PART IV

THE TRANSFORMATION OF SPECIES: ITS ORIGIN IN THE IDIOPLASM

CHAPTER XIII

THE SUPPOSED TRANSMISSION OF ACQUIRED CHARACTERS

1. Difficulties in the Way of a Theoretical Basis for this Assumption

By *acquired* characters I mean those which are not performed in the germ, but which arise only through special influences affecting the body or individual parts of it. They are due to the reaction of these parts to any external influences apart from the necessary conditions for development. I have called them '*somatogenic*' characters, because *they are produced by the* reaction of the body or soma, and I contrast them with the '*blastogenic*' characters of an individual, or those which originate solely in the primary constituents of the germ ('Keimesanlagen'). It is an inevitable consequence of the theory of the germ-plasm, and of its present elaboration and extension so as to include the doctrine of determinants, that somatogenic variations are not transmissible, and that consequently every permanent variation proceeds from the germ, in which it must be represented by a modification of the primary constituents.

I will first attempt to show how this conclusion is arrived at theoretically, and will then proceed to test it by ascertaining how far it is in agreement with actual observation, and whether the theory can be justified by facts.

Somatogenic variations may be classified according to their origin into three categories, — viz., *injuries*, *functional variations*, and variations depending on the so-called '*influences of environment*,' — which include mainly climatic variations.

The hereditary transmission of any of these three kinds of somatogenic variations could be accounted for theoretically only *by the assumption that that part of the soma which had been* changed by external influences, could modify the germ-plasm contained in the germ-cells of the same individual, so that its offspring would, from the germ onwards, undergo similar variations to those which had been acquired by the action of external influences on the parental part in question.

As far as I can see, there are only two ways in which such a *variation could conceivably occur in the germ-plasm in consequence* of a corresponding somatic variation. We should either have to assume the presence in all parts of the body of definite tracks along which each somatogenic variation might be transferred to the germ-cells, in the germ-plasm of which it would produce a corresponding change; or else that gemmules, such as Darwin supposed to exist, are given off from every somatic *cell and are conveyed to the germ-cells, — either* through the vascular system, when one exists, — or by some other means, and that they must then penetrate into these cells, and become incorporated in their germ-plasm. Thus either the presence of hypothetical tracks along which a modifying, though totally inconceivable, influence might be transferred to the germ-cells, or else the discharge of material particles from the modified organ, *must take part in the formation* of the germ-plasm: there is no third way out of the difficulty.

Both these hypotheses have already been used to explain the supposed transmission of somatogenic variations, — the former, it is true, only in vague allusions hinting at 'nerve-influences,' which are supposed to start from the modified part, and to produce a corresponding *alteration in the hereditary substance* of the germ-cells. But no one has yet ventured to state more precisely how nerve-excitation can modify the germ-plasm *materially*, and *in accordance with* the somatic variation. It would probably be useless even to expect an answer to the question as to how a part, such as a muscle, enlarged by functional hypertrophy, is capable of producing a specific nervous current signifying 'enlargement.' If such an explanation were attempted, we should be compelled to imagine that every cell in the body was placed in communication with every germ-cell of the ovary or spermarium by means of a large number of nerve-tracks, and was capable of continually sending information to the germ-cells of what was occurring in its own substance, and of the manner in which it was influenced, and also of giving instructions how each of the millions of units in the germ-plasm should behave. I believe that it would be impossible to avoid absurdities in explanations of this kind, and consider the whole idea inadmissible.

