A THEORY OF HEREDITY.

MR. DARWIN stated, in the year 1868, in the preface to his theory of Pangenesis,* that "every one appears to admit that the body consists of a multitude of 'organic units,' each of which possesses its own proper attributes, and is to a certain extent independent of all others;" and it may be safely asserted that the general expression of biological opinion since that date has been emphatically the same. We may therefore rest assured that the hypothesis of organic units, and all that such an hypothesis implies, must lie at the foundation of the science of heredity. It remains to determine further particulars; we have to examine how far the details of such theories as are based upon the hypothesis of organic units are correct, and to consider how their deficiencies may be supplied.

The facts for which a complete theory of heredity must account may conveniently be divided into two groups; the one refers to those congenital peculiarities that were also congenital in one or more ancestors, the other to congenital peculiarities that were not congenital in any of the ancestors, but were acquired by one or more of them during their lifetime, through change in the conditions under which they lived; as of climate, food, disease, mutilation, or habit.

The first of these two groups is of predominant importance in respect to the number of well-ascertained facts that it contains,

* Darwin: "Variation of Plants and Animals under Domestication," ii. 370.

many of which it is possible to explain, in a broad and general way, by more than one theory based on the hypothesis of organic units. The second group includes much questionable evidence, usually difficult of verification, and which, as I shall endeavour to show, does not, for the most part, justify the conclusion commonly derived from it. In this paper I divide the general theory of heredity into two parts, corresponding respectively to these two groups. The first stands by itself, the second is wholly supplementary and subordinate to it.

No theory of heredity has been enunciated with more clearness and fulness than that of Mr. Darwin's Pangenesis, and the preparatory statement to that theory contains the most elaborate epitome that exists of the many varieties of facts for which a complete theory of heredity must account. What I have now to say is largely based on the arguments and considerations brought forward by Mr. Darwin in support of it; nevertheless the conclusions in this paper will be seen to differ essentially from his own. Pangenesis appears more especially framed to account for the cases which fall in the second of the above-mentioned groups, which are of minor and often doubtful import; and it will be seen that I accept that theory with modification, for the supplementary and subordinate part of a complete theory of heredity, but by no means for the primary and more important part.

Before proceeding, I beg permission to use, in a special sense, the short word "stirp," derived from the Latin *stirpes*, a root, to express the sum-total of the germs, gemmules, or whatever they may be called, which are to be found, according to every theory of organic units, in the newly fertilized ovum—that is, in the earliest pre-embryonic stage—from which time it receives nothing further from its parents, not even from its mother, than mere nutriment. (It is hardly necessary to remind the reader that not a drop of blood from the mother penetrates into the vessels of the embryo, but that the two circulations are wholly distinct; the placenta to which the embryo is attached, and with which it is in vascular connection, being itself nourished from the mother by mere imbibition.) This word "stirp," which I shall venture to use, is equally applicable to the contents of buds, and will be found very convenient, and cannot apparently lead to misapprehension.

The whole of the stirp, together with much of mere nutriment, is packed into a space not exceeding the size of the head of a pin, for that is the size of the newly fertilized ovum, which, curiously enough, is the same in all mammalia. It is evident that direct observation can tell us nothing concerning the form and behaviour of such minute objects as the germs of which the stirp is composed; they would be far beyond the ken of the micro-

scopist, even if their separate actions upon light were different. But even this is not the case, for the fertilized ovum is almost homogeneous in colour. Cells and their contents are, to biologists looking at them through microscopes, much what mail-bags and the heaps of letters poured out of them are to those who gaze through the glass windows of a post-office. Such persons may draw various valuable conclusions as to the postal communications generally, but they cannot read a single word of what the letters contain. All that we may learn concerning the constituents of the stirp must be through inference, and not by direct observation; we are therefore forced to theorize.

We will begin with a statement of the four postulates that seem to be almost necessarily implied by any hypothesis of organic units, and which are included in that of Pangenesis. The first is, that each of the enormous number of quasi-independent units of which the body consists, has a separate origin, or germ. The second is, that the stirp contains a host of germs, much greater in number and variety than the organic units of the structure that is about to be derived from them; so that comparatively few germs achieve development. Thirdly, the germs that are not developed, retain their vitality; they propagate themselves while still in a latent state, and they contribute to form the stirps of the offspring. Fourthly, organization wholly depends on the mutual affinities and repulsions of the separate germs; first in their stirpal, and subsequently during all the processes of development.

