CHAPTER XI.

THE THEORY OF HEREDITY CONSIDERED AS SUPPLEMENTARY TO THE THEORY OF NATURAL SELECTION.

Darwin believes that variations are purely fortuitous—Natural selection cannot give rise to permanent race modifications unless many individuals vary in nearly the same way, at about the same time—The chances against this are very great if variations are fortuitous—Argument from North British Review—Darwin acknowledges the great weight of this objection —It is removed by the theory of heredity—The co-ordinated modification of complicated organs—The time demanded by Darwin practically infinite—Murphy's argument from the complexity of the eye—Herbert Spencer's illustration—Our theory removes this difficulty—Mr. Conn's objection—Saltatory evolution—Evidence that it occurs—Spike-horn buck—Ancon and Mauchamp sheep—Black-shouldered peacock—The theory of heredity accounts for saltatory evolution—Parallel variation—Evidence of its occurrence—Evolution of the medusæ—General and special Homologies.

According to Darwin's view, variations, though determined by definite causes (for the most part unknown), are, so far as their usefulness to the organism goes, fortuitous, and he makes use of the following illustration to explain his conception:

"I have spoken of selection as the paramount power, yet its action absolutely depends upon what we in our ignorance call spontaneous or accidental variability. Let an architect be compelled to build an edifice with uncut stones, fallen from a precipice. The shape of each fragment may be called accidental, yet the shape of each has been determined by the force of gravity, the nature of the rock, and the slope of the precipice—events and circumstances all of which depend on natural laws; but there is no relation between these laws and the purpose for which each fragment is used by the builder. In the same manner the variations of each creature are determined by fixed and immutable laws; but these bear no relation to the living structure which is slowly built up by the power of selection, whether this be natural or artificial selection."

"If our architect succeeded in rearing a noble edifice, using the rough wedge-shaped fragments for the arches, the longer stones for the lintels, and so forth, we should admire his skill even in a higher degree than if he had used stones shaped for the purpose. So it is with selection, whether applied by man or by nature; for though variability is indisputably necessary, yet when we look at some highly complex and excellently adapted organism, variability sinks to a quite subordinate position in comparison with selection, in the same manner as the shape of each fragment used by our supposed architect is unimportant in comparison with his skill" (*Variation*, xxi. p. 301).

It is quite possible that Darwin may be right in attributing the modification and adaptation of organisms almost entirely to the influence of natural selection, *and, at the same time, wrong in his belief that the variations are fortuitous.* Several critics have pointed out that if it is true that variations have no relation whatever to the needs of the organism, there are grave difficulties in the way of natural selection; but the theory rests upon too firm a basis to be easily set aside, and *these objections have hardly received the attention* which they fairly deserve, for those authors who have pointed them out have, at the same time, attacked the general theory in a hostile spirit without proposing any-thing to take its place. This has not prevented Darwin himself from perceiving the weight of the criticism, but it has certainly caused the objections to be ignored or overlooked by other less candid writers.

Natural selection cannot act unless many individual vary together.

One of the most serious objections to Darwin's theory is based upon the fact that while natural selection requires that great numbers of individuals shall vary in essentially the same way at nearly the same time, the chance against this, if variations are fortuitous in Darwin's sense, is great beyond all computation.

In 1864 the writer of what Darwin terms "an able and valuable article" in the *North British Review*, called attention to the fact that, according to the law of chances, slight variations, however useful, will tend to be obliterated, instead of perpetuated, by natural selection, unless they simultaneously appear in a great number of individuals. Unless we can show that the causes of variability act in such a way as to affect many individuals at the same time, and cause the same part to vary in all of them, we must regard this as a very serious objection to the theory of natural selection, and Darwin himself acknowledges (*Origin of Species*, p. 72) that the justice of this objection cannot be disputed. He admits in the later editions of the *Origin of Species*, p. 71, that until reading the able and valuable article in the *North British Review*, he did not appreciate how rarely single variations, whether slight or strongly marked, would be perpetuated.

The reviewer points out that it is difficult to see how a species can be changed by the survival of the descendants of a few individuals which possess some favorable variation, even when the variation is of the very greatest advantage to its possessor; and that this difficulty is very much greater when as must usually be the case, the advantage gained is very slight.

He says: "The advantage, whatever it may be, is utterly out-balanced by numerical inferiority. A million creatures are born; ten thousand survive to produce offspring. One of the million has twice as good a chance as any other of surviving; but the chances are fifty to one against the gifted individual being one of the hundred survivors. No doubt the chances are twice as great against any one other individual, but this does not prevent their being enormously in favor of *some* average individual. However slight the advantage m^y be, if it is shared by half the individuals produced, it will probably be present in at least fifty-one of the survivors, and in a larger proportion of their offspring; but the chances are against the preservation of any one 'sport' (*i.e.*, sudden marked variation) in a numerous tribe. The vague use of an imperfectly understood doctrine of chance has led Darwinian supporters, first, to confuse the two cases above distinguished; and, secondly, to imagine that a very slight balance in favor of some individual sport must tend to its perpetuation. All that can be said is that in the above example the favored sport would be preserved once in fifty times. Let us consider what will be its influence on the main stock when preserved. It will breed and have a progeny of say 100; now this progeny will, on the whole, be intermediate between the average individual and the sport. The odds in favor of one of this generation of the new breed will be, say, one and a half to one as compared with the average individual; the odds in their favor will, therefore, be less than that of their parents; but, owing to their greater number, the chances are that about one and a half of them would survive. Unless these breed together, a most improbable event, their progeny would again approach the average individual; there would be 150 of them, and their superiority would be, say, in the ratio of one and a quarter to one; the probability would now be that nearly two of them would survive and have 200 children with an eighth superiority. Rather more than two of these would survive, but the superiority would again dwindle, until after a few generations it would no longer be observed, and would count for no more in the struggle for life than any of the hundred trifling advantages which occur in the ordinary organs. An illustration will bring this conception home. Suppose a white man to have been wrecked on an island inhabited by negroes, and to have established himself in friendly relations with a powerful tribe, whose customs he has learned. Suppose him to possess the physical strength, energy and ability of a dominant white race, and let the food and climate of the island suit his constitution; grant him every advantage which we can conceive a white to possess over the native; concede that in the struggle for existence his chance of a long life will be much superior to that of the native chiefs; yet from all these admissions there does not follow the conclusion that, after a limited or unlimited number of generations, the inhabitants of the island will be white. Our shipwrecked hero would probably become king; he would kill a great many blacks in the struggle for existence; he would have a great many wives and children. In the first generation there will be some dozens of intelligent young mulattoes, much superior in average intelligence to the negroes. We might expect the throne for some generations to be occupied by a more or less yellow king; but can any one believe that the whole island will gradually acquire a white or even a yellow population?

