration of the eye has been already carried in the *Proteus*; even if we assume that it is merely due to the cessation of the conserving influence of natural selection.

But it is unnecessary to depend upon this assumption alone, for when a useless organ degenerates, there are also other factors which demand consideration, namely, the higher development of other organs which compensate for the loss of the degenerating structure, or the increase in size of adjacent parts. If these newer developments are of advantage to the species, they finally come to take the place of the organ which natural selection has failed to preserve at its point of highest perfection.

In the first place, a certain form of correlation, which Roux[1] calls 'the struggle of the parts in the organism,' plays a most important part. Cases of atrophy, following disuse, appear to be always attended by a corresponding increase of other organs: blind animals always possess very strongly developed organs of touch, hearing, and smell, and the degeneration of the wing-muscles of the ostrich is accompanied by a great increase in the strength of the muscles of the leg. If the average amount of food which an animal can assimilate every day remains constant for a considerable time, it follows that a strong influx towards one organ must be accompanied by a drain upon others, and this tendency will increase, from generation to generation, in proportion to the development of

[1] W. Roux, 'Der Kampf der Theile im Organismus,' Leipzig, 1881.

the growing organ, which is favoured by natural selection in its increased blood-supply, etc.; while the operation of natural selection has also determined the organ which can bear a corresponding loss without detriment to the organism as a whole.

Without the operation of natural selection upon different individuals, the struggle between the organs of a single individual would be unable to encourage a predisposition in the germ towards the degeneration or non-development of a useless organ, and it could only limit and degrade the development of an organ in the lifetime of the individual. If, therefore, acquired characters are not transmitted, the disposition to develope such an organ would be present in the same degree in each successive generation, although the realization would be less perfect. The complete disappearance of a rudimentary organ can only take place by the operation of natural selection; this principle will lead to its elimination, inasmuch as the disappearing structure takes the place and the nutriment of other useful and important organs. Hence the process of natural selection tends to entirely remove the former. The predisposition towards a weaker development of the organ is thus advantageous, and there is every reason for the belief that the advantages would continue to be gained, and that therefore the processes of natural selection would remain in operation, until the germ had entirely lost all tendency towards the development of the organ in question. The extreme slowness with which this process takes place, and the extraordinary persistence of rudimentary organs, at any rate in the embryo, together with their gradual but finally complete disappearance, can be clearly seen in the limbs of certain vertebrates and arthropods. The blind-worms have no limbs, but a rudimentary shoulder-girdle is present close under the skin, and the interesting fact has been quite recently established[1] that the fore-limbs are present in the embryo in the form of short stumps, which entirely disappear at a later stage. In most snakes all traces of limbs have been lost in the adult, but we do not yet know for certain whether they are also wanting in the embryo. I might further mention the very different stages of degeneration witnessed in the limbs of various salamanders; and the anterior limbs of *Hesperornis*—the remarkable toothed bird from the cretaceous rocks

[1] Compare Born in 'Zoolog. Anzeiger,' 1883, No. 150, p. 537.

—which, according to Marsh [1], consists only of a very thin and relatively small humerus, which was probably concealed beneath the skin. The water-fleas (*Daphnidae*) possess in the embryonic state three complete and almost equal pairs of jaws, but two of these entirely disappear, and do not develope into jaws in any species. In the same way, the embryo of the maggot-like legless larva of bees and wasps possesses three pairs of ancestral limbs.

There are, however, cases in which, apparently, acquired variations of characters are transmitted without natural selection playing any active part in the change. Such a case is afforded by the short-sightedness so common in civilized nations.

This affection is certainly hereditary in some cases, and it may well have been explained as an example of the transmission of acquired changes. It has been argued that acquired short-sightedness can be in a slight degree transmitted, and that each successive generation has developed a further degree of the disease by habitually holding books etc. close to the eyes, so that the inborn predisposition to short-sightedness is continually accumulating.

