

## CHAPTER XIV

## VARIATION

## I. NORMAL INDIVIDUAL VARIATION

HEREDITY is the transmission of the physical nature of the parent to the offspring. We have seen that this transmission affects the whole organism, and extends to the most trifling details; and we also know that it is never complete, and that the offspring and parent are never identical, but that the former always differs more or less from the latter. These differences give rise to the phenomenon of *variation*, which thus forms *an integral part of heredity, for the latter always includes the former*.

A theory of heredity must therefore include a theoretical substantiation of variation, such as I will now attempt. Why is the offspring never an exact duplicate of its parent, even when it possesses but one parent, as is the case in parthenogenesis and reproduction by budding? And what forms the basis of the constant '*individual variations*' which, after the precedent of Darwin and Wallace, we regard as the foundation of all processes of natural selection, and as the means which rendered possible such a rich development of organic forms of the most diverse kinds on the face of the earth?

Darwin himself considered the difference between parent and offspring as due to the diversity of external influences, and I was essentially of the same opinion formerly, and stated that 'all dissimilarities of organisms must depend upon the individuals having been affected by dissimilar external influences during the course of the development of organic nature.'<sup>\*</sup> At that time I attributed to the organism the virtual 'power of

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<sup>\*</sup> 'Studien zur Descendenztheorie,' II., Leipzig, 1876, p. 304. English edition, 'Studies in the Theory of Descent,' translated and edited by R. Meldola, with a prefatory note by Charles Darwin, London, 1882, Vol. II., p. 677.

giving rise by multiplication only to exact copies of itself'; but this capacity, in my opinion, did not produce accurate results, because the organism is also capable of reacting to external influences, and may therefore deviate from the inherited tendency in one or another direction, according to the nature of these influences.

Variation would consequently not depend upon a special force existing in the organism, but would simply be the result of external influences, which, either directly or indirectly, are capable of preventing the organism from keeping strictly to the inherited course of development.

Although I still consider this view to be in general correct, the origin of individual variation, on which the transformation of species is based, cannot be deduced so easily from the action of dissimilar external influences as seemed possible when I wrote the passage quoted above. I have discussed this question in full on a previous occasion, and will here only briefly refer to it.\*

At that time, no one supposed that any difference existed between the modifications which may be brought about in the soma and those which proceed from the germ-plasm. Since then, however, we have been compelled — at least in my opinion — to consider that only those variations which are '*blastogenic*,' and not those which are '*somatogenic*,' can be transmitted. We can no longer regard the direct influence of external impressions on the soma as a means of producing hereditary individual variations. It therefore remains to be seen what is the origin of these variations, upon the existence of which we imagine the entire development of organic nature to depend.

This development could be accounted for most easily on Nägeli's hypothesis, according to which the idioplasm is so constituted, that in the course of generations it could exert a definite and regular transforming influence upon itself, and by this means could convert one species into another. Many reasons may, however, be urged against this hypothesis. In the first place, development by internal forces only is contradictory to the close adaptations of organisms to their conditions of life; and secondly, we should not make use of unknown

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\* Cf. 'Die Bedeutung der sexuellen Fortpflanzung für die Selectionstheorie,' Jena, 1886. English Edition, Oxford, 1889, p. 255.

forces for the explanation of natural phenomena until we have proved that the known ones are insufficient.

Such a phyletic principle of development would naturally not produce ordinary individual variations, but would lead to modifications *which affect all the individuals of a species in the same manner*. All the individual modifications which actually exist would, in that case, have to be considered insignificant in phyletic development; and in plants Nägeli actually looked upon them to be transitory, and not hereditary habitat-modifications ('Standorts-Modificationen'). But this view is opposed by the transmission of an immense number of individual differences in man and animals.

If we recognise that the processes of selection are the chief factors in organic development, we must attach the greatest importance to these hereditary differences in individuals, and must try to discover their origin.

Brooks accepts this view, and has propounded a theory of heredity which is based on Darwin's hypothesis of pangenesis, and according to which variation is in the main dependent on sexual reproduction.\* Variability, in his opinion, is caused by every 'gemmule' of the spermatozoon uniting with 'that particle of the ovum which is destined to give rise in the offspring to the cell which corresponds to the one which produced the germ or gemmule. . . . When this cell becomes developed in the body of the offspring *it will be a hybrid, and it will therefore tend to vary.*' Brooks, moreover, assigns different functions to the two kinds of germ-cells, and represents them as being charged or filled to different degrees with 'gemmules,' the egg-cell containing a much smaller number than the sperm-cell. In his opinion the egg-cell is the conservative principle which controls the transmission of purely racial or specific characters, whereas the sperm-cell is the progressive element which causes variation.

Brooks has ingeniously advanced every argument which could be brought forward in favour of his theory, but I doubt whether he still holds to it, for many new discoveries have since been made which contradict it. Although the view that 'acquired' characters are not hereditary is not universally admitted, it has

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\* W. A. Brooks, 'The Law of Heredity: A Study of the Cause of Variation and the Origin of Living Organisms,' Baltimore, 1883.

been accepted by Brooks; and the assumption of a diversity of the hereditary substances contained in the male and female germ-cells, on which his theory is based, is rendered untenable if it is recognised that the idants of both cells remain precisely the same as regards number and quality during the process of amphimixis. It will not, therefore, be rash to conclude that the few observations which seem to be in favour of the dissimilar effect of male and female germ-cells are not convincing, although we may not be able at present to explain them fully. To these belong certain rare cases, which have, perhaps, not been very accurately observed, and possibly form exceptions to the rule that hybrids of two species are *identical*, whether the father or mother belonged to the species A or B.

If we are forced to reject the assumption of the dissimilar action of the two germ-cells, together with that of an internal force of transformation, we can only refer hereditary individual variability to the inequality of external influences; and it then remains to be seen how such influences can produce *hereditary* differences if *somatogenic* modifications are not hereditary: for external influences act directly, and often exclusively, upon the *body*, and not on the *germ-cells*.

In a former essay I have already attempted to show that the constant occurrence of individual variability and the continual transformation in the intermixture required by selection is brought about by amphimixis, although it is not the primary cause of this variability; and that the accomplishment of sexual reproduction is even based in almost all the known organic forms on this necessity of preserving and continually remodelling the hereditary variability of individuals. I am convinced that *the two forms of amphimixis—namely, the conjugation of unicellular, and the sexual reproduction of multicellular organisms—are means of producing variation*. The process furnishes an inexhaustible supply of fresh *combinations* of individual variations which are indispensable to the process of selection.

Hatschek\* has contested this view of the significance of sexual reproduction, and states that 'transformations of species occur far too rarely to admit of their explaining such an uninterruptedly active process as sexual reproduction.' It seems to me, how-

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\* B. Hatschek, 'Lehrbuch der Zoologie,' Jena, 1888, p. 10.

ever, that he has overlooked the fact that the *transformation* of a species, as well as the *preservation* of its constancy, are based upon natural selection, and that this is incessantly at work, never ceasing for a moment.

From what was said in the chapters on the struggle of the determinants of the two parents in ontogeny, and on the 'reducing-division' of the germ-plasm which is indispensable in amphimixis, it follows that by means of the latter process fresh combinations of the possible variations in a species must constantly be produced. On the one hand, the germ-plasm of a new individual produced by amphimixis never receives more than half the ids of each parent—and these are differently selected and arranged in each case; and on the other, the co-operation of the ids of both sides would not always strike an average in all parts of the new organism, but each part would resemble that either of the father or the mother in proportion to the number and controlling force of the individual homologous determinants; the resultant of the co-operating forces may be different in different parts.

Although the process of amphimixis is an essential condition for the further development of the species, and for its adaptation to new conditions of existence amongst the higher and more complicated organisms, *it is not the primary cause of hereditary variation*. By its means those specific variations which already exist in a species may continually be blended in a fresh manner, but it is incapable of giving rise to new variations, even though it often appears to do so.

When it first occurred to me that sexual reproduction was necessary to produce the variations required for the action of selection, I imagined that its influence upon the germ-plasm was still more powerful. Since all differences—even the qualitative ones—are ultimately of a *quantitative* nature, and as the union of the primary constituents of the parents may either strengthen or weaken a 'character,' I imagined that the combination of very strong primary constituents for the same part in both parents would not only cause the part to reappear especially markedly in the child, but would also double the strength of the primary constituents of the part in the germ-cells of the child; and thus the continued intercrossing of offspring in which this part is strongly developed, might cause it to be increased more and more, so that it exhibited far more than an ordinary individual

difference. If we suppose this process to go on in the various parts of the body, the transformation of a species would thus be accounted for.\*

The production of races by artificial selection appears, in fact, to be in part due to such an accumulation of parental 'characters'; but I shall show later on that it is not accompanied by an actual *variation* of the determinants, which alone could gradually lead to a transformation of the species. We know that the paternal and maternal idants do not fuse in the process of amphimixis, and the immense number of cases of perfect transmission proves that the determinants of both sides undergo no alteration by being brought together. The modification of the determinants is a process which is not directly connected with sexual intermingling, but follows its own course, and must be due to special causes.

