CHAPTER VII.

THE EVIDENCE FROM VARIATION.

Causes of variation—Changed conditions of life induce variability—No particular kind of change is necessary—Variability is almost exclusively confined to organisms produced from fertilized ova—Bud variation very rare—History of the Italian orange—The frequency of variation in organisms produced from sexual union, as compared with its infrequency in those produced asexually, receives a direct explanation by our theory of heredity—Bud variation more frequent in cultivated than in wild plants—Our theory would lead us to expect this—Changed conditions do not act directly, but they cause subsequent generations to vary—Tendency to vary is hereditary—These facts perfectly explicable by our theory—Specific characters more variable than generic—Species of large genera more variable than those of small genera—A part developed in an unusual way highly variable—Law of equable variation—Secondary sexual characters variable—Natural selection cannot act to produce permanent modification unless many individuals vary together—Our theory is the only explanation of the simultaneous variation of many individuals—This theory also simplifies the evolution of complex structures—Saltatory evolution—This is explained by our theory of heredity—Correlated variation of homologous parts—Parts confined to males more variable than parts confined to females—Males more variable than females—Summary of last two chapters.

The Causes of Variation.

CERTAIN authors have held that variability is a necessary accompaniment of reproduction; that it is determined by something within rather than without the organism, but Darwin, after long and careful study of the subject, reaches the conclusion that each variation is excited by a change of some kind in the environment. It is impossible to expose animals for any length of time to absolutely uniform conditions, and we therefore find that when careful attention is given to the subject, minute individual differences may be detected in animals which are apparently most uniform. A shepherd easily learns to recognize each sheep in a large flock, and ants are able to perceive a difference between the members of their own community and those from another nest.

It is impossible to show by direct proof that uniform conditions of life would prevent variation; but it is quite possible to approach the subject from the other side, and to show that slight external changes cause slight variability, and greater changes greater variability.

Wild animals and plants vary somewhat and have individual peculiarities, for each one is under slightly different relations to the external world from all the others, but as compared with domesticated species their conditions of life are very uniform.

A wild animal has become habituated to the circumstances under which it lives, by exposure, for generations after generations to the action of natural selection, and a host of competing animals tend to keep it in its place, but domesticated animals are protected from their enemies and competitors, they are removed from their natural conditions, and they are frequently carried from their native land and are exposed in other countries to unnatural food and climate. They are compelled to change their habits, and they are never left long at rest, or exposed for any considerable length of time to closely similar conditions, but they are carried from district to district, and their food and treatment varies considerably.

We accordingly find that, with few exceptions, all our domesticated animals and plants vary more than their wild relations. Even the goose, one of the least variable of domesticated animals, varies more than almost any wild bird, and according to Darwin, hardly a single plant can be named, which has long been propagated and cultivated by seed, that is not highly variable.

These considerations force us to conclude that variability is not a necessary contingent of reproduction, but that the production of the gemmules which give rise to variation is excited by changes in external conditions, and we must agree with Darwin that "it is probable that variability of every kind is directly or indirectly caused by changed conditions of life; or to put the case under another point of view, if it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life, there would be no variability."

When we come to examine the effect of different conditions of life we find that we cannot attribute the variability to one rather than the other. The essential thing is change, but not any particular kind of change.

Variation is frequently caused by a change of climate, but this is by no means essential, for most cultivated plants yield more varieties when cultivated in their native country than when removed to other climates. (Darwin, *Variation*, ii. p. 310.)

Change of food is often a cause of variation, but that this is not necessary is shown by the fact pointed out by Darwin, that fowls and pigeons are the most variable of domesticated animals, although their food is nearly the same as that of their wild allies, but is much less varied than that which they would find for themselves in a state of nature.

Excess of food often causes variation, yet the turkey and goose have been encouraged and tempted for generations to feed to excess, and they have varied but little.

These examples show that the character of the change is unimportant, and that variability cannot be attributed to the exclusive influence of any particular class of external conditions; that the exciting cause of variation is change, but not any particular kind of change.

