

VIII.

THE SUPPOSED TRANSMISSION OF
MUTILATIONS.

1888.

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WE know well the manner in which Lamarck imagined that the gradual transformation of species occurred, when he first made the attempt to penetrate into the mechanism of the process of evolution, and to ascertain the causes by which it is produced. In his opinion, a change in the structure of any part of an organism was chiefly brought about when the species in question met with new conditions of life and was thus forced to assume new habits. Such habits caused an increased or diminished activity, and therefore a stronger or weaker development, of certain parts, and the modified parts were then transmitted to the offspring. Inasmuch as the offspring continued to live under the same changed conditions, and kept up the altered manner of using the part in question, the inherited changes would be increased in the same direction during the course of their life, and would be further increased in each successive generation, until the greatest possible change had been effected.

In this way Lamarck was able to give an apparently satisfactory explanation of at any rate those changes which consist in the mere enlargement or diminution of a part; such, for instance, as the great length of neck in the swan and other swimming birds, which he believed to have been produced by the habit of stretching after food at the bottom of the water; or the webbed feet of the same animals, supposed to be produced by the habit of striking the water with outspread toes, etc. In this way he was also able to explain the disappearance of a part after it had ceased to be of use; as, for

instance, the degeneration of the eyes of animals inhabiting caves or the sunless depths of lakes or the sea.

But it is obvious that such an explanation tacitly assumes that changes produced by use or disuse can be transmitted to the offspring; *it assumes the transmission of acquired characters.*

Lamarck made this assumption as a matter of course, and when half a century later Charles Darwin, his more fortunate successor, refounded the theory of organic evolution, he also believed that we could not entirely dispense with the Lamarckian principle of explanation, although he added the new and extremely far-reaching principle of natural selection. But he certainly attempted to decide whether the Lamarckian principle of the effects of use and disuse is truly efficient, by asking himself the question whether such changes, as for example those produced by exercise during an individual life, can be transmitted to the offspring. Many observations appeared to him, if not to prove the transmission directly, yet to render it extremely probable; and he thus came to the conclusion that there is no sufficient reason for denying the transmission of acquired changes. Hence, in Darwin's works, use and disuse still play important parts as direct factors of transformation, in addition to natural selection.

Darwin was not only an original genius, but also an extraordinarily unbiassed and careful investigator. Whatever he expressed as his opinion had been carefully tested and considered. This impression is gained by every one who has studied Darwin's writings, and perhaps it in part explains the fact that doubts as to the correctness of the Lamarckian principle adopted by him have only arisen during the last few years. These doubts have, however, culminated in the decided denial of the assumption that changes acquired by the body can be transmitted. I for one frankly admit that I was in this respect under the influence of Darwin for a long time, and that only by approaching the subject from an entirely different direction was I led to doubt the transmission of acquired characters. In the course of further investigations I gradually gained a more decided conviction that such transmission has no existence in fact.

Doubts on this point have been expressed not only by me but also by others, such as du Bois-Reymond and Pflüger. Indeed, concerning a certain class of acquired characters, viz. mutilations,

the great German philosopher, Kant, has distinctly denied that transmission can take place¹; and in more recent times Wilhelm His has expressed the same opinion².

But if the transmission of acquired characters is truly impossible our theory of evolution must undergo material changes. We must completely abandon the Lamarckian principle, while the principle of Darwin and Wallace, viz. natural selection, will gain an immensely increased importance.

When I first expressed this opinion in my essay 'On Heredity³,' I was well aware of the consequences of such an idea. I knew well that apparently insurmountable obstacles would be raised against any explanation of evolution, from which the principle of the direct transformation of the species by external influences had been excluded. I therefore endeavoured to show that these difficulties are not in reality insurmountable, and that it is quite possible to explain certain phenomena, such as the degeneration of useless parts, without the aid of the Lamarckian principle. Furthermore it can be shown that a not inconsiderable number of instincts, viz. all those which are exercised only once in a lifetime, cannot possibly have arisen by transmitted practice. This fact renders it unnecessary to make use of the Lamarckian principle for the explanation of other kinds of instinct. I do not mean to deny the existence of phenomena for which such an explanation has not yet been found, or at least has not been brought forward; but on the other hand it appears to me that it has never been proved that we cannot dispense with the Lamarckian principle in the explanation of these phenomena. At any rate, I do not know of any facts which could induce us to abandon from the first any hope of finding an explanation without the aid of this hypothesis.

If we are able to prove that we may dispense with the assumption of the transmission of acquired characters in explaining such phenomena, of course it by no means follows that we *must* dispense with it; or, in other words, it does not follow that the transmission

¹ It is true that he based his opinions upon entirely erroneous theories as to the constancy of species. Compare Brock, 'Einige ältere Autoren über die Vererbung erworbener Eigenschaften' in 'Biolog. Centralblatt,' Bd. VIII, p. 491 (1888): see also Hugo Spitzer, 'Beiträge zur Descendenz-theorie und zur Methodologie der Naturwissenschaft,' Leipzig, 1886, pp. 515 et seq.

² W. His, 'Unsere Körperform,' Leipzig, 1875.

³ See Essay II in the present volume.

of acquired changes cannot take place. It would be as unsafe to make this assertion as to state of a ship seen at a great distance, that it is only moving by sails and not by steam simply because the movement appears to be explicable by sails alone. We ought first to attempt to show that the ship does not possess a steam-engine, or at least that the existence of such an engine cannot be proved.

I believe that I am able to show that the actual existence of the transmission of acquired characters cannot be directly proved; that there are no direct proofs supporting the Lamarckian principle.

If we ask for the facts which can be brought forward by the supporters of the theory of the transmission of acquired characters, if we inquire for the observations which induced Darwin, for instance, to adopt such an hypothesis, or which at least prevented him from rejecting it,—a very brief answer can be given. There are a small number of observations made upon man and the higher animals which seem to prove that injuries or mutilations of the body can, under certain circumstances, be transmitted to the offspring.

A cow which had accidentally lost its horn, produced a calf with an abnormal horn; a bull which had accidentally lost its tail, from that time begat tailless calves; a woman whose thumb had been crushed and malformed in youth, afterwards had a daughter with a malformed thumb, and so on.