The second possible explanation appears to me to be less acceptable at the present day than when it was put forward by Darwin in the form of a hypothesis of pangenesis. And, as already stated in earlier essays, I believe that the talented author of this hypothesis of heredity did not look upon it as a well-grounded assumption, but considered it merely as a working hypothesis, only intended to lead to a better insight. Meanwhile, many changes have been made, and we have become acquainted with facts which compel us to reject the idea of a 'circulation of gemmules,' and I am surprised that this has not hitherto been done. This hypothesis is rendered inadmissible, not merely because we must imagine that the gemmules are *given off*, and then *circulate* through the body, but principally on accouut of the implied *addition of gemmules —i.e., of primary constituents—to the germ-plasm of the germ-cells!*

According to Darwin's idea, there must be a constant addition of 'primary constituents' or gemmules to the germ-plasm already present in the germ-cells, unless, indeed, it is assumed that the entire nuclear substance in the germ-cells is formed by gemmules which migrate into them. Such an assumption is, however, contradicted by the fact that the *hereditary substance of the germ-cells, which we observe in the form of nuclear rods or idants, receives no addition to its organised bodies, the primary constituents.* I have come to this conclusion, not from the fact that we have never observed an addition of this kind, but from the way in which the hereditary substance has been shown to behave during its multiplication. We know that the cell contains a most wonderful mechanism which apparently has the sole function of distributing the idants quantitatively and qualitatively, according to the primary constituents which they contain; and this is done as equally as possible, or, at any rate, in a definitely prescribed manner. Why should the centrosomes and spindle-threads be present, and the longitudinal fission of the idants occur, if myriads of primary constituents of the germ-plasm circulate separately through the body, and are capable of entering the germ- and other cells from without, as well as of becoming properly arranged in them in the order in which they subsequently undergo development? Why should nature be so scrupulously careful to divide the idants as accurately as possible, if their composition were open to alteration at any moment by the entrance of new primary constituents or gemmules? *The process of the fission of the idioplasm in nuclear and cell-division seems to me directly and conclusively to refute the whole idea of the circulation of gemmules.* For the very reason that these nuclear rods or idants can never receive an addition of new primary constituents from without, the most extreme care is required, during their multiplication by division, to prevent the different qualities of the mother-cell from being distributed improperly amongst the daughter-cells, and causing an irreparable loss of certain primary constituents to one of the latter and its descendants.

It is impossible to assume the transmission of somatogenic variations in any theory which accepts the nuclear substance of the germ-cells as germ-plasm or 'hereditary substance'; for it is theoretically impossible to account for these variations, no matter how ingeniously the theory is constructed.

At the present day I can therefore state my conviction still more decidedly than formerly, that *all permanent — i.e., hereditary — variations of the body proceed from primary modifications of the primary constituents of the germ*; and that neither injuries, functional hypertrophy and atrophy, structural variations due to the effect of temperature or nutrition, nor any other influence of environment on the body, can be communicated to the germ-cells, and so become transmissible.

This statement naturally implies the rejection of Lamarck's principle of variation; for those factors which this talented philosopher and investigator believed to be all-important in the modification of species, — viz., the use and disuse of parts, — can have had no direct share in the process. I am by no means the only one to hold this view at the present day; and although the truth cannot be decided by a consensus of opinion, it is nevertheless a significant fact that the views of such naturalists as Ray Lankester,* Thiselton Dyer, Brooks, Meynert,† van Bemmelen,‡ and others, coincide with my own.

The fact, however, that we deny the transmission of the effects of use and disuse, does not imply that these factors are of no importance; and I have already attempted to show in former essays that both use and disuse may lead indirectly to variations, — the former wherever an increase as regards the character concerned is useful, and the latter in all cases in which an organ is no longer of any importance in the preservation of the species, and in which, so far as the disused organ is concerned, 'panmixia' occurs.

Want of space prevents me from discussing these questions in detail; their consideration belongs rather to a work on the theory of descent than to one on that of heredity, and I need only refer to my former essays,§ in which, I think, sufficient proof is given to show that the gradual degeneration of organs which are no longer of use does not require the assumption of the transmission of somatogenic variations, and that consequently the facts do not compel us to adopt a hypothesis which we seem unable to accept theoretically.

It therefore remains to be seen whether we are not acquainted with other facts which are explicable only on such a hypothesis: one side of this question will now be treated of in particular.

