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ON THE SUPPOSED BOTANICAL PROOFS

OF THE

TRANSMISSION OF ACQUIRED CHARACTERS.

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TRANSMISSION OF ACQUIRED CHARACTERS.

In a lecture on heredity, delivered in 1883[1], I first brought forward the opinion that acquired characters cannot be transmitted; and I then stated that there are no proofs of such transmission, that its occurrence is theoretically improbable, and that we must attempt to explain the transformatio of species without its aid. Since that time many biologists have expressed their opinions upon the subject, some of them agreeing with me, while others have taken the opposite side. It is unnecessary to allude to those who have attacked my opinions without first understanding the real point in dispute, which turns upon the true meaning of the phrase 'acquired character.' I think it is now generally admitted that a very important problem is involved in this question, the solution of which will contribute in a decisive manner towards the formation of ideas as to the causes which have produced the transformation of species. For if acquired characters cannot be transmitted, the Lamarckian theory completely collapses, and we must entirely abandon the principle by which alone Lamarck sought to explain the transformation of species,—a principle of which the application has been greatly restricted by Darwin in the discovery of natural selection, but which was still to a large extent retained by him. Even the apparently powerful factors in transformation—the use and disuse of organs, the results of practice or neglect—cannot now be regarded as possessing any direct transforming influence upon a species. And the same is true of all the other direct influences, such as nutrition, light,

[1] See the second Essay 'On Heredity.'

moisture, and that combination of different influences which we call climate. All these, with use and disuse, may perhaps produce great effects upon the body (*soma*) of the individual, but cannot produce any effect in the transformation of the species, simply because they can never reach the germ-cells from which the succeeding generation arises. But if—as it seems to me—the facts of the case compel us to reject the assumption of the transmission of acquired characters, there only remains one principle by which we can explain the transformation of species—the direct alteration of the germ-plasm, however we may imagine that such alterations have been produced and combined to form useful modifications of the body.

The difficulty of understanding these processes of transformation is by no means lightened by abandoning the Lamarckian theory. The difficulty in fact becomes much greater, for we are now compelled to seek a different explanation of many phenomena which were previously believed to be understood. But this can hardly be regarded as a reason for not accepting the view: for we are in want of a correct explanation rather than one which is easy and convenient. We seek truth, and when we recognize that our path is leading in a wrong direction, we must leave it and take another road even if it presents more difficulties.

My theory rests, on the one hand, upon certain theoretical considerations which will be mentioned below, and which I have attempted to develope in previous papers [1]. On the other hand, it rests upon the want of any actual proof of the transmission of acquired characters. My theory might be disproved in two ways,—either by actually proving that acquired characters are transmitted, or by showing that certain classes of phenomena admit of absolutely no explanation unless such characters can be transmitted. It will be admitted, however, that we must be very cautious in accepting proofs of this latter kind, for the impossibility of explaining a given phenomenon may be merely temporary, and may disappear with the progress of science. No one could have explained the useful adaptations so common in animals and plants, before the

[1] Consult 'Ueber die Vererbung,' Jena, 1883; 'Die Kontinuität des Keimplasmas,' Jena, 1885; 'Ueber die Zahl der Richtungskörper und über ihre Bedeutung für die Vererbung,' Jena, 1887. These papers are translated as the second, fourth and sixth Essays in the present volume.

light of the theory of natural selection had fallen on these phenomena; at that time we should have been far from right if we had assumed that organisms possess a power which causes them to respond to external influences by useful modifications, a power unknown elsewhere, entirely unproved and only supported by the fact that at that time it did not seem possible to explain the phenomena in any other way.

Although my theory has not been disproved, I will nevertheless attempt to bring into further accordance with it certain phenomena which seem at first sight to oppose it. I first began to take this course in my paper 'On Heredity[1].' In that paper I attempted to show how the fact that disused organs become rudimentary may be readily explained without assuming the transmission of acquired characters; and also that the origin of instincts may in all cases be referred to the process of natural selection[2], although many observers had followed Darwin in explaining them as inherited habits,—a view which becomes untenable if the habits adopted and practised in a single life cannot be transmitted.

Other phenomena which appeared to present difficulties were also considered and brought into accordance with the theory, and I think that I have been successful in showing that adequate and simple explanations may be given.

There certainly remain many phenomena which seem to be opposed to my theory and for which a new explanation must be found. Thus Romanes[3], following Herbert Spencer[4], has recently pointed to the phenomena of correlation as a proof of the transmission of acquired characters; but, at no distant time, I hope to be able to consider this objection, and to show that the apparent support given to the old idea is in reality insecure and breaks down as soon as it is critically examined. I believe that I shall be able to prove that correlation cannot be used as the indirect proof of an hypothesis, of which all direct evidence is still com-

[1] See the second Essay.

[[2] See R. Meldola in Ann. and Mag. Nat. Hist., 1878, vol. i. pp. 158–161. The author discusses many cases among insects in which instinct is related to protective structure or colouring: he also considers that instinct is to be explained by the principle of natural selection which accounts for the other protective features.—E. B. P.]

[[3] See 'Nature,' vol. 36, pp. 491–407.—E. B. P.]

[[4] See 'The Factors of organic Evolution' in 'The Nineteenth Century' for April and May 1886.—E. B. P.]

pletely wanting. It must not be forgotten that the *onus probandi* rests with my opponents: they defend the assertion that acquired characters can be transmitted, and they ought therefore to bring forward actual proofs; for the mere fact that the assertion has been hitherto accepted as a matter of course by almost everyone, and has only been doubted by a very few (such as His, du Bois-Reymond, and Pflüger), cannot be taken as any proof of its validity. Not a single fact hitherto brought forward can be accepted as a proof of the assumption. Such proofs ought to be found: facts ought to be discovered which can only be understood with the aid of this hypothesis. If, for instance, it could be shown that artificial mutilation spontaneously re-appears in the offspring with sufficient frequency to exclude all possibilities of chance, then such proof would be forthcoming. The transmission of mutilations has been frequently asserted, and has been even recently again brought forward, but all the supposed instances have broken down when carefully examined. I think I may here safely omit all further reference to the proofs dependent upon transmitted mutilations, especially as Döderlein[1] has already, in the most convincing manner, disposed of the argument derived from the tailless cats which were so triumphantly exhibited at the last meeting of the Association of German Naturalists[2].

I now come to the real subject of this paper—the supposed botanical proofs of the transmission of acquired changes. The botanist Detmer has recently brought forward certain phenomena in vegetable physiology[3], as a support for the transmission of such changes, and although I do not believe that they will bear this interpretation, the discussion of them may perhaps be useful. I am even inclined to think that these and a few other phenomena in vegetable physiology, upon which I shall also touch, are very likely to throw new light upon the whole question which has been so frequently misunderstood. I should have preferred to leave this discussion to a botanist, but I do not know whether my views will meet with any support from the followers of this subject, and I must therefore attempt the discussion myself. And perhaps it is of some assistance in clearing up the question, for one who is not

[1] See 'Biol. Centralbl.' Bd. VII. No. 23.

