THE DIRECT ACTION OF ENVIRONMENT ON PLANTS

THE great question which now above all others interests the biologists and divides them into two camps is the question of the relative importance of Natural Selection on the one side, and the Direct Action of environment on the other side, in the process of evolution of new species. We know Darwin's position and his conception on the dominant part of Natural Selection. But his views did not remain unaltered, and we saw in a previous essay[1] how Darwin himself, especially when he went into the details of variation in domesticated plants and animals, was brought to make some concessions. He began to doubt the adequacy of Natural Selection alone, and to assign more and more importance to the Direct Action of surroundings, which his precursors—Buffon, Lamarck, Geoffroy Saint-Hilaire, and Erasmus Darwin—had considered as the main factor of evolution. These are also the views which decidedly prevail now among biologists.

'Is it really sufficient,' they are asking themselves, 'that there should appear in a species of plants or animals an infinite number of purely accidental, individual variations in all possible directions; and out of this mass of slight, contradictory, fluctuating changes Natural Selection, in an acute struggle for life, will work out new varieties, and eventually new species, as perfectly adapted to their surroundings as if they had been the work of the surroundings themselves? Take any species of birds—for instance, the sparrows. Is it sufficient that there should be born, by mere chance, short-legged and long-legged sparrows, birds with shorter beaks and others with longer beaks, with smaller and with larger wings, light-coloured and dark-coloured, dull, bright, spotted ones, and so on—all in equal numbers each way, variation being supposed to be purely accidental, *indeterminate*, *i.e.* guided by no special cause one way more than another—and struggle for life will assort precisely those lengths of beak, legs, and wings, those

[1] *Nineteenth Century and After*, January 1910, p. 86 *sq.*

colours and those instincts which are best suited for making the sparrows thrive in given surroundings? Is it really enough that spots and markings of all possible colours and patterns should appear in a haphazard way? that the size, the form, and the inner structure of every organ, every muscle, every vessel and nerve, every bone, every tissue, should vary in every individual in all possible directions, by mere accident; and out of this lottery, which offers infinitesimally small chances of success for every separate character, Natural Selection will pick out and assort precisely those sets of tissues, vessels, bones, and nerves which answer best to the needs of adaptation? And if such a process may be imagined, does it really take place in nature? Is it true that variation is guided by no structural cause whatever, due to the conditions of life of the organism—that none of its possible causes ever prevails over the others?'

Is it not more consistent with modern observation and experiment to recognise that the variations which appear in a species at a given moment—being a combined result of the inherited *possibilities of variation* (determined by all the previous evolution of that branch of living beings) *and the modifying influences of a changing environment*—appear and accumulate in certain *definite* directions? And have we not reason to affirm that such a definite variation would be already an adaptation, just as in a tree that grows on the sea coast the prevailing winds check the growth of its branches on one side, and favour growth on the opposite side?

But if variation is not a mere accident due to a haphazard shuffling of cards representing thousands of inherited characters, if it is a result of the action of environment, then it is a *physiological fact.* It is due to certain definite causes—to changes in the food of the organism, in the composition of the inhaled air, in its temperature and moisture, in the amount of sunshine received. And each of these causes has definite effects on the composition of the blood of the animal or the sap in the plant, on the texture of the different tissues, on the anatomical structure and functions of each of the organs. Variation, in this case, loses its accidental character and emerges from the mysteries with which it was veiled. It becomes a subject of experiment, and many of the difficulties which stood in the way of the selectionist disappear.

To begin with, there is no need to assume that the very first beginnings in the variation of every organ are already so well pronounced as to have a 'selection value'—that they are already helpful in the struggle for life—as we are bound to assume if variation is accidental and is not reinforced gradually by the action of environment. A serious difficulty is thus removed, so serious that the best-informed Darwinists recognise it, even though they repudiate the exaggerations of Darwin's critics.[2]

We understand, moreover, why variation must be *cumulative*. If it is due to some definite cause, it is bound to accumulate so long as this cause lasts; while there would be no reason whatever to suppose that a character which appeared by mere accident in one generation should be reinforced in the next, since there is no external or inner cause to produce such an effect. Such a supposition is in fact contrary to all we know of accidental deviations, and is contradicted by research in that new branch of science, Biometry.[3]

And finally, we understand why variation must be *correlative*: why several organs should vary at once and support each other's variation—a fact quite general in nature, and yet representing one of the greatest difficulties for the theory of accidental variation. Thus if the wings of a group of birds are slightly increasing in consequence of increased exercise, supported by better food, we see the physiological cause of the increase; and we understand why all the muscles, the bones, the blood vessels, and the nerves connected with the wings *must* undergo a correlative development. Or, if the eyes of a cave animal, having become useless in the dark cave, begin to be atrophied, we understand how, the function of the eyes being performed no more, a physiological deficiency of the nerves leading to the eyes, of the blood vessels, and the muscles connected with them necessarily follows. We need not resort to an improbable hypothesis and maintain that those animals survive best which best realise an economy of their life-forces by rapidly getting rid of a useless organ, with its muscles, nerves, and blood vessels. The economy is usually too small to involve a life-advantage. The same is true of the correlative development of all the teeth of a mammal corresponding to a given change of its food; or the degeneration of the toes in the bovine race and the horses, and all those striking instances indicated by the American palæontologists, Cope and Marsh, showing how difficult it is to explain the correlative variation of several organs, both in development and degeneracy, so long as we do not recognise that variation is due to a definite action of the environment.[4]

[2] See, for instance, the discussion of this point by a well-informed Darwinist, Dr. L. Plate, in the third edition of his work (published now under the title of *Selektionsprinzip und Probleme der Artbildung: ein Handbuch des Darwinismus*, Leipzig, 1908, pp. 76-121), which can be recommended as a model of scientific criticism. Needless to say that, like his great teacher, Dr. Plate fully recognises now the importance of the direct action of surroundings, including, of course, the hereditary transmission of the so-called 'acquired' characters.

