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CHARLES DARWIN AND THE MUTATION THEORY*

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PROFESSOR HUGO DE VRIES, in his American lectures on "Species and Varieties, their Origin by Mutation," claims that his work is "in full accord with the principles laid down by Darwin,"[1] and boldly asserts that Darwin recognized both "mutation" and individual variation, or "fluctuation,"[2] as steps towards what Professor Cope aptly called "the origin of the fittest." I think many persons unfamiliar with Darwin's writings must have been much surprised on reading Professor De Vries's statement, for it has been a common belief in the scientific world for many years that the establishment of the mutation theory would be fatal to Darwinism, or would at least take from it its most original and essential features. The perpetuation of this impression has been due, very largely, to Mr. Wallace and certain of his followers who have steadfastly refused to admit the possibility of the evolution of species and varieties by any form of saltation and have insisted more uncompromisingly than did Mr. Darwin himself upon the exclusive efficiency of selection exercised upon small, recurring individual fluctuations. In fact, many of Mr. Wallace's views have out-Darwined Darwin and yet Darwin, somewhat unreasonably, has been held responsible for them.

* Presidential address at the annual meeting of the New York Academy of Sciences, December 21, 1908.

[1] Preface by the author, p. ix.

[2] Second edition, p. 7.

Accordingly Darwin has been charged with a radicalism which he never professed and champions of a *supposed* Darwinism have felt called upon to do battle against theories which he never distinctly repudiated or which he might even have accepted if he had known of them. Thus, Professor Poulton, in his recently published "Essays on Evolution," attacks with great severity, under the name of "Batesonians," believers in the validity of mutation as a factor in the process of evolution, although, as he admits, "mutation was of course well known to Darwin."[3] Now, I think we are justified in saying that if mutation was "*known*" to Darwin, it must have been, and still is, a veritable fact; and, if evolution is a universal law of nature it can not, in that case, exclude mutation. We, therefore, who believe in general evolution are compelled to decide for ourselves whether mutation has taken place and is now occurring; and we who are really Darwinians—that is to say, we who believe that Darwin set forth correctly the essential steps in the evolutionary process—are interested in knowing whether he actually recognized the fact of "discontinuous variation" or mutation, and, if so, how he fitted it into or reconciled it with his system.

The essential factors in organic evolution, from the Darwinian point of view, are: (1) Variation, (2) inheritance, (3) over-reproduction, (4) competition, (5) adaptation, (6) selection and survival. The general explanation of these factors is as follows:

1. All organisms vary continually and in every part of their structures—that is to say, no two individuals are exactly alike in any particular.

2. Nevertheless, characters anatomical, physiological and psychological are in general transmitted to descendants; in other words, progeny essentially resemble their parents.

3. More animals and plants are brought into the world than can possibly find means of subsistence.

[3] "Essays on Evolution," 1908, p. xviii.

4. There results competition for what subsistence there is, or, as it is otherwise called, a struggle for life.

5. Since out of all the variations that occur in the constitutions or characters of organisms some must happen to be in directions to give their possessors an advantage, or advantages, in procuring the means of existence, as compared with other individuals of the same class, some of the new-born animals and plants are best adapted to their surroundings or "conditions of life."

6. These best-adapted forms ("the fittest") will win in the struggle for life and are figuratively said to be selected; the unfit will in the end be exterminated. The result is the origination (evolution) of new classes of organisms out of the old ones and their substitution for the earlier classes or groups.

Not one of these factors was originally discovered by Darwin, but he first discerned their interrelations and bound them together by a consistent and convincing philosophy. He, for example, was not the earliest observer of progressive change in the organizations and external characters of animals and plants, but no one before him had had the insight to perceive that this changeability was the manifestation of a force great enough to burst the artificial limits placed about the groups called species and varieties and to enable them to transform themselves into other groups better adapted to the changing environment. Before Darwin's time every one, of course, had ocular demonstration of the fact that there were differences between individuals and that descendants were not in every respect like their ancestors. There was universal belief, however, that these variations never exceeded certain narrow boundaries built round species like inviolable walls. Curiously enough, Darwin, who first broke down these boundaries, took the same individual variations as the principal foundations of his selection theory. He assumed—for he admitted that it could not be proved for any particular case—that these small differences, which ordinarily fluctuate about a cer-

tain average for each species or variety, are at times accumulated to such a degree as to carry all the members of the group forward to a new center of oscillation so as to constitute in effect a new group. It was not at first his idea that a single individual, or a small number of individuals, might occasionally develop evolutionary force enough to over-leap suddenly the imaginary boundary and become the nucleus of a new colony beyond; that is the substance of the mutation theory; and, while I think it can be shown that Darwin more or less clearly recognized the possibility of the occasional origin of permanent races by this method of saltation, there can be no doubt that he entertained a strong bias in favor of the evolution of species generally by slow and minute steps.

As far as cultivated plants and domesticated animals were concerned Darwin was willing to grant the widest range of variation and the most abrupt changes, but as to animals and plants in a state of nature he was more sparing of his admissions that great and sudden departures from specific types might occur. This tenure of the two points of view was due to his belief that the domesticated animals and plants were more variable than feral forms because of the direct influence of man upon their surroundings and habits of life. Inasmuch as his theory of the origin of species through natural selection is founded on analogy between the deliberate operations of breeders in choosing the most desirable individuals of their flocks and gardens, and the inevitable sifting out of feral forms through their competition with one another in the struggle for existence, it is difficult to see why Mr. Darwin hesitated about carrying the comparison to its logical conclusion in the admission that what we now call mutations, but what he referred to as "spontaneous variations," "sports," "monstrosities," etc., stand upon substantially the same basis in nature as in cultivation. According to the present-day views of scientific students of animal and plant breeding, I understand, there is no

