German East Africa. Portugal might retain, for her own exploitation on right lines, the large remaining province of Mozambique proper from the Lucio as far south as Quelimane, disposing by sale to the British Empire of inner Zambezia and South-East Africa. The alternative to such proceedings, and the course which should be adopted *in any case* in the Portuguese as well as the French colonies (if an important German grievance is to be removed), would be *the abolition of all differential* duties in the Customs tariff. Such differential duties exist nowhere in the German colonies, in the Indian Empire, or the Crown Colonies of Great Britain, and the present writer is certainly not one who favours their continuance even in the tariffs of the Daughter Nations.

We hear a great deal of Portuguese pride forbidding Portugal to do this and that, under a republic as under a monarchy. But this pride is based on that ignorance that still keeps the Portuguese nation under its cruel yoke, a nation of which some 70 per cent. amongst its people are unable to read and write. There is no reason whatever why Portugal should withdraw from her Asiatic possessions, which are quite manageable with her existing means, especially with the British Empire as her friend and ally. But a portion of the Portuguese dominions in Africa should be sold or leased at a fair valuation, and the proceeds be most carefully employed by the Portuguese Government in developing the resources of Portugal itself, a land, with its annectant islands, of 35,500 square miles, extraordinarily blessed by Nature and yet possessing a population which scarcely reaches the total of London and its suburbs. Even if the Portuguese sold Guinea to the French; the Congo province and North Mozambique (Ibo) to the Germans; Zambezia, Beira and Delagoa Bay to the British, they would still remain the recognised and effective rulers of an empire of 500,000 square miles, a much larger area than they actually possessed in 1870; while, in addition, they should have acquired a fund which would suffice to build a network of light railways over Portugal itself and enable that land to become the greatest fruit-producing region of Europe.

H. H. Johnston.

INHERITANCE OF ACQUIRED CHARACTERS

THEORETICAL DIFFICULTIES

I

The facility with which animals and plants vary under the direct action of altered surroundings, both in their specific and secondary features, has been proved lately by a vast amount of observations and experiments. The forms of animals, their colour, their skin, their skeletons, all their organs, and their habits are easily modified as soon as the animal's food and the general conditions of its existence and its biological surroundings are altered. The same is true of plants, even to a still greater extent. So many striking facts have been accumulated lately in this direction that the chief interest of such researches is now to study the inner physiological and anatomical modifications which take place in the tissues under the influence of changing surroundings. The reason why the modifications so well answer in most cases the new requirements as to represent adaptations is what now chiefly interests the biologist. The study of variation and evolution is thus tending more and more to become a physiological problem. These were the points I dealt with in my previous articles on 'The Direct Action of Surroundings upon Plants and Animals.' [1]

An important question arises, however, in connexion with all similar researches. Are the modifications of the individuals transmitted, entirely or partially, to their offspring? Even if we see that a modification produced in some individuals reappears in their descendants, are we sure that it is not produced anew in each generation? And, supposing it is inherited, will it continue to appear for some time, even though the offspring be taken back to the old surroundings?

Let us take, for instance, the modifications which Viré obtained in some crustaceans after he had transferred them from open rivers and ponds to a laboratory established in the darkness of the Paris catacombs.[2] After a few months' stay in the darkness the eyes of

[1] *Nineteenth Century and After*, July, November and December 1910.
[2] See *Nineteenth Century and After*, November 1910, p. 861.

these little animals, being used no more, were atrophied, while their organs of touch and smell, chiefly used in the dark surroundings, took a rapid development. An important adaptation to new conditions of life, formerly explained by natural selection acting upon accidental congenital variations, was thus accomplished by the surroundings themselves within the individual's life. However, before we recognise in the direct action of environment a powerful factor of the evolution of new species, it must be known whether the adaptations just mentioned, or at least an increasing disposition for acquiring them, are transmitted to the next generation of crustaceans born in the catacombs? And this is what we have not yet learned from direct experiments.

The same question must be asked concerning plants taken from the plains of Middle Europe to Alpine, maritime, or desert surroundings. They rapidly acquire in their new environment the anatomical structure and the forms characteristic for Alpine, maritime, or desert plants.[3] But are these new forms and structure inherited? And, if so, how long will the newly acquired characters last after the plant has been taken back to its old environment?

Unfortunately, the replies to these questions obtained till now by experiments are not quite clear. And yet the questions are most important. For, if characters acquired by individuals under the influence of a new environment and new habits are inheritable, then the whole problem of evolution is immensely simplified. Variation becomes the beginning of evolution, and the function of natural selection is quite comprehensible. Selection has not to *increase*, or to *accentuate* a variation; it has only to weed out those individuals which are not capable of varying rapidly enough in accordance with the new requirements. Those crustaceans whose organs of smell and touch do not develop rapidly enough in an underground river, those plants the tissues of which do not rapidly increase their powers of assimilation in an Alpine climate perish, while those which vary in the proper direction with a sufficient rapidity survive. Nothing is thus expected from natural selection which it could not accomplish.

Darwin and his contemporaries—Herbert Spencer, Haeckel, Moritz Wagner, Huxley, and a host of practical biologists—did not doubt of the inheritance of acquired characters whenever they substantially affect the inner structure of a plant or an animal.[4] It was only after Darwin's death, in the years 1883-1887, that doubts were raised upon this point, especially by the Freiburg professor of entomology, A. Weismann.

[3] See *Nineteenth Century and After*, July 1910.

[4] See, for instance, the quotations in point given by Herbert Spencer from Darwin's works, in *Nature*, li. 414.

A naturalist accustomed to rely upon the experimental method would be disposed to think that some decisive experiments proving the non-transmission of acquired characters were made about that time. But there was nothing of the sort, and up till now we are waiting in vain for such experiments.[5] True, that Weismann announced in 1888 that he had clipped the tails of some twelve to fifteen white mice for five generations, but had obtained no tailless mice; nor had he noticed any tendency towards a shortening of the tails.[6] Later on he extended his experiment to twenty-two generations, and came to the same negative result.[7] Cope and Rosenthal experimenting on mice, and Ritzema on mice and rats, came to the same conclusion.[8] We may thus take as granted that a superficial mutilation, such as the clipping of the tails of mice (which were left to breed a few weeks after their birth), is not inherited.