But we must remember that variations in the refraction of the human eye have been for a long time independent of the preserving control of natural selection. In the struggle for existence, a blind man would certainly disappear before those endowed with sight, but myopia does not prevent any one from gaining a living. A short-sighted lynx, hawk, or gazelle, or even a short-sighted Indian, would be eliminated by natural selection, but a short-sighted European of the higher class finds no difficulty in earning his bread.

Those fluctuations on either side of the average which we call myopia and hypermetropia, occur in the same manner, and are due to the same causes, as those which operate in producing degeneration in the eyes of cave-dwelling animals. If, therefore, we not infrequently meet with families in which myopia is hereditary, such results may be attributed to the transmission of an accidental disposition on the part of the germ, instead of to the transmission of acquired short-sightedness. A very large proportion of short-sighted people do not owe their affliction to inheritance at all, but have acquired it for themselves; for there is no doubt that a normal eye may be

[1] O. C. Marsh, 'Odontornithes, a Monograph on the extinct toothed Birds of North America,' Washington, 1880.

rendered myopic in the course of a life-time by continually looking at objects from a very short distance, even when no hereditary predisposition towards the disease can be shown to exist. Such a change would of course appear more readily if there was also a corresponding predisposition on the part of the eye. But I should not explain this widely spread predisposition towards myopia as due to the transmission of acquired short-sightedness, but to the greater variability of the eye, which necessarily results from the cessation of the controlling influence of natural selection.

This suspension of the preserving influence of natural selection may be termed *Panmixia*, for all individuals can reproduce themselves and thus stamp their characters upon the species, and not only those which are in all respects, or in respect to some single organ, the fittest. In my opinion, the greater number of those variations which are usually attributed to the direct influence of external conditions of life, are to be ascribed to panmixia. For example, the great variability of most domesticated animals essentially depends upon this principle.

A goose or a duck must possess strong powers of flight in the natural state, but such powers are no longer necessary for obtaining food when it is brought into the poultry-yard, so that a rigid selection of individuals with well-developed wings, at once ceases among its descendants. Hence in the course of generations, a deterioration of the organs of flight must necessarily ensue, and the other members and organs of the bird will be similarly affected.

This example very clearly indicates that the degeneration of an organ does not depend upon its disuse; for although our domestic poultry very rarely make use of their wings, the muscles of flight have not disappeared, and, at any rate in the goose, do not seem to have undergone any marked degeneration.

The numerous and exact observations conducted by Darwin upon the weight and measurement of the bones in domestic fowls, seem to me to possess a significance beyond that which he attributed to them.

If the weight of the wing-bones of the domestic duck bears a smaller proportion to the weight of the leg-bones than in the wild duck, and if, as Darwin rightly assumes, this depends not only upon the diminution of the wings, but also upon the increase of the legs, it by no means follows that this latter increase in organs which are now more frequently used, is dependent upon hereditary influences alone.

It is quite possible that it depends, on the one hand, upon the suspension of natural selection, or panmixia (and these effects would be transmitted), and on the other hand upon the direct influence of increased use during the course of a single life. We do not yet know with any accuracy, the amount of change which may be produced by increased use in the course of a single life. If it is desired to prove that use and disuse produce hereditary effects without the assistance of natural selection, it will be necessary to domesticate wild animals (for example the wild duck) and preserve all their descendants, thus excluding the operation of natural selection. If then all individuals of the second, third, fourth and later generations of these tame ducks possess identical variations, which increase from generation to generation, and if the nature of these changes proves that they must have been due to the effect of use or disuse, then perhaps the transmission of such effects may be admitted; but it must always be remembered that domestication itself influences the organism,—not only directly, but also indirectly, by the increase of variability as a result of the suspension of natural selection. Such experiments have not yet been carried out in sufficient detail [1].

It is usually considered that the origin and variation of instincts are also dependent upon the exercise of certain groups of muscles and nerves during a single life-time; and that the gradual improvement which is thus caused by practice, is accumulated by hereditary transmission. I believe that this is an entirely erroneous view, and I hold that all instinct is entirely due to the operation of natural selection, and has its foundation, not upon inherited experiences, but upon the variations of the germ.

