

## MUTATIONS IN HEREDITY<sup>1</sup>

**S**INCE the publication of the two volumes of my "Mutation Theory" ten years have elapsed. At that time the prevailing opinion was that very small and often even invisible changes could gradually be increased and accumulated, and that this process could lead to specific differences, and even to the production of the characters of genera and larger groups. This conception was the principle of the theory of selection as proposed by Darwin, as well as the starting-point for the hypothesis of orthogenesis, of the direct influence of environment, and of many others. It was generally accepted in the teachings of plant improvement in agriculture, and, as a matter of fact, the origin of new varieties by leaps and bounds was a fact well known only to horticulturists.

In opposition to this conception, I tried to show that the origin of new forms complies, in nature as well as in agriculture, to the mode which was observed to be followed in horticulture, and that the whole evolution of the plant kingdom has been brought about by a long series of successive small leaps. The extraordinarily slow evolution which was a necessary consequence of the then prevailing opinion required an almost unlimited duration of time; but the new principle of mutations reduced the biological time to the limits which had been determined by physicists and geologists for the duration of life on this earth. The starting-point for the new ideas was the distinction between two main types of

<sup>1</sup> A lecture delivered at the inauguration of the Rice Institute, by Professor Hugo de Vries, Director of the Hortus Botanicus and Professor of Botany in the University of Amsterdam.

variability: fluctuation and mutation. I had deduced this principle from my interpretation of Darwin's well known provisional hypothesis of pangenesis, and convinced myself of its truth by means of a series of experiments. On the basis of these theoretical considerations I proposed the mutation theory, which means that the characters of all organisms are built up of sharply distinguished units. These qualities may be combined into groups, and in allied species the same units and groups may be met with. They do not pass gradually into one another; transitions fail between them, although they may often be observed between the external forms of plants and animals.

The changes in the number and the position of these units, as well as those in their relative connections, constitute the domain of mutability. They are the causes of discontinuous variation, or of the sudden appearance of externally visible deviations. The steps are, as a rule, only small ones; but are inherited as such from the very beginning, without transitions. Apart from these, the different organs and qualities continually vary in number as well as in measure and weight. In doing so they are observed to follow the laws of probability and to be influenced by external factors; favorable conditions may increase them in one way, while unfavorable circumstances may determine their augmentation in the opposite direction. Such changes are described as fluctuations or as fluctuating variability. On the basis of the investigations of Quetelet, their laws have been very completely studied. All these phenomena are governed by internal as well as by external causes. The internal ones are given by the hereditary units and determine the nature of the changes which may take place; while the external factors decide when and to what extent the deviations from the average will occur.

As well as fluctuations, mutations are induced by external and internal causes, as I have distinctly pointed out. The determination of these, however, is far more difficult than in the case of fluctuations. It is only in a general way that my experiments show that mutability may be increased by favorable conditions of life. In connection with this fact, we may assume that, in nature, the origin of new forms is not due to a hard struggle, but is promoted by a luxuriant environment and by easy conditions of development. It is true that a struggle for life must be; but this comes in after the new forms have already been produced, and, as it seems, often only after a considerable lapse of time. Such a struggle for life demands no greater sacrifices than those which are unavoidable, even under the common conditions of the field; while in the old selection theory the sacrificing of thousands of lives was required for every step in progressive development.

In the last ten years the principle of character units has gained a firm hold for itself in evolutionary science. It has transferred the problems from the domain of speculation to that of experiment, and has brought the teachings of Mendel (which had been disregarded up to that time) to universal acknowledgment. The generally accepted view of the continuous intergradation of characters into one another had for a long time been in the way of a broad appreciation of the merits of the principle of Mendel; but the theory of pangenesis has led me to experiments in hybridization which fully confirmed the results of Mendel, and clearly showed their high importance. Moreover, the lines of research laid down by Mendel proved to be of easy application to an almost unlimited number of cases, and so the study of the last ten years has turned in the main to them, and thereby to

a great extent neglected the direct investigation of the origin of new forms.

The theory of mutation is not intended to take the place of the theory of selection of Darwin. It is only one step further in the development of our appreciation of evolutionary phenomena. The problem of the theory of selection is the explanation of the overwhelming richness of living forms in nature. It has succeeded in bringing this under the grasp of our understanding; but it has the disadvantage of easily conducing to poetical speculations whenever one tries to apply the general views to single cases. In such cases many authors are content with hypothetical descriptions of what the relations of the phenomena may be supposed to be. Contrary to this method, the theory of mutation deals with the problem of the origin of the material from which natural selection chooses. At the time of Darwin the distinction between fluctuation and mutation had not yet been discovered; but as soon as this was the case it was clear that only the latter process could supply the material for further selection. This principle at once got rid of numerous difficulties which up to that period seemed to be inherent in the teachings of Darwin.

Among those who supported the new theory in its first years, although with some reserve, I cite in the first place Strasburger, who wrote as early as 1902 "that the formation of species does not start from fluctuating variability, but from mutations," and that especially "for the place of an organism in the natural system the degree of development reached by all the successive mutations is decisive."<sup>1</sup> He was soon followed by the larger part of the botanists, although many among them took exception for the adaptation of species to their environment.

<sup>1</sup> "Jahrb. f. wiss. Bot.," T. 37, 1902, p. 518.

Among paleontologists, Charles A. White was the first to take publicly the side of the theory of mutation,<sup>1</sup> and the most prominent representatives of this science soon adhered to his ideas. It might perhaps be said that in no other domain has the new principle been so rapidly and so generally acknowledged. Here numerous facts are in evident contradiction to the idea of an extremely slow evolution among fossil plants as well as animals. Other facts clearly show "that the degree of mutability of species has not always been the same during the geological periods of their existence, but is evidently subjected to changes" (p. 638). This sentence corresponds exactly to my conception of periods of mutability. Life before the Cambrian times is wholly unknown to us; but in this period all the main branches of the animal kingdom at once make their appearance, with the exception of the vertebrates only. Only by means of very complicated hypotheses could the old conception explain these broad facts. Among the floras of all times that of the Carboniferous period has without any doubt been by far the richest; it appeared suddenly, and afterward disappeared almost at once. Many types of organisms have escaped the changing influence of natural selection during a long succession of geological times, as, for instance, the genus *Unio*, which has come to us almost without any modification from the Mesozoic period. In the Tertiary layers of Florida, Dall has pointed out the occurrence of numerous forms which have come over from one period into the succeeding one, and which are still in part among living species. The evolution of the pedigree of the vertebrates during Tertiary times has been an exceedingly rapid one—by far too fast to be compatible with the old view of slow improvement. The same conclusion holds good for birds, for fishes, for

<sup>1</sup> Smithsonian Report for 1903, pp. 631-640.

phanerogamic plants, and for quite a number of smaller groups. All in all, the geological facts plead against a slow and for a relatively rapid evolution, thereby justifying the conception of modification by leaps. Such were the arguments of White, but it would take me too long to cite them in all their details.

In the domain of zoölogy the old and the new conception are still sharply opposed. The new ideas easily comply with the celebrated theory of Hubrecht concerning the evolution of the pedigree of the vertebrates, and the author of this view has more than once vigorously supported my ideas. On the other hand, Plate is still among the adherents of the validity of the unmodified theory of selection.

In the field of agriculture the new conceptions are found to be in full harmony with the experience of Hjalmar Nilsson, the director of the Swedish agricultural experiment station at Svalöf. By means of elaborate experiments this investigator has shown that a selection of fluctuating differences has no value at all for the improvement of agricultural plants, especially cereals; and that all breeding of new races must start from a careful choice of the best among the elementary races, which are found in the present cultivated varieties. The unexpectedly large results which this method has rapidly produced have gained for it a general acknowledgment in agricultural circles, and the principle of slow improvement of races has since been replaced almost wholly by that of the choice of single mother-plants ("*enstaka moderplanterna*") and of the cultivation of pure races from their seed.

But still there is always much discussion and much opposition, and therefore it may be useful to give a short review of the main arguments which seem to plead against the new theory. Before doing so, I might, however, point out two

volumes which, from different points of view, deal with almost all the questions which are still open in this field and give a fair appreciation of the arguments brought forward by different authors. One of them is a German treatise on "Abstammungslehre" by Buekers<sup>1</sup>; the other, a volume in French on "Transformations brusques des êtres vivants," written by L. Blaringhem.<sup>2</sup> The first of these two books deals mainly with the questions from a critical point of view, and is very exhaustive in this respect; while Blaringhem supports his opinion by a thorough study and accurate description of a number of new mutations which occurred in his cultures.

Some authors have asserted that the theory of mutation has been deduced from the doctrine of hybridism. Others have pretended that my experiments with the evening primrose of Lamarck were its starting-point. Both these opinions are erroneous from the historical point of view as well as from a logical one. The mutation theory originated from the hypothesis of pangenesis.<sup>3</sup> This hypothesis suggested to Darwin the principle of the units which he called gemmules. Every one of these represented, in his opinion, a visible part of the organism, even of a single cell.

According to my conception, the units correspond to the qualities by the coöperation of which the whole character of the organism is built up. Each of these units may express itself in different parts of the individual. It is from this conception, as stated above, that I derived the hypothesis of the two main types of variability. In order to control this deduction by means of experiments, I studied, on the one hand, variability itself; and, on the other, hybridism. The

<sup>1</sup> Dr. P. G. Buekers, "Abstammungslehre," Leipzig, 1909, § 354.