[2] See the next Essay (VIII).

[3] Detmer, 'Zum Problem der Vererbung,' Pflüger's Archiv f. Physiologie, Bd. 41, (1887), p. 203.

accustomed to the usual botanical views, and is more conversant with other classes of biological knowledge, to consider the facts brought to light by modern botany, from a general point of view. Of course I shall not attempt to question the validity of the observations, nor even the accuracy with which the facts have been interpreted. I shall only deal with the conclusions which may be drawn from the facts, and I do not think that it is absolutely necessary that such criticism should be made by a botanist. Questions of general biological significance such as that of heredity cannot be entirely solved within the single domain of either zoological or botanical facts. Both botanists and zoologists must give due weight to the facts of the province which is not their own, and must see whether the views which they have chiefly gained in the one province can be applied to the other, or whether phenomena occur in the latter which are in opposition to their previously formed views and which cause them to be abandoned or modified.

Detmer begins by bringing forward certain facts which prove, as he believes, that rather important changes in the organism can be directly produced by external influences. He is of opinion that I under-estimate the weight of these influences, and that I make light of the changes which may thus arise in a single individual life. But obviously, it is of no importance for the question of the transmission of acquired characters, whether the changes directly produced by external influences upon the *soma* of an individual are greater or smaller: the only question is whether they can be transmitted. If they can be transmitted, the smallest changes might be increased by summation in the course of generations, into characters of the highest degree of importance. It is in this way that Lamarck and Darwin have supposed that an organism is transformed by external influences. It is therefore interesting to see what Detmer considers to be a change which has been directly effected. We can in this way gain a very distinct appreciation of the difference in views which is caused by the different spheres of experience which belong to botany and zoology. It will be useful to gain a clear idea of the differences which are thus caused.

Detmer first alludes to the dorso-ventral structure of the shoots of *Thuja occidentalis*, chiefly shown in the fact that the upper sides of these shoots contain the green palisade cells, while the under sides which are turned away from the light possess green spheroidal (isodiametric) cells. If the branches of *Thuja* are turned upside down and fixed in this position before the production of new shoots, it is found that the anatomical structure of the latter, when developed, is reversed. The side of the shoot which was destined to become the under side, but which was artificially compelled to become the upper side, assumes the structure of the upper side and developes the characteristic palisade parenchyma; and on the other hand, the under side which was intended to become the upper side developes the spongy parenchyma which is characteristic of the under side. From these facts Detmer concludes that the dorso-ventral structure of the shoots of *Thuja* has resulted from the continual operation of an external force, and that the light must be considered as the cause of the structural change.

But such a conclusion obviously depends upon a confusion of ideas. No one will doubt that the light was the stimulus which led to the reversal of the structures in the shoot, but this is a very different thing from maintaining that it was the cause which conferred upon the *Thuja*-shoot the power of producing palisade and spongy parenchyma. When a phenomenon only occurs under certain conditions, it does not follow that these conditions are the cause of the phenomenon. A certain temperature is necessary for the development of a bird in the egg, but surely no one will maintain that the temperature is the cause of the capacity for such development. It is obvious that the egg has acquired the power of producing a bird chiefly as the result of a long phyletic course of development which has led to such a chemical and physical structure in the egg and the fertilizing sperm-cell, that after their union and development, a bird, and only a bird of a particular species, must be produced. But of course certain conditions must be fulfilled in order that such development may take place; and a definite temperature is one of these conditions of development. Thus we may briefly say that the physical nature of the egg is the cause of its development into a bird, and we may similarly maintain that the physical nature of a *Thuja*-shoot, and not the influence of light, is the cause of the development of tissues which are characteristic of the species. In the development of such a shoot the light plays precisely the same part which is played by temperature in the development of a bird: it is one of the conditions of development.

There is nevertheless a difference between these two cases in that the *Thuja*-shoot possesses the possibility of development in two different ways instead of only one. The upper side of the shoot can assume the structure of the under side and *vice versa*, and this structural reversal depends upon the way in which the light is thrown upon the shoot. But even if the light causes the structural reversal, does this justify us in assuming that the structure itself is also the direct consequence of the influence of light? I see no reason for rejecting the supposition that the physical nature of part of a plant may be of such a kind that this or that structure may be produced according as this or that condition of development prevails. Thus with stronger light the structure of the upper side of the shoot developes; with weaker light, the structure of the under side. But this physical nature of the *Thuja*-bud depends, like that of a bird's egg, upon its phyletic history, as we must assume to be the case with the germs producing all individual developments. It is therefore quite impossible to interpret the reversal of the structure in the *Thuja*-shoot as the result of modification produced by the direct influence of external conditions. It is an instance of double adaptation—one of those cases in which the specific nature of a germ, an organism, or a part of an organism, possesses such a constitution that it reacts differently under the incidence of different stimuli.

An entirely analogous example of reversal occurs in the climbing shoots of the Ivy, and is described in Sachs' lectures on the physiology of plants. Such shoots produce leaves only on the side directed towards the light, and roots (which are made use of in climbing) only upon the opposite side. If however the position of the plant be altered so that the root-bearing side is turned towards the light, while the leafy side is shaded, a reversal occurs, so that from that time the former only produces leaves, and the latter nothing but roots. In other words, the Ivy-shoot reacts under strong light with the production of leaves and under weak light with the production of roots, just as litmus-paper becomes red with an acid and blue with an alkali. The physical nature of the Ivy-shoot was present before the production of either structure, and was no more due to the action of light itself, than the physical nature of litmus-paper is due to an acid or an alkali. But this is quite consistent with the possession of a physical nature which reacts differently under the two different conditions afforded by light and shade.

No one would think of bringing forward the changes in the colour of the green frog (*Hyla*) as a proof of the power of direct influences in causing structural modifications in the animal body. The frog is light green when it is resting upon green leaves, but it becomes dark brown or nearly black when transferred to dark surroundings. This is an obvious instance of adaptation, for the changes in the colour of the frog depend upon a complex reflex mechanism. The changes in the shape of the chromatophores of the skin are not produced by the direct influence of the different rays of light upon the body-surface, but in consequence of the action of these rays upon the retina. Blind frogs do not react under the changes of light. Hence it is impossible that any one can maintain that the skin of the frog has gained its green colour as the direct result of the green light reflected from its usual surroundings. It must be admitted that in this and in all similar cases, there is only one possible explanation, viz. an appeal to the operation of natural selection. It may be objected that we are not here dealing, as in the *Thuja* and Ivy, with changes in the course of ontogenetic development following upon the occurrence of this or that external condition, but only with the different reactions of a mature organism. But nevertheless, cases of the former kind appear to be also present in the animal kingdom.

