The Direct Action of Environment and Evolution

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[*Since this article was written Prince Kropotkin, whose efforts on behalf of the Russian people forty years ago resulted in his imprisonment in the Fortress of St. Peter and St. Paul, has been incarcerated in the same prison by the accursed Bolshevists who now misrepresent that people. The Editor is unable to obtain any news of Prince Kropotkin, but there is only too much reason to fear that he has been murdered in the name of those whom he befriended.*]

> There can be no doubt that species may become greatly modified through the direct action of environment. I have some excuse for not having formerly insisted more strongly on this head in my *Origin of Species*, as most of the best facts have been observed since its publication.
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> Darwin, *Life and Letters*, iii. 232

When we cast a general glance upon the work accomplished during the last half-century in connexion with the theory of evolution, we see that the question which underlay most of the theoretical discussions and inspired most of the study of Nature and experimental research was the great fundamental question as to the part played by the Direct Action of Environment in the evolution of new species. This question was one of the absorbing thoughts of Darwin in the later years of his life, and it was one of the chief preoccupations amongst his followers.

A mass of researches having been made in this direction, I analysed them in a series of articles published in this Review during the last seven years. Beginning with the evolution of the conceptions of Darwin himself and most evolutionists about Natural Selection,[1] I next gave an idea of the observations and experiments by which the modifying powers of a changing physical environment were established beyond doubt.[2] Then I discussed the attempt made by Weismann to prove that these changes could not be inherited, and the failure of this attempt.[3] And finally I examined the experiments that had been made to ascertain how far the changes produced by a modified environment are inherited.[4] What we have to do now is consider the conclusions which may be drawn from all these researches and discussions.

I

When Darwin was leaving England for a cruise in the *Beagle* he was warned by one of his friends that he must not let himself be influenced by what he might see in Nature in favour of the variability of the species. 'None of these French theories,' he was told (I quote from memory), which meant: 'Nothing of the ideas of Buffon, Lamarck, and Geoffroy Saint-Hilaire, according to whom the direct action of the ever-changing conditions of life originated the infinite variety of vegetable and animal forms peopling the globe.'

Darwin carefully observed Nature and studied its life, and he felt the spell of 'the French ideas.' And both in 1842, when he wrote a first sketch of his conceptions about evolution,[5] and in 1859, when he published his *Origin of Species*, where he insisted upon the dominating part played in the

[1] *Nineteenth Century and After,* January 1910

[2] 'The Direct Action of Environment in Plants,' July 1910; and 'The Response of Animals to their Environment,' November and December 1910.

[3] 'Inheritance of Acquired Characters: Theoretical Difficulties,' March 1912.

[4] 'Inherited Variations [???] ober 1914, and "inherited variations in Animals," November 191[??]

[5] *The Foundations of t [???] Species*, a sketch written in 1842. Edited by his son Francis [??] bridge 1909.

evolution of new forms by Natural Selection, he indicated at the same time the part that is played by the Buffon-Lamarckian factor — the Direct Action of Environment. Lyell even reproached him with the 'Lamarckism' of the *Origin of Species.* However, at that time Darwin postponed a thorough discussion of the subject to a work on Variation, for which he was collecting materials. Only nine years later he published the first part of this work; but in the meantime, already in the third edition of the Origin of Species, he felt bound to introduce important matter dealing with the direct action of environment. His great work on *Variation*, as well as the sixth edition of *Origin of Species*, contained, in fact, a straightforward recognition of the importance of the environment-factor in the evolution of new species. He did not hesitate to admit that in certain cases 'definite' and 'cumulative' variation under the influence of environment could be so effective for originating new varieties and species adapted to the new environment, that the role of Natural Selection would be quite secondary in these cases.

The reasons for such a modification of opinion were acknowledged by Darwin himself. In the 'fifties there were no works dealing on a scientific basis with variation in Nature; while Experimental Morphology, although it had been recommended already by Bacon,[6] was called into existence after the appearance of Darwin's work. Still, the new data, rapidly accumulated in these two branches of research after 1859, were such as to convince Darwin of the importance of the direct action of environment, and he frankly acknowledged it.

Of course he did not abandon the fundamental conception of his *Origin of Species.* He continued to maintain that a purely individual, accidental variation *could* supply Natural Selection with the necessary materials for the evolution of new species. But he also had seriously pondered upon the following question that was raised by his first great work: Granting all that has been said about the importance of the struggle for existence — *Would Natural Selection be capable of increasing, or merely accentuation, from generation to generation a new useful feature, if this feature appeared accidentally, in a few individuals only, and was therefore submitted to the law of all accidental changes?* Is it not necessary, for obtaining a gradual increase of the new character, that some external cause should be acting in a definite direction for a number of generations upon the majority of the individuals of a given group, and its effects be transmitted more of less from one generation to the next?

The reply that Darwin gave to this question in 1868 in the revised (sixth) edition of his *Origin of Species* was pretty definitely in the affirmative. He wrote:

> It should not, however, be overlooked that certain rather strongly marked variations, which no one would rank as mere individual variations, frequently recur, owing to a similar organisation being similarly acted on — of which fact numerous instances could be given with out domestic production … There can also be no doubt that *the tendency to vary in the same manner has often been so strong that all individuals of the same species have been similarly modified without the aid of any form of selection.*[7]

Besides, everyone who will take the trouble (or rather, give himself the pleasure) of re-reading *Variation* will see that such a thing as an indefinite, haphazard variation, even with the aid of Natural

[6] In Sylva Sylvarum [????] 1824, section 526) the great founder of inductive science wrote: [???]fore, you must make account, that if you will have one plant [???] another, you must have the nourishment overrule [the inherited dispositions]…You shall do well, therefore, to take marsh-herbs, and plant them upon tops of hills and champaigns; and such plants as require much moisture, upon sandy and very dry grounds…This is the first rule for transmutation of plants.'