But this was known long since. Darwin, who had studied with his usual carefulness the experience of the breeders concerning the cutting of the tails in certain breeds of sheep, and of ears in dogs, came long ago to the conclusion that 'a part of an organ may be removed during several successive generations, and if the operation be not followed by disease, the lost part reappears in the offspring.'[9] But, of course, he did not consider the non-inheritance of superficial mutilations as an argument against the hereditary transmission of acquired characters. In fact, there are many reasons why the *absence* of a tail or a digit has little chance of being transmitted: one of them being, as suggested by Professor Nussbaum, that 'the young embryo would promptly regenerate its missing portion.'[10]

On the other side, in conformity with the just-mentioned views of Darwin, when Professor Brown-Séquard studied the physio-

[5] 'The obligation to give the proof lies with the Lamarckians, who believe in the transmission,'—we are told sometimes by English anti-Lamarckians. But this attitude, not unfrequent in law courts, is certainly not that of men of science. If Darwin were still among us he surely would have begun long ago a series of well-planned experiments to test a statement so fundamental for the theory of evolution.

[6] 'The Supposed Transmission of Mutilations,' in *Essays upon Heredity and Kindred Biological Problems* (Oxford, 1891, 2nd edition), i. 444-445.

[7] *Vorträge über die Descendenztheorie* (2nd edition: Jena, 1904), ii. 56.

[8] For an examination of all the cases in point, see Prof. J. Arthur Thomson's capital work, *Heredity* (London, 1898), pp. 224-225. Contradictory experiments were once mentioned in an American report, but nothing more was heard of them.

[9] *The Variation of Animals and Plants under Domestication* (2nd edition, 1899), ii. 391.

[10] *Die Vererbung erworbener Eigenschaften*, 1903, quoted by Prof. Th. H. Morgan in his capital work, *Experimental Zoology* (New York: 1907), p. 57. The long-continued inheritance of a part which has been removed during many generations is even not an argument against the Pangenesis hypothesis, 'for gemmules formerly derived from the part are multiplied and transmitted from generation to generation.' (Darwin's *Variation*, ii. 392.)

logical effects of more serious lesions, he found that these effects *were* transmitted; and his experiments were confirmed later on by Romanes. With guinea-pigs, an injury made to the spinal cord or to the sciatic nerve provoked epilepsy, or at least a disposition for it; and in a number of cases this disposition was transmitted to the offspring. Otherwise epilepsy never appeared among the guinea-pigs bred in very large numbers by Brown-Séquard—not even among the individuals he had operated upon, but in a different way. The possibility of explaining an inherited disposition for epilepsy as a bacterial infection, which took place during the operation, is thus excluded. Several other results, due to other lesions, were also inherited. Altogether, these experiments were conducted so carefully, during a long succession of years, that the opinion which has prevailed among specialists is, that they really prove the hereditary transmission of certain abnormal states of different organs, provoked by certain lesions.[11]

II

If Weismann's experimental contribution to the question of inheritance of acquired characters was worthless, his critical revision of the whole subject was, on the contrary, very valuable.[12] Besides, Weismann gave a new interest to the whole matter under discussion by bringing forward an ingenious hypothesis of heredity, in defence of which he wrote quite a number of essays and books, always in a form both attractive and accessible to a large circle of readers.

It is evident that a discussion about the part played by environment in the evolution of organic beings ought never to have been made to depend upon our preferences for this or that hypothesis of heredity. It is the hypothesis of heredity which must be built up so as to explain the facts established by our knowledge of evolution; and this is what Darwin did when he worked out his Pangenesis hypothesis. But if we had a hypothesis of heredity,

[11] Prof. T. H. Morgan, who in his earlier work, *Evolution and Adaptation* (1903), had made restrictions, concerning the value of these experiments, wrote as follows in his later work, *Experimental Zoology* (New York, 1907), p. 54: 'I have given somewhat fully these remarkable results of Brown-Séquard because the experiments appear to have been carried out with such a care, and the results are given in such detail, that it seems that they must be accepted as establishing the inheritance of acquired characters.'—Weismann's reply (*Vorträge über die Descendenztheorie*, 2nd edition, ii. 57, 58) consists in repeating that, 'probably' a microbe infection took place. He says moreover that once *the lesion itself* was not inherited, the experiments are no proof of an inheritance of an 'acquired character.' But why the inheritance of an anatomical modification of portions of operated nerves, resulting in the offspring in the same morbid phenomena as those that were provoked in the parents, should not be considered as the transmission of an acquired character, remains unexplained.

[12] An excellent review of Weismann's *critical* contribution in this field will be found in J. Arthur Thomson's *Heredity*.

which would so well explain all the facts of inheritance as to permit us to foretell them, it would have some weight as an argument in the discussion, because evolution and heredity are undoubtedly two portions of the same process. However, that much cannot be said of the series of hypotheses worked out by Weismann to meet the objections of his critics; but as they enjoy a certain favour with a number of biologists, we are bound to examine them, and to see what bearing they may have upon our opinions about the inheritance of acquired characters.

All we can expect now from a hypothesis of heredity is that it should give us some plausible physiological explanation of two sets of facts: the reproduction in the offspring of the characters belonging to the *species*—that is, the maintenance of the ancestral type—and the appearance of *new* features, without which there would have been no evolution. All the hypotheses which were brought out during the last fifty years had in view this double purpose; but there are only two of them—Darwin's Pangenesis and Weismann's Germ-plasm—among which the suffrages of biologists are divided by this time.

Everyone knows more or less the Pangenesis hypothesis. Following Spencer's idea of 'physiological units,' Darwin suggested that all the cells of the body of a plant or an animal throw off during their life extremely minute living particles which are capable, like cells or spores, of multiplying by subdivision, and thus reproducing their mother-cells. Darwin described them as *gemmules*. Being extremely small, the gemmules wander through the body, passing through the membranes of the cells, and finally they collect in the reproductive cells of the individual, which thus contain representatives of all the cells and all the groups of cells of the whole organism. Every organ, every tissue, every bone, muscle, nerve, blood-vessel, and so on, has its representative gemmules in the reproductive cells. And when the time comes for these cells to reproduce a new being, they transmit to it the gemmules capable of reproducing all the features of the race, as also, to some extent, the modifications which the parents may have gone through during their own lifetime.