Why, for instance, should not the instinct to fly from enemies have arisen by the survival of those individuals which are naturally timid and easily startled, together with the extermination of those which are unwary? It may be urged in opposition to this explanation that the birds of uninhabited islands which are not at first shy of man, acquire in a few generations an instinctive dread of him, an instinct which cannot have arisen in so short a time

[1] C. Darwin, 'Variation of Animals and Plants under Domestication.' Vol. I.

by means of natural selection. But in this case are we really dealing with the origin of a new instinct, or only with the addition of one new perception ('Wahrnehmung,' Schneider)[1], of the same kind as those which incite to the instinct of flight—an instinct which had been previously developed in past ages but had never been called forth by man? Again, has any one ascertained whether the young birds of the second or third generation are frightened by man? May it not be that the experience of a single life-time plays a great part in the origin of the habit? For my part, I am inclined to believe that the habit of flying from man is developed in the first generation which encounters him as a foe[2]. We see how wary and cautious a flock of birds become as soon as a few shots have been fired at them, and yet shortly before this occurrence they were perhaps playing carelessly close to the sportsmen. Intelligence plays a considerable part in the life of birds, and it by no means follows that the transmission of individual habits explains the above-mentioned phenomena. The long-continued operation of natural selection may very well have been necessary before the perception of man could awake the instinct to flee in young, inexperienced birds. Unfortunately the observations upon these points are far too indefinite to enable us to draw conclusions.

There is again the frequently-quoted instance of the young pointer, 'which, untrained, and without any example which might have been imitated, pointed at a lizard in a subtropical jungle, just as many of its forefathers had pointed at partridges on the plain of St. Denis,' and which, without knowing the effect of a shot, sprang forward barking, at the first discharge, to bring in the game. This conduct must not be attributed to the inheritance of any mental picture, such as the effect of a shot, but to the inheritance of a certain reflex mechanism. The young pointer does not spring forward at the shot because he has inherited from his forefathers a

[1] Compare 'Der thierische Wille,' Leipzig, 1880.

[2] Steller's interesting account of the Sea-cow (*Rhytina Stelleri*) proves that this suggestion is valid. This large mammal was living in great numbers in Behring Strait at the end of the last century, but has since been entirely exterminated by man. Steller, who was compelled by shipwreck to remain in the locality for a whole year, tells us that the animals were at first without any fear of man, so that they could be approached in boats and could thus be killed. After a few months however the survivors became wary, and did not allow Steller's men to approach them, so that they were difficult to catch.—A. W., 1888.

certain association of ideas,—shot and game,—but because he has inherited a reflex mechanism, which impels him to start forward on hearing a report. We cannot yet determine without more experiments how such an impulse due to perception ('Wahrnehmungstrieb,' Schneider) has arisen; but, in my opinion, it is almost inconceivable that artificial breeding has had nothing to do with it; and that we are here concerned—not with the inheritance of the effects of training—but with some pre-disposition on the part of the germ, which has been increased by artificial selection.

The necessity for extreme caution in appealing to the supposed hereditary effects of use, is well shown in the case of those numerous instincts, which only come into play once in a lifetime, and which do not therefore admit of improvement by practice. The queen-bee takes her nuptial flight only once, and yet how many and complex are the instincts and the reflex mechanisms which come into play on that occasion. Again, in many insects the deposition of eggs occurs but once in a life-time, and yet such insects always fulfil the necessary conditions with unfailing accuracy, either simply dropping the eggs into water, or carefully fixing them on the surface of the earth beneath some stone, or laying them on a particular part of a certain species of plant; and in all these cases the most complicated actions are performed. It is indeed astonishing to watch one of the *Cynipidae* (*Rhodites rosae*) depositing her eggs in the tissue of a young bud. She first carefully examines the bud on all sides, and feels it with her legs and antennae. Then she slowly inserts her long ovipositor between the closely-rolled leaves of the bud, but if it does not reach exactly the right spot, she will withdraw and re-insert it many times, until at length, when the proper place has been found, she will slowly bore deep into the very centre of the bud, so that the egg will reach the exact spot, where the necessary conditions for its development alone exist.