[7] *Origin of Species*, 6th edition, p.72; the italics are mine.

Selection, hardly had any importance for the great founder of the theory of evolution at the time when he wrote this last work.[8] Over and over again he repeated in it that variability depended entirely upon the conditions of life; so that if the latter remained unaltered for several generations, 'there would be no variability, and consequently no scope for the work of Natural Selection.' And, on the other hand, where the same variation continually recurs, owing to 'the action of some strongly predisposing cause,' *the appearance of new varieties is rendered possible, independently of Natural Selection.* In chapter xxiii. He gave the facts he was able to collect before 1868, 'rendering it probable that climate, food, etc., have acted so definitely and powerfully on the organisation of our domestic productions that new sub-varieties or races have been thus formed without the selection of by or Nature.' It is also evident that if Darwin had had at his disposal the data we have now he would not have limited his conclusions to domesticated plants and animals. He would have been able to extend them to variation in free Nature.

II

For the first twenty or thirty years after the appearance of the *Origin of Species* research was chiefly directed to the study of the direct action of environment as it works in free Nature and is made to work in our experiments. The chief result of these researches was to prove, first, that there are no such specific characters, either in plants or in animals, as could not be altered by modifying their physical conditions of life; and, second, that the variations obtained experimentally under certain conditions of heat or cold, dryness or moisture, rich or poor nutrition, and so on, were exactly those which are characteristic for animals and plants living in the Artic and Torrid zone, in a dry and in a wet climate, in fertile prairies and in deserts. It was thus proved that if a species of plants or animals migrated from a warmer into a cooler region, or from the sea-cost inland, or from a prairieland into a desert, *Variation itself amongst the new immigrants, apart from Natural Selection, would tend to create a variety representing an adaptation to the new conditions.* The same would happen if the climate of a given locality underwent a change for some physiographical reason. In both cases Natural Selection would thus play a quite subordinate part — that of a 'handmaid to Variation,' as Hooker wrote in one of his letters to Darwin. It would have only to weed out the weaklings — those who would not possess the necessary plasticity for undergoing the necessary changes in their tissues, their organs, and (with animals) in their habits.

The researches of those years having shown how the floras and the faunas of the Artic barren lands, the Alpine summits, the African swamps, the sea-casts, the deserts, and the Steppes were adapted to withstand the climate and the general conditions of life in each of these surroundings, the first steps were also made, especially by botanists, to prove that most of these wonderful adaptations could be reproduced in a short time in our experiments. It was sufficient for that to rear the plants or the animals into those conditions of temperature, moisture, light, nourishment, and so on which prevail in the different regions of the earth. Hence, already then — especially for those who were acquainted with Nature itself, it appeared most improbable that the adaptations of plants and animals which we see in Nature should be the results of *merely accidental, fortuitous variations.*

To take one of the simplest instances — we had learned form experiments that when a plant was grown under a glass bell in a very dry air, its leaves soon ceased to develop succulent lobes, and the ribs of the leaves were turned into spines or prickles. And when we saw that spiny plants were

[8] See *Variation in Domesticated Animals and Plants*, vol. ii. Pp. 289, 291, 300, 321, 322, 347, and so on, of the 1905 popular edition of Mr. Murray.

characteristic of the vegetation of dry regions, we could not be persuaded that the unavoidable transformation of leaves into prickles and spines in all plants immigrating into a desert, or growing in a gradually desiccating region, should count for nothing in the evolution of spiny species. We could not believe that all the evolution of the so-called 'adaptive' structures in deserts, sea borders, Alpine regions, and so on, which is going on in Nature on an immense scale *as a physiological result of the conditions themselves*, should leave no trace in the evolution of the desert, sea-border, and Alpine species; that the adjustments which are *in the individual a direct consequence of the physico-chemical action of the environment upon its living matter, should have in the evolution of a species a merely accidental origin.*

Already then many biologists took the Lamarckian point of view; and very soon Darwin himself, after having gained what he considered to be the main point of his teaching — the variability of species,[9] made the next step. He recognised the powers of the direct action of environment in the evolution of new varieties, and eventually new species. The part of Natural Selection in this case was to eliminate those individuals which were slow in acquiring the new adaptive features, and to keep a certain balance in the evolution of new characters. Its function was thus to give a certain stability to the new variety. Of course this stability did not mean immutability. *There being no immutable species*, it meant only that the new features would be retained for a certain number of generations, even if the new variety was placed once more in new surroundings, or was returned to the old ones.

III

That changes produced in plants and animals by the direct action of a changing environment are inherited, was not a matter of doubt for Darwin. He had carefully studied and sifted the experience of breeders and cultivators, and he found in it ample proofs of such an inheritance. He was aware, of course, that mutilations are not, and cannot be, inherited *as such* (this had been known, in fact, since the eighteenth century); but he also knew that characters developed in a new environment *were* transmitted to the offspring — if the modifying cause had acted upon a certain number of generations. This last limitation was well known to both Lamarck and Darwin and repeatedly mentioned by them.

Having already discussed in a previous article the teachings of Weismann who opposed this view, I shall refer the reader to that article,[10] and only mention here and further develop one or two of its points.

Going back to an early and not generally known work of Weismann, *Upon the Final Causes of Transmutations*,[11] I found that the origin of his teachings was *not* experimental: it was theological. In 1876 Weismann was still a Darwinist. His own experiments on seasonal dimorphism had confirmed the facts discovered by Dorfmeister concerning the effects of temperature in producing two different races of butterflies; while the experiments that Weismann made subsequently on mice to prove the non-transmission of a mutilation (the clipped tail) added absolutely nothing to our previous knowledge. If Weismann had taken the trouble of consulting Darwin's *Variation* before he had written his eighth essay, he would have seen that clipped tails are *not* inherited, and he would have learned

[9] See his *Letters*

[10] *Nineteenth Century and After*, March 1912.