This is made still clearer if we reflect that the lower organisms — *e.g.*, sponges and polypes — must possess a very small number of determinants compared to those in higher forms, such as birds and mammals. *The number of determinants in an id of germ-plasm has therefore increased considerably, and even enormously, in the course of phyletic development.* A single peacock's feather may possibly be controlled by as many determinants as an entire polype. Amphimixis alone, however, could never produce a multiplication of the determinants.

*The cause of hereditary variation must lie deeper than this; it must be due to the direct effect of external influences on the biophors and determinants, which I imagine to take place in the following way.*

The entire substance of the earliest organisms must have consisted of equivalent biophors, the nucleus and cell-body not having yet become differentiated. In these lowest forms, whether they exist or not at the present day, the perfect constancy of the composition of the body may occasionally have been disturbed by external influences of different kinds, and these modifications must have been preserved, as they persisted in the two parts resulting from reproduction by binary fission.

When the morphoplasm and idioplasm subsequently became differentiated, and the latter was enclosed in the nucleus as the

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\* Compare my essay 'Die Bedeutung der sexuellen Fortpflanzung,' *Jena*, 1866, p. 40. English edition, Oxford, 1889, p. 279.

hereditary substance and controlled the body of the cell, variations which had been produced solely by the direct action of external influences on the *body of the cell*, could no longer be transmitted to the offspring as an inheritance, for they were dependent on the part of the morphoplasm in which they originated, and did not pass into the idioplasm, which comprises all the primary constituents of the species. Every hereditary variation must therefore have originated in the nucleus, even in unicellular organisms — which in this respect therefore resemble the Metazoa and Metaphyta, the sole difference being that in the unicellular form we are concerned with the characters of one cell and not of many. In many unicellular organisms — *e.g.*, the higher Infusoria — the cell-body is very highly differentiated: it may possess a complex arrangement of cilia, undulating membranes, trichocysts, and flagella, each having a definite position in the body, — as well as a protective case of a definite form, with a lid capable of being closed; the animal, moreover, is capable of reconstructing all these parts should any of them become injured. We are therefore forced to admit that this minute organism must have a centre in which the latent germs for all these structures slumber, and from which reproduction may take place. This centre is the nucleus, and modifications of the nuclear matter can alone give rise to transformations of a *hereditary* nature in the cell-body.

The fact that species have remained sharply defined as long as we have known them, proves that these transformations occur neither easily nor rapidly.

The germ-plasm of multicellular forms is obviously also very constant, and the biophors constituting it are capable of nourishing themselves and of growing, so as to furnish exact duplicates of themselves when they divide. We could not otherwise understand how it would be possible, in spite of the enormous growth of the germ-plasm from one generation to another, for the specific characters, and even the most minute individual characteristics, to be preserved through so many generations.

The difficulty with which the germ-plasm becomes changed is not so clearly proved by the instances of constancy displayed by some species of ancient Egyptian animals — the ibis and crocodile — through thousands of years, which were formerly advanced by Nägeli and myself for this purpose. It may be objected that these species were always subject to the

control of natural selection, which eliminated every case of deviation from the perfectly adapted form. If insignificant individual characteristics which are of no use to the species can, however, be preserved in the human race for several generations, this must be owing to the fact that the corresponding determinants have very little tendency during their growth and multiplication to suffer any marked variation, and that, on the contrary, they reproduce exact duplicates of themselves. I was therefore quite justified in supposing that the germ-plasm possessed a great power of remaining constant.\*

We can none the less avoid assuming that *the elements of the germ-plasm—i.e., the biophors and determinants—are subject to continual changes of composition* during their almost uninterrupted growth, and that *these very minute fluctuations, which are imperceptible to us, are the primary cause of the greater deviations in the determinants, which we finally observe in the form of individual variations.*

The assumption that such very minute fluctuations occur, naturally follows from the impossibility of a complete uniformity as regards nutrition existing during growth; and in fact, though underestimating its importance,† I formerly made this assumption, in correctly supposing that the influences producing these fluctuations 'are mostly changeable, and occur sometimes in one and sometimes in another direction.' I had not then taken into consideration the fact that the fluctuations accumulate in consequence of the process of amphimixis. If a single determinant increases to a hundred thousand during the multiplication of the germ-cells of an individual, it is not likely that the nutrition of all these determinants during the process will be absolutely the same in strength and kind. If this is not the case, minute differences could not fail to appear in the subsequent determinants. These minute fluctuations may undoubtedly again disappear, as I formerly assumed, provided that the modified determinant is exposed to counteracting influences, and *alone* they are quite incapable of producing an individual variation of any perceptible character; but they may become cumulative. For the germ-plasm always consists of a large number of ids, each of which contains one of the homologous determinants in

\* Cf. my essay 'Die Bedeutung der sexuellen Fortpflanzung,' Jena, 1886, p. 28. English edition, Oxford, 1889, p. 271.

† *Loc. cit.*, p. 272.



question, and the co-operation of all of these determines the character. *A hereditary individual variation will therefore arise if many of the homologous determinants vary in the same way.*

We can thus understand the process of *doubling* of the determinants, which must have occurred repeatedly, as more complicated structures arose in phylogeny. More abundant nourishment would cause a determinant to grow and multiply more rapidly, and if the first multiplication occurs before the 'reserve germ-plasm' for the next generation has become separated off, this double determinant will be permanently retained by the species. The corresponding part of the body, however, will only display a perceptible variation when the majority of the homologous determinants have become doubled.

Minute fluctuations must thus continually occur in the composition of the biophors and determinants. Their variability depends on the same principle as the systematic disintegration of the determinants in the germ-plasm, and is due to the *dissimilar composition of the elements of the growing substance*. If the determinants consisted of masses which were all exactly alike, inequality of nutrition could never transform determinant A into A<sub>1</sub>:—it could only alter its rate of growth. They are, however, composed of biophors of different kinds, which react dissimilarly under different conditions of growth. This renders possible a disarrangement of the proportional numbers of the different biophors in a determinant, and consequently also the variation of the latter. It is therefore quite conceivable that all the qualities of a cell are not affected by these influences, but that only certain of them vary, and that only a few amongst a large number of similar determinants need become modified.

The facts already mentioned with regard to the *climatic variation of butterflies*, prove that such an alteration can actually occur. In these insects the determinants of certain coloured wing-scales are slowly changed in the course of generations, in consequence of the rise in temperature of the climate, and thus the colour of the scales becomes considerably modified. Such cases of conspicuous variation are not often met with; all species of butterflies, at any rate, are not affected in this way by changes of temperature, and those that are thus influenced do not display the variation in all the different kinds of scales. This indicates that the determinants have a strong tendency to remain constant,

and that the deviations to which they are subject on account of inequalities of nutrition are as a rule so infinitesimal that their effect is unnoticeable.

These deviations are nevertheless of great significance, *for they form the material from which the visible individual variations are produced by means of amphimixis together with selection*; and new species arise by the increase and combination of these variations.

The hypothesis that the germ-plasm consists of ids is quite indispensable in this case. Every determinant is represented in the germ-plasm as many times as there are ids in the latter, for every id contains all the kinds of determinants. The determinant N, for example, is represented a hundred times if the germ-plasm consists of a hundred ids. Most of these ids must differ slightly from one another, for in the course of generations they are continually brought together in new combinations by the process of amphimixis. On the occurrence of this process, however, the diversity of the ids persists, even if we go back to the origin of the multicellular forms, or of the unicellular ones from the primordial organism. A condition in which all the ids could be considered similar is never found; in fact, as already stated, *the dissimilarity of individuals must be traced to the primordial organism*, at a period when neither the process of amphimixis nor idioplasm had come into existence, and in which every individual organism derived its individuality directly from the dissimilarity of external influences. From these organisms the dissimilarity was transmitted to the unicellular forms, which cannot all have originated from one primordial organism, but each species must have arisen polyphyletically from a large number of similarly modified organisms. This point has often been misunderstood, and I have been asked to explain, for example, how the adaptations of flowers, fruits, and seeds in Phanerogams, could have been derived from a combination of characters acquired by the shapeless primordial ancestors. *The characters were not inherited from the primordial beings, but variability, or the dissimilarity of individuals.*

We might, however, be inclined to believe that external influences must affect *all* homologous determinants of a germ-plasm in the same way, and must cause them to vary; but this would be erroneous.