good evidence that cultivated plants and animals are more subject to wide and abrupt variations than are those living under natural conditions. On this point Professor De Vries remarks that "it is not proved, nor even probable, that cultivated plants are intrinsically more variable than their wild prototypes."[4] As to distinct mutations, we must remember that plants and animals preserved and nurtured by man are constantly under the eyes of many thousands of pecuniarily interested observers, while those in a state of nature are closely studied by but a handful of scientific investigators. We must also remember that it is only within a few years that a small fraction of these men of science have been led to look for cases of mutation, while all gardeners, farmers and breeders have had the inducement of financial profit to watch for marked variations among their stock and to preserve such variations if desirable. The naturalists specially interested in evolutionary questions are exceedingly few in number, but their field of research is immensely extended and varied. The number of those who have raised animals and plants for gain, however, has always been large, though the number of forms which they have been called upon to consider have been relatively few. The two fields have consequently had exceedingly different degrees of scrutiny. But since De Vries and others opened up the subject an astonishing number of clearly proven cases of mutation have been discovered in very various classes of organisms, just as numerous paleontological evidences of evolution have been brought to light as a consequence of Darwin's turning men's minds in that direction.

As I have already intimated, Mr. Darwin undoubtedly dealt with numerous cases of mutation among domesticated animals and plants, and they gave him little or no intellectual disquietude. In his work on "Animals and Plants Under Domestication" he gives a long catalogue of "spontaneous variations" or "sports," many of which

[4] "Species and Varieties, their Origin by Mutation," 2d ed., 1906, p. 66.

he freely acknowledges were the starting points of new and constant races; and there is good reason to believe that some of them occurred before the animals and plants which underwent the sudden changes had been actually brought under domestication or cultivation; in fact, that the mutations themselves suggested to men the directions in which their breeding operations should be conducted. For example, take the case of the tumbler pigeon: Mr. Darwin remarks concerning this that "no one would ever have thought of teaching or probably could have taught, the tumbler pigeon to tumble,"[5] but it seems to me obvious that no one would ever have thought of accumulating slight variations in the direction of tumbling. It is much more reasonable to suppose that the birds which were artificially selected as the progenitors of the present race of tumbler pigeons actually tumbled—that is to say, they were mutants. As to the origin of domestic races through modifications so abrupt as to have been thought by Darwin entirely independent of selection, he gave it as his judgment, as late as 1875, that

> It is certain that the Ancon and Mauchamp breeds of sheep, and almost certain that the Niata cattle, turnspit and pug-dogs, jumper and frizzled fowls, short-faced tumbler pigeons, hook-billed ducks, &c. suddenly appeared in nearly the same state as we now see them. So it has been with many cultivated plants.[6]

Now, considering, as I said a moment ago, that Mr. Darwin's theory of the origin of species by means of natural selection has for its main foundation-stones facts derived from observation of the effects of man's selection among domesticated animals and plants,—without which, indeed, he admitted that he had no actual proof of the operation of natural selection,—it is difficult to realize the state of mind which led Mr. Darwin to add to the sentence just quoted the following caution:

> The frequency of these cases is likely to lead to the false belief that natural species have often originated in the same abrupt manner. But

[5] "Origin of Species," 6th ed., 1882, p. 210.

[6] Ans. and Plnts. Under Dom., 2d ed., 1875, Vol. II, pp. 409–10.

we have no evidence of the appearance, or at least of the continued procreation under nature, of abrupt modifications of structure; and various general reasons could be assigned against such belief.

I am not aware that Mr. Darwin ever presented definite and convincing reasons for the sharp demarkation here attempted and, indeed, I can not see how the state of knowledge in his time could have justified it, for, as I have already stated, mutations had not been much looked for among feral plants and animals. In fact, by absolutely excluding from his theory the idea that mutation could occur under nature, Mr. Darwin, by the force of his great authority and influence, would have prevented a careful weighing of the pros and cons, if the human mind had at that time been prepared to weigh them. It is practically only since the Darwinian hypotheses have themselves been subjected to prolonged scrutiny, and since De Vries and a few others entered upon detailed experimental examination of this particular subject, within the last twenty years, that the matter can be said to have received anything like scientific treatment.

But, after all, Darwin was not *wholly* prejudiced against a belief in the occurrence of mutations in nature, for he several times expressed the opinion that the establishment of such a fact would in some ways be an advantage to the evolution theory. For instance, in a letter of August, 1860, to W. H. Harvey, he says:

> About sudden jumps: I have no objection to them—they would aid me in some cases. All I can say is that I went into the subject and found no evidence to make me believe in jumps; and a good deal pointing in the other direction.[7]

This of course refers to discontinuous variations in organisms under natural conditions, for he had certainly found evidence to make him believe in similar variations among domesticated animals and plants. I think Mr. Darwin never specified the directions in which a belief in mutation would be a help to him, but, from casual remarks made in various places, I fancy he had in mind

[7] "More Letters," Vol. I, p. 166. See also, "Life and Letters," 1886, Vol. II, p. 333.

the way in which it would ease him over that difficult subject, the imperfection of the geological record, and would reconcile him with the physicists and cosmogonists who were not disposed to allow him the lapse of past time he required for the evolution of species by the accumulation of successive minute or "insensible" individual variations. But I will not discuss these points now. What I wish to dwell upon at the moment is that Darwin recognized and accepted the fact of mutation among animals and plants under domestication, although it is worth while to repeat the statement that some of his cases probably happened in a state of nature, since they occurred at the very beginning of, and were the points of origination for, man's selective operations. As Mr. Darwin himself says: "Man can hardly select, or only with much difficulty, any deviation of structure excepting such as is externally visible,"[8] which means, as I take it, that nature usually presents some quite manifest variation before artificial selection begins, and this must have been the case at the time when man's first choices were made, particularly when half-civilized and unobserving men began the cultivation of our now domesticated animals and plants. It is necessary to remember, however, in this connection, that the mutation theory, as interpreted by De Vries, requires for its starting point only a variation which marks a distinct separation of a form from its parent group without connecting gradations, and not necessarily any great or extraordinary change of characters; for, as he says: "Species are derived from other species by means of sudden small changes which, in some instances, may be scarcely perceptible to the inexperienced eye."[9] None the less it remains true that man is apt to select only striking variations and hence Mr. Darwin, in treating of "sports," or what we should now call mutants, among cultivated plants and animals, usually speaks of them as wide departures from type, or, rather, he deals only with such as *are* large deviations.