[11] 'Ueb[????] Ursachen der Transmutationen,' in *Studien zur Descendenz*[???] 1876, chapter "Mechanismus und Teleologia.' I don't know [???] exists an English translation of this chapter.

why such mutilations have little chance of being inherited (embryonal regeneration), and why their non-transmission did not affect Darwin's views upon the inheritance of variations.

It was under the influence of Schopenhauer's, Hartmann's, and Karl Baer's criticisms of the philosophical substance of Darwinism that Weismann accepted the idea of Baer that evolution without a teleological guidance from above was an unscientific conception. He thus came to the conclusion that, although evolution is a mechanical process, it must have been predetermined by a supreme power in accordance with a certain plan. And, in order 'to reconcile teleology with mechanism,' he borrowed from Näeli and partly from Nussbau the idea of 'continuity' of the germ-plasm; and thus he came to a Hegelian conception of an 'immortal soul.' His hypothesis was thus suggested by those same considerations, lying outside the domain of Science, that Darwin had had to combat.

In his *Essays upon Heredity*, written in 1881–1887, Weismann represented his germ-plasm hypothesis as an outcome of the remarkable microscopical discoveries made in those years by a number of well-known anatomists, concerning the processes taking place during and immediately after the fertilisation of the egg. Bt as early as 1897 Professor Hartog made the quite correct remark that the cardinal defect of the theory of Weismann was its 'objective baselessness.'

> *It professes [he wrote] to be founded on the microscopic study of the changes in the nucleus in cell-division, but there we find nothing to justify the assumption of two modes of nuclear division in the embryo — the one dividing the determinants, and the other only distributing them between the daughter-cells.*[12]

Later on, two of the leading microscopists who took part in the just-mentioned discoveries, far from giving support to Weismann's contention that no material influences can be transmitted from the protoplasm of a cell to the germ-plam of its nucleas, distinctly contradicted it.[13]

More than that. The fundamental point of all the hypotheses brought forward by Weismann was the isolation of the germ-plasm and the impossibility of its being influenced by the changes going on in the body under the influence of the outer agencies. But the more we advanced in the study of heredity the more we were brought to realize the close interdependence of all the organs and tissues of the living beings — plants and animals alike — and the impossibility of one of their organs being affected without a disturbance being produced in all parts of the organism.[14] We learned from the best embryologists that the living substance which is bearer of inheritance is *not* localised in the nucleus of the germ-cells; and that an intercourse of substances between the nucleus and the cell-plasm must

[12] 'The Fundamental Principles of Heredity,' in *Natural Science*, xi. October and November 1897. Reproduced in Professor Marcus Hartog's *Problems of Life and Reproduction*, London 1913.

[13] Oscar Hertwig, *Der Kampf un Kerntragen der Entwickelungs und Vererbungslehre*, Jena 1909, pp. 44–45 and 107–108. See also *Nineteenth Century*, March 1912, p. 520.

[14] To a review of this question in his capital work, *Heredity* (London 1908, p. 64), Professor J. Arthur Thomson added the following words: 'Holding firmly to the view which we have elsewhere expressed, that life is a function of inter-relations, we confess to hesitation in accepting without saving clauses any attempt to call this or that part of the germinal matter the exclusive vehicle of the hereditary qualities.'

be taken as proved.[15] Finally, we have no experiments tending to prove that even unimportant lesions of the body may be followed by important modifications in the reproductive cells.[16]

The difficulties which the hypothesis too hastily framed by Weismann had to contend with when it was confronted with the scientific observation of Nature, and the new hypotheses he brought forward to meet the rapidly accumulated contradictory facts, were discussed in my above-mentioned article. Sufficient to say here that, after having emphatically denied at the outset that his 'immortal' germ-plasm could be influenced by external agencies in the same direction as that taken by the somatogenic changes [in the body] which follow the same causes'[17] ; and after having maintained that the mixture of two germ-plasms in sexual reproduction [that is, Amphimixis] was 'the only way' that hereditary influences 'could arise and persist,[18] Weismann soon had to abandon his Amphimixis hypothesis (already repudiated long since by Darwin). Gradually he came to the hypotheses of 'Germinal Selection,' or struggle for food between the determinants of the germ-plasm, as a probable cause of inherited modifications, and 'Parallel Induction.' In these two hypotheses he thus acknowledged that the germ-cells *are* modified by external causes, so as to reproduce in the offspring the somatic, or body changes produced in the parent by the environment. Only in his second hypothesis he suggested that the germ-cells are influenced *directly* by the external agencies — not through the modifications produced by the environment in the organs and tissues of the body. It hardly need be said that most biologists received this last suggestion, not as a new working hypothesis, but as a veiled concession of Weismann to his opponents. In fact, the hypothesis was *not* a generalisation born from the study of changes going on in germ-cells under the action of external agencies: it was advocated only as an hypothetical explanation for the facts that contradicted the previous hypotheses of Weismann. But till now — we are told by the specialists who have studied the subject — it is impossible to ascertain in one single concrete case of inheritance how the modification was produced in the germ-cells: through the body-cells, or independently of them.[19]

Some biologists saw in 'parallel induction' an interesting new line of research, and they followed it. But Darwin, who already knew this hypothesis long before Weismann resorted to it, pointed out with full right, in *Variation*, that although a simultaneous modification in some definite direction of the body-cells and the germ-cells takes place in certain special cases, this cannot be a general cause of the hereditary transmission of variations. Like Amphimixis, this hypothesis does not account for the

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[15] Rabl, *Ueber Organ-bildende 'Substanzen und ihre Bedeutung fur die Vererbung;* E. Godlewski jun., in Roux's Archive, vol. xxviii. 1908, pp. 278–378. The connexion between all the cells in plants has been proved by observation, and now it begins to be proved for animals. The lively intercourse between the cells of the animal's body by means of the wandering cells, which was observed during regeneration processes, seems not to be limited to these processes.' The researches of His, Kupffer, Loeb, Roux, and Herbst are tending to prove that the same cells also take part in the ontogenetic processes. (See the articles of Herbst in *Biologisches Centralblatt*, vols. xiv. And xv.) As to Nussbaum, whose work is suggested to Weismann the 'continuity' of the germplasm, his idea is that the germ-cells *are exposed to the same modifying agencies as the body-cells (Archiv fur mikroskopische Anatomie*, xviii. 1908, quoted by Professor Rignano in *La transmissibilite des caracteres acquis,* p. 169.) Many other biologists come to the same conclusion.