Since reproduction is connected with amphimixis in the

multicellular organisms, and the latter process is never entirely wanting in any species, the germ-plasm of these forms consists of many ids from different sources,—one half of them being derived from the father, and one half from the mother, each half, again, containing ids from the grandparents in varying proportions; the ids of the grandparents, moreover, are derived from one, two, or even three great-grandparents, and so on. As I have shown above, the proportions in which the individual ancestors may be represented by ids may vary very much; and consequently the germ-plasm of different individuals, even when they are closely related, must always differ.

Each id contains all the determining elements of the species, but in a manner peculiar to the individual. If a determinant  $N$  differs slightly in every id, it will also vary a little during growth if exposed to modifying influences; so that, for example, the determinant  $N$  may remain unaltered in id  $A$ , while  $N^1$  varies in  $B$ . On the other hand, the modifying influence of nutrition may very likely be slightly different in  $A$  and in  $B$ , and may produce a variation in  $N$ , while  $N^1$  remains unaltered. Sufficient factors would thus be present to cause a variation of one or more homologous determinants in certain, but not in all ids. In the only carefully observed cases of blastogenic variation, due to the direct influence of external conditions,—viz., those of the climatic variations of *Polyommatus phlæas*,—it is evident that the influence of temperature was not quite uniform. Some of the captive Neapolitan specimens of this species are darker and others lighter, although they were raised in a room under conditions as nearly the same as possible; and in those caught in the neighbourhood of Naples, the amount of black-dusting—the character modified by the climate—varied considerably. The same influences, even when they act during many successive generations, do not necessarily cause the individuals of a species to vary to the same extent; and I account for this by the fact that the ids of every animal contain different variants of a particular determinant  $N$ , some of which are more susceptible to heat than others. The germ-plasm, as a whole, will vary to a greater or less extent in proportion to the number of the determinants which are more or less variable.

Many enigmatical points, however, still remain. Thus the transformation by heat of many of the original reddish-gold wing-scales of *P. phlæas* into black ones does not occur evenly,

so as gradually to change the entire reddish-gold upper surface of the wing into black; but certain parts first become darker, and then other adjacent ones, the whole surface being blackened only in the very darkest specimens. The margin and base of the wing first turn black, and the change then spreads slowly towards the middle, which, however, remains unaltered in most individuals. Since we must suppose that scales of the same colour arise from similar determinants, why are they affected to such an unequal extent by the modifying influence of heat?

The explanation previously used can, however, be applied in this case also.

It was shown in the chapter on reversion that although new specific characters are produced by the modification of certain determinants or groups of determinants, this modification never affects the homologous determinants in *all* the ids of the germ-plasm simultaneously. It must, on the contrary, be assumed that variation affects only a small majority of modified determinants at first, but increases by the selection and preference of the most modified individuals, until finally a predominant majority of all the ids contain modified determinants.

This evidently implies that *new and old specific characters are respectively represented by a small and a large majority of modified determinants*. If this statement be applied to the case of *P. phlæas*, we obtain a principle by the aid of which the dissimilar effect of heat on the determinants for the middle and the margin of the wing respectively may be understood. It is very improbable that the surface of the wing of the brown ancestral form of *P. phlæas* has changed uniformly into reddish-gold, and it is much more likely that a lighter spot in the middle became modified first and took on a reddish-gold colour, in consequence of sexual selection, and that this then gradually extended towards the margin. If this were so, the reddish-gold scales of the centre must be represented in the germ-plasm by a greater majority of homodynamous determinants than are those at the margin: and in this way we can understand why the black-dusting of the wings affects the sides first, and the middle last of all. This must be so if the old 'brown' determinants under the influence of heat give rise to black scales more easily than do the 'reddish-gold' ones. Whether this explanation be correct in this particular case or not, it is nevertheless true that *the diversity of the extent to which the determinants for the same*

*character are represented in different regions of the body, affords us a principle by which we can understand the unequal effect produced by similar modifying influences upon various regions of the body.*

Even though it can no longer be doubted that climatic and other external influences are capable of producing permanent variations in a species, owing to the fact that, after acting uniformly for a long period, they cause the first slight modifications of certain determinants to increase, and gradually affect the less changeable variants of the determinants also, the countless majority of modifications is not due to this cause, but to the processes of selection. The question then arises as to the origin of variations which are sufficiently considerable for natural selection to act upon them. External influences at first produce only very slight fluctuations in the determinants — presumably not only in some, but in all; *a continual supply of the most minute variations of the different determinants will thus always be present.*

I do not, however, believe that variations, as we perceive them, are the direct result of these minute fluctuations on the part of individual determinants: they can only *be produced by the accumulation of a large number of fluctuations of this kind.* This is an immediate consequence of the theory. Since the germ-plasm consists of many ids, each of which contains the same number of homologous determinants, and as, moreover, any character is the result of the interaction of all its homologous determinants, the variation of a single determinant would be imperceptible; a character can only be modified to an appreciable extent when a majority of the determinants are equivalent, or at any rate are similarly modified.

In my opinion, a variation of this kind is produced by solitary homodynamous determinants in different ids and individuals being brought together in *one* germ-plasm by means of the processes of 'reducing division' and amphimixis, so that they can thus form a majority.

I will illustrate this by a simple example. A small brown European butterfly, *Lycæna agestis*, Hb., has a small black spot formed by a few scales in the centre of the wing. Let us suppose that this spot is controlled by a *single* determinant F, and that the germ-plasm in this species contains a hundred ids, and consequently a hundred determinants F; and that, in

consequence of a change in nutrition, some of these determinants F in different individuals constantly vary in such a manner that if they were in the majority in the germ-plasm they would give rise to a white spot instead of a black one. It will sometimes happen that they are in the majority; for, in consequence of the process of amphimixis, the modified determinants F may become accumulated in the course of generations, so as to exceed fifty in one or more individuals. The black spot will then turn white, and among thousands of individuals belonging to this species some will exhibit this variation.

The subsequent course of the phyletic development of this white spot depends upon its *physiological value* to the species. Even if it is only of slight importance, it will gradually come to be possessed by an increasing number of individuals, and will ultimately be transmitted to *all* of them: *i.e.*, it will become a specific character. This extension could hardly occur without amphimixis; for by its means any minority of determinants F<sup>1</sup>, wherever produced, may accumulate so as to constitute a majority; and otherwise they could not have been effective, since a minority could never have produced a white spot.

This example was selected because it is based on facts. A variety of *Lycæna agestis* actually exists which possesses a milky-white spot on each of the four wings in the place of the black one; it is known as the variety *artaxerxes*, and occurs in the north of England. It is immaterial whether sexual selection or a protective resemblance has caused the dominance of this modification.

Many variations of one species or another are merely due to the modification of a few or a large number of determinants; changes in the colour of individual parts or of the whole body may occur without an accompanying increase in the total number of determinants of the germ-plasm, but, on the other hand, as was shown above, many modifications do result from an *increase in their total number*. We have already seen that the doubling of a determinant of the germ-plasm may be referred to the influences of nutrition, and no difficulties therefore arise in the application of the principle just propounded to the multiplication of the determinants. The important modifications in species, including all enlargement of parts and higher differentiation of organs, must be connected with this increase: and the accumulation

of double determinants of single ids, as well as their purely qualitative modifications, may be increased by means of the 'reducing division' and amphimixis, till the variation becomes perceptible, and natural selection comes into play.

The 'increase' of a character derived from two parents which merely possessed it to a slight extent, is an entirely different matter. A *fusion* of the primary constituents of a character common to both parents, and a consequent increase of these primary constituents, such as was hitherto supposed to take place, evidently do not occur: such an assumption is contradicted by ordinary experience; for if the primary constituents of the parents could accumulate in this way, all parts of the offspring must be twice as large, or at any rate larger than, those of the parent, and this is not the case. If, however, it were maintained that it is merely a question of the differences in the primary constituents, and that the offspring receives half the sum of the characters of the two parents, it could be replied that this might be approximately true in some cases, but no explanation would be given as to how an increase of a characteristic can occur, and may even be produced artificially by pairing animals which exhibit a certain tendency to vary in the desired direction. If two animals are paired which possess the character  $a$  in the degree  $2a$ , the offspring would contain  $\frac{2a + 2a}{2}$  — *i.e.*,  $2a$ , and no increase would be produced. Moreover, the real meaning of the term 'halving' would then remain perfectly vague. Hensen\* thought that 'the effect of transmission was to halve the characters of the parents,' since 'a similar whole can only result from two equal half-transmissions.' I believe that this is to a certain extent true, but not in the sense which would entail the halving of an *indivisible* primary constituent.