[8] "Origin of Species," 6th ed., p. 28.

[9] "Plant Breeding," 1907, p. 9.

Even when treating of organisms in a state of nature, however, he admits that "there will be a constant tendency in natural selection to preserve the most divergent offspring of any one species."[10] Returning to the subject of artificial selection, Mr. Darwin says:

> No man would ever try to make a fan-tail till he saw a pigeon with a tail developed in some slight degree in an unusual manner, or a pouter till he saw a pigeon with a crop of somewhat unusual size; and the more abnormal or unusual any character was when it first appeared the more likely it would be to catch his attention.[11]

In another place he says:

> It is probable that some breeds, such as the semi-monstrous Niata cattle, and some peculiarities, such as being horuless, &c. have appeared suddenly owing to what we may call, in our ignorance, spontaneous variation; . . . During the process of methodical selection it has occasionally happened that deviations of structure more strongly pronounced than mere individual differences, yet by no means deserving to be called monstrosities have been taken advantage of.[12]

Now, in his work on Animals and Plants under Domestication Darwin has given a long list of these widely varying forms from each of which has descended a new race conforming to his own test of a species, namely its possession of "the power of remaining for a good long period constant . . . combined with an appreciable amount of difference."[13] One of the most striking of these cases is that of the "japanned" or "black-shouldered" peacocks which have occasionally appeared "suddenly in flocks of the common kind," which "propagate their kind quite truly," which, according to good authority, "form a distinct and natural species," and which tend "at all times and in many places to reappear."[14] Mr. Darwin rejects the idea that these birds are the result of hybridization and reversion and declares in favor

[10] "Origin of Species," 6th ed., 1882, p. 413.

[11] *Ibid.*, p. 28.

[12] "Animals and Plants under Domestication," 2d ed., 1875, Vol. I, p. 96. See also, Vol. II, pp. 189–90.

[13] "More Letters of Charles Darwin," 1903, Vol. I, p. 252.

[14] "Animals and Plants under Domestication," 2d ed., 1875, Vol. I, pp. 305–7.

of their being "a variation induced by some unknown cause," and says that "on this view the case is the most remarkable one ever recorded of the abrupt appearance of a new form which so closely resembles a true species that it has deceived one of the most experienced of living ornithologists." In all points this case agrees with the modern idea of a mutation, even in the respect that it comes from a family of birds not usually considered very variable.

Concerning fowls Mr. Darwin remarks that

> Fanciers, whilst admitting and even overrating the effects of crossing the various breeds, do not sufficiently regard the probability of the occasional birth, during the course of centuries, of birds with abnormal and hereditary peculiarities. Whenever, in the course of past centuries, a bird appeared with some slight abnormal structure, such as with a lark-like crest on its head, it would probably often have been preserved from that love of novelty which leads some persons in England to keep rumpless fowls and others in India to keep frizzled fowls. And after a time any such abnormal appearance would be carefully preserved from being esteemed a sign of the purity and excellence of the breed; for on this principle the Romans eighteen centuries ago valued the fifth toe and the white ear-lobe in their fowls.[15]

But Mr. Darwin's cases of what we must regard as saltations are not confined to the animal kingdom. We might easily cull from his list numerous more or less pertinent examples under the peach, plum, cherry, grape, gooseberry, currant, pear, apple, banana, camellia, cratægus, azalea, hibiscus, althæa, pelargonium, chrysanthemum, dianthus, rose and perhaps other plants. Concerning useful and ornamental trees he says: "All the recorded varieties, as far as I can find out, have been suddenly produced by one single act of variation,"[16] and as to roses, he remarks on their marked tendency to "sport" and to produce varieties "not only by grafting and budding, but often by seed," and quotes Mr. Rivers as saying that "whenever a new rose appears with any peculiar character, however produced, if it yielded seed" he "ex-

[15] "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 242–4.
[16] *Ibid.*, p. 384.

pects it to become the parent of a new family." In this connection Mr. Darwin called attention to the now well-known fact that the mutative tendency is an inheritable one by citing the case of the common double moss-rose, imported into England from Italy about the year 1735, which "probably arose from the Provence rose (*R. centifolia*) by bud-variation," the White Provence rose itself having apparently originated in the same way.[17] He also called attention to the significant fact that many abrupt variations were not to be attributed either to reversion or to the splitting-up of hybrids. Thus he declares:

> No one will maintain that the sudden appearance of a moss-rose on a Provence rose is a return to a former state, for mossiness of the calyx has been observed in no natural species; the same argument is applicable to variegated and laciniated leaves; nor can the appearance of nectarines on peach-trees be accounted for on the principle of reversion.[18]

Further on in the same work he says:

> Many cases of bud-variation . . . can not be attributed to reversion, but to so-called spontaneous variability, as is so common with cultivated plants raised from seed. As a single variety of the chrysanthemum has produced by buds six other varieties, and as one variety of the gooseberry has borne at the same time four distinct kinds of fruit, it is scarcely possible to believe that all these variations are due to reversion. We can hardly believe . . . that all the many peaches which have yielded nectarine-buds are of crossed parentage. Lastly, in such cases as that of the moss-rose, with its peculiar calyx, and of the rose which bears opposite leaves, in that of the Imantophyllum, &c., there is no known natural species or variety from which the characters in question could have been derived by a cross. We must attribute all such cases to the appearance of absolutely new characters in the buds. The varieties which have thus arisen can not be distinguished by any external character from seedlings. . . . It deserves notice that all the plants which have yielded bud-variations have likewise varied greatly by seed.[19]

Now, Darwin was here treating of saltations among cultivated plants, but it is instructive to read in this con-

[17] "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 405–6.