"Darwin says that in the struggle for life a grain may turn the balance in favor of a given structure, which will then be preserved. But one of the weights in the scale of nature is due to the number of a given tribe. Let there be 7000 A's and 7000 B's, representing two varieties of a given animal, and let all the B's, in virtue of a slight difference of structure, have the better chance of life by a $\frac{1}{7000}$ part. We must allow that there is a slight probability that the descendants of B will supplant the descendants of A; but let there be only 7001 A's against 7000 B's at first, and the chances are once more equal, while if there be 7002 A's to start, the odds would be laid on the A's. True, they stand a greater chance of being killed, but then they can better afford to be killed. The grain will only turn the scales when these are very nicely balanced, and an advantage in numbers counts for weight, even as an advantage in structure. As the numbers of the favored variety diminish, so must its relative advantages increase, if the chance of its existence is to surpass the chance of its extinction, until hardly any conceivable advantage would enable the descendants of a single pair to exterminate the descendants of many thousands, if they and their descendants are supposed to breed freely with the inferior variety, and so gradually lose their ascendancy."

Darwin acknowledges that the justice of these remarks cannot be disputed, and there is no escape from the conclusion that if variations do not appear simultaneously in a great number of individuals, the theory of natural selection fails to explain the origin of species. But the theory itself is so firmly estabished by other facts, that the logical conclusion seems to be, not that natural selection is at fault, but that Darwin's opinion, that variations are fortuitous, is an error.

According to our view of the cause of variation, it is plain that a change in the environment, affecting many individuals of a species in the same way, will cause, in succeeding generations, variation of the same cells in all or nearly all of them. It is also clear that since a change in one cell of an organism will disturb the harmonious adjustment of all adjacent or related cells, any variation which makes its appearance will become more marked instead of being obliterated, in the offspring of successive generations.

I think it is clear, without further discussion, that our theory of heredity entirely does away with this very serious difficulty, *and furnishes a firmer basis for the* theory of natural selection. It is also clear that this cannot be said of the Pangenesis hypothesis, or of any other hypothesis which has been proposed.

The Formation of Complicated Organs by the Natural Selection of Fortuitous Variations demands Unlimited Time.

There is another objection of nearly the same character, which must have struck every thinker with more or less force. How are the various organs of a highly complicated organism, or the various structures which enter into the formation of a complicated organ, kept in harmonious adjustment to each other by the selection of variations which are, in Darwin's sense, fortuitous? It is plain that, as soon as one part has varied in any direction, *the harmonious adjustment of related parts will be* disturbed, and that they too must vary correspondingly in order to restore the proper tone to the whole, and it is equally clear that even a slight change in a complicated organ will thus, if the various modifications are really fortuitous, require a very great number of generations to supply the necessary variations.

There does not seem to be any logical ground for doubting that any of the adaptations of nature *might have been* produced by the natural selection, from an indefinite number of fortuitous variations, of those which happened to be favorable; but in the case of any complex adaptation, an indefinite and almost infinite period of time would be required.

Darwin says (*Origin of Species*, p. 143) that reason tells us that if numerous gradations from a simple and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor, as is certainly the case; if further the eye ever varies, and these variations be inherited, as is likewise certainly the case; and if such variations should be useful to any animal under changed conditions of life, then the difficulty of believing that a perfect and complex eye *could be formed* by natural selection, though insuperable by our imagination, should not be considered as subversive of the theory. Before we can accept as possible this view of the evolution of the eye "we must suppose each new state of the instrument to be multiplied by the million; each to be preserved until a better one is produced, and then the old ones to be all destroyed. . . . Let this process go on for millions of years; and during each year on millions of individuals of many kinds; and may we not believe that a living optical instrument *might* thus be formed as superior to one of glass as the works of the Creator are to those of man?"

To show that complex adaptations *might have been* produced by the selection of fortuitous variations is by no means to prove that they *have* thus been produced, and we may well doubt whether life has existed long enough upon earth, to allow all the harmonious adjustments of living things to be slowly perfected in this way.

The vast number of changes which must be co-ordinated in order to produce any considerable modification of one of the higher animals, and the length of time which must be necessary if the successive steps are purely fortuitous, are points which must have attracted the notice of every one who has read the "Origin of Species." The difficulty is obvious, and it has been noticed by many writers, but Murphy, in his discussion of the evolution of the vertebrate eye (*Habit and Intelligence*, p. 319), has stated it with great force. He says: "The higher the organization, whether of an entire organism or of a single organ, the greater is the number of the parts that co-operate, and the more perfect is their co-operation; and consequently the more necessity there is for corresponding variations to take place in all the co-operating parts at once, and the more useless will be any variation whatever unless it is accompanied by corresponding variations in the co-operating parts; while it is obvious that the greater the number of variations which are needed in order to effect an improvement, the less will be the probability of their all occurring at once. It is no reply to this to say, what no doubt is abstractly true, that whatever is possible becomes probable, if only time enough is allowed. There are improbabilities so great that the common-sense of mankind treats them as impossibilities. It is not, for instance, in the strictest sense of the word, impossible that a poem and a mathematical proposition should be obtained by the process of shaking letters out of a box; but it is improbable to a degree that cannot be distinguished from impossibility; and the improbability of obtaining an improvement in an organ by means of several spontaneous variations, all occurring together, is an improbability of the same kind. If we suppose that any single variation occurs on the average once in m times, the probability of that variation occurring in any individual will be $\frac{1}{m}$; and suppose that x variations must concur in order to make an improvement, then the probability of the necessary variations all occurring together will be $\frac{1}{m^x}$. Now suppose, what I think a moderate proposition, that the value of m is 1000, and the value of x is 10, then $\frac{1}{m^x} = \frac{1}{1000^{10}}$ 30 $= \frac{1}{10^{30}}$. A number about ten thousand times as great as the number of waves of light that have fallen on the earth since historical time began. And it is to be further observed that no improvement will give its possessor a certainty of surviving and leaving offspring, but only an extra chance, the value of which it is quite impossible to estimate."