2. The Hypothesis Tested by Facts

A few words will suffice concerning the hypothesis of the *transmission of injuries and mutilations*, which has been accepted for so long a time, and is obstinately defended even at the present day; for since the appearance of my essay on 'The

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* Ray Lankester, 'The History and Scope of Zoology,' 'Enc. Brit.,' Vol. xxiv.

† Meynert, 'Mechanik der Physionomik,' a Lecture held at the Meeting of German Naturalists at Wiesbaden, 1887.

‡ J. F. van Bemmelen, 'De Erfelijkheid van verwooven Eigenschappen,' s'Gravenhage, 1890.

§ *Cf.*, 'Uber die Verebung,' Jena, 1883, and 'Die Continuität des Keimplasma's als Grundlage einer Theorie der Verebung,' Jena, 1885. English translation, 'Essays upon Heredity,' pp. 71 and 165.

Supposed Transmission of Mutilations,' * no new observations on this point have appeared.† The old arguments, on the scientific worthlessness of which I then expressed my opinion, are constantly being brought forward, — in part altered, and in part with a new interpretation. It is now even less necessary than ever to return to the matter, as even among those observers who supported *the view of the transmission of functional variations, a few* agree with me in denying the transmission of mutilations. As an instance, I may mention Osborn, who, however, goes a little too far when he compares the contest of the old view of the transmission of mutilations with Don Quixote's celebrated fight with the windmills.‡ Only a few years ago, at a meeting of the German association of naturalists,§ two *'tailless' cats were exhibited, in which the absence of the* tail was supposed to be due to their mother having accidentally lost hers; and biologists of such eminence as Ernst Haeckel‖ have accounted for similar cases in the same way. Since such men still regard the inheritance of mutilations as possible, the exposition of the subject has not been a superfluous task.¶

There is, however, *a third kind of somatogenic variation*, produced by *the influence of environment*, *the mode of nutrition*, *the climate*, and so on; this often appears to be transmissible, and consequently capable of becoming increased in the course of generations. I myself called attention to this fact a number of years ago in the following words: — 'I only know of *one* class

* Jena, 1889, 'Essays upon Heredity,' Oxford, 1889, p. 421.

† None, that is to say, which are in opposition to my views. My experiments with mice have been confirmed by Ritzema Bos and by Rosenthal. I have now continued these experiments to the nineteenth generation — always with the same negative results; cutting off the tails has no influence on the tails of the descendants. A similar result was obtained by both the above-mentioned observers from experiments on rats (*cf.* 'Biolog. Centralblatt,' Vol. xi., 1891, p. 734, &c.).

‡ Osborn, 'Are Acquired Variations Inherited?' Boston, 1890, p. 3.

§ At the meeting at Wiesbaden, 20th September 1887.

‖ Haeckel, 'Natürliche Schöpfungsgeschichte,' 3rd ed., 1889, p. 194. English edition, 'The History of Creation,' London, 1876, Vol. i., p. 214.

¶ See the Section on the Transmission of Mutilations in Eimer's book entitled 'Die Entstehung der Arten,' &c., Jena, 1888. (*Cf.* 'Organic Evolution as the Result of the Inheritance of Acquired Characters,' &c., translated by J. T. Cunningham, London, 1890.) A whole collection of 'proofs' are there given.

of changes in the organism which is with difficulty explained by the supposition of changes in the germ; these consist in modifications which appear as the *direct consequence of some alteration in the surroundings*. But our knowledge on this subject is still very defective, and we do not know the facts with sufficient precision to enable us to pronounce a final verdict as to the cause of such changes.' Mention was then made of a few of the large number of cases which have been repeatedly quoted, and I attempted to show that none of them stood criticism, that they could not be explained in the way some investigators supposed, and that somatogenic variations are only apparently hereditary; for in reality a change must first be brought about in the germ-plasm by the influence of the surroundings before such a variation can be produced. I then continued:—'It must be admitted that there are cases, such as the climatic varieties of certain butterflies, which raise some difficulties against this explanation. I myself, some years ago, experimentally investigated one such case, and even now I cannot explain the facts otherwise than by supposing,' as I did then, that somatic variations were transmissible. 'It must be remembered, however, that my experiments,' which have been repeated upon several American species by H. W. Edwards, 'were not undertaken with the object of investigating the question from this point of view alone. New experiments, under varying conditions, will be necessary to afford a true explanation of this aspect of the question.' *