In a great number of such cases every guarantee for the trustworthiness of the statements is entirely wanting, and, as His and still earlier Kant have already said, they are of no greater value as evidence than the merest tales. But in other cases this assertion cannot be made without further examination; and a small number of such observations can indeed claim a scientific investigation and value. I shall presently discuss this point in greater detail, but I wish now to lay stress upon the fact that, as far as direct evidence goes, we cannot bring forward any proofs in favour of the transmission of acquired characters, except these cases of mutilations. There are no observations which prove the transmission of functional hypertrophy or atrophy, and it is hardly to be expected that we shall obtain such proofs in future, for the cases are not of a kind which lend themselves to an experimental investigation. The hypothesis that acquired characters can be transmitted is therefore only directly supported by the above-mentioned instances of the transmission of mutilations.

For this reason, the defenders of the Lamarckian principle, who have come forward in rather large numbers recently¹, have endeavoured to show that these observations are conclusive, and therefore of the highest importance. For the same reason I believe that it is my duty, as I take the opposite view, to explain what I think of the value of these apparent proofs of transmitted mutilations.

It can hardly be doubted that mutilations are acquired characters: they do not arise from any tendency contained in the germ, but are merely the reaction of the body under external influences. They are, as I have recently expressed it, purely somatogenic characters², viz. characters which emanate from the body (*soma*) only, as opposed to the germ-cells; they are therefore characters which do not arise from the germ itself.

If mutilations must necessarily be transmitted, or even if they might occasionally be transmitted, a powerful support would be given to the Lamarckian principle, and the transmission of functional hypertrophy or atrophy would thus become highly probable. For this reason it is absolutely necessary that we should try to come to a definite conclusion as to whether mutilations can or cannot be transmitted.

We will now consider in greater detail the facts which have hitherto been brought forward upon this point. It is not my purpose to discuss every single case which has been mentioned anywhere or by anybody; such a discussion would hardly lead to any result. I propose to select a small number of such instances, in order to show why they cannot be maintained as proofs. I shall chiefly deal with cases which have been brought forward as

[¹ One of the most remarkable forms of this revival of Lamarckism is the establishment in America of a 'Neo-Lamarckian School,' which includes among its members many of the most distinguished American biologists. One of the arguments upon which the founders of the school have chiefly relied is derived from the comparative morphology of mammalian teeth. The evolution of the various types are believed to be due to modifications in shape, produced by the action of mechanical forces (pressure and friction) during the life of the individual. The accumulation of such modifications by means of heredity explains the forms of existing teeth.

It may be reasonably objected that the most elementary facts concerning the development of teeth prove that their shapes cannot be altered during the lifetime of the individual, except by being worn away. The shape is predetermined before the tooth has cut the gum. Hence the Neo-Lamarckian School assumes, not the transmission of acquired characters, but the transmission of characters which the parent is unable to acquire!—E. B. P.]

² See p. 412 of the preceding Essay (VII).

especially strong proofs by my opponents, and which have been carefully and completely examined. I shall attempt to show that these are not conclusive and that they must be explained in an entirely different manner. The insufficiency of the proof does not always depend upon the same circumstances, and, according to the latter, we may distinguish different classes of cases.

First of all we may briefly mention those instances in which the necessary precautions have not been taken before drawing conclusions.

To this class belong the tailless cats which were shown at last year's (1887) Meeting of the Association of German Naturalists, at Wiesbaden. These cats had inherited their taillessness, or rather their rudimentary tails, from the mother cat, which 'was said' to have lost her tail by the wheel of a cart having passed over it. Not only did the owner of the cats, Dr. Zacharias, consider them as a proof of the transmission of mutilations, but in a recently-published work, entitled 'On the Origin of Species, based upon the Transmission of acquired characters' ('Ueber die Entstehung der Arten auf Grundlage des Vererbens erworbener Eigenschaften'), the author, Prof. Eimer, speaks of these cats in the preface as a 'valuable' instance of the transmission of mutilations: these examples therefore form part of the foundation upon which the author builds up his theoretical views.

Certainly, the want of tails in young cats, of which the mother had lost its tail by an accident, would have been well worth consideration, but unfortunately there is no trustworthy record as to how the mother cat became tailless. Without absolute certainty upon this point the evidence becomes utterly worthless; and Dr. Zacharias has acted very wisely in afterwards admitting that this is the case, for inherent taillessness has been known in cats for a long time. The tailless race of the Isle of Man is mentioned in the first edition of 'The Origin of Species'; of course I am referring to Darwin's work, and not to the above-mentioned book of the same name, by Prof. Eimer. As to the first origin of the tailless Manx breed we know no more than about the origin of that remarkable race of cats with supernumerary toes, which E. B. Poulton has recently described from Oxford, and has traced through several generations¹. These are innate mon-

[¹ See 'Nature,' vol. xxix. p. 20, and vol. xxxv. p. 38. In the latter article nine generations are recorded, and in both articles figures of the normal and abnormal feet

strosities which have arisen from unknown changes in the germ. Similar monstrosities have been known for a long time, and no one has ever doubted that they can be transmitted.

It would be equally justifiable to derive the cats with extra toes from an ancestor of which the toes had been trodden upon, as to derive the tailless cats of the Isle of Man from an ancestor of which the tail had been cut off by a cart passing over it, and thus to regard the existence of the race as a proof of the transmission of mutilations.

But even if it were certain that the tail of the mother cat had been mutilated, such a fact would not necessarily prove that the rudimentary tails of the offspring were due to transmission from the mother: they might have been transmitted from the unknown father. This is probably not the case with Dr. Zacharias' cat, for tailless kittens occurred in several families produced by the same mother; but in other cases the possibility of the possession of innate taillessness by the father must be taken into account. The following case is, in this respect, very instructive.

Last summer, my friend, Prof. Schottelius, of Freiburg, brought me a kitten with an innate rudimentary tail, which he had accidentally discovered as one of a family of kittens at Waldkirch, a small town in the southern part of the Black Forest. The mother of the kitten possessed a perfectly normal tail; the father could not be identified.

A closer investigation resulted in the following rather unexpected discovery. For some years past, tailless kittens have frequently appeared in the families of many different mother cats at Waldkirch, and this fact is explained in the following manner.

are given. Additional generations and many more families have been since observed, and an account of these observations will shortly be published in the same paper. The breed originally came from Bristol. In the observations recorded, the abnormality of the offspring is an indication of the hereditary strength of the female parents, while the degree of normality is a similar test of heredity through the male parents; for the female parents were always abnormal, the male parents always normal. The most abnormal kitten observed possessed seven toes on each forefoot, seven toes on the right hind foot (three more than the normal number), and six on the left hind foot. Kittens with seven toes on the forefeet and six on the hind were comparatively common, and all intermediate conditions between this and the normal were of frequent occurrence. Cats with extra toes are, I think, not uncommon in most countries, and the fact that the peculiarity is transmitted is also well known. The object of the investigation alluded to was to observe the transmission systematically through many generations.—E. B. P.]