The solution of the problem is to be found in *the multiplicity of the ids and determinants*, and in distinguishing carefully between the vague idea of the 'character' and the definite one of the *determinate* or hereditary part. Each determinate is controlled by as many determinants as there are ids in the germ-plasm; but half the ids of each parent, together with half the determinants of *every kind*, are removed from the germ-plasm by the reducing division of the germ-cell. Half the primary constit-

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\* V. Hensen, 'Physiologie der Zeugung.'

uents are, however, not removed in this process; on the contrary, the occurrence of 'pseudo-monogenic heredity' proves that every parent-organism transmits the whole of them to the offspring; *every primary constituent is, however, represented by only half the number of determinants.*

From this theoretical basis, the results arrived at by breeders are easy to understand. '*Like begets like,*' is their chief maxim, and this is true whenever two individuals are coupled which possess a certain character as an inheritance transmitted through a long series of generations. For such a character must be represented by homodynamous determinants in the great majority of ids in the germ-plasm; and as it consequently will not be entirely removed from either half of the latter by the reducing division, it will in most cases be represented in a majority of ids in the offspring.

The idea that the '*increase*' of a 'character' can be produced simply by crossing, is due to an inaccuracy of expression. '*Like begets like,*' but not something else; and in this respect theory and practice agree. It is theoretically inconceivable that precisely the same part—that is to say, the same determinate or group of determinates—may be increased merely by the pairing of parents possessing it. If, for instance, two individuals of *Lycæna agestis* pair, and each of them possesses a white spot instead of a black one, in the centre of the wing, none of the offspring could exhibit a spot twice as large as, or even any larger than, that of the parents. For the spot is controlled by one or more homologous determinants, and if those of the white variety are in the majority, the spot will be of this colour; but the adjacent determinants cannot thereby become modified. The spot can at any rate only become pure white in case it was previously merely grey, owing to the relatively larger number of 'black' determinants which took part in the control of the spot in the parents having now been completely excluded from the control of the cells by a preponderating majority of 'white' determinants.

The term 'quality' or 'character' ('Eigenschaft') is the real cause of confusion in this instance. In the Introduction to this book I pointed out that this term may have several different meanings with regard to heredity. *Whiteness* in plumage, for example, is a 'quality' which a breeder tries to obtain by always selecting the whitest bird for breeding purposes. From a breed



of blue pigeons, for instance, a bird with a white head is paired with another possessing a white tail, and in this way some young may be obtained with white heads and tails. The 'qualities' of the white head and white tail are here, therefore, combined. The feathers of both parts of the body, however, have their own determinants; and in this cross the process which took place in the idioplasm was not the accumulation of homologous determinants, but the acquisition of a majority by the 'white' determinants for the feathers of the head and tail over the 'blue' ones. This is, therefore, not a case of the summation of like with like, but a victory of similar determinants in different parts of the body.

Surprise has often been expressed at the case, mentioned by Darwin, of two crested canaries which produced young none of which possessed larger crests, while many, at any rate, were bald. As Darwin himself pointed out, the crest in birds is due to a sparser covering of feathers on the head, and this peculiarity may be increased so as to result in baldness in the offspring. This is also an instance of the increase of a 'quality,' but only that of baldness, and not of the crest which is valued by the breeder. In terms of the idioplasm, this may be explained in the same way as was done with regard to the increase of the character of whiteness in pigeons. It is due to the arrangement of 'bald' determinants,— if I may use such an expression,— some of which are derived from the father and control the region *a*, the others from the mother controlling the region *b*. In the father the region *b*, and in the mother the region *a*, still possessed a 'feather' determinant; in the offspring the 'bald' determinants for both regions were accidentally brought together owing to the reducing division and the subsequent amphimixis. It is shown by our theory that bald-headed offspring need not invariably result in such a case; and, as a matter of fact, all the young birds did not exhibit this peculiarity.

The increase in the number of feathers in any particular part, such as has occurred, for instance, in a fantail pigeon, is another case of this kind. The tail of this bird consists of about forty quill-feathers, instead of twelve, as in the original form; and the breed has undoubtedly been produced by artificial selection, those pigeons always being chosen for breeding purposes which possessed an extra feather in the tail. The young frequently,

or at any rate in some cases, would thus exhibit more tail-feathers than either of the parents. But this would not by any means be an 'increase in the force' of a 'character,' but simply *an increase in the number of new feathers in the individual*. Let us suppose that the male bird possessed two extra feathers which were situated at  $a^1$  and  $d^1$  between the normal feathers  $a$  and  $b$  and  $c$  and  $d$ , and that the mother had two supernumerary feathers in the positions  $f^1$  and  $h^1$ : a majority of the determinants for the extra feathers of the two parents might then be united in the germ-plasm of one of the offspring, so that the latter would possess all the four new feathers. This 'increase' in the character of additional feathers in the tail, therefore, depends upon the constitution of the germ-plasm, and can consequently be transmitted to the next generation.

This example clearly shows that *all really new structures are not merely the result of transmission, but are due to the variation and frequent multiplication of the determinants*. The mere extension of a 'character' over larger regions or the whole of the body, even if we choose to speak of it as an 'increase,' may be produced by pairing individuals which possess the desired 'character' in different parts. But an increase which is connected with the formation of new structures, and consequently with the *multiplication of the determinants in the germ-plasm*, can never be produced by such means alone. When this results, the cause of the modification must be the *variation of the determinants themselves*.

Thus in the case of the fantail, a new feather can never be produced by transmission alone: the offspring can merely possess new combinations of such feathers as were present in the parents. All really new structures can only originate in a previous modification of the germ-plasm.

Let us now take an example from among *sexually dimorphic* forms, in which we are quite certain of the phyletic modification, apart from the complication arising from the existence of sexual double-determinants. *The long tail-feathers of male humming birds* have arisen by a gradual lengthening of the ordinary tail-feathers, such as are possessed by the females at the present day. As already remarked, this lengthening is the result of a considerable multiplication of the determinants which give rise to the feather: the process of lengthening implies that variations in the ids which possessed a larger number of

determinants than those of the original feather were exposed to selection. It was stated above that fluctuations in the structure of the determinants, caused by inequalities of nutrition, may also be produced in consequence of their more rapid growth and earlier division. If, then, certain determinants for the feather of the original form underwent division at an early stage in individual males, so that their number became doubled, a lengthening of the feather must have resulted as soon as the doubling occurred in the majority of the ids. The majority need not have appeared in one individual from the first, but, like every other simple variation of a determinant, it may have originated sporadically, in separate ids of different individuals, and have become increased by the repetition of the process of amphimixis in every generation. *The modification would become apparent* and the processes of selection could take place, as soon as these ids had attained a majority in any individual.

## 2. Pathological Variation

The above theoretical explanation of the 'increase' of a character possesses the important advantage of *accounting for the sudden appearance of more extensive variations*. If more abundant nourishment can cause the doubling of a determinant in the germ-plasm, it is possible, and even probable, that many or all the contiguous determinants for the same feather will become doubled. The feather must consequently *at once* increase to twice the size. Doubts have often been justly raised as to whether the process of sexual selection at first produces very slight variations, which would scarcely be noticed and preferred by the selecting sex. We learn from the doctrine of determinants that it is unnecessary to take such minute variations into account, and that more extensive ones may suddenly arise directly from the germ-plasm.

The doubling by division, not only of biophors and determinants, ids and idants, but even of *individual groups of congruent determinants*, such as must be contained in the germ-plasm in the form of primary constituents of any organ—*e.g.*, a feather—is theoretically possible. But this is one of the more special questions, the details of which may be reserved for subsequent investigations. I think it is highly probable that many *congenital deformities*, such as the occasional doubling of the tarsus in the hind-limbs of beetles and other

insects, are due to the doubling of a group of determinants, and perhaps the much-discussed and debated problem concerning *supernumerary fingers and toes in human beings* may be explained in a similar way. There is nothing impossible in the assumption that the latter phenomenon is due to reversion 'to an extremely remote, lowly-organised, and many-fingered ancestor,' for we know of other cases of reversion to very distant ancestral forms. But in none of the reliable instances does reversion to ancestral characters extend through such an enormous lapse of time or immense number of generations as must be assumed in this case. The striping on mulcs points back to an early equine ancestor, and we are led to the conclusion that at the present day the germ-plasm of horses and asses still contains solitary 'zebra' determinants. Reversion may occur to yet more remote ancestors of the modern horse, — even to those possessing three toes; but cases of reversion to still earlier ancestors can hardly be proved with any degree of certainty; nor is it probable, from a theoretical point of view, that any groups of determinants of such extremely remote primitive mammals should have been preserved in the germ-plasm of human beings. Moreover, it is not at all certain that the primitive mammals possessed more than five fingers and toes; and it would be necessary to go back to much more remote ancestors before obtaining any support for the explanation of human polydactylism given by Darwin, and formerly accepted by Bardeleben, Wiedersheim, and others.

Not only is there no firm foundation for this latter assumption, but there appear to me to be very weighty reasons against it. We must not, in the first place, overlook the fact that these primitive ancestors did not possess 'human' fingers; supernumerary fingers are, nevertheless, real fingers, and though they are not always perfect, they are furnished with the form of nail typical of the human finger, and not with claws. In my opinion, we are not justified in assuming that such a supernumerary finger is represented in the germ-plasm by a group of determinants derived from the primitive ancestor, and that this group has in the meantime become transformed into the type of the human finger.