[16] Experiments of Ignaz Schiller on *Cyclops* and Tadpoles; preliminary report in Roux's *Archiv*, xxxiv. Pt. 3, pp. 469–470.

[17] *Essays*, ii.190.

[18] [...]

[19] Cf. L. Plate, *Selekionsprinzip*, 4th edition, 1913, pp.441–442. The same view, as it was pointed out by Professor Hartog, is held by E.B Wilson, the author of a standard work on the cell: 'Whether the variations [he writes] first arise in the idioplasm [the germ-plasm] of the germ-cells, or whether they may arise in the body-cells, and then be reflected back upon the idioplasm, is a question to which the study of the cell has thus far given no certain answer' (*The Cell in Development and Inheritance,* 2nd edition 1900, p.433, quoted by Marcus Hartog in his work, *Problems of Life and Reproduction*, London, Murray, 1913, p. 198, chapter on the inheritance of acquired characters).

inherited *adaptive* variations, the necessity of which for the evolution of new species Darwin already saw in 1868, and we still better see now.

In short, Weismann's attempt to combine the pre-Darwinian ceonception of innate pre-determined variations with the Darwinian principle of National Selection has failed; and an attentive reader of his last work, *Vorträe zur Descendenztheorie* (especially the pages 258–315 of the second volume), will himself see how little there remained from that attempt. By his criticisms of some facts which formerly used to be quoted as proofs of the inheritance of acquired characters, he certainly induced biologists to go deeper into the subject of heredity. But that was all. In his attempts at constructive work he failed. He had not that power of inductive generalisation which leads modern science to its great discoveries. His hypotheses were brilliantly and imaginatively developed *suggestions*; but they were not brilliant inductive generalizations. They even lacked originality.

IV

However, it may be asked: 'Why don't we know more cases where the hereditary transmission of acquired characters has been proved by experiment? Why have we not yet proofs of acquired characters being retained for a number of generations, even though the offspring was taken back to its old environment? These two questions certainly deserve a careful examination.

The reasons are many. To begin with, it is extremely difficult to breed plants, and still more so higher animals, in surroundings sufficiently different from the normal ones for altering the distinctive characters of a species. Especially is it difficult to make animals reproduce themselves in such conditions. In the best-conducted experiments it happened over and over again that the second generation, when it was bred in an unusual environment, perished entirely; in the best cases only one or two individuals survived.

Besides, it was only gradually learned by the experimentators in order to obtain an inheritable variation, the modifying cause must act at a certain period fo the individual's life, when its reproductive cells are specially sensitive to new impressions.[20] And then the experiments require time. While it is very difficult to breed several generations in succession in unusual conditions, it is precisely several, or even many, generations which must be under the influence of a modifying cause in order to produce a more or less stable variation. Lamarck, in stating his two laws of variation, was careful to indicate that the changes must be slow, and that they must take place for a succession of generations, in order to be inherited and maintained later on for some time. Darwin repeatedly insisted upon this. But only now the conditions under which such experiments must be conducted are beginning to be realized in special climateric stations and laboratories. Up till quite lately such experiments were not in favour in most of the West-European universities.

Finally, during the first decades after the appearance of the *Origin of Species*, research was chiefly directed, as we have seen, to prove the very fact of a great variability of the species, even in their typical specific characters — this being denied then by a great number of zoologists and botanists. And later on a mass of experiments had to be made in order to prove that if plants and animals be placed in such conditions of temperature, moisture, light, and so on, as are offered in different regions of the Earth, they will display exactly those variations which are characteristic for the floras and faunas of these regions, without any interference of natural or artificial selection. Besides, it was

[20]Darwin knew it and mentioned it in several places in *Variation*; but when the fact was established by the experiments of Merrifield, Standfuss, and so on, it was received as a new discovery.

important to prove, and it was proved, that these variations, representing in most cases adaptations to the new conditions of life, could be produced by the new conditions themselves, which stimulate certain physiological functions (nutrition, evaporation, the elaboration of fats, and so on), and through them modify different organs.[21]

Only after this immense work had been done — and it took more than forty years — did biologists begin to investigate how far such variation is capable of giving origin to new races, and how many generations must be submitted to the modifying influences in order to produce a more or less stable variety.[22]

It must also be noted that at the outset inheritance experiments were chiefly made with variations in the colours and the markings of insects, and only now are they beginning to be directed towards the far more important study of variations in physiological functions, which are (as was indicated long since by G. Lewes and Dohrn, and lately by Plate) the chief agencies in the evolution of new races.

These are the causes which explain why the inheritance of environment-variations has not yet been proved by more experiments. However, it must not be forgotten that we know already two important groups of variations, both due to environment, *which are inherited*, and the inheritance of variations by means of bud-reproduction, and the other includes the so-called 'sports,' described by de Vries as 'mutations.'