Thus the very careful and extensive investigations of Poulton[1] upon the colours of certain caterpillars have distinctly shown that some species possess the possibility of development in two directions, and that the actual direction taken by the individual is decided by the influence of external conditions. Poulton surrounded certain larvae of Geometrae with an abundance of dark branches, in addition to the leaves upon which they fed. When such conditions prevailed from the beginning of larval life, the caterpillars as they developed, gradually assumed the dark colour of the twigs and branches upon which they rested. When other larvae of the same species (and in

[[1] Dr. Weismann is here alluding to experiments upon the larvae of *Rumia Crataegata*. A short account of the results will be found in the Report of the British Association at Manchester (1887), and in 'Nature,' vol. 36, p. 594. I have now obtained similar results with many other species (see Trans. Ent. Soc., Lond. 1888, p. 553); but many of the results are as yet unpublished.—E. B. P.]

many experiments hatched from the same batch of eggs) were similarly exposed to the green leaves of the same food-plant, they did not indeed become bright green like the leaves, but were invariably of a much lighter colour than the other larvae, while many of them gained a brownish-green tint. The larvae of *Smerinthus ocellatus*[1] also possess the power of assuming different shades of green and of thus approaching, to some extent, the green of the plant upon which they happen to live. It is quite impossible to explain the phyletic development of the green colour of these and other caterpillars as due to the direct action upon the skin of the green light reflected from the leaves upon which they sit. The impossibility of such an effect was pointed out long ago by Darwin, and also followed from my own investigations. Here, as in the other cases, the only possible solution is afforded by natural selection. The colour of the caterpillars has become gradually more and more perfectly adapted to the colour of the leaves,—and often to the particular side of the leaves upon which these animals rest, —not by the direct effect of reflected light, but by the selection of those individuals which were best protected. Poulton's experiments quoted above prove that certain species which occur upon different plants with different colours (or even in some cases upon the differently coloured parts of the same plant), present us with a further complication in the process of adaptation, inasmuch as each individual has acquired the power of assuming a lighter or darker colour[2]. The light which falls upon a single individual

[[1] See the editorial notes by Raphael Meldola, in his translation of Weismann's 'Studies in the Theory of Descent' (the Essay on 'The Origin of the Markings of Caterpillars,' pp. 241 and 306): also E. B. Poulton, in 'Proc. Roy. Soc.,' vol. xxxviii. pp. 296–314; and in 'Proc. Roy. Soc.,' vol. xl. p. 135.—E. B. P.]

[[2] Professor Meldola first called attention to the scattered instances of the kind here alluded to by Professor Weismann, in 1873: see 'Proc. Zool. Soc.,' 1873, p. 153. The author explains the relation of this 'variable protective colouring' to other protective appearances, and he is strongly of the opinion that the former as well as the latter is to be explained by the action of the 'survival of the fittest.'

The validity of Dr. Weismann's interpretation of these effects as due to adaptation, through the operation of natural selection, is conclusively proved by the following facts. The light reflected from green leaves becomes the stimulus for *the production of dark brown pigment* in those cases in which the leaves constitute the surroundings for many months. Under these circumstances the leaves of course become brown at a relatively early date, and protection is thus afforded for the remainder of the period, although the dark pigment is produced before the change in the colour of the leaf. Instances of this kind are seen in the colours of cocoons spun among leaves by certain lepidopterous larvae (see 'Proc. Ent. Soc. Lond.,' 1887, pp.

caterpillar during the course of its growth determines whether the lighter or darker colour shall be developed. Here therefore we have a case exactly parallel to that of the *Thuja*-shoot in which the palisade or spongy parenchyma is developed according to the position in which the shoot is fixed.

As far as it is possible in the present condition of our knowledge to offer any opinion upon the origin of sex in bisexual animals, it may be suggested that this problem is also capable of an essentially similar solution. Each germ-cell may possess the possibility of developing in either of two directions, the one resulting in a male individual, and the other resulting in a female, while the decision as to which of the two possible alternatives is actually taken may rest with the external conditions. We must, however, include among the external circumstances everything which is not germ-plasm. Moreover, this explanation is by no means certain, and I only mention it as an instance which, if we assume it to be correct, further illustrates my views upon the phenomena presented by the *Thuja*-shoot.

The two other facts brought forward by Detmer as proofs of the transforming power of external influences can be explained in precisely the same manner. These instances are—the fact that *Tropaeolum* when grown in moist air produces leaves with anatomical characters different from those produced when the plant is grown in dry air; and the differences in the structure of the leaves of many plants, according as they have been grown in the sun or shade respectively. Such differences do not by any means afford proof of the direct production of structural changes by means of external influences. How would such an explanation be consistent with the fact that the leaves are, in all these cases, changed in a highly purposeful manner? Or is it assumed that these organs were so constituted from the beginning, that they are compelled to respond to external conditions by the production of useful

l, li, and 1888, p. xxviii), the cocoons of the same species being of a creamy white colour when spun upon white paper.

Conversely, the light reflected from the same surfaces serves as the stimulus for *withholding pigment* in the cases alluded to by Dr. Weismann (larvae of *R. Crataegata*, &c.), in all of which the organism only remains in contact with the leaves while they are green, viz. at a time when the dark colour would be disadvantageous.

Hence precisely opposite effects are produced by the operation of the same force; the nature of the effect which actually follows in any case being solely determined by the advantage afforded to the organism.—E. B. P.]

changes? Any one who made such an assertion nowadays, or who even thought of such a thing as a possibility, would prove that he is entirely ignorant of the facts of organic nature, and that he has no claim to be heard upon the question of the transformation of species. The very first necessity in any scientific question is to gain acquaintance with that which has been thought and said upon the subject. And it has been frequently shown that whole groups of useful characters cannot by any possibility have been produced by the direct action of external influences. If a caterpillar, which hides itself by day in the crevices of the bark, possesses the same colour as the latter, while other caterpillars which rest on leaves are of a green colour, these facts cannot be explained as the results of the direct influence of the bark and leaves. And it would be even less possible to explain upon the same principle all the details of marking and colour by which these animals gain still further protection. If the upper side of the upper wings of certain moths is grey like the stone on which they rest by day, while in butterflies the under side of both wings which are exposed during rest, exhibits analogous protective colours, these facts cannot be due to the direct influence of the surroundings which are resembled, but, if they have arisen in any natural manner, they must have been indirectly produced by the surroundings. One may reasonably complain when compelled to repeat again and again these elements of knowledge and of thought upon the causes of transformation!