Apart from polydactylism, cases of the doubling of the limbs are known, which, from their nature, cannot be looked upon as atavistic: insects, for example, have never possessed a double tarsus. There must, therefore, be another way in which this doubling might originate.

The sudden appearance of polydactylism and its great tendency to transmissibility can, moreover, be easily understood if we suppose that excessive local nutrition has caused the group of determinants in question to become doubled.\* For when this doubling has once occurred in several ids in the germ-plasm, it must be capable of being transmitted on account of the continuity of the germ-plasm; and the degree of certainty with which this will take place will increase as the number of ids in which it has occurred becomes greater. I am entirely of Ernst Ziegler's opinion that polydactylism is due to a germ variation: this *must* be so whenever it is hereditary, for it would not otherwise be transmissible.

In this way we can also understand why polydactylism, after it has once arisen and has been transmitted through several generations, may finally disappear; for at every fresh 'reducing division' the number of abnormal ids is increased or decreased, and in the latter case their effect may be entirely obliterated, in consequence of their meeting with perfectly normal ids during the process of amphimixis; and in the next generation they may be for ever eliminated. Like all individual variations, they may be absent from one generation and appear again in the next; but in case of continual crossing in normal human beings, theoretically they may be expected once more to disappear completely. This agrees with fact, for supernumerary fingers have never been observed in more than five consecutive generations.

We know that variation consists not only in the addition of parts, but also in their disappearance. *The process of degeneration of parts* must be attributed to the disappearance of the respective determinants from the germ-plasm. In the chapter on reversion, I have already attempted to show that regressive transformations need not occur in *all* the ids of the germ-plasm *at the same time*, and that reversion to long-lost ancestral characters may be ascribed to the preservation of a minority

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\* Dr. R. Zander has recently declared himself in favour of the view that supernumerary fingers, &c., are formed by the mechanical constriction of the rudiments of the embryonic fingers by amniotic threads. But if this is true, they would not be transmissible, and another explanation must be made for the doubling of the tarsus in beetles, (*Cf.* 'Ist die Polydactylie als thermorphe Varietät oder als Missbildung anzusehen?' *Virch. Arch.*, Bd. 125, 1891, p. 453.)

of the determinants in question, which gradually decreases in course of time. The cause of the regression of a determinant is to be looked for in insufficient nutrition, — which condition may occur in a determinant quite as likely as that of more abundant nutrition. If this occurs in the majority of the ids either directly, or in consequence of the accumulation produced by *amphimixis*, the character controlled by these determinants becomes regressive in that particular individual. If, however, it no longer has a physiological value, it becomes slowly but surely suppressed by *panmixia* in an ever-increasing number of individuals until it disappears. Specific characters which have long been unrecognisable externally, instead of disappearing entirely, may still be retained in individual ids in the form of incompletely-degenerated determinants; and, as already mentioned, these may cause the reappearance of a character under particularly favourable circumstances.

### 3. *Summary of Sections 1 and 2, and Conclusions*

The above remarks may be briefly summarised as follows: —

*The origin of a variation* is equally independent of selection and of *amphimixis*, and is due to the constant recurrence of slight inequalities of nutrition in the germ-plasm which affect every determinant in one way or another, and differ even in the same germ-plasm, — not only in different individuals but also in different regions. These variations are at first infinitesimal, but may accumulate; and, in fact, they must do so when the modified conditions of nutrition which gave rise to them have lasted for several generations. In this way deviations may occur in the structure of single determinants or of groups of them, — never, perhaps, in all ids at once, but at any rate in several or even many of them. A doubling of certain determinants of the germ-plasm may originate in the same way. The process of *amphimixis* has an important share in the accumulation of these modified determinants, for it may raise the minority previously existing in the two parents to a majority by combining their halved germ-plasms. Then, and then only, does selection begin to take place.

The extreme importance of sexual reproduction in processes of transformation only becomes evident, however, when we realise that adaptations are usually concerned with several variations at the same time, and rarely or never arise in connection

with a single one. *The process of amphimixis alone rendered it possible for such manifold combinations of characters to be offered to selection, so that the proper choice could be made.* If the view which I have long held is correct, a *single* character is never alone acted upon by natural selection, but the whole aggregate of specific characters is incessantly exposed to this process. The constancy as well as the transformation of the existing specific characters, the removal of superfluous ones, and the development of new characters, is due to the incessant and uninterrupted control of selection. This is only rendered possible by the continual intermingling of all the existing varieties of characters, which can only be effected by amphimixis. Hence, although the latter process is not the primary cause of individual variation, it is nevertheless an indispensable factor in selection, for by its means alone can the material from which variations arise be so arranged that selection can operate.

The theory of variation here propounded also affords a more satisfactory explanation of a further difficulty than can be obtained by any other. In considering the unlimited number of adaptations of organisms to the conditions of existence, we must be surprised at the wonderful plasticity of the species. It gives us the impression that every variation, however unexpected, might be produced by a species as soon as the species has use for it. On reflecting how certain animals and plants, or parts of plants, are imitated in colour, form, and marking by other animals, we might be inclined to suppose that every part of an animal may assume any required form, colour, or marking, according to requirement.

This must not, however, be taken literally; an organism cannot assume every form, though it may become adapted in so many ways that we cannot possibly attribute its immense number of adaptations to *rare, fortuitous variations, occurring only once*. The *necessary variations* from which transformations arise by means of selection, *must in all cases be exhibited over and over again by many individuals*.

The presence of such an ever active material for primary variations is a direct consequence of the theory here propounded, according to which every part or 'determinate' of a species must present every possible variant in different individuals in the course of generations, and will sometimes be represented in a larger, and sometimes in a smaller majority of modified ids. Since an

absolute equality of nutrition in homologous determinants, either in different individuals or in the different ids of the same germ-plasm, is inconceivable, and as every minute variation of a determinant does not disappear of itself with the individual in which it is present, but is transmitted directly to the germ-plasm of the next generation, there can be no scarcity of variations of every determinant, and the presence of the material required for all the *possible* variations of all parts seems to be supported theoretically.

Before considering the modifications which the germ-plasm must undergo *as a whole* during the transformation of species, I should like to meet an objection which might be raised. If all determinants are incessantly exposed to slight inequalities of nutrition and consequently suffer slight variations, what is the cause of the extraordinary pertinacity by means of which the species is preserved without the type undergoing variation,—*what is the cause of the constancy of species?* We might expect that all organic forms must be in a constant state of transition, and that no form, and no organ, could be retained for any length of time.

Several points are disregarded in such a question. In the first place, every species is under the uninterrupted control of natural selection, as is clearly shown by the degeneration of parts which have become useless. And since the old hypothesis of the transmission of somatic variations must, it appears to me, be definitely rejected, this process of degeneration can only be explained as the result of panmixia, *i.e.*, the cessation of the control of natural selection over that part which is no longer of use. We may, however, conclude from the fact that such degeneration is universal, that the determinants are in a constant state of fluctuation; and as degeneration takes place very slowly in all cases, I further infer that, in spite of the frequency with which these fluctuations occur, *they only increase very gradually so as to give rise to perceptible variations.*

As at first stated, the individual fluctuations of the determinants must be regarded as excessively small. Natural selection could produce no *direct* result from an individual variation, for it could not produce a cumulative effect; an accumulation can only be produced by amphimixis, and I am inclined to assume that much of the importance of the latter process is due to this fact. It can cause minorities of modified



determinants to accumulate into majorities by mingling the halved germ-plasms of two individuals. By the aid of the 'reducing division' it can also level and equalise matters by fortuitously dispersing the homologously modified determinants of an individual.

It must not be forgotten that slight primary variations of a determinant need not always continue in the same direction: influences of nutrition in the reverse direction will frequently cause them once more to disappear. Only after a determinant has been modified to a considerable degree by the action of a uniform influence during a long period, and the determinants of many ids have become similarly and simultaneously modified, can a variation become visible — after being first accumulated by amphimixis. And even then it by no means forms a permanent specific character, for the question as to whether it will or will not give rise to one is decided by natural selection.

Thus several powerful influences prevent the constant variation of the specific type.

An answer to the question as to *what variations the idio-plasm undergoes in the transformation of species* will be found in the chapter on reversion, and it will here only be necessary to summarise what I have already said.

