
A Theory *of* Heredity. By Francis Galton, F.R.S.*

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 inborn or congenital peculiarities that were also congenital in one or more ancestors, the other to those that were not congenital in the ancestors, but were acquired for the first time by one or more of them during their lifetime, owing to some change in the conditions of their life.

The first of these two groups is of predominant importance, in respect to the number of well-ascertained facts that it contains, 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 of which the evidence is questionable or difficult of verification, and

and boy; (2) boy and girl; (3) girl and boy; (4) girl and girl. All these events would in the supposition be equally likely, and they give two cases of the same, and two of opposite sexes.

* This memoir was in type for publication in the December number of the *Contemporary Review*, at the time when it was read before the Anthropological Institute. I have taken the opportunity afforded by a reprint, to revise it considerably, and to amend it in many particulars.—F. G.

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

which, as I shall endeavour to show, does not, for the most part, justify the conclusion commonly derived from it. In this memoir I divide the general theory of heredity into two parts, corresponding respectively to these two groups. The first stands by itself, the second is 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 Pangenesis; 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 a less striking and assured character than those in the first group, and it will be seen that I accept the theory of Pangenesis with considerable modification, as a 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 fertilised 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, I think, 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 about the size of the newly fertilised 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 microscopist, even if their separate actions upon light were different. But even this is not the case, for the fertilised ovum is almost homogeneous in colour. Ova 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 theorise.

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 bodily structure that is about to be derived from them; so that comparatively few individuals out of the host of germs, achieve development. Thirdly, that the undeveloped germs retain their vitality: that they propagate themselves while still in a latent state, and contribute to form the stirps of the offspring. Fourthly, that organisation wholly depends on the mutual affinities and repulsions of the separate germs; first in their earliest stirpal stage, and subsequently during all the processes of their 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 a variety of ancestral peculiarities to his children, that he did not himself possess. But since everything that reached him from his ancestors must have been packed in his own stirp, it follows that his stirp contained in addition to such peculiarities as were developed in his own bodily structure, 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 organisation 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 must 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, at least of the higher races, admits of being long maintained through any system of unisexual parentage; but that a deterioration, which we may reasonably ascribe to a deficiency of some of the structural elements, is always observed to set in and gradually to increase, the race ultimately perishing from that cause. A system of double parentage is therefore a very important requirement, some think an essential one, to secure the indefinite maintenance of any race whose organisation is complex. What is the explanation of this? In the first place, double parentage should be looked upon as the primary requirement, and sex as the consequence, not the cause of that requirement. There are not of a necessity two sexes,

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

because swarms of creatures of the simplest organisations mainly multiply by some process of self-division. On the other hand, as I shall endeavour to show, there is a theoretical advantage in a system of double parentage, which grows to be of paramount importance, as organisations increase in complexity. But it is through the evolution of sex, that a system of double parentage is secured, and, therefore, I would submit, it is to the need of the latter that we must ascribe the existence of the former. The opposite view is certainly erroneous, namely, that sex is an inherent necessity, and that double parentage is the simple consequence of it. Such a sequence, which, perhaps, represents the common and unreasoned theory, is, to use a common phrase, "putting the cart before the horse." As has been just remarked, in many of the lowest forms of organised life, double parentage exists, but sex apparently does not, because any two cells seem able to conjugate and to 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 a stage where the differentiation of sex is complete, and the power of unisexual propagation is wholly lost. Now the necessity of a system of double parentage in complex organisations, is the immediate consequence of a theory of organic units and germs, as we shall see if we 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, this particular line of descent 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.*

* It might be worth the while of the mathematical reader to refer to a paper on an analogous subject, "The Extinction of Surnames," by the Rev. H. W. Watson, in the Journal of the Anthropological Institute, 1874, p. 138, to which there is a page of preface by myself.