Since 1883 I have waited in vain for some skilled entomologist or for one of the numerous advocates of the transmission of acquired characters, to carry out the proposed experiments. In the meantime, as far as the time and material at my disposal permitted, I have myself made a start on this line of research, and now possess the results of a series of new experiments, which, though not so numerous, complete, or exhaustive as I could have wished, are nevertheless sufficient to form a more trustworthy basis for a theory dealing with variations of this kind. Some of these are described in the following section, a more detailed account of them being left for another occasion.

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* *Cf.* my essay, 'Uber Vererbung,' Jena, 1883. English edition, Oxford, 1889, pp. 98–99.

3. Climatic Variation in Butterflies

Polyommatus phlæas, a butterfly belonging to the family *Lycænidæ*, is distributed over the whole of the temperate and colder parts of Europe and Asia. It also occurs on the shores of the Mediterranean, in Maderia, the Canaries, and in part of North America. Before the glacial epoch this species must have inhabited the more northern circumpolar regions, and have been driven southward during that epoch; subsequently it must have again migrated towards the north. In our latitudes the upper surface of the wings of this form is of a beautiful reddish-gold colour, and hence it has received the popular name 'Feuerfalter' (fire butterfly). Further south, the reddish-gold colour is more or less thickly dusted with black, and specimens from Sicily, Greece, or Japan often display only a few reddish-gold scales, the general appearance being almost black. In Germany this butterfly is double-brooded, and the two generations are similar; but in certain districts of Southern Europe, such as the Riviera di Levante, the first generation is reddish-gold, — the second, which flies in midsummer, and is known as the variety *eleus*, having the wings well dusted with black. As in Germany, during exceptionally hot summers, individuals with a blackish tint have repeatedly been caught together with the ordinary form, and as, moreover, in the extreme southern limit of their range — so far as my experience extends — both generations have a blackish colour, it would appear at first sight that the modifications are merely due to the effect of heat; — the butterfly becomes red when exposed to a moderate temperature, and black when the heat is greater.

The following experiments, however, prove that this conclusion cannot be a correct one. Caterpillars were raised from the eggs of the German form of *P. phlæas*, and the pupæ were then exposed to a much higher temperature till the emergence of the butterfly. The result was that many of the butterflies were slightly dusted with black, *but none of them resembled the darkest forms of the southern variety eleus*. I then made the reverse experiment, subjecting caterpillars which had just entered the pupal stage, and had been raised from the spring generation of the Neapolitan form, to a very low temperature.*

* I must take this opportunity of expressing my warmest thanks to Dr. Schiemenz, of the Zoological Station at Naples, for the kind and generous

Many butterflies were thus obtained which were not so black as those which had emerged from pupæ kept at a higher temperature, *but none were so light-coloured as the ordinary German form. The difference between the Neapolitan specimens which had become light-coloured from exposure to cold, and the normal German form, on the one hand; and that between the German specimens artificially darkened by warmth, and the normal Neapolitan form, on the other, is too great to be attributable to the incompleteness of the experiments.* The German and the Neapolitan forms are therefore *constitutionally distinct*, the former tending much more strongly towards a pure reddish-gold, and the latter towards a black coloration.