Darwin quotes a number of cases to show how slight a change may result in variability.

Thus the wild horses of the pampas of South America are of one of three colors, and the wild cattle are of one color; but when the same horses and cattle are domesticated, although they are not confined, but are allowed to run at large like the wild forms, they entirely lose their similarity of color, and display the greatest diversity in this particular. In India several species of fresh-water fishes are reared in great tanks as large as natural ponds, and they are all very variable. Darwin quotes from Downing the statement that varieties of the plum and peach which breed truly by seed, lose this power, and like other worked trees give variable seedlings when grafted on another stock.

Variability almost Exclusively Confined to Organism Produced from Fertilized Ova.

The only method open to us besides the study of hybrids for observing the influence of the sexes in heredity, is by a comparison of sexual with asexual heredity. As I shall show in another place, all the various forms of asexual reproduction are so connected that we may pass from fission, or the formation of two new organisms by the splitting of one old one, to parthenogenesis, or reproduction from unfertilized ova, without finding any important gap in the series, and we may safely conclude that all these forms of reproduction are fundamentally alike.

So far as regards the physical side of the problem of heredity, the only essential difference between asexual reproduction and sexual reproduction is the absence of fertilization or union with a male cell in the one case, and its occurrence in the other case.

It is therefore extremely important to compare the two processes, in order to discover whether this physical difference is accompanied by any difference in the result. In the one case we have heredity with the male factor omitted, and in the other we have heredity with a male factor, and if there is any constant difference in the result, we may safely attribute it to this factor.

In making this comparison we are almost compelled to restrict ourselves to plants, for although asexual reproduction is not at all unusual in animals, it is restricted, with one exception, to animals which are not domesticated or reared by man, and we therefore know too little about the minute details of their life to make use of them for our purpose. The number of plants which have been cultivated and carefully observed and studied by man is very great, and as most of them multiply asexually by budding, as well as by fertilized seeds, we here have abundant material for comparative study, and it is well established by hundreds of thousands of observations that the presence or absence of the influence of the male element does have an influence upon the result of the reproductive process, and that this result is exactly what our view of the nature of the process would lead us to expect. Plants produced from fertilized seeds differ from those produced from buds only in their greater tendency to vary. Bud variations do occur, but they are very unusual, while more or less variation in seedling plants is almost universal.

As we suppose that any cell may, when excited by unfavorable conditions, throw off gemmules, the gemmules may find their way, by a sort of accident, to growing buds, and thus cause variation. We should therefore expect bud variation to occur occasionally, but very much less frequently than variation in seedlings.

This is so well known to be the case that many authors have held that there can be no variation without sexual union. Darwin has shown, however, by a long list of instances of bud variation in plants, that this is not absolutely true, and the weight of his authority has led to the almost universal acceptance of his conclusion that there is no essential difference between asexual and sexual heredity. I shall discuss this conclusion at length in another place, as I believe that the facts demand an interpretation which is somewhat different from the one which Darwin furnishes. At present I simply wish to call attention to the fact that all authorities agree that variation is almost infinitely more common in sexual than it is in asexual offspring.

Asexual multiplication in animals is restricted to the lower forms which are of little use to man, and as these forms have not been domesticated and carefully observed, our knowledge of the variability of organisms produced asexually is almost entirely derived from the study of plants.

The only instance in domesticated animals of anything like asexual reproduction is the parthenogenetic reproduction of bees, and it is therefore interesting to note that the hive-bee is the least variable of all domesticated animals (Darwin, *Variation,* Vol. ii. p. 307).

Darwin says (*Variation,* Vol. i. p. 360) that he procured a hive full of dead bees from Jamaica, where they have long been naturalized, and on carefully comparing them under the microscope with his own bees, could not detect a trace of difference.

With plants it is well known to all cultivators that forms which are highly variable as seedlings can be kept perfectly true by asexual propagation, and we have Darwin's authority (*Variation,* Vol. ii. p. 307, and Vol. i. p. 429) for the statement that while hardly a single plant can be named which has long been cultivated and *propagated by seed* that is not highly variable, the total number of instances of bud variation *is as nothing* in comparison with seminal varieties.

