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It is a well-established fact that what are commonly called variations include modifications of quite different import in relation to the process of evolution. Whether or not the variations that are induced in the soma, either by its own activities or through the influences of the environment, have any effect in shaping the course of evolution as they were held to do by Lamarck and his followers, it is evident that they do not count in this process in the same way as variations that arise in the germ. But among the germinal variations themselves there are classes of unequal significance. Variations differ markedly in regard to their stability or permanence. Many variations after their first appearance persist with little modification for an apparently indefinite time. Of these what are commonly called mutations afford conspicuous examples; these are abrupt variations which breed true or nearly so from the start, having their own fluctuating variability, to be sure, but around a mean which does not approach that of the parental type in successive generations. Other variations behave quite differently. They may be selected generation after generation, modifying the stock up to a certain point, after which, if the variety is left to itself, there is revision towards the original parent. It is held by many that these two classes of variations are fundamentally distinct, and that only the first, so-called discontinuous variations, play an important rôle in the origination of new species.

A considerable proportion of what is described as fluctuating variability is, in many cases, simply somatic variation, having no relation to the germ plasm. It is evident, however, that all fluctuating variability can not be such, otherwise species could not be modified by ordinary methods of continued selection. Our mathematical curves represent two kinds of variability lumped together and which it is in most cases practically impossible to separate. The character of height, for instance, in human beings is to a certain extent an inherited one, but it is determined to a marked degree by influences operating after birth. The usual curves of variation represent both and may even include also variations in the nature of mutations which fail of discrimination from the rest of the aggregate.

De Vries distinguished three kinds of germinal variations, elementary species, retrograde varieties and fluctuations. These three kinds he conceives to be sharply distinguished and produced in different ways. All congenital variability is regarded by him as resting upon qualitative or quantitative changes in the pangens or the organic units of which he conceives living matter to be built up. The pangens form the basis of the unit characters, or independently variable elements of the organism, there being a special kind of pangen for each such character. Variations in the number of pangens cause variations of the fluctuating type which obey Quetelet's law of chance frequency distribution. De Vries maintains and attempts to prove by the citation of several examples that through the selection of such variations modification may be carried to a certain point, but soon a limit is reached beyond which selection is incompetent to effect further improvement. Moreover, continued selection must be practised in order to maintain the condition which has been reached, else the stock will in the course of a few generations revert more or less completely to the ancestral mean.

Retrograde varieties, according to De Vries, are sharply distinguished from fluctuations. They are, as a rule, constant from the start, and differ from the type in only one or at most a very few respects.

> They originate for the greater part in a negative way by the apparent loss of some quality and rarely in a positive manner by acquiring a character seen in allied species." "By far the greatest part of the ordinary garden-varieties differ from their species by a single sharp character only. In derivative cases, three or even more such characters may be combined in one variety, for instance, a dwarfed variety of the larkspur may at the same time bear white flowers or even double white flowers, but the individuality of the single characters is not in the least obscured by such combinations.

These varieties, says De Vries, "do not possess anything really new." The loss of a character is merely apparent. "On a closer inquiry we are led to the assumption of a latent or dormant state. The presumably lost characters have not absolutely, or at least not permanently disappeared. They show their presence by some slight indication of the quality they represent, or by occasional reversions. They are not wanting, but only latent." In other words, the only difference between retrograde varieties and the types is the latency or patency of certain characters. The same kinds of pangens are present in the germ plasm of both.

Elementary species, on the other hand,

> are distinguished from their nearest allies in almost all organs. There is no prominent distinctive feature between the single forms of *Draba verna,* Helianthemum or of Taraxacum; all characters are almost equally concerned. The elementary species of Draba are characterized, as we have seen, by the forms and the hairiness of the leaves, the number and height of the flower stalks, the breadth and incision of the petals, the forms of the fruits, and so on. Every one of the two hundred forms included in this collective species has its own type, which it is impossible to express by a single term. Their names are chosen arbitrarily. Quite the contrary is the case with most of the varieties, for which one word ordinarily suffices to express the whole difference.