[3] Cf. *Nineteenth Century and After*, January 1910, p. 105.

[4] Part II. ('The Causes of Variation') of the admirable work of Professor E. D. Cope has become so classical that it hardly needs a special mention. Suffice it to say that his chapter on 'Physiogenesis' (modification by physical causes) and especially the chapter on 'Kinetogenesis' (effects of use and disuse), which contains

It is self-evident that those biologists who recognise the dominant influence of a direct action of environment do not necessarily deny the intervention of Natural Selection. On the contrary, they fully recognise its usefulness as an auxiliary. They only limit its powers. It ceases to be a selection of haphazard variations—necessarily indifferent in most cases in their incipient stages—but becomes a physiological selection of those individuals, societies, and groups which are best capable of meeting the new requirements by new adaptations of their tissues, organs, and habits. It is not so much a selection of individuals as a selection of groups of individuals, modified all at once, more or less, in a given direction. It is also, in the animal world, a selection of those who best exercise their collective intelligence for the diminution of inner competition and inner war, and for the rearing of their offspring by combined effort. And finally, as it does not depend upon an acute struggle between all the individuals of a group, it does not require for its full action those exceptionally bad seasons, droughts, and times of calamities which Darwin considered as especially favourable for Natural Selection. It goes on in times of plenty as well as in times of scarcity, especially in times of plenty and during the good seasons, when an abundance of food and vitality favours variability, and gives a certain plasticity to the organisms. Progressive evolution becomes thus comprehensible, and our hypotheses meet what we really learn of variation and evolution in nature.

In short, many serious difficulties which beset the way of the selectionist disappear, and we feel no more the need of the many hypotheses made by the Neo-Darwinists in support of Natural Selection, once we see in it but an auxiliary to the direct action of environment. Let us examine, then, how far such a view is borne out by modern research.

I

Already in Darwin's lifetime the investigations he was making and those to which his work had given birth induced him to recognise the importance of the direct action of environment. He only added—and his excuse was, of course, absolutely true—that at the time he wrote his *Origin of Species* the researches which proved the importance of this cause did not exist. Now, the amount of work already done in that direction is immense and its bulk increases every year. At Vienna we have now a special

the analysis of the origin of the osseous tissue in the vertebrate animals, the moulding of the articulations, the origin of the different types of foot in mammals and of their dental types, remain models of truly scientific analysis in support of the Direct Action of environment and the impossibility of explaining these structures by Natural Selection.

physiological laboratory established for the study of the different agencies—food, temperature, light, &c.—which alter the inner structure and the forms of living beings; and a special review was founded in Germany for the sole purpose of dealing with the same subject.[5] Two new branches of science, experimental morphology and experimental embryology, have grown up lately, and every year there appears some fundamental work devoted to the general position of Darwinism and Lamarckism.[6]

A good-sized volume would be required merely to sum up the results of the modern experimental researches into the direct action of environment upon plants and animals. Consequently, beginning with plants, I will mention here but some of the most convincing of these researches. Let me only remark at once that the character of such investigations has quite changed of late. Formerly the explorers directed their chief attention to changes in the *forms* of organisms, which could be obtained experimentally. The biologist continued, so to say, in his laboratory the work of the practical grower or the breeder. But now the inquiry goes deeper. It becomes a physiological investigation into the substance and the causes of variation. Variation is treated as a branch of plant or animal physiology and histology, and it is thus studied in the only proper way which is capable of revealing its causes and throwing light upon the much debated question as to whether variation, acquired by one generation, is transmitted to the next, and how the transmission takes place.

[5] *Archiv für Entwicklungsmechanik.* Having lately gone through the recent literature of the subject, I found that I had to examine the contents of more than two hundred memoirs and works, chiefly experimental, published during the four years 1906 to 1909. And yet the American literature was far from being fully represented.

[6] Besides the works of Professor H. W. Conn (*The Method of Evolution*, New York, 1900), R. H. Lock (*Recent Progress in the Study of Variation, Heredity, and Evolution*, London, 1906), and H. de Vries (*Die Mutationslehre*, Vol. I.), which I have mentioned previously, the following must be warmly recommended to the general reader: *The Primary Factors of Organic Evolution*, by Professor E. D. Cope, London and Chicago, 1896; *Darwinism To-day*, by Professor V. L. Kellogg, New York, 1907; *Les Théories de l'Evolution*, by Professor Yves Delage and M. Goldsmith, Paris, 1909; and the third, much enlarged edition of Dr. L. Plate's work, now entitled *Selektionsprinzip und Probleme der Artbildung: ein Handbuch des Darwinismus*, Leipzig, 1908: all four full of facts and ripe thought. So many side-issues have been introduced into the subject of Evolution, and so much that is purely dialectic has been dragged into the discussion, that a substantial portion of these works is given to heredity and the discussion of the rapidly altered and readjusted hypotheses of Weismann and his 'Neo-Darwinist' followers, as also to the sudden 'mutations' observed by de Vries, in which some naturalists saw a rival to, and some others a support of, Darwinism; to the rules of hybridism discovered by Mendel; and to the half-mystical reasonings of Pauly. In some modern works, and especially in R. H. Francé's *Der heutige Stand der Darwin'schen Fragen*, Leipzig, 1907, one will find, by the side of serious scientific analysis, a large tribute paid to the metaphysical and half-mystical views of some German biologists who try to revive the Hegelian *Naturseele*, in order to explain evolution, and most improperly describe themselves as 'Neo-Lamarckians.'

