THE THEORY OF EVOLUTION AND MUTUAL AID

In a series of articles, published originally in this Review and reproduced since with additional matter in book form,1 I endeavoured to show the importance of sociability and habits of mutual aid in the evolution of both the animal world and the human race. Later on, in an essay, 'The Morality of Nature,'2 I examined the influence which sociability and mutual aid, representing a dominant feature in the life of animals, must have exercised upon the development of the first ethical conceptions of our earliest human ancestors, at a time when they were living in close contact with Nature. I spoke also in this essay of the remarkable attempt made by Darwin to explain the origin of the moral sense of man by a general prevalence, among sociable animals, of the social instinct over the individual instinct.

This essay was an introduction to a study of the growth of ethical ideals in mankind from those modest beginnings to the great heights reached in the course of history. It appears, however, that before proceeding further with such a study it is necessary to clear up a certain misunderstanding. There is not the slightest doubt that the hesitation of many biologists to recognise sociability and mutual aid as a fundamental feature of animal life is due to the contradiction they see between such a recognition and the hard Malthusian struggle for life which they consider as the very foundation of the Darwinian theory of evolution. Even when they are reminded that Darwin himself; in the Descent of Man, recognised the dominating value of sociability and ‘sympathetic’ feelings for the preservation of species, they cannot reconcile this assertion with the part that Darwin and Wallace assigned to the individual Malthusian struggle for individual advantages in their theory of Natural Selection.

It is useless to deny that a certain contradiction exists. If a

1 Nineteenth Century, September and November 1890, April 1891, January 1892, August and September 1894, January and June 1896; Mutual Aid: a Factor of Evolution, 1902 (Heinemann).
2 Nineteenth Century and After, March 1905.

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strenuous Malthusian struggle for food and for the possibility of leaving progeny is carried on within each animal group to the extent admitted by most Darwinsians (which must be admitted if the natural selection of individual variations plays the part that is attributed to it), then it excludes the possibility of association being a prevalent feature among animals. And, *vice versa*, if association prevails in the animal world to the extent we see it depicted in the works of our best field zoologists—the very founders of descriptive zoology: Pallas, Azara, Rengger, Audubon, Naumann, Prince Wied, Brehm, &c.; if sociable feelings among animals are so developed that they fight in common their enemies, send out scouts before repairing to their feeding grounds, keep sentries, protect the retreat of their herds, and so on, up to self-sacrifice in the interest of the group—then struggle for life cannot possibly have the aspect of an acute inner war within each tribe and group. It cannot be a struggle for *individual* advantages. It must be an *associated* struggle of the group against its common enemies and the hostile agencies of environment. Natural selection in this case also takes a quite different aspect.

The contradiction must therefore be cleared up; and the only way to do it is to examine the gradual evolution of Darwinism since the appearance of the *Origin of Species*, and to see what ideas prevail now as regards the part of Struggle for Life in the present conceptions of evolution.

The subject is immense. So let us limit it, always keeping in view our special point: the place of Mutual Aid and of Struggle for Life in the theory of evolution. For that purpose we will examine, first, the evolution of Darwin's ideas as it appears from his voluminous correspondence; we shall see how, after having himself indicated the three different aspects which Struggle for Life may take in Nature, he gradually came, in an indirect way, to attribute less and less value to the *individual* struggle inside the species, and to recognise more significance for the *associated* struggle against environment; and next we shall have to see how the mass of experimental researches made within the last twenty-five years about the influence of surroundings upon the forms of plants and animals, has modified opinion in favour of the direct action of environment, which lays much less stress on struggle for life as a species-producing agency than is required by the theory of Natural Selection.

I

When Darwin began to think about the variability of species, the dominant opinion in academic circles, especially in this country, was entirely in favour of immutability. To believe that species
could vary otherwise than temporarily, and that two or more species might have descended from common ancestors, was a heresy sufficient to destroy for ever the reputation of a man of science. Even the more courageous thinkers, like Huxley, feeling that once they admitted doubt about immutability they would have to go to the end, preferred to retain an attitude of scepticism and not to touch this subject at all. ‘It is like confessing a murder,’ Darwin wrote to Hooker in 1844, when he told him that he was almost convinced that species are not immutable, and that, after a good deal of reading, he thought he had ‘found out (here’s presumption!) the simple way by which species become exquisitely adapted to various ends.’

Under such conditions, the main point for Darwin was to demonstrate, first, that there are no immutable species: that all of them give birth to countless variations which can be transmitted to the offspring. Once variability could be proved to that extent, the study of it would reveal those natural causes which are capable of giving stability to certain variations, and of transforming temporary varieties into those more stable forms which we describe as species. To study, then, the variations of domestic animals obtained by our breeders was an excellent way of attacking the prejudice of invariability. This is what Darwin did. He collected an immense mass of data showing that amid the domesticated animals accidental variation continually goes on in all directions, to a degree quite unsuspected by men of science.

The next step was to suppose that a similar variability exists among the wild animals as well, and that there goes on in Nature, under certain conditions, a process of selection similar to the selection resorted to by the breeders. Variability in the state of Nature being proved in its turn, there would remain only the necessity of finding a substitute in Nature for the breeder’s conscientious choice of certain forms in preference to others. Malthus’s Essay on Population, which Darwin came across in 1838, supplied him, as is known, with a possible cause for natural selection. It was ‘struggle for life’—the survival of the fittest.

Plants and animals, he reasoned, breed in such proportions that if a considerable portion of those that are born every year was not exterminated, every square mile of the earth’s surface would soon be peopled with far more living beings than it could ever support. There must be, therefore, a violent ‘struggle for existence’ between the competitors, before a considerable

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number of them succumb; and during this struggle those which are less suited to their conditions of existence will be eliminated, while the best suited will survive. These last will leave more progeny, and in the subsequent generations those variations which had helped the parents to survive will go on increasing in the same direction, owing to a continued selection of the fittest. This double process of elimination and survival he described as natural selection. It plays in Nature the same part as the breeder plays among the domesticated animals with an artificial selection guided by his taste or fancy.  

If the external conditions change at the same time—so much the better, because there will be a greater number of variations to choose from (changing conditions increase the tendency to vary) and a greater number of competitors—the birth-rate often increasing in new conditions. Consequently there will be a sharper struggle for life and a better selection.