<sup>2</sup> "Bibliothèque de Philosophie scientifique," Paris, E. Flammarion, 1911.

<sup>3</sup> See A. A. W. Hubrecht, in "Popular Science Monthly," July, 1904, p. 222, and V. Haecker, "Allgemeine Vererbungslehre," 2<sup>e</sup> Aufl., 1912, p. 287.

first of these two groups of experiments included over a hundred different species, some of which showed signs of mutability, while by far the larger number did not. A small degree of the propensity to produce new forms was observed in *Linaria vulgaris*, *Dahlia variabilis*, *Chrysanthemum segetum* and *Dracocephalum moldavicum*. Among all the species studied by me, I found, however, only a single one which showed the new quality in quite a large degree, producing new types almost every year, and thereby stimulating to an extensive as well as intensive study. I supported this inquiry by a critical review of the numerous facts scattered through the literature in the fields of agriculture, horticulture, teratology and other sciences; and, almost at the same time, the whole range of observations which pleaded for a sudden origin of cultivated varieties was exhaustively collected by Korshinsky from the horticultural literature.

Another widely distributed error is the opinion that the theory of mutation is opposed to the principle of selection. It is even asserted sometimes that the theory of selection should have been replaced by it. I have already pointed out that the real service done by Darwin to evolutionary science lies in the proposition of his principle of explaining the development of the organisms from one another, in its main lines as well as in its details, on the basis of well ascertained facts only. His means to reach this aim were the struggle for life and the survival of the fittest—or, in one word, natural selection. The question whence the material for this selection was derived was of course duly and fully dealt with; but our knowledge of the phenomena of variability was at that time still in its infancy, and far from being adequate to the demands Darwin made upon it. This was the reason why he did not succeed in convincing his contemporaries. It is only on this weak point that the theory of



mutation has to come in. Its aim is not to be sought in the explanation of the different forms of life. It starts from the principle that the changes which find their expression in variability are intrinsically connected with the germ-plasm; that they are provoked within this substance before fecundation, either in one or both of the sexual elements, and come to light only afterward, during the development of the new individual. Although evidently dependent on external factors, such as nutrition, etc., they are not each related to these in such a manner that it would already be possible for us to explain this dependency in its details. The older and some of the still prevailing theories consider that the changes take place first in the growing or even in the adult organs, and are only transferred afterward to the sexual cells.

From a general point of view, the chances of a new idea finding adherence often depend in a great degree on its applicability to other fields of inquiry besides its own experimental domain. General considerations are often more decisive than pure facts. In this respect the mutation theory has the great advantage of easily complying with the most widely divergent conceptions of the phenomena of adaptation. It may be combined with these even more intimately than the older views, as I shall show later on.

The empirical basis of the new teachings is the distinction between fluctuation and mutation. The first is the ordinary form of variation, often called individual, gradual or continuous variation, and well known to Darwin himself. It is almost always and everywhere active in a lesser or in a greater degree. Mutation, on the other hand, is a rare and most sporadic phenomenon only rarely occurring in groups, but by means of it new types are seen to arise suddenly, sharply, although often not widely distinct from the parental type. With this proposition many authors have since ex-

pressed their agreement, and in one of the newest manuals Karsten summarizes the now prevailing conviction by saying, "Spontaneous variation or mutation is sharply distinct from fluctuation, since it proceeds by leaps and at once produces hereditary differences."<sup>1</sup> And even the most ardent opponent of my view—Plate—in concluding his lecture on "Inheritance and the Theory of Descent," says that "phyletical evolution is discontinuous in the changes of the determinants, although ordinarily continuous in its external display";<sup>2</sup> and in doing so he evidently concedes the main point in discussion.

Fluctuations are quantitative variations, but mutations are of the qualitative kind. Under the influence of selection, the first do not produce constant races which become independent from that selection, while the products of mutation are at once of an hereditary nature and constant. This principle has brought the study of elementary species into the first rank of biological interest. The investigations of Jordan, de Bary and many others had not succeeded in convincing biologists and systematists of the truth that the species of Linnæus are in reality collective entities, and that the real units of nature are the so-called small species. It is quite evident that it is impossible to observe the origin of such a collective species, since the conception is partly, at least, of an artificial nature. But now the origin of the small species has become an object of direct inquiry. One of the oldest objections against the theory of descent has thereby been surmounted forever. Even in the field of pure description the new ideas have their influence. It is conceded that even the so-called type specimens might not be homogeneous

<sup>1</sup> Nussbaum, Karsten und Weber, "Lehrbuch der Biologie für Hochschulen," Leipzig, 1911, p. 295.

<sup>2</sup> L. Plate, "Festschrift zum sechzigsten Geburtstage Richard Hertwigs," Bd. II, 1910, p. 607.

if they are based on different individuals collected in the field. Small differences of the nature of those existing between elementary species might occur among them and sooner or later become the source of misunderstanding. A pure prototype can evidently not be secured in this way, or at least its purity cannot be guaranteed. Starting from these considerations, Kellerman and Swingle have lately pointed out the necessity of taking all the type specimens for one species from one single individual, and proposed to distinguish those which comply with this principle by the name of merotypes.<sup>1</sup>

One of the greatest difficulties of the theory of selection as worked out by Darwin is found in the fact that changes which after some degree of development may be advantageous to their possessors cannot be of any use to them at their first appearance as almost invisible deviations from the old type, and even during a long period afterward. Notwithstanding this, the theory requires their being selected from among the others, and this on the ground of their usefulness. This objection has been dealt with exhaustively by a large number of authors; but in the last ten years all of them agree in conceding that it has been successfully met with by the principle of mutation.

One of the main supports for the ideas of Darwin was a comparison of selection as used in agricultural practice with the corresponding phenomena in nature. Unfortunately, the descriptions of their procedures given by the leading agriculturists were far from adequate to the use Darwin wanted to make of them. On the one hand, he succeeded in proving the analogy between artificial and natural selection by heaping up an overpowering material of facts, and it seems to me that this proof has been one of the principal factors in the

<sup>1</sup> Journal of the Washington Academy of Sciences, Vol. II, May, 1912, No. 9, p. 222.

victory which his theory has so completely gained. But the agriculturists themselves did not clearly understand their practice, and even partially explained it in an erroneous way, and these errors were transferred unobservedly to the theory of natural selection. It was only a critical study of the classical and thoroughly scientifically conducted cultures of Rimpau in selecting his rye which yielded a satisfactory, although belated, understanding of the whole phenomenon.<sup>1</sup> I found out that Rimpau, although believing he was selecting only the richest ears from among a uniform race, in reality chose the best elementary species from a motley mixture of types. From the progeny of his handful of chosen ears he subsequently eliminated the minor ones, until by means of a selection of some ten to twenty ears he finally reached a pure race, which, according to our present conception, must have consisted only of the progeny of the very best one of the ears he chose in the beginning. Such a pure race was no longer exposed to reversions, and this has been thoroughly proved in the case of the rye of Rimpau by the cultures of Schribaux in northern France. At present the principle is universally recognized. We may safely transfer it to the comparison of artificial and natural selection as proposed by Darwin, and conclude from it that Nature herself does not select her new species from fluctuating variations, but from the existing small types, or, in the end, from mutations that occurred at a previous time.

I now come to a consideration of the two principal theories which have secured for themselves quite a number of adherents and are still defended by many authors as auxiliaries of the old theory of selection. I mean the principles of orthogenesis and neo-Lamarckism, or the theory of direct influences. The former of these refers to the main

<sup>1</sup> Proceedings, American Philosophical Society, Vol. XLV, 1906, pp. 149-156.

lines in the pedigree of the animal and vegetable kingdoms, the latter to the adaptations in the ultimate branches of these pedigree trees. In my opinion, neither of them is opposed to the teachings of the theory of mutation, especially since they are destined for quite another field of phenomena.

This is clearly shown by the curious circumstance that the adherents of orthogenesis recognize the validity of the new theory for the explanation of adaptations, while the neo-Lamarckists declare it to be valuable only for the origin of the larger branches of the system. All of them recognize the process of mutation as the normal mode of origin of species, and make an exception only for the field in which they are especially engaged.<sup>1</sup>

Before continuing this discussion, it is, however, necessary to deal with the distinction between characters of organization and those of adaptation as proposed by Nägeli. The former are the marks of natural families and of higher groups; they have been evolved in very old geological times, and our knowledge concerning the climate and the life conditions of those periods is necessarily limited to a general outline and does not justify us in making a distinct idea of the environmental conditions of the single species and of the claims made upon them by the struggle for life. Therefore it is hardly possible to deal with the causes of their evolution and of the origin of new types of life with any higher degree of probability than that of more or less poetical descriptions.<sup>2</sup> These characters of organization are often supposed to have originated in a manner essentially different from that of the characters of adaptation. In the former case,

<sup>1</sup> Von Wettstein, "Handbuch der systematischen Botanik," 1901, p. 36; Strasburger, "Jahrb. f. wiss. Bot.," 1902, T. 37, p. 518 u. A.

<sup>2</sup> This expression is not meant to include the least reproach. On the contrary, I myself often prefer using such forms of speech, trusting that my readers will recognize them for what they are intended to be. Critics who failed to see this point more than once have given me great amusement.

internal causes are assumed to be the most essential factors; while in the latter this rôle is given to the external conditions.