It would be needless to repeat what has been already said in the pages of this Review in my 'Recent Science' articles about this important category of researches in the domain of plant physiology.[7] One illustration only—the experiments of Professor Gaston Bonnier—I shall have to repeat; and, with a couple or so of examples taken from more recent works, this will do to show the bearing of all similar investigations upon the question which we have in view. Let me only remind the reader that we have in this domain such capital investigations as Rauwenkof's, Koch's, and Batalin's into the influence of light upon the structure of the cells; the modification of aërial stems and their inner structure obtained by Constantin by cultivating them in the ground; and especially the extensive researches of Stahl, Dufour, Pique, Surozh, Vesque, and Viet, and many others, some of which will be mentioned presently, into the changes of form, colour, hair-growth, and tissues of the leaves, according to the amount of sunlight and moisture they receive. All these researches, undertaken without any preconceived idea—as mere contributions to different chapters of plant physiology—prove nevertheless that most plants suit their environment so well only because environment itself has produced their actual forms. Let us then cast a glance upon some such instances.

We all know that the plants of the Arctic regions, as also the plants growing at high altitudes in the Alps, the Pyrenees, the Himalayas, the mountains of Borneo, and so on, have certain characters in common which compel botanists to describe them as separate varieties, sub-species, and even separate species, quite distinct from their next of kin growing in the lowlands of the temperate zone. As a rule, both the Arctic and the Alpine plants are often dwarfed, their main stem is often arrested in its growth, and a rosette of radical leaves only is formed. If there is a stem, the leaves upon it are usually crowded and reduced in size; the flowers, too, have shorter stalks, but they are often more brilliant and fragrant. Altogether, the plant has a 'tufted,' compact aspect and is often covered with hairs.

Now all these Alpine characters were obtained experimentally by a member of the Paris Academy of Sciences, Gaston Bonnier. Taking several plants from the valley, and dividing each of them into two parts, he planted one part in the valley and the other in a protected place at a high level. Two or three years later both sets of plants were compared, and the results were striking. Without the slightest interference of natural selection, Alpine varieties were obtained out of the plants of our valleys. Taking,

[7] *Nineteenth Century*, April 1894, pp. 684-691; and September 1901, pp. 423-437.

for instance, a common inhabitant of our meadows, the rock-rose (*Helianthemum vulgare*), with its slender stalks bearing each a pretty flower, the same plant became at an altitude of 6660 feet a thickly interwoven, shapeless ball of leaves, out of which ball protruded tiny star-like flowers with narrow petals. It certainly could be described as a distinct variety, and probably would have been described as a separate sub-species if it had been found in Laponia or in the barren lands of Canada.[8]

As a rule, in all plants grown at the high-level stations the internodes were short, the leaves were smaller and thicker, and when the plants were not placed too high, their flowers were more brilliant in colour and more fragrant than those of their congeners in the valley. An anatomical examination of their tissues proved that in the Alpine surroundings they had taken such characters as to reduce transpiration, and especially waste, obtain a better assimilation, and store more starch, more sugar, more volatile oils, and more colouring pigments. They were thus adapted, without the aid of natural selection, by the action itself of the surroundings, to take better advantage of the short Alpine summer, and better to resist its cold nights and blighting wind.[9]

In order to be still more sure of his results, Professor Bonnier made further experiments. He grew plants in boxes, wherein artificial surroundings of heat, cold, and moisture were maintained. The results were still more striking. When the plants were submitted during their growth to extremes of temperature and moisture—as is the case in an Alpine climate—they took, after only two months, the above-mentioned Alpine characters, including even the reddish colour of the leaves, due to the presence of a special colouring matter, anthocyan.[10]

At the same time the opposite results were obtained when seeds of germander (*Teucrium*), gathered at an altitude of 5000 feet in the Pyrenees, were sown near Paris. They gave, after three years, plants with longer stems and longer internodes, leaves of a brilliant green, and so on—plants, in short, quite similar to those which grow wild in that neighbourhood. In the surroundings of the low plains Alpine seeds thus gave plants bearing the character of lowland vegetation—this experiment being a reply to those who

[8] De Vries, in his *Mutationstheorie*, I. 102, has reproduced the photographs of the mother-plant and its Alpine variety.

[9] G. Bonnier, 'Culture expérimentale dans les Alpes et les Pyrénées,' in *Revue générale de botanique*, 1890, p. 213; 'Recherches expérimentales sur l'adaptation des Plantes au Climat alpin,' in *Annales des Sciences naturelles, Botanique*, 7e série, 1894, t. xx. p. 217; *Recherches sur l'Anatomie expérimentale des Végétaux*, Corbeil, 1895, with plates.

[10] *Comptes Rendus* of the Paris Academy of Sciences, 1898, t. cxxvii. p. 307; 1899, t. cxxviii. p. 1143.

had objected that Bonnier's plants, in taking an Alpine character, were probably 'reverting' to an ancestral form.

Taking next forty-three different species from Fontainebleau, and growing them at La Garde, near Toulon, Professor Bonnier obtained on the coasts of the Mediterranean—in the first, and still more so in the second generation (the characters acquired in the first generation being thus transmitted by heredity to the next, to be further increased)—plants with a distinct Mediterranean aspect: woody stems, broader and thicker leather-like leaves without nerves. The Fontainebleau Ragwort Senecio (*Senecio Jacobæa*) took several of the characters of the Mediterranean species *Senecio nemorosus*. Our common ash (*Fraxinus excelsior*) became similar to the ash of the Mediterranean coasts, *Fraxinus parvifolia*, and so on.[11]

I have dwelt on purpose upon these experiments, as they represent a complete cycle of researches the accuracy of which has been recognised by competent botanists, while at the same time they contain replies to the usual objections: 'reversion to ancestral types,' 'non-inheritance of acquired characters,' and the like. The characters acquired in one generation *were* transmitted to the next; and those characters which are described as 'hereditary' were as liable to vary as those which are described as 'acquired.' All we can say of these experiments, and all the others to be mentioned presently, is that those characters which had been maintained during a very long period of evolution (in our case, those of the Helianthemum *genus* and those of the Cistaceæ *family*, to which it belongs), being of a more ancient descent than those of the different *species*, have more stability than the latter.