This was, then, the so often misunderstood substance of Darwin's ideas. 'Variability and Natural Selection.' The one supplying the material for selection, and the other giving a certain fixity to those variations which are useful for a given portion of the species under its actual conditions of existence. Of these two elements the first, i.e. Variability, was amply proved by the immense mass of facts collected by Darwin. As to Natural Selection, it was offered as a working hypothesis only, which had to be tested before it should be accepted as a probable theory—this being the usual way in inductive science. Darwin's hypothesis had, however, a great advantage. It explained the wonderful adaptations of animals and plants to their surroundings, which had always been a puzzle for all observers of Nature, and it was free at the same time both from a supernatural, teleological intervention, and from all metaphysics. Such metaphysical 'words' as 'the conscious adaptation of the organism to its surroundings,' which Lamarck had introduced, in addition to the effects of use and disuse of different organs, disappeared. The hypothesis of natural selection permitted the explorers, whom it invited to enter a new field of research, to study and to group the facts, and thus to discover those other natural causes besides the

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5 At the outset, A. R. Wallace remarks, no discrimination was made between natural preservation, which is the true domain of natural selection, and 'selection' properly speaking. A great deal of confusion resulted therefrom. (See Darwinism, an Exposition of the Theory of Natural Selection, with Some of its Applications, 2nd edition, London, 1888.)

6 This was not always understood by the early reviewers of Darwin's work. 'Indeed,' he wrote, 'I have over and over again said in the Origin that Natural Selection does nothing without variability. . . . But I agree that I have somehow (Hooker says it is owing to my title) not made the great and manifest importance of previous variability plain enough.' (More Letters, i. 193; letter to Charles Lyell, August 21, 1861.)
natural selection of chance variations, which might also give the same wonderful adaptations of organic forms to an infinite variety of surroundings.'

It is certainly true that Darwin felt a sort of paternal predilection for his hypothesis of Natural Selection, and that he unduly minimised the direct action of separations upon the living beings. He openly acknowledged it later on. But one sees from his letters how anxious he was at the outset that his views on the origin of species should not be confounded with those of Lamarck, and still more so with the bold hypotheses that had been brought forward in the famous book, *Vestiges of the Natural History of Creation*, especially in its first edition. He was careful, therefore, to state that his views, although they led to similar conclusions of transformation, were widely different as to the means by which transmutation was achieved.

*Creation or Modification—that was for Darwin the main point.* 'I only mean change of species by descent. That seems to me the turning point,' he wrote to his friend Asa Gray even as late as May 1863. 'Personally, of course, I care much about Natural Selection; but that seems to me utterly unimportant; compared to the question of Creation or Modification' (*Life and Letters*, ii. 371). 'Indeed, I have never hinted,' he wrote to Hooker in 1860, 'that Natural Selection is the efficient cause to the exclusion of the other'—i.e. variability from climate &c. The very term *selection* implies something, i.e. variation or difference to be selected....' Many passages from his letters express the same idea.

Darwin knew perfectly well that Natural Selection was only an hypothesis, and that to be accepted as a theory it required two tests: its capacity of explaining a vast number of facts, including the difficult cases, and some proof to show that the processes it appealed to are really going on in Nature. And when one studies

... Speaking of Huxley's lecture, Darwin wrote to Hooker on the 14th of February 1860: 'He gave no just idea of Natural Selection. I have always looked at the doctrine of Natural Selection as an hypothesis which, if it explained several large classes of facts, would deserve to be ranked as a theory deserving acceptance; and this, of course, is my own opinion.' (*More Letters*, i. 120-140.)

... 'Heaven forbid me,' he wrote to Hooker in the already mentioned letter, 'from Lamarck's notion of a tendency to progression, 'adaptations from the slow willing of animals,' &c. But the conclusions I am led to are not widely different from his; though the means of change are wholly so.' (*Life and Letters*, ii. 40.)

*Life and Letters*, iii. 317. By 'Climate' Darwin understands in this and many other letters the sum of external physical conditions.

1 Speaking of Huxley's lecture at the Royal Institution, he wrote to Hooker (February 14, 1860) that he was glad to find that Huxley agrees with his manner of looking at the subject; 'only that he rates higher than I do the necessity of Natural Selection being shown to be a vera causa always in action' (*More Letters*, i. 140). 'It seems to me that an hypothesis is developed into a theory solely by explaining an ample lot of facts,' he wrote to Asa Gray in 1860 (*Life and Letters*, ii. 40).
his work and letters, one is really struck by the infinite pains he took to test the value of Natural Selection as an hypothesis capable of explaining the greatest imaginable variety of biological facts and the most complex problems offered by evolution.

As to the second of the tests to which an hypothesis has to be submitted—the extent of the processes it appeals to—Darwin apparently left it to the study he was going to make of Struggle for Life and Natural Selection in his great work on *Variation in the State of Nature*. This is probably why, in the *Origin of Species*, he gave, as proofs of an acute Malthusian struggle, only the arithmetical argument of possible—not actual—increase of animals, the fact of rapid increase of European species imported into other countries, and a paragraph of a few lines only containing a few indirect proofs, some of which appear now to be open to a different interpretation. He mentioned in the *Origin* (p. 50) the three different forms which struggle for life may take in nature, saying that 'there must be in every case a struggle for existence, either one individual with another of the same species, or with individuals of distinct species, or with the physical conditions of life' (*Origin*, p. 50); but he did not even try to discriminate between these three aspects of struggle, so widely different as to their consequences for the genesis of new species and for natural selection altogether. He left it for a future occasion. 'In my future work,' he wrote, 'this subject will be treated, as it well deserves, at greater length.' And we know from his letters that he tried to get information about the birds, in order to see whether the majority of the arithmetically computed competitors which disappear every year are not destroyed already in the eggs, or as fledglings, so as to deprive the struggle for life of its competitive character and render it entirely metaphoric. Unfortunately, he never terminated this part of his researches.