The germ cells of—let us say—a cart-horse would thus contain gemmules capable of reproducing all the typical organs and features of a cart-horse of a given race; and they would also bear traces of the changes which the individual horse had undergone during its life in consequence of a good or a bad food, over-exertion, and so on.

The inheritance of both the racial and the individually 'acquired' characters is thus rendered more or less comprehensible. But with our present ignorance of the inner life of organic tissues, the difficulty is to conceive how the gemmules are carried from the spot where they originate to the reproductive cells. How can they reach them in due proportions, and why, later on, when the germ begins to develop into an embryo, do they enter into action in due succession—each group at the proper moment? These difficulties certainly are great; and yet, with all that, the Pangenesis hypothesis so well explains various aspects of heredity that Professor Delage, the author of an elaborate work on the subject, is quite right in saying that all the subsequent hypotheses which retained the idea of 'representative units' added nothing substantial to the explanation proposed by Darwin.[13] Still, the fact is, that the Pangenesis hypothesis, including Brooks's attempt to improve it, has not yet met with much support, and, for some time at least, the hypothesis of Weismann—before he was compelled to introduce into it the hypothesis of germinal selection—rallied the majority of suffrages.[14]

III

Weismann started from the idea that the inheritance of characters acquired by individuals under the direct action of surroundings is not needed for explaining evolution. Variation is not something coming from without: it comes from within—from the organisms themselves, and it is regulated by natural selection, which, given the spontaneous variations of the germ-plasm, is sufficient to explain all the adaptations of the organisms to the conditions of their existence. However, this hypothesis so much runs against all the tendencies of modern empiric science, that I referred to the earlier writings of the Freiburg professor to find in them some indications as to its origin. If I am not wrong, an essay written by him in 1876, with the idea of reconciling Darwin's teachings with a teleological conception of evolution, contains such an indication.[15]

Karl von Baer, in his criticism of Darwin's hypothesis of natural selection, had made the remark that the followers of this

[13] Yves Delage and M. Goldsmith, *Les théories de l'hérédité* (Paris, 1909), pp. 113-115. The main work of Delage is *L'hérédité et les grands problèmes de la biologie générale* (2nd edition: Paris, 1903).

[14] Besides Spencer and Darwin, the same idea of self-multiplying representative particles was developed also by Francis Galton, the botanists Nägeli and De Vries, the anatomist Kölliker, and Oscar Hertwig. But I am compelled to pass over these extremely interesting hypotheses. The general reader will find them analysed in Prof. J. Arthur Thomson's *Heredity* (London, 1908), and Delage and Goldsmith's *Théories de l'évolution* (Paris, 1909). For excellent critical analyses of Weismannism, see S. R. Romanes's *An Examination of Weismannism* (London, 1893), H. W. Conn's *The Method of Evolution* (New York, 1900), and Dr. Plate's *Selectionsprinzip und Probleme der Artbildung* (Leipzig, 1908).

[15] A. Weismann, 'Ueber die letzten Ursachen der Transmutationen,' second essay in *Studien zur Descendenztheorie* (Leipzig, 1876), chapter 'Mechanismus und Teleologie,' pp. 314 *seq.*

hypothesis being brought more and more to deny 'all purpose' in evolution—scientific recognition could be granted to the hypothesis only if it recognised a universal tendency towards reaching a certain purpose.[16] To which Weismann, after having quoted these words with approval, as also those of Hartmann, who considered Darwinian evolution as a 'mad chaos of stupid and capricious forces,' added that it was necessary, indeed, 'to combine in a theory of evolution the teleological principle with a mechanical conception.' Formerly, he thought it impossible. Now, he was going to prove that it was *unavoidable*.

Baer (he wrote) is right, for 'the phenomena of organic and inorganic nature cannot possibly be imagined as a work of accident. They can be conceived only as a process directed in accordance with a certain great plan' (p. 315). And he came to this conclusion: 'We must not hesitate to recognise the existence of a force acting with a purpose (*einer zweckthätigen Kraft*); only we must not represent it as directly interfering in the mechanism of the universe: we must conceive it rather *behind* the mechanism, as a final cause.'[17]

Causality and purpose—he wrote further on—by no means exclude one another: we see them combined by a watchmaker in a watch; and they are likewise combined in the universe by 'the Mechanic of the universe.' 'The apparent contradiction between teleology and mechanism can be conciliated,' and he concluded with these significative words which contain the key to his subsequent conceptions of heredity: 'Why should we not return to the idea of "matter endowed with a soul?"'[18]

This matter endowed with an immortal soul—this conciliation of determinism with teleology—found, I am inclined to think, its expression in Weismann's 'immortal' germ-plasm. This was evidently the 'teleological mechanism' through which the Baconian and Darwinian 'mad chaos of capricious forces' was avoided in the universe.

To avoid Hartmann's reproach Weismann eliminated from his hypothesis of heredity the very possibility of Buffon's and Lamarck's factor of evolution—the direct action of the *monde ambiant*, and the effects of use and disuse. To deny these effects upon the *individuals* was impossible, they are evident; but their hereditary transmission, he maintained, was *inconceivable*, *impossible*. Upon this postulate, borrowed from his conception of evolution, he built up his hypothesis of heredity.

[16] 'Soll der Darwin'schen Hypothese wissenschaftliche Berechtigung zuerkannt werden, so wird sie sich dieser allgemeinen Zielstrebigkeit fügen lassen. Kann sie das nicht, so wird man ihr die Geltung zu versagen haben' (p. 315).

[17] P. 324.

[18] P. 327.