The great value of the experiments of G. Bonnier is generally recognised. Still, in the last edition of Dr. Plate's excellent work on Darwinism we find the remark that, after having considered first the experiments of Bonnier as conclusive, Dr. Plate began to doubt lately,

> whether in this case, as in the case of adaptation of mammals to life at a high altitude, there were not set free such reactions only, which occasionally will take place in the lowlands. If I nevertheless accept the possibility of direct adaptation [Dr. Plate continues], it is because, according to the rules of probability, the variations due to mechanical causes may also occasionally happen to be useful.[12]

That the variations which took place in Bonnier's plants at a high altitude should belong to the category of those which take place *accidentally* in the lowlands as well, seems extremely unlikely, and remains a mere guess. Wherever changes *in the same direction* (though to a smaller extent) take place in the lowlands, we are sure

[11] *Comptes Rendus*, 1899, t. cxxix. p. 1207.
[12] *Selektionsprinzip*, p. 436.

to find some causes at work similar to those which exist in the high altitude surroundings, though on a smaller scale. This would be just one of those cases which Lamarck mentions, speaking of variation in a meadow plant.[13] Still less probability is there in Dr. Plate's suggestion, since we know from a later communication of Bonnier to the Academy of Sciences[14] that the morphological variations in his plants were brought about by variations of their inner structure, and therefore by no means can be described as *accidentally* useful. The diminished surfaces of transpiration and the shortened stems were the necessary results of the Alpine surroundings; the increased storage of starch and sugar was due to the long hours of intense light; and so on. None of these changes was accidental. That so serious and impartial a thinker as Dr. Plate is should have conceived such doubts seems to me probably due to the fact that at the time he wrote he did not yet know Bonnier's later work on the anatomy of his Alpine plants.[15] Besides, like all the recent writers on Darwinism and Lamarckism, he has chiefly studied variations in animals, while it is for variation and adaptation in plants that we have the best experimental data.

II

Taking now another series of experiments, made by H. Klebs, we learn how and why not only the lower plants—fungi and algæ—but also the flowers of the higher plants are altered under the influence of surroundings in their form, their size and colour, the number of their different parts, and their disposition (the inflorescence). A change in the food, or in the temperature and the moisture of the air, in the amount or even in the colour of light received by the plant, alters all the characters of the flowers.

If the common nettled-leaved *Campanula* be submitted to a high temperature during the winter, its usually blue bell-flowers turn to white. The cause of it is, that the stem grows faster under the influence of a raised temperature, and for its forced growth it absorbs a considerable amount of food. But the intensity of light is relatively small during the winter in our latitudes, and therefore the formation of food-stuffs is slow within the plant; the result

[13] *Philosophie zoologique*, edit. 1907, p. 44.

[14] 'On the anatomical and physiological characters of plants rendered Alpine by means of an alternately changing temperature,' in *Comptes Rendus*, 1899, t. cxxviii. p. 1143.

[15] From Dr. Plate's most conscientious list of the works which he has consulted, or only knows in abstracts, we see that he knows only the first two works of Bonnier—of 1890 and 1894—the first through De Vries. In the first edition of his work (made in 1890) he did not yet speak of Bonnier's experiments.

is that the colouring matters of the flower, which require sugar for their formation, are not prepared in sufficient quantities. The flowers become paler and often smaller than usual. Something similar happens also with the red primula. The usual equilibrium between the supplies of heat and light being broken, the effect is the same.

Taking next various species of *Sempervivum*, which belongs to the thick-leaved Crassulaceæ family and requires plenty of sunshine and a dry atmosphere for blooming, important changes were produced by altering these two conditions. The keeping of the plants in a warm temperature of from 85 to 89 degrees Fahrenheit, but in the dark, prevented them from blooming; and if they received afterwards a full light, the few flowers they produced were poor and of a lighter colour. On the other hand, the moment of blooming could be advanced by keeping the plants in a dry atmosphere and reducing at the same time the amount of food. By varying his experiments, H. Klebs altered at will the form of the plant, the forms of the flowers, the numbers of their separate parts, and the disposition of the flowers, *i.e.* the inflorescence, which often serves to distinguish species from each other.[16]

The conclusions drawn by Professor Klebs from his experiments are worthy of note.

> Under different conditions of life [he writes] independent variations take place on a large scale in all parts of the flowers. The sepals, the petals, the stamens, &c., all undergo variation. All the organs of a plant vary under the influence of the outer world, even when crossing is rigorously excluded. Even those characters which are constant under the usual conditions (the so-called 'organisation characters' of Naegeli) obey the same rule, provided the outer world acts at the proper moment. The distinction between the so-called 'constant' and the so-called 'variable' characters—those which are supposed to have been fixed by heredity and those which are not—disappears. *All* the characters of a species depend upon its inner structure, which depends in its turn upon the outer conditions; a change in the latter always produces a change in the former, which results in modifying the different *specific* characters of the plant.

Species, in Klebs's opinion, remain invariable so long only as the outer conditions are unchanged; and their variations are determined, on the one side, by 'the sum of potentialities' of the finest particles of their protoplasm and the action of environment. Let me add also that Klebs, in common with most plant physiologists who also speak from their own experimental knowledge, maintains that the anomalies of development due to a change of environment can be transmitted by heredity.[17]

[16] *Jahrbücher für wissenschaftliche Botanik*, 1905, Bd. xlii. pp. 155-320; Tobler's abstract in *Naturwissenschaftliche Rundschau*, 1906, xxi. pp. 254 *sq.* Also the Croonian lecture delivered before the Royal Society on the 26th of May, 1910.