With his really wonderful powers of generalisation, Darwin had conceived the problem of evolution on such a wide scale that his work tended to become a synthesis of all biological knowledge. Besides variability and natural selection, he studied such wide branches as the evolution of instincts, sexual selection, the geologi-

Gray in 1869 (*Life and Letters*, ii. 286); and he enumerated the various groups of facts which Natural Selection could explain. Very similar views are stated by Huxley in the article he contributed to the edition of Darwin's letters: 'We wanted,' he says, 'not to pin our faith to that or any other speculation, but to get hold of clear and definite conceptions which could be brought face to face with facts and have their validity tested. The *Origin* provided us with the working hypothesis we sought' ('On the Reception of the *Origin of Species*, in *Life and Letters*, ii. 197).

cal proofs of evolution, the geographical distribution of organisms, spontaneous variations and hybridism, the effects of isolation, the collective instinct, the value of specific characters, and, finally, the immensely vast problem of heredity. After the publication of the *Origin of Species*, which was, as is known, but a summary of the great work he began in 1837, he took in hand its first part, *Variation of Animals and Plants under Domestication*, and this book came out so full of data in support of an unlimited variability, that after its appearance it was no longer possible to speak of immutable species, or of a preconceived plan in their variation.

After having spent a tremendous amount of labour upon this book, in which he introduced also his ‘Pangenesis’ theory of heredity, Darwin published one more summary of his great work: on the descent of man, including the origin of his intellectual faculties and moral sense, and on sexual selection. But in this way he never went beyond the first ten chapters—unfortunately, not yet published—of his great work on *Variation in the State of Nature*, in which he certainly would have dealt with Struggle for Life and Natural Selection with as much care as he had bestowed on artificial selection.

In the meantime Darwin’s health was failing, and he frequently complained in his letters of feeling unable to deal with such a vast problem as the relative value of the different factors of evolution. Since he had broken the spell of immutability, a legion of biologists had rushed to the study of a multitude of factors involved in evolution, and the more they advanced in their studies the more complicated rose before them the interaction of these different agencies. So that Darwin, after having himself started all these researches, and vivified them by a general idea, and shown the way to deal with them, had to leave them to his followers.

II

We saw that Darwin divided his task into two parts: Variability and Natural Selection. The former he had proved by an immense array of facts. As to the second, his ideas fluctuated all the time between natural selection in the struggle for life and the direct action of the environment. And, with his unbounded love of truth, in proportion as new experimental data were forthcoming in favour of the factor of direct action indicated by Buffon and Lamarck, he did not hesitate to recognize their importance. His letters, published in five volumes by his son Francis Darwin, contain a remarkable illustration of this gradual change of his mind; and a careful study of these letters is of the utmost value for appreciating in favour of direct action.

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From Darwin's note-books we see that in 1837, before he had read (in October 1838) Malthus's *Essay on Population*, he explained the appearance of new species chiefly by adaptation to changing circumstances. Even in 1844, after he had read the *Essay* of Malthus, he continued to give prominence to the direct action of surroundings. But later on his opinions changed, and by the end of 1856 he already wrote to Hooker that, after having studied variation under domestication, he came to the conclusion that 'external conditions (to which naturalists so often appeal) do by themselves very little.' He added, however: 'How much they do is the point of all others on which I feel myself very weak. I judge from the facts of variation under domestication, and I may yet get more light.' At that time he admitted that the effect of the external conditions was only to cause more variability; which is, of course, very different from the formation of new species. As to this last, he said: 'The formation of a strong variety, or species, I look at as almost wholly due to the selection of what may be incorrectly called chance variations, or variability' (*Life and Letters*, ii. 87). In the same letter, replying to a remark of Hooker, he maintained that even during a period of migration of a species, whether short or long, 'there would be little tendency to the formation of a new species . . . though considerable variability may have supervened.' To utilise variations, so as to produce a new species, Natural Selection was an absolute necessity.

In studying the letters from that period I cannot refrain from the idea that the more he was told by his friends (especially since the appearance of the *Vestiges of the Natural History of Creation*) of the near resemblance between his ideas and those of Lamarck popularised in that book, the more he insisted upon showing in what they differed. He recognised that the Lamarckian factor of 'direct action' of environment may increase variability; but, for giving stability to any variation—for giving origin to a new species possessed of a certain fixity of its forms—

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14 This was pointed out by Huxley. After having read the Sketch of Darwin's ideas, written in 1842, he wrote to Francis Darwin that in this Sketch 'much more weight is attached to the influence of external conditions in producing variation, and to the inheritance of acquired habits, than in the *Origin*' (*Life and Letters*, ii. 14). The Sketch of 1842 has now been published. See *The Foundations of the Origin of Species, a Sketch written in 1842*, by Charles Darwin, edited by his son Francis Darwin (Cambridge, 1909). The passages on pp. 32-33 fully confirm Huxley's appreciation.
15 The first edition of the *Vestiges* appeared in 1844. Several scientific errors of this book seem to have been eliminated from the subsequent editions. It is now known that it was written by R. Chambers.
something else was needed, and this something was Natural Selection. He even shows a sign of impatience when his great friend Lyell repeatedly brings forward Lamarck in his letters.

In 1859 Darwin once more reminded Lyell that he repudiated the Lamarckian idea that a mysterious power of adaptation was inherent to animals; he felt no need of such a metaphysical explanation. However, in June 1860, after having pondered over the criticisms of his *Origin of Species*—some of which were very foolish, but some very serious—he wrote to Hooker that he was not opposed to admitting the direct action of the surroundings. He was only cautious to point out that the variations called forth by a change of conditions must be submitted to Natural Selection. This last will preserve those of them that are useful, by weeding out those that are not. He compared the variations to the squared stones, or the bricks, or the timber of which the architect builds. They certainly influence the character of the building. 'Yet, in the same manner as the architect is the all-important person in a building, so is selection with organic bodies.' Direct action is for him only a 'handmaid' who offers her 'mistress,' Natural Selection, the entirely accidental, purposeless materials for a choice.

He thus insisted still upon two different moments in the genesis of a species: the appearance of indiscriminate variations of all sorts—both useful and harmful, or indifferent, without a prevalence of either; and the extermination of those individuals which have not the variations that are useful under given conditions, or have them to a smaller degree than other individuals. Natural Selection is thus the 'natural preservation' of the fittest.