Proofs of the reasonableness of these postulates are especially to be found in the arguments of Mr. Darwin: that there is at least a fair ground to believe in their reasonableness, may be shown in a cursory manner. Thus, the independent origin of the several parts of the body may be argued from the separate inheritance of their peculiarities. If a child has its father's eyes and its mother's mouth, these two features must have had a separate origin. Now, it is observed that peculiarities, even of a microscopic kind, are transmissible by inheritance, and therefore it may be concluded that the minutest parts of the body have separate origins. That the stirp contains a much greater variety of germs than achieve development, is proved by the fact that a person is capable of transmitting ancestral peculiarities to his children, that he did not himself possess. Everything that reached him from his ancestors must have been packed in his stirp; therefore his stirp contained not only such peculiarities as were developed in his own bodily structure, but also those numerous other ancestral peculiarities of which he was personally destitute, but which he bequeathed to one or more of his descendants. Therefore every stirp must be held to contain a great variety of germs in addition to those that may achieve development in the person who grows out of that

stirp. It further follows that these residual germs retain their vitality, and contribute to form the stirp of the descendants, as will be explained more fully further on. The fourth and last postulate, that organization wholly depends on the mutual affinities of the separate organic units, commends itself to acceptation by the simplicity and sufficiency of what is asked; much of what I have to say in this paper will testify to this. We should also bear in mind that the alternative hypothesis of a general plastic force resembles that of other mystic conceptions current in the early stages of many branches of physical science, all of which yielded to molecular views, as knowledge increased. The science of heredity is still in an early stage, and analogy disposes us to expect that its course will be similar to that of its predecessors. The possibility of such minute objects as the germs possessing sufficient delicacy of perception to ensure that each of so enormous a variety of them should find its place, was illustrated by Mr. Darwin through the delicate perception of the pollen grains of the different species of plants. He says:* "About 10,000 compositæ exist, and there can be no doubt that if the pollen of all the species could be simultaneously or successively placed on the stigma of any one species, this one would elect, with unerring certainty, its own pollen." The partial failures in the action of these affinities are most instructive, as where a mark of any kind on the skin is transmitted by inheritance in an altered situation, to a neighbouring or to an homologous part. Having stated thus much by way of preface, we may now proceed freely.

Much wonder is expressed by physiologists at the apparent fact that none of the higher races admit of being long carried on by any system of unisexual parentage; but that deterioration, apparently due to a deficiency of some of the structural elements, gradually sets in, and the race ultimately perishes. It appears to be a universal law, that a system of double parentage is a very important, some think an essential requirement, for the indefinite maintenance of any race whose organization is complex; and I would submit that the differentiation of a race into two sexes is the result, and not the cause, of this requirement. In the lowest forms of organized life double parentage exists, but sex apparently does not, because it appears that any two cells may conjugate and combine their contents within a single cell; these forms are also capable of easy unisexual multiplication by self-division or by budding. Proceeding higher in the scale of life the sexual differentiation becomes increasingly marked, and unisexual propagation is of rarer occurrence. At length we reach the stage where the differentiation of sex is complete, and the power of unisexual propagation is wholly lost.

* "Variation of Plants and Animals under Domestication," ii. 380.