[17] *Abhandlungen der Naturforschenden Gesellschaft zu Halle*, 1906, Bd. xxv. pp. 133 *sq.* In a second series of experiments the same explorer confirms

III

We have just seen that Professor G. Bonnier produced the 'Mediterranean characters' in plants taken from Fontainebleau which he grew on the Mediterranean coast. But the characters of maritime plants were also produced artificially by Lesage. One of the most typical features of maritime plants is that most of them have thicker leaves, due to a greater development of the palissade tissue (accompanied by a reduction of both the spaces between the cells and the empty spaces known as 'lacunae'). The fleshy character of the leaves is also met with in desert plants when they grow in a salty soil. Now, these same characters were obtained by Lesage simply watering our commonest plants with water containing some table-salt. The leaves of the common pea and the watercress became more fleshy and succulent under such a treatment, owing to an increase in the palissade tissue (the epidermis and the nerves of the leaves becoming only a trifle thicker); and these so easily 'acquired' features were transmitted by inheritance: plants grown 'from seed obtained from plants of cress which were somewhat succulent in the first year's experiment became still more so in the following.' [18]

Taking now another division of typical plants—the plants of the deserts and the sub-deserts, we see that the most characteristic feature, the spines and the prickles, can be produced artificially in a dry atmosphere; and, *vice versa*, they disappear when a desert plant is cultivated in a sufficiently moist air.

It will be remembered that Darwin considered the thorns and prickles borne by certain plants—especially by the desert plants —as a good proof of natural selection. In the plains peopled with large numbers of browsing animals, the more so in the arid plains where the grass is burnt in the summer, only those bushes and shrubs would have a chance of survival which had accidentally developed prickles and spines. True that the very fact of prickly plants being especially characteristic of dry and hot deserts suggested a causal connexion between the hot and dry atmosphere of the desert and the development of thorns and prickles; but so long as it was not demonstrated by experiment

his previous conclusions in these words: 'All the characters of a species, even those inherited characters which seem to have been quite firmly established, can be changed within certain limits by *influencing the potentialities of an organ at the moment of its formation.*'

[18] *Revue générale de Botanique*, t. ii.; *Comptes Rendus*, 1899, t. cix., and 1891, t. cxii. I quote this last passage from Rev. Geo. Henslow's *Plant Structures*, pp. 50 and 128-131.

that a dry atmosphere develops thorns, the hypothesis of natural selection seemed to be very probable. Now, we have such experiments.

Lhôtelier has demonstrated that if two stocks of barberry, the stems of which have been cut a few inches above the ground, are grown under two glass bells, one of which has a very dry atmosphere and the other a very moist one, two different sorts of plants are obtained. In the moist atmosphere all the leaves are fully developed, while in the dry atmosphere of the other bell the lobes of the leaves are not developed at all and their nerves become woody and are transformed into thorns.[19] The strong transpiration which takes place in a dry atmosphere reduces the formation of the tissues out of which the lobes of the leaves are formed, and it lignifies—*i.e.* makes hard and woody—the tissues of the nerves of the leaves. The surroundings themselves thus develop the thorns and the prickles.

The reverse experiment has also been made by W. Wollny. By growing various species in three different glass-houses, one of which was kept very dry, the other very moist, and the third of average moisture, he demonstrated that under the influence of great dampness the thorns of the common furze (*Ulex europæus*) were entirely transformed into full leaves.[20] Similar experiments were repeated more than once with the same result. Besides, we have the experiments of Marloth, which prove how easily all the traits which give the desert flora its special aspect can be obliterated. It was sufficient to transport plants from the sunburnt deserts of the Tangua Karoo to the less sunny and moister climate of Capstadt (where they still get 54 per cent. of the astronomically possible sunshine) to see them lose their desert features. Their globular shape and their dull or ochre colouring, due to a coating of wax, or gum, or to a thick coating of hair, disappeared. The *Crassula columnaris* lost its globular form and grew in the shape of a column; and the *Mesembryanthemum truncatum*, which is usually of an ochre colour, produced only green leaves at Capstadt. Other dull-coloured or grey plants of the desert were covered with a green foliage during the rainy season; but, having lost the protective epidermis and the special supplement of scales which they usually have in the desert, they were burnt during the dry season.[21]

A great amount of similar evidence could be produced. Hugo de Vries, who is an experienced botanist and grower, obtained two

[19] For more details see my 'Recent Science' article, *Nineteenth Century*, April 1894, p. 690.

[20] *Forschungen aus dem Gebiete der Agrikulturphysik*, Bd. xx. 1898, p. 397.

[21] R. Marloth, 'Die Schutzmittel der Pflanzen gegen übermässige Isolation,' in *Berichte der deutschen botanischen Gesellschaft*, Bd. xxvii. p. 362 *sq.* Also *Naturwissenschaftliche Rundschau*, 1909, p. 643.

quite different sorts of plants by cultivating the South African Compositæ, *Othonna carnosa* and *Othonna crassifolia*, in a moist and in a dry atmosphere.[22] From Rev. Geo. Henslow we learn that the *Zilla myagroides*, from the Cairo deserts, when it was raised from seed in the Botanic Garden at Cairo by Dr. Sickenberg, 'not only bore developed leaves, but the spines, though formed through the forces of heredity, were very slender and sub-flaccid, instead of being intensely rigid.' So also the ordinary spiny form of *Ononis* (*O. spinosa*), when it is grown either in a very rich soil with abundance of water, or in a moist atmosphere, gradually loses its spines. But they reappear as soon as the plants are allowed to grow in the ordinary way.[23]

Another feature characteristic of plants growing in the dry soil of the deserts and sub-deserts is the production of tubers and bulbs, which are storehouses of starch and sugar, and also apparently of water.[24] But this feature, too, disappears when the plant is cultivated in a moist soil. On the other side, Duchartre, by making tubers of the yam-plant (*Dioscorea Batatas*) produce long shoots without being allowed to have water, obtained that other feature of the desert plants: the hardening of the stem, due to a hardening of the walls of the fibres and a diminution of their inner diameters.[25]

I ought also to mention the varied and striking experiments of Vöchting, who, by varying the temperature and the amount of light given to a plant, obtained rampant varieties, maintained asexual reproduction, and so on,[26] as also many other similar experiments. In fact, a volume ought to be written on the subject which I am sketching in this article.