Adaptation is limited to the very youngest qualities of animals and plants, and this is carefully pointed out by the most prominent among living neo-Lamarckists, von Wettstein. He says, "As far as experience goes, we may assert that by means of direct adaptation nothing absolutely new is produced but that its results are in the main directed to an augmentation or a diminution of properties already present." And to this sentence he joins another, which eliminates all possible doubt, and which says that, after long times of direct adaptation and after the disappearance of such transitional forms as it may have produced, "the impression of an essential deviation" may be made upon us.<sup>1</sup>

From this discussion it is clear that the characters of organization and adaptation do not cover the whole field of systematic differences. The former are limited to those between the larger groups; and it is characteristic of them that they do not show any relation to the struggle for life—at least not at the present time. The characters of adaptation, on the other hand, are the marks of the youngest of all the systematic groups, and are, as a rule, limited to species and subspecies. Between the two divisions there is a wide gap; but this field includes, curiously enough, exactly those cases which are the most interesting ones for the great principle of evolution. Large, and therefore, at all events, not very young groups, like most of the cactaceous and euphorbiaceous plants, in many cases show the most beautiful and stringent arrangements for a life under strongly specialized conditions. These, however, are to be included neither with the marks of organization as described by Nägeli, nor with those of adaptation as proposed by von Wettstein. There-

<sup>1</sup> R. von Wettstein, "Handbuch," *l. c.*, p. 44.

fore it seems unavoidable to collect them into a new division, for which it seems practical to choose the name of *characters of specialization*. For the cases to be covered by this expression are taken from plants which show a high degree of differentiation on very special lines; and the question whether this is useful or only innocuous to them is one which it is at best hardly possible to decide on a purely empirical basis. But on the layman they make the impression of the most beautiful adaptations.

Warming has distinctly pointed out that the real nature of orthogenesis, as well as of direct influence, is not clear to us. The latter of the two principles assumes an intimate correlation between the external factors and the usefulness of the deviations produced by them, but in Warming's opinion this relation is "of obscure nature."<sup>1</sup> Therefore it seems justifiable to assume that this direct influence is not a single mystic force of nature, but the result of the combination of a larger or lesser number of such forces. But in this case it must be possible to make an analysis of them, and it strikes me that the theory of mutation is capable of supplying us with precisely the necessary means for this purpose.

The same reasoning and conclusion hold good for the principle of orthogenesis. Concerning this Coulter says: "Long ago it seemed possible to consider it to be 'a mysterious principle inherent in organic life,' or as an internal force which determined the direction of variability; but in our time, since the rôle of environmental conditions and the whole group of external factors have come into the foreground of biological interest, this conception can no longer be considered as sufficient. But, at all events, we hardly know how these external factors really influence evolution,

<sup>1</sup> Warming, "Ecology of Plants," 1909, p. 370.

and which is their true nature."<sup>1</sup> And in connection with this he remarks that natural selection, mutation and orthogenesis are far from excluding one another.

Let us now consider these three groups separately. In the case of orthogenesis we may limit ourselves to two points. First, the suggestion that it is not variation, but selection, which has been working in the same direction during long geological times. And although, as already pointed out, we know very little about the factors of the struggle for life in those remote times, this question seems to claim full appreciation. If we decide for a continuity in the selection, variability may be assumed as occurring in indistinct directions, even at those times. If, however, we take the opposite point of view, it remains an open question whether the one-sided variability which we must then assume was of the nature of fluctuation or of mutation. And since the former determines only an augmentation or a diminution of qualities already present, we should conclude with the conception of series of mutations taking place in an unchanged direction. This would bring us in line with the proposition of indistinct mutability, since evidently all mutations which would take place in divergent directions would sooner or later have to disappear. Be this as it may, my aim is only to show that, even in such an hypothetical field, the theory of mutation has the best chance of complying with our knowledge of the available facts, without the need of recurring to secondary hypotheses. I have already pointed out that the paleontologists are best prepared to recognize the principle of mutation for orthogenetic evolution. In concluding it seems to me that orthogenesis may best be explained as produced by successive mutations, which themselves have been conducted by orthogenetic selection.

<sup>1</sup> Coulter, Barnes and Cowles, "Textbook of Botany," Vol. I, p. 290.



The conception that characters of adaptation cannot be due to selection, but must be induced by direct environmental influences, was formerly derived in the main from the fact that very small deviations from a given type can have hardly any advantage in the struggle for life, while the theory of natural selection must assume a distinct activity of its principle from the very beginning.<sup>1</sup> As is well known, this difficulty is met with in the most satisfactory manner by the theory of mutation, and on this point almost all authors agree. Different propositions for reconciliation have been made. Thus, for example, the direct influence of the environment seems sufficient to von Wettstein, while Strasburger holds the opinion that it must always be accompanied by selection in order to take its effect. Evidently such an assumption would make the whole theory superfluous.

Two objections must still be considered. In the first place, it should be pointed out that the differential characters on which the diagnostic descriptions of species are based are rarely of the nature of adaptations. In the second place, a most common source of confusion is the lack of a sharp distinction between plasticity and phylogenetic adaptation.

If, in botanical excursions or in determining the identity of collected plants, we have an eye open for the question concerning the meaning of the distinguishing characters for the plants themselves, we must usually concede that they are in reality far from having any real usefulness, or that at least we cannot point out their use if we limit ourselves to purely empirical arguments; for example, *Ranunculus bulbosus* and *R. Philonotis* have the slips of their calyx turned downward; *Myosotis versicolor* opens its flowers before the corolla assumes the blue color; *Viola arvensis* has a calyx which is longer than the corolla; umbelliferous plants are often dis-

<sup>1</sup> Von Wettstein, "Handbuch," p. 39.

tinguished by the occurrence or the absence of a common or a partial involucre; *Spergula Morisonii* has a narrow membranaceous ring around its seeds; the species of *Taraxacum* and other groups are often apogamous; and so on in an endless series of arguments. What is the use of such qualities? The answer is, as a rule, none at all, since the nearest allies are as successful in their struggle for life without them. This is true in a still higher degree for the distinguishing marks of elementary species, and, as has been pointed out by Willis, for those endemisms which are not relicts but are growing still in the midst of their presumed ancestors.<sup>1</sup> Very often erroneous conceptions concerning the use of distinct qualities are seen to prevail. Thus the red color of many flowers is presumed to attract some species of insects and to find its use in this; but as a matter of fact it is often only a local expression of a quality which may be seen in activity in other parts of the organism as well. Many white varieties of red or blue species are weaker in the struggle for life than their ancestors, and this is the reason why they so regularly disappear very soon after making a local appearance. This struggle for life is not fought out by means of the flowers, but during the vegetative period, wholly independent of the visits of insects and the question of fecundation. This is best seen in perennial plants or in small shrubs where the red or blue flowering forms are often seen to hold their ground, while the white ones are incapable of doing so. I cite, for instance, a culture of *Daphne Mezereum* and of its white variety, both in a number of specimens. The white ones were weak and succumbed to our climate after some years; while the red ones were continually seen to thrive. Between *Ranunculus bulbosus* and *R. Philonotis* it is not those characters that may be studied on dried material which are

<sup>1</sup> See F. Graebner, "Lehrbuch der Pflanzengeographie," 1910, p. 70.

decisive in the struggle for life. On the contrary, the result depends on the predilection of the former for a dry soil, and of the latter for moist meadow-land. Numerous instances of the same kind might be given, and it seems to me that they would exceed by far the number of those cases in which elementary characters, as opposed to compound ones, might be proved to be useful.

Those cases in which the production of new species has been ascribed to the direct influence of the environment may commonly be explained on the principle of mutations as easily as on that of the accumulation of very small and almost invisible deviations.

Seasonal dimorphism is one of the most widely known arguments of von Wettstein. Some plants of the alpine meadows occur in two elementary forms, one of which flowers and ripens its seeds before the summer period of mowing, while the other begins its vigorous growth only as soon as this period is over. At that time, when the great significance and the general occurrence of elementary species were not yet realized, it seemed allowable to assume for this case a special process of adaptation. But, in the light of our present knowledge, the other assumption is at least as fully justified—viz., that the mowing has simply selected, from among a group of preëxisting forms, those which did not suffer by it in the one way or in the other. Unconscious selection would then have acted here just in the same way as conscious artificial selection does elsewhere. In this way the proposition of direct environmental influences may be easily and advantageously combined with the principle of the origin of species by mutation. Species have the power of adapting themselves to the prevailing conditions of life, but they do this by means of the great number of elementary forms of which each of them consists.

The other objection was that connected with the phenomena of plasticity. By this term is meant the power of many species to live under quite different conditions. Not rarely this is associated with striking changes in their dimensions and in other characters; and these differences may be so large as to be taken for specific ones on first inspection. The best known example is that of *Polygonum amphibium*, which has a terrestrial form and a floating one. Some authors have described the former of these as another species and have given it the name of *Polygonum Hartwrightii*. But Massart has shown that by transferring one of the two forms to the life conditions of the other it is always possible to change it into the other type, and that even both types may be developed as branches from the same plant, provided this is growing just at the margin of the water. In the case of alpine plants Bonnier has shown that it suffices to transplant a part of a rhizome into the plain to make the new stems assume the type that is known to be characteristic for the new conditions. In almost all cases where plants may be multiplied in a vegetative way it is possible, in accordance with this principle, to show that their plasticity (which is often called their adaptability) is a latent quality capable of coming into action at once in response to changes in environmental conditions. From perennial species we may conclude that the same must hold good for annual ones too. The capability of many ordinary weeds, which like a soil rich in saltpeter or in other nitrogenous substances, to attain gigantic dimensions under such conditions while they remain dwarfish on poor or dry soil, even in such a degree as to conclude their growth after the production of a single fruit, as, for example, is seen in *Datura Stramonium*, is no doubt one of the most beautiful instances of adaptability; but it is

evident that it does not involve any change in the hereditary qualities.