A clergyman, who lived for some time at Waldkirch, had married an English lady who possessed a tailless male Manx cat. The probability that all the tailless cats in Waldkirch are more or less distant descendants of that male cat almost amounts to certainty. Since a male Manx cat has reached the Black Forest, it might equally well arrive at some other place.

But we will now leave observations such as these, which do not prove the transmission of a mutilation, because the mutilation itself has not been established; and we will turn to more serious 'proofs.'

Let us still consider the tails of domesticated animals. In these animals a spontaneous and considerable reduction of the tail occurs not uncommonly, and since the habit of cutting off part of the tail of young animals prevails in many countries, the coincidence has been explained as a causal relation, and the question has been raised whether the disposition towards the spontaneous appearance of rudimentary tails has not arisen in consequence of the artificial mutilation practised through many generations. This supposition appears very plausible at first sight, but the keen scientific criticism of Döderlein, Richter, and Bonnet, together with careful anatomical investigations, have shown that, at least in the cases which were carefully examined, such a causal connection did not exist. It has been shown that the spontaneous rudimentary tails which occasionally appear in cats and dogs have an entirely different origin from the transmission of artificial mutilation. They depend upon an innate peculiarity of the germ, a peculiarity which is easily and strongly transmitted. They are monstrosities, like the sixth finger or toe, or, rather, like the rudimentary fingers and toes, which also occasionally appear. Bonnet¹ has shown that the rudimentary tails of dogs depend upon the absence of several vertebrae, together with an abnormal ossification, and sometimes also with a premature coalescence, of the vertebrae of the tail.

Bonnet states that in the two first cases examined by him the reduction occurred at the distal end of the vertebral column in the tail, the more or less malformed vertebrae being ankylosed. A membranous appendage extended beyond the end of the reduced

¹ Bonnet, 'Die stummelschwänzigen Hunde im Hinblick auf die Vererbung erworbener Eigenschaften,' *Anat. Anzeiger*, Bd. III, 1888, p. 584; see also 'Beiträge zur patholog. Anatomie und allgem. Pathologie' by Ziegler and Nauwerck, Bd. IV, 1888.

caudal vertebrae, as the so-called 'soft tail.' These characters were shown to have been inherited from the mother and to have undergone progressive development as regards the number of missing vertebrae and the proportion of individuals with rudimentary tails.

In a third instance Bonnet found that four to seven of the normal caudal vertebrae were absent, and that the column in the region of the tail was characterised by a tendency towards premature ankylosis along its whole length and not merely in its distal portion. Furthermore the last three to four vertebrae were distorted and were either placed transversely to the long axis of the tail, or were so greatly curved that the tip of the tail was directed forwards.

It is obvious that these changes are not such as we should expect as a result of the transmission of the mutilation of the tail which is so commonly practised. If the artificial injury were transmitted we should not expect that a variable number of the mesial vertebrae would be absent, but rather those of the tip. There would be no reason why the existing vertebrae should be degenerate as in the majority of the caudal vertebrae of the dogs examined by Bonnet.

Entirely similar phenomena have been observed by Döderlein in the tailless cats which not infrequently occur in Japan. In these cats the rudimentary vertebrae of the tail were reduced to a short, thin, inflexible spiral, which formed a knot densely covered with hair on the posterior part of the animal.

Such a reduction of the tail occurs quite independently of artificial injury, in individuals of which the parents were not injured; it is even found in races, such as the dachshund, which, as far as we know, have never been habitually mutilated.

But the fact is rendered especially interesting because the reduction of the vertebral column in the region of the tail takes place in very various degrees. Sometimes only four vertebrae are absent, sometimes as many as ten. The degree of abnormality in shape and the degree of coalescence between the vertebrae also differ greatly. Hence Bonnet rightly concludes that a slow and gradual process of reduction is going on in these animals, a process which tends, as it were, to shorten the tail. I intentionally say 'as it were,' for of course the statement must not be taken literally, and we must not conclude that the process of reduction is a consequence of some hypothetical developmental force seated in the

organism, of which the purpose is to remove the tail. On the contrary, this instance shows very clearly that the appearance of a development guided in a certain direction may be produced without the existence of any motive developmental force.

The disposition of the tail to become rudimentary, in cats and dogs, may be explained in the simplest way, by the process which I have formerly called panmixia. The tail is now of hardly any use to these animals; and neither dog nor cat would perish because they possessed only an incomplete tail. Hence natural selection does not now exercise any influence over these parts, and an occasional reduction is no longer eliminated by the early destruction of its possessor: therefore such reduction may be transmitted to the offspring.

The race of tailless foxes which, according to Settegast, existed during the present century on the hunting-grounds of Prince Wilhelm zu Solms-Braunfels, very soon disappeared; while cats and dogs with rudimentary tails have been preserved in many cases. Such results are to be expected, because in these domesticated animals the absence of the tail did not cause any inferiority in the struggle for existence.

But these facts appear to me to be remarkable in another direction. I previously mentioned the tailless race of Manx cats. Tradition does not tell us how it happened that the descendants of the first tailless cat in the Isle of Man were able to increase and spread in such a manner as to form the dominant race in the island. But we can easily imagine how it happened, when we learn that tailless cats are especially prized¹ in Japan, because people think that they are better mousers. Every one in Japan wishes to possess a tailless cat, and people even cut off the tails of normal cats when they cannot obtain those with congenital rudimentary tails, because they believe that cats become better mousers in consequence of taillessness. In Waldkirch the same account of the superiority of tailless cats is curiously enough also found. We thus see how a slight but striking variation may at once cause an energetic process of artificial selection, which helps this variation to predominance: a hint for us to be careful in passing judgment upon

¹ See the interesting remarks by Döderlein on this point, which Dr. Ischikawa of Japan tells me are quite correct. Döderlein, 'Ueber schwanzlose Katzen,' Zool. Anzeiger, vol. x. Nov. 1887, No. 265.

sexual selection, for the latter also works upon such functionally indifferent but striking variations. In the case of the cats, man has favoured a particular variation, because the novelty rather than the beauty of the character surprised and attracted him. He has attached an imaginary value to the new character, and by artificial selection has helped it to predominate over the normal form. I see no reason why the same process should not take place in animals by the operation of sexual selection.

But now, after this little digression, let us return to the transmission of mutilations.

