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Unisexual Inheritance

by

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The chief question on which biologists are divided in opinion at the present time is that of the inheritance of acquired characters. Darwin himself believed in such inheritance, although he attributed to it only a subordinate importance as a factor of evolution. It would perhaps be generally admitted that the question is still open, that on the one hand the hereditary transmission of such characters has not been finally disproved, and on the other hand that there is not sufficient satisfactory evidence to prove that it occurs. But nearly everyone interested in evolution, in spite of this formal admission, is firmly convinced on one side or the other. The followers of one school, are scarcely willing to consider any arguments in favour of the affirmative side in the absence of direct experimental verification, while the heretics frequently make damaging attacks on the system of doctrine by which the facts of evolution are supposed to be explained on the principle of selection alone.

The rejection by many evolutionists of one factor which Darwin admitted, is due chiefly to the influence of Weismann's writings, and Weismann's opposition to it was not founded on an inductive method of investigation such as that employed by Darwin, but arose from his able and persevering endeavours to formulate a detailed conception of the process and mechanism of heredity. Finding no facts or data on which to base a conception of the process by which a change in parts or organs of the body could be transmitted to the germ cells in the reproductive organs, Weismann started from the assumption that

the powers of development in the germ cells are entirely independent of the body, that germ cells derive all their properties from the germ cells of previous generations. Thus a hen's egg develops into a chick, not because it is produced by a hen but because it is descended from the eggs of previous generations which also had the power of developing into chicks. When one egg develops into a chick, it divides into numerous cells, some of which form the body of the bird, while others are the germs of new eggs, and the body of the bird has no influence on these new germs. The developmental powers of the germ-cells themselves however, as they multiply by subdivision, and unite in sexual union, undergo variations, and therefore the individuals developed from them are not exactly alike for all time, but show, as we observe, individual peculiarities. By constant selection from numerous individuals with small or great peculiarities evolution is supposed to be effected.

The body of the individual, as distinguished from the germ cells in its reproductive organs, may be modified by accident or exercise or stimulation. A muscle grows larger when exercised, sunlight causes the skin to become pigmented, the friction of a boot may produce a corn. But such physiological changes, according to Weismann, begin and end with the individual, with the body or soma. We can thus definitely distinguish between variations which arise in the soma, somatogenic variations, and variations which have their origin in the germ-cell, blastogenic, and according to Weismann somatogenic variations have no effect on the germ cells and therefore never become hereditary.

That I am justified in attributing the disbelief in the inheritance of somatogenic variations to theoretical prejudice is proved I think by a passage which Herbert Spencer quotes from a letter addressed to him by a zoological expert at Cambridge. The passage contains this statement: „Most of us here at Cambridge are intensely opposed to the doctrine of the inheritability of acquired variations. Even assuming that the developmental power of a germ is determined by its molecular structure, we still fail to conceive any means by which for instance a change in the development of a muscle or nerve can effect a corresponding change in that part of the germ which is destined to produce a corresponding part in the descendant."

There is however another way of testing the rival theories of heredity, besides the possibility of conceiving the mechanism of the process, and that is by comparing the necessary logical consequences of the theories with observed and admitted facts. The theory whose deductions agree more closely with the facts of observation is likely to be the nearer the truth. I have lately devoted considerable labour to making such a comparison for the facts concerning secondary sexual

characters. The existence of structural differences between the sexes, apart from the essential reproductive organs, is one of the most interesting phenomena in zoology. An adult stag has an enormous pair of branching bony structures attached to his skull, and the female has generally no trace of such organs. The stag is the father of deer both male and female, his male progeny develop antlers like his own, his female progeny show no trace of antlers. Do these familiar facts agree with the hypothesis that only blastogenic variations are hereditary? We know well enough that some variations are blastogenic, hare lip for example, or the existence of a sixth finger or toe. But these are transmitted indifferently to male or female progeny.

We have no reason to believe that any kind of selection whether sexual selection or natural selection can explain the limitation of inheritance to one sex. This question has been discussed at length by Darwin in his „Descent of Man", 2nd Edition, chapter XV. Darwin was led to examine the subject very carefully in consequence of Wallace's contention that the variations which led to the special male characters in birds tended at first to be transmitted equally to both sexes, but that the female was prevented from acquiring the conspicuous characters of the male through natural selection, because of the danger she would thus have incurred during incubation. Darwin states that he knew of no facts rendering it probable that a character could be limited to one sex by selection when it was not originally sexually limited in transmission.