It is most significant that in those years Darwin did not anywhere admit the suggestion—which for us is now an established fact—that under the influence of external conditions the variations themselves are produced chiefly in a certain definite direction, and therefore have already a protective character—just as the 'Alpine' features that are induced by climate in plants transported by man from the lowlands into Alpine surroundings protect them from perishing in the new surroundings. Such an

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15 This epoch-making work appeared on the 24th of November 1859.
16 Letter to Lyell, June 14, 1860 (Life and Letters, ii. 319).
17 *Life and Letters*, ii. 320. To Hooker he wrote on the 5th of June 1860:
18 By the way, I think, we entirely agree, except perhaps that I use too forcible language about Selection. I entirely agree—indeed, would almost go further than you—when you say that climate (i.e. variability from all unknown causes) is 'an active handmaid, influencing its mistress [Natural Selection] most materially.'
19 The very term selection implies something, i.e. variation or difference to be selected' (*Life and Letters*, ii. 317). And to Lyell, on the 14th of June: 'I have expressly stated that I believe physical conditions have a more direct effect on plants than animals. But the more I study, the more I am led to think that natural selection regulates, in a state of nature, most trifling differences' (*ibid.*, pp. 319-320).
idea does not occur to him. That direct action might be—to use Herbert Spencer’s terminology—a direct adaptation he still repudiates, or does not mention at all. The admission will come only later.  

It is evident that such an attitude of Darwin was not a mere matter of predilection. One need only remember the vagueness of all that was written in those years (nearly fifty years ago!) about the action of external conditions upon the organisms, and the veil which surrounded them. Besides, he had a substantial argument, borrowed from the geographical distribution of species. It was the fact that most species keep constant forms, even though they are spread over a wide area, which apparently offers a great variety of local conditions. This argument seems to have had great weight in his opinion, both in this question and in that of the influence of isolation.

"I see in Murray and many others"—he wrote at the same date of the 6th of June 1860—"one incessant fallacy, when alluding to slight differences of physical conditions as being very important, namely, oblivion of the fact that all species, except very local ones, range over a considerable area, and though exposed to what the world calls considerable diversities, yet keep constant."—Life and Letters, ii. 319.

At the present time, especially since we have the works of Gulick on the two hundred different species of snails limited to separate valleys of one of the Sandwich Islands, or of Hyatt on fossil Cephalopodes, and a number of local faunas and florae, published since more attention began to be paid to local sub-species and species—our ideas of constancy of the type have undergone a substantial change. Besides, since we know better the interior of the continents of Asia and America, we can better understand both the constancy of the type over large areas and its local variations.

When we see now that a given animal type keeps pretty constant over such a large area as the interior of Asia, from the Himalayas to Lake Baikal, or the interior of North America from Mexico to the borders of Alaska, we know that along the plateaux which run along the axes of these continents, the physical conditions are not so widely different as mere differences of latitude

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18 In August 1861 he writes to Lyell, in reply to a remark of John Herschell: 'It seems to me that variations in the domestic and wild conditions are due to unknown causes, and are without purpose, and in so far are accidental; and that they become purposeful only when they are selected by man for his pleasure, or by what we call Natural Selection in the struggle for life, and under changing conditions' (More Letters, i. 181-83). It must be said, however, that Darwin had so much to struggle at that time against objections raised from religious, teleological considerations, that he had to lay more stress upon the "accidental" character of variations than he probably would have done had the question been asked in terms of pure science: 'Does the influence of external conditions produce chiefly adaptive variations, or not?"
may suggest. We know, indeed, since we have become better acquainted with the orography of Asia, that an immense plateau stretches through the interior of the continent, from the Himalayas to the latitude of Lake Baikal, diminishing in altitude from 16,000 feet to 3000 feet as it advances towards the north; so that the climate, the vegetation and the fauna of the plateau do not vary so much as the difference of latitude between Tibet or Persia and the banks of the Lena would make us believe. On the contrary, I have shown that a striking similarity of conditions prevails along large tracts on that succession of plateaux, and we know from the modern explorers of Asia that the animals continually move along that line, from the south-west to the north-east, and back. This explains why the tiger and many other species spread from Persia and the Himalayas to Lake Baikal. But the moment we compare the florae, and partly also the faunae on the north-western (Siberian) and the south-eastern (Manchurian) slope of the same plateau, we find the most striking differences in the same latitudes at relatively short distances. The contrast between the West Siberian flora on the western slope of the High Plateau, and the Manchurian flora on its eastern slope, is simply striking. As for the fauna, when we study somewhat closer those animals, like the tiger, whose range extends over the whole plateau and its south-eastern slope (thirty-five degrees of latitude and as many of longitude), we find among them notable differences. Thus Brandt, the father, mentioned in his remarkable monograph of the tiger that the representatives of this species which are met in Bengal and in China—that is, on the southern and south-eastern slope—have much in common in their colouration, sufficient to distinguish them from the tigers met elsewhere in Asia. The same differences between the two slopes are met with, so far as I know, in Canada, and the same similarity of conditions prevails along the line of plateaux which stretches from Mexico to Calgary and the Saskatchewan. In short, I am inclined to believe that the wide range of many species would have offered to Darwin no argument against the direct action of local conditions and the effects of isolation, if he could have taken into account—as we can do now—the uniformity of conditions on the surfaces of immense plateaux and the migration of animals and plants along the axes of these upheavals.

Returning now to the gradual evolution of Darwin's ideas in favour of a direct action of external conditions, we see that in 1862 a change began to take place in his mind in this respect. Amidst occasional remarks about the progress of his work on Variation among the domesticated animals and plants, he dropped

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20 Letter to Hooker. Also More Letters, in Domesticated Animals, which, he says, have some 'effect.'

21 See the above.
the following confession: ‘I hardly know why I am a little sorry, but my present work is leading me to believe rather more in the direct action of physical conditions. I presume I regret it, because it lessens the glory of Natural Selection, and it is so confoundedly doubtful. Perhaps I shall change again, when I get all my facts under one point of view, and a pretty hard job that will be.’