Any one who remembers these things, and is aware of the countless number of purposeful characters which cannot possibly depend upon such direct influences, will be very cautious in yielding to any single instance which at first sight appears to be the direct consequence of external conditions. If Detmer had been thus cautious he would hardly have written the following sentence as a *résumé* of the physiological experiments on plants which have been already alluded to: ‘In certain cases it is possible, as we have seen, to artificially modify the anatomical structure of certain parts of plants. In such cases the relation between the structure and the external influences is undoubtedly clear: the latter act as the cause; the anatomical structure of the members of the plant is the consequence of this cause.’ A little more logic would have prevented the author from expressing such an opinion, for, as has been already shown, it is founded on a confusion between the true cause of a phenomenon and one of the conditions which are necessary for its production. We might as well consider the phenomena of *geotropism*, *hydrotropism*, and *heliotropism*—which have been established, and investigated in such a brilliant way by modern vegetable physiologists—as the direct results of the attraction of the earth, of water, and of light; and it is not improbable that some botanists are even inclined to make this assumption. And yet it is perfectly easy to show that this cannot be the case. By geotropism we mean the power possessed by the parts of a plant of growing along lines which make certain angles with the direction of the earth's attraction. For example, the chief root grows parallel with the earth's attraction, viz. towards the centre of the earth, and it is described as positively geotropic: conversely the main shoot grows along the same line but in an opposite direction, and it is negatively geotropic. But geotropism is not a primitive attribute of the plant, and it is even now absent from those plants which, like many Algae, have no definite position. Geotropism cannot have arisen before plants first became fixed in the earth. If any one were to assume that the direct influence of gravity, continuous through countless generations, had at length conferred upon the root the power of growing in a geotropic direction, how would it be possible to explain the fact that the shoot which has been under precisely the same influence has acquired the power of growing in an exactly opposite direction? The characteristic differences between root and shoot cannot have appeared until the plant became fixed in the ground, and how can we imagine that the same influence of gravity has since that time directly produced the two antagonistic results of positive and negative geotropism, in two structures, which were originally and essentially similar? It should also be remembered that it is only the main root which exhibits true positive geotropism. The lateral roots form angles with the main root, and do not therefore grow towards the earth's centre; and the same is true of the lateral shoots which grow obliquely, and not perpendicularly upwards, like the main shoot. Moreover the angles which the lateral roots make with the main root, and the lateral shoots with the main shoot, are quite different in different species. How is it possible that all these different modes of reaction witnessed in the different parts of plants can be the direct results of one and the same external force? It is quite obvious that these are all cases of adaptation. The main root has not acquired the power of growing perpendicularly downwards under the stimulus of gravity, because this force has acted upon it for numberless generations, but because such a direction for such a part was the most useful to the plant. Hence natural selection has conferred upon the root the power of reacting under the stimulus of gravity by growing in a direction parallel to this force. For the main shoot, the opposite reaction was the most useful and has been established by natural selection, while still another reaction has been similarly established for the lateral roots and another for the lateral shoots.

Each part of a plant has received its special mode of reacting under the stimulus of gravity because it was useful for the whole plant, inasmuch as the position of its different parts relatively to one another and to the soil became thus fixed and regulated. These modes of reaction have become different in different species, because the conditions of life peculiar to each require special arrangements.

The same argument also holds with regard to heliotropism. The power of growing towards the light possessed by green shoots cannot be a primitive character of the plant: it must have arisen secondarily. If it were an essential and original character it could not be reversed in certain parts of the plant; but the roots are negatively heliotropic, for they grow away from the light. There are also shoots, such as the climbing shoots of Ivy, which are similarly negatively heliotropic. Whenever the heliotropic power is thus reversed in shoots, the change is of a useful kind. Thus the shoots of the Ivy gain the power of clinging closely to a perpendicular wall or to some horizontal plane [1]. In this case, however, it is only the shoot which is negatively heliotropic, its leaves turn towards the light; and the same is true of the flower-bearing shoots which do not climb. All these are clearly adaptations and not the results of direct influence. The light only provides the stimulus which calls forth the characteristic reaction from each part of the plant, but the cause of each peculiar reaction lies in the specific nature of the part itself which has not been produced by light, but as we believe by processes of natural selection. If this explanation

[1] Compare Sachs, 'Lectures on the Physiology of Plants,' translated by H. Marshall Ward, p. 710.

does not account for the facts we may as well abandon all attempts at understanding the useful arrangements in organisms.

Sachs has used the term *anisotropism* to express the fact that the various organs of a plant assume the most diverse directions of growth under the influence of the same forces. He also states that anisotropism is one of the most general characteristics of vegetable organization, and that it is quite impossible to form any idea as to how plants would appear or how they could live if their different organs were not anisotropic. Since anisotropism is nothing more than the expression of different kinds of susceptibility to the action of gravity, light, &c., it is obvious that the configuration of the plant is to be traced to such specific susceptibilities.

Now these specific susceptibilities cannot have been produced by the direct effect of the various external influences (as was shown above), and the only other possible explanation is to recognise them as adaptations, and to admit that they have arisen by the operation of natural selection upon the general variability of plant organization.

Simple as these conclusious are, I have failed to meet with them in any of the writings of botanists, and they may perhaps be of use in helping to shake the vaguely-felt opinion that the characters of plants are to be chiefly referred to the direct action of external influences.

At all events it cannot be maintained that the phenomena of anisotropism support the opinion mentioned above; and the mere assertion that it is highly probable that hereditary characters arise as the result of external influences, is no more than the expression of an unfounded individual opinion. It is remarkable that Detmer should make such an assertion as the outcome of his discussion of the reversed *Thuja*-shoot, &c., for even if we admit that the dorso-ventral structure of the shoot is—as Detmer believes—the direct and primary effect of the action of light, the experiment with the reversed shoot would prove that no part of this effect has become hereditary. Although the upper side of the shoot has produced the palisade parenchyma under the influence of light for thousands of generations, there is nevertheless no tendency towards the establishment of any hereditary effect, for as soon as the upper side of the growing shoot is artificially transformed into the under side, its normal structure is at once abandoned. Hence so far from lending any support to the assumption that acquired characters can be transmitted, Detmer's experiment rather tends to disprove this opinion.

I think I have sufficiently shown that Detmer's reproach—that I have under-estimated the effects of external influences upon an organism—may be fairly directed against its author. If we can believe that every structural arrangement in plants, which depends upon certain external conditions, has been produced in a phyletic sense by these latter, it becomes very easy to explain the transformation of species; but in accepting such an explanation we are building without any foundation, for the proof that acquired characters can be transmitted has yet to be given.