I am not aware that since 1885 any new facts have been produced which would diminish the validity of Darwin's conclusion. We must assume therefore that the variations which give rise to unisexual characters are from their first appearance unisexual in their occurrence and transmission. If we deny the inheritance of acquired characters we can only assume this without any explanation. We can only observe with Darwin that variations occurring late in life are more likely to be unisexually inherited than others, but we can give no reason why changes should occur in the determinants within the germ which produce characters late in life limited in inheritance to one sex. We can only say that they do occur, like other variations equally inherited by both sexes, and that when they occur they may be preserved and accumulated by selection.

Weismann in his treatise on the „Keimplasma" has considered in detail the mechanism of unisexual heredity, but he has not satisfactorily explained the first origin of unisexual variations. He refers to the fact that a character not appearing in the female may yet be transmitted through the female from grandfather to grandson. The ovum from which the female was developed therefore contains the determinants of, i. e. the living particles which determine, the male cha-

racters, and hands them on to the germ cells of the following generation, although the characters themselves do not actually show themselves in the female. But more than this he points out is required. The determinants exist also in the cells of the body of the female, because in certain cases when the female has become sterile from old age the male characters are developed. Conversely the determinants of the female characters exist in the male, because when the latter is castrated at an early age the male characters are not developed or, as Weismann interprets the matter, female characters are developed instead. Weismann's explanation of the facts then is that in each rudiment of an organ in the developing soma there are two sets of determinants or a set of double determinants, one set of which is active and the other latent, while the latent may be called into activity by special conditions such as castration, or sterility.

But so far as I can discover Weismann has made no attempt to explain how on his own theory the activity of one or other set of homologous determinants in the soma, in an external organ for example, can be in any way affected by the removal of the primary generative organs, or by the condition of those organs. He conceives the development of the individual, as in the first place a subdivision of the fertilised ovum into a number of cells, some of which will become the germ cells of the next generation. The rest then are the somatic cells, and these as they divide become differentiated, each cell as it is formed taking with it only the determinants of the organ or organs in whose formation it is going to take part. According to the theory the fate of these somatic determinants can have no influence on the determinants in the germ cells, for if they had we should have the possibility of the inheritance of acquired characters. Consider then the cells of the frontal bone in a young stag from which the antlers will grow. These cells contain the determinants of the antler, and presumably no female determinants, since the female possesses no antlers. Yet if the testes are removed the determinants of the antlers refuse to act, and remain latent. It is evident therefore that the action of these determinants depends on the presence of the primary generative organs, i. e. of the germ cells of the next generation, in another part of the body. There must therefore be some connection, some continuity between the germ cells and the determinants of the antlers, while the theory postulates that there is none.

It may perhaps be argued that the activity of the antler-determinants depends not on the presence of the germ cells, but on nervous excitement or other conditions of the soma, which are due to the functional activities concerned in the liberation of the germ cells. In that case how are we to conceive the origin of the variations which originally gave rise to the antlers? Variations according to the theory

arise by changes in the determinants within the germ plasm, changes which are independent of the condition of the soma. How then do these modified determinants ever come to depend for their behaviour on the condition of the soma?

It is perhaps easy enough for the follower of Weismann to say that the variation which arose in certain germ cells originally was not merely production of determinants which would in development produce antlers, but of determinants which would only produce antlers when the body was in the condition caused by the activity of the reproductive organs. But since the variations of the determinants in the germ cells are supposed to be entirely independent of the soma or its condition there is no reason why such a variation should ever arise. The periosteum of the frontal bones, the formative action of which produces the antlers, has not originally any sexual character, is not in other animals specially affected by the periodical activity of the generative organs. Why then should the variation in the determinants which gives rise to antlers be correlated with the sexual function?

It is I think impossible in this case to explain the facts by the process of selection, for if the development of the antlers took place like that of teeth at a certain stage of life independently of the sexual functions, the antlers would be equally effective as weapons. A tiger does not lose his teeth when castrated, what advantage then is it to the deer tribe that the development of the antlers should be so profoundly affected when the reproductive organs are removed? Selection does not even explain the presence of antlers in deer and their absence in other tribes of mammals, such as horses or swine. There is no valid evidence, in spite of the fabled occurrence of horned horses, of antlers occurring as occasional spontaneous variations, in animals that do not normally possess them.