[18] *Ibid.*, Vol. II, p. 242.

[19] "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 439–40.

nection the following passage in which he prepares the ground for a belief in the possibility of similar abrupt and wide variations under natural conditions. He remarks:

> Domesticated animals and plants can hardly have been exposed to greater changes in their conditions of life than have many natural species during the incessant geological, geographical, and climatal changes to which the world has been subject; but domesticated productions will often have been exposed to more sudden changes and to less continuously uniform conditions. As man has domesticated so many animals and plants belonging to widely different classes, and as he certainly did not choose with prophetic instinct those species which would vary most, we may infer that all natural species, if exposed to analogous conditions, would, on an average, vary to the same degree.[20]

But now let us take a specific example of spontaneous variability which deeply impressed Mr. Darwin. It is a case which was brought to his attention in 1860 by Professor W. H. Harvey concerning *Begonia frigida*, as to which Mr. Darwin says:

> This plant properly produces male and female flowers on the same fascicle; and in the female flowers the perianth is superior; but a plant at Kew produced, besides the ordinary flowers, others which graduated towards a perfect hermaphrodite structure; and in these flowers the perianth was inferior. To show the importance of this modification under a classificatory point of view, I may quote what Professor Harvey says, namely, that had it "occurred in a state of nature, and had a botanist collected a plant with such flowers, he would not only have placed it in a distinct genus from *Begonia*, but would probably have considered it as the type of a new natural order." . . . The interest of the case is largely added to by Mr. C. W. Crocker's observation that seedlings from the *normal* flowers produced plants which bore, in about the same proportion as the parent-plant, hermaphrodite flowers having inferior perianths.[21]

This was written in the first edition of "Animals and Plants under Domestication" (1868) and was allowed to stand in the second and last edition (1875). In both editions, however, Mr. Darwin made the statement in an entirely different part of the work, that "the wonderfully anomalous flowers of *Begonia frigida*, formerly described, though they appear fit for fructification, are

[20] *Ibid.*, Vol. II, pp. 401–2. See also *ibid.*, Vol. II, p. 278.

[21] "Animals and Plants Under Domestication," 2d ed., Vol. I, p. 389.

sterile."[22] The last point, however, does not invalidate the claim to this new type of Begonia as a mutant, since the facts which determine its position in this regard are, first, the sudden appearance of the form bearing three kinds of flowers and, second, the production by seed of descendants also bearing three kinds of flowers.

It is very evident that this case troubled Mr. Darwin, for he referred to it a number of times and did not relish Professor Harvey's assertion that "such a case is hostile to the theory of natural selection, according to which changes are not supposed to take place *per saltum*," and Harvey's further declaration that "a few such cases would overthrow it (natural selection) altogether."[23] Sir Joseph Hooker attempted to explain the matter so as to weaken Professor Harvey's argument against the doctrine of natural selection, but Darwin himself wrote Hooker, saying:

> As the "Origin" now stands Harvey is a good hit against my talking so much of the insensibly fine gradations; and certainly it has astonished me that I should be pelted with the fact that I had not allowed abrupt and great enough variations under nature. It would take a good deal more evidence to make me admit that forms have *often* changed by *saltum*.

About the same time, namely early in 1860, Darwin wrote to Lyell on this subject, saying:

> It seems to me rather strange; he (Harvey) assumes the permanence of monsters, whereas monsters are generally sterile and not often inheritable. But grant this case, it comes that I have been too cautious in not admitting great and sudden variations.[24]

There is an added point of interest about this discussion in the fact that it is the earliest record in print of the consideration of saltation or mutation by Mr. Darwin.

You have doubtless noticed Mr. Darwin's protest against the belief in the occurrence of important changes "*per saltum.*" He uses this expression with disapproval a number of times and yet his condemnation of

[22] *Ibid.*, 1st ed., Vol. II, p. 166. Also *ibid.*, 2d ed., Vol. II, p. 150.
[23] "Life and Letters," 1886, Vol. II, p. 274.
[24] *Ibid.*, p. 275. Also, "More Letters," 1903, Vol. I, p. 141.

the idea involved is not entirely unqualified, as is shown by the following significant statement:

> On the theory of natural selection we can clearly understand the full meaning of the old canon in natural history, "Natura non facit saltum." This canon, if we look to the present inhabitants alone of the world, is not strictly correct; but if we include all those of past times, whether known or unknown, it must on this theory be strictly true.[25]

This I understand to be in effect a protest against deducing proof of separate creations from the imperfection of the geological record, coupled with an admission that saltation or mutation does, at least occasionally, occur among existing living forms. I trust you perceive the importance of the concession that *natura non facit saltum* is not strictly correct as applied to *the present inhabitants of the world.*

Having noticed Mr. Darwin's repeated use of the words *per saltum,* I now wish to revert to his frequent use of the words *monster* and *monstrosity* and to call your attention to the fact that they are not always employed with exactly the same meanings. Sometimes by "monstrosity" he evidently intends to indicate a mere deformity of the nature of an accidental injury, or aborted or perverted development, but more generally he refers to a deviation from type wide enough, or discontinuous enough, to exclude it from the category of variations to which he supposed the operation of natural selection must be confined. Among domesticated animals and plants, however, the word monster as used by him often meant no more than the word "sport." In most cases when he used this term or one of its derivatives he took care to explain that monstrosities could not be qualitatively separated from other kinds of variations. Thus, in writing to R. Meldola, in 1873, he says:

> It is very difficult or impossible to define what is meant by a large variation. Such graduate into monstrosities or generally injurious variations. I do not myself believe that these are often or ever taken advantage of under nature.[26]

[25] "Origin of Species," 6th ed., p. 166. See also *ibid.,* pp. 156. 234, 414.