Suffice it to say in this place that we have now a considerable number of experimental works which did not exist when Darwin wrote his *Origin of Species*, but by means of which it has been established, beyond any reasonable doubt, that the adaptations of the inner structures and the outer forms of plants, which were a puzzle fifty years ago, must have been produced by the direct action of environment. And we have seen also in the above that the hereditary transmission of the so-called 'acquired' characters in plants has been proved in most cases by direct experiment.

[22] *Die Mutationstheorie*, Bd. i., Leipzig, 1901, p. 105, where the photographs of both series of plants are reproduced.

[23] Rev. Geo. Henslow, *The Origin of Plant Structures by Self-Adaptation to the Environment* (London, 1895), pp. 38-40.

[24] Such is, at least, the opinion of Dr. Volkens.

[25] *Plant Structures*, pp. 78, 79 and 42.

[26] *Jahrbücher für wissenschaftliche Botanik*, 1893, Bd. xxv. p. 149; *Berichte der deutschen botanischen Gesellschaft*, 1898, xvi. 37.

IV

With such an *experimental* knowledge as we possess now, the *observations* of botanists relative to the adaptations of plants to environment in different typical regions of the globe acquire a new meaning. They become a strong corroborative evidence in favour of the direct action of environment having itself produced these adaptations.

Let us take a concrete example to fix our ideas. Let us examine, for instance, the flora of the caverns as it appears from the investigations of M. Jacques Maheu, who has explored scores of caves, *gouffres*, and *avens* in France, in the German portion of the Vosges, in Belgium, and partly in Italy.[27] The flora of all these caverns originates from plants growing in the immediate neighbourhood, but all these plants are so modified in their new surroundings as to represent a special type of cavern flora. Want of light, a low temperature, extreme humidity, and a meagre calcareous soil are their conditions of growth; and all the cavern plants have acquired precisely those characters which one may have anticipated under such conditions, judging from the experiments of Dufour on the action of light,[28] and those abovementioned of Bonnier and Lhôtelier. Altogether, the cavern vegetation stands between the Arctic and the aquatic and is perfectly well adapted to its own special surroundings.

If we take now the classical work of Grisebach on the vegetation of the globe and examine the floras of different typical regions of the earth and their protective features, or if we study under the same aspect any one of the fundamental works on the flora of some typical region, we find the same coincidences between the local conditions and the adaptations of the vegetation to these conditions. The flora of the Arctic regions, of the high altitudes, the deserts, the sea coasts, and so on, have each their distinctive features, and these features are precisely those which we obtain experimentally if we take plants from the plains of Middle Europe and grow them in Arctic, Alpine, desert, or maritime surroundings. We may thus conclude that although these numerous coincidences between the characters of the plants and their environment are not yet *proofs* of those characters having been produced by the direct action of the surroundings,

[27] Jacques Maheu, 'Contribution à l'étude de la flore souterraine de France,' in *Annales des Sciences naturelles, Botanique*, 9e série, t. iii. 1906, pp. 1-190. The paper is illustrated by many drawings and contains a copious bibliography. The anatomical process of disappearance of the mechanical support tissue and the changes from sexual to vegetative reproduction are especially worthy of note.

[28] 'Influence de la lumière sur la forme et la structure des feuilles,' in *Annales des Sciences naturelles, Botanique*, 7e série, t. v., 1887, p. 311.

they establish, by their very number, a high degree of *probability* in favour of the hypothesis of Direct Action.

This is the thesis which G. Henslow develops in his work on plant structures,[29] and in support of which he brings forward a considerable amount of evidence. Taking first the desert and sub-desert vegetation, and next the Alpine, the Arctic, the maritime, and the aquatic vegetations, he shows that the same coincidences are found between these types of vegetation, the climatic conditions they belong to, and those plants which were obtained experimentally in conditions similar to those of the deserts, the high altitudes, and so on. And he concludes that these coincidences are so numerous that it would be contrary to all probabilities to attribute all these well adapted forms to an infinity of *indiscriminate, indefinite* variations out of which only those in harmony with environment have survived.[30]

It is very probable that his suggestion to the effect that there are '*no* indiscriminate and wasted variations at all' will not meet with general acceptance. Each plant is a complex result of all the modifications which its ancestors underwent during the long process of past evolution, and its possible variations are determined by all the past modifications. It seems difficult, therefore, to deny the possibility of indiscriminate variation, due to the inner causes of heredity. But once by the side of indiscriminate variation there is going on a process of *variation in a definite direction*, due to the direct action of environment, and the effects of this action are *inherited*, as we saw it proved more than once in the above-mentioned experiments—then the accidental variation is necessarily subordinated to the determinate one.

With this limitation, most botanists will certainly agree with the conclusions of Henslow—namely, that the facts he has brought together represent strong corroborative evidence in favour of the adaptations being produced by the direct action of the environment itself. They render this hypothesis so probable as to attain almost certainty.

And now I must mention a third vast series of researches, pursued for the last thirty years, into the effects of mechanical, electrical, and chemical irritations, as well as changes of light, tem-

[29] *The Origin of Plant Structures*, 1895.

[30] The question, Henslow writes, is this: 'Which probability or hypothesis do *the facts* of the case seem to favour most, viz. that *indefinite* variations arise from some assumed internal causes, of which variations only those in harmony with the environment survive, and are said, therefore, metaphorically to be selected by it; or is it that the external forces of the environment excite the variability which is inherent in plants, and call into action the responsive power of the protoplasm in the various species of plants, which thus *all* tend to put on the same, or similar, or at least adaptive and *definite* variations of one sort or another, so that there are *no* indiscriminate and wasted variations at all?' (Introduction, pp. 9-10).

perature, moisture, and composition of the air received by a plant, upon its physiological processes and the structure of its tissues. Here we have another immense array of facts which could be described as experimental anatomy, or experimental histology (the experimental science of the organic tissues), giving us a fresh insight into the inner life-processes which lead to changes of external forms.