The transformation of species is due to the variation of some, and frequently even of most, of the determinants. Many species do not possess a single character which resembles that of an allied species, and in this case *all* the determinants must be different. But this only implies that all the determinants  $a-x$  have been modified *in the majority of ids*; a minority of the latter will contain unmodified ancestral determinants. As the transformation of a species proceeds, the number of modified determinants increases together with the number of ids in which they occur. Nevertheless the dominating principle of selection only permits the transformation of *all* the ids to occur very gradually, so that the germ-plasm of a young species may often contain completely unmodified ids of the ancestral species; and even older species may contain solitary groups of unmodified determinants in many of their ids. This, and this alone, renders reversion possible.

It has been recently maintained that, as a consequence of my theory, I must adopt one of two alternatives, and assume either that the germ-plasm of the higher animals consists of ids

of the primitive protozoan ancestors,\* or that every id is constructed in accordance with the existing character of the species: my real view, however, is intermediate between these two. I believe that the germ-plasm of a species always consists to a great extent of specific ids, amongst which, however, some more or less unmodified ancestral ones are present, the number being largest when the species is young. The germ-plasm varies in different species, and must differ very much in the higher and lower forms; but its transformation does not go on at the same rate in all the ids, for some are modified only gradually, or are transmitted unaltered through long lapses of time till they are at last casually removed by a 'reducing division.'

This might be regarded as a defect in the process of the transformation of species, for the possibility of reversion, as well as the retention of inactive ancestral ids in the germ-plasm, can scarcely be considered useful to the species. But in nature no contrivance is absolutely perfect,—not even the marvellously developed human eye: all structures are only as perfect as *possible*,—that is to say, as perfect as they need be in order to perform their required functions. This statement also applies to the mechanism for the transformation of species:—it approaches perfection as nearly as is necessary for the performance of its function.

#### 4. VARIATIONS ON A LARGER SCALE

##### *a. The Origin of these Variations*

We have till now chiefly confined our attention to the question of general individual variation, as exemplified by those minor hereditary differences which distinguish individuals from one another. But there can be no question that variations sometimes occur on a larger scale, and these usually appear suddenly, are met with only in single individuals, and are as a rule hereditary. Darwin has given a large number of instances of this kind. Although the special peculiarity of the black-shouldered peacock, for example, may be due to reversion to an unknown ancestral form, there are many well attested cases in

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\* Compare Marcus Hartog, 'Nature,' Vol. 44, December 1891. The deductions made by this author from my former views are logically correct, but are no longer justifiable, since in the meantime I myself have gained further insight into the problems concerned.

which a given structure in a species has suddenly become considerably modified. How far such modifications have to do with the formation of new species need not concern us at present: we have only to consider the causes and method of origin of these modifications.

A large number of cases of this kind have been observed, especially amongst plants. Not only *fruits*, but *leaves*, *blossoms*, and *entire shoots* have been found to vary suddenly, and in a striking manner. Several varieties of fruits must be included in this category—such as the variety of peach known as the nectarine, as well as the moss-rose, copper-beech, copper-hazel, the varieties of the beech, hornbeam, and oak, the fern-leaved variety of the maple, and numerous other plants cultivated in our gardens.

These varieties in some cases first appeared as seedlings, *i.e.*, as entire plants, and in others as simple branches or shoots, in which latter case they are usually known as *bud variations*.

Let us first take into consideration the *varieties which have originated from seeds*. These occur most frequently in cultivated plants, *i.e.*, in species which have existed for some length of time under conditions which differ more or less from the natural ones. We are therefore undoubtedly justified in attributing the cause of the variation to the influence of changed external surroundings. But a wild plant, which is transplanted into a garden soil, does not always begin to vary at once: it has, in fact, been shown by Hoffmann's experiments, of which we have already given an account, that many generations often elapse before conspicuous variations occur. And even then they do not appear in all the seedlings, occurring perhaps only in one among several hundreds or thousands.

As in the case of ordinary individual variations of a minor kind, the modification begins a long time before it becomes apparent. A few determinants are first changed, and then a gradually increasing number, until at last, by means of the 'reducing division' and amphimixis, they occur in such numbers in certain germ-cells that they form the majority. The fact that these variations occur on a larger scale than the ordinary ones is due to the *permanent* action of *uniform* changes in nutrition, which give a constant direction to the modification of susceptible determinants, so that an increase is effected. This is wanting in the case of the ordinary and constantly varying nutrition.

'*The accumulative action of changed conditions of life,*' suggested by Darwin,\* is consequently theoretically supported to a certain extent by the theory of the continuity of the germ-plasm: those determinants which varied in the first generation continue to do so in a similar direction in the second and third.

Professor Hoffmann has for many years been making very interesting experiments in the Botanical Garden at Giessen which bear on this point, some of which I will now describe.

Various plants, bearing flowers of the normal structure, were exposed during a number of generations to greatly modified conditions of life; they were, for example, grown crowded together in small pots, so that each plant restricted the amount of food obtainable by the others, and were thus scantily nourished. Under this treatment some species—such as *Nigella damascena*, *Papaver alpinum*, and *Tagetes patula*—bore a number of non-typical *double* flowers more or less frequently. The fact that these deviations from the ordinary type in no case appeared in the first generation, proves that they were due to an influence exerted upon the germ-plasm, and not to the *direct* influence of the abnormal conditions of nutrition upon the soma of the plant. Seeds of normal wild flowering plants of different species, when grown in cultivated soil or even when thickly sown in pots, *never produced plants possessing even one double flower*. Only in the course of several, and often many generations, did any of these wild plants exhibit a greater or less number of double flowers, or occasional modifications in the leaves or in the colour of the flowers. It seems to me that only one explanation can be given of this fact, viz., that the altered conditions at first only produced *imperceptible* variations in the germ-plasm of an individual plant,—such, for instance, as alterations in the determinants for the leaves or flowers in *individual* ids, but not in *all* of them at once. These modified determinants were transmitted to the next generation in consequence of the continuity of the germ-plasm; but since the causes of variation continued to operate, the homologous determinants in several other ids also became modified, and thus the number of modified determinants for the leaves and flowers continued slowly to increase, until finally they exceeded the normal determinants in number, and the

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\* Darwin, 'Animals and Plants under Domestication,' Vol. II., p. 249.

abnormality became apparent as a variation in the flower or in the leaf.

The reason why I lay special stress on these cases is, that natural selection plays no part in them, for we are here dealing with artificial, and not with the natural conditions of life. The imperceptible variations of the germ-plasm naturally did not increase continuously, for the processes of 'reducing division' and amphimixis exerted their influence on every fresh generation, and helped to bring about either a marked decrease of the modified determinants, or their sudden increase -- a doubling, or a still greater augmentation. In this way it is easy to understand all the particulars connected with the occurrence of the abnormal flowers and leaves. As a rule, the number of these abnormalities increased in the course of generations with a fairly constant regularity. The following results, for example, were obtained from four generations of *Nigella damascena*, when sown close together: —

1883. No double flowers.

1884. " " "

1885. Six double and twenty-three typical flowers, or 24 per cent.

1886. One double and ten typical flowers, or 10 per cent.

The number of double flowers was, however, not always constant, and in some cases they again disappeared entirely. *Papaver alpinum*, for instance, which Hoffmann had cultivated uninterruptedly since 1862, displayed 'a trace of variability in the form of the leaves, and a more decided variation in the colour of the flowers in 1882.' These experiments were continued from 1882 to 1886, and yielded the following proportion of double and normal flowers: —

In 1881 the proportion was 40.0 per cent.

In 1882 " " 4.0 "

In 1883 " " 5.3 "

In 1884 " " 13.0 "

In 1885 " " 0 "

In 1886 " " 0 "

The complete disappearance of abnormal flowers in the two last of these years seems inexplicable at first sight; but it is easily accounted for if we bear in mind the fact that natural, and not artificial fertilisation occurred, — *i.e.*, the plants were crossed at random, — and that every reducing division and subse-

quent amphimixis were capable of reducing the modified determinants to a minority, and even of removing them completely from the germ-plasm. The modification of the determinants manifestly occurs very gradually, as the small number of modified flowers in most of the years shows; and the chances must have been greatly in favour of the union in amphimixis of germ-cells which contained few or no modified determinants.

Had fertilisation been produced artificially, and abnormal flowers always employed for the purpose, it would have been easy in the course of a moderate number of generations to modify the species entirely, and these cases would then have served as an illustration of the process of natural selection. It would have been still easier to produce the contrary effect by selection,—that is to say, to keep the species constant, and suppress any subsequent variation in this direction. For in the present instance, variation evidently occurred slowly, and most of the determinants were not easily affected by it; and these experiments furnish additional proof of the truth of the statement propounded above that the elements of the germ-plasm only change slowly, and with difficulty: they merely fluctuate to a very slight degree, and only undergo an important change of *any duration* when uniform influences continue to act on them in one direction for a longer time.

It by no means follows from what has just been said that influences of environment and nutrition exist, which, when they have acted for a long time, are able to modify the majority of the determinants for certain parts of the body, and thus to produce purely climatic variations, in the origin of which natural selection has no share. Many—perhaps even most—of the ‘climatic’ varieties are rightly so called.