In all such cases it is clear that the assumed analogy between these adaptations and the origin of new species is only apparent. Qualities may lie dormant for thousands of years, as in the case of the alpine plants, and under changed conditions come suddenly into activity again; they will evidently do this every time that the corresponding stimulus excites them. Without any doubt, many of these qualities are useful, but this does not prove that they have originated on account of their usefulness. The conception that they owe their existence to some mutation, and in this respect follow the general rule, has at least the same degree of probability. In this case no supplementary hypotheses would be necessary. The researches of Costantin, Goebel, Klebs, Stahl, Vöchting, Frank, Karsten and many others have brought our knowledge concerning the phenomena of plasticity to a high degree of development; everywhere it may be seen, however, that the resemblance to the processes of the origin of species has no real signification. Nature often gives us the impression of a most beautiful harmony between living organisms and their environment, and thereby between the latter and their ontogenetic evolution, and it is all too tempting to conclude from this that organisms as a rule have been adapted to their life conditions. This conclusion, however, is in many cases only a postulate and does not rest upon an empirical ground. It goes without saying that animals and plants cannot live under extremely unfavorable or injurious conditions, and that, for this reason, we must find everywhere better or less fitted forms. But, as a matter of fact, most plants are contented in nature with an environment which is far from being the best for them; and where the trade happens to bring their seeds to other countries, they are often seen to

thrive far better and to multiply with unexpected rapidity. It is a curious fact that they are best adapted to conditions which are quite new to them and which they never enjoyed before.

Our third division was that of the characters of *specialization*. It lies between that of the qualities of organization of Nägeli, which have no relation to the surrounding world, and the consequences of adaptation of von Wettstein, which do not produce any really new steps in the line of evolution. Every student must be struck by the fact that the most beautiful examples of so-called adaptations are found in the distinguishing marks, not of species but of genera and the larger groups, even of whole families. In a geological sense they are therefore so old that an appreciation of the single factors of the environmental conditions under which they have originated must necessarily be impossible. As a rule, such adaptations do not consist in a single quality, but in very complicated and highly developed arrangements, which can have been attained only by a series of successive changes. I refer to the flowers of the orchids, to insectivorous plants, to many cases of climbing species, to the tubers on the roots of the leguminous plants, to the *Cactaceæ* and *Euphorbiaceæ* of the desert, and so on. All of them are specialized in a very high degree, and this we assume to be of use to them, at least in many cases. But it seems to me that this usefulness is most liable to overestimation, and in reality consists mostly in a compensation of other hurtful qualities. Later investigations have shown, more than once, that the presumed use does not exist at all—in any case, not at the present time. For instance, let us take the heterostyly of the primroses, which according to Weiss, is more hurtful than useful; or the flowers of *Orchis* and *Ophrys*, which discourage insects rather than invite them to visit, as was discovered by Detto.

The anthers of *Mimulus* and *Torenia*, which contain a large supply of good pollen but never open, must be considered simply a useless waste of material. The *Drosera* has no apparent advantage at all in its ability to catch insects, when we compare its distribution and the rate of its multiplication with that of the species with which it lives; on a rich soil it thrives just as well without the food supplied to it by the insects. The species of *Utricularia* are adapted in the most beautiful manner to capture small animals, but that this should be advantageous to them in their struggle with neighboring plants nobody can prove.

If, however, we concede that they have originated as the result of their usefulness, we do not gain any real understanding of the different factors of these complicated qualities. Neither this assumption nor experience can decide whether the units out of which these qualities have been built up have had their origin in sudden leaps, or in the accumulation of slow and originally invisible changes. In other words, they may be due to mutations as well as to fluctuations, and to the activity of orthogenesis as well as to that of direct environmental influence. From this point of view, there is not the least justification in assuming special supplementary hypotheses for their explanation. The conception that these characters of specialization have originated in quite the same manner as any other distinguishing marks of species as well as of the larger groups has evidently the same right, and perhaps even a greater right, to our appreciation than any special assumption.

Leaving these considerations of a more general nature, we may now return to the experimental side of the question. Here two propositions demand a careful treatment. The first of them is the sentence that fluctuations cannot, by means of the coöperation of selection, lead to constant races,

which should be independent of a continuance of that same selection. The second proposition is the contention that mutations do produce such constant races.

In the realm of selection the first principle is to distinguish sharply between pure elementary species and the collective species of the systematists. On the one hand, we may try to improve the small species themselves by means of selection; on the other, we are concerned simply with a choice from among the mixed groups of already constant and hereditary types. Any doubt which may have existed concerning the reality of this distinction has of late been completely surmounted by the practical processes of breeding which have been introduced by Nilsson into agriculture, and which were founded on his deep scientific knowledge of the problems with which he had to deal. The pure races which he succeeded in isolating from the old mixed varieties of cereals may still produce deviations in the way of mutations or as a result of accidental crosses, but these changes always occur suddenly. It is not possible to improve his strains as such by means of continuous selection. The same is true of many of the older agricultural races which have been won by a more or less unconscious process of selection.

Within the elementary species, artificial selection in many cases may be conducive to real improvements which in a sense are hereditary. In others, however, this result seems not to be attainable. But in any case such races do not become independent of continued selection. Especially instructive in this respect is the history of the cultivated sugar-beets. From a broader point of view, our beets consist of a number of elementary species, and any large breeder has, as a rule, his own kind which he has purified by means of selection. The principle of the culture of separate families is followed. It starts from single mother-plants, and



every family is the progeny of only one such specimen. The possible, and often practically unavoidable, influence of foreign pollen must afterward be eliminated by means of well directed selection during some of the next generations. Such families are called *élite races*, and from them every year a branch is taken for the production of the seed needed for culture in the fields or for the trade. Accordingly it must be multiplied in a high degree, but this multiplication must always be accompanied by a continued selection on the basis of external characters as well as of the amount of sugar. One, or at best two, generations without such selection are allowed; but if a breeder should multiply his seed entirely without it, the value would soon sink far beneath the limit required in practice. There are no races rich in sugar which would maintain themselves without such continued help.

Next to the sugar-beets come a number of garden plants in their varieties with double flowers. Ordinarily, such a variety has originated only once, and is in this sense a true elementary species. But the breeder chooses his seeds from the best individuals only, in order to secure a high percentage of beautifully doubled flowers among the progeny. This improvement of the seeds, however, is effective only for the very next generation, and therefore it is necessary to repeat the selection every year. Numerous instances could be given, and it seems that the rule prevails that the selected characters are in a high degree dependent upon the conditions of nourishment; or, in other words, that in reality the selection is only the choice of the best nourished individuals as seed-bearers. Whenever this nourishment, by means of a fuller development of the seeds, is effective through some successive generations, the races are called *high-bred*, and are liable to decline in a few generations after the subsidence of the selection.

Excellent material for the study of such high-bred races is afforded by some deviations of seedling plants, and especially by tricotylous and syncotylous races. I have cultivated some of these races and found them, in the main, to contain about fifty per cent. of deviating individuals. By means of selection it was easy to bring this standard, in a few years, up to ninety per cent. and more, or down to ten per cent. and less. The selector, however, must not be content with choosing the most perfectly tricotylous or syncotylous seedlings for the continuance of the race. This external mark has only a very secondary value. We have to breed from those individuals whose progeny is the richest in the desired deviation, and therefore to determine this standard for a number of seed-bearers, in order to choose from among them the one with the highest percentage figure. It is a fact well worthy of notice that such breedings succeed almost as easily by insect fecundation as by means of artificially conducted pure self-pollination (*Oenothera hirtella*, *Antirrhinum majus*), the reason being that the obnoxious effects of foreign pollen are at once eliminated by the selection itself.

Among the most interesting of these cases are the middle races, or those which continually oscillate between two ideal types, without being able to transgress their limits and to change into one of those types. Tricotylous races, for instance, oscillate between pure dicotyly and pure tricotyly; and although the single individuals may apparently show both these types, the race never reaches the one end, to the complete exclusion of the other. In such cases the range of variation is evidently an exceptionally wide one, and therefore it must be easy for selection to encroach upon it. But we should always keep in mind that the basis of selection should never be sought in the externally visible qualities of single individuals, but only in the average amount of these

qualities among their progeny. In other cases the width of variation within the limits of an elementary species is much smaller, and wherever this condition prevails it is often difficult to reach any amount of durable improvement by means of selection. Johannsen has studied such instances, and his results may be considered as one of the best supports of the theory of mutation. For it must be clear to every one that, when selection can bring no improvement at all, it cannot even be supposed to be conducive to the production of new species and varieties. In order to be wholly sure of the purity of his cultures, Johannsen has limited his experiments to such forms as are fertile with their own pollen; but, unfortunately, this condition is far from being the general rule in nature. Moreover, he starts from a single self-pollinated individual, and in this point he follows the principle laid down in my mutation theory and introduced by Nilsson into agricultural practice. To such cultures, derived from single selected mother-plants, he gives the name of "pure lines." His method soon found universal approval, and by this means strongly contributed to the spread of the new ideas. Within these pure lines and in the examples chosen by him, selection does not provoke any real changes. High-bred races do not occur in this field, and so there is also no chance of winning new and constant races by means of them. The significance of this principle seems to me to be a very large one, and to hold good for far longer periods than those of ordinary experiments. We may deduce this from the cultures of Bonnier with the alpine plants. In this case natural selection has been at work during centuries, and in many instances probably since the last of the glaciary periods. But this has been of no avail—at least, not in such a degree that alpine plants would have become purely and exclusively adapted to their environment. For, as is well known, they

have not at all lost the property of accommodating themselves to the conditions of a low country.