Both experiments, however, prove the correctness of the old assumption of Lepidopterists that the action of heat on a single generation is capable of giving the German form of a blackish tint; and since, moreover, it is clear that the development a single generation at a lower temperature can render the colour of the Neapolitan butterfly less black, it appears that the two varieties may have originated owing to a gradual cumulative influence of the climate, the slight effects of one summer or winter having been transmitted and added to from generation to generation. *This would then seem to be an instance of the transmission of acquired characters.*

I do not believe, however, that this is the correct interpretation of the facts. If it were, there could be no region in which the species is seasonally dimorphic, as I have myself ascertained it to be on the Ligurian coast. The germ-plasm would then contain either the primary constituents of the red variety, if the colony had been exposed for many generations to a low temperature; or those of the black one, if a high temperature had influenced it for the same length of time. It would then make no difference to what degree of temperature a single generation were exposed at the present day in artificial breeding, for the colour would have already been determined in the germ-plasm, which would contain, to use my own phraseology, either 'reddish-gold' or 'black' determinants for the wing-scales in question. Hence it would be quite impossible for the spring generation to develop reddish-gold, and the summer one

assistance he has given me in my efforts. Without his help I should have been unable to obtain the necessary living specimens.

black scales, for the germ-plasm would only contain either 'red' or 'black' determinants for a certain spot on the wing.

The theory of determinants will, I believe, supply a very simple explanation of this apparently complicated case, which I consider of great value, because it confirms this theory. Instead of supporting the doctrine of the transmission of somatogenic characters, this example shows how *such a process may apparently be brought about*, and on what it depends. A somatogenic character is not in this case inherited, but the modifying influence — the temperature — *affects the primary constituents of the wings in each individual*, — *i.e.*, a part of the soma, — *as well as the germ-plasm contained in the germ-cells of the animal.* It modifies the *same* determinants in the rudiments of the wings of the young chrysalis as in the germ-cells, — namely, those of the wing-scales. The variation cannot be transmitted from the wings to the germ-cells, but only affects the coloration of these organs of the individual in question; whereas it is transmitted from the germ-cells to successive generations, and consequently controls the coloration of their wings in so far as this is not again modified by *subsequent* influences of temperature; for the same determinants which are now present in the germ-cells of generation I are afterwards passed into the rudiments of the wings in the caterpillar and chrysalis of generation II, and the change which they underwent while lying in generation I may be increased or weakened by the influence of the temperature to which they are exposed after entering into generation II.

Since warmth affects the whole body, it is not surprising that the determinants which are modified by it should undergo these modifications, whether they are contained in the germ-plasm of a young egg or sperm-cell of the caterpillar, chrysalis, or butterfly, or in certain cells in the rudiments of the wings in the chrysalis or caterpillar. This, however, does not imply that they must undergo the *same amount* of variation in both places, for they have not by any means the same environment in the two situations. In the germ-plasm they are grouped amongst thousands of determinants of the species, all of which constitute the germ-plasm; while in the rudiments of the wings, they are associated with only a few other kinds of determinants, and a time must come when *each of them controls a cell by itself*, and transforms it into a red or a black wing-scale.

We know, however, of a fact which definitely proves that the susceptibility of the scale-determinants to the influence of temperature is greatest at a certain stage in the development of the butterfly — much greater than either before or afterwards. I have frequently noticed in seasonally dimorphic species like *Vanessa prorsa-levana*, that the modifying influence of heat or cold only acts at the *beginning of the pupal stage*. Although I have not yet been able to ascertain the time at which this occurs more precisely, it can be definitely stated that the winter pupæ of *Vanessa levana*, for instance, which have been exposed to a high temperature even only a month after entering the pupal stage, are never transformed into the *prorsa* form; they all emerge as *V. levana*.

This is not due to the fact that the colour of the wings is already deposited a month after the insect has entered the pupal stage, for at this time there is no trace of colour whatever. *There must, consequently, be a period in the disintegration of the determinants when they are most susceptible to the influences of temperature:* subsequently this is no longer the case, and although they are susceptible *before* this period, I nevertheless venture to suppose that they were so to a *far slighter extent*. This may be due to their connection with other determinants, or to other causes which we are not yet able to discover.