But in a free state of nature, where the weakly plants are supplanted by those that remain sound, a new consideration is introduced. Here we have to consider, on the one hand, the growing chance against the deterioration of each 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, again, this excess would become an impossibility 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") necessarily diminishes. On the other hand, when there are two parents, and therefore a double supply of material, the chance deficiency in the contribution from either of them, of any particular species of germ, tends to be supplied by the other. No doubt, cases must still occur, though much more rarely than before, 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 each succeeding 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 those few who do, tend to become rehabilitated. There is yet another advantage in double parentage, namely, that 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 place among the competing germs, and the success, as we may infer, of the fitter half of their numerous varieties.

The limitation of space in the stirp must compel a limitation not only to the number of varieties of each species of germ, but also to the number of individuals in each variety. The knowledge of such a fact 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 now considering cases of the slow loss of some characteristic of a race, which proceeds by minute gradations, and which may be ascribed, at least in part, to a change in the quality of the germs, nor am I now speaking of cases where it is clear that one of two alternative qualities has overpowered the other, but of instances where they are equipotent and in no way antipathetic. Thus, in the gradual breeding-out of negro blood, we may find the colour of a mulatto to be the half, and that of a quadroon to be the quarter of that of his black ancestors; but as we proceed further, the subdivision becomes very irregular; it 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 many 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 fertilised 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 as 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 directions of the mutual influences of the germs to be limited to lines, like those that cause the blood-corpuscles to become attached face to face, in long rouleaux, when coagulation begins; neither can we suppose them limited to planes, like those that 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 those connected with the struggle for place and power, with election, and with representation. 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. We may compare the stirp to a nation and those among its germs that achieve development, to the foremost men of that nation who succeed in becoming its representatives; lastly, we may compare the characteristics of the person whose bodily structure consists of the developed germs, to those 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 views on heredity.

The great dissimilarity frequently observed between brothers or sisters is to be accounted for and easily illustrated by a political metaphor. We have to recognise, on the one hand, that the stirps of the brothers and sisters must have been nearly alike, because the germs are simple organisms, and all such organisms breed true to their kind, and on the other hand, that very different structures have been developed out of those stirps. A strict analogy and explanation of all this is afforded by the well-known conditions and uncertainties of political elections. We have abundant experience that when a constituency is very varied, trifling circumstances are sufficient to change the balance of parties, and therefore, although there may be little real variation in the electoral body, the change in the character of its political choice at successive elections may be abrupt. A uniform constituency will always elect representatives of a uniform type; and this result precisely corresponds to what is found to occur 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.

In twins of the same sex a dissimilarity is not unfrequently found of a more marked description than that between ordinary brothers and sisters, notwithstanding that the embryonic conditions of the twins must have been closely similar. This is a very curious subject, 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 exist two groups of cases that contrast strangely with one another, while there are, comparatively speaking, only a few intermediate cases. In the larger of the two 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 comparatively rare, so 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 alike, and the circumstances under which the bodily structure is developed out of them being almost identical, the results must be closely similar. On the other hand, as regards the dissimilarity, we might expect that if there had happened to be a sufficient delay before the division of the primary stirp, to allow its germs to arrange themselves somewhat according to their affinities, the twin halves of the primary stirp would be strongly contrasted. Political analogies may again be appealed to with advantage. In the case of an ordinary single birth, each germ that achieves development may be compared to the sole representative of a body of electors,

* For some general results of these inquiries, see the paper printed in the miscellanies of this volume. 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; Späeth'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.

each of whom has a single vote; then, in the case of twins, two representatives have to be elected, each elector still having only a single vote. If one of the political parties slightly predominates, and if the electoral body be divided by an accidental line, the same party would predominate in each division; consequently if the election happened to be so conducted, both representatives would be men of the same predominant party, and of identical politics. But if the electoral body acted as a whole, the predominating party would be unable to return more than a single candidate; consequently the two representatives would be men of opposite politics.