[26] "More Letters," 1903, Vol. I, p. 350.

In the "Origin of Species" he wrote:

> At long intervals of time, out of millions of individuals reared in the same country and fed on nearly the same food, deviations of structure so strongly pronounced as to deserve to be called monstrosities arise; but monstrosities cannot be separated by any distinct line from slighter variations.[27]

He frequently repeats this statement and it is quite clear that he intends to convey the idea that all variations are merely quantitative; at any rate he failed to adopt a nomenclature that would enable his readers to judge as to the degrees of difference he meant to indicate by such adjectives as "insensible," "minute," "slight," "large," "wide," "sudden" and "abrupt," as applied to variations. I am convinced, however, that he had in mind an idea that there were two different kinds of variations, namely, first, what he oftenest called "individual variations," by which he referred to the ordinary differences between the single organisms of the same group, or what mutationists now call "fluctuations," and, second, those radical and generally extensive deviations from type which constitute an actual break with the species, variety or race, and which are substantially what we of these later times have named "mutations." There are places in Darwin's works where the two kinds of variation just mentioned are spoken of as "indefinite" and "definite" and as results, respectively, of the *indirect* and the *direct* action of the conditions of life, and once only, I think, he uses the term "*fluctuating variability*" as synonymous with *indefinite* variability.[28] Now I do not assume to say that the recognition of these distinctions by Mr. Darwin proves that he clearly foresaw the present-day mutation theory with its foundation in the principle of unit characters, but I think it is true that he had at least a glimpse of the coming modifications

[27] "Origin of Species," 6th ed., p. 6, also p. 33. See also "Animals and Plants Under Domestication," 2d ed., Vol. I, pp. 312, 322. Also "More Letters," 1903, Vol. I, p. 318.

[28] "Animals and Plants Under Domestication," 2d ed., Vol. II, pp. 280, 281, 345.

to be required in his own theory to meet the then dawning truth. De Vries declares that his own field researches and testing of native plants are based "on the hypothesis of unit-characters as deduced from Darwin's Pangenesis," which conception, De Vries points out, "led to the expectation of two different kinds of variability, one slow and one sudden."[29]

But the main point I wish to dwell upon at present is that Darwin recognized, at least dimly, a kind of variability the results of which were essentially different from the "individual" or "indefinite" variations, which mistakenly seemed to him alone capable of being acted upon by selection. He was sorely puzzled by what he saw and realized in this direction, for he had spent more than twenty years of intense thought in elaborating his theory that new species were evolved from older ones by the gradual building up of new characters from extremely small differences, and he feared that the admission of saltation in any form meant the undermining of the foundations he had labored so hard to construct. He had once said:

> When we remember such cases as the formation of the more complex galls, and certain monstrosities, which cannot be accounted for by reversion, cohesion, &c., and sudden strongly-marked deviations of structure, such as the appearance of a moss-rose on a common rose, we must admit that the organization of the individual is capable through its own laws of growth, under certain conditions, of undergoing great modifications, independently of the gradual accumulation of slight inherited modifications.[30]

In the last edition of the "Origin of Species," however, which was published in the year of the author's death, although he introduces this apology: "In the earlier editions of this work I underrated, as it now seems probable, the frequency and importance of modifications due to spontaneous variability,"[31] he still later inter-

[29] "Species and Varieties, their Origin by Mutation," 2d ed., 1906, p. 689.

[30] "Origin of Species," 5th ed., 1869, p. 151.

[31] "Origin of Species," 6th ed., 1882, p. 171.

polates the following rather sweeping recantation:

> There are, however, some who still think that species have suddenly given birth, through quite unexplained means, to new and totally different forms; but, as I have attempted to show, weighty evidence can be opposed to the admission of great and abrupt modifications. Under a scientific point of view, and as leading to further investigation, but little advantage is gained by believing that new forms are suddenly developed in an inexplicable manner from old and widely different forms, over the old belief in the creation of species from the dust of the earth.[32]

In this sixth, and last, edition of the "Origin of Species" Mr. Darwin devotes to the task of answering criticisms made by St. George Mivart far more space than he had ever allowed to any other one critic and the passage just read is evidently one of those inspired by Mr. Mivart's attacks. The sore point with Mr. Darwin at that time was the doctrine of natural selection and, as I have already remarked, he had adopted the erroneous belief that this important principle must be greatly weakened if not entirely sacrificed if any form of saltation was to be admitted in nature. He had, therefore, wavered between his loyalty to his cherished hypothesis and his fearless devotion to truth. By this time, however, he had so long contemplated the possibility of the origin of new species and varieties through single long steps and had had so many convincing examples brought to his attention, that his hesitancy and doubt concerning the validity and sufficiency of the arguments urged in favor of this mode of evolution were ready to give way, and I regard the passage, which I am about to quote, as a virtual surrender on this point. The fact that, in this emphatic form, it was written at the close of his life, as his last word on this subject, and that he must have felt that it contained a concession very damaging to the theory to the establishment of which that life had been devoted, gives it, in my mind, a deeply pathetic significance. Mr. Darwin says:

[32] "Origin of Species," 6th ed., 1882, p. 424.