No one can be more firmly convinced of the great potency of natural selection than I am, but I am sure every one will feel that the problem of the origin of species would be greatly simplified if it could be shown that variations are not fortuitous in Darwin's sense of the word, but that natural selection is in some way provided with variation in those parts where change is needed.

Mivart has discussed this subject at considerable length. He points out that the modification of domesticated animals by the continued selection of slight variations, is a very slow process, and after quoting Darwin's statement that wild species probably change much more slowly than domesticated forms, he continues as follows: "Let us take for an example the proboscis monkey of Borneo. According to Mr. Darwin's own opinion, this form might have been sensibly changed in the course of two or three centuries. According to this, to evolve it as a true and perfect species one thousand years would be a very moderate period. Let ten thousand years be taken to represent approximately the period of substantially constant conditions, during which no considerable change would be brought about. Now, if one thousand years may represent the period required for the evolution of this species and of the other species of the genus, ten times that period should, I think, be allowed for the differentiation of that genus, the African Circopithecus, and the other genera of the family Simiidæ, the differences between the genera being certainly more than tenfold greater than those between the species of the same genus.

". . . For the differentiation of the families Simiidæ and Cebidæ—so very much more distinct and different that any two genera of either family—a period ten times greater should, I believe, be allowed than that required for the evolution of the subordinate groups. A similarly increasing ratio should be granted for the successive developments of the difference between the Lemuroid and the higher forms of primates; for those between the original primates and other root-forms of placental mammals; for those between primary placental and implacental mammals; and perhaps, also, for the divergence of the most ancient stock of these and of the monotremes, for in all these cases modifications of structure appear to increase in complexity in at least that ratio. Finally, a vast period must be granted for the development of the lowest mammalian type from the primitive stock of the whole vertebrate sub-kingdom. Supposing this primitive stock to have arisen directly from a very lowly original animal indeed (such as a nematoid worm, an ascidian, or a jelly-fish), yet it is not easy to believe that less than two thousand million years would be required for the totality of animal development by no other means than minute, fortuitous, occasional and intermitting variations in all considerable structures. If this be even an approximation to the truth, then there seem to be strong reasons for believing that geological time is not sufficient for such a process. . . . .

"Now, it will be a moderate computation to allow 25,000,000 years for the deposition of the strata down to and including the Upper Silurian. If, then, the evolutionary work done during this deposition only represents a hundredth part of the sum total, we shall require 2,500,000,000 (two thousand five hundred million) years for the complete development of the whole animal kingdom to its present state. Even one quarter of this, however, would far exceed the time which physics and astronomy seem able to allow for the completion of the process.

". . . Now all these difficulties are avoided if we admit that new forms of animal life of all degrees of complexity appear from time to time with comparative suddenness, being evolved according to laws in part depending on surrounding conditions, in part internal, similar to the way in which crystals (and perhaps, from recent researches, the lowest forms of life) build themselves up according to the internal laws of their component substance, and in harmony and correspondence with all environing influences and conditions."

Darwin himself seems to believe that in order to explain the harmonious co-ordination of all the inter-related parts of a complicated animal, we must believe that natural selection is greatly aided by other influences, such as the inherited effect of use and disease, the direct action of external conditions, and especially the law of correlated variability.

Our theory of heredity furnishes exactly what we need to escape this difficulty, for we can understand that a change in any part of the body, disturbing, as it must, the harmonious adjustment of related parts, acts directly to produce variations in these parts in succeeding generations, by causing the transmission of gemmules. The time which is needed for the evolution of a complicated organ by natural selection is thus brought within reasonable limits, and one of the most serious and fundamental objections to Darwin's explanation of the origin of species is completely done away with.

He says: "We may borrow an illustration from Mr. Herbert Spencer, who remarks that when the Irish elk acquired its gigantic horns, weighing above one hundred pounds, numerous co-ordinated changes of structure would have been indispensable, namely, a thickened skull to carry the horns; strengthened cervical vertebræ with strengthened ligaments; enlarged dorsal vertebræ to support the neck, with powerful fore-legs and feet; all these parts being supplied with proper blood-vessels, muscles and nerves. How, then, could these admirably co-ordinated structures have been acquired? According to the doctrine which I maintain, the horns of the male elk were slowly gained through sexual selection, that is, by the best armed males conquering the worse armed, and leaving a greater number of descendants. But it is not at all necessary that the several parts of the body should have simultaneously varied. Each stag presents individual differences, and in the same district those which had slightly heavier horns, or stronger necks, or stronger bodies, or were the most courageous, would serve the greatest number of does, and consequently have the *greatest number of offspring. The offspring would* inherit in a greater or less degree these same qualities; would occasionally intercross with each other, or with other individuals varying in some favorable manner; and of their offspring, those which were the best endowed in any respect would continue multiplying: and so onwards, always progressing, sometimes in one direction, and sometimes in another, towards the present excellent co-ordinated structure of the male elk.

"To make this clear, let us reflect on the probable steps, as shown in the twentieth chapter, by which our race and dray horses have arrived at their present state of excellence: if we could view the whole series of intermediate forms between one of these animals and an early unimproved progenitor, we should behold a vast number of animals not equally improved in each generation throughout their entire structure, but sometimes a little more in one point, and sometimes in another, yet on the whole gradually approaching in character to our present race or dray horses, which are so admirably fitted in the one case for fleetness, and in the other for draught.