As a further disproof of my views Detmer quotes the so-called phenomena of correlation in plants, and he believes that these instances help us to conceive how the acquired changes of the body (*soma*) of the plant may also influence the sexual cells. If the apical shoot of a young spruce fir be cut off, one of the lateral shoots of the whorl next below the section rises and becomes an apical shoot: it not only assumes the orthotropic growth of such a shoot, but also its mode of branching. The phenomenon itself is well known, and I have often observed it myself in my garden without making any botanical experiments; for this experiment is not uncommonly made by Nature herself, when the apical shoot is destroyed by insects (for example the gall-making *Chermes*). The change of the lateral into an apical shoot occurs here in consequence of the loss of the true apical shoot, and is therefore really dependent upon it. The only difficulty is to understand how these and many other kindred phenomena can be considered to prove the transmission of acquired characters. That correlation exists between the parts of an organism, that correlated changes are not only common but nearly always accompany some primary change, has been perfectly well known since Darwin's time, and I am not aware that it has been disputed by any one. I further believe that hardly any one would maintain that it is impossible for the reproductive organs to be influenced by correlation. But this is very far from the admission that such changes would occur in the germ-cells as would be necessary for the transmission of acquired characters. For such transmission to occur it would be necessary for the germ-plasm (the bearer of hereditary tendencies) to undergo a transformation corresponding to that produced by the external influences;—such a transformation as would cause the future organism to spontaneously develope changes similar to those which its parent had acquired. But since the germ-plasm is not an organism in the sense of being a microscopic facsimile which only has to increase in size in order to become a mature organism, it is obvious that the developmental tendencies must exist in the specific molecular structure, and perhaps also in the chemical constitution of the germ-plasm itself. It therefore follows that the changes in the germ-plasm which would be required for the transmission of an acquired character must be of an entirely different nature from the change itself acquired by the body of the parent plant: and yet it is supposed that the former is produced by the latter as a result of correlation. I will illustrate this by an example. Let us suppose that the influence of climate had caused a plant to change the form of its leaves from an ovate into a lobate shape: now such a change could not be transferred to the germ-plasm in the pollen and the ovules, as anything similar to leaves or the form of leaves; for such specialized morphological features have no existence in the germ-plasm. The only thing which could happen would be changes in its molecular structure which bear no resemblance to those changes which are implied by the direct alteration of the form of the leaf in the parent plant. Any one who clearly appreciates this difficulty will hesitate in admitting the possibility of the transmission of acquired characters, because it is possible that the sexual cells may be affected by correlated influences. If the change in the form of a leaf exercises any influence at all upon the germ-plasm, why should it produce a corresponding (in the above-mentioned sense) change in its molecular structure? Why should it not produce some other out of the immense number of possible changes? There must be as many possible changes in the structure of germ-plasm as there are possible variations in each part of a plant that arises from it. Why then should the corresponding change always occur,—a change which had never previously existed in the whole phyletic development of the organic world; for the plant with the latest modification can have never existed before? The occurrence of a particular change out of the countless possible changes would be about as likely as if one out of a hundred thousand pins thrown out of a window were to balance on its point when it reached the ground.

The assumption scarcely deserves to be called a scientific hypothesis, and yet it must be made by all who accept the transmission of acquired characters,—that is unless they adopt the hypothesis of pangenesis, which is quite as improbable, and which even Darwin did not look upon as a real, but only as a formal explanation.

Detmer is also greatly mistaken when he says that I refuse to admit the transmission of acquired characters, because I am prejudiced in favour of my doctrine of the continuity of the germ-plasm. This doctrine is either right or wrong, and there is no middle course: to this extent I quite admit that I am prejudiced. But the question as to whether acquired characters can be impressed upon the germ and thus transmitted would not be by any means settled in this way; for even if we admit that the germ-plasm is not continuous from one generation to another, but that it must be produced afresh in each individual, this would by no means necessarily imply that it would potentially receive and retain every change produced in every part of the individual, and at any time in its life. It seems to me that the problem of the transmission or non-transmission of acquired characters remains, whether the theory of the continuity of the germ-plasm be accepted or rejected.

I will now proceed to examine the last group of phenomena which Detmer brings forward in favour of the transmission of acquired characters. He charges me with not having taken into account, in discussing the problem of heredity, the very important facts which are known about the strange phenomena of 'after-effect' in plants. Among these 'after-effects' are the following.

If vigorous plants of the sun-flower, grown in the open air, be cut off close to the ground and transferred to complete darkness, the examination of a tube fixed to the cut surface of the stem will show that the escape of sap does not take place uniformly, but undergoes periodical fluctuation, being strongest in the afternoon and weakest in the early morning. Now the cause of this daily periodicity in the flow of sap depends upon the periodical changes due to the light to which the plant was exposed when it was growing under normal conditions. When plants which have been grown in darkness from the first are similarly treated, the flow of sap does not exhibit any such periodicity.

Another instance is as follows:—it is well known that darkness accelerates, while light retards the growth of plants, and therefore plants usually grow more strongly by night than by day. If now plants are transferred from the open air into constant darkness, the periodicity in their growth does not immediately disappear, and often persists for a long time as a phenomenon of after-effect.

The opening and closing of the leaves of *Mimosa pudica* also takes place periodically under natural conditions, the leaves closing at dusk as a result of changes in the stimulus provided by the light. In this case also, when the plants are transferred to constant darkness, the periodicity in the movements of the leaves continues for several days.

All this is certainly very interesting, and it proves that periodical stimuli produce periodical processes in the plant, which are not immediately arrested when the stimulus is withdrawn, and only become uniform gradually and after the lapse of a considerable time. But I certainly claim the right to ask what connexion there is between these facts and the transmission of acquired characters. All these peculiarities produced by external influences remain restricted to the individual in which they arose; most of them disappear comparatively soon, and long before the death of the individual. No example of the transmission of such a peculiarity is known. Although successive generations of sunflowers have been exposed for thousands of years to the daily alternation of light and darkness, the periodicity in the flow of sap has not become hereditary, and does not take place at all in plants which have always been kept in darkness. Detmer specially tells us that we can even reverse the periods of opening and closing the leaves in *Mimosa pudica* by keeping them in darkness during the day, but exposed to light at night; an experiment which was performed by Pfeffer. Here again we see the proof that influences which have acted upon countless generations have left no impression whatever upon the germ-plasm.

Detmer himself admits this when he says that the after-effects are only witnessed during the life of the individual, but he nevertheless adds that he has been for many years convinced that the phenomena of heredity and after-effect differ in degree and not in kind. He even goes so far as to assert that, in spite of the obvious non-transmission of after-effect, the similarity between the natures of these two classes of phenomena cannot escape the intelligent observer.

It seems to me that this question does not demand the attention of the observer (for the observations have already been made) so much as that of the thinker. It is not a correct train of reasoning to conclude that after-effect and heredity are identical in nature, from the fact that certain periodical influences, acting upon a single individual, set up periodical physiological processes which continue for a time after the influences have ceased to act. We might almost as well argue that the oscillations of a pendulum, which continue as after-effects when the pendulum has been set going, are of an identical nature with the process of heredity. All these phenomena have indeed this much in common:—a cause which acted at some time in the past, but which is no longer visible at the time when the phenomenon appears. But the likeness ends here, and the supposed identity in nature merely depends upon wild speculation. One difference is very obvious, for the phenomena of after-effect gradually cease after the withdrawal of the stimulus, just like the oscillations of the pendulum, while the phenomena of heredity continue without any interruption. As far as heredity is concerned the physiological processes of after-effect are not distinguishable from any of the other well-known acquired characters which are recognizable as morphological changes. After-effects are not transmitted, and compared with this fact but little importance can be attached to the use of vague analogies by Detmer, who would wish to conclude that heredity is only the after-effect of processes which had been set going in the parent organism.

At the end of his paper Detmer applies the ideas which he has gained from the consideration of after-effect to certain phenomena in the normal life of plants. He suggests that the periodical change of leaf in trees and shrubs may have been produced by the direct effect of climate. If branches bearing winter buds are cut off in the autumn and are placed in a hot-house, with their cut ends in water, the buds do not at once develope, and months may often elapse before they begin to break. He argues that this experiment proves that the annual periodicity of the plant no longer depends directly upon external influences; these latter produced the periodicity at some earlier time, but it has been gradually fixed in the organism by after-effect and heredity (!), so that its disappearance does not now take place when the stimulus is withdrawn, and changes would only happen very gradually under the influence of changed climatic conditions. He considers that this is proved from the fact that our cherry has become an evergreen in Ceylon.