The germ-cells which serve to reproduce the individual are not derived, he maintains, like Darwin's gemmules, from the individual's body-cells and tissues. They represent a speck of 'immortal' matter, transmitted to the now living beings—unchanged in the main features of its chemical and molecular structure—from their remotest unicellular ancestors. Each individual receives it from its parents, and keeps it quite apart from its own organs, tissues, and body-cells (the 'somatic' cells), so as to transmit it, unaltered, to its offspring. These were, at least, Weismann's ideas when he brought out his hypothesis in 1883-1885.[19]

As to the structure of the germ-plasm, Weismann's hypothesis also differs from Darwin's Pangenesis in an essential point. The plasm of the germs is not composed of gemmules capable of reproducing by subdivision the cells from which they originate. They only contain *Anlagen, i.e.* 'predispositions,' 'tendencies' of a molecular or chemical nature) to produce such and such cells, tissues, and organs. When the germ begins to develop into an embryo, its physiological units only *determine* the production of cells, tissues, and organs of a definite character; this is why Weismann gave them the name of *determinants*. There is a group of determinants for each new line of growth in the embryo originated by each new subdivision of its cells: for the outer skin and the inner membranes—for each portion of the body, including such tiny local peculiarities as, for instance, a tuft of grey hair inherited in a family. Besides, there is a strong hierarchy among Weismann's determinants. There are determinants of each arm which govern the development of the arm in the embryo, and there are subordinate determinants for marshalling the development of each finger, each nail, each muscle, etc., of the arm and the hand. The development of the embryo thus

[19] 'The whole foundation' of the Pangenesis hypothesis must be abandoned: 'it is impossible for the germ-cell to be, as it were, an extract of the whole body.' (*Essays on Heredity*, 2nd edition, 1891, i. 169.) Heredity is due to the transference from one generation to the next of part of its germ-plasm, containing the very same 'formative predispositions' as were contained in the germ-plasm of the parents. 'The germ-cells may be contrasted with the rest of the body; . . . as their development shows, *a marked antithesis exists between the substance of the undying reproductive cells and that of the perishable body cells.*' (*Essays*, i. 73-74.) There are 'no conceivable means' by which modifications produced in the body-cells by external agencies, or by use and disuse, could be conveyed to the cells of the germ-plasm (i. 172). Weismann did not assert that the germ-plasm is totally uninfluenced by forces residing in the organism. . . . 'The nutrition and growth of the individual must exercise some influence upon its germ-cells'; but he was disposed to think 'that the influence of nutrition upon the germ-cells must be very slight, and that *it may possibly* leave the molecular structure of the germ-plasm *absolutely untouched.*' 'In fact,' he added, 'up to the present time, it has *never been proved that any changes in general nutrition can modify the molecular structure of the germ-plasm.*' (Essays, i. 172-173.)

reminds one of the mobilisation of an army, of which the determinants are the officers and sub-officers organising its different parts.

IV

Most of the processes of heredity lie unfortunately in a domain which still remains invisible for our best microscopes. We are reduced, therefore, to build up purely hypothetical, more or less probable, mental representations of these processes, and in the impossibility of verifying which of our mental images is nearest to reality, it would not have been worth while discussing them for years. However, even such representations may have a scientific value. It matters little whether we represent to ourselves heredity as a transmission of self-multiplying 'gemmules,' or of 'predispositions' and 'determinants.' But if it were proved, or only rendered very probable, that the germ-cells *cannot* receive from the body-cells impressions which affect them in the same sense as the body-cells are affected by environment, then an important argument would have been furnished against the hereditary transmission of acquired characters. This is the *raison d'être* of the interest taken by our best biologists in the hypothesis of heredity advocated by Weismann. The question at the bottom of this interest is the desire to know: Was modern physiology right when it maintained (to use Cuvier's words) that 'all the organs of an animal represent a unified system, of which all parts act and react upon each other, so that no modification can take place in one of them without producing *analogous* modifications in all others?' Or, as Houssay puts it in *La forme et la vie*: Were Darwin and Lamarck right when they conceived that an individual's inheritance is a resultant from *all* the external forces that had acted upon its ancestors—of all the variations, ancient and modern, they underwent? In a subsequent essay we shall see what data the direct experiments made during the last five-and-twenty years have given us to solve the problem. Now let us see first how the question stands from the theoretical point of view: what our present knowledge of the processes of heredity—so far as it goes—has to say about this question? Let us, then, cast a glance upon the main points won during the discussions upon the complicated framework of Weismann's hypotheses.

To begin with, it was proved that it was wrong to oppose the *body-cells* to the *germ-cells*, or reproductive cells.[20] Germ-plasm is not limited to the germ-cells only. On the contrary, it is contained, in a more or less advanced state of specialisation, in the nuclei of all the cells. Consequently, the idea of a sort of

[20] Weismann had to recognise it in 1885. (*Essays*, i. 209-211.)

sanctuary occupied by the germ-cells, and inaccessible to the influences which modify the body-cells, appeared highly improbable.

Another step in the same direction was made when Maupas, Oscar Hertwig, and Max Verworn demonstrated how intimately are connected in every reproductive cell the protoplasm of its nucleus (the nucleo-plasm), and the protoplasm which surrounds it (the cell-plasm, or cytoplasm). Far from giving support to the idea that the transmission of material influences from the cell-plasm to the nucleus should be impossible, the observations of these leading microscopists proved—as Hertwig expresses it—that the cell-plasm takes a prominent part in the whole process of fecundating evolution, at all its stages.

Altogether, the better we know the processes following fertilisation, the more we are convinced of the intimate connection that exists between the nucleo-plasm and the surrounding cell-plasm. We learn also that the membrane which surrounds the nucleus is no obstacle for the intercourse, and that a constant exchange of substances elaborated in both plasms is going on in both directions during the process of development of the embryo.[21] More than that. Every cell being quite a world, composed of a variety of separate physiological units,[22] all the component parts of the cell are required—we are told—in an equal degree.[23]

Besides, Maupas proved that in unicellular organisms (which may be considered analogous to the germ-cells of the multi-cellular beings) modifications in the cell-plasm, due to external influences, are continually inherited; this proves that they are transmitted to the nucleo-plasm—very probably through the intermediary of the extremely minute constituents of the cell passing through the membrane which encloses the nucleus. All taken, far from yielding support to the idea of its being 'inconceivable' that the germ-plasm should reflect the changes going on in the body-cells, it is the reverse that is rendered more and more probable by modern research.