With regard to the former, I have already mentioned in a previous article[23] that Darwin, who *had* studied the subject, had shown that there is no means of finding any substantial distinction between reproduction by seed. The laws of both are the same, and in both cases the reproduction takes place by means of germ-cells, capable of reproducing the whole plant with its sexual organs and with sexual reproduction, whether the germ-plasm be contained in a seed or a bud, in the leaf of a Begonia, or in the cambial tissue of a Willow. And I have also shown that if Weismann, writing in 1888 under the fascination of his Amphimixis hypothesis, made the grave mistake of thinking that there is no transmission of germ-plam in vegetative reproduction, and therefore described 'bud-variation' as an 'individual variation,' he at least saw his error later on. He recognised in 1904,[24] *using almost the same words as Darwin used in 'Variation,' that a plant obtained through budding is as much a new individual as if it had been reproduced by seed.*[25]

[21] All this has been proved by experiment, and this is why a good-sized book would be required to record the results obtained lately by Experimental Morphology. Cf. T.H. *Morgan's Experimental Morphology*, New York 1907; Przibram's *Experimental-Zoologie*, Vienna 1910; Yves Delage and M. Goldsmith, *Les theories de l'evolution*, Paris 1909; and so on.

[22] That time was an important element in the problem was emphatically asserted by both Lamarck and Darwin, and even by Bacon. But there are Weismannians who overlook it. Thus Lamarck was reproached with having enunciated two contradictory statements in his first and second law. But such a reproach could only be made by *overlooking the time that is required to produce the changes.* To use Lamarck's own words, time is needed 'both in gradually fortifying, developing, and increasing an organ which is active, and in undoing that, effect by imperceptibly weakening and deteriorating it, and diminishing its faculties, if the organ performs no work' (first law; italics mine). All that the second law says is, that what has been acquired or lost in this way is transmitted to the new individuals born from the former; but it says not a word about the length of time that the new character is going to be maintained, if the new-born individuals are placed again in new conditions or returned to the old ones. *These individuals evidently fall in such case under the action of the slow changes mentioned in the first law. Nineteenth Century and After*, October 1914, pp. 821–825.

[23] *Nineteenth Century and After*, October 1914, pp. 821–825

[24] *Vortrage*, 2nd edition, vol. ii. pp. 1 and 29.

[25] Weismann is thus no longer responsible for those who go on repeating his opinions of 1888, when he believed that in vegetative reproduction we have only a subdivision of the same individual, and added: 'But no one will doubt that one

But it must be remembered that in the vegetable world reproduction by buds (rootstocks, runners, and the like) is far more important than reproduction by seed. In fact it seems most probable that the immense majority of the plants which cover the northern part of the northern hemisphere have reproduced themselves since the Glacial period chiefly by buds, runners, rootstocks and the like, as the Artic and many Alpine plants still reproduce themselves. And as they transmitted to their offspring, during this long period of a chiefly vegetative reproduction, the characters they acquired in new surroundings, as they followed the retreat of the ice-sheet, we can already say that an enormous number of sub-Artic and Temperate zone varieties and species owe their origin to the inherited effects of the direct action of changing surroundings.

It is very nice to say in poetical language that the Steppes of South Russia are covered now with the same individuals of Grasses that were withering under the hoofs of the horses during the migration of the Ugrians from the Southern Urals to Hungary; but a botanist who knows that a bud on the rootstock of a Grass contains the very same germ-plasm as the seed in its ear does not take these pretty images for a scientific induction.

V

Much of the same must be said about the so-called 'sports,' or inherited variations which seem to appear all of a sudden and have often given to breeders and growers the possibility of raising new varieties, or sub-species. Darwin paid them a good deal of attention; and in 1900, when the well-known Dutch botanist de Vries described the 'sports' under the name of 'mutations,' and saw in them the real cue to the origin of species, interest in these 'sudden' or 'discontinuous' variations was renewed.

Already in Darwin's times it had been suggested that the 'sports' may represent an important factor in the evolution of new species, and Darwin had shown the reason why this could not be the case (it will be mentioned further on). However, developed as it was by de Vries in a well-written work, rich in original observations, 'the Mutations Theory' obtained for some time some success. The main objection against considering Natural Selection as Nature's means of evolving new species being the insignificance of the first incipient changes in 'continuous' variation, and their little value in the struggle for life, some biologists saw in the sudden variations, or 'mutations,' the means of getting rid of this objection, without resorting to the hateful Direct Action of Environment.

De Vries based his theory chiefly on the sports of a well-known decorative plant, the Evening Primrose, or *Oenothera lamarckiana*, which he found growing wild in a field at Hilversum, near Amsterdam. It displayed there a number of 'sports,' and by cultivating these sports de Vries obtained a number of new 'species.'[26] These observations led him to build up a new theory of descent. According to it, the variations which Darwin described as 'continuous,' or 'fluctuating,' have no value for the appearance of new species — not only because they are too small for having a life-value in the struggle for existence, but also because they are not inherited, and consequently cannot be 'cumulative.' The sudden 'discontinuous' variations (Darwin's 'sports') are known, on the contrary, to be inherited, and they often offer sufficient differences from the normal type to be of value for Natural Selection. In artificial selection they have been the means of obtaining new steady varieties.

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and the same individual can be gradually changed during the course of its life, by the direct action of external influences.' (*Essays*, i. 429.)

[26] Darwin probably would have described them only as 'incipient species.' Professor Plate considers them as *habitus* modifications. They differ, he says, from the mother, plant in many organs, but in each of them in an insignificant degree.

In his earlier researches de Vries, who had studied for fifteen years such inherited 'monstrosities' as the Five-Leaved Clover, and the Many-Headed Poppy, had come, in accordance with Professor J. MacLeod, to the conclusion that rich nutrition in the wide sense of the word (heavy manuring, keeping the seedlings wide apart, and so on) was the first condition for obtaining such inheritable variations.[27] But later on, accepting the teachings of Weismann, he separated the 'nutrition variations' — which, he maintained, were not inheritable — from the 'mutations.' The latter were inherited, because they were originated by 'congenital' variations, suddenly appearing for some causes unknown in the germ-plasm, at certain periods of the life of species. Each species, he said, has such a period, during which it can give origin to new species.