The most important distinction which De Vries draws between retrograde varieties and elementary species is a physiological one. They behave in quite different manner, when subjected to crossing experiments, and the hope is justified that some day crosses may become the means of deciding, in any given instance, what is to be called species, and what variety on physiological grounds.

When varieties are crossed with the parent type the character that is active in one or the other of the forms will usually be patent in the first generation of offspring. In the second generation there is, according to De Vries, a segregation of characters which takes place in conformity to Mendel's law. Ordinary sugar corn, for example, differs from the usual type in having a part of the starch replaced by sugar in the kernels, which consequently become wrinkled when dry. When these two forms are crossed the active character of starchy kernels is present in all the members of the first generation. In the second generation there is a segregation of these characters, one fourth of the offspring being wrinkled kernels, and three fourths smooth ones. Approximately one third of the latter produce only smooth kernels in subsequent generations, while the other two thirds split up again in the expected Mendelian ratio.

In the crossing of varieties it is possible, according to De Vries, for all the corresponding characters of the two forms to become paired. As the distinguishing feature of the variety is the latency or patency of one or more characters, these characters "will unite as well as though they were both active or both dormant. For essentially they are the same, only differing in their degree of activity. From this we can infer that, in the crossing of varieties, no unpaired remainder is left, all units combining in pairs exactly as in ordinary fertilization." As the varieties differ only in the dominance or latency of certain characters, offspring obtained through crossing them differ only in the same way. For such unions De Vries gives the name "bisexual crosses," inasmuch as there is "complete bisexuality, all unit characters combining in pairs."

In the crossing of the elementary species of Œnothera De Vries found that in the first generation there was a splitting up of the progeny in various ratios, but that the second and subsequent generations bred true to type, thus presenting a condition just the reverse of Mendelian inheritance. For instance when the mutant *rubrinervis* was crossed with the parent type *Lamarckiana* the first generation of hybrids were either *rubrinervis* or *Lamarckianas,* the proportion varying greatly in different lots. The two kinds of hybrids did not split up in the second generation but bred true to type. Similar results were obtained by crossing several other elementary species of *Lamarckiana* but this kind of behavior does not seem to be generally characteristic of the elementary species of other forms.

In the crossing of elementary species there is, according to De Vries, one unit character which is not mated, since

> the differentiating mark is present in one of the parents and not in the other. While all other units are paired in the hybrid it is not. It meets with no mate and must therefore remain unpaired. The hybrid of two such elementary species is in some way incomplete and unnatural. In the ordinary course of things all individuals derive their qualities from both parents; for each single mark they possess at least two units. Practically but not absolutely equal, these two opponents always work together and give to the offspring a likeness to both parents. No unpaired qualities occur in normal offspring; these constitute the essential features of the hybrids of species and are at the same time the cause of their wide deviations from ordinary rules.

These differences between variations were predicted by De Vries on the basis of his pangen theory, and in his essay on "Intracellular Pangenesis" published in 1889 he expresses the opinion that fluctuating variability which rests upon numerical variation of the pangens plays but a minor part in the modification of species. The "artbildende" or species forming variability, is dependent upon the appearance of an entirely new kind of pangen. When categories of variation are anticipated *a priori* on the basis of a theory of the constitution of living matter there is naturally produced a temptation or bias towards reading the classification into nature and to the overlooking of transitional stages, and we shall therefore enquire if the distinction which is made between elementary species and varieties is a valid one.

In the first place, there does not seem to be any very good reason why on the pangen theory elementary species should differ in numerous characters from the parent form. A pangen is the basis of a single unit character. Elementary species are produced through the origination of a new kind of pangen. If the becoming latent or dominant of a pangen affects only one unit character of an organism, it is not evident, when a new kind of pangen is produced, why the whole organization of the plant should be so profoundly influenced. Why should not the awakening of a dormant pangen produce as great a change as the production of a new pangen of a somewhat different quality. Says De Vries:

> There can be little doubt but that all the attributes of every new species are derived from one principal change. But why this should affect the foliage in one manner, the flowers in another and the fruits in a third direction, remains obscure. To gain ever so little insight into the nature of these changes, we may best compare the differences of our evening primroses with those between the two hundred elementary species of Draba and other similar instances. In doing so we find the same main feature: the minute differences in nearly all points.