Our second proposition was that mutations can be the source of new and constant races which are independent of selection. In discussing this point, we must distinguish between those cases which have been observed only after the mutation took place, and those which have been controlled for several generations in advance. The former we shall call empirical and the latter pedigree mutations. The former group includes those numerous cases of the origin of well observed novelties either in horticulture or in the field; while the other class is concerned with mutations occurring in carefully guarded cultures in an experimental garden, after at least several generations of the old type have been controlled. In the case of empirical mutations we must base our conclusions concerning the forefathers of the new type on the basis of observations made in the moment of its discovery, and often this may give a very convincing degree of probability. In the other case, the ancestors, however, are empirically known. Moreover, it is only these latter cases which afford us the necessary material for a detailed experimental study of the conditions under which the mutation took place.

The oldest and best known example of an empirical mutation is the sudden origin of *Chelidonium laciniatum*. A compilation of a large number of other cases has been given in my mutation theory and a critical and historical review of the instances recorded in horticultural literature has been published by Korshinsky. To these instances Solms-Laubach has added his *Capsella Heegeri*, and Blaringhem his *Capsella Viguieri* and others; and the list of cases is increasing almost yearly. We may therefore state that the fact itself is now beyond all doubt. Instances of pedigree mutations

have been described in my mutation theory, especially in the case of *Linaria vulgaris peloria* and of the double *Chrysanthemum segetum*, or corn-marigold. Referring for the description of these experiments to the source I mentioned, I will point out here the critical and methodological side of the problems involved.

In the case of the peloric toad-flax, the aim of the experiment was to control experimentally the instances of this mutation which had so often been observed in nature; in other words, to watch the occurrence of such a change in a well guarded pedigree culture. The observations made by different authors clearly pointed to a sudden origin without transitions or visible preparing steps. No intermediates had ever been found. My aim, however, was to see the mutation taking place. Evidently, peloric flowers owe their particularity, in a morphological sense, to the loss or to the latency of the symmetrical structure of the flower; but by far the greatest number of instances of empirical mutations refer to such losses, and as yet there is no ground for supposing that progressive changes should behave differently in this respect. In my experiment the first completely peloric individual—*i.e.*, the plant which had all of its flowers, without exception, in this condition—was seen in the fourth generation. It was soon followed by others, and in a sufficient number to show that the mutation occurred in about one per cent. of all the individuals, and was repeated in succeeding generations. Unfortunately, these peloric plants were almost wholly sterile; and I contrived only with difficulty to raise about a hundred individuals from their seed. These, however, repeated the anomaly, although with a few exceptions, due probably to the extraordinarily difficult conditions of the artificial self-pollination of these almost sterile flowers. Intermediate forms did not occur, neither in the number of

peloric flowers per plant nor in that of the spurs per flower. It is hardly necessary to point out that a single experimental mutation of this kind provides a much deeper insight into the phenomena than all the empirical mutations of this species taken together.

In some respects the case of the double corn-marigold is different from this. The starting-point of this experiment was derived from two empirical theses. One of these is the proposition already mentioned, that within pure races selection is the choice of only the best nourished individuals. The other is the increment of chance of the occurrence of mutations caused by a high degree of nutrition. From a combination of these two empirical rules we may derive the belief that in experiments on mutation a most carefully conducted and luxurious culture is to be combined with sharp-eyed selection. Moreover, we may apply a third rule which deals with the sensitive periods in the development of variable qualities. It says that selection chooses especially those individuals which have been best nourished during this sensitive period of the character in question, and from this we may deduce that the chance of new mutations lies mainly in the direction of those characters which we choose for our selection, or of such as are most intimately connected with them.

The point of this discussion should always be kept in mind in the planning of new experiments on mutation, as we shall easily see by applying it to the case before us. It involves the principle that the chance of winning a double variety may be enhanced by selection in the direction of increasing the number of the ray florets in the flower-heads. This augmentation refers to the outer range of florets, while the doubling consists in the change of the florets of the disk into rays. The two phenomena are therefore essentially different, and

in my cultures they were observed to be not connected by transitional or intermediate forms.

By means of very careful selection I succeeded in bringing the average number of ray florets in the flower-heads from the ordinary type of twenty-one (the number of the variety I started from) up to thirty-four; and in doing so the extremes were seen to reach even sixty-six rays per head. After this was reached a change in the disk suddenly made its appearance, and this in one of the seed-bearers chosen for its extremely high number of rays. Next year the seeds of this one plant were sown separately, and at once they gave the expected double race in full display. It seems justifiable to assume that the numerous double varieties of species of the family of the composites have originated in the same way, in the field or in the garden, and in the latter case probably under the influence of unconscious selection.

After the same method I succeeded in producing a twisted race of *Dracocephalum moldavicum* by means of the selection of tricotylous individuals. To this experiment I was led by the description given by Morren of a most beautiful instance of spiral twisting in another species of the same genus. But from these instances we may not conclude that such pedigree experiments will always give the desired result. Thus, for instance, I have tried in vain to win a double petalomanous variety of *Ranunculus bulbosus*, although such a variety from time to time occurs in the field in Holland. Also, I did not succeed in producing a purely four- or five-leaved race of the red clover; nor even a constant seven-leaved form. But it is still possible that the difficulties in finding out the most favorable methods of growing these wild plants are at least partly to be considered as the causes of this lack of success.

Advance in the study of the question of mutation seems

now to depend mainly on the accumulation of numerous pedigree cultures of this kind. It should be possible to repeat the mutations which are known to have occurred in nature or in horticulture, in an experimental way, with either the same or with allied species. The conclusions which are now derived from empirical mutations should be based upon observations in the experimental garden. In working on this principle, not only more exact proofs may be reached, but we should come into possession of the material needed for a more thorough study of mutations and of their internal and external conditions. Here is the starting-point for the long path which must still be explored in trying to produce intentionally chosen novelties; but it does not seem at all impossible to surmount the difficulties, even in this field, and thereby to open new sources of artificial improvement for our crops.

In nature, probably, the production of new forms has taken place sometimes sporadically and sometimes in groups. It is chiefly a paleontological question which of these two processes has had the prevailing part in the evolution of the vegetable and animal kingdoms. Have the main branches of the pedigree been started from among those rich groups of species and varieties which constitute the so-called polymorphic types, or are these latter types only products of the lesser branches? As far as our present knowledge goes, both cases seem to occur. At the present time the polymorphous genera and species, the misty spots of the older systematists, and the groups of explosive changes of Standfuss, are evidently the consequences of such mutation periods. But most of them are already past that stage, and no traces of mutability have been preserved in them. Or, perhaps, this changeability is limited to a few of the numerous forms, and it has as yet not been possible to discern these among



them. On the other hand, it is clear that cases of the simultaneous production of groups of new forms provide a far more suitable material for experimental researches than do sporadic mutations. The former type may include the most divergent kinds of specific changes. It is on the ground of this conception that in the beginning of my experiments I sought a species which would be in such a condition of mutability. I tried more than a hundred species, mostly of wild plants of Holland; cultivated them for several years in my garden, and finally selected one from among them which seemed best suited for my purpose.

This one was the evening primrose of Lamarck, introduced long ago from America into Europe, and which has run wild in different spots. It was the *Oenothera Lamarckiana*. The processes of the mutation of this evening primrose have been observed of late by so many investigators that no traces of doubt concerning their reality any longer remain. It is true that the whole case is still an isolated one, but it is evident that a further search will sooner or later lead to the discovery of analogous instances. On the other hand, the question of the significance of these observations as typical for the theory of evolution, as well as that concerning the true nature of the mutations themselves, is a subject of much discussion. It is a struggle for and against the *Oenotheras* and their evolutionary value; but this struggle is concerned with the mutations themselves as they occur in our experiments, and not—or at least not directly—with that primary condition of them which I have called the premutations. This internal tendency to mutation is proved by the fact that the same new forms may arise yearly from the main stem of the cultures, and often in a relatively large number of individuals. Generation after generation, the same mutations are repeated, and this re-

veals to us an hereditary condition of the germ-plasm which must have remained unchanged during all the twenty-five years of my experiments and evidently during a much longer period of time. In what way, and when, these internal predispositions have been acquired, the visible consequences of which are the mutations, is a wholly different question, which has until now hardly offered itself to experimental treatment.

This question of the premutation, or of the internal preparation of the mutability, is most intimately connected with that of the duration of the whole period of mutations. In this respect the first proofs have referred to the introduction of the *Oenothera Lamarckiana* into Europe, and have shown that it must have been already in a mutable condition at that time, or about sixty years ago. This conclusion was derived from the fact that the different strains, issued from that introduction shortly after it had taken place, all showed the same phenomena of producing new forms.

Later observations, and a better appreciation of some older ones on the ground of them, then led to the view that the mutability must in this case be older than the species itself, and have developed gradually together with the specific differentiation within the group of the *Onagras* to which *O. Lamarckiana* belongs.