V

Twenty-five years ago, when our knowledge of heredity was in its infancy, it was possible to concentrate our attention upon

[21] For the ideas of O. Hertwig, Max Verworn, C. Rabl and Fick upon this point, see the quotations given by O. Hertwig, *Der Kampf um Kernfragen der Entwicklungs und Vererbungslehre* (Jena, 1909), pp. 44-45 and 107-108.

[22] Some information about this last subject will be found in one of my 'Recent Science' articles (*Nineteenth Century*, May 1892, pp. 756 *seq.*).

[23] See Rabl's suggestive work, *Ueber Organ-bildende Substanzen und ihre Bedeutung für die Vererbung* (Leipzig, 1906). See also E. Godlewski, jun., in *Archiv für Entwicklungsmechanik*, xxviii. 278-378.

the wonderful processes that are going on in a fertilised ovule (the 'Karyokinesis' processes), then recently revealed by the microscope. But now a broader view of the matter must be taken. Here is a mighty oak bearing hundreds of thousands of acorns, and each of these acorns contains a speck of the germ-plasm which is capable of reproducing, not only some sort of oak, but that special sort of oak which has been evolved since the Post-Glacial period in a given geographical region, in certain definite topographical conditions. Or, here is a pine-tree which sheds at a certain part of the year a real rain of pollen, each minutest grain of which is also a bearer of germ-plasm capable of transmitting to the offspring the aspects and properties of a given local variety of a pine-tree. More than that, each of the buds of the oak, each few inches of the cambial tissue of a willow-tree, each leaf of a *begonia*, are capable of reproducing both the species and the variety from which they originate. The same is equally true of the animal, for the miscroscopical particle of germ-plasm inherited from the parents, when the moment comes for sexual awakening, multiplies to such an enormous extent that it produces millions of similar particles, before one of them becomes the beginning of a new living being. One has only to think of the prodigious mass of food that is supplied every year to the germ-plasm for rendering possible such a prolification; one must realise that its structural materials are collected from the whole of the oak, the pine, the animal, that they are elaborated in all its parts, and then it becomes evident how untenable it is for a naturalist to maintain that the changes that are going on every year in the life of the body-cells have no effect upon the germ-plasm originating in such enormous quantities from these same cells.

More than that. As Professor Houssay points out in his elaborate and interesting work, *La forme et la vie*, the communication of living physiological units, at least one way—from the germ-cells to the body-cells—is already an established fact: the suppression of the reproductive glands produces a series of well-known effects in the structure of the body, and these effects find some explanation in what we know about the thyroid glands and the suprarenal capsulæ. Although these glands and capsulæ have no excretory channels, the substances resulting from their cellular activity spread, nevertheless, through all the cells of the organism, either through osmosis or in any other way yet unknown. They are even so important for the organism's life that a complete amputation of one of these two organs in a dog produces a general impoverishment of its health, and its death, while recovery follows an injection of the products of their activity taken from another dog. As to the reverse action, in certain cases, of the body-cells upon the reproductive cells, if not yet *proved*, it is rendered very probable by a number of modern researches.[24] And we shall certainly learn more upon this subject, now that variation begins to be studied under its *physiological* and *biochemical* aspects. Viewed under these two aspects—the only true ones—all discussions about the 'impossibility' for internal variation to reach the material bearers of heredity in the reproductive cells appear utterly unreal.

We know already that in plants there exists an intercourse between the protoplasm of all their cells. The membranes of the cells are not impermeable, and threads of extremely fine particles of protoplasm are flowing through the cell-membranes from cell to cell. They have been well seen and described by many microscopists.[25] Besides, botanists know that a plant—including the germ-plasm of its reproductive cells—can be reproduced by a bud, a tuber, a piece of its underground stem, a piece of its cambial tissue, or even by a leaf (in *begonia* and several other plants). Consequently, in plants, germ-plasm, *capable of reproducing a complete individual* (not only the corresponding portion of it) is contained *in the body-cells* of the stem, the branches, the leaves. And, to say that it leads there a sleeping-beauty existence, free from the influences acting upon the body-cells amongst which and upon which it lives, feeds, grows, and multiplies, appeared so extravagant an assertion to most botanists (Nägeli, de Vries, Vines, and so on), that they repudiated it at once. In plants, at least, the tiny speck of matter which is the bearer of heredity cannot be anything but what Darwin conceived it to be: the result of all the influences which had acted formerly to produce the family, the genus, the species, and now have been acting to produce the individual with its own distinctive features.

It could be said, of course, that if the inalterability of the germ-plasm is highly improbable in plants, it may be a fact in animals. Here the reproductive cells *may* have their inaccessible sanctuary. However, modern research into the processes of *regeneration* in animals has induced many zoologists also to recognise the impossibility of such an isolation of the reproductive plasm.[26]

[24] A few of them are mentioned by Houssay, *La forme et la vie* (Paris, 1900), pp. 834 *seq.*

[25] See O. Hertwig, *Die Zelle und die Gewebe*, which appeared in its second, entirely re-written edition under the title of *Allgemeine Biologie* (Jena, 1906). About the continual exchange of living matter between the different portions of plants, see Prof. Jumelle, in *Revue générale de botanique*, 1891, xiii. 332. W. Pfeffer's *Physiology of Plants* (English translation by A. J. Ewart, Oxford, 1903) also contains most useful information in that direction. It was these cell-bridges which gave to Nägeli the idea of his hypothesis of *micelli* wandering all over the body of the plant, and finally gathering in its reproductive cells.

[26] The researches into regeneration promise to give us a real insight into the processes of heredity. But they are already so numerous that all I can do here is to mention only one or two points having a direct bearing upon the question of inherited modifications, and to refer to such works as Prof. Th. H. Morgan's *Regeneration*, 1907 (completed and rewritten in collaboration with the German translator, Max Moszkowski, 2nd edition, Leipzig, 1908), and to the original memoirs appearing in great numbers in Roux's *Archiv*, the *Zoologischer Anzeiger*, in the publications of different zoological laboratories, and so on.