Now the especial necessity of a system of double parentage in complex organizations is the immediate consequence of a theory of organic units and germs. Let us fix our attention upon any one definite series of unisexual descents, and follow out its history: suppose we select, cut off, and plant the second bud, then after it has grown to maturity we similarly take the second of its buds, and so on consecutively. At each successive stage there is always a chance of some one or more of the various species of germs in the stirp dying out, or being omitted; and of course when they are gone they are lost for ever, and are irreplaceable by others. From time to time this chance must fall unfavourably, and will cause a deficiency in some of the structural elements, and a consequent deterioration of the race. If the loss be vital it will of course be extinguished at once; but on the more favourable supposition, the race will linger on, submitting to successive decrements in its constituent elements, until the accumulation of small losses becomes fatal. What is true for the series of second buds in our example, is of course equally true for any system we please to specify, and therefore it would be generally true in the experience of gardeners and others.* Exactly the same argument applies to every other unisexual process, all of which lead to deterioration and final extinction. On the other hand, when there are two parents, the chance deficiency in the contribution from either of them, of any particular species of germ, will be supplied by the other. No doubt, cases will rarely occur in which the same species of germ is absent from the contribution of both, and a very small proportion of the families will thereby perish. But what if they do become extinct? The remaining families are perfectly sound, or tend to become so in the next generation, and they fill up, only too easily, the gap. Thus we see that in any specified course of unisexual generation, every line of descent is doomed to extinction, sooner or later; but that in bisexual, only a very small proportion of families become extinct, or even temporarily suffer, from the cause we are considering, while the great majority do not suffer a whit, and the remainder tend to become rehabilitated. Again, as the stirp whence the child sprang can be only half the size of the combined stirps of his two parents, it follows that one half of his possible heritage must have been suppressed. This implies a sharp struggle for

* It would not, however, be always true in a free state of nature, where the weakly plants would be supplanted by those that remained sound. Here we have to consider, on the one hand, the growing chance against the deterioration of any single line of descent, and on the other, the growing number of all possible lines of descent. They both proceed in a geometrical ratio; and if the ratio of the latter exceeded that of the former, extinction need not take place. But this would become impossible after a certain degree of complexity had been reached, because with growing complexity, the chance of deterioration must increase, while the fecundity (see H. Spencer's Biology; vol. i., "Multiplication") must diminish.

place among the competing germs, and the success, as we may infer, of the fittest half of their numerous varieties.

The limitation of space in the stirp requires a limitation not only of the varieties of each species of germ, but also of the number of individuals in each variety. The knowledge of such a cause is helpful, and appears to be needed, in accounting for the not very large number of subdivisions in which peculiarities are transmitted. I am not considering cases of the slow loss of some characteristic of a race which proceeds by minute gradations, and may be ascribed, at least in part, to an alteration in the quality of the germs, nor am I speaking of cases where it is clear that one of two alternative qualities has overpowered the other, but of instances where they appear equipotent and capable of merging together. Thus, in the gradual breeding-out of negro blood, we may find the colour of a mulatto the half, and that of a quadroon one quarter that of his black ancestors; but as we proceed further, the subdivision is very irregular, and does not continue indefinitely in the geometrical series of one-eighth, one-sixteenth, and so on, but it is usually present very obviously, or not at all, until it entirely disappears. There are, of course, far more gradations in compound results, as in an expression of the face, because any one of its elementary causes may be present or absent; and as the number of possible combinations or alternatives, among even a few elements, is very great, there must be room for a large number of grades between the complete inheritance of the expression and its total extinction.

It is certain, from the rapidity of the visible changes in the substance of the newly fertilized ovum, that the germs in the stirp are in eager and restless pursuit of new positions of organic equilibrium, due, as we may suppose, to the unequal rates of development of some of the better nourished germs. We see that segregations occur as much as aggregations, and it is reasonable to suppose that repulsions concur with affinities in producing them. We know nothing yet of the nature of these repulsions and affinities, but it seems hardly possible to account for the whole state of affairs on the hypothesis of a purely step-by-step development like that proposed in Pangenesis, where B follows A, and C follows B, and so on. It is difficult to suppose the mutual influences of the germs to be limited to lines like those which attach the blood corpuscules face to face in long rouleaux when coagulation begins; neither can we suppose them limited to planes, like those which govern the harmonious groupings of the flora and fauna on the face of a land left in a state of nature; but we ought rather to expect them to act on many sides, in a space of three dimensions, just as the personal likings and dislikings of an individual in a flying swarm may be supposed to determine the position that he occupies in it. Each germ has many neighbours:

a sphere surrounded by other spheres of equal sizes, like a cannon ball in the middle of a heap of them, when they are piled in the most compact form, is in immediate contact with no less than twelve others. We may therefore feel assured that the germs must be affected by numerous forces on all sides, varying with their change of place, and that they must fall into many positions of temporary and transient equilibrium, and undergo a long period of restless unsettlement, before they severally attain the positions for which they are finally best suited. However ignorant we may be at present of the character of these affinities and repulsions, or of what Mr. Herbert Spencer calls their polarities in his instructive chapters in the first volume of his "Principles of Biology," a conviction of their existence is sufficient to afford general notions of what must be their mode of action, and enables us to illustrate its necessary consequences by many familiar experiences. Chief among these are the events of political life, such as the struggle for place and power, election and representation. For example, we know that the primary cells divide and subdivide, and we may justly compare each successive segmentation to the division of a political assemblage into parties, having, thenceforward, different attributes. Or, again, we may compare the stirp to a nation, and the germs that achieve development to its foremost men, who succeed in becoming its representatives; lastly, we may compare the qualities of the person whose structure is composed of the developed germs, to the political characteristics of the house of representatives of the nation. These are not idle metaphors, but strict analogies; they will be found to bear consideration, and to be worthy of being pursued, as they give a much-needed clearness to our views on heredity.

The great dissimilarity frequently observed between brothers or sisters is easily to be accounted for, and it may be well illustrated by a political metaphor. On the one hand, the stirps must be nearly alike, because the germs are simple organisms, and all such organisms breed true to their kind; on the other hand, we have very different structures developed out of these stirps. The well-known uncertainties of political elections, and their causes, afford a strict analogy and explanation of this. We have abundant experience that when a constituency is very varied, trifling circumstances will change the balance of parties, and therefore, although there may be little real variation in the electoral body, the character of its political choice at successive elections may change abruptly. A uniform constituency will always have representatives of a uniform type; and this precisely corresponds to what occurs in animals of pure breed, whose stirp contains only one or a very few varieties of each species of germ, and whose offspring always resemble their parents and one another. The

more mongrel the breed, the greater is the variety of the offspring. The dissimilarity not unfrequently found between twins of the same sex is more marked than that between ordinary brothers and sisters, notwithstanding that the embryonic conditions were closely similar. The subject is a very curious one, and requires the following explanation. I had occasion to make many inquiries into the resemblances of twins, whence it appeared that among well-formed "true" twins,* so to speak, namely those who, up to the time of their birth, were enclosed in the same membrane, and had therefore been developed out of two germinal spots in the same ovum, there are two groups of cases that contrast strangely with one another, and there are but few intermediate cases. In the larger of these groups, the twins are exceedingly alike in body and mind, also in their growth, illnesses, and decay, and their resemblance is not unfrequently such as to justify the somewhat startling incidents referring to twins that are to be found in many works of fiction. In the smaller group, which contains perhaps one-fourth as many cases as the larger, the twins are absolutely unlike; so much so, that they have occasionally been described as "complementary" the one to the other; the one having what the other lacked. What can be the reason that, out of identically the same primary stirp, either two absolutely dissimilar persons can be developed, or else two closely similar ones; while the intermediate cases are so rare, that they may be considered due to quite another and more common contingency, namely, that in which the twins are not produced out of the same ovum, but from separate ova? The answer I suggest is as follows:—As regards the similarity of true twins, there can be little difficulty; we should expect, on statistical grounds, that the two halves of any assemblage of germs would be much alike. The secondary stirps of the twins being in this case alike, and the circumstances of their development being almost identical, the results must be closely similar. As regards the dissimilarity, we might expect that if there had happened to be a sufficient delay before the commencement of the division of the primary stirp to allow its germs to arrange themselves somewhat according to their affinities, the two halves would be strongly contrasted. In the case of an ordinary single birth, the germ (to make the illustration less complex, I will not say the germs) of each species

* For some general results of these inquiries, see *Fraser's Magazine*, Nov., 1875. I had twenty cases of strong dissimilarity in twins, and in all the cases, the twins were of the same sex. Now, it appears to be a rule without exception that what I have above termed "true" twins are of the same sex. Such twins are by no means uncommon; Spaeth's estimate of their frequency, as compared to that of twin births generally, is as high as 25 per cent., and I understand that his observations rank among the very best; however, the estimates of other observers are much lower. Hence there is much probability that my cases of strong dissimilarity were usually, if not invariably cases of true twins. But I have no direct evidence one way or the other.

that achieves development may be compared to the one representative of a body of electors, each of whom has a single vote. In the case of twins, we may suppose each elector still to have only a single vote, but that two representatives are elected. Let us now suppose one of the political parties slightly to predominate; then, if the electoral body be divided by some accidental line, the same party would predominate in each division; and if the election were conducted on that principle, the two representatives would certainly be men of the same predominant party. But if the electoral body acted as a whole, it would be impossible for the predominating party to return more than one candidate, and the two representatives would be men of opposite politics.