From a letter to Mr. Horace Dobell, written in February 1863, we see that his hesitations continued. In his lectures ‘On the Germs and Vestiges of Disease’ Mr. Dobell spoke of variations in the quantity of force exhibited by an organism in the operations of life (very near, by the way, to the accommodation ‘effort’ of Lamarck), and Darwin agreed with him that ‘the conditions of life must play a most important part in allowing this quantity to increase.’ But how far these conditions act on the forms of organic life he could not see clearly.

‘In fact’—he added (I italicise some passages) —‘no part of my subject has so completely puzzled me as to determine what effect to attribute to (what I vaguely call) the direct action of the conditions of life. I shall before long come to this subject, and must endeavour to come to some conclusion when I have got the mass of collected facts in some order in my mind. My present impression is that I have underrated this action in the “Origin.”’—More Letters, i. 235.

It is evident that at that time Darwin was perplexed how to determine the part which belonged to Natural Selection and that which belonged to the Direct Action of the Surroundings—the ‘mistress’ and the ‘handmaid.’ He apparently realised sometimes that the handmaid who produced the variations could submit to Natural Selection variations so useful that little choice was left for the approval of ‘the mistress.’

Could not new species, better appropriated to new conditions, be produced in the same way as the function produces the organ—as had been indicated by Herbert Spencer? But at other times Darwin and his friends must have asked themselves, Why are there no direct proofs of the action of surroundings being capable of producing a permanent variety, and still less a new species? Why has not even some simple organ, harmonised with the whole of the structure, ever been produced experimentally by altering the conditions of growth of a plant, or of life for an animal?

Experimental Morphology, such as it exists now, did not exist forty years ago; and instead of speculating, as Lamarck

22 Letter to Hooker, 24th of November 1862; Life and Letters, ii. 399, 390. Also More Letters, i. 214. It is known that in preparing his book on Variation in Domesticated Animals and Plants he made measurements and weighings of bones which, he hoped, would convince Hooker that ‘use and disuse’ at least have some ‘effect’ (Letter to Hooker, March 26, 1862, in More Letters, i. 199).

21 See the above-mentioned letter to Hooker (Life and Letters, ii. 317).

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St. Petersburg,
did in 1809, and Spencer in 1832, about the ways in which new functions could modify a group of muscles, or an organ, he preferred to keep to the then safer ground of Natural Selection.

However, there is among his letters a long draft letter to George Lewes, most instructive on this point. It is evidently a reply to an important letter from Lewes, wherein the physiologist suggested that organs may be formed by the direct physiological action of the surroundings upon the organism. Darwin definitely replies that he cannot admit such a view. His study of nature has brought him to the impression that the 'striking harmony between the affinities, embryological development, geographical distribution, and geological succession of all allied organisms,' and, on the other side, the perfect coadaptation of such special organs as the electric organs of fishes, or the thorns of certain plants, 'with the whole rest of the organisation,' are opposed to the view that such organs may have been formed by the direct action of the conditions of life. In regard to thorns and spines, he admits that the abortion of various appendages may result in producing rudimentary thorns; he freely also admits that 'the precise form, curvature and colour of the thorns' are 'the result of the laws of growth of each particular plant, or of their conditions, internal and external'; 'but I must believe,' he adds, 'that their extreme sharpness and hardness is the result of fluctuating variability and the "survival of the fittest." . . . That Natural Selection would tend to produce the most formidable thorns will be admitted by everyone who has observed the distribution in South America and Africa (side Livingstone) of thorn-bearing plants, for they always appear where the bushes grow isolated and are exposed to the attacks of mammals.'

This letter, written in 1868, is extremely instructive. It shows that Darwin distinguished already two different parts in the process of adaptation. The surroundings, by their direct action upon the plant, produce the beginnings of adapted organs —elementary spines and thorns, due to the abortion of the lobes of the leaves. Variation, in this case, is no longer a chance variation. It is directed in the proper, necessary way: it is an adaptation. Speaking metaphorically, it is no longer purposeless, because it is the dry atmosphere which diminishes the evaporating surface of the leaves, maintaining only their veins transformed into elementary spines or thorns. The 'handmaid' offers to Natural Selection something which the 'mistress' dare not reject. It is Natural Selection which becomes a handmaid to direct action.

Nor is the above variation an 'individual variation.' If there

22 More Letters, i. 306-9. Owing to its length I was compelled to condense it.
is in the surroundings a cause—the dryness of the atmosphere—which produces an abortion of the lobes of the leaves, it acts upon all the individuals of the same locality. It is a group variation, and the sharpest struggle for life goes on no longer between the individuals of the same group, but between the group and its competitors from other species. Natural Selection eliminates with preference the individuals of other species which cannot undergo the same useful transformation—those which are more refractory to the action of a dry environment and retain broad leaves. Impressionability, plasticity, become the subject of struggle. But this means that two new conceptions have crept in, totally modifying the struggle for life so as to deprive it of its bitter individualist character.

New elements had, however, to be taken into account in order to bring us a step nearer to the solution of that difficult problem.

III

The new elements which had to be taken into account belonged to three different orders of ideas. One of them was 'isolation'—i.e. the consequences of a portion of the species, in its constant efforts of spreading over a wider territory, becoming separated from the main body by some barrier: a channel, a chain of mountains, an intervening desert. Separation would favour in such cases the formation of a new variety, and eventually a new species. The second element was of a negative character. It was the difficulty for Natural Selection to establish a new species if the variations it had to choose from were purely accidental, and had no tendency to accumulate in a definite direction. And the third element, the chief one, was the direct action of the environment, and its capacity for producing in plants and animals such changes as would be sufficient to give origin to new species adapted to their surroundings.

In all these three directions important researches were made, and Darwin, with his love of truth, did not fail to recognise their value, even though he had to modify his views upon the part played by Natural Selection in the genesis of new species. For our special problem—the part that belongs to Mutual Aid in progressive evolution—these researches have a great value, and we must dwell upon them at some length.

Already in the Galapagos Islands, which Darwin had visited during his Beagle voyage, he had had the opportunity of appreciating the effects of isolation. In fact, it was the new forms of birds and shells which he found in these islands—different from those of South America, and yet undoubtedly derived from them—which had set him thinking about the 'transmutation' of
species. In 1844 he was so convinced of the importance of isolation that he described it as 'the chief concomitant or cause of the appearance of new forms.'