Such are Detmer's opinions, and every one will agree with him in believing that the periodical change of leaf in temperate climates has been produced in relation to the recurring alternation of summer and winter. This is certainly the case, and it cannot be doubted that the character has become fixed by heredity. Where, however, is the proof that this hereditary character has been produced by the direct influence of climate? What right have we to look upon the hereditary appearance of the character as an after-effect of the direct influence exerted by changes of temperature upon previous generations? Such an opinion derives but little support from the previously described experiments upon after-effect, which showed that these phenomena were never hereditary.

It appears to me that there are certain points in this change of leaf and its accompanying phenomena, which distinctly indicate that natural selection has been at work. Can Detmer imagine that the brown scales which form the characteristic protective covering of winter buds have been produced by the direct action of the cold? If, however, the peculiar structure of these buds is to be referred to the specific constitution of the individual rather than to the direct effects of climate, would it be so very improbable for their physiological peculiarity of lying dormant for several months to have been developed simultaneously with the structure, by the operation of natural selection? And if this explanation be correct, we can at once see why the character has become hereditary, for natural selection works upon variations of the germ-plasm, and these are transferred from one generation to another with the germ-plasm itself.

But Detmer attempts to establish the converse conclusion, and he argues that the hereditary change of leaf has been abandoned under the long-continued effect of changed climatic conditions; but this opinion is based upon the single instance of the alteration in the habit of the European cherry in Ceylon. If it were proved that our cherry, grown from seed in Ceylon and propagated by seed for several generations, became evergreen gradually and not suddenly in the first generation: if, under such circumstances, it came to retain its leaves in the autumn and ceased to produce the dormant winter buds:—then indeed the transmission of acquired characters could hardly be doubted. I am not a botanist, but I believe I am right in supposing that the wild cherry reproduces itself by seeds, while the edible domesticated cherry is propagated by grafting. Grafts are, however, parts of the *soma* of a previously existent tree, and we are not therefore concerned, in this method of propagation, with a succession of generations, but with the successive distribution of one and the same individual over many wild stocks. But no one will doubt that one and the same individual can be gradually changed during the course of its life, by the direct action of external influences. The really doubtful point is whether such changes can be transmitted by means of the germ-cells. If, as I presume, the English in Ceylon do not care to eat wild cherries but prefer the cultivated kinds, it follows that the branches which bear fruit in that island have not been developed from germ-cells, at any time since their introduction, and there is nothing to prevent them from gradually changing their anatomical and physiological characters in consequence of the direct influence of climate.

Hence the instance which Detmer looks upon as plainly conclusive, can hardly be accepted in support of such a far-reaching assumption as the transmission of acquired characters.

It is therefore clear that none of the facts brought forward by Detmer really afford the proofs which he believes that they offer. But another botanist, Professor Hoffman of Marburg, well known for his long-continued experiments on variation, has recently called attention to certain other botanical facts in support of the transmission of acquired characters. These facts are indeed conclusive, if we accept the author's use of the term 'acquired,' but it will be found that they lead to hardly any modification in the state of existing opinion upon the subject.

In a short note, dated Jan. 1, 1888, the author communicated to this journal ('Biologisches Centralblatt') the statement that changes in the structure of flowers caused by poor nutrition can be proved to be hereditary to a greater or less extent [1].

A more elaborate account of the experiments will be found in several numbers of the 'Botanische Zeitung,' and the author expresses his final results in the following words (see Bot. Zeit. 1887, p. 773):—'These experiments prove with certainty (1) that

[1] Compare Biol. Centralbl. Bd. VII. No. 21.

insufficient nutrition may cause considerable morphological changes (viz. qualitative variations) which are in the first place acquired by thes exual apparatus of the flower, (2) that the "transient" (Weismann) characters acquired by the individual can be transmitted[1].'

The data upon which Hoffman bases these opinions are certain experiments conducted upon various plants, in order to determine the conditions of life under which abnormal flowers or any other variations occur most frequently: to decide, in short, how far variations are caused by the change of conditions.

It is obvious that the attention of the author was not at first directed to the question of the transmission of acquired characters. His experiments are of a much older date than the present condition and significance of the question before us. Hoffmann has, in fact, re-examined his former results from the new point of view, and this explains why his proofs are not always sufficiently convincing when applied to the present issue. But this is of no great importance, inasmuch as there is no necessity for me to question the correctness of his assumptions.

The essential details of the experiments to which he directs attention are as follows.

Different plants with normal flowers were subjected to greatly changed conditions of life for a series of generations. They were, for example, crowded together in small pots. Under these circumstances the plants were of course poorly nourished, and in the course of generations, several species produced a variable proportion of abnormal—viz. double-flowers. This, however, was not always the case, for such flowers did not appear in *Matthiola annua* and *Helianthemum polifolium*. In other species, such as *Nigella damascena*, *Papaver alpinum* and *Tagetes patula*, they appeared and often increased in numbers in the course of generations, although this was not a constant result. For instance, four successive generations of *Nigella damascena*, when closely sown, produced the following results:—

1883.	No double flowers.
1884.	,, ,, ,,
1885.	23 typical flowers: 6 double flowers.
1886.	10 ,, ,, : 1 ,, flower.

[1] I have used the expression 'transient' ('passant') in the same sense as 'acquired,' in order to enforce the conclusion that they are merely temporary, and disappear with the individual in which they arise. Since the characters of which

But it was not always the case that the double flowers continued to appear after they had been once produced. In *Papaver alpinum*, which Hoffman has cultivated in successive generations since 1862, other changes in addition to the doubling of the flowers first appeared in 1882, viz. a slight variability in the form of the leaf, and a greater variability in the colours of the flowers. The production of double flowers appeared to be favoured by poor nutrition caused by crowding the plants. The results as regards the number of double flowers produced in this species by close sowing, from 1882–1886, have been as follows:—

Experiment XI.	1881.	40	per cent.	of double	flowers.
	1882.	4	,,	,,	,,
	1883.	5·3	,,	,,	,,
Experiment XVII.	1884.	13·	,,	,,	,,
	1885.	0·0	,,	,,	,,
	1886.	0·0	,,	,,	,,

Although in these and some other series of generations the double flowers again disappeared in the later generations, yet there can be hardly any doubt that their first appearance was due to the abnormal conditions of nutrition. This conclusion is also unaffected by the fact that double flowers appeared in nearly the same proportions in consequence of cultivation in ordinary garden soil. The plants which were crowded in pots produced 2879 normal flowers, and 256 (=8·8 per cent.) abnormal and mostly double ones, while 867 normal and 62 (=7·0 per cent.) abnormal ones were produced on garden beds. Hoffman will not indeed admit that such a comparison can be fairly made, for the plants in the garden beds were raised from seed which was in part taken from the double flowers, and was therefore, he believed, under a strong hereditary influence. But this latter assumption is not supported by the results of his own experiments.