De Vries nowhere gives us a much clearer explanation as to why elementary species and varieties should differ in this way and we must probably be content with referring the matter to different degrees of "correlation."

It is evident that there are allied groups separated by small differences throughout the entire organization, and there are other groups which differ apparently in single characters only, such as the presence or absence of hair, spines or certain colors. Hornless cattle and six-toed cats do not seem to present any general or constitutional differences from the other members of their species, but this is a subject upon which we should exercise great caution, as very slight differences in the rest of the organization may be correlated with pronounced differences in a single part.

Among the forms arising by mutation from *Œnothera lamarckiana* De Vries distinguishes three varieties, *lævifolia, brevistylis* and *nanella.* These forms are called varieties instead of elementary species because they differ from the type in a few characters only and because of their different behavior when crossed. But even according to De Vries' own description the points of difference are not limited to a single character. *Lævifolia,* for instance, is

chiefly distinguished from Lamarck's evening primrose by its smooth leaves, as its name indicates. The leaves of the original form show numerous sinuosities in the blades, not at the edge, but anywhere between the veins. The blade shows numbers of convexities on either surface, the whole under surface being undulated in this manner. It lacks the brightness of the ordinary evening-primrose or *Œnothera biennis.* These undulations are lacking or at least very rare on the leaves of the new *lævifolia.* Ordinarily they are wholly wanting, but at times single leaves with slight manifestations of this character may make their appearance. They warn us that the capacity for such sinuosities is not wholly lost, but only lies dormant in the new variety.

The leaves of *lævifolia* are also "a little narrower and more slender than those of the *Lamarckiana.*" But *lævifolia* also shows differences in the flower. "The yellow color is paler and the petals are smoother. Later in the fall, on the weaker side branches these differences increase. The *lævifolia* petals become smaller and are devoid of the emargination at the apex, becoming ovate instead of obcordate."

Brevistylis is characterized by its short style. The stigma is different in shape from that of the parent form; there are differences in the ovaries, and there are only a few seeds produced. These differences may possibly depend upon a single varying character, although

the leaves of the *O. brevistylis* are more rounded at the tip, but the difference is only pronounced at times slightly in the adult rosettes, but more clearly on the growing summit of the stems and branches. By this character the plants may be discerned among the others, some weeks before the flowers begin to show themselves.

Nanella is a dwarf plant, but it is not distinguished by its smaller size alone.

From its first leaves to the rosette period, and through this to the lengthening stem, the dwarfs are easily distinguished from any other of its congeners. The most remarkable feature is the shape of the leaves. They are broader and shorter, and especially at the base they are broadened in such a way as to become apparently sessile. The stalk is very brittle, and any rough treatment may cause the leaves to break off. . . . The stems are often quite unbranched, or branched only at the base of the spike. Strong secondary stems are a striking attribute of the *Lamarckiana* parent, but they are lacking, or almost so in the dwarfs.

So far as morphological evidence is concerned, the difference between the above forms and elementary species are not so sharp as to inspire one with much confidence in the essential distinctiveness of the two classes. All of these so-called varieties differ in various parts of their organization. It may be said that these differences are dependent through correlation upon the variation of a single character, but if any one maintains that smooth leaves and paler flowers, or small size, brittle stem and short leaf stalks are related in this way, the burden of proof is on his shoulders. If a half dozen characters in different parts of the plant vary it would indeed be difficult, amid a considerable amount of fluctuating variability, to separate on morphological grounds a retrograde variety from a true elementary species, especially since experts are sometimes troubled in distinguishing some of the elementary species from one another. Indeed, De Vries admits that it is often very difficult to decide whether a given form belongs to one or the other of these two groups, but he states that in such cases we have a means of testing the matter experimentally by the formation of crosses. Let us see, therefore, how the test of crossing works out.