Individual variation depends upon two factors; the one, is the variability of the germ and of its progeny; the other, is that of all kinds of external circumstances, in determining which out of many competing germs, of nearly equal suitability, shall be the one that becomes developed. The variability of germs under changed conditions, and that of their progeny, may be small, but it is indubitable; absolute uniformity being scarcely conceivable in the condition and growth, and, therefore, in the reproduction of any organism. The law of heredity goes no further than to say, that like *tends* to produce like; the tendency may be very strong, but it cannot be absolute. The effect of the second of the factors mentioned above, is that a very slight variation in the germs may have a momentous effect in the personal structure that is developed out of a comparatively small number of them. There are numerous competing germs in the place of each unit of structure, and only one of the competitors can succeed in each case. When the competition is close, a very slight difference, either in the intrinsic quality of the germ, or in its temporary position at some critical time, or in any other variable circumstance, may determine its success. It may well happen, that some species of germs may have failed in achieving development during very many generations, by the end of which time they may have become considerably modified, and at length, partly owing to their intrinsic improvement, and partly to the accident of favourable circumstances, that species may suddenly vanquish its competitors and achieve development, and be the cause of a marked individual variation. The chain of sequences would have been perfectly continuous, though its manifestation in the form of personal structure would appear strangely capricious. Precisely similar catastrophes are of notoriously frequent occurrence in political and social life.

Those germs which have become developed into cells, have been supposed (I believe universally) to be the important, if not the chief agents in maintaining the progeny of germs; in other words, of influencing heredity. This is certainly an essential condition in the theory of Pangenesis, as the name of that theory testifies; there, each separate cell in its nascent state is supposed to throw off germs that circulate freely in the body along with the others that had been hereditarily transmitted. It is from among the general mass of these, that certain groups are supposed to aggregate themselves, owing to their mutual affinities, and so to form the sexual elements. For my own part, while acknowledging that there is undeniable evidence of the existence of the power of cells to throw off germs, which will be discussed when we come to the second group of cases, I shall endeavour to show that its effects on inheritance generally, are minute and secondary. My argument is this: Of the two groups of germs, the one consisting of those that succeed in becoming developed, and in forming the bodily structure, and the other consisting of those that remain continually latent, the latter vastly preponderates in number. We should expect the latent germs to exercise a corresponding predominance in matters of heredity, unless it can be shown that, on the whole, the germ that is developed into a cell, becomes thereby more fertile than if it had remained latent. But the evidence points the other way. It appears both that the period of fertility is shorter, and the fecundity even during that period is less in the germ that becomes developed into a cell, than they are in the germ that remains latent. Much less then would the entire bodily structure, which consists of a relatively small number of these comparatively sterile units, successfully compete in matters of heredity with the total effect of the much more numerous and more prolific units which are in a latent form. The shortness of the period of fertility of the germ that becomes developed, is implicitly acknowledged even by the author of Pangenesis, who considers it to cease so soon as the cell is completely formed (*op. cit.* ii. 374), and the hypothesis that the developed germ is less fecund, even during its short period of fertility, than the germ that continues latent, 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 in 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 personal elements may be absolutely misrepresentative of the residual elements, 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; where, therefore, according to the above theory, the number of valuable germs were few, and all of them were used up and rendered comparatively sterile in the structure of his own person. The steady tendency to deterioration in exceptional peculiarities is likewise shown by the avowed difficulty, among breeders, of maintaining the high character 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 insure 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 themselves into divisions or septs, and that these septs must subdivide again and again, under the influence of the mutual attractions and repulsions of their units, 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 that are the parents of the sexual elements or buds.

No process of subdivision like that which has just been described could be expected to take place 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 formed out of those germs that have developed into cells, must afford many convenient places for the lodgment and sustenance of the 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-corpuscle 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 the theory of Pangenesis. 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 final result of this would be, that the individual would transmit his or her maternal peculiarities far more than his or her 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 any large number, in the blood-vessels, 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, whereas the supposition of their transgression through a small space beyond their original 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 fertilised pistil of a different variety of plant. The distribution of the germs, by the agency I supposed, all over the body, would account equally with Pangenesis 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, as already quoted, where they are most fully and carefully discussed, and to consider, while reading it, whether 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.