We have seen that the rudimentary tails of cats and dogs, as far as they can be submitted to scientific investigation, do not depend upon the transmission of artificial mutilation, but upon the spontaneous appearance of degeneration in the vertebral column of the tail. The opinion may, however, be still held that the customary artificial mutilation of the tail, in many races of dogs and cats, has at least produced a number of rudimentary tails, although, perhaps, not all of them. It might be maintained that the fact of the spontaneous appearance of rudimentary tails does not disprove the supposition that the character may also depend upon the transmission of artificial mutilation.

Obviously, such a question can only be decided by experiment: not, of course, experiments upon dogs and cats, as Bonnet rightly remarks, but experiments upon animals the tails of which are not already in a process of reduction. Bonnet proposes that the question should be investigated in white rats or mice, in which the length of the tail is very uniform, and the occurrence of rudimentary tails is unknown.

Before this suggestion was made, I had already attacked the problem experimentally. Such a course might, perhaps, have been more natural to those who maintain the transmission of mutilations, to which I am opposed. Although I undertook the experiments expecting to obtain purely negative results, I thought that the latter would not be entirely valueless; and since the numerous supporters of the transmission of acquired characters do not seem to be willing to test their opinion experimentally, I have undertaken the not very large amount of trouble which is necessary in order to conduct such an experimental test.

The experiments were conducted upon white mice, and were

begun in October of last year (1887), with seven females and five males. On October 17 all their tails were cut off, and on November 16 the two first families were born. Inasmuch as the period of pregnancy is only 22-24 days, these first offspring began to develop at a time when both parents were without tails. These two families were together eighteen in number, and every individual possessed a perfectly normal tail, with a length of 11-12 mm. These young mice, like all those born at later periods, were removed from the cage, and either killed and preserved, or made use of for the continuance of the breeding experiments. In the first cage, containing the twelve mice of the first generation, 333 young were born in fourteen months, viz. until January 16, 1889, and no one of these had a rudimentary tail or even a tail but slightly shorter than that of the offspring of un mutilated parents.

It might be urged that the effects of mutilation do not exercise any influence until after several generations. I therefore removed fifteen young, born on December 2, 1887, to a second cage, just after they were able to see, and were covered with hair; their tails were cut off. These mice produced 237 young from December 2, 1887 to January 16, 1889, every one of which possessed a normal tail.

In the same manner fourteen of the offspring of this second generation were put in cage No. 3 on May 1, 1888, and their tails were also cut off. Among their young, 152 in number, which had been produced by January 16, there was not a single one with an abnormal tail. Precisely the same result occurred in the fourth generation, which were bred in a fourth cage and treated in exactly the same manner. This generation produced 138 young with normal tails from April 23 to January 16.

The experiment was not concluded with the fourth generation; thirteen mice of the fifth generation were again isolated and their tails were amputated; by January 16, 1889 they had produced 41 young.

Thus 901 young were produced by five generations of artificially mutilated parents, and yet there was not a single example of a rudimentary tail or of any other abnormality in this organ. Exact measurement proved that there was not even a slight diminution in length. The tail of a newly-born mouse varies from 10.5 to 12 mm. in length, and not one of the offspring possessed a tail

shorter than 10.5 mm. Furthermore there was no difference in this respect between the young of the earlier and later generations.

What do these experiments prove? Do they disprove once for all the opinion that mutilations cannot be transmitted? Certainly not, when taken alone. If this conclusion were drawn from these experiments alone and without considering other facts, it might be rightly objected that the number of generations had been far too small. It might be urged that it was probable that the hereditary effects of mutilation would only appear after a greater number of generations had elapsed. They might not appear by the fifth generation, but perhaps by the sixth, tenth, twentieth, or hundredth generation.

We cannot say much against this objection, for there are actual phenomena of variation which must depend upon such a gradual and at first imperceptible change in the germ-plasm, a change which does not become visible in the descendants until after the lapse of generations. The wild pansy does not change at once when planted in garden soil: at first it remains apparently unchanged, but sooner or later in the course of generations variations, chiefly in the colour and size of the flowers, begin to appear: these are propagated by seed and are therefore the consequence of variations in the germ. The fact that such variations *never* occur in the first generation proves that they must be prepared for by a gradual transformation of the germ-plasm.

It is therefore possible to imagine that the modifying effects of external influences upon the germ-plasm may be gradual and may increase in the course of generations, so that visible changes in the body (*soma*) are not produced until the effects have reached a certain intensity.

Thus no conclusive theoretical objections can be brought forward against the supposition that the hereditary transmission of mutilations requires (e.g.) 1000 generations before it can become visible. We cannot estimate *a priori* the strength of the influences which are capable of changing the germ-plasm, and experience alone can teach us the number of generations through which they must act before visible effects are produced.

If therefore mutilations really act upon the germ-plasm as the causes of variation, the possibility or even probability of the ultimate appearance of hereditary effects could not be denied.

Hence the experiments on mice, when taken alone, do not constitute a complete disproof of such a supposition: they would have to be continued to infinity before we could maintain with certainty that hereditary transmission cannot take place. But it must be remembered that all the so-called proofs which have hitherto been brought forward in favour of the transmission of mutilations assert the transmission of a single mutilation which at once became visible in the following generation. Furthermore the mutilation was only inflicted upon one of the parents, not upon both, as in my experiments with mice. Hence, contrasted with these experiments, all such 'proofs' collapse; they must all depend upon error.

It is for this reason important to consider those cases of habitual mutilation which have been continually repeated for numerous generations of men, and have not produced any hereditary consequences. With regard to the habitually amputated tails of cats and dogs I have already shown that there is only an apparently hereditary effect. Furthermore, the mutilations of certain parts of the human body, as practised by different nations from times immemorial, have, in not a single instance, led to the malformation or reduction of the parts in question. Such hereditary effects have been produced neither by circumcision¹, nor the removal of the front teeth, nor the boring of holes in the lips or nose, nor the extraordinary artificial crushing and crippling of the feet of Chinese women. No child among any of the nations referred to possesses the slightest trace of these mutilations when born: they have to be acquired anew in every generation.

Similar cases can be proved to occur among animals. Professor Kühn of Halle pointed out to me that, for practical reasons, the tail in a certain race of sheep has been cut off, during the last hundred years, but that according to Nathusius, a sheep of this race without a tail or with only a rudimentary tail has never been born. This is all the more important because there are other races of sheep in which the shortness of the tail is a distinguishing peculiarity. Thus the nature of the sheep's tail does not imply that it cannot disappear.