Consequently, when Moritz Wagner published, in 1868, his first essay on the effects of isolation for generating new species,24 Darwin frankly recognised that this was a factor which removed many difficulties unexplained by Natural Selection.25 Later on, he confirmed the same views in a letter to Karl Semper, saying that when a species splits into two, three, or more species, 'nearly perfect separation would greatly aid in their "specification," to coin a new word' (Life and Letters, iii. 160). 'In North America,' he wrote to the same correspondent, 'in going from North to South, or from East to West, it is clear that the changed conditions of life have modified the organisms in the different regions, so that they now form distinct races or even species.' But with respect to all adapted structures, and they are innumerable, Darwin could not see how Wagner's view could throw any light (iii. 161).

The above admission of the part played by isolation in the genesis of new species was most important, and I have shown elsewhere to what consequences it brings us as regards the supposed extermination of 'intermediate links.' Once we admit the successive migrations, in the course of ages, of certain species over several continents (and it seems necessary to admit them, for instance, for the series of ancestors of the wild horse), and once we realise the amount of segregation that ensued, we fully understand the necessary 'absence of intermediate forms.' And yet it was this absence which so much puzzled Darwin and for which he admitted 'extermination' during a severe struggle for life. With isolation, such an extermination is not necessary; very probably it did not take place at all.

Of course, Darwin could not recognise all the claims of Moritz

23 He wrote to Hooker: 'The most general conclusion which the geographical distribution of all organic beings appears to me to indicate is that isolation is the chief concomitant or cause of the appearance of new forms (I well know there are some startling exceptions)' (Life and Letters, ii. 28).
24 'Although I knew,' he wrote to Wagner, 'the effects of isolation in the case of islands and mountain ranges, and knew of a few instances of rivers, yet the greater number of your facts was unknown to me. I now see that from the want of knowledge I did not make sufficient use of the views which you advocate; and I almost wish I could believe in its importance to the same extent with you; for you well show, in a manner which never occurred to me, that it removes many difficulties and objections.' [After having made some restrictions in favour of Natural Selection, Darwin continued:] 'But I admit that by this process [Natural Selection] two or more new species could hardly be found within the same limited area; some degree of separation, if not indispensable, would be highly advantageous, and here your facts and views will be of great value.' (Apparently written in 1863; Life and Letters, iii. 157.)
25 Mutual Aid, pp. 65-66.
Wagner, because in a subsequent work he the German geographer came to maintain that isolation totally dispenses with Natural Selection. So that Darwin reminded him that isolation alone could not explain the manifold adaptive structures of organisms. Besides, Darwin saw in the co-existence, on the surfaces of large continents, of species originated from a common stock, an objection against recognising in isolation a factor of primary importance for the origin of species. 'When I thought of the fauna and flora of the Galapagos Islands I was all for isolation, when I thought of South America I doubted much,' he wrote in 1868 to Karl Semper.

Since Darwin wrote these lines a great deal of attention has been paid to isolation, and it must be said that the importance of this factor is now recognised almost unanimously. Only the sense of 'isolation' has been widened, as it includes now the so-called 'biological' and 'physiological' isolation, in addition to 'geographical isolation,' and it is no longer opposed to Natural Selection, but is recognised as one of the factors of evolution.

The remarks that I have made in the preceding chapter about the rôle of plateaux, which permit certain species to spread over a very wide territory and at the same time isolate them from each other, either on the opposite slopes of the plateau or in the mountains parallel to its border, refer to broad geographical features only. But the segregation of groups of plants and animals may also take place on the surface of a plateau or an elevated plain, in consequence of local topographical depressions. To take an example once more from Asia, the great Central Asian plateau is intersected from east to west on two-thirds of its width by the Tarim depression, which is the remainder of an ancient inner sea, and now introduces into the very heart of Central Asia the vegetation and some other characteristics of the steppes of the border lowlands. However, this is still a large depression. But what is seen here on a large scale is repeated many times elsewhere on a smaller scale. In several places the borders of the Central Asian plateau are diversified by local depressions—the
vestiges of large gulfs, or lakes, formerly connected with each other during the Post-Glacial period, and also with the sea, and now possessing a number of distinct species in their flora and fauna.\footnote{I do not mean, of course, that these lakes were covered by the ocean during the Glacial or Post-Glacial period. They represented only successive series of lakes at different levels, connected by large channels, or fjärden, such as we see now in Sweden and Finland.} To wit, the seal of Lake Baikal (Phoca sibirica), quite distinct from the seal (Phoca caspica) which is found in both the Caspian Sea and Lake Aral; or the Baikal Freshwater Herring (Coregonus omul), quite distinct, too, from the representatives of this genus living in the lakes of Northern Russia and Switzerland. In all these cases we have undoubtedly species which have originated owing to topographical isolation.

However, there is a still more local segregation which has been described as 'biological isolation.' Thus a butterfly, if it does not find enough of the plant upon which it is accustomed to deposit its eggs, deposits them on some other nearly related plant, and, as has been shown by Standfuss, a new variety of that butterfly comes into existence. Or some frogs, accustomed to a wet ground, have been forced to migrate to a dry ground, and we learn from Hutton that not only a new variety was originated in this way, but that it differed from the parent stock by laying its eggs somewhat earlier,\footnote{I take these two examples from L. Plate, Ueber die Bedeutung und Tragweite des Darwin'schen Selektionsprincip, Leipzig, 1900.} so that cross-breeding probably became impossible. Or a portion of the squirrels of a given region, finding a scarcity of cedar cones, moves to a larch forest and feeds on the seeds of the larch and on mushrooms.\footnote{Polyakov, Visit Expedition, 1875, Zoology, p. 37.} Scores of similar cases could be produced. In all such cases the isolation of a portion of the species gives origin to a new variety, and thus we may have in the same region two varieties, and eventually, if they become unfertile in cross-breeding, two sub-species or species.

And, finally, there is the 'physiological isolation' (or rather the 'sexual isolation') indicated by Catchpool and worked out by Romanes. Continually we see in nature that some slight differences in the modes of life of animals and plants produce a slight morphological divergence which leads to, or is accompanied by, sterility between the parent stock and the slightly modified variety. We see also that in animal societies a certain race-feeling is developed, which prevents cross-breeding of that society with other similar societies, in virtue of a merely psychological aversion or some physiological causes. In all these cases we have what may be described as physiological isolation—a factor certainly not opposed to Natural Selection, but helpful in the evolution of new species.