It appears that I formerly underrated the frequency and value of [variations which seem to us in our ignorance to arise spontaneously] as leading to permanent modifications of structure independently of natural selection. But as my conclusions have lately been much misrepresented, and it has been stated that I attribute the modification of species exclusively to natural selection, I may be permitted to remark that in the first edition of this work, and subsequently, I placed in a most conspicuous position—namely, at the close of the Introduction—the following words: "I am convinced that natural selection has been the main but not the exclusive means of modification." This has been of no avail. Great is the power of steady misrepresentation; but the history of science shows that this power does not long endure.[33]

The sting of this vehement declaration is in the underlying implication that the limitation placed upon the applicability of natural selection was deemed necessary because of Mr. Darwin's inability to free his mind from the belief that it could not act upon large and sudden variations as well as upon small and unimportant ones. This point of view seems illogical when we consider his repeated declaration that no qualitative distinction could be established between the two kinds of variation, but it may be partially accounted for by the fact that a slight confusion at times existed in his mind concerning the general *modus operandi* of natural selection, through which he attributed to it a *causal* power as well as a mere sifting effect. Both Lyell and Wallace took him to task for this double use of the term and, therefore, in the third edition of "the Origin" he attempted to clear up this point by means of this statement:

Several writers have misapprehended or objected to the term natural selection. Some have even imagined that natural selection even *induces* variability, whereas it implies only the preservation of such variations as arise and are beneficial to the being under its conditions of life.[34]

Nevertheless, almost side by side with this explanation we find in the last edition of "the Origin," the following sentences which were allowed to come down from the first edition: "Natural Selection will *modify* the

[33] "Origin of Species," 6th ed., p. 421. See also, "Life and Letters," 1886, Vol. III, p. 243, and "More Letters," 1907, Vol. I, p. 389.

[34] "Origin of Species," 3d ed., 1861, p. 84.

structure of the young in relation to the parent, and of the parent in relation to the young.''[35] ''Natural Selection . . . will *destroy* any individual departing from the proper type.''[36] If Darwin had adopted the simile of a sieve, so effectively used by De Vries, he would have drawn nearer to the recognition of the fact of ''selection *between* species,'' even if he had not been prepared to assent to De Vries's counter proposition that there is no ''selection *within* the species.'' He might also have escaped some of his apprehensions concerning the fate of adaptation, which he thought to be endangered by a belief in saltation; for the fact is that adaptedness is only another name for fitness, and this is a quality inherent in the organism and precedent to selection—that is to say, natural selection merely sifts out for preservation the *adapted* or fit, allowing the unadapted or unfit to perish. Now, it is impossible to see why forms both adapted and unadapted to their environment may not arise through mutation and thus be offered to the operation of selection. In fact, Mr. Darwin has supplied us with a good illustration of such a case in a rather naïve passage which has run through every edition of ''the Origin,'' to the following effect:

> One of the most remarkable features in our domesticated races is that we see in them adaptation, not indeed to the animal's or plant's own good, but to man's use or fancy. Some variations useful to him have probably arisen suddenly, or by one step; many botanists, for instance, believe that the fuller's teasel, with its hooks, which can not be rivaled by any mechanical contrivance, is only a variety of the wild Dipsacus; and this amount of change may have suddenly arisen in a seedling.[37]

Surely, if Mr. Darwin could have looked at this case with a perfectly free mind, he must have perceived that the teasel's adaptation to man's needs would not have fallen if man had failed to exercise his power of selection; and that the adaptation was not weakened by the fact that it arose by a mutation. But that he was uncon-

[35] *Ibid.*, 6th ed., 1882, p. 67.

[36] *Ibid.*, 6th ed., 1882, p. 81.

[37] ''Origin of Species,'' 6th ed., p. 22.

sciously biased in this matter is shown by an extract from a letter written to Asa Gray, in 1860, in which he says:

> I reflected much on the chance of favorable monstrosities (*i. e.*, great and sudden variation) arising. I have, of course, no objection to this, indeed it would be a great aid, but I did not allude to the subject [*i. e.*, in "the Origin"] for, after much labor, I could find nothing which satisfied me of the probability of such occurrences. There seems to me in almost every case too much, too complex, and too beautiful adaptation, in every structure, to believe in its sudden production.[38]

The idea involved in this passage is that adaptation is *produced*—rather than *preserved*—by natural selection and that, as natural selection must, according to Mr. Darwin's curious prepossession, act only upon slow and small changes of character, adaptation itself must necessarily be in every case a matter of gradual growth. This sort of argument appears to justify the fear shared by both Lyell and Hooker that Darwin was at times disposed to stake his whole case on the maintenance of an unnecessary assumption. Hooker wrote him as early as 1859 or 1860 that he was making a hobby of natural selection and overriding it, since he undertook to make it account for too much.[39] Darwin mildly protested that he did not see how he could do more than he had done to disclaim any intention of accounting for everything by natural selection.[40] In this discussion, however, it is apparent that while Darwin was overloading the theory of natural selection with a responsibility for the origin of the adapted or fit, he was at the same time unduly limiting it to only one class of the fit, namely those which had arisen by slow degrees. If he had taken the position that natural selection could and would operate upon any kind or any degree of variability, he need not to have imagined that his main doctrine was in jeopardy.

But though Mr. Darwin could be stirred by attack to a vigorous defense, and sometimes even to an *over*-defense, of natural selection, he contended, at other times, with equal vigor, that his main interest was with varia-

[38] "Life and Letters," 1887, Vol. II, p. 333.

[39] "More Letters," 1903, Vol. I, p. 135.