Thus experiment XVIII., conducted upon *Papaver alpinum*, is described in these words,—'Seeds yielded by double flowers from experiment XI. (1883), were sown in pots, and the resulting plants produced from 1884–1886, fifty-three single flowers and no double ones.'

Hoffmann speaks are hereditary, the term cannot be rightly applied to them, and I shall prove later on that they cannot be regarded as acquired characters in the sense required by the theory of descent.

In the converse experiment XIX. 'The seeds of single flowers from different stocks were sown in pots, and the resulting plants produced in 1885 and 1886 forty-three flowers, of which all were typical except one;' while plants produced in the garden by seed from the same sources, yielded 166 single and five double flowers. Hoffman also describes other experiments in which the seeds from double flowers produced plants which also yielded many double flowers. Thus, for example, in experiment XXI. seeds yielded by the double flowers of *Papaver alpinum* were sown in the garden and produced numerous plants, which in 1885 and 1886 bore 284 single and twenty-one double flowers, that is 7 per cent. of the latter.

It will therefore be seen that the transmission of the abnormality is by no means proved beyond the possibility of doubt, for who can decide between the effects due to heredity and changed conditions in the last experiment? I have no doubt however that the results are at any rate in part due to the operation of heredity, for I do not see how the phenomena can be otherwise understood. Nevertheless I cannot admit the transmission of acquired characters on this evidence, for the changes which have appeared are not 'acquired' in the sense in which I use the term and in the sense required by the general theory of evolution. It is true that they may be described by the use of this word: inasmuch as they are characters which the plant has come to possess; we are not however engaged in a mere dispute about terms, but in the discussion of a weighty scientific question. Our object is to decide whether changes in the *soma* (the body, as opposed to the germ-cells) which have been produced by the direct action of external influences, including use and disuse, can be transmitted; whether they can influence the germ-cells in such a manner that the latter will cause the spontaneous appearance of corresponding changes in the next generation. This is the question which demands an answer; and, as has been shown above, such an answer would decide whether the Lamarckian principle of transformation must be retained or abandoned.

I have never doubted about the transmission of changes which depend upon an alteration in the germ-plasm of the reproductive cells, for I have always asserted that these changes, and these alone, must be transmitted. If any one makes the contrary assertion, he merely proves that he does not understand what I have said upon the subject. In what other way could the transformation of species be produced, if changes in the germ-plasm cannot be transmitted? And how could the germ-plasm be changed except by the operation of external influences, using the words in their widest sense; unless indeed we assume with Nägeli, that changes occur from internal causes, and imagine that the phyletic development of the organic world was planned in the molecular structure of the first and simplest organism, so that all forms of life were compelled to arise from it, in the course of time, and would have arisen under any conditions of life. This is the outcome of Nägeli's view, against which I have contended for years.

If we now use the term 'acquired characters' for changes in the *soma* which, like spontaneous abnormalities, depend upon previous changes in the germ-plasm—it is of course easy to prove that acquired characters are transmitted; but this is hardly the way to advance science, for nothing but confusion would be produced by such a use of terms[1]. I am not aware that any one has ever doubted that spontaneous characters, such as extra fingers or toes, patches of grey hair, moles, etc., can be transmitted. It is true that such characters are sometimes called 'acquired' in pathological works, but His has rightly insisted that such an obviously inaccurate use of the term ought to be avoided, in order to prevent misunderstanding. If every new character is said to be 'acquired'

[1] Compare a paper by J. Orth, 'Ueber die Entstehung und Vererbung individueller Eigenschaften,' Leipzig, 1887. This author considers my theory of the non-transmission of acquired characters to be incorrect, because he will insist upon using the term 'acquired' for those characters which are due to spontaneous changes in the germ; although he considers that they are only indirectly acquired. He also reproaches me with not having discriminated with sufficient clearness between the two modes in which new characters are acquired by the body, and with having altogether failed to take into account the class of characters which are due to variations in the germ. On the very same page he quotes the following sentence from my writings:—'Every change of the germ-plasm itself, however it may have arisen, must be transmitted to the following generation by the continuity of the germ-plasm; and hence also any changes in the *soma* which arise from the germ-plasm must be transmitted to the following generation.' Not only does the transmission of Orth's 'indirectly acquired characters' necessarily follow from this sentence, but it is even distinctly asserted by it. I cannot understand how any one who is aware of what happened at the meeting of the Association of German naturalists at Strassburg in 1885, can charge me with the confusion of ideas which has prevailed since Virchow took part in the discussion of this question.

the term at once loses its scientific value, which lies in the restricted use. If generally used, it would mean no more than the word 'new'; but new characters may arise in various ways,—by artificial or natural selection, by the spontaneous variations of the germ, or by the direct effect of external influences upon the body, including the use and disuse of parts. If we assume that these latter characters are transmitted, the further 'assumption of complicated relations between the organs and the essential substance of the germ becomes necessary' (His), while the transmission of the other kinds of characters do not involve any theoretical difficulties. There is therefore obviously a wide difference between these two groups of characters as far as heredity is concerned, quite apart from the question as to whether acquired characters are really transmitted. It is at all events necessary to have distinct terms which cannot be misunderstood. His [1] has proposed to call those characters which are due to selection 'changes produced by breeding' ('erzüchtete Abänderungen'), those which appear spontaneously—'spontaneous changes' ('eingesprengte Abänderungen'), and these two groups of characters would then be opposed to those which he calls 'acquired changes' ('erworbene Abänderungen'), of course using the term in the restricted sense. Science has always claimed the right of taking certain expressions and applying them in a special sense, and I see no reason why it should not exercise this right in the case of the term 'acquired.' It appears moreover that this word has not always been used in this vague sense by pathological anatomists, such as Virchow and Orth; for Weigert and Ernst Ziegler have employed it in precisely the same sense as that in which it has been used by Darwin, du Bois-Reymond, Pflüger, His and many others, including myself.

It is certainly necessary to have two terms which distinguish sharply between the two chief groups of characters—the primary characters which first appear in the body itself, and the secondary ones which owe their appearance to variations in the germ, however such variations may have arisen. We have hitherto been accustomed to call the former 'acquired characters,' but we might also call them '*somatogenic*,' because they follow from the reaction of the *soma* under external influences; while all other characters might be contrasted as '*blastogenic*,' because they include all those

[1] His, 'Unsere Körperform,' Leipzig, 1874, p. 58.

characters in the body which have arisen from changes in the germ. In this way we might perhaps prevent the possibility of misunderstanding. We maintain that the '*somatogenic*' characters cannot be transmitted, or rather, that those who assert that they can be transmitted, must furnish the requisite proofs. The *somatogenic* characters not only include the effects of mutilation, but the changes which follow from increased or diminished performance of function, and those which are directly due to nutrition and any of the other external influences which act upon the body. Among the *blastogenic* characters, we include not only all the changes produced by natural selection operating upon variations in the germ, but all other characters which result from this latter cause.