But each *Cynips* lays eggs many times, and it may be argued that practice may have led to improvement in this case; we cannot however, as a matter of fact, expect much improvement in a process which is repeated, perhaps a dozen times, at short intervals of time, and which is of such an excessively complex nature.

It is the same with the deposition of eggs in most insects. How can practice have had any influence upon the origin of the instinct which leads one of our butterflies—(*Vanessa levana*)—to lay its green eggs in single file, as columns, which project freely from the stem or leaf, so that protection is gained by their close resemblance to the flower-buds of the stinging-nettle, which forms the food-plant of their caterpillars?

Of course the butterfly is not aware of the advantage which follows from such a proceeding; intelligence has no part in the process. The entire operation depends upon certain inherent anatomical and physiological arrangements:—on the structure of the ovary and oviducts, on the simultaneous ripening of a certain number of eggs, and on certain very complex reflex mechanisms which compel the butterfly to lay its eggs on certain parts of certain plants. Schneider is certainly right when he maintains that this mechanism is released by a sensation, arising from the perception (whether by sight or smell, or both together) of the particular plant or part of the plant upon which the eggs are to be laid [1]. At any rate, we cannot, in such cases, appeal to the effects of constant use and the transmission of acquired characters, as an explanation; and the origin of the impulse can only be understood as a result of the process of natural selection.

The protective cocoons by which the pupae of many insects are surrounded also belong to the same category, and improvement by practice is entirely out of the question, for they are only constructed once in the course of a life-time. And yet these cocoons are often remarkably complex: think, for instance, of the cocoon spun by the caterpillar of the emperor moth (*Saturnia carpini*), which is so tough that it can hardly be torn, and which the moth would be unable to leave, if an opening were not provided for the purpose; while, on the other hand, the pupa would not be defended against enemies if the opening were not furnished with a circle of pointed bristles, converging outwards, on the principle of the lobster pot, so that the moth can easily emerge, although no enemy can enter. The impulse which leads to the production of such a structure can only have arisen by the operation of natural selection—not, of course, during the history of a single species, but during the development of numerous, consecutive species—by gradual and unceasing improvements in the initial stages of cocoon-building.

[1] Compare Schneider, 'Der thierische Wille.'

A number of species exists at the present day, of which the cocoons can be arranged in a complete series, becoming gradually less and less complex, from that described above, down to a loosely-constructed, spherical case in which the pupa is contained.

The cocoon spun by the larva of *Saturnia carpini* differs but little in complexity from the web of the spider, and if the former is constructed without assistance from the experience of the single individual—and this must certainly be admitted—it follows that the latter may be also built without the aid of experience, while there is neither reason nor necessity for appealing to the entirely unproved transmission of acquired skill in order to explain this and a thousand other operations.

It may be objected that, in man, in addition to the instincts inherent in every individual, special individual predispositions are also found, of such a nature that it is impossible that they can have arisen by individual variations of the germ. On the other hand, these predispositions—which we call talents—cannot have arisen through natural selection, because life is in no way dependent upon their presence, and there seems to be no way of explaining their origin except by an assumption of the summation of the skill attained by exercise in the course of each single life. In this case, therefore, we seem at first sight to be compelled to accept the transmission of acquired characters.

Now it cannot be denied that all predispositions may be improved by practice during the course of a life-time,—and, in truth, very remarkably improved. If we could explain the existence of great talent, such as, for example, a gift for music, painting, sculpture, or mathematics, as due to the presence or absence of a special organ in the brain, it follows that we could only understand its origin and increase (natural selection being excluded) by accumulation, due to the transmission of the results of practice through a series of generations. But talents are not dependent upon the possession of special organs in the brain. They are not simple mental dispositions, but combinations of many dispositions, and often of a most complex nature: they depend upon a certain degree of irritability, and a power of readily transmitting impulses along the nerve-tracts of the brain, as well as upon the especial development of single parts of the brain. In my opinion, there is absolutely no trustworthy proof that talents have been improved by their exercise through the course of a long series of generations. The Bach family shows that musical talent, and the Bernoulli family that mathematical power, can be transmitted from generation to generation, but this teaches us nothing as to the origin of such talents. In both families the high-water mark of talent lies, not at the end of the series of generations, as it should do if the results of practice are transmitted, but in the middle. Again, talents frequently appear in some single member of a family which has not been previously distinguished.