That part of the stirp which has become developed has been supposed (I believe universally) to be the chief agent in maintaining the progeny of germs. It is certainly an essential condition in the theory of Pangenesis, as the name of that theory testifies; where each separate cell in its nascent state is supposed to throw off germs which circulate freely in the body along with others which had been hereditarily transmitted, and which aggregate themselves owing to their mutual affinities, and so form the sexual elements. For my own part, while acknowledging that there exists undeniable evidence of the existence of this power, which will be discussed when we come to the second group of cases, I shall endeavour to show that it can, at the most, be effective in a very minute degree. The germs that become developed into structure, are relatively too few to exert much hereditary influence, and when fully developed they would be passive and sterile. I argue, that as fertility resides somewhere, it must have been vested in the non-developed residue of the stirp, or rather in its progeny and representatives (whatever, or however numerous, they may be) at the time when the individual has reached adult life.

The hypothesis that the developed germs are relatively few and sterile agrees singularly well with many classes of fact. Thus it explains why, although hereditary resemblance is the general rule, the offspring is frequently deficient in the very peculiarity for which the parent was exceptionally remarkable. We can easily understand that the dominant characters in the stirp will, on the whole, be faithfully represented by the structure of the person who is developed out of it; but if the personal structure be a faithful representative of the dominant germs, it must be an over-favourable representative of the germs generally, and therefore, *à fortiori*, of the undeveloped residue; nay, in extreme cases, the person may be absolutely misrepresentative of the residue, the accidental richness of the sterile sample in some particular valuable variety of germ, having drained the fertile residue of every germ

of that variety. The possibility of this occurrence is the more credible, since, as we have already seen, the number of germs of each variety cannot be very large. Experience testifies to the fact that children of men of extraordinary genius have not unfrequently been singularly deficient in ability, and this condition has been especially remarked in instances where the man of genius was himself the offspring of a mediocre ancestry; therefore where, according to the above theory, the number of valuable germs were few, and all of them were used up and rendered sterile in the structure of his own person.

The steady tendency to deterioration in exceptional characters is likewise shown by the avowed difficulty, among breeders, of maintaining the characters of any valuable variety that has been produced by accident (that is, by some happy combination of a number of unknown variable causes).

Another result of the best elements of the stirp being rendered sterile is the strong tendency to deterioration in the transmission of every exceptionally gifted race. That this is a universal tendency among races in a state of nature, is proved by the fact that existing races are only kept at their present level by the severe action of selection. If they were left unpruned even for a single generation, the weaker members would survive, and the average quality of the race would necessarily diminish.

Again, the sterility of the developed elements of the stirp explains the fact of certain diseases skipping one or more generations, if the further very reasonable postulates are granted, that the germs of those diseases are both prolific and gregarious. Thus, nearly all the gout molecules in the stirp whence A sprang might, owing to their gregarious nature, become developed in the person of A, and so be rendered sterile; the small fertile residue in his stirp would be insufficient to supply that of his son B with enough gout germs to dominate and achieve development in the person of B, consequently they would be husbanded; then, owing to their prolific character, they would so multiply in a latent form in the structure of B, as to ensure transmission in sufficient numbers to the stirp of C the son, or D the grandson, to enable them to achieve development in the person of C or D, just as they had done in that of A; and so the cycle would be repeated.

The conclusion from what has thus far been said is amply confirmed by observation; it is:—(1.) That the contents of the stirp must segregate into septs, or divisions, and that these septs must subdivide again and again, just as a large political party may repeatedly subdivide itself into different factions. (2.) That the dominant germs in each successive sept are those that achieve development. (3.) That it is the residual germs and their progeny that form the sexual elements or buds.