It will be convenient at this place to contrast the views that have been thus far set forth with those of Mr. Darwin in his theory of Pangenesis. That theory affirms as follows:—

(1.) There are cells, and there are a great number of gemmules.

(2.) The cells multiply by self-division, and during this process they throw off gemmules. [I look upon this process of throwing off gemmules to be of such minor importance as to have no effect whatever upon the cases we have thus far considered. Its existence is granted, but only as a subordinate process, to account for the exceptional cases to be hereafter considered, and not as the primary process in heredity.]

(3.) The gemmules multiply by self-division, and any gemmule admits, under favourable circumstances, of being developed into a cell. [I look upon this as the primary process in heredity.]

(4.) The personal structure is formed by a process analogous to the fertilisation of each gemmule that becomes developed

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

into a cell, by means of the partially developed cell that has preceded it in the regular order of growth. [I look on it as due, first, to the successive segmentations of the host of gemmules that are contained in the newly fertilised ovum, owing to their mutual affinities and repulsions; and, secondly, to the development of the dominant or representative gemmules in each segmentation, the others remaining dormant, and are called, for convenience, in the next paragraph, the "residue."

(5.) The sexual elements are formed by aggregations out of the gemmules, all of which are supposed to travel freely throughout the body. [I look on the sexual elements as directly descended from the "residue," and do not suppose the gemmules to travel freely. I allow some very moderate transgression across the bounds of their domiciles, and something more than that, under the limitations that will be described in the latter part of this memoir.]

[I account for all varieties of the gemmules being found in all parts of the body, by the above-mentioned segmentations being never clean and precise. Hence it follows that each segmentation must contain stray and alien gemmules, and I suppose that many of these become entangled and find lodgment in the tissue developed out of each segmentation.]

We will next proceed to examine the cases that fall into the second group; they are those in which characters created artificially in the person of the parents, are transmitted by inheritance to their offspring. In considering what appear at first sight to be cases in evidence of this, 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 organised 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 these cases 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 his 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, when similar germinal matter is everywhere affected by the same conditions, we should expect that it would be everywhere affected in the same way. The particular kind of germ 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 changes in the germs would everywhere be collateral, although the moments when any of the changed germs happened to receive their development, might be different. So far from there being evidence that the changed structure of the hair causes the germs in the sexual organs to vary, it may often happen that the latter are the first to change. Thus the progeny of thick-fleeced sheep, newly imported into the tropics, may begin to lose wool earlier 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. Another instance of simultaneous action is to be found in the fact that a drunkard is often known to have imbecile children, although his offspring previous to his taking to drink were healthy. The alcohol pervades his tissues, and, of course, affects the germinal matter in the sexual elements as much as it does that in the cells which form the structure of his own nerves. Exactly the same result must occur in the case of many constitutional diseases that have been acquired by long-continued irregular habits. The case is different as regards those conditions that have a local influence; but races are very slow in adapting themselves to these.

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 no 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 has just been 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 certain purely physical effects that were produced on 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 of the disused parts. 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 indeed 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 like, and the results of 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 about them; but 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 thereby to acquire a chance of occasionally finding their way to the sexual elements, and of becoming naturalised 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 organised 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

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

the *representative governments* of the parent nations. This, at least, is a first approximation: the second approximation consists in making allowance for the small power that exists, of transmitting acquired peculiarities; that is, for the power of the personal structure to react upon the sexual elements, and thereby upon the future stirp. To effect this, the analogy may be revised by supposing the governments of the parent states to have the power of nominating a certain proportion of the colonists.

It now remains to summarise briefly. I began by showing that certain postulates were admitted by most biologists, and that they gave a firm base whereon to develope 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. Next I 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). Then, I spoke of individual variation. Then, 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 ultimately 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.