¹ It is certainly true that among nations which practise circumcision as a ritual, children are sometimes born with a rudimentary prepuce, but this does not occur more frequently than in other nations in which circumcision is not performed. Rather extensive statistical investigations have led to this result.

A very good instance is mentioned by Settegast, although perhaps with another object in view. The various species of crows possess stiff bristle-like feathers round the opening of the nostrils and the base of the beak: these are absent only in the rook. The latter, however, possesses them when young, but soon after it has left the nest they are lost and never reappear. The rook digs deep into the earth in searching for food, and in this way the feathers at the base of the beak are rubbed off and can never grow again because of the constant digging. Nevertheless this peculiarity, which has been acquired again and again from times immemorial, has never led to the appearance of a newly hatched individual with a bare face.

Thus there is no reason for the assumption that such a result would occur in the case of the mice even if the experiments had been continued through hundreds or thousands of generations. The supposition of the accumulative effect of mutilation is entirely visionary, and cannot be supported except by the fact that accumulative transformations of the germ-plasm occur; but of course this fact does not imply that mutilations belong to those influences which are capable of changing the germ-plasm. All the ascertained facts point to the conclusion that they have not this effect. The transmission is all the more improbable because of the striking form of the mutilation in all cases which are relied upon as evidence. The only objection which can be raised is to suppose that the absence of the tail is less easily transmitted than other mutilations, or that mice possess smaller hereditary powers than other animals. But there is not the slightest evidence in favour of either of these suggestions; the supporters of the Lamarckian principle have, on the contrary, always pointed to the transmission of mutilated tails as one of their principal lines of evidence.

The opinion has often been expressed that such transmission need not occur in every case, but may happen now and then under quite exceptional conditions with which we are unacquainted: for this reason it might be urged that all negative experiments and every refutation of the 'proofs' of the transmission of mutilations are not conclusive. Only recently, a clever young zoologist said in reference to Kant's statements upon the subject, that perhaps the most decided opponent of the transmission of mutilations would not venture

nowadays to maintain his view with such certainty, 'for it must be admitted that the transmission of acquired characters may take place at any rate as a rare exception.' Similar opinions are often expressed, especially in conversation, and yet they can mean nothing except that the transmission of acquired characters has been proved; for if such transmission can take place at all, it exists, and it does not make the least difference theoretically whether it occurs in rare cases or more frequently. Sometimes heredity has been called capricious, and in a certain sense this is true. Heredity appears to be capricious because we cannot penetrate into its depths: we cannot predict whether any peculiar character in the father will reappear in the child, and still less whether it will reappear in the first, second, or one of the later children: we cannot predict whether a child will possess the nose of his father or mother or one of the grandparents. But this certainly does not imply that the results are due to chance: no one has the right to doubt that everything is brought about by the operation of certain laws, and that, with the fertilization of the egg, the shape of the nose of the future child has been determined. The co-operation of the two tendencies of development contained in the two conjugating germ-cells produces of necessity a certain form of nose. The observed facts enable us to know something of the laws under which such events take place. Thus, for instance, among a large number of children of the same parents some will always have the form of the nose of the mother or of the mother's family; others will have the nose of the father's family, and so on.

If we apply this argument to the supposed transmission of mutilations, such transmission, if possible at all, must occur a certain number of times in a certain number of cases: it must occur more readily when both parents are mutilated in the same way, or when the mutilation has been repeated in many generations, etc. It is extremely improbable that it would suddenly occur in a case where it was least expected, while it did not occur in 900 cases of the most favourable kind. Those who recognise in the doubtful cases of transmission of a single mutilation present in only one of the parents, proofs of the existence of the disputed operation of heredity, quite forget that the transmission presupposes a very marvellous and extremely complex apparatus which if present at all ought, under certain conditions, to become manifest regularly, and not only

in extremely exceptional cases. Nature does not create complex mechanisms in order to leave them unused: they exist by use and for use. We can readily imagine how complex the apparatus for the transmission of mutilations or acquired characters generally must be, as I have tried to show in another place. The transmission of a scar to the offspring e.g. presupposes first of all that each mechanical alteration of the body (*soma*) produces an alteration in the germ-cells: this alteration cannot consist in mere differences of nutrition, only affecting an increased or decreased growth of the cells: it must be of such a kind that the molecular structure of the germ-plasm would be changed. But such a change could not in the least resemble that which occurred at the periphery of the body in the formation of the scar: for there is neither skin nor the pre-formed germ of any of the adult organs in the germ-plasm, but only a uniform molecular structure which, in the course of many thousand stages of transformation, must tend to the formation of a *soma* including a skin. The change in the germ-plasm which would lead to the transmission of the scar, must therefore be of such a kind as to influence the course of ontogeny in one of its later stages, so that an interruption of the normal formation of skin, and the intercalation of the tissue of the scar, would occur at a certain part of the body. I do not maintain that equally minute changes of the germ-plasm could not occur: on the contrary, individual variation shows us that the germ-plasm contains potentially all the minutest peculiarities of the individual; but I have in vain tried to understand how such minute changes of the germ-plasm in the germ-cells could be caused by the appearance of a scar or some other mutilation of the body. In this respect I think that Blumenbach's condition is nearly fulfilled: he was inclined to declare himself against the transmission of mutilations, but only if it were proved that such transmission was *impossible*. Although this cannot be strictly proved, it can nevertheless be shown that the apparatus presupposed by such transmission must be so immensely complex, nay! so altogether inconceivable, that we are quite justified in doubting the possibility of its existence as long as there are no facts which prove that it *must* be present. I therefore do not agree with the recent assertion¹ that Blumenbach's condition cannot be fulfilled to-day, just as it was impossible at the time when it was first

¹ See Brock, 'Biolog. Centralblatt,' Bd. VIII. p. 497, 1888.

brought forward. But if nevertheless such a mysterious mechanism existed between the parts of the body and the germ-cells, by means of which each change in the former could be reproduced in a different manner in the latter, the effects of this marvellous mechanism would certainly be perceptible and could be subjected to experiment.

But at present we have no evidence of the existence of any such effects; and the experiments described above disprove all the cases of the supposed transmission of single mutilations.