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However—and this is what interests us most from our special point of view—the necessity of a bitter struggle for life inside the species, for the origin of new species, vanishes more and more. This struggle is simply avoided. Over-multiplication is prevented by portions of the species taking to new grounds, or to different sorts of food, or to different modes of life. Countless examples of such a colonisation are found with all sociable animals. With the ants they are especially striking, colonisation undoubtedly contributing very much to maintain the immense extension of the different species of ants. And the results of such a colonisation are invariably to avoid that individual Malthusian struggle which arithmetical calculations may have led us to assume.

IV

The above-mentioned letter of Darwin to Moritz Wagner was important in another respect. He frankly admitted in it that he had underrated the Lamarckian factor—the direct action of environment.

'In my opinion,'—he wrote—'the greatest error I have committed has been not allowing sufficient weight to the direct action of environment, i.e. food, climate, &c., independently of Natural Selection. Modifications thus caused, which are neither of advantage nor disadvantage to the modified organism, would be especially favoured, as I can now see, chiefly through your observations, by isolation in a small area, where only a few individuals lived under nearly uniform conditions. When I wrote the Origin, and some years afterwards, I could find little good evidence of the direct action of environment; now there is a large body of evidence, and your case of Saturnia is one of the most remarkable of which I have heard' (Life and Letters, iii. 169).

And in March 1877, writing to the Vienna Professor Neumayr about the work of Mr. Hyatt on extinct Cephalopods in America, he expressed himself in nearly the same words. 'There can be no doubt,' he wrote, 'that species may become greatly modified through the direct action of environment. I have some excuse;' he added, '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.'

These admissions by Darwin have a double importance. Not only do they show that already during his lifetime researches were accumulating sufficiently to prove that the 'direct adaptation' advocated by Lamarck and Spencer was much more than a mere lucky guess; they also imply that Darwin's views must have

Life and Letters, iii. 232. A few weeks later he wrote to E. S. Morse, speaking of the work of an American zoologist: 'I quite agree about the high value of Mr. Allen's works, as showing how much change may be expected apparently through the direct action of the conditions of life' (iii. 233).
changed about mere chance variations being sufficient for producing new species.

As regards the sense he attributed to the word 'chance,' he warned his readers against a possible misunderstanding. In using this word he simply wanted to emphasise that nature shows no evidence of evolution being in accordance with a 'preconceived aim,' or being governed by a 'guiding power.' The multitude of variations which appear in every generation of plants and animals without any preconceived plan, as a consequence of the multitude of forces acting in all possible directions, is quite sufficient, he maintained, for producing all the wonderful adaptations of organic beings to their surroundings, once there is struggle for life and Natural Selection. But he certainly never forgot that every fact in nature is a necessary consequence of the so-called laws of nature. Therefore he reminded his readers that when he spoke of 'chance variations,' he simply meant variations the causes of which were unknown.

However, the words 'chance variations' have in science another meaning, especially familiar to the physicist and the astronomer. These last say that the variations are mere chance variations when in a given series of deviations from an expected result they find no cause affecting the series one way or another, with preference to all others. Suppose that an astronomer, taking his seat at a given spot in Greenwich, the latitude of which is known with great exactitude, makes twenty determinations of its latitude with a given instrument. In his calculations he eliminates all possible causes of error: the effects of refraction in the atmosphere, the errors of his instrument, his own personal error due to his individual perception, and so on. And he expects then to find some of his determinations in excess of the true latitude, and some others below it, but equally distributed on both sides of the true one. He expects, in other words, to find only chance variations—only accidental deviations. If he finds, however, that his determinations have, nevertheless, a tendency to fall above the correct latitude (or below it), he concludes that there was some constant cause of deviations which affected most of his determinations. The deviations are no longer chance deviations only.

The same with a sharpshooter. His shots may deviate more or less from the centre of the bull's-eye according to his skill, his rifle, or his mood on a given day; but so long as the sum of the deviations to the right and to the left of the centre, above and beneath it, counterbalance each other, they are chance deviations. No constant cause is at work tending to affect either way all his shots. And, rice versa, there is such a cause, external or personal, if the average result of all his shots does not fall in the centre; there is then definite deviation in addition to chance variations.

Now, Darwin's idea and with them a hard fact will do to explain gradually new species. Variations some that exist, Natural Selection have them not, or have given an additional chance to those who have the prevailed fifty years a. with the embryonal at its causes, such a suggest the whole question of present time we need chance variations only that when the conditions not only increases variety processes: it produces many cases the variant them? We don't know of logical investigation fact is there, and we.

On the other hand works in which the very the so-called individuals under their quantitative errors, are treated in Biology—Biometric Francis Galton having Natural Inheritance. Ludwig, Duncker, I studied this sort of gradual, reversible, slow.

The results of the full meaning of a tree, or the Cambridge University men—as Galton did done by Kuhn with sugar-works, or if everywhere we find the same as the sciences under the rule.

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Now, Darwin's idea was this: give me chance variations only, and with them a hard struggle for life and Natural Selection, and this will do to explain the appearance of new varieties, and eventually of new species. As there will always be among the chance variations some that are useful under the given conditions of existence, Natural Selection will eliminate those individuals who have them not, or have them in a smaller degree, and will thus give an additional chance of survival and of further multiplication to those who have the variation. With the prejudices which prevailed fifty years ago against the 'mutation' of species, and with the embryonal state of our knowledge about variation and its causes, such a suggestion proved to be most useful. It placed the whole question on a purely scientific ground. But at the present time we need not limit the species-producing activity to chance variations only. Darwin himself was forced to recognize that when the conditions of life are altered, the change of habits not only increases variability by acting somehow upon the genetic processes: it produces also variation in a definite direction; and in many cases the variations are adaptations. How does it produce them? We don't know yet, and it would require a special physiological investigation in each separate case to explain it; but the fact is there, and we must recognize it.