If, then, the determinants for the scales are only influenced very slightly by the temperature as long as they are situated in the germ-plasm, and are subsequently greatly affected by it at a certain period in the development of the wings, the above-mentioned phenomena admit of a simple explanation. The germ-plasm of the southern colony of *P. phlæas* must contain many determinants among those for the wings, which, in consequence of the exposure of thousands of generations to heat, have been adapted for the production of black scales, together with a large number of others which only require a small increase of temperature during pupation in order to give rise to a black colour. These latter kind cause such fluctuations in the coloration as occurred in my experiments; while the former produce the black coloration of the wings, which has become fixed in the constitution of the southern colony, and can no longer be removed by the action of cold on the young chrysalis.

In this case it is taken for granted that the ancestral form possessed pure reddish-gold wings, and that it inhabited high northern latitudes, — an assumption which alone enables us to understand the present distribution of the species, and which has been adopted by Hofmann * in his splendid researches on the origin of European butterflies. This, however, is of no great importance in the present question, but we must assume that either the reddish-golden tint, or the deep black dusting is the primary colour. The seasonal dimorphism and the occurrence of blackish specimens in Germany in hot summers are easily acounted for on the former assumption.

In consequence of the increase in temperature of the habitat of the species, many scale-determinants in the germ-plasm would gradually become so modified that the action of only a slight further increase on the rudiments of the pupal wings would lead to the production of black scales. In Germany the species has attained this point in its phyletic modification; and if the weather happens to be hot when the second annual brood enter upon the pupal stage, some butterflies of a blackish tint will be produced. This will be more likely to happen as the internal transformation of the determinants in question advances further, and the blackish tint will become more conspicuous as the scale-determinants which have reached this stage of modification in the germ-plasm become more numerous. These two conditions will obtain most often in districts where the summer is usually tolerably warm; and the fact is thus accounted for that dark specimens of *P. phlœas* are rarely caught in northern Germany, and in the far north not at all, although very dark forms occur comparatively often in the warm valleys of Valais.

In still warmer districts, like the Riviera, the summer brood of *P. phlœas* is almost always exposed to a high temperature, and hence the transformation of the determinants for the scales has become so great, that with the help of the usual summer heat at the time when the caterpillar enters the pupal stage, the variety *eleus* has been produced. This variety does not appear in the spring brood, because the additional heat required for the complete transformation of the determinants for the scales is absent during the pupal stage.

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* Ernst Hofmann, 'Isoporien der europäischen Tagfalter,' Stuttgart, 1873.

If the area of distribution of the species extended uninterruptedly from the Polar regions to South Italy or North Africa, all the intermediate forms would occur, from the pure reddish-gold single-brooded form in Lapland to the black double-brooded variety *eleus:* there would thus be — first, two similar reddish-gold broods; then similar ones, — those butterflies which are exposed to a higher temperature during the pupal stage having a tendency to develop a black tint; and then seasonal dimorphic forms, the butterflies being black in the summer and reddish-gold in spring, as is actually the case in Genoa. A still longer action of a higher temperature would at first change a small and then an increasing number of determinants for the scales into the 'black' variety, so that finally two broods, both consisting of the black form *eleus,* would occur. The case of the Neapolitan colony is somewhat similar to the last-mentioned one, for many black specimens certainly occur amongst the spring brood, although there are also many light-coloured ones; none, however, are as light as the northern reddish-gold form of *P. phlæas.* I do not know whether a complete change of colour has been attained by *both* annual broods in any locality; but if it has, I should expect it to be seen in Southern Japan rather than elsewhere, for the butterflies which I possess from the neighbourhood of Tokio display an unusually dark colour.

This case has been discussed at length because it appears to me to be especially significant, not only in the explanation of the climatic varieties of butterflies, but also as regards *the theory of heredity, and the assumption of material determinants which exist in the germ-plasm and are passed on from one generation to another.* The facts are so evidently in favour of this assumption that no other explanation seems possible. It must, however, be remembered that the artificial modification of the colour on the wings does not take place if the change in temperature occurs only when the scales begin to become coloured. The colouring matter is consequently not produced by the *direct* influence of chemical transformations, but by an indirect influence, which we may suppose to be due to a mutual disarrangement and rearrangement of the 'biophor-material' of which the determinants consist, by the co-operation of which latter the chemical process forming the colour is derived.