Such sudden variants, however, appear not only in *entire* plants which have been produced sexually, but also in the individual shoots of a plant. These *bud-variations* are rarely met with; but in cases in which they occur, they can be propagated by cuttings or grafting, and often even by seeds.

When I ventured some years ago to suggest that sexual reproduction has come into force in organic nature in order to preserve the variability which had existed since the time of the primordial beings, facts concerning bud-variation were put forward by several persons to prove that variability may occur in the absence of sexual reproduction. At that time I certainly

did not attach sufficient importance to the variation of the germ-plasm in consequence of influences acting directly; but the existence of bud-variations does not prove that variation occurs without amphimixis. For all those plants in which bud-variation has been observed are reproduced sexually, and their idioplasm therefore contains ids and determinants which differ individually: the different intermingling and behaviour of these in the process of growth would alone form a basis for variations.

In my opinion, indeed, this heterogeneous composition of the germ-plasm produced by amphimixis is an essential factor in bud-variation, notwithstanding the fact that it may not in this case give the first stimulus to variation, any more than it does in ordinary individual variation. Plants which have for a long time been propagated by means of buds and shoots, like the potato and sugar-cane, must possess a germ-plasm consisting of different kinds of ids; for they were formerly reproduced sexually, and the complex intermingling of their determinants thus produced, cannot have undergone an appreciable modification during the period in which they have multiplied asexually. Their germ-plasm must therefore present far more favourable conditions for variation than would one composed of identical ids or of one kind of id only, — did such a germ-plasm exist.

The primary cause of bud-variation must be the same as that of variation from seeds, and must be due to *inequality of nutrition in the germ-plasm*; — the term 'nutrition' being used in its widest sense, so as to include differences in temperature, &c. This view not only receives support from theoretical considerations, — for theoretically it could only be replaced by the assumption of an internal phyletic developmental force, — but it is also supported by observation. For all recorded observations go to prove that bud-variations are most likely to occur when the plant is placed under abnormal conditions, and especially when it is cultivated. As the direct modification of the soma caused by these conditions is not hereditary (*Nägeli*), and *cannot* be so, — for somatic variations are only hereditary when they proceed from the germ, — we are obliged to assume that the modification of several or many determinants in the germ-plasm is due to inequality of nutrition.

That bud-variations are produced by the same causes as those which occur in reproduction by seeds, is borne out by

the fact that the former occur most frequently in those species which have already varied greatly in multiplying by seeds.\* Expressing this in terms of the idioplasm, we may say that it occurs oftenest *in those species in which the homologous determinants already exhibit considerable differences.*

We attribute these variations to influences of nutrition, which at first bring about slight, and then more marked deviations in certain determinants of the germ-plasm during the course of their growth and multiplication, if these influences continue; but this alone does not fully account for the process. The question then arises as to how the modifying influences can cause a *particular* bud to undergo variation while all the rest remain unchanged, although they are exposed to the same influence. Some other influence is therefore required before a modification of this kind can appear.

If we remember that bud-variations sometimes occur in wild plants, or in those which, like the forest-trees of our parks, exist under practically the same conditions as many wild ones, it will appear still more probable that the inequalities of nutrition, while constituting the primary cause of bud-variation, cannot *alone* bring it about.

My own conception of the process is as follows. Just as in the case of ordinary individual variation, bud-variation is primarily due to those slight, fluctuating, structural changes which all determinants undergo in consequence of minute and inevitable fluctuations in nutrition. As in the former case, the homologous determinants of the various ids are not all affected to the same extent; some become greatly modified, and others little or not at all. A difference is, however, seen in the fact that in this case the *same* influence of change—*e.g.*, generally improved nutrition—occurs for a considerable time, and throughout several generations. As in the case of variations in plants raised from seeds, a modification of greater extent can thus be produced in these determinants.

Up to this point the process is quite similar to that of the spasmodic variation of seedlings. A difference, however, results owing to the non-occurrence of amphimixis in the case of gemination, for the variable bud does not arise from the germ-plasm of a seed, but from '*blastogenic*' *germ-plasm* ('Knospen-Keim-

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\* Darwin, *loc. cit.*



plasma'). The latter is derived directly from the former, from which the plant in question — or one of its ancestors, if the plant itself was raised from a cutting — arose. If, during the growth of a tree, one of the determinants, N, varied in the same way in certain ids, and tended, for example, to produce red leaves instead of green ones, red leaves would nevertheless not be produced till all, or at any rate a majority, of the determinants N had become transformed into the red variety. If a 'reducing division' intervened between the germ-plasm of the bud and the growth of the latter into a shoot, a minority of 'red' determinants might give rise to a majority in one of the two daughter-cells; but this reducing division is exactly what does not take place in ordinary cell-multiplication.

Since bud-variations are of very rare occurrence, and only *one* of many thousand buds on the *same* plant varies so as to produce red leaves, for instance, while the altered conditions simultaneously affect all the buds, I conclude that the modified determinants which the tree contains *may sometimes attain a majority in consequence of an abnormal differential nuclear division*. Should this take place in the apical cell or cells of a bud, the resulting shoot might, to return to our former example, bear both green and red leaves; for, according to our pre-supposition, the 'green' and 'red' determinants of the apical cells would have been separated during the cell-divisions in such a manner that in some leaves the green determinants, and in others the red ones, might be in the majority. If the separation occurs at an earlier stage, before the apical cells are formed, — that is to say, in the cambium, — a shoot bearing red leaves alone might arise from the cell which receives the 'red' group at the differential division of the nucleus.

There is nothing impossible about this assumption; for during the process of mitotic nuclear division, irregularities might occur in the complex apparatus by which this process is effected, and individual cases of such irregularity have actually been observed: — even the possibility of a *direct* nuclear division cannot be entirely overlooked. I am, however, far from considering this hypothesis as established, and merely offer it as a suggestion.

Nägeli was of the opinion that all variations are slowly prepared in the idioplasm in the course of generations before

they become apparent, and in stating this view he also specially referred to bud-variations. I fully agree with him in this respect, and in the course of this book have repeatedly shown how these gradual modifications ('Umstimmungen') of the germ-plasm, or of individual parts of it, are to a certain extent the natural result of its assumed structure. In the case of bud-variations these invisible modifications may occur in a much earlier generation than that in which they appear; and hence it is easy to understand why this form of variation mostly occurs in those plants which, like the rose and Azalea, have already varied in reproduction by seed. For modified determinants are more readily accumulated by amphimixis; and a germ-plasm which has inherited such determinants from its ancestors may, after these have been still further modified, give rise to a bud in which, by a fortuitous differential nuclear division, the modified determinants are in the majority, and can thus become effective.

Unfortunately it has not been observed whether complicated modifications, like that of the moss-rose, owe their origin to bud-variation. This is quite possible theoretically, for the invisible preliminary to variation—the modification of certain determinants—is just as likely to affect a single determinant as a whole group; even the formation of two or more new determinants, by the multiplication of a primary one, is quite as possible here as in the case of the ordinary transformation of species. The sudden appearance of such modified groups of determinants is due therefore to fortuitous differential nuclear division. Such cases prove that the preparation for the modification is a slow process, for it appears impossible to conceive of any cause producing a sudden variation of an entire group of determinants by any method.

The *extent* of any spasmodic variation will depend on the extent to which the various groups of determinants have been permanently exposed to abnormal nutrition. It would doubtless be as yet premature to bring their *qualitative* characteristics into any causal relation with definite influences producing variation. We can only state the necessity of assuming, *a priori*, that the extraordinarily complex germ-plasm is provided with special means for the transmission of nutrient fluid, the increase or diminution of which must produce purely local *differences* of nutrition; and that, on the other hand, the vital units must, owing to slight changes in their structure, modify

the characteristics of the part of the body which they represent, in some inexplicable way. It is not yet possible, for instance, to give an exact account of the changes in the group of determinants for the legs which led to the sudden production of a bow-legged 'otter'-sheep, or of the modifications of certain determinants in the rudiments of the leaves which caused the formation of the notches characteristic of a certain variety of birch.

*b. The Transmission of these Variations*

The transmission of 'sports' in plants has hitherto been a very obscure problem. Seed-variations are often propagated by means of seeds, but cannot always be thus reproduced, or at least only in individual cases. Bud-variations can usually only be propagated by cuttings or grafting, but some instances are known in which they have also been reproduced by seeds, though only in a certain percentage of cases. The origin of these irregularities was unknown, and no previous theory of heredity could offer a reason for them; all that could be said was, that in these instances transmission was very capricious. The theory of the germ-plasm, however, offers a very simple explanation of them. We will first consider certain facts recorded by Darwin, which are very valuable in respect of this theory.