[40] *Ibid.*, Vol. I, pp. 172, 213.

tion, however produced, which was the necessary basis of the whole evolutionary process. He admitted, however, that the cause of variation was to him inexplicable and, like all beginnings, it remains to this day a deep mystery. Darwin said of it:

> Our ignorance of the laws of variation is profound. Not in one case out of a hundred can we pretend to assign any reason why this or that part has varied.[41]

In another place he remarks:

> When we reflect on the millions of buds which many trees have produced before some one bud has varied, we are lost in wonder as to what the precise cause of each variation can be.[42]

He never definitely undertook to solve this mystery, though he reflected and reasoned on it much. The nearest he came to formulating a law concerning it was the expression of his conviction that variability was more a matter of organic constitution than a result of external agencies. Thus he declares:

> If we look to such cases as that of a peach tree which, after having been cultivated by tens of thousands during many years in many countries, and after having annually produced millions of buds, all of which have apparently been exposed to precisely the same conditions, yet at last suddenly produces a single bud with its whole character greatly transformed, we are driven to the conclusion that the transformation stands in no *direct* relation to the conditions of life.[43]

From examples like this Mr. Darwin deduced a "general rule that conspicuous variations occur rarely, and in one individual alone out of millions, though all may have been exposed, as far as we can judge, to nearly the same conditions"[44] and while this is, in a general way, in accordance with the admission of De Vries that although mutations are "not so very rare in nature,"[45] the numbers "under observation are as yet very rare,"[46] we shall see a little later that Mr. Darwin's deduction is not

[41] "Origin of Species," 6th ed., p. 131.
[42] "Animals and Plants Under Domestication," 2d ed., Vol. II, p. 281.
[43] *Ibid.*, 2d ed., Vol. I, p. 441. See also, *ibid.*, Vol. II, pp. 277, 279, 282.
[44] "Animals and Plants Under Domestication," 2d ed., Vol. II, p. 276.
[45] "Species and Varieties, their Origin by Mutation," 2d ed., p. 597.
[46] *Ibid.*, p. 8.

strictly accurate since it excludes the idea of a whole genus or species or variety mutating at once.

While on this subject, I may mention that Mr. Darwin anticipated the doctrine of the mutationists to the effect that "when the organization has once begun to vary, it generally continues varying for many generations."[47] But as to variability having periods of activity Mr. Darwin's opinion seems to have been unsettled. In a letter to Weismann, in 1872, he remarks on the strangeness "about the periods or endurance of variability,"[48] but in a letter to Moritz Wagner, in 1876, he says:

> Several considerations make me doubt whether species are much more variable at one period than at another except through the agency of changed conditions. I wish, however, that I could believe in this doctrine, as it removes many difficulties.[49]

Practically this is the dilemma of the mutationists of the present day: they are not in a position to prove that plants and animals have periods of mutation, but they assume that it must be so, because the belief "removes many difficulties."

One of Darwin's perplexities, however, has been explained away, as I have already pointed out, by the discovery that mutation is not confined to a single case out of millions of individual forms, nor even to a single generation out of a long genetic line, but that, as in the case of the Œnotheras (evening primroses), a whole genus is likely to be in a mutating condition at the same time, producing from each of several species numberless individual mutants, which are themselves often in a mutating condition, the parent stock meanwhile remaining perfectly constant. Such has been the case with *Œnothera* (*Onagra*) *lamarckiana,* which, while throwing off, since it has been under scientific observation, in large numbers not less than a dozen elementary species and retrograde varieties, has bred true to its original type through at least one hundred and sixteen years, although there is

[47] "Origin of Species," 6th ed., p. 5.

[48] "Life and Letters," 1886, Vol. III, p. 155.

[49] *Ibid.,* p. 158.

considerable proof that it is itself a mutant from *Œnothera grandiflora,* and none whatever for the assertion, often made, that it is a hybrid. As at least nine of its mutants have also bred true through many generations in pedigree cultures and doubtless had been constant forms for a long time in a state of nature, there appears to be no ground for Darwin's fear that, granting the occurrence of mutation, the mutants would be liable to speedy extermination through inability to propagate. Of course this would not be the case with even a single self-fertilizing plant and it would not be true with animal mutants if, like plant mutants, they were produced in numbers by the mutating stock. As to swamping by intercrossing, it has been shown that, under Mendel's law, in the extreme case of the production of a solitary mutant obliged to cross with the parent form, if it possesses characteristics having a certain relation to the parent, it can establish a race like itself and even supplant the parent form, if it is only *as well* fitted for the battle of life as is the progenitor.[50]

If Darwin had known these facts he would not have written, or he would have greatly amended, the following passage:

> He who believes that some ancient form was transformed suddenly through an internal force or tendency into, for instance, one furnished with wings, will be almost compelled to assume, in opposition to all analogy, that many individuals varied simultaneously. It can not be denied that such abrupt and great changes of structure are widely different from those which most species apparently have undergone. He will further be compelled to believe that many structures beautifully adapted to all the other parts of the same creature and to the surrounding conditions, have been suddenly produced; and of such complex and wonderful co-adaptations, he will not be able to assign a shadow of an explanation. He will be forced to admit that these great and sudden transformations have left no trace of their action on the embryo. To admit all this is, as it seems to me, to enter into the realms of miracle, and to leave those of science.[51]

Of course Mr. Darwin was not entirely oblivious to the fact that every important advance in knowledge must

[50] See Lock's "Variation, Heredity and Evolution," 1906, p. 205.