It was just mentioned that in plants extremely fine threads of protoplasm are seen to connect the cells. But the same connections were proved to exist, by Siegfried Garten's experiments upon his own arm, between the epithelial cells of man; and the existence of intercellular bridges between the epithelial cells and various others cells of the muscles and the connective tissue was proved by Hedenhain and Schuberg.[27] It may be possible, of course, that these 'intercellular bridges' are only the means of transmission of nerve-currents, but it seems far more probable that minute particles of living matter travel along them, as they do in plants.[28] Of course, we know yet very little about the intercellular communications in animals, but the little we know shows at any rate how cautious one must be in his assertions about the 'impossibility' of communication between the body-cells and the germ-cells.

That a communication *exists* between them may be taken now as highly probable. As to what sort of effects a modification produced in the body-cells may have upon the germ-plasm of the reproduction cells, we shall see presently, after we have cast a glance upon the facts we have learned from another vast series of investigations into regeneration, about the germ-plasm scattered all over the body.

VI

The main point established by these investigations is that while both in plants and animals there is germ-plasm scattered all over the body, this germ-plasm is capable of reproducing not only those cells in which it is lodged, but also the cells of quite different parts of the organism. The extraordinary powers of regenerating, not only parts of tissues and amputated members, but even, in some divisions of the animal kingdom, the whole animal out of a small piece of it, alter many of our previous conceptions about heredity. It is well known that a piece, a few square millimetres in size, will do to regenerate a whole Hydra. And when a Planaria was cut crossways into nine pieces, seven of them regenerated the whole animal.[29] A worm, the *Lumbriculus*,

[27] S. Garten, in *Archiv für Anatomie und Physiologie* (1895), pp. 407-409; Heidenhain, in *Anatomischer Anzeiger*, viii. (1893), 404-410; Schuberg, in *Sitzungsberichte* of the Würzburg Physico-Medical Society; all quoted in Eugenio Rignano, *La transmissibilité des caractères acquis* (Paris, 1908, pp. 34-41.

[28] The transmission of irritations along these 'bridges'—O. Hertwig remarks—is slower than that of a nerve-current.

[29] See for a rich array of facts Th. H. Morgan's *Regeneration*

which lives in the mud of small lakes and ponds, having been cut into twenty-seven pieces, each of only two millimetres in length, every piece reproduced the whole creature. Even the much higher organised Tritons have an astounding power of regeneration : thus it is known long since that Spallanzani saw one of them regenerating an amputated leg six times in succession.

The most striking fact with regeneration, recently discovered, is that an organ may be regenerated by tissues quite different from those from which it originates in the embryo.[30] Besides, in most cases the regenerating power does not come from the surface of amputation : it comes from cells lying far from it, much deeper in the body, and of a quite different character. We see it very well in the Planaria, which regenerates its head, with all its organs, after the whole of the anterior part of the body has been cut off.

Only two possible explanations of these facts can be given : either the whole of the germ-plasm scattered in the body-cells is capable of supplying the elements necessary for the regeneration of all parts of the body, as we have it in plants; or particles of germ-plasm, capable of regenerating such an important part as the head, with its brain, its eyes, its mouth, etc., are scattered in certain parts of the body, far away from the germ-cells, and they wander to the necessary spot whenever their constructive powers are required. In both cases it follows that germ-plasm, capable of reproducing other parts than those it is lodged in, stands in continual intercourse with whatever is going on in the body; and whatever hypothesis of heredity we adopt—a hypothesis of representative elementary units (Darwin's 'gemmules,' Galton's 'stirp,' Nägeli's 'micelli,' De Vries's 'pangenes,' Weismann's 'determinants'), or some hypothesis of a central ruling body (the 'epigenetic' hypotheses of Hertwig, Delage, and several others), it must account for the just-mentioned facts.

In this respect the recent researches of Józef Nusbaum and Mieczyslaw Oxner on regeneration in Nemertinae offer a special interest, as they seem to open a new field of research. The experiments were made on the small Nemertina, *Lineus ruber*, which was cut into two parts at different distances from its front end, and the regeneration process was studied under the microscope on

[30] Thus O. Hertwig, in the Introduction to his *Handbuch der Vergleichenden und Experimentalen Entwicklungslehre der Wirbelthiere*, Bd. i. (1906), speaks of the astonishment produced in anatomical circles by the discovery made by Colucci and Wolff, confirmed by Erik Müller and others, that in the eye of a Triton, after a complete extraction of the lens, a quite normal new lens was re-developed—not from the original mother-cells, but from the epithelium of the upper rim of the iris, which stands in no connexion with the lens at the time of its embryonal development.

living specimens. When the animal was cut into two parts just behind the cerebral ganglion and above the beginning of the digestive tube, so as not to leave the slightest part of this last organ in the front piece, the hind part was nevertheless regenerated in full, including the whole of the digestive tube. The regeneration in full of such an important organ was thus accomplished by another organ, from which the former is quite independent, both anatomically and genetically. The new organ was grown 'in consequence of a re-differentiation of the elements of a neighbouring, quite different organ.'[31]

Another fact, still more interesting for all theories of heredity, was established by the same experiments. It was the important part taken in regeneration by the so-called 'wandering cells.' As soon as the regeneration process had begun, these cells became active, and they acted as phagocytes; they absorbed particles of reserve materials lodged in the tissues, as also the grains of pigment, and then themselves were eaten up by the cells of the regenerated parts, and thus aided the growth of the latter.

From the few facts just mentioned it is already obvious that the researches on regeneration do not yield support to those hypotheses of heredity which make no allowance for the inheritance of modifications acquired by the body-cells. In fact, when Weismann framed his hypothesis in the years 1883-1885, he paid little attention to regeneration. But after the work of Götte and Fraisse he had to take it into account, and so he did in his *Germ-Plasm*, published in 1892. It was shown by Götte that when the amputated leg of a Triton is regenerated, all the parts of the leg—its bones, its muscles, the connective tissue, the mucous glands, the nerves, and the blood-vessels—are regenerated in full. And the question arose : Wherefrom come the determinants which 'marshal' the regeneration?