No process of subdivision like this could be expected to be carried on with perfect accuracy; no political party was ever split with such clean precision into two political septs, that none of the A party were included in the ranks of B, and *vice versâ*. We must therefore feel assured that germs of many alien species would be included in each successive sept. Also, we may reasonably suppose that the structure of the developed germs must afford many convenient places for the lodgment and sustenance of these alien germs; consequently, representatives of all parts of the residue of the stirp would be found dispersed all over the body. Lastly, we cannot but expect that these alien germs, when they thrive and multiply, would somewhat transgress the bounds of the cell or cell-interspace in which their progenitors had lodged, knowing that even so large an object as a blood-corpuscule will occasionally find its way through the unruptured wall of a capillary vessel. This is a very different supposition to that of the free circulation of gemmules in Pangenesis, yet it seems to have the merits of that theory (so far as the group of cases are concerned which we are now considering, namely, the inheritance of qualities that were congenital in the ancestry), and at the same time to be free from the many objections that are urged against it. These are as follows:—On physical grounds, we cannot understand how colloid bodies, such as the Pangenetic gemmules must be, could pass freely through membranes. Moreover, if they did, the paternal gemmules in the body of the unborn child would diffuse themselves equally over the body of the child and that of its mother; consequently there would be very few remaining in the body of the child, while, on the other hand, there would be an invasion of maternal gemmules. The result of this would be, that the child would transmit its maternal peculiarities far more than its paternal ones; in other words, people would resemble their maternal grandmothers very much more than their other grandparents, which is not at all the case. That the gemmules are not contained in the blood-vessels circulating with the blood, is proved by my own experiments, in which I largely transfused the blood of an alien species of rabbit into the blood-vessels of male and female silver-grey rabbits, from which I afterwards bred. I repeated this process for three generations, and found not the slightest sign of any deterioration in the purity of the silver-grey breed.*

Again, a free circulation of the gemmules, such as Pangenesis supposes, would cause various events to be extremely common,

* The experiments on the first generation were published Proc. Royal Society, 1871, p. 393, to which see Mr. Darwin's remarks in *Nature*, 1871, p. 502. I subsequently carried on the experiments with improved apparatus, and on an equally large scale, for two more generations.

whereas the supposition of a small transgression of their limits shows them to be possible, though infrequent; just as they actually are. I mean such cases as the zebra-marks on the foal out of a thoroughbred mare by a thoroughbred horse, owing to the former having once borne a mule to a zebra; the action of pollen on the tissues adjacent to the fertilized pistil of a different variety of plant. The distribution of the germs, by the agency I supposed, all over the body, would fully account for the replacement of a lost limb in the lower animals, and the reparation of simple tissues in the higher ones. It would much transcend my limits if I were to enter at length into these and kindred questions, but it is not necessary to do so, for it is sufficient to refer to Mr. Darwin's work already quoted, where they are most fully and carefully discussed, and to consider, while reading it, whether or no the theory I have proposed could, as I think it might, be substituted with advantage for that of Pangenesis. I must repeat, that I limit these remarks to the very large proportion of cases that fall into the first of the two groups in which I am discussing the facts of heredity. We will next proceed to consider those that fall into the second group.

The cases now before us are those in which characters created artificially in the person of the parents are transmitted by inheritance to their offspring. In considering these, we must be extremely careful not to confuse the effects of totally different processes.

We have thus far dealt with three agents—(1) the stirp, which is an organized aggregate of a host of germs; (2) the personal structure, developed out of a small portion of those germs; and (3) the sexual elements, generated by the residuum of the stirp. The cases before us are those which are supposed to prove that 2 reacts on 3—that is, the personal structure upon the sexual elements. The first and the largest class of the cases now before us refer to adaptivity of race. It is said that the structure of an animal changes when he is placed under changed conditions; that his offspring inherit some of that change; and that they vary still further on their own account in the same direction, and so on through successive generations, until a notable change in the congenital characteristics of the race has been effected. Hence, it is concluded, that a change in the personal structure has reacted on the sexual elements. For my part, I object to so general a conclusion, for the following reasons. It is universally admitted that the primary agents in the processes of growth, nutrition, and reproduction are the same, and that a true theory of heredity must so regard them. In other words, they are all due to the development of the same germinal matter, variously located. Consequently, where it is everywhere affected by the