However, it was soon recognised by most botanists that the value of the *Oenothera* sports for a theory of descent had been over-estimated. From accurate researches made in the United States, at Harlem, and in the environs of Liverpool, it appeared that the species described as *Oenothera lamarckiana* had a long history: it was cultivated in Europe as early as the middle of the eighteenth century; and it easily could be a crossing of two other species of the Evening Primrose. Hence its great variability.[28] Moreover — and this is an essential point, already noticed by Darwin — a variation is often described as a 'sudden' one simply because the minute changes which were leading to its appearance were not taken notice of. In reality, leaving aside those unimportant individual differences which but feebly affect some organs, Darwin found no substantial difference between the sports and the inheritable fluctuating variations due to environment.[29] As to the idea that sports might explain the appearance of new species, Darwin very wisely pointed out that purely accidental sports could not have played such a part in the evolution of new species, *because they would not offer that accommodation to the environment which can only be supplied by a definite and cumulative variation under the influence of a new environment,*—this variation being aided by Natural Selection.

At any rate, those who have seriously studied the whole subject of evolution and heredity, like Yves Delage, Johannsen, Plate, and many others, do not now attribute to 'mutations' the importance that was going to be attributed to 'mutations' the importance that was going to be attributed to them a few years ago.[30] Professor Ed. Bordage, who has published lately a special study of the whole question of mutations, also came to a similar conclusion.[31]

To begin with, Bordage points out that the *Oenothea lamarckiana* is, according to different botanical authorities, a hybrid, either between *Oe. Grandiflora* and *Oe. biennis,* both imported to Europe in the

[27]Cf. *Die Mutationstheorie*, vol. i., Leipzig 1901, pp. 93, 97–100, and in fact all the fouth chapter. Also his earlier articles, *L'unite dans la variation* and *Alimentation et selection* summed up in *Mutationstheorie.*

[28]Many important data concerning variation in *Oenotheras* will be found in the monograph of Messrs. D. T. MacDougal, A. M. Vail, and G. H. Shull, *Mutation, Variation and Relationships of Oenatheras*, Washington (Carnegie Publications) 1907.

[29]'Monstrosities graduate so insensibly into mere variations that it is impossible to separate them' (*Variation*, ii. 297–298). He considered that 'variability of every kind is directly or indirectly caused by changed conditions of life' (p. 300); and 'of all causes which induce variability, excess of food, whether or not changed in nature, is probably the most powerful' (p. 302)

[30]Thus, fully recognising that 'de Vries has established in the domain of heredity a mass of facts, the theoretical value of which still remains in some respects to be established by further research,' Professor Plate, in analyzing the Mutation theory in his monumental critical work (*Selektionsprinzip*, pp. 384–435), wrote: 'The mutation theory obtained an apparent temporary success because it introduced new words for well-known facts and conceptions, and thus awakened the idea that a new knowledge had been won. It is evident that for the theory of descent no real progress in advance of Darwin had been won in that direction.' In another, very elaborate work, *Vererbungslehre* (vol. ii. of his *Handbucher der Abstammungslehre*, Leipzig 1913, pp. 430–475), Plate returned once more to this subject, and after a careful examination of the whole question (including Mendelism) he worded his final conclusion as follows: 'Those thoughts in it [the Mutations theory] which are correct are not new, and its new components cannot be accepted' (p.473).

[31]'Les nouveaux problemes de l'heredite: la theorie de la mutation,' in *Biologica*, ii. 1912.

eighteenth century (the former was known at Harlem since 1756), or between different varieties of *Oe. biennis*, which is a very variable species.[32] But even if it was not a hybrid, the Evening Primrose has undergone so many changes in the conditions of its culture during the last hundred or hundred and fifty years, that its present considerable variability may be a consequence of these changes.

All taken, Professor Bordage comes to the opinion that a mutation of not something substantially different from an ordinary variation. It is only

> a sudden external expression of internal processes, accomplished gradually and without interruption … Between the sudden and the slow variation there is no absolute difference. Both can be considered as the effects of the same law, manifesting themselves more or less rapidly.

VI

'Mutations,' we have just seen, were described as 'congenital variations.' But *every* variation of form and structure, once it is inherited, implies a 'congenital variation': some change must have taken place in the germ-cells, whatsoever the origin of the variation, or the position of the germ-cells in the organism may be. We learn, it is true, from the experiments of MacDougal and Tower that certain inheritable changes may be obtained by a direct action of external agencies (temperature and so on) upon the germ-cells. Of course, they *may*. But nobody has yet proved that changes produced in the body-cells *cannot* affect the germ-cells; while modern research tends to prove quite the contrary.

Consequently, we are not astonished to learn that de Vries, having recognised in his last work, *Gruppenweise Artbildung*, that every mutation must have 'not only an inner cause, but also an exterior case,' and that the high variability of the Oenotheras must be 'to some extent a consequence of the special conditions of the soil,'[33] has thus given a hard blow to the idea of a fundamental distinction between 'mutations' and ordinary variation. Both are inherited, the difference being only one of degree in the modifying cause.

It may be added the Erwin Baur, who also has carefully studied the subject, comes to a similar conclusion in his 'Introduction to the Experimental Theory of Heredity.' As a rule (he writes) mutations are rare (one in a thousand individuals, or less); and 'what are their causes in most cases we don't know.' Only lately experiments were made showing that mutations, i.e. inheritable variations, can be provoked by exterior influences, depending on our will. Such are the experiments on the Colorado beetle made by Tower, who used high temperatures, dryness of the air and low atmospheric pressure, those of Blaringhem who provoked inherited variations by mutilations of plants, and MacDougal who acted directly on the reproductive cells.[34]

[32] The latter is the opinion of Mr. Boulenger, an authority on the subject; and the former is the view taken by Davy and several other botanists.

[33] De Vries, *Gruppenweise Artbildung*, pp. 342–343; also *Species and Varieties: their Origin by Mutations*, Lectures before the University of California, edited by D.T MacDougal, Chicago, 1906, p.451.