Weismann answered this question by adding a new hypothesis to his previous ones. The cells which are capable of producing regeneration—he wrote in *Germ-Plasm*—must contain, besides the principal idioplasm (*Haupt-Idioplasm*), additional idioplasm (*Neben-Idioplasm*), which consists of the determinants of those parts which it may have to regenerate. 'Thus all the cells of the bone of the [amputated] front leg must contain, beside the determinant No. 2, also the determinants 3 to 35 of the additional idioplasm, as they have to reconstitute all the succession of bones

[31] Józef Nusbaum und Mieczyslaw Oxner, 'Studien über die Regeneration der Nemertinen,' i., in Roux's *Archiv für Entwicklungsmechanik der Organismen*, Bd. xxx. (Festband), Th. I., 1910, p. 115. These researches—the authors remark—are a further development of the observations made in 1909 by Prof. Davydoff, and a similar process was also described by MM. Salensky and Lebedinsky in 1897.

in the front leg.'[32] Besides, there is a sufficient number of 'lieutenant' or 'reserve-determinants' (*Ersatz-Determinanten*) lodged along special 'germ-tracks' running from the reproductive cells to different parts of the body. There are even two different reserve-determinants in the middle portions of the *Lumbriculus*: one for regenerating, in case of need, the front part of the animal, and another for regenerating its hind part.[33]

One may be tempted to treat all these suggestions as a mere work of imagination; but, let us not forget what Tyndall said in one of his brilliant lectures about the part of imagination as a scout in scientific research. Let us suppose that the imagined picture corresponds to some extent to reality. What would be the result? It would be that the 'impossibility' for the germ-plasm to be influenced in the proper way by modifications in the body-cells—the 'inconceivability' of the process would be irretrievably gone!

Once more we are thus compelled to recognise the existence of a close intercourse between the germ-cells and the body-cells. The fact is more and more firmly established. There remains only to see what sort of intercourse that may be. Are not the germ-cells influenced by the changes going on in the body-cells in the same sense as the latter, so as to be capable of reproducing the changes in the offspring?

VII

One of thechief results of the discussion which took place in the years 1880-1893, and in which Herbert Spencer took a prominent part,[34] was to define more accurately the proper *rôle* of natural selection in the evolution of new species. It was shown that natural selection cannot be the *origin* of the so-called 'determinate' or 'cumulative' variation, unless there is at work some cause affecting many individuals at the same time, in the same direction, and for a succession of generations. A great number of biologists sought, therefore, the origin of variation—as Darwin had done—in the direct action of the surroundings; while those for whom the main thing was to repudiate the hateful 'Lamarckian factor' followed their spokesman, Weismann, who

[32] *Das Keimplasma*, p. 137.

[33] *Das Keimplasma*, p. 169.

[34] *Contemporary Review*, February to May 1893. Spencer's articles were reprinted separately as a pamphlet under the title *The Inadequacy of Natural Selection* (Williams & Norgate, 1893). Prof. Marcus Hartog contributed also an important paper to the same Review, 'The Spencer-Weismann Controversy,' July 1893.

was maintaining at that time the *Allmacht*—the 'all-sufficiency' of natural selection.

Weismann, however, soon abandoned this position, thinking that he had found the true origin of variation in sexual reproduction, *i.e.* in the mixing together of the germ-plasms of the two parents during the process of fertilisation, to which he gave the appropriate name of *Amphimixis*.

Microscopical investigation had shown, a few years before, that in sexual reproduction an actual mixing together of the two parent plasms takes place in the fertilised egg, whereupon one-half of the coalesced two plasms is thrown out—the remaining half only going for the development of the embryo. To take a familiar example, things go on as if two packs of cards, one of which represents the characters inherited from the father, and the other represents those of the mother, were shuffled together; whereupon the double pack is divided into two equal parts, one of which is put aside and the other retained. The number of determinants corresponding to the immense variety of characters of each parent being extremely great, the possible combinations of them are countless, and this is why two children of the same parents, or even two puppies of the same litter, are never quite alike.

This was the idea developed by Weismann in 1886 and 1891.[35] He was so much taken by it that he saw in Amphimixis the *true* cause of all inheritable individual variation—'the keystone of the whole structure' of the theory of heredity.[36] Therefore he still more emphatically denied the possibility of the germ-plasm being influenced by external agencies 'in the same direction as that taken by the somatogenic changes which follow the same cause.'[37] The only source from which inheritable individual differences could be derived was sexual reproduction—Amphimixis. 'It was *only* in this way that hereditary individual differences *could arise and persist*';[38]—only in this way new species could originate with the aid of natural selection.

There is no need to say that such a position could not be maintained. The believers in the sufficiency of Amphimixis as a cause of variation were shown that if variation were limited to a redistribution of already existing characters, no progressive evolution would have been possible, and Weismann himself had to recognise the force of this remark, so that in 1904 he

[35] 'The Significance of the Sexual Reproduction in the Theory of Natural Selection,' in *Essays*, i. 257-342, and 'Amphimixis; or, the Essential Meaning of Conjugation and Sexual Reproduction,' in *Essays*, ii. 99-222.

[36] *Essays*, ii. 101.

[37] *Essays*, ii. 190.

[38] *Essays*, i. 296.

abandoned the Amphimixis hypothesis in his *Vorträge über die Descendenztheorie* (*The Evolution Theory* in the English version).

Even now [he writes in this work] I still consider Amphimixis as the process by means of which new *re-combinations of variations* are produced—a process without which the building up of an organic world infinitely rich in forms and incomprehensively complicated could not have taken place. But I do *not* consider it as the true root of the variations themselves, because the latter cannot possibly depend upon a mere *exchange* (*Austausch*) of ids: they must rather depend upon a *modification* of the ids. . . . Amphimixis, *i.e.* the coalescence of two plasms, certainly does not modify the determinants: it only produces new and new combinations of the ids (the ancestral plasms). If the appearance of variations were limited to this cause, the transmutation of species and genuses would have been possible only within a very limited scope.[39]

But this abandonment of the Amphimixis hypothesis was not sufficient. Every hypothesis of heredity is bound to indicate the source of 'definite,' or 'cumulative' variation which accumulates from generation to generation certain changes in a given direction. In Weismann's terminology, it had to indicate the possible cause of a *continued modification of the determinants* of the germ-plasm in a given direction.