same conditions, it would be everywhere affected in the same way. One of the species of germs whence the hair sprang, that was induced to throw out a new variety in the cells nearest to the surface of the body under certain changed conditions of climate and food, might be expected to throw out a similar variety in the sexual elements at the same time. The essential changes would be collateral, although the moment when the changed germs received their development might be different. So far from the changed structure of the hair causing the germs in the sexual organs to vary, it may often happen that the latter are the first to show change. Thus the progeny of thick-fleeced sheep, newly imported into the tropics, have less wool than their parents. There is not a shadow of proof that the adaptivity of a race to changed conditions, *affecting all parts of the body alike*, is due to the reaction of changed personal structure upon the sexual elements. The fact that a drunkard will often have imbecile children, although his offspring previous to his taking to drink were healthy, is another instance of simultaneous action. The alcohol pervades his tissues, and, of course, affects the germinal matter in the sexual elements as much as it does that in his own structural cells, which have led to an alteration in the quality of his own nerves. Exactly the same must occur in the case of many constitutional diseases that have been acquired by long-continued irregular habits. There is not the shadow of a proof that the adaptivity of a race to changed conditions, which affect all parts of the body alike, is due to the action of changed structure upon the sexual elements. The case is different as regards conditions that have a local influence, but races are very slow in acquiring these, such as the callosities on the knees of animals who use them much.

Another class of evidence brought forward in proof of the inheritance of non-congenital peculiarities concerns mutilations. No doubt the industry of M. Prosper Lucas, and of many others, has brought together several curious cases; but the negative evidence, that is to say, the certainty of the non-inheritance of mutilations in a vast number of cases (see Darwin: "Variation of Plants and Animals under Domestication," ii. 23), is so overpowering, that it may still be reasonable to look upon the former as more than a collection of coincidences. The earliest instance that I know of, that seems worthy of serious consideration, is that of Dr. Brown-Séquard's epileptic guinea-pigs, because it admits of verification; but this, if I understand his account rightly (Proceedings of Royal Society, x. 297), is open to some objection. It appears that Dr. Brown-Séquard found, during his researches into the cause of epilepsy, that, by a particular operation on the spinal cords of guinea-pigs, he could induce a convulsive disease very much like

epilepsy. He operated upon many guinea-pigs, and kept them apparently apart from the rest of his stock, and noticed that their young were at times attacked with "epileptiform" convulsions, while the young of the rest of his stock never were; hence he concludes that the artificially induced epilepsy was transmitted hereditarily. My objection to this conclusion is, that if persons were brought up from childhood in a ward of epileptic patients, they would certainly acquire a tendency to epileptiform seizures by the mere effect of imitation. It is notorious that many an epileptic person has had his fits first brought on by witnessing the epileptic seizure of another. This however, may be an unfounded objection, due, as was remarked, to misapprehension of an experiment, whose details deserve a fuller description. It is much to be regretted, that two subsequent memoirs, read by Dr. Brown-Séquard at the British Association in 1870, do not appear to have been published; their titles only are to be found in its Journal (p. 134). But he has communicated a most important *résumé* of other results to the *Lancet* (Jan., 1875, p. 7) regarding the inheritance of purely physical effects, that were produced in the parent guinea-pigs by nerve mutilation, and their occurrence in the offspring, in the same order in which they had appeared in the parents.

A special cause may be assigned for the effects of disuse in causing hereditary atrophy; it has already been shown that all exceptionally developed organs tend to deteriorate; consequently those that are not protected by selection will dwindle. The level of muscular efficiency in the wing of a strongly flying bird is like the level of water in the leaky vessel of a Danaid, only secured to the race by constant effort, so to speak; let the effort be relaxed ever so little, and the level immediately falls.

In addition to much else that might be said in disparagement of evidence on which overmuch reliance has hitherto been put, we should recollect that it is hazardous to adduce the very gradual adaptation of a race to changed conditions as a proof that acquired habits are hereditarily transmitted, because when several generations elapse before any appreciable result can be observed, selection will have had many opportunities of operating. It is noticeable that a race is much longer in adapting itself to conditions that affect one part only of the body, than to those whose influence is more general; and this is just what we should have expected from the views already expressed. It is hard to find evidence of the power of the personal structure to react upon the sexual elements, that is not open to serious objection. That which appears the most trustworthy lies almost wholly in the direction of nerve changes, as shown by the inherited habits of tameness, pointing in dogs, and the results of Dr. Brown-Séquard.