This contrast is the more remarkable when we recollect that in most of our cultivated plants the number of buds which develop is thousands of times greater than the number of seeds which give rise to plants. It is clear that if the chance of variation were the same in both cases the number of bud variations would be thousands of times greater than the number of seedling variations. If there were thousands of chances of seedling variation for one chance of bud variation, the number of bud varieties would still be equal to the number of seedling varieties.

The fact that with all this probability in their favor, bud varieties are very rare as compared with seedling varieties, shows that the chance of bud variation is almost infinitely small as compared with the chance of seedling variation.

While we cannot deny that variation may sometimes occur in organisms produced asexually, I think we are justified in giving great emphasis to the law that variability is almost exclusively the characteristic of organisms produced from fertilized ova.

Darwin says (*Variation*, Vol. ii. pp. 351 and 377), "When we reflect on the millions of buds which many trees have produced before some one bud has varied, we are lost in wonder what the precise cause of each variation can be." "Habit, however much prolonged, rarely produces any effect on a plant propagated by buds: it apparently acts only through successive seminal generations."

The curious history of the naturalization of the orange in Italy, quoted by Darwin on the authority of Gallesio (*Theoria della Riproduzione Veg*, 1816, p. 125), is very interesting in this connection. During many centuries the sweet orange was propagated exclusively by grafts, and so often suffered from frost that it required protection. After the severe frost of 1709, and more especially after that of 1763, so many trees were destroyed that seedlings from the sweet orange were raised, and to the surprise of the inhabitants their fruit was found to be sweet. The trees thus raised were larger, more productive and hardier than the former kinds, and seedlings were now constantly raised.

Hence Gallesio concludes that much more was effected for the naturalization of the orange in Italy by the accidental production of new kinds from seeds during a period of about sixty years than had been effected by grafting old varieties during many ages.

It is hardly necessary to give other illustrations of this law, for no one with any knowledge of the subject will be inclined to question it. It is strange that its significance has been overlooked, but this is probably due to the failure of students of the subject to perceive that it is possible to believe that the transmission of variability is the peculiar function of the male cell, and also to acknowledge that variation may occasionally occur without its influence.

Our theory that variation is caused by the transmission of gemmules, and that there is no especial arrangement for their transmission to buds or to unfertilized eggs, while there is a special adaptation which has been slowly evolved during the evolution of sex for transmitting them to fertilized eggs, gives us a simple explanation of the fact that while bud variation is perfectly possible, it is extremely rare as compared with the variability of sexual offspring.

Darwin has been led, through the study of variability, to a conclusion which is very much like the explanation which is here presented. He says (*Variation*, Vol. ii. p. 325) that "we may infer from the occurrence of bud variation that the affection of the female element through external conditions may induce variability, for a bud seems to be the analogue of an ovule. *But the male element is apparently much oftener affected by changed conditions, at least in a visible manner, than the female element or ovule.*"

Bud variation is much more frequent in cultivated plants than it is in wild ones. Very few instances have ever been observed in plants growing wild or under strictly natural conditions, and Darwin states that "bud variation is most common in plants which have been highly cultivated for a long time."

The adjustment between a cultivated organism and its artificial or unnatural environment must, in most cases, be less perfect than that which has been slowly established between a wild organism and its natural environment. We should, therefore, expect domesticated and cultivated forms to be more prolific of gemmules than wild species. The fact that bud variation, like ordinary variation, is most common in cultivated forms, seems to show that the tendency to vary is excited in buds, as it is in fertilized ova, by the influence of gemmules which are thrown off by the cells of the body under new or unnatural conditions, and we can easily understand why it should be more frequent where gemmules are abundant than in a form with few gemmules, for the chance in favor of the accidental transmission of a gemmule to a growing or nascent bud will increase as the number of gemmules increases.

Changed Conditions do not act directly, but they cause Subsequent Generations to vary.