On the other hand we have now a considerable number of works in which the variations from all sorts of indefinite causes—the so-called individual or chance variations—have been studied under their quantitative aspects, just as accidental deviations, or errors, are treated in physics and astronomy. Quite a new branch of Biology—Biometry—has been created by these researches. Francis Galton having opened the way by his epoch-making work, Natural Inheritance, he was followed by Weldon, Bateson, Ludwig, Duncker, Karl Pearson, and many others, who have studied this sort of variability under the names of fluctuating, gradual, reversible, statistical, or individual variation.

The results of these researches are extremely interesting and full of meaning. Whether we take the sizes of the leaves of some tree, or the stature of several thousand Englishmen at Cambridge University, or the strength of pull of several hundred men—as Galton did—or the contents of sugar in beetroot, as was done by Kuhn with nearly 20,000 samples of beet at the Narden sugar-works; the sizes of various seeds, as de Vries did—everywhere we find that the laws of variation in organic beings are the same as those with which we are familiar in physical sciences under the name of laws of errors in the theory of proba-

34 They varied from 13 to 19 per cent., which means that in some samples the percentage of sugar was by about one-third higher than the average, which was 15.2 per cent. I take these figures from de Vries.
bilities. Quetelet, in 1845, had already extended these laws to facts of organic life; now we see that they fully apply to variation —provided we take a considerable number of cases.

This means a great deal, as it appears that the greater the divergence from the average type, the smaller is the chance of its appearance. Thus, if the average length of several hundred beans taken from one plant is found to be 12 millimetres, there will be among them a few beans as short as 8 mm., and some as long as 16 mm.; but out of 448 beans measured by de Vries only one was as small, and one as big as that; two had a length of 9 mm., and seven attained 15 mm. in length, which makes a total of only eleven beans the lengths of which were not within the limits of from 10 to 14 mm.; while the number of beans of an average size—that is, 11, 12 or 13 mm. long—reached 381 (108, 167, and 106 respectively). The chance of meeting a variation of one-third of the average size was thus only two in 448; even a variation of one-sixth of the average did not occur in one case out of forty. What prevailed to an enormous extent in this and in all other similarly studied cases was the 'happy medium.'

The law according to which the small variations are numerous, but the considerable ones are few, and their rarity grows as the square of the size of the variations, holds good for the above-mentioned leaves, the size of beans and many other seeds, the percentage of sugar in beet, the pull of men, their stature, and so on. It may be taken as a general law. But it has also another aspect. Whichever of the just-mentioned variations be taken, in all cases the number of variations above the average is equal to the number of variations below it, so long as there is not some definite cause of perturbation. If we represent the distribution of these variations by a curve, the curve is always symmetrical on both sides of the average. It has the same

The general reader will find a very good exposition of these biometrical researches in two excellent English works: The Method of Evolution, by H. W. Conn, New York, 1900, which I have had already the pleasure of recommending, and Recent Progress in the Study of Variation, Heredity, and Evolution, by R. H. Lock, London, 1906 (with the necessary diagrams). De Vries has given a general review of these researches in the introductory pages of his well-known Mutationstheorie, Ed. I., Fig. 1.

The examples of variation quoted by A. R. Wallace in Darwinism seem to contradict the above result. Having taken measurements, chiefly of birds, on museum specimens, he has found a much greater proportion of considerable variation in the lengths of wings, toes, and so on, even though the numbers of measured specimens were only from ten to fifty-eight. However, it must be borne in mind that the specimens brought in by specimen-collectors are not numerically representative of variation in a species, because, if some specimen-collectors followed the advice of Linnaeus and cared only for 'typical' representatives, the others were interested especially in 'variety.' Besides, we know from such authorities as Eyvertrito and several others that the effects of hybridism in birds must be taken into account. The laws of variation deduced from a great number of measurements are certainly more reliable.

character as in the sharpshooter.

were not symmetrically more numerous (or at once that there to produce variation such a cause of surroundings or so like).

True that A. R. does not agree with a particular kind of vari itself goes on increase not attempt to prove matter the opinion of de Vries, he position, and shows of arguments borrow apples.

To be cumulate chance variations, a direct action of the nature and the forms direction. This is there is such a cause of the individuals of The acting cause in the subsequent the struggle for life necessary, once v concrete cause produce that for some the winter makes the acquire a lighter, need to suppose separate individual enemies of their colouring prevalent is why it prevail in herds on the one and in the extreme factor of direct prominence by t separately in a
character as in the above-mentioned cases of the astronomer or the sharpshooter. And this is so general a law that if the curve were not symmetrical—if the variations above the average were more numerous (or less) than those below it—we should conclude at once that there was some permanently acting cause tending to produce variation in one definite direction. In organic variation such a cause would be either the direct action of the surroundings or some form of cross-breeding.

True that A. R. Wallace in his admirable book Darwinism does not agree with this view. He maintains that "if any particular kind of variation is preserved or bred from, the variation itself goes on increasing to an enormous extent." But he does not attempt to prove his assertion. And when we take upon this matter the opinion of so experienced a breeder as Professor de Vries, he positively denies it on the ground of direct experiment, and shows why he cannot be convinced by Wallace's arguments borrowed from the breeding of different sorts of apples.

To be cumulative in its effects, there must be, beside the chance variations, a cause, such as hybridism, or still more so the direct action of the environment, which tends to alter the structure and the forms of the animal or the plant in a certain definite direction. This is the result of all these researches. But once there is such a cause, there is no need of an acute struggle between the individuals of the species to preserve the effects of variation.

The acting cause will itself accumulate them, and increase them in the subsequent generations. The hypothesis which saw in the struggle for life the cause of accumulated variation is no longer necessary, once we have in the direct action of environment a real cause producing the same effects. In fact, if it be proved that for some physiological reason the cold of the sub-Arctic winter makes the fur of an animal, both wild and domestic, acquire a lighter, and eventually a white colour, then there is no need to suppose that it is a severe competition between the separate individuals for food, or in concealing themselves from their enemies (or their intended prey), which makes the white colouring prevail in the long run. And so it is in reality. This is why it prevails alike with the tame Yakut horse which lives in herds on the open prairies, in the now unsociable polar bear, and in the extremely sociable polar fox. However, this important factor of direct action, which has been brought so much into prominence by the Neo-Lamarckians, will have to be examined separately in a subsequent essay.

P. Kropotkin.

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