"Although natural selection would thus tend to give to the male elk its present structure, yet it is probable that the inherited influence of use has played an equal or more important part. As the horns gradually increased in weight, the muscles of the neck, with the bones to which they are attached, would increase in size and strength; and these parts would react on the body and legs. Nor must we overlook the fact that certain parts of the skull and extremities would, judging from analogy, tend from the first to vary in a correlated manner. The increased weight of the horns would also act directly on the skull in the same manner as when one bone is removed in the leg of the dog, the other bone, which has to carry the whole weight of the body, increases in thickness. But from the facts given with respect to horned and hornless cattle, it is probable that the horns and skull would immediately act on each other through the principle of correlation. Lastly, the growth and subsequent wear and tear of the augmented muscles and bones would require an increased supply of blood, and consequently an increased supply of food; and this again would require increased power of mastication, digestion, respiration and excretion."

It will be seen by a careful examination of this extract that Darwin is compelled, by cases of this kind, to believe that other influences have played a part equal to or more important than that of natural selection, and he is compelled to attribute the co-ordinated modification of related parts to the action of the law of correlated variability.

I have already called attention to the fact that this law of correlated variation is a necessary result of our view of the nature of heredity, for a change in one part must cause variation in co-ordinated parts; and gemmules thrown off by a certain organ of the body may cause co-ordinated variation in all the homologous parts of a descendant. I believe that it will be clear to every one, without further explanation, that the acceptance of our theory will greatly simplify our conception of the action of natural selection, and will enable us to understand the rapid evolution of co-ordinated structures, without being compelled to attribute them to other influences.

Darwin appears to have felt the need of something of the kind, for we find evidence that he has hunted long and faithfully, but in vain, for something to show that changed conditions produce, directly, the proper modifications, and failing to find any such proof, he has accepted, as the only alternative, the view that variations are fortuitous. This is not the only alternative, for we see that there is a third view, namely, that changed conditions cause the variation, but do not determine its character.

In his exhaustive essay on *Variation*, Darwin has discussed the question whether the external conditions of life have such a direct and definite influence that the exposure of many individuals for many generations to any change in their physical conditions will result in the modification of all or nearly all of them in the same direction, thus producing a new sub-variety without the aid of selection.

He points out that many animals and plants which range widely and are exposed to great diversity of conditions remain nearly the same in character; that the two hundred plants which are distributed over every English county, and which must have been exposed for an immense period to considerable differences of climate and soil, are uniform throughout the whole area; and that certain birds, insects and plants which range over large portions of the world, nevertheless retain the same character.

He calls attention to the fact that fowls and pigeons have varied, and will no doubt go on varying, in directly opposite ways, though kept during many generations under nearly the same conditions; and he therefore concludes that the amount of modification which animals and plants have undergone under domestication does not correspond with the degree to which they have been exposed to changed circumstances. He lays especial stress, in this connection, upon the phenomena of bud-variation, and says: "It is well worth while to reflect maturely on some striking case of bud-variation—for instance, that of the peach. This tree has been cultivated by the million in various parts of the world, has been treated differently, grown on its own roots and grafted on various stocks, planted as a standard against a wall, and under glass; yet each bud of each sub-variety keeps true to its kind. But occasionally, at long intervals of time, a tree in England, or under the widely different climate of Virginia, produces a single bud, and this yields a branch which ever after bears nectarines. . . . Now is it possible to conceive of conditions more exactly alike than these to which the buds on the same tree are exposed? Yet one bud alone, out of the many thousands borne by the same tree, has suddenly, without any apparent cause, produced a nectarine. But the case is even stronger than this, for the same flower-bud has yielded a fruit, one half or one quarter a nectarine, and the other half or three quarters a peach. Again, seven or eight varieties of the peach have yielded, by bud-variation, nectarines; the nectarines thus produced, no doubt differ a little from each other, but still they are nectarines. Of course there must be some cause, internal or external, to excite the peach-bud to change its nature; but I cannot imagine a class of facts better adapted to force on our minds the conviction that what we call the external conditions of life are quite insignificant, in relation to any particular variation, in comparison with the organization or constitution of the being which varies. We are thus driven to conclude that in most cases the conditions of life play a subordinate part in causing any particular modification; like that which a spark plays, when a mass of combustibles bursts into flame, the nature of the flame depending on the combustible matter and not on the spark. . . . Hence, although it must be admitted that new conditions of life do sometimes definitely affect organic beings, it may be doubted whether well-marked races have often been produced by the direct action of changed conditions, without the aid of selection, either by man or nature" (*Variation*, 347–352).

While we acknowledge the great weight of this reasoning we must bear in mind that evidence to show that new forms of life are not produced, without the aid of selection, by direct modification, is not necessarily proof that the causes of variation have no relation to the purpose of the modification—that variations are, so far as their use goes, purely fortuitous.

Even if external changes do not give rise to useful modifications, unless they are aided by natural selection, it may still be true that they play an important and essential part.

It may be true that a change of conditions does not necessarily produce a change of structure, and yet true that when a change of structure does take place it is due to the changed conditions.

It may be true that an unfavorable change in the environment has no power to produce a compensating change of hereditary structure without the aid of natural selection, and yet true that this external change may be the cause of variation in the part affected.

If this latter supposition be a fact the work of natural selection will be almost infinitely simplified, for in place of an indefinite number of fortuitous variations, it will be furnished with variation of the part in which change is needed, and it is only an even chance whether a change in a part which is out of harmony with its environment be favorable or unfavorable.

According to our theory of heredity, when an organism, placed under new conditions, becomes modified to meet the change in its environment, the existence of the internal change is caused by the external change, while its precise character is determined by other factors, chiefly by the hereditary characteristics of the corresponding part, in both parents.