The conclusion to be drawn from the foregoing arguments is, that we might almost reserve our belief that the structural cells can react on the sexual elements at all, and we may be confident that at the most they do so in a very faint degree; in other words, that acquired modifications are barely, if at all, *inherited*, in the correct sense of that word. If they were not heritable, then the second group of cases would vanish, and we should be absolved from all further trouble; if they exist, in however faint a degree, a complete theory of heredity must account for them. I propose, as already stated, to accept the supposition of their being faintly heritable, and to account for them by a modification of Pangenesis. Each cell may be supposed to throw off a few germs that find their way into the circulation, and have thereby a chance of occasionally finding their way to the sexual elements, and of becoming naturalized among them. In illustration of this process, we may recur to political metaphor, and imagine the stirp to be represented by some country, and the germs by its inhabitants. We know that, in every country, travellers from other nations occasionally find a place, which they can fill more suitably than at their own homes or elsewhere, and they become settlers. The population of the country may be as highly organized as it is needful to consider the sexual elements to be; every trade and profession may seem to be full; and yet the stranger obtains a lodgment, either through superiority or luck. He may displace one of the native-born inhabitants, or he may find an unoccupied corner which he can fill; anyhow, as a matter of fact, he becomes a permanent citizen.

The hypothesis of organic units enables us to specify with much clearness the curiously circuitous relation which connects the offspring with its parents.* The idea of its being one of direct descent, in the common acceptation of that vague phrase, is wholly untenable, and is the chief cause why most persons seem perplexed at the appearance of capriciousness in hereditary transmission. The stirp of the child may be considered to have descended directly from a part of the stirps of each of its parents, but then the personal structure of the child is no more than an imperfect representation of his own stirp, and the personal structure of each of the parents is no more than an imperfect representation of each of their own stirps. The political analogy to the common, but false, idea of the filial relationship is that which connects colonists to their parent nations: the relationship, according to the views in this memoir, is much more circuitous and feeble; it resembles that which connects the *representative government* of the colony with that of the parent nations. This, at least, is a first approximation:

* I endeavoured to explain this in a paper, Proc. Royal Soc., 1872, p. 394.

the second approximation consists in making allowance for the small power of transmitting acquired peculiarities; that is, for the reaction of the personal structure upon the sexual elements, and thereby upon the future stirp. This may be effected by supposing the governments of the parent states to have the power of nominating a certain proportion of the colonists.

It now remains to summarize briefly. I began by showing that certain postulates were admitted by most biologists, and that these gave a firm base whereon to develop a theory of heredity. By these, and by what appear to be their necessary consequences, I explained the object of double parentage, and therefore of sex. Then I dwelt on the restless movements of the germs in the stirp and the variety of their attractions and repulsions, and explained how it arose that brothers or sisters were often very dissimilar; also, on other grounds, why twins derived from the same primary stirp were either very much alike or extraordinarily contrasted (this being a fact that had resulted from inquiries of my own). Next, I argued that the developed part of the stirp was almost sterile, and that it was from the undeveloped residue that the sexual elements were derived. By this I explained the almost complete non-transmission of acquired modifications; also the occasional deficiency in the offspring, of qualities for which the parent had been exceptionally remarkable, and for certain diseases skipping alternate generations. The theory was proposed that the successive segmentations of the stirp were not perfectly clean and precise, but that each structure included many alien germs, whereby the progeny of all the contents of the residue of the stirp were distributed over the body. This accounted for much that Pangenesis over-accounted for, and was free from objections raised against the latter.

The assumed evidence that structural changes reacted on the sexual elements was then discussed, and it was pointed out that certain changes were really collateral which had been commonly thought to be effected by inheritance. Some of the evidence that structural changes might react on the sexual elements was, however, accepted, and to account for its existence, a modification of Pangenesis was adopted; each nascent cell being supposed to throw off germs which occasionally found their way into the circulation and obtained a lodgment in the already constituted sexual elements; this process being therefore independent of and subordinate to the causes which were supposed mainly to govern heredity. Finally, the exact relationship was defined, which connects the parents with their offspring.

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