Another important peculiarity of antlers is their annual loss and recrescence. According to Weismann's conception the determinants are used up when the cells which they determine have been definitely formed. In his treatise on Das Keimplasma he expressly refers to the antlers of stags in the chapter on regeneration, or as I prefer to call it, recrescence. He believes that recrescence is not a process due to a common original property of organisms, but is a special adaptation produced by selection. This means that as an occasional variation there occur in certain cells not merely the determinants of the cells developed from them, but also extra sets of determinants which can provide the regenerated tissues when the first are removed. The formation of these extra or reserve determinants is supposed to occur in the germ, as a blastogenic variation, and selection alone is supposed to decide whether the possibility of recrescence shall belong to a given

organ or not. Again the selectionist merely assumes that the required variation occurred in the germ, and gave rise to the observed phenomena in development. It is difficult to see how selection can be made to assist in the explanation of the annual recrescence of antlers, for permanent antlers would have been equally effective as weapons. It may be urged that antlers once formed do not grow, but it is not evident that either the periodical renewal or the characteristic branching give to antlers any superiority as weapons over the permanent horns of antelopes, and cattle.

It may be fully granted that, since the growth and periodical renewal of the antlers take place in existing stags as a hereditary and constitutional process, independent of all exciting causes except the functional activity of the testes, there must be something in the constitution of the ovum from which a stag is developed, which „determines" all these peculiarities in the antlers. The fertilised ovum of a deer or a rabbit is to our perceptions a minute mass of protoplasm, and although the two may not be exactly alike in size and other respects, yet it is perfectly impossible for us to distinguish in them the differences which cause one to develop into a stately stag, the other into a defenceless rabbit. Yet we know that there is as much difference between the two ova as between the two animals into which they develop. The characters of the adult animals are not due to the different food they eat, nor to differences of climate, nor even to the fact that the embryo in one case is developed in the body of female deer in the other in that of a doe rabbit: they are due entirely to some peculiarities in the ova, of whose existence we are certain, but of whose nature we are profoundly ignorant.

So far there is no objection in principle to Weismann's attempt to construct a theory of the mechanism of development, a theory of the constitution and properties of the ovum. But when we ask whence was derived this power of the stag's ovum to give rise to antlers having such a marvellous history, what is the reply? Merely that the properties which are in the ovum arose in the ovum.

The hypothesis of Weismann then is that the properties of the deer's ovum which cause antlers to develop were originally of the same nature as the blastogenic variations which occasionally in the human ovum cause the development of supernumerary fingers, or hare lip, or even a double head. That such blastogenic variations occur is admitted, and it may even be possible in course of time to find the causes of them, but the question to be considered is whether all hereditary peculiarities are of the same kind. What evidence have we of the observed occurrence of blastogenic variations limited to one sex, and correlated with the functional activity of normal reproductive organs?

There is one well known abnormality in the human race which appears at first sight to offer evidence of this kind. I refer to the disease called haemophilia, a congenital tendency to excessive bleeding. This disease is comparatively rare, but its importance from our present point of view is due to the fact that it is strongly hereditary, and that it occurs chiefly in men, rarely in women. According to Wickham Legg, one of the principal authorities on the subject, the disease generally appears in the sons of women who belong to an affected family, though the women themselves show the symptoms but slightly or not at all; on the other hand fathers are said rarely to transmit the disease to their sons. The exact nature of the abnormality to which the bleeding is due seems to be doubtful, Dr. Gamgee considered the fault lay rather in the blood vessels than in the blood. Weismann refers to this disease, and explains it according to his theory. He suggests that the determinants of the blood-vessels in the human ovum are double determinants, one set developing in the male, the other in the female, and that the congenital variation giving rise to haemophilia has arisen only in the male determinants. But it is to be observed that the disease does not exactly correspond to a secondary sexual character. It generally shows itself in boys during the first year of life, though sometimes the symptoms do not appear until a few years later, whereas secondary sexual characters generally do not appear much before the period of puberty. It seems to me quite possible that the actual defect, or variation, whatever it may be, is equally present in both sexes, but produces more serious results in males in consequence of differences normally present between the sexes. That there are normal differences between man and woman in the blood, is certain, in man there are more red corpuscles and the specific gravity is higher. The general blood pressure also may be higher in man. Haemophilia therefore is not shown to be a case of a unisexual congenital variation at all.

Evidence to be of real importance in this enquiry should consist of cases in which a unisexual congenital variation is observed to occur in a species in which the male and female are normally similar. Wild species of pigeons fulfil this condition, and it is a fact that sexual differences have appeared to a certain degree in pigeons under domestication. Darwin refers to a Belgian breed in which the males alone are marked with black striae, and the peculiarities of the pouter and carrier are more developed in the male than in the female. But it is by no means certain that these differences arose as blastogenic variations: it seems to me more probable that they are to be explained in the same way as I explain the sexual differences in wild animals. The occurrence of unisexual variations in individual pigeons has not I believe been described.