This strange and, as I hope to show, highly significant law has been noted by many observers, and a long list of illustrations might be quoted.

As Darwin points out, it is certainly a remarkable fact that changed conditions should at first produce, so far as we can see, absolutely no effect, but that they should subsequently cause the character of the species to change.

The late Dr. Jared P. Kirtland told me that for more than forty years he tried in vain to obtain varieties from the common red cherry, but that when at last varieties began to appear the variability was very great: that after it had once become established it continued for many years with no diminution.

It is well known that when new flowers are first introduced into gardens they do not vary, although all, with rarest exceptions, ultimately vary.

Darwin, in his *Variation*, Vol. ii. p. 316, quotes the following illustrations of this law: "Mr. Salter remarks that every one knows that the chief difficulty is in breaking through the original form and color of the species, and every one will be on the lookout for any natural sport, either from seed or branch; that being once obtained, however trifling the change may be, the result depends upon himself. M. de Jonghe, with reference to pears, says the more a type has entered into a state of variation, the greater is its tendency to continue doing so, and the more it is disposed to vary still further. Vilmorin says that when any particular variation is desired the first step is to get the plant to vary in any manner whatever, and to go on selecting the most variable individuals, even though they vary in the wrong direction; for the fixed character of the species once broken, the desired variation will sooner or later appear.

Darwin gives quite a list of authorities to show that after English dogs have been bred for a few generations in India they degenerate, not only in their mental faculties, but in form.

According to Bachman, turkeys reared from the eggs of wild ones lose their metallic tints and become spotted with white in the third generation.

It will be seen from the instances which have been given that the number of generations which are exposed to the new conditions before variation is induced varies greatly. In the case given by Dr. Kirtland, fifty years elapsed before variations of the red cherry began to appear. In the case last quoted, variation appeared in the third generation, and Yarrell says that Australian dingos bred in the Zoological Gardens of England, almost invariably produced in the first generation puppies marked with white and other colors.

Sir Charles Lyell mentions that some Englishmen engaged in conducting the operations of the Real del Monte Company in Mexico, carried out with them some greyhounds of the best breed to hunt the hares which abound in that country. It was found that the greyhounds could not support the fatigues of a long chase in this attenuated atmosphere, and before they could come up with their prey they lay down gasping for breath; but these same animals have produced whelps, which have grown up, and are not in the least degree incommoded by the want of density of the air, but run down the hares with as much ease as do the fleetest of their race in this country.

It is interesting to note in this connection that a tendency to vary is strongly inherited independently of the inheritance of any particular variation. Darwin believes that this tendency to vary may be transmitted by either parent, and he says (*Variation*, ii. 325) it is certain that variability may be transmitted through either sexual element, whether or not originally excited in them, for Kölreuter and Gärtner found that when two species were crossed, if either one was variable the offspring were rendered variable.

We have already pointed out that the crossing of species is in itself one of the most efficient causes of variation, and we can hardly base upon the observations above given the conclusion that variability may be transmitted by either sex.

The fact that changed conditions do not directly produce variation, but cause subsequent generations to vary, is precisely what we should expect, according to our theory: for a change in the environment of an animal or plant must disturb the harmonious adjustment which natural selection has brought about between the cells of its body and their conditions of life. Such a change, if considerable, could hardly fail to affect certain cells unfavorably; and it would therefore cause the production of gemmules, thus inducing variation in later generations.

We can also understand how a tendency to vary may be hereditary, for if certain cells of the body vary, they will exercise a disturbing effect upon adjacent or related cells, and these, transmitting gemmules, will hand on the tendency to vary to succeeding generations.

Secondary Laws of Variation.

The law that variability is itself hereditary involves a number of secondary laws, all of which find a ready explanation in our theory of heredity.

Among these secondary laws is the law that "*specific characters are more variable than generic characters.*" Darwin has given the evidence of the existence of this law ("Origin of Species," p. 122), so it will not be necessary to discuss it, or to do more than point out that the theory of heredity furnishes an explanation of it.