The occurrence of seasonal dimorphism alone, shows with certainty that the determinants for the scales are influenced by temperature in the germ-plasm to a much slighter extent than in the rudiments of the wings. If the modifying influence had the same effect in both cases, the germ-plasm in the germ-cells of a butterfly of the summer generation would be modified as much as the wings of the same individual; and consequently the offspring, even if exposed to a low temperature, would necessarily display a greater tendency towards the summer coloration, because the latter was already potentially contained in the germ. This, then, would only be the case if the influence of the cold were stronger than that of the heat. In any case, however, a coloration intermediate between that produced by cold and by heat respectively would result, and would be transmitted to both generations, even when the two influences were equally strong. If we indicate the winter and summer colorations respectively by A and B, the coloration of each generation would then be 1 A + 1 B. It is only when the germ-plasm is modified to a much smaller extent than the determinants which have already entered the rudiments of the wings, that an alteration of coloration can become permanent.

In many other animals and plants influences of temperature and environment may very possibly produce permanent hereditary variations in a similar manner; but it is difficult — in fact almost impossible — to identify such cases with anything like certainty from the observations which have hitherto been made. Thus we find it stated that 'in Cashmere dogs soon become covered with a woolly hair;'* but we do not know who observed this, or who ascertained that such a change — if it really does occur — is transmitted. 'Merino sheep lose their fine wool when they are transported to a tropical climate;' but I have not been able to discover whether this loss occurs in the first, or in the course of several, generations. *We are thus left in uncertainty* as to the possibility of a direct climatic variation of a somatic part having taken place in these instances, which would again disappear in the next generation provided that the descendants were placed under the original climatic conditions. The same applies to the races of naked dogs from the tropics, such as the

* These statements are quoted from an essay by Giard, who takes them as a proof of the transmission of somatogenic modifications. *Cf.* 'L'Hérédité des modifications somatiques,' *Revue Scientifique*, December 6th, 1890.

Guinea dog, for 'they do not become covered with hair when transported to a temperate climate.' *

Many climatic varieties of plants may also be due wholly or in part to the simultaneous variation of corresponding determinants in some part of the soma and in the germ-plasm of the reproductive cells, and these variations must of necessity be hereditary. Temperature, and nutrition in its widest sense, affect the whole body of the plant, — the somatic-cells as well as the germ-cells. It cannot, however, at present be stated whether the determinants in the soma are in this case influenced more strongly than those which are still in the germ-plasm. It is conceivable, and, I am inclined to think, even most usual, that certain determinants are affected to the same extent whether the influence of the environment happens to act on them in the germ-plasm, or in any stage of somatic transformation. In this case the change may have been perhaps scarcely or not at all noticeable in the first generation, and may gradually have become apparent, and also transmissible, in the course of subsequent generations. On the other hand, there are probably many influences of environment which produce a considerable change in the body of the plant, without, however, modifying the corresponding determinants in the germ-plasm. The experiments made by Nägeli and many others on the genus *Hieracium* at any rate support this view, though they have hardly been carried on long enough to exclude the possibility of a very faint and gradual alteration occurring in the germ-plasm.

The question as to which influences are capable of simultaneously modifying the developing and growing soma and the corresponding determinants in the germ-plasm, even in a very different degree, can only be solved by future experiments. The cases of an apparent inheritance of somatogenic variations are due to this coincidence; — no others are, it seems to me, conceivable. All those influences, however, such as the use and disuse of a part, which can only affect this part itself in a specific manner, are incapable of producing a *corresponding* change in the respective determinants of the germ-cells, and consequently cannot lead to hereditary modifications. In such cases the

* Compare also the cases of degeneration in the descendants of the European dog in India, which have been carefully collected by Darwin in his 'Variation of Animals and Plants under Domestication,' Vol. I., p. 45.