Two or three examples chosen from a mass of material will do. Thus in an interesting little work R. Prein studied the effects of mechanical pressure upon the tissues of the roots (Bonn, 1908). We know what will happen if a growing root is passed through a glass tube which prevents it from increasing in thickness. Unless the tube be extra strong, it will be broken—the root creating a tissue strong enough to break the resistance. As the root continues to grow, and its cells continue to increase and subdivide, they exert a pressure upon each other where they meet with a mechanical obstacle, and this pressure stimulates further growth. The cells subdivide more rapidly and become more numerous, remaining smaller at the same time. The walls of the parenchym cells consequently grow thicker, especially those walls which run parallel to the lines of pressure, while those which are parallel to the surfaces of the glass tube grow thinner, or even disappear. The tissue of the root thus acquires a greater solidity. But as the transpiration current of the plant and the transport of assimilation products go on unabated along the root, the life processes are intensified in the compressed zone, and finally the growing root breaks the tube. Of course the formation of a more solid tissue may be described as an adaptation, but it is merely a small alteration of the process of growth, which has a purely mechanical cause. And we need not resort to heredity, or to natural selection, when we see that, as a rule, the roots grow harder in a hard soil, and their tissues become softer in a friable soil—a change, by the way, which has permitted our gardeners to obtain the eatable radish out of its wild ancestor.

The experiments of R. Hegler, showing that the application of artificial strains to seedlings provokes a remarkable development of the mechanical tissues of the seedlings, and those of Henslow, who obtained the same result with leaf-stalks of the horse-chestnut, belong to the same category.

A wide series and a great variety of researches into the effects of mechanical lesions upon growth, of different sorts of food upon the characters, both racial and specific, of carbonic acid and different narcotics upon the assimilation of oxygen, and so on, might be mentioned in this place. They would deserve mention the more so as from most of them we learn over and over again—in defiance of Weismann's hypotheses—that characters acquired in new conditions *are* transmitted by heredity to the offspring, and are retained by it for some time after the plant has been returned to its previous conditions. But another score of pages would be needed to do justice to these instructive and varied researches. So I shall limit my illustrations to one more—namely, the investigations made by Vöchting and Haberlandt for explaining the well-known capacity of the leaves in many plants for taking such positions as to receive more light in a direction perpendicular to the surface of their lobes.

It appears from the investigations of G. Haberlandt, who has worked at this subject for the last five years, that the cause of such changes of position of the leaf—so appropriate that they seemed to suggest a conscious will—lies in the structure of its epidermis. The latter contains a number of slightly swollen cells, which, being filled with sap, act as so many microscopic lenses for admitting light into the interior of the leaf. Haberlandt describes them even as *ocelli*, or eyelets, and compares them to the *ocelli* of some lower animals. This discovery having been contested, Haberlandt continued his researches, and it may be taken now as proved that it is really the direct action of the light falling on the epidermis, and transmitted through the small lenses to the protoplasm of the lobe, which produces a certain irritation in its tissue. This irritation is apparently transmitted further to the stalk (probably by means of the protoplasm filaments connecting the cells), and makes it alter the position of the lobe.[31] The same capacity of reflex action in response to light is well known in seedlings, in the inflorescence axis of the daisy and many other plants, as also in the eyes of animals. We do not know yet how it acts, but it requires no special act of volition.

Altogether we have in these and many similar researches ample proofs of the fact that many adaptive variations, which were a puzzle for the botanist, are direct results of purely mechanical causes due to the conditions of growth.

With these illustrations our series of evidence in favour of the direct action of environment, considered as the true cause of determinate variation, may be concluded. We took that evidence from three distinct domains: the experiments which show that all the typical characters of the different floras on the surface of the globe can be obtained experimentally by placing plants in the conditions of growth that are characteristic of the Arctic, the Alpine, the desert, the maritime, and the aquatic flora. We

[31] G. Haberlandt, *Die Lichtsinnesorgane der Laubblätter*, Leipsig, 1905; *Berichte der Botanischen Gesellschaft*, Bd. xxii. 1904, and xxvi. 1906; *Biologisches Centrallblatt*, Bd. xxvii. 1907; *Sitzungsberichte der Wiener Akademie der Wissenschaften*, Bd. cxvii. 1908; *Jahresbericht der wissenschaftlichen Botanik*, 1909. Good summing up, by O. Damm, in *Naturwissenschaftliche Rundschau*, Bd. xxiv. 1909, p. 389.

then rapidly passed in review the corroborative evidence offered by the typical representatives of each of these floras, whose inner structure and external forms always correspond to their conditions of life. And, finally, we took a few illustrations from a third, still wider domain of researches, which throw some light, by an anatomical study of the tissues and a physiological study of the different organs, on how it is that a given external cause, such as excessive evaporation or want of light, produces those morphological changes which counterbalance the noxious effects of this cause; how is established the equilibrium between cause and effect which permits plants to live in the sun-burnt dry deserts and in the over-moist, dark caves, by the side of the glaciers of Spitzbergen, and in the moist, tropical atmosphere of the coasts of the Malay Archipelago.

Going over these three categories of data, we have found that the environment, acting on the tissues of the plants, is capable of itself producing, and really produces, those features which render life possible in each of the just named conditions. Plants are so plastic that they respond at once to changed conditions of life.

Of course, it would be contrary to all our present knowledge to believe that natural selection has nothing to do with the evolution of new species. On the contrary, it has much to do to maintain in purity the races which undergo the necessary changes under the influence of the direct action of environment. But its chief function must be to weed out those individuals and races which have not enough vitality and enough plasticity to undergo the changes imposed upon them by a change of environment. The great difficulty which confronted biologists so long as they considered natural selection as the mainspring of evolution—namely, the accumulation of change in a given direction, if variation does not go itself in that direction under the influence of the surroundings—this difficulty, which Darwin saw very well and which no amount of speculation can remove, does not exist any more once we recognise that the main factor of all evolution is the direct action of surroundings, and agree to consider natural selection as an extremely useful but not unavoidable auxiliary.