As long as the harmony which has been gradually established, by natural selection, between any particular cell and its conditions of life, remains undisturbed, this cell will continue to perform its function as a part of the body, and will have little tendency to give rise to gemmules. When through any change, either in the conditions of life external to the organism, or in other parts of the body, this cell comes to be placed in circumstances which are unfavorable to the performance of its function, it will exert the tendency to throw off gemmules; for each cell being, in a morphological sense, an independent organism, possesses this power, by inheritance, although natural selection has gradually acted, during the past history of the evolution of life, to prevent the useless manifestation of the tendency, as long as surrounding conditions are favorable and no change is needed.

These gemmules, when transmitted to the egg, by impregnation, will, by sexual union with the corresponding parts of the egg, cause variation in the homologous cells of the offspring, and will thus produce a congenital hereditary change at the very time when, and in the very part where, such change is needed.

Instead of being purely fortuitous on the one hand, or due on the other hand to the direct modifying influence of external conditions, congenital variations are due to the manifestation of a general law, which has gradually become established, during the evolution of life, for this very purpose. I believe that the gradual establishment of this law of heredity is due to the action of natural selection; to the divergent specialization of the two sexual elements; and to a physiological division of labor, each step in the production of which has been advantageous, and has therefore been perpetuated like any other useful variation.

According to this view, we must recognize in the law of natural selection, not simply a great means of modification, but the agency to which organic evolution is almost exclusively due; but we must also believe that, in the higher multicellular organisms it acts indirectly, and is subordinate to another law, the law of heredity, which itself owes existence to the law of natural selection.

Objection to the View that the Variation of any Part is Caused by the Transmission of Gemmules, which owe their Existence to the Action of Unfavorable Conditions upon the Corresponding Part of the Parent.

Mr. H. W. Conn has called my attention to the fact that in many cases it is difficult to see any connection between the function of a new variation and a failure to perform that function in the parent. He instances the mimetic colors of insects, and the long neck of the giraffe, and says that it is difficult to see how the action of unfavorable conditions upon the parents could have given rise to these variations. He says that if an insect were dangerously conspicuous its unfavorable conditions of life would not affect the cells to which its color is due, in any especial way, but would lead to the destruction of the entire animal.

So, too, if a series of dry seasons should place the giraffe under conditions of hardship, the individuals with the shortest necks would suffer most, from inability to reach their food, but he says that this would not affect the cells of their necks especially, but would result in general disadvantage to the whole body.

The validity of this objection cannot be denied, and I do not think it would be difficult to find many instances which are much more striking than the two which have been referred to.

It is very difficult to understand how our explanation of the origin of variation can apply to instances of modification in animals which, like worker bees, do not produce descendants.

It is proper to point out, however, that these cases are no more difficult to explain after our theory of heredity is accepted than without it. Its acceptance does, in many cases, greatly simplify our conception of natural selection, and the fact that it still leaves difficulties unexplained, is no reason for rejecting it, provided it does not add to these difficulties.

In the case of the giraffe it is not difficult to understand that if circumstances should compel this animal to stretch frequently after foliage almost beyond its reach, this might cause hardship in the cells of the neck, and thus result in the production of gemmules, and in consequent variation of this part of the body.

As sterile insects are simply sexual insects which have not become perfectly developed, we must believe that all their characteristics are shared by the sexual insects, and there is therefore no great difficulty in understanding how the action of unfavorable conditions upon the sexual form might cause variation in the sterile form.

The various cells of the body stand in such intimate relations to each other, and are mutually dependent upon each other in so many ways, that it is quite impossible to trace out in its completeness the effect of an external influence. A change outside the body may have an obvious and direct effect upon the cells of a certain part, and these cells may influence other cells and so on indefinitely. Any of the cells which are thus affected may give rise to gemmules, and may thus result in a favorable variation which will be seized upon and perpetuated by natural selection. *A new variation may* therefore follow from an external change which has no direct influence upon the part in which the variation occurs. This would be an apparent but not a real objection to our view that the cause of a variation is to be sought in the unfavorable action of changed conditions upon the part in which the variation occurs, but our inability to trace the connection between a variation and the external change to which it is due, is no reason for doubting the reality of the connection.

Saltatory Evolution.

The origin of species by the natural selection of minute fortuitous variations, demands time which is so long that it is practically infinite, and many naturalists have accordingly held that the successive changes may possibly not be so minute as Darwin believes. Thus Huxley says: "We greatly suspect that Nature does make considerable jumps in the way of variation now and then, and that these saltations give rise to some of the gaps which appear to exist in the series of known forms."

Galton compares the evolution of an organism to the rolling of a rough stone, which has, in consequence of its roughness, a vast number of natural facets on any one of which it might rest in stable equilibrium. When pushed, this stone would yield a little; but it would fall back again on the withdrawal of the pressure, unless this was great enough to overpass the limit of the facet on which it has been resting.

In this case it would tumble over into a new position of stability, which it will retain until the pressure again becomes great enough to dislodge it and roll it another step onwards. He says, "*The various positions of stable* equilibrium may be looked upon as so many typical attitudes of the stone, the type being more durable as the limits of its stability are wider. We also see clearly that there is no violation of the law of continuity in the movements of the stone, though it can only repose in certain widely separated positions."

Mivart, who has discussed this subject at some length, has given many reasons for believing, in opposition to Darwin, that such sudden jumps do occur, and that evolution is not always by minute changes.

It is clear to every one that any theory of the cause of variation, which recognized the possibility of sudden and extensive modification, would very greatly *diminish the* time which is demanded for the origin of species by natural selection, and would thus greatly simplify our conception of the working of this law.

We have just seen that as our theory of heredity explains how a variation in one part causes related parts to vary, it removes one great objection to the theory of natural selection, and I wish now to call attention to the fact that, since a change in any part will disturb the harmony of related parts, thus causing their cells to throw off gemmules, a slight change in one generation may become, in following generations, a very considerable modification. There is therefore no reason why natural *selection should not often be presented with* great and extended variations—the saltations which Mivart believes in—and the evolution of organisms may therefore be a much more rapid process than Darwin believes.