The main support of this view is the discovery of the fact that the European type of *O. biennis* has the same property of producing dwarfs which is so prominent in *O. Lamarckiana*. This has of late been observed by Stomps in his cultures of *O. biennis cruciata*, and it has occurred also in my experimental garden. The common view takes this *O. biennis* to be one of the forefathers of *O. Lamarckiana*, and therefore present indications assume that the property of producing dwarfs has been inherited by *O. Lamarckiana*

from such ancestors. This view is supported by that curious quality of the dwarfs of being sensitive in a high degree to the attacks of some kinds of bacteria of the soil; this sensitiveness and the changes in the structure which it produces being exactly the same in both of these kinds of dwarfs. I shall have to refer to this disease later on.

Elsewhere, also, among the nearest allies of the evening primrose of Lamarck, phenomena of mutability may be seen to occur. *Oenothera cruciata* has given in my cultures from their very beginning three types, which differed from each other especially in the form of the flower-buds; it has shown the same elementary forms in the cultures of MacDougal. This author studied also the *Oenothera grandiflora* from Alabama, and the origin of new derivative forms from it, and stated that analogous deviating types are also met with in its original station near Tensaw. Moreover, the cultures of Davis have given evidence of a wide range of subordinate forms within the type of *Oenothera grandiflora*. In the neighborhood of Courtney, Missouri, I observed, among numerous specimens of the ordinary American type of *O. biennis*, a deviating individual with narrow leaves. Analogous mutations have arisen from the seed collected in that station from normal plants and sown in my garden. One among them proved especially interesting in being of lower stature and of a more slender structure than its very stout ancestor.

According to some stray observations, mutability is not at all limited to these examples, but occurs in different allied species also. From all of these facts we may safely conclude that mutability is a wide-spread phenomenon in the group of the *Onagras*, and that it has not originated with the origin of *O. Lamarckiana*. This weighty conclusion has of late found an unexpected support in the discovery of Stomps that

the European *O. biennis* is liable to the production not only of dwarfs, but also to that of the main progressive type among my mutants, the *gigas*. As a matter of fact, it has not as yet been observed to throw off *gigas*-plants as such. But it has given a half-*gigas*—*Oenothera biennis semigigas*—characterized by intermediate marks between real *gigas* and ordinary *O. biennis*, and especially by having in its nuclei in the one half the fourteen chromosomes of the former, and in the other, the seven of the latter. In other words, it has twenty-one chromosomes, being in this respect wholly analogous to the triploid mutants of *O. Lamarckiana* so fully and ably described of late by Miss Anne M. Lutz.<sup>1</sup>

Returning to our general discussion, it is clear that the other species are only mutating in a lesser degree than *O. Lamarckiana*, and from this fact we conclude that the extent of this property must have increased gradually during the phyletic evolution of the group. Or, in other words, the present mutability of *Oenothera Lamarckiana* is built up by a number of factors, more than one of which have evidently originated already with its ancestors. It goes without saying that the single steps of this process must themselves be regarded, on the basis of our theory, as constituting each of them a special mutation.

By means of the facts which I have just described, many objections made by different authors may easily be surmounted. The question whether *O. Lamarckiana* has still one or more wild stations is no longer of interest, since most of the other mutating species are recognized to be good wild types. This is especially the case with *O. grandiflora*. From my discovery that *O. Lamarckiana* produces twin hybrids, *O.*

<sup>1</sup> Since the reading of this address numerous cases of mutability in allied species of *Oenothera* have been discovered by H. H. Bartlett. (Note of 1915.)

*læta* and *O. velutina*, when it is crossed with certain of the older species, some authors have drawn the conclusion of a hybrid nature. But Davis has shown that *O. grandiflora* produces the same twins in analogous crosses; and in order to explain this fact by a hybrid condition the adversaries would either have to assume such a condition separately for the two species, or suppose a hybrid origin for their common ancestors. Both suppositions seem to lie far beyond the realm of credible scientific hypotheses.

Other grounds for assuming a hybrid nature for *O. Lamarckiana* must disappear before the same group of facts. As a matter of fact, it is generally conceded that in polymorphous groups of species some forms may have been the result of crosses between others. This opinion was held by Linnaeus, and for the cereals it is evidently true, as is proved by the researches of Nilsson and others. Any one who has studied the species of *Oenothera* in botanic gardens must have been struck by the fact that they are very rich in constant hybrids. But all such observations are far from containing even a single trace of proof in favor of the assertion that mutations should be a consequence of previous crosses.

Some authors deal with the struggle against the *Oenotheras* in a rather inconsiderate way, especially among those who enjoy any argument pleading for "the possibility of the Mutation Theory being based on false premises." As an example, I may give the observation of Boulenger.<sup>1</sup> He found a station for *Oenothera Lamarckiana* in Bretagne, not far from La Garde St. Cast (Côtes du Nord). Here it had started from the neighborhood of the hotel and spread

<sup>1</sup> G. A. Boulenger, in "Journal of Botany," October, 1907.

through the surrounding dunes during several years. He found that it showed a high degree of variability, especially in the direction of the characters of the European *O. biennis*, a long line of transitions and intermediate steps being clearly made out. He tried to recognize among them the types of my mutants, but they proved to be wholly of another nature. Neither did he succeed in determining a limit which would separate two groups, the one belonging to *O. Lamarckiana* and the other to *O. biennis*. From these facts he concluded that *O. Lamarckiana* may locally revert to some ancestral form which would have been very similar to, if not identical with, the *O. biennis*. Every botanist would of course have come to a different conclusion and assumed that *O. biennis* had already been present on that spot, being a common inhabitant of the dunes, and that it had readily crossed with the introduced *Lamarckiana* so as to produce quite a number of intermediates of hybrid origin. And even the pointing out of this possibility would have destroyed the whole basis on which Boulenger thought it safe to attack the new theory.

Moreover, it is rather easy to prove that the transitions of Boulenger must really have been such hybrids. In crossing the species in question, we come upon three clearly distinct types, two of which have been already dealt with. These are *Oenothera hybrida læta* and *velutina*. They result from the cross *O. biennis*  $\times$  *Lamarckiana* and constitute its twin hybrids. The former has broader and flatter, the other narrow and rolled leaves; but aside from this mark, they differ in almost all their organs and qualities. The third hybrid results from the reciprocal cross, *O. Lamarckiana*  $\times$  *biennis*; its characters are very similar to those of *O. biennis*, from which in some specimens it is often hardly discernible. To determine the limits of these five

types in a mixed group of plants may seem a difficult task even to an experienced eye; in any case, Boulenger failed to recognize them. *O. biennis* is one of the more common species in many parts of the dunes of Holland, where it is known to have grown already at the time of Linnæus. Not rarely *O. Lamarckiana* is sown on the same spots, being a favorite food for birds; in such cases the hybrids will arise by the natural processes of fecundation by insects. This of course also happens from time to time in the dunes of Holland, and I have observed it in an unusually broad area for the *Oenotheras* in the neighborhood of Zandvoort, where I studied it with special care in 1905 and 1910. In the spring of 1906 I sowed seeds of this motley group in my experiment garden; and in 1911 I introduced a set of rosettes and got them to flower. The hybrid types were easily recognized, although, on account of their transgressive variability, they seemed to constitute continuous lines of variation in many characters. In the dunes these differences are less evident than in the experiment garden, on account of the very different life conditions. In groups, however, it is easy to ascertain the types, but from such a station I would never use the seeds for any experiments in mutability. Every single individual must always be regarded with some doubt as to the purity of its origin.

In England, also, the two species often grow together. Charles Bailey has described such a station from the neighborhood of St. Anne's on the Sea, near Liverpool. Therefore I asked one of my friends to visit this station for me, and he informed me that in some of the valleys *O. Lamarckiana* was seen to be pure, while in others it was mixed with *O. biennis* and the hybrids.

In order to give a general review of the single mutants

which have arisen from the *Oenothera Lamarckiana*, we may bring them into certain groups:

- A. Progressive mutations: *O. gigas*.
- B. Retrogressive and degressive mutations:
  1. Mendel cases: *O. brevistylis*.
  2. Half Mendel cases: *O. nanella*, *O. rubrinervis*.
  3. Not Mendelizing mutants: *O. lata*, *O. scintillans*,  
*O. oblonga*, *O. levifolia*.

Besides these, there is a long list of instances which have not as yet been studied by means of crosses, as, for example, *O. albida*, *O. elliptica*, *O. leptocarpa*, *O. semilata*, *O. spathulata*, *O. sublinearis*, *O. subovata*, and many others to which no names have been given on account of their sterility or of their excessive feebleness. Mutations have also been won by other investigators; among them the *O. rubricalyx* of Gates, the *O. ammophila* of Abromeit, and the *O. blanda* of Schouten must here be mentioned. During the last ten years I have not tried to increase the number of the mutants; but notwithstanding this, I have secured some interesting novelties. The fact that in this whole group only one species is of a progressive nature, while the large majority are either degressive or retrogressive, has had stress laid upon it by some authors as a strong objection, but it is just what we should expect on the ground of our knowledge of other polymorphous groups.

As is well known, a certain group of authors assert that all hybrids and all characters must necessarily follow the rules of Mendel. A criticism of this evidently one-sided conception would take me too far from my real subject. At the present moment I will therefore limit myself to the contention that conclusions drawn from immutable plants are



not *a priori* applicable to those which are in a condition of mutability. On the contrary, these latter behave in many respects differently, and it is only with them that I shall have to deal here.