The reasons then for regarding secondary sexual characters as due to blastogenic variations are by no means conclusive, and such a view affords no explanation of the remarkable correspondence between the development of such characters and the life and habits of the animal possessing them. On the other hand such characters have a much greater resemblance to acquired characters, and when so regarded their peculiarities are seen to be due to antecedent conditions, instead of arising by a kind of spontaneous generation in the germ plasm.

The growth of the antlers of a stag resembles physiologically the formation of a knob of bone or exostosis which occurs when the periosteum or membrane covering the bone is mechanically irritated. Stags fight with their antlers, and if they fought originally with their foreheads before antlers existed, we could understand the origin of these structures. The females do not butt with their heads, and these have no antlers. When the antler is developed the external skin and periosteum are removed in the process known as the peeling of the velvet. Now bone denuded of its periosteum by injury or disease sooner or later dies and dead bone is absorbed or thrown out of the body. The antler likewise when the velvet is shed becomes a mass of dead bone, although the circulation of blood and the life of the bone may continue for some time in the centre. Absorption then takes place at the base of the dead structure and the antler is shed, to be followed by a larger successor. The phases in the history of the antler correspond to the phases in the activity of the reproductive organs. The growth of the antler takes place in summer, when the testes are quiescent but maturing. The velvet is shed in August after which the stag begins to fight and the testes are active. The fighting and pairing season lasts from September to December, and the antlers are shed usually in the following April.

All these facts become intelligible if we regard them as the hereditary repetition of processes of growth and absorption originally produced directly by the mechanical irritations caused by fighting. Stags are in the habit of rubbing the velvet from the fully developed antlers purposely, but probably the shedding of the velvet and all the other processes in the history of an antler would take place in a stag at the present day by heredity alone. It is consistent with physiological science however to suppose that originally the antler began to grow in consequence of the blows received in fighting, that the velvet was torn from the same cause and that the shedding of the antler followed in consequence. After the old antler was shed the same results would be produced at the next rutting season. The unisexual inheritance and the remarkable effects of castration are explained by the hypothesis that the new processes of growth and absorption are necessarily

repeated by heredity in their original associations. As acquired characters they were produced when the testes were active and the brain and nervous system irritated by sexual excitement, as inherited characters they only develop when these conditions are present or approaching. On this hypothesis there is no need for a double set of determinants in both male and female. The determinants, the living elements, are the same in both, but their action depends on the condition of the generative organs, and of the whole body.

(Schluss folgt.)

Versuch einer Einteilung der nicht-nervösen Reflexe[1]).

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I. Allgemeinheit der nicht-nervösen Reflexe.

Alle Vorgänge, welche sich im lebenden Protoplasma eines Organismus abspielen, können zum mindesten von zwei verschiedenen Gesichtspunkten aus betrachtet werden. Man kann entweder die chemische Seite der Frage ins Auge fassen und die stofflichen Veränderungen studieren, sowie die zur Ausführung notwendige Kraft, oder man untersucht vom Standpunkt der Reizbarkeit, durch welche Reize eine Reaktion eintritt.

Diese zweite, physiologische Seite der ganzen Frage ist von denjenigen, welche sich mit dem Chemismus beschäftigten, beinahe ganz vernachlässigt worden, gerade so, als ob sie vergessen hätten, dass nichts in einem Lebewesen spontan ist, dass alle Veränderungen, selbst die unbedeutendsten, durch Reize bedingt sind, folglich dem Gebiet der Reizbarkeit zugezählt werden müssen. Mit einem Worte, jede protoplasmatische Thätigkeit ist ein elementarer Reflex, der auf seine größte Einfachheit zurückgeführt ist.

Bei den Metazoen ist ein eigener Apparat vorhanden, welcher die verschiedenen Teile des Organismus miteinander verbindet und so den Zusammenhang herstellt zwischen der Stelle der Reizung und der, welche die Reaktion hervorbringen soll. Aber dem Nervensystem unterstehen bezüglich ihrer Reizbarkeit nicht alle Zellen der Metazoen. Die freien Zellen (Leukocyten, Spermatozoen, Wanderzellen des Bindegewebes) stehen in keiner Verbindung mit dem Nervensystem. Ueberdies hat das Nervensystem durchaus nicht die allgemeine Leitung über alle Vorgänge in den Zellen, mit denen es sich verbindet; es reguliert nur die gröberen Vorgänge (Kontraktion, Drüsensekretion etc.), und es giebt dem Tiere nur Auskunft über die gröbsten Abänderungen der

1) Auf Wunsch des Herrn Verfassers übersetzt aus den „Annales de l'Institut Pasteur“ (25 août 1901).