Of course, I do not maintain that such cases are to be always explained by want of sufficient observation. In order to make my position clear, I propose to discuss two further classes of observations. First of all, there are very many cases of the apparent transmission of mutilations in which it was not the mutilation or its consequences which was transmitted, but the predisposition of the part in question to become diseased. Richter¹ has recently pointed out that arrests of development, so slight as to be externally invisible, frequently occur, and that such arrests exhibit a tendency to lead to the visible degeneration of parts in which they occur, as the result of slight injuries. Since therefore the predisposition towards such arrest is transmitted by the germ—occasionally even in an increased degree—the appearance of a transmitted injury may arise. In this way Richter explains, for instance, the frequently quoted case of the soldier who lost his left eye by inflammation fifteen years before he was married, and who had two sons with left eyes malformed (microphthalmic). Microphthalmia is an arrest of development. The soldier did not lose his eye simply because it was injured, but because it was predisposed to become diseased from the beginning and readily became inflamed after a slight injury. He did not transmit to his sons the injury or its results, but only microphthalmia, the predisposition towards which was already innate in him, but which led in his sons from the beginning, and without any obvious external injury, to the malformation of the eye. I am inclined to explain the case which Darwin in a similar manner adduced, during the later years of his life, in favour of the transmission of acquired characters, and which seemed to prove that a malformation of the thumb produced by chilblains can be transmitted. The skin of a

¹ W. Richter, 'Zur Vererbung erworbener Charaktere,' *Biolog. Centralblatt*, Bd. VIII. 1888, p. 289.

boy's thumbs had been badly broken by chilblains associated with some skin disease. The thumbs became greatly swollen and remained in this state for a long time; when healed they were malformed, and the nails always remained unusually narrow, short, and thick. When this man married and had a family, two of his children had similarly malformed thumbs, and even in the next generation two daughters had malformed thumbs on both hands. The case is too imperfectly known to admit of adequate criticism; but one may perhaps suggest that the skin of different individuals varies immensely in its susceptibility to the effects of cold, and that many children have chilblains readily and badly, while others are not affected in this way. Sometimes members of the same family vary in this respect, and the greater or less predisposition towards the formation of chilblains corresponds with a different constitution of the skin, in which some children follow the father and others follow the mother. In Darwin's instance a high degree of susceptibility of the skin of the thumb was obviously innate in the father, and this susceptibility was certainly transmitted, and led to the similar malformation of the thumbs of the children, perhaps very early and after the effect of a comparatively slight degree of cold¹.

The last class of cases which I should wish to consider, refer to observations in which the mutilation of the parent was certain, and in which a malformation similar to the mutilation had appeared in the child, but in which exact investigation shows that the malformations in parent and child do not in reality correspond to each other.

In this class I include an instance which has only become known during the present year (1888), and which has been observed as

¹ This case was not observed by Darwin himself, but was communicated to him by J. P. Bishop of Perry, in North America (see 'Kosmos,' vol. ix. p. 458). Quite apart from the fact that it is by no means certain whether the father did not already possess an innate malformation of the thumb, exact data are wanting as to the time during which the thumb was diseased, and as to the time when the malformation of the thumb was first observed in the children and the grandchildren; whether at birth or at a later period. For a thorough criticism it would also be necessary to have figures of the thumbs. I should not have alluded to this case, because of its incomplete history, if it had not appeared to me to illustrate the ideas mentioned above. Of course I do not maintain that I have suggested the right explanation in this particular case. It is possible that the father possessed an inherent malformation of the thumb which he had forgotten by the time that he came to have children and grandchildren, and was struck by the abnormality of their thumbs.

exactly as possible by an anthropologist and physician, who has worked up the history of the case. Dr. Emil Schmidt communicated to this year's meeting of the German Anthropologists' Association at Bonn a case which indeed seems at first sight to prove that mutilations of the human ear can be transmitted. As Dr. Schmidt has been kind enough to place at my disposal all the material which he collected upon the subject, I have been able to examine it more minutely than is generally possible in such cases; and I will discuss it in detail, as it seems to me to be of fundamental importance in the history of human errors upon this subject.

In a most respectable and thoroughly trustworthy family, the mother possesses a cleft ear-lobe upon one side. She quite distinctly remembers that when playing, between the ages of six and ten years, another child tore out her ear-ring, and that the wound healed so that the cleft remained. Later on a new hole was made in the posterior part of the lobe. She had seven children, and the second of these, who is now a full-grown man, has a cleft ear-lobe on the same side as the mother. It is not known whether the mother possessed an innate malformation of the ear before it was mutilated, but, judging from the present appearance of the ear, this is extremely improbable. Furthermore, the existence of an innate cleft in the ear-lobe has never been previously observed. The parents of the mother did not possess any malformation of the ear. The conclusion seemed to be therefore inevitable that the transmission of an artificial cleft in the ear-lobe had really taken place.

But we must not be too hasty in forming an opinion. When we compare the figures I. and II., representing the two ears, we are first of all struck by the fact that the malformation of the ear of the son has an entirely different appearance from that of the mother. The ear-lobe of the latter is quite normally formed; it is broad and well-developed, and only exhibits a median vertical furrow which is the result of the mutilation. The ear-lobe of the son, on the other hand, is extremely minute, one might even maintain that it is completely wanting. In my opinion a cleft is not present at all, but the far higher posterior corner of the ear forms the end of its posterior margin—the so-called helix. But even if another opinion were pronounced with regard to the interpretation of this part, there is one other circumstance to be taken into account, which appears to me to be absolutely conclusive, and which com-

FIG. I.

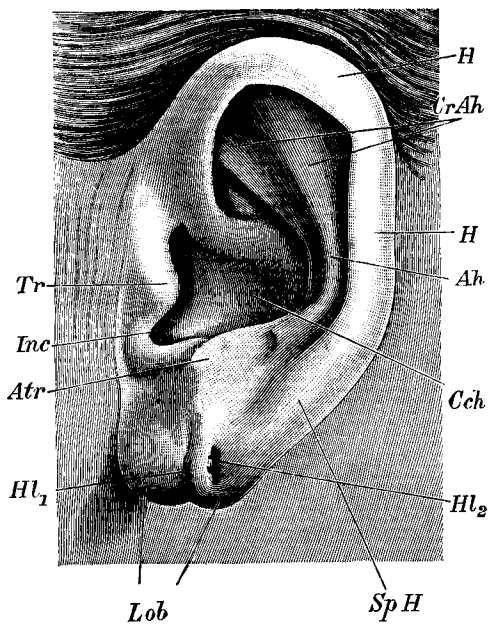
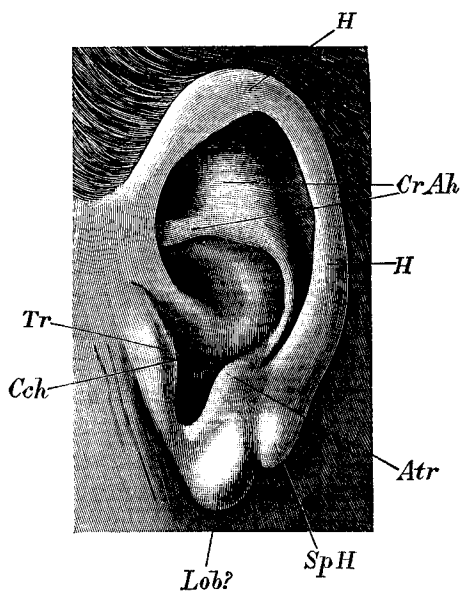


FIG. II.