Gauss was not the son of a mathematician; Handel's father was a surgeon, of whose musical powers nothing is known; Titian was the son and also the nephew of a lawyer, while he and his brother, Francesco Vecellio, were the first painters in a family which produced a succession of seven other artists with diminishing talents. These facts do not, however, prove that the condition of the nerve-tracts and centres of the brain, which determine the specific talent, appeared for the first time in these men: the appropriate condition surely existed previously in their parents, although it did not achieve expression. They prove, as it seems to me, that a high degree of endowment in a special direction, which we call talent, *cannot have arisen from the experience of previous generations, that is, by the exercise of the brain in the same specific direction.*

It appears to me that talent consists in a happy combination of exceptionally high gifts, developed in one special direction. At present, it is of course impossible to understand the physiological conditions which render the origin of such combinations possible, but it is very probable that the crossing of the mental dispositions of the parents plays a great part in it. This has been admirably and concisely expressed by Goethe in describing his own characteristics—

> Vom Vater hab' ich die Statur
> Des Lebens ernstes Führen,
> Vom Mütterchen die Frohnatur
> Die Lust zum Fabuliren, etc.

The combination of talents frequently found in one individual, and the appearance of different remarkable talents in the various branches of one and the same family, indicate that talents are only special combinations of certain highly-developed mental dispositions which are found in every brain. Many painters have been admirable musicians, and we very frequently find both these talents developed to a slighter extent in a single individual. In the Feuerbach family we find a distinguished jurist, a remarkable philosopher, and a highly-talented artist; and among the Mendelssohns a philosopher as well as a musician.

The sudden and yet widespread appearance of a particular talent in correspondence with the general intellectual excitement of a certain epoch points in the same direction. How many poets arose in Germany during the period of sentiment which marked the close of the last century, and how completely all poetic gifts seem to have disappeared during the Thirty Years' War. How numerous were the philosophers that appeared in the epoch which succeeded Kant; while all philosophic talent seemed to have deserted the German nation during the sway of the antagonistic 'exact science,' with its contempt for speculation.

Wherever academies are founded, there the Schwanthalers, Defreggers, and Lenbachs emerge from the masses which had shown no sign of artistic endowment through long periods of time [1]. At the present day there are many men of science who, had they lived at the time of Bürger, Uhland, or Schelling, would probably have been poets or philosophers. And the man of science also cannot dispense with that mental disposition directed in a certain course, which we call talent, although the specific part of it may not be so obvious: we may, indeed, go further, and maintain that the Physicist and the Chemist are characterized by a combination of mental dispositions which differ from those of the Botanist and the Zoologist. Nevertheless, a man is not born a physicist or a botanist, and in most cases chance alone determines whether his endowments are developed in either direction.

Lessing has asked whether Raphael would have been a less distinguished artist had he been born without hands: we might also enquire whether he might not have been as great a musician as he was painter if, instead of living during the historical high-water mark of painting, he had lived, under favourable personal influences, at the time of highly-developed and widespread musical genius. A great artist is always a great man, and if he finds the outlet for his talent closed on one side, he forces his way through on the other.

From all these examples I wish to show that, in my opinion,

[[1] The author refers to the Academy of Arts at Munich. S. S.]

talents do not appear to depend upon the improvement of any special mental quality by continued practice, but they are the expression, and to a certain extent the bye-product, of the human mind, which is so highly developed in all directions.

But if any one asks whether this high mental development, acquired in the course of innumerable generations of men, is not dependent upon the hereditary effects of use, I would remind him that human intelligence in general is the chief means and the chief weapon which has served and still serves the human species in the struggle for existence[1]. Even in the present state of civilization—distorted as it is by numerous artificial encroachments and unnatural conditions—the degree of intelligence possessed by the individual chiefly decides between destruction and life; and in a natural state, or still better in a state of low civilization, this result is even more striking.