We will now examine the evidence to show that sudden changes of this kind do sometimes occur. This evidence is of necessity drawn almost entirely from our domesticated animals and plants. A great gap between fossil forms might be attributed to the imperfection of the record, and if a wild form were to come into existence suddenly it would simply be recorded as a very rare species, and there would be no way to tell whether it is the first or the last of its race. If a considerable modification of a well-known wild species should appear suddenly in a region which is well known and thoroughly explored, we might have sufficient evidence to be certain that it is due to recent variation: and there are a few instances of this kind, the spike-horned buck of the Adirondacks being the most conspicuous one with which I am acquainted. In Dec., 1869, a writer in the *American Naturalist* says that he has hunted in the Adirondacks where the Cervus Virginianus abounds for the last twenty-one years. About fourteen years ago he first heard of spike-horn bucks. These became from year to year more common; about five years ago he shot one, and subsequently another, and now they are frequently killed. He says that the spike-horn differs greatly from the common antler of C. Virginianus. It consists of a single spike, more slender than the antler, and scarcely half as long, projecting forward from the brow, and terminating in a very sharp point. He believes that it gives a considerable advantage to its possessor over the common buck, as it is a more effective weapon than the common antler, at the same time that it enables him to run more swiftly than the common buck through thick woods and underbrush.

This certainly seems to be an instance of the sudden appearance, in a wild species, of a very considerable modification, and although it is true that few similiar instances have been recorded, the study of variation in domesticated animals leads us to believe that many similar cases must occur in wild forms, although our means of observation do not allow us to prove that this is the case.

In 1791 a ram lamb was born in Massachusetts, having short crooked legs and a long back, like a turnspit dog. From this one lamb the well-known ancon breed of sheep was raised (Darwin, *Variation*, I. p. 126). Darwin says that in 1828 a single ram-lamb was born on the Mauchamp farm with long, smooth, straight silky wool. The ram was of small size, with a large head, long neck, narrow chest, and long flanks. This one ram is the founder of the Mauchamp-merino breed of sheep, and has transmitted all his desirable peculiarities to a whole race of descendants, although certain undesirable peculiarities have been eliminated by judicious selection.

Darwin says (*Variation*, I. p. 350): "There is one strange fact with respect to the peacock, namely, the occasional appearance in England of the 'japanned' or 'black-shouldered kind.' This form has lately been named on the high authority of Mr. Sclater as a distinct species, *Pavo nigripennis*, which he believes will hereafter be found wild in some country, but not in India, where it is certainly unknown. These japanned birds differ considerably from the common peacock in the color of their secondary wing-feathers, scapulars, wing coverts and thighs; the females are much paler, and the young, as I hear from Mr. Bartlett, likewise differ. They can be propagated perfectly true. Although they do not resemble the hybrids which have been raised between

P. cristatus and *muticus*, nevertheless they are in some respects intermediate in character between these two species; and this fact favors, as Mr. Sclater believes, the view that they form a distinct and natural species.

On the other hand, Sir H. Heron states that this breed suddenly appeared within his memory in Lord Brownlow's large stock of pied, white, and common peacocks. The same thing occurred in Sir J. Trevelyan's flock composed of common and pied peacocks. It is remarkable that in these two latter instances the black-shouldered kind increased to the extinction of the previously existing breed. I have also received, through Mr. Sclater, a statement from Mr. Hudson Gurney that he reared, many years ago, a pair of black-shouldered peacocks from the common kind, and another orinthologist, Prof. A. Newton, states that, five or six years ago, a female bird, in all respects similar to the female of the black-shouldered kind, was produced from a stock of common peacocks in his possession, which, during more than twenty years, had not been crossed with birds of any other strain. Here we have five distinct cases of japanned birds suddenly appearing in flocks of the common kind kept in England. Better evidence of the first appearance of a new variety could hardly be desired. If we reject this evidence, and believe that the japannned peacock is a distinct species, we must suppose in all these cases that the common breed had at some former period been crossed with the supposed *P. nigripennis*, but had lost every trace of the cross, yet that the birds occasionally produced offspring which suddenly and completely reacquired, through reversion, the characters of *P. nigripennis*. I have heard of no other such case in the animal or vegetable kingdom. . . . So remarkable a form as *P. nigripennis*, when first imported, would have realized a large price; it is therefore improbable that it should have been silently introduced, and its history subsequently lost. On the whole the evidence seems to me, as it did to Sir H. Heron, to preponderate strongly in favor of the black-shouldered breed being a variation, induced either by the climate of England or by some unknown cause, such as reversion to a premordial and extinct condition of the species. On the view that the black-shouldered peacock is a variety, the case is the most remarkable ever recorded of the abrupt appearance of a new form which so closely resembles a true species that it has deceived one of the most experienced of living ornithologists."

Mivart quotes from Naudin, Godron, and others, several very similar cases in plants. From the seeds of a poppy, which suddenly took on a remarkable variation in its fruit, a crown of secondary capsules being added to the normal central capsule, a field of poppies was grown. These resembled the form from which the seed was taken, and gave seed which again reproduced the variation. In 1861 Godron "observed among a sowing of *Datura tatula*, the fruits of which are very spinous, a single individual of which the capsule was perfectly smooth. The seeds taken from this plant all furnished plants having the character of this individual." These seeds were cultivated up to the fifth and sixth generations, and the latest descendants did not exhibit the least tendency to revert to the spinous form.

These cases show us that very considerable variations may suddenly appear in cultivated plants and domesticated animals, and that these sudden modifications may be strongly inherited, and may thus give rise to new races by sudden jumps.

The analogy of domesticated forms would lead us to believe that the same thing sometimes occurs in nature, and that Darwin has over-estimated the minuteness of the changes in wild organisms, and has thus failed to see that natural selection may give rise to new and well-marked races in a few generations.

Our theory of heredity would lead us to expect much of this sudden modification, and it gives us a simple explanation of its origin, and thus gives to the law of natural selection a much simpler and therefore a much more probable form than that in which it presented itself to the mind of its discoverer.

Parallel Variation.