external influence affects only the fully-formed organ, — such as a muscle which has become enlarged by exercise; for the influence consists in the increased activity of the organ, which takes place within it alone; the germ-plasm of the germ-cells, and even the determinant in the germ-plasm for the muscle in question, are not thereby affected. In all cases of functional hypertrophy or atrophy, the external influence affects none of the determinants, but only the fully-formed organs, — *i.e.*, groups of specific cells produced from determinants. In my opinion it is very probable that such twofold modifying influences of environment as we meet with in *P. phlœas*, can only occur when the determinants which have not yet been transformed into the organ, as well as the germ-cells, have been affected by the modifying influence. And this will be most likely to happen in those structures which, like the scales on the wings of butterflies, are formed at a later stage of the animal's existence, *and the determinants of which are consequently stored in an undeveloped condition in the idants of certain somatic cells during a great part of the ontogeny.* The wings of the butterfly arise as outgrowths from the hypodermis of the caterpillar. Before these outgrowths can be formed, the determinants for the wing-scales must be contained in the idioplasm of some of the cells of the hypodermis, but after their appearance they would be found in some of the cells in the rudiments of the wings. The wings at first are small, and contain by no means so large a number of cells as when full-grown, so that inactive determinants for several wing-scales must be contained in the idants of *one* nucleus. At a certain period in the course of further growth, however, the number of cells increases to such an extent that each determinant constitutes the idioplasm of a particular cell, and the modifying external influences seem then to have the greatest effect on these determinants. By means of experiments it may be possible to ascertain exactly when this occurs.

It might have been expected that in this section I should enter into the whole question of the possibility of the transmission of acquired variations, about which there has been so much dispute of late years, and that all the arguments and facts which have been put forward in favour of the theory should be discussed. But, as I have already remarked, this seems to be out of place in a theory of heredity, the object of which is to show whether this form of transmission is or is not possible from a theoretical point of view, and to ascertain further whether in the latter case such an *apparent* transmission might not possibly occur under certain circumstances, and to account for this theoretically. I have always emphasised the fact that it is easier to explain the transformation of species on Lamarck's principle; but this is no reason for the retention of a theory which cannot be accepted on theoretical grounds, unless no other explanation can be given for the facts. So far, my opponents have been unable to prove that this is the case.

The above explanation of the causes of the climatic variations of butterflies may perhaps convince some of those who have till now opposed my views that we are here not dealing blindly with mere principles, but with inductive methods. The view of the non-inheritance of acquired modifications has been especially opposed in America, principally by the palæontologists. It can certainly not be denied that certain facts in palæontology, such as the development of the feet and teeth in Ungulates, furnish us with an extremely fine and uninterrupted series of forms which may apparently be very easily explained on the assumption of the inheritance of acquired modifications. But is not this exactly what would be expected, in case phylogeny essentially depends on selection — that is, on an increasingly complete adaptation to certain external conditions of life of a purely general nature? It appears to me that neither the completeness of the developmental series, nor the close relation of the nature of the modifications to function, give any clue to the causes which have produced these series. They may quite as well have originated by continued selection alone, as by continued transmission of functional variations.

The eminent American naturalist, Lester Ward,* is, however, in error if he supposes that the proof that climatic influences are capable of modifying the germ-plasm, contains all that is required by the neo-Lamarckian school. Further details will be given in the next chapter as to the manner in which I now suppose variation has originated: but quite apart from this, the supposition that climatic influences can produce modifications of the germ-plasm, has certainly nothing to do with the view that

* *Cf.* the essay directed against my views by this author ('Neo-Darwinism and Neo-Lamarckism,' Washington, 1891), which is written from the thoroughly objective and truly scientific point of view.

functional modifications of any particular organ can cause a corresponding change in the germ-plasm. I believe I have here furnished a proof that the former supposition is a correct one: the onus of proof of the latter lies with the neo-Lamarckians.