Darwin states that 'when a new peculiarity first appears, we can never predict whether it will be inherited.'\* If both parents exhibit the variation, 'the probability is strong that it will be transmitted to at least some of their offspring.' Bud-variations are propagated to a much smaller extent than seed-variations, but the power of transmission often appears to be very capricious, inasmuch as one and the same modification on a single plant is transmitted by seed in one case and not in another. Thus vain attempts were for a long time made to propagate the weeping ash by seeds. Over twenty thousand seeds developed into trees of the ordinary form, but offspring with hanging boughs were finally raised from the seeds of another specimen of this variety. The same ash-tree, however, did not transmit this character to all its offspring, but only to a certain

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\* 'The Variation of Animals and Plants under Domestication,' Vol. I., London, 1888, p. 460.

percentage of them; and Darwin mentions a famous weeping oak at Moccas Court which transmitted its special character to all its seedlings, though in *varying degrees*.

According to our theory, the transmission of a variation by seeds depends on the presence of a corresponding modification in the majority of the determinants in the germ-plasm of the seeds. If the germ-plasm contains a hundred ids, the controlling forces of which are equal, more than fifty determinants  $N$  must be transformed into  $N^1$  before the modification would be perceptible in the seedling. Since therefore, as was remarked above, new variations probably never appear simultaneously in *all* the determinants, but only in a varying percentage of the ids, the chances are greatly against all the seedlings produced by the transformed plant exhibiting this modification. For every germ-cell has undergone a 'reducing division,' and hence many of them will always only possess a minority of the modified determinants  $N^1$ , and this may even be a very small one if the majority in the germ-plasm of the parent-plant was small. When two such cells unite in the process of amphimixis, the resulting germ-plasm contains only a small minority of modified determinants  $N^1$ , and the modification is inappreciable. This accounts for the fact that the seedlings of a variety hardly ever reproduce the variety in *all* cases; and that in rarer instances, such as that of the weeping oak already mentioned, all the seedlings may exhibit the corresponding variation, although in varying degrees. For the composition of the germ-plasm must differ in each of them in consequence of the processes of 'reducing division' and amphimixis, even when the parent-plant contains only a small but ever varying minority of ancestral determinants.

We can, moreover, easily account for the fact that seedlings of a variety, such as the balsamine, may resemble the parent-plant, without transmitting the character of the variety to their offspring. In this case all the daughter-plants of the variety in question must retain a majority of the modified determinants, but in very varying degrees. In those which contain a very large majority in their germ-plasm, it necessarily follows that the larger number of the germ-cells produced must contain a majority of modified determinants; but in the case of those in which the proportions are more equal, the chances are in favour of the seedlings containing only minorities of these determinants.

Darwin mentions that only thirty per cent. of the seedlings of the wild variegated variety of *Ballota nigra* possessed the variegated leaves of the parent-plant; but sixty per cent. in the second generation were variegated. This is also quite in accordance with our theory; for the determinants for the leaves in the mother-plant cannot all have been modified, but only the majority; these would then become differently grouped by means of the reducing divisions of the germ-cells. A seed reproduces either the variety or original form according to whether modified determinants, which were brought together in fertilisation, constituted the majority or minority. As in the instance first quoted, variegated plants were alone retained for cultivation in the second generation, and consequently a greater number of the determinants of the variety were brought together at fertilisation: *the percentage of the variety was therefore bound to rise in the third generation.* This proportion would have increased still further if a fourth and fifth generation had been raised in the same way; for in those seeds which yield variegated plants the germ-plasm must of necessity contain more modified determinants than in the case of those producing the original form. Hence with every generation the chances of an increased majority of modified determinants become greater; and I have no doubt that in this instance, by the constant selection of the most variegated plants for further cultivation, a 'pure' variegated race might eventually have been obtained, which would have transmitted its character to the great majority of its offspring — or as we usually express it — 'to all its offspring.'

The fact that many weeping ashes transmit their special character to many, but not all, the seedlings is also attributable to the diverse effects of the 'reducing division' and amphimixis, the former of which causes the introduction into the germ-plasm of a large majority of modified determinants, and the latter of only a slight one. The *manner in which the variety arises* must here, however, be taken into account. *Bud-variations are much more rarely reproduced by seeds than are variations arising from seeds*; but, on the other hand, they can almost always be propagated by grafting, budding, or by cuttings. Hence the capacity of a certain individual for transmitting the variation to its seeds may be owing to its having arisen from a seed, while in another case the same variation arose in a bud, and it could therefore rarely or never be transmitted by seeds.

The most difficult point to explain theoretically, is why bud-variation is *not* generally, but only occasionally, transmitted by seeds. Even this may to a certain extent be accounted for by the present theory.

A bud is a growing point, enveloped by scales. It arises from the apical cells, which produce the other cells of the shoot by means of continual division, and these form the interfoliar parts, leaves, and flower-stocks. In accordance with the principle of the continuity of the germ-plasm, a part of the 'blastogenic' germ-plasm of the apical cells must be transmitted in an 'unalterable' ('gebundenen') condition to certain cells of the shoot as accessory idioplasm ('Neben-Idioplasma') or '*reserve germ-plasm.*' From these cells it is passed on to the sexual organs, where it is used for the formation of germ-cells. This reserve germ-plasm remains undisintegrated, and is perfectly distinct from, and independent of, the 'blastogenic' germ-plasm, which is gradually distributed during the ontogeny of the shoot into groups of determinants.

The fact that bud-variations are so rarely transmitted by seeds seems to me to be owing to the cause just mentioned; for the majority of modified determinants required to make a modification apparent may evidently be present in the 'blastogenic' germ-plasm, though absent in the reserve germ-plasm. If we remember that these variations have been prepared long beforehand in the germ-plasm, and that at first a few, and then gradually a larger number of determinants become modified in a similar way, and that finally a fortuitous differential nuclear division must, on our assumption, intervene before the 'blastogenic' germ-plasm of a certain apical cell can contain a majority of modified determinants, it becomes comprehensible why the reserve germ-plasm contained in this cell may behave differently, and contain only a few or none of the determinants in question in a modified condition. We must not forget that the influences which produce the variation are not those of the nutrition of the bud in which the modification appears, but those which affected the determinants during their long course from the ancestral plant of a past generation to the bud in which they now appear.

This explanation seems to me to sufficiently account for the fact that the seeds which give rise to 'sports' indirectly, need not necessarily transmit the modification.

The question as to why this transmission is of *such rare occurrence* must, however, be considered more closely. I am inclined to seek the causes of this fact in the processes of 'reducing division' and amphimixis, to which the reserve germ-plasm, but not the 'blastogenic' germ-plasm, is subjected. Let us suppose that the two were precisely similar at first with respect to their contained modified determinants  $N^1$ , each possessing a small majority of them: the shoot must then exhibit the variation, but only certain germ-cells would contain a majority of  $N^1$ , the rest containing a minority of these determinants in consequence of the diversity resulting from the reducing division. It is true that two germ-cells containing majorities of  $N^1$  might unite in fertilisation; but this extremely favourable case would only occur very rarely, — when, as assumed, the majority in the reserve germ-plasm was only a *slight* one; while the other cases, in which amphimixis leads to  $N^1$  being in the minority, would take place much more frequently.

It is, however, by no means certain that reserve germ-plasm and 'blastogenic' germ-plasm must contain a similar percentage of  $N^1$ . The two may very well differ in this respect, and it is extremely probable that a larger percentage of  $N^1$  in the reserve germ-plasm leads to the formation of seeds which give rise to seedlings exhibiting variation. We may therefore suppose that in the one case, when the 'blastogenic' germ-plasm contains even a small majority of  $N^1$ , the modification of the shoot will actually occur; and that in the alternative case, in which the reserve germ-plasm alone contains a majority of  $N^1$ , variation will take place in a larger or smaller number of seedlings in the following generations. When both contain a majority of  $N^1$ , the shoot must vary, and some of the seeds arising from it must transmit the variation.

This explanation is not so hypothetical as it might appear. Certain facts point with certainty to the conclusion that these 'sports' in many cases really contain only a very slight majority of modified determinants. In most bud-variations *reversions to the original form* are of frequent occurrence, both in the buds themselves and in the generation derived from them either by seeds or buds. This has already been mentioned in the chapter on reversion, and is so well known that a brief statement of a few cases will suffice. In the botanical gardens at Bonn, Professor Strasburger showed me an immense horn-

beam with deeply notched leaves, like those of the oak, a large branch of which had reverted completely, and bore leaves of the ordinary form. I have in my garden a 'fern-leaved' beech, some of the leaves of which have the usual form; Darwin states, in fact, that some shoots of this variety may produce fern-like leaves, normal leaves, and various intermediate forms. Slight inequalities in the nuclear divisions may in this case displace the controlling resultant of the determinants  $N$  and  $N^1$ , supposing that the majority of  $N^1$  is only a small one.