According to the view that variations are purely fortuitous, the chances are almost inconceivably great against the independent modification of several forms along parallel lines, by the action of natural selection, yet Darwin gives many instances in which this has actually occurred.

He says that by the term "analogous or parallel variation" he wishes to express that similar characters occasionally make their appearance in the several varieties or races descended from the same species, and more rarely in the offspring of widely distinct species. For instance the nectarine is the offspring of the peach; and the varieties of both these trees offer a remarkable parallelism in the fruit being white, red or yellow-fleshed, clingstone or freestone, in the flowers being large or small, in the leaves being serrated or crenated, furnished with globose or reniform glands, or quite destitute of glands. In this case we know that the two forms have independently varied in parallel lines, and that each variety of the nectarine has not derived its character from a corresponding variety of the peach. The several varieties of the apricot, which belongs to a closely allied genus, differ from each other in nearly the same parallel manner. Darwin gives many similar instances, and we must acknowledge that in these cases we have homologies which are not due to inheritance from a common ancestor, but to secondary modification.

It is true that, in all the cases which Darwin gives, the parallelism exists between forms which are very much alike, and which have quite recently diverged from a common ancestor, but there is reason to believe that this is not always the case. Morphologists assume that homology or morphological resemblance is, in itself, evidence of community of descent, and when two widely separated organisms present features which show fundamental similarity of plan, they take it for granted that they owe their resemblances to inheritance from a common ancestor, which exhibited all the characteristics which they share in common.

This is no doubt true as a general rule, and even if it were not true it would usually be extremely difficult to prove its falsity; but there are a few cases where great groups of animals are related to each other in such a peculiar way that the view that all their homologies are due to descent is untenable.

The Medusæ present such a case. These animals resemble each other in many particulars. They have a muscular contractile gelatinous umbrella by the pulsations of which they swim through the water. The digestive organs are suspended from the concave centre of the umbrella, and they give rise to diverticula which penetrate its gelatinous substance. Their reproductive organs are developed upon the digestive tract or upon its diverticula, while their organs of sense are placed around the margin of the umbrella. They usually pass through a fixed polyp-like larval stage before maturity is reached, and this polyp larva is destitute of a swimming umbrella, and of organs of special sense. It has an elongated cylindrical body, by one end of which it is attached, while the mouth is placed at the opposite end and is surrounded by a crown of tentacles.

The group is divided into two grand divisions, the medusæ with a veil or diaphragm across the opening of the umbrella, and the medusæ without a veil. The two groups resemble each other in all essential particulars, and no naturalist has doubted that they are truly homologous with each other, but they present certain constant differences, such as the presence of a veil and the absence of gastric filaments in the one group, and the absence of a veil and the presence of gastric filaments in the second group. The larva of a veiled medusæ is a hydroid-polyp, which has a simple digestive cavity, and the power of multiplication by lateral budding, while the polyp-larva in the veilless medusæ is known as a scyphistoma. It has gastric filaments in its digestive cavity, and it multiplies by terminal budding or fission. In other respects, the two kinds of larvæ show a close homology with each other, but the points of resemblance are not the same as those which unite the two groups of mature medusæ.

Haeckel has devoted many years to the study of the medusæ, and his opinion is entitled to very great weight, and he believes that the resemblances between the larvæ are due to community of descent, but that the resemblances between the adults are not. He believes that the remote ancestor of all the medusæ was a polyp which united in itself the features which now distinguish the hydra-larvæ of the veiled medusæ from the scyphostoma larvæ of the veilless forms, and that these two larval forms have diverged in two directions from this ancestor, from which they inherit all that they have in common.

Haeckel believes that after this separation took place, the veiled medusæ were developed from hydroid polyps, while the veilless medusæ were developed from scyphistoma polyps. The many points of resemblance between the two forms of medusæ are, therefore, not due to common inheritance, but have been secondarily acquired. They are due to the fact that the two groups of medusæ have been evolved along parallel but distinct lines.

Haeckel's familiarity with the medusæ entitles him to speak with great authority; but still he may possibly be wrong, and the origin of the two groups may not have been as he supposes.

There are four possible hypotheses as to the origin of the medusæ, in favor of each of which something may be said. We may hold with Haeckel that the two larval polyps are the divergent descendants of a common ancestral polyp, which had no medusa stage, and that each has subsequently developed medusæ, or we may believe that the common ancestor was a medusa without a polyp larva, and that the hydra larva and the scyphistoma larva have been independently acquired, or we may believe that the ancestral form had both a larval polyp-like stage, and an adult medusa stage, or finally we may assume what seems to us the most probable view, that the ancestral form was neither a true swimming medusa nor a true sedentary polyp, but something half-way between, like the actinula of Tubularia or the embryo of Cunina. I do not see any fifth alternative, and one of these four suppositions must correspond with the actual evolution of the group. Now whichever one we accept, we are compelled to believe that there has been parallel evolution, and that certain homologies between the various forms are not due to inheritance, but to independent modification.

Haeckel's view compels us to believe that the resemblances between the two groups of medusæ have been independently acquired. If we accept the second alternative, and derive the two forms from an ancestral medusæ, the resemblances between the larvæ must be due to parallel variation. Suppose, then, that we accept the third or the fourth view, and derive both groups from an ancestral form which had a polyp-like larval stage, and a medusa-like adult stage, or else from an ancestral form which united in itself certain of the larval and certain of the adult characters.

Among the veiled medusæ there are some which, like Liriope, do not pass through a hydra stage, but lay eggs, which develop directly into medusæ; and there are also forms which, like the fresh water hydra, have no medusæ stage. Among the veilless forms there are also some which have no medusa stage, but which, like Lucernaria and the Tesseridæ, remain permanently as scyphistoma-polyps, and it is probable that in others, as the Charybdeadæ, the eggs hatch into medusæ, as they do in Liriope, without the intervention of a larval polyp stage.

It is therefore impossible to frame any hypothesis as to the origin of the medusæ, which will do away with the necessity for the belief that parallel modification, along independent lines, has occurred in the different subdivisions of the group.