H. Helix. *Cr. Ah.* Crura anthelics. *Ah.* Anthelix. *Cch.* Concha. *HL¹*, and *HL²*, Holes 1 and 2 for ear-rings. *Lob.* Ear-lobe. *Sp. H.* Spina helicis. *Inc.* Incisura intertragica. *Tr.* Tragus. *Atr.* Antitragus.

pletely excludes the interpretation of this malformation as the transmission of a mutilation.

If we compare the ears with each other, that of the mother with that of the son, not only the anatomist but every trained observer will at once be struck by the fact that they are totally different in their outlines as well as in every detail. The upper margin of the ear is very broad in the mother, in the son it is quite pointed; the so-called *crura anthelialis* are normally developed in the mother, in the son they can hardly be distinguished and open in an anterior direction, while in the mother they are directed upwards. The concha itself, the *incisura intertragica*, in short everything in the two ears, is as different as it can possibly be in the ears of two individuals.

But this fact obviously proves that the son does not possess the ear of his mother, but probably that of his father or grandfather. Unfortunately the father and grandfather have been now dead for a long time, so that we cannot obtain certain evidence upon this point. At all events, the son does not possess the ear of his mother, and it would be very rash to suppose that he has inherited the ear from the father, but the malformation of the ear-lobe from the mother—a malformation which, as it seems to me, is certainly quite different from that of his mother's ear. I said that this case was of fundamental importance chiefly because it shows very distinctly, on the one hand, how difficult it is to bring together the material which is absolutely necessary for the correct understanding of a single case, and on the other hand, how carefully the abnormalities must be compared and examined if we wish to escape wrong conclusions. Such precautions have hitherto been rarely taken with the necessary accuracy; people are in most cases satisfied with the knowledge that an abnormality is present in the child on the same part which had been malformed by mutilation in the parent.

But if we are to speak of the transmission of a mutilation, it must be shown, before everything else, that the malformation of the child corresponds precisely to the mutilation of the parent.

For this reason the older observations upon this subject are, in most cases, entirely valueless.

The readiness with which we may be deceived is shown by the fact that I myself nearly became a victim during the past year (1888). A friend of mine, in order to convince me of the

transmission of mutilations, called my attention to a linear scar on his left ear, which extended from the upper margin of the helix for some distance upon the posterior part of the anthelix, giving it the appearance of a small, rather sharp ridge. The scar had been caused by a cut from a duelling sword, which the gentleman had received during his residence at the University. Strangely enough, the left ear of his daughter, who is five years old, exhibits a similar peculiarity. The posterior part of the anthelix forms a rather sharp and narrow ridge like that of the father, although the scar itself is wanting.

I must admit that I was at first rather puzzled by this fact, but the mystery was soon solved in a very simple manner. I asked the father to show me his right ear, and I then saw that this ear possessed a similar ridge on the posterior part of the anthelix. Only the scar was absent, which in the left ear brought the crest of the ridge into still greater prominence. The ridge was therefore only an individual peculiarity in the formation of the ear of the father,—a peculiarity which had been transmitted to one ear of the child. No transmission of the mutilation had taken place.

In the same manner, many of the so-called proofs of the transmission of mutilations would be shown, by a careful examination, to be deceptive. We must not expect to succeed in all of them, for in most cases the investigation cannot be completed, chiefly because the condition of the part in question in the ancestors is not known or is only known in an insufficient manner. This is the reason why fresh examples of such so-called proofs continue to appear from time to time,—proofs which do not admit of a searching criticism because something, and in most cases very much, is invariably wanting. But it will be admitted that even a very large number of incomplete proofs do not make a single complete one. On the other hand, it may be asserted that a single instance of coincidence between a mutilation in the parent and a malformation in the offspring, even if well established, would not constitute a proof of the transmission of mutilations. Not every *post hoc* is also a *propter hoc*. Nothing illustrates this better than a comparison between the 'proofs' which are even now brought forward in favour of the transmission of mutilations and the 'proofs' which supported the belief in the efficacy of so-called 'maternal impressions'

during pregnancy, a belief which was universally maintained up to the middle of the present century. Many of those 'proofs' were simply old wives' fables, and were based upon all kinds of subsequent inventions and alterations. But it cannot be denied that there are a few undoubtedly genuine observations upon cases in which some character in the child reminds us in a striking manner of a deep psychical impression by which the mother was strongly affected during pregnancy.

Thus a trustworthy person told me of the following case. A well-known medical authority cut his leg above the ankle with a knife: his wife was present at the time and was much frightened. She was then in the third month of pregnancy: the child when born was found to have an unusual mark upon the same place above the ankle. People almost forget nowadays the tenacity with which the idea of maternal impressions was kept up until the middle of this century; but it is only necessary to read the received German textbook on physiology of fifty years ago, viz. that of Burdach, in order to be convinced of the accuracy of this statement. Not only does Burdach give a number of 'conclusive' cases in man and even in animals (cows and deer), but he also attempts to construct a theoretical explanation of the supposed process. This is undertaken in the following manner,—'Imagination influences the function of organs;' but the function of the embryo is the 'tendency towards development, and hence the influence [of maternal imagination] can make itself felt only as variations in the mode of development.' Thus by exchanging the conception of function for that of the development of organs, Burdach comes to the conclusion that 'homologous organs of the mother and the embryo are in such connexion' that when the former are disturbed a corresponding 'change in the formation of the latter may arise.'

It seems to be not without value for the appreciation of the questions with which we are dealing to remember that the idea of 'maternal impressions' was only comparatively recently believed to be a scientific theory, and that the proofs in support of it were brought forward in form and language as scientific proofs. In Burdach's book we even meet with detailed 'proofs' that violent mental shocks produced by maternal impressions may not only exercise their influence upon one but even upon several children born successively, although with diminishing strength. 'A young

wife received a shock during her first pregnancy upon seeing a child with a hare-lip, and she was constantly haunted with the idea that her child might have the same malformation. She was delivered of a child with a typical hare-lip: her next child had an upper lip with a less-marked cleft; while the third possessed a red mark instead of a cleft.'