The characters which are common to all the species of a genus, and which distinguish it from other genera, are, as a rule, much older than those which distinguish one species of the genus from the other species. The specific characters or features which distinguish each species of a genus from the others, are features which have appeared as new variations since the time when the various species diverged from the common ancestor from whom they inherit their common or generic characters. As specific characters are of more recent acquisition than generic characters, natural selection will have had less time to act upon the former than upon the latter. The adjustment between a specific character and its environment will therefore be, as a rule, less complete and perfect, and the cells which are involved will therefore have a greater tendency than those involved in generic characters to throw off gemmules. These characters will therefore be more variable in the descendants than generic characters.

Another law, the evidence for which is given by Darwin on page 44 of the "Origin of Species," is that "*species of the larger genera in each country vary more frequently than the species of the smaller genera.*"

When a country contains a great number of species of a genus it is generally safe to conclude that they have recently varied and diverged from each other. As the tendency to vary is in itself hereditary, and as one variation is in itself a cause of other variations, our theory of heredity would lead us to expect species which have recently undergone considerable change to show a tendency to vary still further, and we should therefore expect the species of large genera to be, as a rule, more variable than the species of small genera, although there is no reason why this rule should be absolute.

A still more interesting law is that "*a part developed in any species in an extraordinary degree or manner, in comparison with the same part in allied species, tends to be highly variable*" ("Origin of Species," p. 119).

When one species of a genus agrees with the other species in most particulars, but differs from them all in some one respect, we may conclude that the peculiar organ or feature has recently been modified. Natural selection has therefore had less time to perfect the adjustment between this part and the remainder of the body than it has had to perfect the relations between other parts, or between the same parts in the other species.

This peculiar part will accordingly be in a favorable state for the production of gemmules, and it will therefore be more likely than a part which has not recently varied to vary still farther.

Walsh has called attention ("Proc. Entomolog. Soc.," Philadelphia, October, 1863, p. 213) to what he calls the "Law of Equable Variation," which is, "*if any given character is very variable in one species of a group, it will tend to be variable in allied species, and if any given character is perfectly constant in one species of a group, it will tend to be constant in allied species.*"

This is by no means an absolute law, but simply a general rule. Darwin points out that something of the same kind occurs in domesticated races, and that in the forms which are now undergoing rapid improvement those parts or characters which are most valued vary the most.

We can readily see that circumstances which cause a certain part to throw off gemmules, and thus induce variability, in one species, will be likely to produce the same effect on allied species living under similar circumstances. We can also understand that the divergent modification which has resulted in the formation of several species or races from a parent form, will in itself be a cause of still further modification in the same general direction.

Another well-known law, of which many examples will be given in Chapter IX. is that secondary sexual characters are highly variable. In the chapter on this subject I shall show that the distinctive sexual characters of a species are usually due to recent modification. Their great variability is therefore due to the same cause as that which renders specific characters more variable than generic, and is exactly what our theory would lead us to expect.

Natural Selection cannot produce Race Modification unless the Same Part tends to vary in a Number of Individuals at the Same Time.

This argument, which seems to me to be the most important one which has ever been adduced against the theory of natural selection, was first advanced by a writer in the *North British Review* in June, 1876.

The author points out that since the chance of survival of any particular individual which is born is very slight indeed, the birth of an individual with any particular slight advantage, and its consequent superiority over its fellows, would not be sufficient to over-balance the chance of its destruction. The objection, which is purely logical, and not experimental, will be stated at length in another place. At present the fact that those who are best qualified to judge, Darwin among them, have acknowledged its great weight, will suffice to show that it is a real and valid objection, and that the foothold of the theory of natural selection would be greatly strengthened if we could show that the causes which produce variation act in such a way as to cause the same part to vary at the same time in great numbers of individuals.

According to our theory of heredity, this will generally be the case. We suppose that an unfavorable change in the environment of a particular cell causes this cell to throw off gemmules. It is plain that a change in the external world, which unfavorably affects any particular cell or group of cells in one individual, will usually affect the corresponding cells of other individuals of the species at the same time. When any particular cell is prolific of gemmules in one individual of a species, the same thing will usually be true of the same cell in other individuals, and the corresponding cell will therefore be a hybrid, and will tend to vary in many descendants.