If we accept Darwin's view of the origin of variation, parallel modification is not absolutely impossible, although the chances against it are very great indeed.

The cases where it can be proved to have occurred are not very numerous, it is true, but there are enough of them to present a serious difficulty. On our view that an external change which acts upon a certain part of the body may cause variation in that particular part, the chances against the parallel modification of allied organisms are very greatly diminished, so much so that the occasional occurrence of such modifications might be expected. If such cases were the rule they would be equally fatal to the theory of natural selection, whether our theory of heredity were accepted or not; but the cases are very far from frequent.

General and Special Homology: and the Significance of Serial Homology, Symmetry and Polymorphism.

We have, so far, been occupied in studying the evidence for the law of heredity which is afforded by the slight and recently acquired differences between the sexes of the same species, between the young and the adult, between domesticated and wild races, between the hybrid offspring of allied species, between reciprocal hybrids, etc.

The bearing of this law upon the more profound problems of morphology has hardly been referred to, for the field which we have examined, although we have passed over it very rapidly, has furnished material for a treatise of considerable length. The discussion of the general problems of morphology would require another volume of even greater length, for I believe, and hope to show in another place, that the acceptance of my view will lead to considerable change in our manner of handling these problems ; and will so shift our view as to remodel some of the fundamental principles of the science.

I believe that it will throw light upon many obscure and perplexing questions, such as the significance of symmetry and general homology, the origin of polymorphism, the definition of an individual or person, etc.; but the end of a book is not the place to enter upon a a new field, and I am forced to reserve this subject for future discussion, although I will now indicate very briefly the nature of this explanation.

The basis of modern morphology is the doctrine that homology indicates genetic relationship.

Homology is fundamental similarity of plan, as distinguished from difference or similarity in physiological function. For example a man's arm and hand are fitted for grasping, and a bird's wing for flight, and their different uses render them unlike each other in a superficial view, although there is below and behind this obvious difference a more deep-seated resemblance. The feathers which cover the bird's wing have the same histological structure and the same origin as the hairs upon the human arm; the skin which covers the limb has the same character in both cases; the wing, like the arm, has a supporting skeleton, which consists of a shoulder and upper arm, a forearm, a wrist, and a hand; the muscles have the same structure and the same general arrangement, and the way in which they are supplied with nerves and blood-vessels is the same.

This fundamental identity of structure which is obscured, but not destroyed by the difference of use, is homology. In a superficial view the wing of a bird resembles the wing of a dragon-fly more closely than it resembles a man's arm, but careful examination shows that the insect's wing is not a limb at all, but a peculiar outgrowth from the body. The resemblance between a bird's wing and an insect's wing is not an homology, and it has no morphological significance: it does not indicate that there is any close relationship between a bird and an insect.

It is sometimes difficult to determine whether a resemblance is an homology or not, and in simple cases we decide by asking whether it can be due to similarity of use. We know that a bird's wing is more closely related to a man's arm than it is to an insect's wing, because the resemblance between the two wings is no more than we should expect in organs adapted to the same purpose; but there is nothing in the use of the arm and wing to explain what they have in common.

In cases too complicated to be settled in this simple way we appeal to embryology, and ask whether the resemblance becomes more marked or less marked when we study it in its younger stages. The arm and the wing are more alike in the embryo than they are in the adults, and the features which they share in common make their appearance earlier than their distinctive characteristics.

An homology then is a resemblance which is not due to similarity of use, and which is more conspicuous in the embryo than in the adult.

This is the doctrine of homology considered from its structural side; historically considered, an homology is a resemblance due to community of descent, as distinguished from one due to recent modification. The modern morphologist believes that the resemblances between a bird's wing and a man's arm are due to inheritance from a remote ancestor in which the limb had all the characteristics which are common to the wing and arm; that during the evolution of birds and mammals along two divergent lines from this ancestral form, the distinctive features which fit the wing for flight and the hand for grasping have been gradually acquired.

The doctrine that homology is an indication of ancestral relationship, and that the past history of organisms can be traced by studying their anatomy and embryology, is the basis of the modern science of morphology.

Now there are two kinds of homology, special homology and general homology. Homologies between corresponding parts of different animals are known as special homologies, and those between different parts of the same animal as general homologies. As examples of general homology we may instance the serial homology of a cray-fish, the bilateral symmetry of mammals, and the radial symmetry of a star-fish.

So far as structure goes the homology between a man's arm and a man's leg is precisely like the homology between his arm and a bird's wing. It is a resemblance which is not due to similarity of use, but to fundamental resemblance, and it is more marked in the embryo than it is in the adult, and we seem, at first sight, to be justified in concluding that, if special homologies indicate genetic descent, general homologies must also; and that if general homologies cannot be explained in this way, the explanation of special homologies cannot be accepted.

Mivart has pointed out that it is impossible to explain general homologies by attributing them to inheritance from a common ancestor, and he therefore concludes that special homologies do not prove genetic evolution. On the other hand many authors have held that since special homologies indicate descent, general homologies must have the same meaning, and this belief has led to such speculations as the attempt to trace the vertebrates back to an annelid with a number of equivalent segments, to trace the echinoderms back to a community of worms, and to trace the polymorphic siphonophores back to unspecialized communities of hydroids.

I hope to show in another place that the acceptance of my view of the nature of heredity enables us to avoid both of these results, since it shows that special homologies may be due to heredity of one sort, and general homologies to heredity of another sort. Since corresponding cells in the homologous parts of the body of any individual are derived from closely related parts of the egg, they may be affected by similar gemmules and may thus give rise to what Darwin calls analogous variations. This form of inheritance I propose to call ontogenetic heredity, to distinguish it from ordinary inheritance from an ancestor. I shall point out, in another place, that while special homologies are due to ordinary or phylogenetic heredity, that is, to descent from a common ancestor, general homologies are, in many cases, due to ontogenetic heredity; that special homologies are old, and that *they indicate genetic relationship*, and thus enable us to trace the origin and history of animals, while general homologies are, in many cases, new, and recently acquired by secondary modification, and they do not indicate ancestry.