If we now wish to place Hoffmann's results in their right position, we must regard all of them as '*blastogenic*' characters, for no one of them can be considered as belonging to the group which has been hitherto spoken of as 'acquired,' in the literature of evolution: they are not due to *somatogenic* but to *blastogenic* changes. The body of the plant—the *soma*—has not been directly affected by external influences, in Hoffman's experiments, but changes have been wrought in the germ-plasm of the germ-cells and, only after this, in the *soma* of succeeding generations.

There is no difficulty in finding facts in support of this statement, among Hoffmann's experiments. The proof chiefly lies in the fact that in no one of his numerous experiments did any change appear in the first generation. The seeds of different species of wild plants, with normal flowers, were cultivated in the garden and in pots (thickly sown in the latter case), but no one of the plants produced by these wild seeds possessed a single double flower. It was only after a greater or less number of generations had elapsed that a variable proportion of double flowers appeared, sometimes accompanied by changes in the leaves and in the colours of the flowers. This fact admits of only one interpretation;—the changed conditions at first produced slight and ineffectual changes in the idioplasm of the individual, which was transmitted to the following generation: in this again the same causes operated and increased the changes in the idioplasm which was again handed down. Thus the idioplasm was changed more and more, in the course of generations, until at last the change became great enough to produce a visible character in the *soma* developed from it, such as, for example, the appearance of a double flower. Now the idioplasm of the first ontogenetic stage (viz. germ-plasm) alone passes from one generation to another, and hence it is clear that the germ-plasm itself must have been gradually changed by the conditions of life until the alteration became sufficient to produce changes in the *soma*, which appeared as visible characters in either the flower or leaf[1].

In addition to the above-mentioned cases Hoffmann also quotes some facts of a somewhat different kind. He succeeded in inducing considerable changes in the structure of the root of the wild carrot (*Daucus carota*) by means of the changes in nutrition implied by garden cultivation. These changes also proved to be hereditary.

Unfortunately, I have not the literature of the subject at hand, and hence I am unable to read the accounts of these older experiments *in extenso*; but it is sufficiently obvious that in this case we are also concerned with a change which did not become visible until after some generations had elapsed, and which was therefore a change in the germ-plasm.

Many instances of a precisely similar kind have been long known, and one of them is to be found in the history of the garden pansy, which Hoffmann has succeeded in producing from the wild form, *Viola tricolor*, in the course of eighteen years. Darwin some time ago pointed out in his work upon 'The Variation of Animals and Plants under Domestication,' that, in the case of the pansy and all other 'improved' garden flowers, the wild form remained unchanged for many generations after its transference to the garden, apparently uninfluenced by the new conditions of life. At length single varieties began to appear, and these were further developed by artificial selection and appropriate crossing, into well-marked races distinguished by peculiar colours, forms, etc.

In these cases also, changes in the germ-plasm are the first

[1] Compare on this point Nägeli in his 'Theorie der Abstammungslehre.' This writer also concludes from similar facts that external influences have wrought in the idioplasm, changes which were at first ineffectual, and which only increased during the course of generations up to a point at which they could produce visible changes in the plant. He does not, however, draw the further conclusion that these changes only influence the germ-plasm, for he was not aware of the distinction between germ-plasm and somatoplasm.

results of the new conditions, and there is no evidence for the occurrence of acquired characters, using the term in its restricted sense.

I now come to the last botanical fact brought forward by Hoffmann in support of the transmission of acquired characters. He states that specimens of *Solidago virgaurea* brought from the Alps of the Valais, commenced flowering in the botanical garden at Giessen, at a time which differed by several weeks from that at which specimens from the surrounding country, planted beside them, began to flower. In other words, the time of flowering must have been fixed by heredity in the alpine *Solidago*, for the external conditions would have favoured a time which was simultaneous with that of the Giessen plants.

What conclusions can be drawn from these facts? Hoffmann of course sees in them the proof of the transmission of acquired characters, but this presupposes that the time of flowering was originally an acquired character. Hoffmann indeed appears to entertain this opinion when he somewhat vaguely states that the time at which flowering begins has been acquired by accommodation —that is by the influence of climate—during a long series of generations, and has become hereditary. But what does Hoffmann mean by 'accommodation'? He presumably means that which, since the appearance of Darwin's writings, has been generally called adaptation:—that is a purposeful arrangement, suited to certain conditions. The majority of biologists have followed Darwin in believing that such adaptations have been produced by processes of natural selection. Hoffmann seems to imagine that they have arisen in some other way: perhaps he believes, with Nägeli, that they have been directly produced by external influences.

The fixation of the time at which flowering begins, is an adaptation which formerly could have been very well explained as the direct result of external conditions. The question we have to decide is whether such an explanation is the true one. We might imagine that the plant would be forced into quicker development by an earlier appearance of the warm season. Hence when transferred into a warmer climate the plant would at first flower rather earlier, the habit would then be transmitted, and would increase in successive generations from the continued influence of climate, until it advanced as far as the organization of the plant permitted. But in this explanation, as in so many others of the same kind, it has unfortunately been forgotten that the transmission of acquired characters which is presupposed in the explanation is a totally unproved hypothesis. It is sufficiently obvious that by interpreting a phenomenon in a manner which presupposes the transmission of acquired characters, we cannot furnish a proof of the existence of such transmission.

It always seemed to me that the fixation of the commencement of flowering, together with similar physiological phenomena in the animal kingdom (for example, the hatching of insects from winter eggs), could be explained very satisfactorily by the operation of natural selection: and even now this explanation appears to me to be the simplest and most natural. In Freiburg, where the vine is largely grown, the harvest is often injured by frosts in spring, which kill the young shoots, buds and flowers. Accordingly, different kinds of vine, which do not push their buds so early, have now been planted. Any one, who has seen all the shoots of the former destroyed by the frosts at the end of April, while the latter, not having opened their buds, were spared, would not doubt that the former must have been long ago exterminated, if they had been compelled to struggle for existence with the others, under natural conditions. Now the time of flowering fluctuates slightly in the individuals of every species of plant, and can therefore be modified by natural selection. It is therefore difficult to see why the time at which each plant flowers should not have been fixed in the most favourable manner for each habitat, by natural selection alone.

Hoffmann is obviously unaware of the fundamental distinction between the characters primarily acquired by the *soma*, and the secondary characters which follow from changes in the germ-plasm.

If the author had appreciated this distinction he would not have attempted to strengthen his opinions by following up the botanical facts which exclusively belong to the second class of characters, with the enumeration of certain instances selected from the animal kingdom (viz., the supposed transmission of mutilations), all of which belong to the first class. I will not discuss these latter instances, for most of them are old friends, and they are all far too uncertain and inaccurate to have any claim on scientific consideration.

I believe that I have shown that no botanical facts have been hitherto brought forward which prove the transmission of acquired characters (in the restricted sense), and that there are not even any facts which render such transmission probable.

A. W.

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