Let us take, as an instance, the classical example, worked out by Professor Marsh, of the horse's hoof evolved out of the median toe. It so happens that we have a practically complete chain of the ancestors of the present horse since the Eocene period; and we see how, these ancestors having dwelt in regions with a hard ground, where increased rapidity of locomotion was an advantage, the median toe, which was becoming the chief support of the foot, gradually developed more and more, and its nail became a hoof; while the other digits, touching the ground no more, ceased to be used, and were atrophied, so that now they are only splint-bones. This is what the determinants' hypothesis had to explain, without recognising the inheritance of acquired characters which it repudiated.

Weismann tried to do so by means of a new hypothesis—of 'germinal selection,' or of struggle between the determinants in the germ-plasm. W. Roux had just published at that time a remarkable work in which he described the sometimes conflicting claims of the different organs upon the disponible stock of nutritive stuffs in the organism as a struggle between them. Weismann applied the same conception to the determinants within the germ-plasm, and described the effects of that competition as 'germinal selection.'

[39] *Vorträge* (2nd edition), ii. 163.

However, the new hypothesis did not help to solve the difficulties. We certainly may use the word 'struggle' as a metaphoric expression for processes far more complex in reality than a competition for nutritive stuffs; but we must not forget the physiological facts covered by our vague expression—those facts which Roux and his co-workers precisely are studying now at his laboratory for the study of 'the mechanics of evolution,' and of which the *Archiv für Entwicklungsmechanik* is the organ. Thus, reverting to the causes which may secure to the mediane toe a 'victory' over the other toes, they are of a physiological nature; namely, an increased *use* of the toe, leading to a *stimulation* of its tissues, and consequently to an increased *nutrition* of that toe. But how do these changes of nutrition of the different toes affect the germ-plasm determinants of these toes? Do they affect them at all? and, if they do, is there any parallelism in the changes of nutrition of the toes and the nutrition of the respective determinants? Formerly, Weismann used to assert most positively that there is no such correlation: not even an approach to it.

'I must thus affirm to-day, even more decidedly than I formerly did (Weismann wrote in 1892 in *Germ-Plasm*) that all lasting, *i.e.* inheritable, modifications of the body originate in primary modifications of the germs' predispositions (*Keimesanlagen*), and that neither mutilations, nor functional hypertrophy or atrophy, nor any changes that have originated in the body as the effects of temperature, or food, or any other influences of environment, are transmitted to the germ-cells, so that therefore they might become inheritable.' [40]

The transmission of differences of nutrition from the digits of the horse to the determinants of these digits, so as to provoke an increased nutrition of the mediane toe determinants, and a decreased one for the determinants of the other toes, was thus absolutely excluded. Germinal selection having no relation whatever to the 'struggle' that is going on between the toes, it could even run in the opposite direction and favour the development of all the digits but the mediane one, thus counterbalancing the cumulative increase of the latter.

Only in 1904, when Weismann published his *Lectures on the Theory of Descent*, he seemed to make a concession; he recognised that the effects of a varying nutrition may be such as better to feed and to increase certain determinants more than the others, in which case the organs they determine would also increase; but he expressed no opinion as to the possibility, or the impossibility, of the reverse effect: he did not say that the increase of an organ (of the mediane toe in our case) should result in a

[40] *Das Keimplasma: eine Theorie der Vererbung* (Jena, 1892), p. 518.

corresponding increase of force in the determinants of that toe lodged in the germ-plasm: he only did not deny it.[41]

Only in one passage, where he spoke of the seasonal variations of colour in butterflies, did Weismann recognise that the change, both in the germ-plasm and in the butterfly's wings, takes place in consequence of the same cause—temperature. This change is inherited; but this is, Weismann maintains, *only an 'apparent' inheritance of an acquired character*. The changes in the body and the germ-plasm simply take place simultaneously.

This statement, quite unproved and unprovable, evidently renders all further discussion about the inheritance of acquired characters from a theoretical point of view absolutely useless—so long as we are not able to study the 'determinants,' and the still more minute 'biophores' of which they are composed, their 'struggles' and their 'selection' under the microscope. Keeping still to our illustration—if it be asserted that an increased nutrition of the determinants of the middle toe of the horse is a pure matter of accident: that it may happen in some individual horses while in other horses the determinants of the other toes will receive an excess of nutrition—then there is no determinate variation; everything is left again to be accomplished by natural selection, and the whole discussion begins again from the beginning. Or, the fact that the middle-toe determinants receive an excess of nourishment, as soon as the middle toe itself is better fed in consequence of an increased use, is admitted; and then the 'impossibility' for the germ-plasm of being influenced in the same sense by the causes affecting the body-cells is abandoned, in which case the admission ought to be recognised in plain words. Of course, there is a third way out of the difficulty: some new hypothetical suggestion, still more difficult to verify, may be made; but then we should be landed in the domain of pure dialectics.

At any rate, we must say that the attempt to prove the 'impossibility' of an hereditary transmission of acquired characters, and, as Professor Osborne remarks, the attempt to explain evolution without recognising that transmission, have failed. So we can now return from the domain of speculation to the true domain of science—the experimental study of the question. Here

41 'Of course (he wrote) we know nothing certain and nothing exact about the component units of the germ-plasm, we have no definite representation about the relations which exist between the changes going on in the determinant and those that are going on in the part which it determines'; we have only the right to suppose 'that to a stronger development of the one [the determinant] corresponds a stronger development of the other, and that the reverse cannot be true at the same time. If the determinant X disappeared from the germ, the determinate X_1 would also disappear from the *soma*. So we have also the

we have such a mass of rapidly accumulating data that I must leave for another article the analysis of the experimental proofs of the hereditary transmission of acquired characters.

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right to conclude from the degree of development of an organ about the force (*Stärke*) of its determinants, and to consider the *positive* variations and the *negative* variations of both the organ and its determinants as corresponding quantities (*entsprechende Grössen*).' (*Vorträge*, ii. 129.)