In each of these descendants this hybrid will be composed of almost identical elements, and they will all tend to vary in the same or nearly the same manner; and as each variation causes other cells to throw off gemmules, the number of individuals which are similarly modified will tend to increase from generation to generation, and natural selection will therefore act, not on a single exceptional individual, but upon a great number, all of which are modified in essentially the same way.

If Variation is Purely Fortuitous, the Evolution of a Complicated Organ composed of Many Parts by Natural Selection demands a Period of Time which is almost Infinite.

This obvious objection to the law of natural selection has been so frequently discussed that it is unnecessary to dwell upon it at present, especially as I shall examine it in detail in another place. At present I will only call attention to the fact that a variation in any part of a complicated organ will, in itself, disturb the harmonious adjustment of other parts, and will thus cause them to throw off gemmules, and thus to induce variability in the next generation.

The fact that change is needed in any part will be the cause of variation in this part, and the time which is needed to restore all parts of an organ to a position of equilibrium will thus be almost infinitely reduced. The argument of those who hold that life has not existed upon the earth long enough for the evolution of all the adaptations of nature by the selection of fortuitous variations will thus lose all its weight.

Saltatory Evolution.

Darwin believes that the evolution of wild species is due, like the formation of many domesticated races, to very slow modification by the natural selection of great numbers of very slight and inconspicuous variations, but many other authors have given reasons for believing that this is not the case.

Many of our most peculiar domestic races have originated suddenly, and there are reasons for believing that the history of the evolution of each species is divided into periods of abrupt and extensive modification, alternating with periods of comparative stability. This subject, like those which have been briefly noted in the last two sections, will be fully discussed in Chapter XI., and I will only dwell upon it long enough at present to point out that our view of the cause of variation implies that any particular change should in itself be a fruitful source of still greater modification, so that as soon as a tendency to vary becomes established it will continue to increase until an equilibrium is again established by the natural selection of those modifications which are adapted to the environment.

Correlated Variation.

This subject will be fully discussed in the chapter on homology, but a few words upon it will not be out of place here.

Darwin, who frequently uses the term, includes under it facts which belong to two somewhat different classes. When any part varies, the organs with which it is most directly associated also tend to vary in such a way as to restore the harmonious adjustment between the various parts: and a variation in one part is often accompanied by variation in homologous parts.

These two cases shade into each other somewhat, but it will be convenient to treat them separately. The first has just been briefly examined, p. 156, and what follows relates only to the second class of cases—the variation of homologous parts.

The most familiar illustration of this law is the fact that in most bilateral organisms homologous parts on both sides of the body tend to vary together. The law holds in radially symmetrical organisms also. All the petals of a regular flower generally vary in the same manner, but there are many exceptions.

The front and hind limbs of vertebrates tend to vary in the same manner, as we see in long and short legged or in thick and thin legged races of horses and dogs.

It is stated that when the muscles of the arm depart in number or arrangement from the proper type they almost always imitate those of the leg, and so conversely the varying muscles of the leg imitate the normal muscles of the arm. There are many cases where a parent with extra fingers has produced a child with extra toes, or the reverse, and in other cases a parent with only one extra digit on one hand has had children with supernumerary digits on both hands and both feet.

In certain pigeons and fowls, especially in the trumpeter pigeon, long feathers, like the primary wing feathers, grow on the outside of the leg and on the two outer toes, and in pigeons with the feet thus feathered the two outer toes are partially connected by skin, thus showing a marked anatomical resemblance to a wing.

The various appendages which are formed from the skin, such as hoofs, horns, hair, feathers, teeth, etc., are homologous organs, and it is interesting to notice how frequently a peculiarity in one of these structures is associated with similar peculiarities in others.