Here again, therefore, we encounter the effects of natural selection, and to this power we must attribute, at any rate, a great part of the phenomena we have been discussing, and it cannot be shown that—in addition to its operation—the transmission of characters acquired by practice plays any part in nature.

I only know of one class of changes in the organism which is with difficulty explained by the supposition of changes in the germ; these are the modifications which appear as the direct consequence of some alteration in the surroundings. But our knowledge on this subject is still very defective, and we do not know the facts with sufficient precision to enable us to pronounce a final verdict as to the cause of such changes: and for this reason, I do not propose to consider the subject in detail.

These changes—such, for example, as are produced by a strange climate—have been always looked at under the supposition that they are transmitted and intensified from generation to generation, and for this reason the observations are not always sufficiently precise. It is difficult to say whether the changed climate may not have first changed the germ, and if this were the case the accumulation of effects through the action of heredity would present no difficulty. For instance, it is well known that increased nourishment not only causes a plant to grow more luxuriantly, but it alters the plant in some distinct way, and it would be

[1] Compare Darwin's 'Descent of Man.'

wonderful indeed if the seeds were not also larger and better furnished with nutritive material. If the increased nourishment be repeated in the next generation, a still further increase in the size of the seed, in the luxuriance of the plant, and in all other changes which ensue, is at any rate conceivable if it is not a necessity. But this would not be an instance of the transmission of acquired characters, but only the consequence of a direct influence upon the germ-cells, and of better nourishment during growth.

A similar interpretation explains the converse change. When horses of normal size are introduced into the Falkland Islands, the next generation is smaller in consequence of poor nourishment and the damp climate, and after a few generations they have deteriorated to a marked extent. In such a case we have only to assume that the climate which is unfavourable and the nutriment which is insufficient for horses, affect not only the animal as a whole, but also its germ-cells. This would result in the diminution in size of the germ-cells, the effects upon the offspring being still further intensified by the insufficient nourishment supplied during growth. But such results would not depend upon the transmission by the germ-cells of certain peculiarities due to the unfavourable climate, which only appear in the full-grown horse.

It must be admitted that there are cases, such as the climatic varieties of certain butterflies, which raise some difficulties against this explanation. I myself, some years ago, experimentally investigated one such case [1], and even now I cannot explain the facts otherwise than by supposing the passive acquisition of characters produced by the direct influence of climate.

It must be remembered, however, that my experiments, which have been repeated upon several American species by H. W. Edwards, with results confirmatory of my own in all essential respects, were not undertaken with the object of investigating the question from this point of view alone. New experiments, under varying conditions, will be necessary to afford the true explanation of this aspect of the question; and I have already begun to undertake them.

Leaving on one side, for the moment, these doubtful, and

[1] 'Studien zur Descendenztheorie, I. Ueber den Saison-Dimorphismus der Schmetterlinge.' Leipzig, 1875. English edition translated and edited by Professor Meldola, 'Studies in the Theory of Descent,' Part I.

insufficiently investigated cases, we may still maintain that the assumption that changes induced by external conditions in the organism as a whole, are communicated to the germ-cells after the manner indicated in Darwin's hypothesis of pangenesis,—is wholly unnecessary for the explanation of these phenomena. Still we cannot exclude the possibility of such a transmission occasionally occurring, for, even if the greater part of the effects must be attributed to natural selection, there might be a smaller part in certain cases which depends on this exceptional factor.

A complete and satisfactory refutation of such an opinion cannot be brought forward at present: we can only point out that such an assumption introduces new and entirely obscure forces, and that innumerable cases exist in which we can certainly exclude all assistance from the transmission of acquired characters. In most cases of variation in colour we have no explanation but the survival of the fittest [1], and the same holds good for all changes of form which cannot be influenced by the will of the animal. Very numerous adaptations, such, for instance, as occur in the eggs of animals,—the markings, and appendages which conceal them from enemies, the complex coverings which prevent them from drying up or protect them from the injurious influence of cold,—must have all arisen entirely independently of any expression of will, or of any conscious or unconscious action on the part of the animals. I will not mention here the case of plants, which as every one knows are unconscious, for they are beyond my province. In this matter, there can be no suggestion of adaptation depending upon a struggle between the various parts of the organism (Roux)[2]. Natural selection cannot operate upon the different epithelial cells which secrete the egg-shell of *Apus*, since it is of no consequence to the animal which secretes the egg-shell whether a good or a bad shell is produced. Natural selection first operates among the offspring, and the egg with a shell incapable of resisting cold or drought is destroyed. The different cells of the same individual are not selected, but the different individuals themselves.