Now what can be said about such 'proofs'? We may probably rightly conjecture that Burdach, who was in other respects a clever physiologist, was in this subject somewhat credulous: but there are also instances about which there is not the slightest doubt. I may remind the reader of a case which has been told by no other than the celebrated embryologist, Carl Ernst von Baer¹.

'A lady was very much upset by a fire, which was visible at a distance, because she believed that it was in her native place. As the latter was seven German miles distant, the impression had lasted a long time before it was possible to receive any certain intelligence, and this long delay affected the mind of the lady so greatly, that for some time afterwards she said that she constantly saw the flames before her eyes. Two or three months afterwards she was delivered of a daughter who had a red patch on the forehead in the form of a flame. This patch did not disappear until the child was seven years old.' Von Baer added, 'I mention this case because I am well acquainted with it, for the lady was my own sister, and because she complained of seeing flames before her eyes before the birth of the child, and did not invent it afterwards as the "cause" of the strange appearance.'

Here then we have a case which is absolutely certain. Von Baer's name is a guarantee for absolute accuracy. Why then has science, in spite of this, rejected the whole idea of the efficacy of 'maternal impressions' ever since the appearance of the treatises by Bergmann and Leuckart²?

Science has rejected this idea for many and conclusive reasons, all of which I am not going to repeat here. In the first place, because our maturer knowledge of the physiology of the body shows that such a causal connexion between the peculiar characters of the child and, if I may say so, the corresponding psychical im-

¹ See Burdach, 'Lehrbuch der Physiologie,' Bd. II, 1835-40, p. 128.

² See Handwörterbuch der Physiologie von Rud. Wagner, Artikel 'Zeugung,' von Rud. Leuckart.

pressions of the mother, is a supposition which cannot be admitted ; but also and chiefly because a single coincidence of an idea of the mother with an abnormality in the child does not form the proof of a causal connexion between the two phenomena.

I do not doubt that among the many thousands of present and past students in German Universities, whose faces are covered with scars, there may be one with a son who exhibits a birth-mark on the spot where the father possesses a scar. All sorts of birth-marks occur, and why should they not sometimes have the appearance of a scar? Such a case, if it occurred, would be acceptable to the adherents of the theory of the transmission of acquired characters ; it would in their opinion completely upset the views of their opponents.

But how could such a case, if it were really established, be capable of proving the supposed form of hereditary transmission, any more than von Baer's case could prove the theory of the efficacy of 'maternal impressions'?

I am of opinion that the extraordinary rarity of such cases strongly enforces the fact that we have to do with an accidental and not a causal coincidence. If scars could be really transmitted, we should expect very frequently to find birth-marks which correspond to scars upon the face of the father,—viz. in almost all cases in which the son had inherited the type of face possessed by the father. If this were so we should have to be seriously concerned about the beauty of the next generation in Germany, as so many of our undergraduates follow the fashion of decorating their faces with as many of these 'honourable scars' as possible.

I have spoken of 'maternal impressions' because I wished to show that, until quite recently, distinguished and acute scientific men have adhered to an idea, and believed that they possessed the proof of an idea, which has now been completely and for ever abandoned by science. But in addition to this, there is a very close connexion between the theory of the efficacy of maternal impressions and that of the transmission of acquired characters, and sometimes they are even confounded together.

Last year a popular scientific journal quoted the following case as a proof of the transmission of mutilations. I do not, however, wish to imply that the editor must be held responsible for the errors of a correspondent. 'In November, 1864, a pregnant merino

sheep broke its right fore-leg, about two inches above the knee-joint; the limb was put in splints and healed a long time before the following March, when the animal produced young. The lamb possessed a ring of black wool from two to three inches in breadth round the place at which the mother's leg had been broken, and upon the same leg.' Now if we even admitted that a ring of black wool could be looked upon as a character which corresponds to the fracture of the mother's leg, the case could not possibly be interpreted as the transmission of a mutilation, but as an instance of the efficacy of maternal impressions; for the ewe was already pregnant when she fractured her leg. The present state of biological science teaches us that, with the fusion of egg and sperm-cell, potential heredity is determined¹. Such fusion determines the future fate of the egg-cell and the individual with all its various tendencies.

Such tales, when quoted as 'remarkable facts which prove the transmission of mutilations,' thoroughly deserve the contempt with which they have been received by Kant and His. When the above-mentioned instance was told me, I replied, 'It is a pity that the black wool was not arranged in the form of the inscription "To the memory of the fractured leg of my dear mother."'

The tales of the efficacy of 'maternal impressions' and of the transmission of mutilations are closely connected, and break down before the present state of biological science. No one can be prevented from believing such things, but they have no right to be looked upon as scientific facts or even as scientific questions. The first was abandoned in the middle of the present century, and the second may be given up now; when once discarded we need not fear that it will ever again be resuscitated.

It is hardly necessary to say that the question as to the transmission of acquired characters is not completely decided by the unconditional rejection of the transmission of mutilations. Although I am of opinion that such transmission does not take place, and that we can explain the phenomena presented by the transformation of species without this supposition, I am far from believing that the question is settled, simply because the transmission of mutilations may be dismissed into the domain of fable. But at all events we have gained this much,—that the only facts which appear to directly

¹ See V. Hensen, 'Physiologie der Zeugung.' Leipzig, 1881.

prove a transmission of acquired characters have been refuted, and that the only firm foundation on which this hypothesis has been hitherto based has been destroyed. We shall not be obliged, in future, to trouble about every single so-called proof of the transmission of mutilations, and investigation may be concentrated upon the domain in which lies the true decision as to the Lamarckian principle, it may be concerned with the explanation of the observed phenomena of transformation.

If, as I believe, these phenomena can be explained without the Lamarckian principle, we have no right to assume a form of transmission of which we cannot prove the existence. Only if it could be shown that we cannot now or ever dispense with the principle, should we be justified in accepting it. I do not think that I can represent the state of the subject better than by again referring to the metaphor of the ship. We see it moving along with all sails set, we can discern the presence of neither paddles nor screw, and as far as we can judge there is no funnel, nor any other sign of an engine. In such a case we shall not be justified in concluding that an engine is present and has some share in the movement of the vessel, unless the movement is of such a kind that it is impossible to explain it as due to the unaided action of the wind, the current, and the rudder. Only if the phenomena presented by the progress of organic evolution are proved to be inexplicable without the hypothesis of the transmission of acquired characters, shall we be justified in retaining such an hypothesis.