[51] "Origin of Species," 6th ed., p. 204. See also, *ibid.,* p. 202.

have the appearance, at first, of a move into a region of mystery and uncertainty. The lapse of time and the growth of familiarity with it are necessary to the reclamation of a *terra incognita.*

Before leaving this branch of my subject, I desire to call your attention to the very interesting fact that Mr. Darwin himself once conducted a long series of experiments which, it can hardly be doubted, resulted in the production of mutants and that he just missed the discovery of principles which are now the basis of scientific pedigree cultures and are occupying the attention of investigators of the problems of variation and heredity. In a letter to J. H. Gilbert, dated February 16, 1876, Mr. Darwin writes:

> Now, for the last ten years I have been experimenting in crossing and self-fertilizing plants; and one indirect result has surprised me much, namely, that by taking pains to cultivate plants in pots under glass during several successive generations, under nearly similar conditions, and by self-fertilizing them in each generation, the colour of the flowers often changes, and, what is very remarkable, they became in some of the most variable species, such as Mimulus, Carnation, &c., quite constant, like those of a wild species. This fact and several others have led me to the suspicion that the cause of variation must be in different substances absorbed from the soil by these plants when their powers of absorption are not interfered with by other plants with which they grow mingled in a state of nature.[52]

The point I particularly wish you to notice in this case is that Mr. Darwin was employing practically the methods now used by Professor De Vries, Professor MacDougal and others who are engaged in species testing, by growing naturally variable or mutating plants under conditions of rigid control, so as to exclude crossing or, as De Vries calls it, *vicinism.* In this view of the matter, it would be interesting to know what percentage of Mr. Darwin's plants exhibited the new and constant characters and through how many generations his mutants were found to breed true, for then we could compare his results with those of investigators of our day. But his attention was centered upon the endeavor to find a cause

[52] "Life and Letters," 1886, Vol. III, p. 343.

for the abrupt variations and not on the formulation of laws of their action. Apparently he considered isolation to be the principal secondary cause or favoring condition, upon which view the obvious comment is that it requires no great stretch of imagination to conceive of similar isolation as occurring in nature and thus favoring mutation among uncultivated forms.

Having now hastily reviewed the oscillations in Darwin's opinions concerning the kinds, the causes and the laws of variation with relation to the origin of species, it is not my purpose to enter upon a discussion of the present-day mutation theory, which has grown out of a closer study, and a more scientific treatment, of the problems of variation and heredity than were attempted, or were perhaps possible in Darwin's time. It is desirable, however, to compare Darwin's views with generalizations from the mutation theory, which we can do, well enough for our present purpose, by merely recalling the seven laws which De Vries claims to be the logical outcome of his twenty years of cultural experiments upon plants. They are, with slight modifications as to wording and order, as follows:

1. New elementary species appear suddenly without intermediate steps.
2. New forms spring laterally from the main stem.
3. New elementary species attain their full constancy at once.
4. Some of the new strains are elementary species, while others are to be considered as retrograde varieties.
5. The same new species are produced in a large number of individuals.
6. Mutations take place in nearly all directions and are due to unknown causes.
7. Species and varieties have originated by mutation, but are, at present, not known to have originated in any other way.

Now, looking back over what Darwin wrote concerning variation, I can not believe that he would seriously have

disputed any of De Vries's propositions except the last. All would have had to stand or fall with that. He recognized the fact that new species had sometimes appeared suddenly without intermediate steps and that the new forms had sprung laterally from the main stem. I think he also substantially admitted that such new species attained their full constancy at once. As to the fourth affirmation of De Vries, with reference to elementary species and retrograde varieties, Darwin had no knowledge, for the distinction is original with De Vries. Darwin believed, as a general proposition, that "species are only strongly marked and permanent varieties, and that each species first existed as a variety,"[53] but, of course, in admitted cases of mutation this can not be true; and if Darwin had been obliged to concede De Vries's seventh proposition, the fourth might well have been allowed to go with it. The same is doubtless the case concerning De Vries's fifth law, which sets forth in effect that similar mutants are thrown off by many individuals of the same species at about the same time. As we have already seen, Mr. Darwin was convinced that if, for example, he were to admit the origin by mutation of a species of flying animal, for the reasons urged by Mr. Mivart, he would be compelled to assume "that many individuals varied simultaneously." I, therefore, do not see that he would have been interested, from a theoretical point of view, in disputing either of the two last-named declarations of De Vries except in connection with his seventh and last law, to which I shall presently refer. The sixth law of De Vries, which affirms that mutations take place in nearly all directions, is practically the equivalent of Darwin's first law that all organisms vary continually and in every part of their structure, provided it is agreed that mutations are only quantitatively different from Darwin's "individual variations," which was Darwin's own view. In so far as Darwin admitted the occurrence of mutation at all, he must have agreed that it could proceed in any

[53] "Origin of Species," 6th ed., 1882, p. 412.

direction. But now we come to the conclusion of De Vries which we know Darwin would not have accepted, at least in its entirety. As we have seen, he was compelled to concede that what we now call mutation had occasionally taken place and become the starting point of new races, but he was none the less unshaken in the conviction that this process was exceptional and extraordinary, and that, as a rule, a new species originated by the gradual building up of minute and even insignificant deviations from the average characters of an old species, which deviations we now call fluctuations. We know with what tenacity he held this view to the end of his life. For the doctrine of "insensible gradations," which touched mainly a minor premise in his general argument for evolution, Mr. Darwin was, unhappily, almost willing to relinquish the essence of the whole matter, which was his claim to the discovery of a *vera causa* in the evolutionary process. Notwithstanding the prior claim of Patrick Matthew, and the partial anticipation of Alfred R. Wallace and others, the establishment of the theory of natural selection was Mr. Darwin's most original and greatest achievement. Time has proved that he could have afforded to stand upon the general validity and applicability of this theory though every step in his argument in its favor had needed review and modification; for each passing year but adds to the impregnable mass of proofs by which it is affirmed and supported. Properly regarded, the mutation theory does not antagonize nor weaken the doctrine of natural selection—on the contrary, it merely offers itself as a helpful substitute for, or adjunct to, one of Darwin's subordinate steps in the approach to a consistent philosophy of the origin of species, leaving the last great cause of evolution as efficient as ever. It is, therefore, one of the tragedies of science that in this matter Darwin should have been ready to surrender his main position rather than to receive and to join forces with those who were coming to his aid, but whom he failed to recognize as friends.