Tropical sheep with long coarse hair usually have goat-like horns. Inherited baldness in man is often accompanied by deficient teeth, and the renewal of the hair in old age by a renewal of the teeth. The famous hairy Burmese had deficient teeth, and both peculiarities were hereditary. A Spanish dancer, Julia Pastrana, had a full beard and a double set of teeth, and the daily papers have recently contained an account of a man, living near Lebanon, Pennsylvania, with no hair, teeth, or sweat glands.

The homologous parts of plants often vary in the same way, as is well shown by certain compound flowers, in which the stamens and pistils closely resemble petals.

According to our view of the cause of variation we can easily see how gemmules from a cell in one hand might hybridize, and thus cause variation in the corresponding cells of all four extremities, or perhaps in the embryonic cell from which all these cells are derived, for in the same way that an animal can unite sexually either with another of its own race or with one which is somewhat less closely related to it, so I assume that a gemmule may unite with the particle of the ovum which corresponds to it, or with some other closely related particle. For example, a gemmule which is thrown off from a particular epithelial cell may simply cause modification in the corresponding cell of the offspring, or it may cause modification in a cell which is to produce this particular cell and a number of others.

If each variation is purely fortuitous the number of generations which would be necessary in order to convert a species with black hair into a species with every hair brown or with every hair red is almost inconceivable, but this difficulty entirely disappears as soon as we recognize that gemmules from one part of the parent may affect all the homologous parts of the offspring in the same way and at the same time.

Males more Variable than Females.

One of the most remarkable and suggestive of the laws of variation is that in all the higher animals a part which is confined to males, or is more developed or of more functional importance in males than it is in females, is very much more variable than a part which is confined to females or is more important in females than it is in males.

The evidence for this remarkable law will be presented at length in Chapters VIII. and IX. The existence of such a law is absolutely inexplicable without the theory of heredity, but it is exactly what this theory would lead us to expect, for an organ which is most important in one sex is most likely to be influenced in this sex by changed conditions, and is therefore more likely to form gemmules in the body of the sex where it is most important than in the body of the opposite sex. An organ which is most important in males will therefore be most prolific of gemmules in males, while an organ which is most important in females will be most prolific of gemmules in females. Gemmules which are formed in the male body are vastly more likely to be transmitted to descendants than those which are formed in the female body. It follows that an organ which is most developed or most important in males must be vastly more likely to transmit gemmules to descendants, and therefore to vary in successive generations than an organ which is most developed or most important in females.

Another law which follows from the one which has just been stated is that males are as a rule more variable than females. This law has been noticed by Darwin and others, but no explanation has ever been advanced.

Summary of Last Two Chapters.

The study of hybrids and of variation has led to the discovery of a great number of general laws, all of which are perfectly explicable by the theory of heredity, and are precisely what it would lead us to look for, although most of them are absolutely inexplicable without it, and have no place in any other hypothesis which has ever been proposed to account for the phenomena of heredity.

The study of hybrids gives us a means of analyzing to a certain extent the influence of each sex in heredity, but our experiments in this direction are limited by the fact that organisms must be very closely related in order to breed together, and parents which are very closely related must be essentially alike in everything except the most recently acquired modifications. So far as they enable us to analyze the influences of the sexes, the results furnished by hybrids agree with the demands of our theory. This furnishes an explanation of the great variability of hybrids, as compared with the pure parents, and it also enables us to understand why hybrids from domestic races should be more variable than those from wild races.

The remarkable fact that the descendants of hybrids are more variable than the hybrids themselves receives a simple explanation by our assumption that exposure of the various cells of the body to unnatural conditions is the prime cause of variability, and that it acts indirectly by causing the production of gemmules.

Some of the recorded facts regarding hybrids are so very peculiar that it would be difficult to devise better tests than they furnish of the truth of our theory. What could be more curious or more opposed to the view that the sexes play similar parts in heredity than the fact that the offspring of a male hybrid and the female of a pure species is much more variable than the offspring of a female hybrid by a father of pure blood? Darwin's pangenesis hypothesis furnishes no explanation of this most remarkable fact, and none of the hypotheses of heredity which have been proposed from time to time are sufficiently definite to have any bearing upon a concrete case like this, but our theory that changed conditions of life cause a production of gemmules, and that these are stored up in and transmitted by the male element, fits this case exactly.