In all such cases we have no explanation except the operation of natural selection, and if we cannot accept this, we may as well

[1] The colours which have been called forth by sexual selection must also be included here.

[2] Wilhelm Roux, 'Der Kampf der Theile im Organismus.' Leipzig, 1881.

abandon any attempt at a natural explanation. But, in my opinion, there is no reason why natural selection should be considered inadequate to the task. It is true that the objection has been lately urged, that it is inconceivable that all the wonderful adaptations of the organism to its surroundings can have arisen through the selection of individuals; and that for this purpose an infinite number of individuals and infinite time would be required; and stress is laid upon the fact that the wished-for useful changes can only arise singly and very rarely among a great number of individuals.

This last objection to the modern conception of natural selection has apparently some weight, for, as a matter of fact, useful variations of a conspicuous kind seldom appear, and are often entirely absent for many generations. If we expect to find that qualitative changes take place by sudden leaps, we can never escape this difficulty. But, I think, we must not look for conspicuous variations—such as occur among domesticated animals and plants—in the process of the evolution of species as it goes on in nature. Natural selection does not deal with qualitative but quantitative changes in the individual, and the latter are always present.

A simple example will make this clearer. Let us suppose that it was advantageous to some species—for instance the ancestors of the giraffe—to lengthen some part of the body, such as the neck: this result could be obtained in a relatively short time, for the members of the species already possessed necks of varying length, and the variations which form the material for natural selection were already in existence. Now all the organs of every species vary in size, and any one of them will undergo constant and progressive increase, as soon as it acquires exceptional usefulness. But not only will the organ fluctuate as a whole, but also the parts composing it will become larger or smaller under given conditions, will increase or diminish by the operation of natural selection. I believe that qualitative variations always depend upon differences in the size and number of the component parts of the whole. A skin appears to be naked, when it is really covered with a number of small fine hairs: if these grow larger and increase in number, a thick covering is formed, and we say that the skin is woolly or furry. In the same way the skin of many worms and

Crustacea is apparently colourless, but the microscope reveals the presence of a number of beautiful pigment spots; and not until these have increased enormously does the skin appear coloured to the naked eye. The presence or absence of colour and its quality when present are here dependent upon the quantity of the most minute particles, and on the distance at which the object in question is observed. Again, the first appearance of colour, or the change from a green to a yellow or red colour depends upon slight variations in the position or in the number of the oxygen atoms which enter into the chemical combination in question. Fluctuations in the chemical composition of the molecules of a unicellular organism (for example) must continually arise, just as fluctuations are always occurring in the number of pigment granules in a certain cell, or in the number of pigment cells in a certain region of the body, or even in the size of the various parts of the body.

All these quantitative relations are exposed to individual fluctuations in every species; and natural selection can strengthen the fluctuations of any part, and thus cause it to develope further in any given direction.

From this point of view, it becomes less astonishing and less inconceivable that organisms adapt themselves—as we see that they obviously do—in all their parts to any condition of existence, and that they behave like a plastic mass which can be moulded into almost any imaginable form in the course of time.

If we ask in what lies the cause of this variability, the answer must undoubtedly be that it lies in the germ-cells. From the moment when the phenomena which precede segmentation commence in the egg, the exact kind of organism which will be developed is already determined—whether it will be larger or smaller, more like its father or its mother, which of its parts will resemble the one and which the other, even to the minutest detail. In spite of this, there still remains a certain scope for the influence of external conditions upon the organism. But this scope is limited, and forms but a small area round the fixed central point which is determined by heredity. Abundant nourishment can make the body large and strong, but can never make a giant out of the germ-cell destined to become a dwarf. Unhealthy sedentary habits or insufficient nourishment makes the factory-hand pale and stunted; life on board ship, with plenty of exercise and sea air, gives the sailor bodily strength and a tanned skin; but when once the resemblance to father or mother, or to both, is established in the germ-cell it can never be effaced, let the habit of life be what it will.