[34] Erwin Baur, *Einfurhrung in die experimentelle Vererbungslehre*, Berlin 1911, pp. 202–204. In a recently published work by R. Ruggles Gates, *The Mutation Factor in Evolution, with particular reference to Oenothera* (London 1915), we have an important contribution to this subject. Its chief interest is in the researches made by the author to discover the changes which take place in the germ-cells when an inherited variation takes place in the extremely variable complexus of species and varieties represented by the Oenothera. These researches have not yet brought the author to a definite conclusion as to the causes of mutations (p. 321); but they open an interesting branch of investigations in the great question of Heredity.

Finally we learn from another most careful and gifted experimentator, Professor Klebs, that those characters of a plant which belong to the most constant ones under the ordinary conditions of culture can become most variable under properly chosen conditions; and that both the so-called continuous and the discontinuous variations (the mutations) can be obtained in the same individual, according to the external conditions into which it is placed.[35]

The consensus of opinion is thus against attributing to mutations an origin quite different from the origin of habitus-variations. But once it is so, we have in the so-called 'mutations' another vast category of characters 'acquired' under the influence of a changed nutrition in a new environment, *and inherited.*[36] And these two vast categories immensely reduce the part that Natural Selection may have to play in the evolution of new species. With this reduced function it becomes quite comprehensible.

VII

The dominating tendency of modern research is thus to come to a synthesis of the two chief factors of evolution: the Buffon-Lamarckian factor including the variations called forth by a changing environment, and the Darwin-Wallacian factor of Natural Selection. Darwin, as we saw, frankly acknowledged it.

Herbert Spencer had already come to this conclusion, only giving even more importance to the first factor.

The forgoing chapters — he wrote in the second enlarged edition of his *Principles of Biology* — imply that neither extreme (i.e. Natural Selection alone, or the Direct Action of Environment without the aid of Natural Selection) is here adopted. Agreeing with Mr. Darwin that both 'factors have been operative, I hold that the inheritance of functionally caused alterations has played a larger part than he admitted even at the close of his life; and that, coming more to the front as evolution has advanced, it has played the chief part in producing the highest types.

It is most interesting to note that Weismann, although his starting-point was quite different from that of Darwin and Spencer, also came, after all, to the same views. He began by proclaiming the 'All-Sufficiency of Natural Selection' for giving origin to new species, and rejected the necessity of inheritable adaptive changes being produced by the environment. But we saw how he gradually came to new hypotheses which actually recognised the part played in the evolution of new species by inherited variation.

Pages could be covered to show how biologists engaged in experimental work came, after some hesitation, to recognize the modifying influence of environment. But a few quotations will do to show the general tendency of modern research.

Standfuss has summed up the results of his twenty-eight years' experiments in a carefully worded lecture. He sees in the predominance of an older type upon a newly appearing variation the key to

[35] 'Studien uber Variation,' in Roux's *Archiv*, vol. xxiv. pp. 29–113; review in *Annee biologique*, xiv. p. 357

[36] With all the respect I have for the always most accurate work of Professor J. Arthur Thomson, I confess that, whatever his other reasons in favour of discontinuous variation may be, the facts he mentions in *Heredity* (London 1908, pp. 86–89) hardly prove that 'Variation leads by leaps and bounds.' The very words with which Professor Thomson accompanies, with his habitual, fairness, each of the examples he mentions, suggest that there is no reason to affirm, and some reason to doubt, that the new characters appeared suddenly. About the wonder-horse with an extremely long mane we are told that 'the parents and grandparents had unusually long hair'; about the Shirley poppy, that the 'single discontinuous variation' from which it was obtained 'may have occurred often before Mr. Wilks saved it from elimination,' but no reason is given to suggest that it was a 'sudden' variation; the same applies to the Star Primrose, the Moth *Amphidasys*, and the Medusoid *Pseudoclitia pentata*, which is said to be 'remarkably variable.'

the difficulty of a transmission of acquired characters to the offspring. The grip of the Old stirp — of what has become strongly established during a succession of generations — cannot, Standfuss says, be easily overpowered by the New (a view, by the way, expressed already by Bacon). And after having proved by his experiments that sometimes the New is inherited, Standfuss concluded his lecture with these words:

The mutual inter-action between the agencies of the outer world and the organisms gives origin to fluctuating (*schwankenden*) new forms; they are inherited more or less, then they are sifted by Selection, and kept by it within definite lines of development.[37]

Wettstein, who has been experimenting for years upon the modification of plants by exterior agencies, openly accepts the hereditary transmission of acquired characters in his 'Handbook of Systematical Botany. He writes:

In the immense majority of cases, adaptive characters are originated by the so-called 'direct adaptation'; in other words, we must recognize in the plant the of adapting itself directly to the prevailing conditions of life, and inheriting these acquired adaptation-characters.[38]

J.P Lotsy, the author of a well-known elaborate work on the theories of descent, comes to the conclusion that

unless we accept a *Vis vitalis* [a Life-force] which, after all, would explain nothing, it is impossible to find another reason for the origin of variations but the influence of the external conditions on the substance of the protoplasm; and without an inheritance of the acquired variation, or character, there is no reason for its being fixed. If one absolutely denies the possibility of biometamorphoses (variations due to environment) being inherited, this means to deny evolution itself.[39]

D.T. MacDougal, after having analysed the work of Buchanan, Gages, Klebs, Zederbaum, and de Vries, finds that their discoveries, coupled with his own and other botanists' work at the Desert Botanical Laboratory in the United States and elsewhere, enforce upon us the conclusion that structural changes and implied functional accommodations are without doubt direct somatic responses, which became fixed and permanent in the consequence of their annual repetition through the centuries.[40] W. Johannsen, whose main work, 'Elements of the Exact Science of Heredity,'[41] is kept in high esteem by biologists of all schools, comes, in one of his latest writings, to the conclusion that without inherited variations 'Selection would have no hereditary influence.'[42] And so on.