Let us first look at the progressive mutations. According to our theoretical conceptions, they owe their origin to the appearance of a new kind of hereditary unit, or pangens, which must have been split off by some one of the previously existing units. This latter can be in a condition of premutability, and thereby able to repeat the same mutation from time to time. Whether this premutation is caused by its own condition, or is due to the influence of neighboring pangens, is a question which is not now in need of an answer. It is only a few progressive mutations that are of a phyletic nature—*i.e.*, made for contributing to the building up of the pedigree of the whole system; by far the greatest number must, of course, be limited to ordinary specific differences.

In the foreground of our discussion of *Oenothera gigas* we may put the fact that it possesses, in its nuclei, a double number of chromosomes in comparison with the species from which it arose and with almost all of its other derivatives. *O. gigas* has twenty-eight instead of fourteen in the vegetative cells, or fourteen instead of seven in the generative elements. This important fact was discovered in 1907 by Miss Anne M. Lutz and corroborated shortly afterward by Gates, and later on by my pupils Geerts and Stomps. It has brought the new species to the foreground of cytological interest. Similar duplications of the set of chromosomes constitute important specific marks in other groups of plants; and in no single case are there arguments in favor of regarding it as a retrogressive change.

For the origin of a progressive mutant, in this case of a plant with a double number of chromosomes, it is obviously

necessary that two mutated sexual cells should combine, as was first pointed out by Stomps. This condition is not the same for retrogressive and digressive mutations, as we shall see later on. It is true that Gates has expressed a different opinion and asserted that the duplication takes place only after fecundation, not being a real mutation, but more in the nature of an accident.<sup>1</sup> This, however, would bring the whole phenomenon into the class of acquired characters which are now generally considered as not hereditary. From this point of view, the conception is in evident contradiction to the facts, since the *gigas* has continued its existence already during several generations. In this connection I may point to the double-nucleated cells of *Spirogyra* in the experiments of Gerassimow, which retain this special mark during all the vegetative divisions, but lose it as soon as fecundation comes into play. Moreover, the facts since discovered fully disprove the view of Gates.

*Oenothera gigas* has been seen with sufficient evidence to arise only once in my cultures. This was in 1895, from pure seeds of 1891. It is only of this race that the chromosomes have been counted. In the beginning I believed that I saw it in other years also; but at that time I did not know the characters of the hybrid between it and *Lamarckiana*. Looking back to those cases, it now seems to me that they were only half mutants, produced by the conjugation of a mutated sexual cell with a normal one. In this case they should have had twenty-one chromosomes in their nuclei, but they have not been studied in this respect and did not bear any seed. Such supposed half mutants have since been seen to arise more than once, because it was now known that there are reasons for expecting them and looking for them. For one of these the chromosomes have been counted by Stomps,

<sup>1</sup> R. R. Gates, "Archiv für Zellforschung," 3 Bd., 4 Heft, 1909, p. 549.

who found the expected number of twenty-one. This observation proves, first, that the duplication takes place before fecundation, and secondly, that the mutation is not so rare in the germ-cells themselves that we should be justified in considering it as an accident. By means of a careful and extensive study, Miss Lutz has discovered the same fact. In her cultures she observed ten half-*gigas* mutants arising from *O. Lamarckiana*, and in counting the number of chromosomes for all of them, she found it, without exception, to be twenty-one.<sup>1</sup>

It may here be mentioned that Heribert Nilsson discovered in 1907, in Sweden, a mutation of *O. Lamarckiana* in *gigas*.<sup>2</sup> It gave an hereditary race, but nothing has been published in regard to the nuclei. Another important fact is the discovery of Geerts, who met once, in his cytological studies of *O. Lamarckiana*, with a mother-cell of an embryo sac which showed in its division twenty-eight instead of fourteen chromosomes. Controlling these observations, I have accurately compared my half mutants with the artificial hybrids between *O. gigas* and *O. Lamarckiana*, and convinced myself of their external identity in all respects.

On the basis of these experiences it is possible to calculate the mutation coefficient for *O. gigas*. Most suitable for this purpose are crosses of *O. Lamarckiana* with such species as produce only, or almost only, yellow, very weak and soon dying hybrid germs. This is the case when *O. Lamarckiana* is pollinated with the pollen of *O. cruciata*, *O. muricata* or *O. Millersi* (*nov. sp.*). We have only to count the germinating seeds and to cultivate the few green ones among them. As in *Lamarckiana*, all of its derivatives give such yellow seedlings, the only exception being that of *O. gigas*.

<sup>1</sup> Miss Anne M. Lutz, "Triploid mutants in *Oenothera*," *Biol. Centralbl.*, Bd. 32, July, 1912, p. 384.

<sup>2</sup> "Bot. Not.," 1909, pp. 97-99.

Those sexual cells which have been mutated into this form will therefore produce green seedlings, which it will then be easy to isolate from the rest. In growing up they may soon be recognized by their much stouter stature, and for this reason Stomps has proposed to call them *Hero*. In counting their chromosomes, he found them to be twenty-one in each nucleus, this number being the sum of seven chromosomes derived from the father (*O. cruciata*, etc.) and of fourteen derived from the mutated egg. This, of course, is a sufficient proof; but the *Hero* plants may afterward be easily recognized as such by their stout flower-buds and other characteristics.

Among fifteen thousand yellow seedlings, forty-five examples of *Hero* were counted, giving a percentage of 0.3. If now we assume that the mutations are as numerous in the male sexual cells, the chance of their meeting together and thereby producing a full *gigas* will obviously be equal to the quadrate of this number, or 0.0009,—say about 0.001%. In my mutation theory I had provisionally conjectured this number to be 0.01%.

The size of the cells and of some of the organs of *O. gigas* has increased in consequence of this doubling of the chromosome number and in accordance with the laws discovered by Boveri and Marchal. This fact was first pointed out by Gates. This author extended his conclusions to all the differences between *O. gigas* and *O. Lamarckiana*; but this has been shown by Stomps to be unjustifiable. Neither the biennial habit, nor the large seeds in the small capsules, nor the adhesion of the axillary buds to the stem above the leaf can be explained in this way. The same is the case with other marks. Here I might, however, lay stress on two points which can hardly be considered as consequences of a double set of chromosomes, but which have of old been con-

sidered as true specific characteristics as opposed to mere varietal marks. I am thinking of the strongly diminished fertility of almost all the crosses and hybrids of *O. gigas*; and, in the second place, of the fact that the hybrids are intermediates between their parents and constant as such in their progeny, whenever they have any.

*O. Lamarckiana*, as a rule, gives a normal harvest of seeds, after being crossed with allied species, amounting to about 0.3 cc. per capsule. *O. gigas*, however, does not produce after the same crosses more than 0.01 to 0.02 cc. of seeds per capsule; and if sometimes the harvest is found to be larger, the seeds are, as a rule, not capable of germinating, although apparently of good structure. Often it is very difficult to win hybrid seeds at all; as, for instance, in the crosses with the European and the American species of *O. biennis* with *O. strigosa*, with *O. Hookeri* and even with *O. Lamarckiana* and the larger number of its derivatives. Moreover, the hybrids, if once produced, prove afterward to be almost, or wholly, sterile after self-fecundation, and the second generation often embraces only a very few individuals. Reciprocal hybrids are identical, provided the nature of the other parent permits it, and the externally visible qualities are apparently just the mean between the two parents.

On the ground of all these facts I take it for granted that *O. gigas* is a good species, arisen in a progressive way from its parent, although distinguished from this by only a single unit character. In all these respects it behaves differently from all the other mutants.

We now come to a discussion of *O. brevistylis*. It is distinguished from its parent form mainly by the partial loss of the epigynous condition of the flowers. Besides this, it is the only one among all the derivatives of *O. Lamarckiana*

that exactly follows the law of Mendel; and this in its crosses with the parental species as well as with its derivatives and with the older species. In some crosses it may be seen to split into the twin hybrids *læta* and *velutina* in the same manner as its ancestor, but then both of the twins will split in respect to the length of the style, according to Mendel's formulæ.

Of course the same splitting must occur in the field where it grows together with *O. Lamarckiana*. As a matter of fact, it is not possible to distinguish the hybrids from that species on first inspection; but in bringing numbers of rosettes of root-leaves to the garden from time to time a single plant may be met with, the progeny of which contains the short-styled individuals in the number required by Mendel's rule. Such a case I happened to find in my cultures in 1905. From this we may infer that the short-styled specimens (which almost every year are seen to grow in the field) may be offspring of such hybrids, and thus their existence is far from proving the presence of another source, such as a direct mutation from *O. Lamarckiana*. Moreover, it seems that this mutability is wholly exhausted, since the mutation has never repeated itself in my cultures.

If we try to penetrate into the mechanism of the original mutation to which my race owes its existence, we find that obviously the change of a single sexual cell must be considered as sufficient. Its fecundation by a normal cell will give rise to a hybrid, from the seeds of which the pure type of *O. brevistylis* will come into existence. The hybrid could not be recognized in the field, but the short-styled individuals at once strike the eye by wholly different qualities. These themselves produce no seed at all, or hardly any; but in fecundating the surrounding *Lamarckianas* they will give rise to hybrids, from which the pure type may once more be

produced. There can be no doubt that it is in this way that the *O. brevistylis* has kept its place in the field during the almost twenty years of my observations.

We may now turn our attention to those mutants which follow the laws of Mendel only half-way. They do not comply with these rules in their crosses with the parental form, nor with the majority of its derivatives. But in those crosses with other species which split them into twins the rule is that one of the twins follows these formulæ while the other does not. To this group we may bring *O. nanella* and *O. rubrinervis*.