But if the essential nature of the germ-cell dominates over the organism which will grow from it, so also the quantitative individual differences, to which I referred just now, are, by the same principle, established in the germ, and—whatever be the cause which determines their presence—they must be looked upon as inherent in it. It therefore follows that, although natural selection appears to operate upon the qualities of the developed organism alone, it in truth works upon peculiarities which lie hidden in the germ-cells. Just as the final development of any predisposition in the germ, and just as any character in the mature organism vibrates with a certain amplitude around a fixed central point, so the predisposition of the germ itself fluctuates, and it is on this that the possibility of an increase of the predisposition in question, and its average result, depends.

If we trace all the permanent hereditary variations from generation to generation back to the quantitative variations of the germ, as I have sought to do, the question naturally occurs as to the source from which these variations arose in the germ itself. I will not enter into this subject at any length on the present occasion, for I have already expressed my opinion upon it [1].

I believe however that they can be referred to the various external influences to which the germ is exposed before the commencement of embryonic development. Hence we may fairly attribute to the adult organism influences which determine the phyletic development of its descendants. For the germ-cells are contained in the organism, and the external influences which affect them are intimately connected with the state of the organism in which they lie hid. If it be well nourished, the germ-cells will have abundant nutriment; and, conversely, if it be weak and sickly, the germ-cells will be arrested in their growth. It is even

[1] Consult 'Studien zur Descendenztheorie, IV. Über die mechanische Auffassung der Natur,' p. 303, etc. Translated and edited by Professor Meldola; see 'Studies in the Theory of Descent,' p. 677, &c.

possible that the effects of these influences may be more specialized; that is to say, they may act only upon certain parts of the germ-cells. But this is indeed very different from believing that the changes of the organism which result from external stimuli can be transmitted to the germ-cells and will re-develope in the next generation at the same time as that at which they arose in the parent, and in the same part of the organism.

We have an obvious means by which the inheritance of all transmitted peculiarities takes place, in *the continuity of the substance of the germ-cells, or germ-plasm.* If, as I believe, the substance of the germ-cells, the germ-plasm, has remained in perpetual continuity from the first origin of life, and if the germ-plasm and the substance of the body, the somatoplasm, have always occupied different spheres, and if changes in the latter only arise when they have been preceded by corresponding changes in the former, then we can, up to a certain point, understand the principle of heredity; or, at any rate, we can conceive that the human mind may at some time be capable of understanding it. We may at least maintain that it has been rendered intelligible, for we can thus trace heredity back to growth; we can thus look upon reproduction as an overgrowth of the individual, and can thus distinguish between a succession of species and a succession of individuals, because in the latter succession the germ-plasm remains similar, while in the succession of the former it becomes different. Thus individuals, as they arise, are always assuming new and more complex forms, until the interval between the simple unicellular protozoon and the most complex of all organisms—man himself—is bridged over.

I have not been able to throw light upon all sides of the question which we are here discussing. There are still some essential points which I must leave for the present; and, furthermore, I am not yet in a position to explain satisfactorily all the details which arise at every step of the argument. But it appeared to me to be necessary to state this weighty and fundamental question, and to formulate it concisely and definitely; for only in this way will it be possible to arrive at a true and lasting solution of the problem. We must however be clear on this point—that the understanding of the phenomena of heredity is only possible on the fundamental supposition of the continuity of the germ-plasm. The value of experiment in relation to this question is somewhat doubtful. A careful collection and arrangement of facts is far more likely to decide whether, and to what extent, the continuity of germ-plasm is reconcilable with the assumption of the transmission of acquired characters from the parent body to the germ, and from the germ to the body of the offspring. At present such transmission is neither proved as a fact, nor has its assumption been shown to be unquestionably necessary.