VIII

The idea of Natural Selection apparently did not occur to Lamarck, although several passages in his works suggest that he had noticed the struggle for existence. As to the modern Lamarckians, while nearly all of them indicate the limitations of Natural Selection, they do not exclude its action

[37] M. Standfuss, 'Zur Frage der Gestaltung und Vererbung,' lecture before the Zurich Naturalists' Society , in January 1902. Zurich 1905 (separate reprint).

[38] *Handback der systematischen Botanik*, Vienna 1901 seq. I quote from Adolpha Wagner's *Geschichte des Lamarckismus*, Stuttgart 1909, p. 215.

[39] *Vorlesungen uber Descendenztheorien,* vol. ii., Jena 1908.

[40] 'The Inheritance of Habitat Effects in Plants,' in *Plant World*, xiv. 1911; analysed in *Botanisches Centralblatt*, Bd. Exxii. 1913, p.134.

[41] *Elemente der Exakten Erlichkeistslehre*, Jena 1909, pp. 308, 449 etc.

[42] 'The Genotype Conception of Heredity' in *American Naturalist*, xlv. 1911, quoted by Semon in *Verhandlungen des Naturforschers-Verein in Brunn,* vol. lxix.

form their schemes of Evolution. The only object to the exaggerated part attributed to it by those whose conceptions of descent are influenced by their sociological or super-natural considerations; and they understand that Natural Selection surely gives stability to the effects of the Direct Action of Environment. Most of them also recognize that by the side of these two main factors of Evolution one must take into consideration the two aspects — individual and social — of the struggle for life, the development of protective instincts in the higher animals, and the effects of use and disuse of organs, crossing, and the occasional appearance of more or less sudden variations — all these having their part in the evolution of the unfathomable variety of organic forms.

Among the modern biologists, Professor Plate has perhaps best understood the necessity of a synthetic view of the factors of Evolution, which he has developed in his elaborate work, now known under the title of *Selektionsprinzip*. He examined first in detail the scope and the possibilities of Natural Selection under the different forms of the struggle for life; and after having shown that Natural Selection steps in where the Lamarckian direct adaptation fails, and that single-handed it would not be sufficient to solve the problem of the origin of species, Professor Plate sums up his opinions in the following lines, which, in the present writer's opinion, are a fair statement of the case:

The only real difficultly for Darwinism is [he writes] that the variations must attain a certain amplitude before they are 'selection-worth' — that is, before they give to Selection the opportunity to step in. Minimal individual differences can call forth no selection. However, I have shown already at some length (pp. 109–179) that after a careful study of the problem this difficulty proves to be illusory, because, on the one hand, it is impossible to deny that there are variations worthy of being selected,[43] and on the other hand there are in Nature different ways for increasing the minimal differences, so that they do become worthy of selection. Of these different ways, the modification of function, the changes in the conditions of life, use and disuse, and orthogenesis enter into the category of the factors indicated by Lamarck, and therefore the Selection theory cannot refuse the collaboration of the Lamarckian factors. Darwinism and Lamarckism,[44] taken together, give a satisfactory explanation of the growing up of species, including the origin of adaptation, while neither of these two theories, taken separately, gives it. (*Selektionsprinzip*, pp. 602–603.)

Let me only add, to avoid misunderstandings, that the Lamarckism of which I have spoken in these pages, and which Plate has in view in the just-given quotation, means the teachings of Lamarck as they appeared in his *Philosophie zoologique*, his remarkable *Discours d'ouverture de l'an X et de l'an XI*, delivered at the Academy of Sciences at Paris, and his *Systeme analytique des connaissances positives de l'homme* — of which the last two are entirely ignored in this country, and the first is frequently misquoted. These teachings show that Lamarck had not the least leaning toward a metaphysical *Natur-Philosophie*, and they have nothing to do with the vitalist and other theories of the German Neo-Lamarckians, of whom France (a distinguished botanist) and Dr. Adolph Wagner are prominent representatives.[45]

A synthesis of the views of Darwin and Lamarck, or rather of Natural Selection and the Direct Action of Environment, described by Spencer as Direct and Indirect Adaptation, was thus the necessary outcome of the researches in biology which have been carried on for the last-thirty or forty years. If considerations lying outside the true domain of biology, such as those which inspire the

[43] One must however ask whether such sudden variations appear in sufficient numbers? — P.K

[44] 'I mean, of course [he adds in a footnote], only the causal-mechanical part of Lamarckism, not its auto-genetical and psychical ideas. See pp. 501, 504.'

[45] See R.H France, *Der heutige Stand der Darwin'schen Fragen*, Leipzig 1907; and Dr. Adolf Wagner, *Geschichte des Lamarckismus*, Stuttgart 1909.

Neo-Lamarckians and inspired Weismann, cease to interfere, a synthetic view of Evolution (in which Natural Selection will be understood as a struggle for life carried on under both its individual and its still more important social aspect) will probably rally most biologists. And if this really takes place, then it will be easy to free ourselves from the reproach which has been addressed to nineteenth-century science: the reproach that while it has aided men to liberate themselves from superstitions, it has ignored those aspects of Nature which ought to have been, in a naturalistic conception of the universe, the very foundations of human Ethics, and of which Bacon and Darwin have already had a glimpse.[46]

Unfortunately the vulgarisers of the teachings of Darwin, speaking in the name of Science, have succeeded in eliminating this deeply philosophical idea from the naturalistic conception of the universe worked out in the nineteenth century. They have succeeded in persuading men that the last word of Science was a pitiless individual struggle for life. But the prominence which is now beginning to be given to the direct action of environment in the evolution of species, by eliminating the Malthusian idea about the necessity of a competition to the knife between all the individuals of a given species for evolving new species, opens the way for quite different comprehension of struggle for life, and of Nature altogether.

P. Kropotkin

[46]Cf. 'The Morality of Nature,' in *Nineteenth Century*, March 1905.

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The Direct Action of Environment and Evolution

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