V

Professor V. L. Kellogg, in his *Darwinism To-day*, makes the remark that if one carefully re-reads now the *Origin of Species* in the light of modern controversies, he will be astonished to see how often Darwin calls on Lamarckian factors of evolution to explain the difficulties met by the theory of Natural Selection.[32] That

[32] *Darwinism To-day*, 1907, p. 39, note. Professor T. H. Morgan seems to have made the same remark in *Evolution and Adaptation*.

there is much Lamarckism even in the first edition of the *Origin* was also Lyell's impression. In fact, determinate variation under the direct action of environment and the effects of use and disuse of organs are recognised in many places in the *Origin of Species*; still more so in the second volume of *The Variation of Animals and Plants under Domestication*, and in the seventh chapter of the sixth edition of the *Origin*, which was much modified by Darwin and partly written anew for that edition. About Darwin's later days' 'Lamarckism' there is no doubt; but what especially induced him to oppose Lamarck, apart from his personal predilection for Natural Selection, was, as we see from his letters, that Lamarck had spoken of a 'tendency to progression' and 'adaptation from the slow willing of animals.'[33] In such ideas Darwin probably saw a danger, as they were opening the way for teleological conceptions which might once more bar the way for a truly scientific study of evolution.[34]

It must be owned that so long as biologists studied chiefly the variations *of forms only*, and saw in variability a process due in the main to the obscure causes of heredity, there really was a danger of such an intrusion of teleological metaphysics into the theories of evolution. However, scientific research soon opened new channels. Variation having been taken in hand by physiologists and anatomists, they began to study how the different tissues of plants and animals and their functions are altered by changes in environment. And then we began to understand that what we described as 'adaptations' was nothing but changes produced *in the organs and the intimate structure of tissues by the altered surroundings themselves*. An increased or diminished assimilation, a greater or smaller activity in the preparation of the food reserves in the organism, a change in the composition of the sap of the plant or the blood of the animal—changes, in short, in the physiological processes, due to the action of the external conditions of life—these, we learned, are the real causes and the true components of variation. And, having learned that, we began to understand *how* the external agencies *can* produce in the organism those changes which already are protective adaptations.

It is self-evident that the protoplasm of the plants is not

[33] Cf. *Nineteenth Century and After*, January 1910, p. 90 and note.

[34] If it is well worth re-reading now the *Origin of Species* in the light of modern discussions, it is equally well worth while to re-read Lamarck's *Philosophie zoologique* in the same light. One is struck on reading it now to find how much of the future work of Darwin, especially on domesticated plants and animals and modern biology altogether, was outlined by the great French zoologist (see pp. 190-194, 200-201 of the new French edition by Schleicher frères, Paris, 1907). One sees also that the idea which he attaches to 'progression' in the development of new forms of organisms is nothing but the idea which Spencer and Darwin attached to 'evolution'—that of a growing complexity of organisation—the '*composition croissante*' (p. 187; the whole passage must be re-read).

possessed of any unknown, mysterious capacity of answering irritations from the outside by corresponding 'adaptations'; but it undergoes under the action of the external forces some changes in its activity which permit the life-processes to go on with the greatest possible intensity under the new conditions to which the plant is exposed. It is these changes in the life of the protoplasm which result in so-called 'adaptive' changes in the tissues, which produce, in their turn, the 'adaptations' of form and functions of the different organs to the requirements of a new environment. This is the main substance of what we know as 'variability.'

In short, botanists acquire more and more the certitude that all the changes taking place in plants when they are placed in new surroundings can be explained, as Lamarck foresaw, by the action of the physical and chemical forces affecting their tissues. Of new 'unknown' or 'unknowable' forces they feel no need. Therefore, if Darwin's fears are justified, since a number of biologists with a metaphysical turn of mind—known as 'Neo-Lamarckians'—appeal to a Hegelian *Naturseele* in order to explain evolution, Lamarck is as little responsible for such a misreading of his work as Darwin is for the doctrines which preach mutual extermination in the name of 'Darwinism.' The reality is, that, on the contrary, those biologists who went deepest into the ideas, and especially those botanists who went deepest into the matter, do not feel the need of any other causes for explaining adaptations, and evolution altogether, but those causes which they see at work, the phenomena of growth.[35]

This is the lesson we learn from the plants. As to the animals' response to their environment, it must be discussed separately on some future occasion.

P. KROPOTKIN.

[35] As to the exaggerated 'interference of the animal's will in the formation of new organs,' of which metaphysically inclined writers have lately tried to make so much, Lamarck distinctly said (in chapter vii., devoted entirely to variation) that variation in plants is fully due to change in food, in absorption and transpiration, and in the quantities of heat, light, air, and moisture received. 'Plants have no will.' And as to animals he insisted, repeating that it is only in insects and the classes superior to them that 'sensation and effort,' originated from a need, can be effective in producing new *habits* which will contribute to modify structure—it being the function which creates the organ, not the reverse. Altogether, I am much inclined to think that it is the vulgarisers and commentators of Lamarck who have especially contributed to create a prejudice against him. It is his works that must be read—in the original if possible (his French terms requiring a cautious translation). Let us add that one ought to read also the last work of Lamarck, *Système analytique des Connaissances positives de l'Homme*, before speaking of his philosophical conceptions. Unfortunately, this work exists only in very few copies, of which the British Museum has one. I learned of it through the Russian translation, by Professor Lesshaft, in the *Izvestia* (*Bulletin*) of the Biological Laboratory of St. Petersburg, vols. iii. and iv., 1899 and 1900.