Before detailing the results of the crosses of these two new species, I must call your attention to one of the most curious objections that have been made in the struggle of some authors against the *Oenotheras*. I mean the contention that the dwarfs should not be a pure hereditary race, but only diseased individuals of the ordinary *Lamarckiana*. Of course nobody who ever saw the two cultures side by side can hold such an opinion, since transitions are always absent. The dwarfs do not attain half the height of the parental form, and are almost all of the same stature. This is purely reproduced from seed, without exceptions or deviations. The contention I mentioned starts from a discovery made by Zeylstra. He observed a curious type of bacterium within the cells of the dwarfs, and showed that the presence of this parasite is the cause of some of their characters, formerly held for specific marks: thus, for instance, the broadened bases of the leaves, the brittleness of their stalks, the frequent curvature of the flower-buds, the failure of the style in some flowers, and others. But in opposition to these minor points, the stature of the dwarfs is neither caused nor sensibly affected by the parasite. This may be proved in an easy way by cultivating the dwarfs on a soil rich in phosphate

of lime and relatively poor in nitrogenous manure. Under such conditions the phenomena of the disease are seen to disappear completely, or almost so.<sup>1</sup> The leaves become narrow and stalked, the internodes longer, the brittleness is lost, the flower-buds are straight, and the flowers open in a normal way. Often one or the other leaf still shows signs of the disease, and so betrays the presence of bacteria in the cells. But the main point is that the stature remains the same; the dwarfs are still dwarfs, even when they are in the best of health. They constitute a distinct mutation, which, however, is distinguished from the parental type in two points—viz., the stature and the sensitiveness to certain kinds of bacteria of the soil. As already stated, the same holds good for the dwarfs of the *Oenothera biennis*.

From the crosses of *O. nanella* and *O. rubrinervis* with some of the older species the same twins arise as from the analogous crosses of *O. Lamarckiana* itself. They are the *leta* and *velutina*, of which I have already spoken more than once. In such cases dwarfs are lacking in the first generation; and from this we should expect a splitting in the second, according to Mendel's law. As a matter of fact, this splitting does occur, but only among the progeny of one of the twins. The other gives a constant race without dwarfs. And since the twins are usually produced in about equal numbers, it is one half of the progeny which complies with Mendel's law. Hence the name of "half-Mendel hybrids." As a rule, it is the *velutina* which produces the dwarfs, while the *leta* remains constant.<sup>2</sup>

It is evident that such splittings cannot occur in the field

<sup>1</sup> "Science," N. S., Vol. XXXV, No. 906, pp. 753-754, May, 1912.

<sup>2</sup> For more details see my book, "Gruppenweise Artbildung," which is soon to be published. A modification of the process of splitting may be introduced into these experiments by the use of heterogamous species, as, for instance, *O. muricata*. See also "Ber. d. d. bot. Ges.," Bd. XXVI a. 1908, p. 667.



on spots where the *Lamarckiana* is free from the admixture of other species. In such cases we are concerned only with the crosses of the derivatives among themselves and with the parent type. From these crosses only the parental types are repeated, and, as a rule, to the exclusion of others. Fecundating themselves, they will prove constant. From these experimentally ascertained facts we may conclude as to what must happen in the field. A mutation may keep its hold there in three different ways: first, by means of self-fecundation; secondly, by means of intercrossing with the parental species; and thirdly, by being produced anew, from time to time, from the main stock. To which of the three processes a given individual owes its origin can of course not be seen in the field; and so there is almost never a direct proof of mutations occurring there, except in those cases where the mutants succumb in the struggle for life before opening their flowers. And this is not at all rare under the adverse conditions of the field at Hilversum.

The results of our crosses show that in many cases the coöperation of two mutated sexual cells is not a necessary condition for a mutation to be produced. It is often quite sufficient that the mutated cell be fecundated by an ordinary one. If this does not occur too rarely—as a rule, in one half of the instances—the mutation will be lost; while in the other half it will dominate and develop its qualities in the new individual. For this is the rule governing artificial crosses. In those cases where it is lost, the new individuals will be identical externally with the ordinary *Lamarckiana*; but it might be possible that such individuals should prove to possess a greater liability for mutating than do others. This point, however, has not as yet been investigated. It might be suggested that it is in just this way that mutability is maintained in the field; but the results of some artificial

crosses do not plead in favor of this opinion, since the *Lamarckiana* individuals produced from such crosses do not show any increase in their mutability.

The facts which we have now described could be used as a starting-point for answering the question concerning the nature of the process of premutation, or of the initial change which induces the condition of mutability. In doing so we should have to assume that originally some mutation had occurred in a sexual cell and that from the copulation of this with a normal plant no mutant, but a seemingly ordinary *Lamarckiana*, had arisen. Then we might assume that this copulation had induced a mutable condition, which must be supposed to have become hereditary and to have given rise to an hereditary race. If such a change had taken place in the lapse of time, first for the mutability into *O. nanella*, it could have been followed by a similar change for *O. rubrinervis*, then for *O. lata* and *O. scintillans*, and so on for the whole range of known and as yet unknown mutants.

But such speculations hardly throw any light on the real nature of the processes of premutation, nor on that of the premutated condition, nor on the power of mutating derived from it. I have only mentioned them in order to show that the hypothesis of Bateson concerning this process is as superfluous as it is erroneous. This author contended (1902) that mutability might be a result of crosses with other pre-existing species, which would have been in the possession of the qualities afterward displayed by the mutants. In opposition to this supposition, many authors, and among them MacDougal, have pointed out that the species required for the justification of this view do not, as a matter of fact, occur. And if we review the qualities of the different new types produced by *O. Lamarckiana* as mutants, the number of which amounts to more than twenty, we shall soon be

convinced that the large majority of them are too weak in some respect or another to be able to exist in nature. They would have been crowded out almost as soon as they had arisen. The only way of escaping this difficulty would be to assume that those hypothetical species had possessed the desired qualities only in a latent condition. But this supposition would, in another respect, be contrary to the views of Bateson. Under these circumstances, I think it must be conceded to be a more simple supposition to leave out the conception of a long row of hypothetical ancestors, and only to assume a succession of those premutations the consequences of which may yearly be observed in the mutations they produce.

But still one could be inclined to consider the premutation as a consequence of the cross of a mutated sexual cell with an unchanged one. In order to produce the desired result, such crosses would have to occur more than once, since only half of them may be expected to produce mutable *Lamarckiana* plants; and the reason for such repetitions would then remain an obscure point in the discussion. But, as already stated, all these considerations do not bring us nearer to an understanding of the phenomena. Therefore I will limit myself to the citing of the extensive criticism of Blaringhem (*l. c.*, pp. 173-186), and to pointing out the most important fact described by Geerts—namely, that the rudimentary condition of the pollen grain, which plays so large a part in those hypotheses which ascribe a hybrid nature to *O. Lamarckiana*, is not at all characteristic of this species and its nearest allies, but is seen to occur throughout almost the whole family of the *Onagraceæ*. It is evident from this that it cannot be considered as proof of a hybrid nature of any species of that family.

Moreover, I might once more lay stress on the assertion

that it is not permissible to apply conclusions drawn from immutable plants in an explication of the conditions of mutable ones. Such a process would be justifiable only in case it were experimentally shown to be possible to change the ordinary immutable types into the rare and so much desired mutable forms, only by means of artificial crosses. But as yet all experience is contrary to such a conclusion.

The last group we have to consider embraces those mutants which in no respect comply with the laws of Mendel. It may be sufficient to deal with them only very briefly here. Their first generation, after being crossed with the parental species, is as a rule a twofold one which only repeats both of the parental forms. In the case of *O. lævifolia* and *O. oblonga* these types are at once constant, while in that of *O. lata* and *O. scintillans*, which are inconstant types themselves, the form which externally corresponds to them does so in respect to its constancy also. Only the *Lamarckiana* individuals sprung from these crosses remain constant when self-fertilized.

It is clear that the discussion given above for the appearance of individuals deviating in the field, as well as that for the process of premutation, is directly applicable to this case too. It would be useless to repeat them. But the results of my crosses indicate a long range of possibilities, which it is as yet hardly possible to combine into a simple and clear scheme. They have only one feature in common, and this is the total absence of splittings conforming to Mendelian laws.

Of course it is not possible to review here all the objections made against the significance of the *Oenotheras* for the mutation principle. The theory does not stand or fall with the validity of a single example. It has been derived from general considerations, and is supported by a critical review of numerous facts taken from the most diverse fields of

natural science. It has found rapid recognition in almost all circles of biological inquiry, and has caused the principle of pangenesis, laid down by Darwin, to become the starting-point for the theory of heredity.<sup>1</sup> It is true that, as I have already pointed out in the introduction to my mutation theory (Vol. I, p. v), work on the basis of this principle is far more easy in the domain of hybridology than in that of pure heredity. The development of the experimental studies within the last ten or twelve years has fully justified this assertion. Hybridology, or at least that part of this science which deals with Mendelism, has developed to a bright and flourishing science, while only a few investigators have devoted their work to the study of pure descent. In the next few years the main interest will probably turn to the production of new species within pure and well-guarded strains,<sup>2</sup> partly in order to get extensive proofs of the fact itself, and partly to find their explanation. Along these lines scientific research is gradually approaching its highest scope: the artificial production of new forms of life—forms planned beforehand.

HUGO DE VRIES.

<sup>1</sup> See C. Stuart Gager, "Intracellular Pangenesis," English edition (Chicago, The Open Court), 1911.

<sup>2</sup> See L. Blaringhem, "Transformations brusques," *l. c.*