The curious phenomena of reciprocal crosses, again, are just what our theory would lead us to expect, and it also furnishes us with an explanation of the fact that crossing so frequently causes reversion.

A comparison of sexual with asexual reproduction also gives us a means of analyzing the influences of the two sexual elements, for asexual reproduction is essentially reproduction with the male element left out, and the result of this omission is, as we should expect, the reduction of the tendency to vary to a minimum. At the same time that our theory explains the great rarity of bud variations, it admits of their occasional appearance, and it gives an explanation of the singular fact that bud variation is much less rare in plants which have long been cultivated than it is in wild forms.

The most remarkable of the laws of variation is the well-known law that changed conditions do not directly produce variation, but cause subsequent generations to vary. As changed conditions do not in themselves cause hereditary modification, but simply lead to the production of gemmules, we see why their effect should be manifested in succeeding generations, and we also see why variation is itself hereditary, for the variation of any particular cell will cause adjacent or related cells to throw off *gemmules, and thus to produce variation in* successive generations.

We can also understand why specific characters should be more variable than generic characters; why the species of large genera should vary more than the species of small genera; why a part developed in an unusual way or to an unusual degree should show a marked tendency to vary, and why secondary sexual characters should exhibit a similar tendency.

Unless our theory is true, what possible reason can there be why a part which is excessively developed in males should vary more than a part which is similarly developed in females alone, or why the males of our higher domesticated animals should be more variable than the females? Its power to deal with and interpret special cases of this kind separates our theory from all other attempts to explain the phenomena, and seems to show that there can be but one choice between it and any other explanation which has ever been proposed.

If we accept Darwin's view that variations are purely fortuitous, there are certain grave difficulties which must prevent us from giving the theory of natural selection unqualified acceptance as an adequate and complete explanation of the origin of species.

Natural selection can rarely lead to permanent modi*fication unless many individuals tend to* vary in nearly the same way at about the same time, and if variation is fortuitous the chance against this is very great indeed. While there is no reason to doubt that natural selection might bring *about all the changes which have led to the* formation of a complicated organ, by the preservation of fortuitous variations, if time enough were given, there is reason to doubt whether life has existed long enough to permit the evolution of existing forms in this way, and natural selection gives no account of the sudden appearance of considerable modifications, although the history of domestic animals shows us that such saltations do sometimes occur.

On the one hand we find that Darwin's assumption that variations are fortuitous involves us in grave difficulties, but on the other hand we find scarcely any evidence to show that permanent hereditary race modifications are ever directly produced by the action of external conditions, while we do find evidence for the opinion that race modifications are, as a rule, not due to this direct action, but to congenital variation.

Our theory furnishes an explanation which lies midway between Darwin's view of the origin of variation and the Lamarkian view, and thus enables us to escape both these difficulties, for it shows us how the influence of changed conditions upon an organism may give rise to congenital variation in later generations, and it also shows us why variations tend to appear at the time and place where they are needed. It also shows how a considerable modification may appear suddenly and become hereditary.

The correlated variation of homologous organs and the correlated modification of the various parts of a complicated organ are accepted by Darwin without explanation, but the theory of heredity shows us that these phenomena, the chance against the fortuitous occurrence of which is almost infinite, are due to the working of a very simple law.

When we review the ground and see how all the phenomena of hybridization and variation fall into their proper places; how the same simple explanation fits the most anomalous and exceptional phenomena as well as the more ordinary and simple cases, I think we must acknowledge that our theory is at least an approximation to the truth.

If it leads us to the discovery of truth, and thus ultimately contributes to the establishment of an explanation of the phenomena of heredity, its final acceptance in its present form is a matter of little moment. That it is a great advance beyond all the attempts which have been recorded seems obvious, and an examination of the ground which it covers certainly seems to show that it is a step in the right direction.