In the case of the varieties of *Œnothera lamarckiana* there is in the second generation a splitting according to the Mendelian ratio when the variety is crossed with the parent form, but with varieties of other forms this does not seem to be an invariable occurrence. Davenport has shown that albinism in poultry is in some cases a non-Mendelian character, and the same is probably true, according to Castle, for the lop-eared condition in rabbits. In the inheritance of long and short hair in guinea pigs there is also a marked departure from Mendelian ratios. In silkworms Kellogg has shown that while most features are Mendelian, cocoon color in some cases follows Mendelian ratios, but in others it proved to be "inconstant as to dominance and recessiveness and numerical proportions, and may even break down and blend." Deaf-mutism also refuses to come under Mendelian categories according to the statistics compiled by Bell. The foregoing are cases of apparent retrograde variations which form an exception to Mendel's law, but it must be admitted that the majority of such variations which have been investigated show a fair approximation to Mendelian ratios.

In the crosses between the elementary species of *Œnothera lamarckiana* there is commonly a splitting up in the first generation with absence of splitting in the second and subsequent ones. Hybrids of *O. Lamarckiana* and *O. biennis,* however, have nearly the aspect of the latter species and remain true in the second and subsequent generations without reversion or splitting. Crosses between *O. muricata* and *O. hirtella* produced hybrids showing the characters of both parents. These were propagated through four generations and remained "true to this type, showing only slight fluctuations and never reverting or segregating the mixed characters." Instances of constant hybrids between different species are very common and it is unnecessary to specify them here. Such constancy according to De Vries is "one of the best proofs of unisexual unions" or unions between distinct elementary species in which there is always one unpaired pangen.

The attempt to make a general rule for the hybridizing of elementary species leads to many difficulties. In poultry, as Davenport has pointed out, such characters as pea and rose comb, extra toes and the presence of muffs and beards on the head, are acquisitions which developed since the domestication of the original ancestral species. They certainly can not be regarded as the outcropping of latent characters which are represented in allied forms, but are in the line of progressive variation and therefore according to theory dependent upon the production of new kinds of pangens. In breeding experiments some ~~any definite rule of inheritance and none~~ of them follow Mendel's law, the extra toes do not seem to come under any definite rule of inheritance, and none of them follow the rule for the hybridization of elementary species.

Consider the forms of the common potato beetle studied by Tower. These arise suddenly, breed true to type and differ from the parent form in many characters, some of which are apparently in the line of progressive evolution. They seem to be as truly elementary species as the mutants of *Œnothera lamarckiana.* Yet when crossed with the parental type they produce hybrids which in most cases give a mixed progeny segregating according to Mendel's law. If we can not call these forms elementary species there is no way of distinguishing such except through breeding experiments, and the distinction De Vries draws between elementary species and varieties amounts to nothing more than the fact that crosses between certain groups follow Mendel's law, while crosses between others do not. There is no correlation between any structural criterion of species and the criterion afforded by breeding experiments.

Now when we attempt to make a classification on the basis of breeding experiments alone we fare little better. With blended inheritance in the first and all subsequent generations, partially blended inheritance, total resemblance of hybrid to one or another parent with or without subsequent splitting, incomplete segregation of characters, splitting of offspring of hybrids in various inconstant and non-Mendelian ratios, and many other irregular manifestations of heredity, the difficulty of maintaining a sharp distinction between varieties and elementary species on the basis of behavior in inheritance is apparent. Are we to classify a six-toed cat as a variety or an elementary species? The variation is apparently limited to a single character and it has therefore one of the marks of a variety, but the variation is doubtless a progressive one and not due to an awakening of a latent character, and hence possesses one of the features of an elementary species. When crossed some of the offspring of the first generation may inherit the variation and some not, and the same is true for the following generation; but there is apparently no splitting according to the law of Mendel. So far as our knowledge goes the situation is the same in respect to polydactylism in man.

The second volume of the Mutationstheorie, which seems to have been little read by most expositors of De Vries, affords several examples of irregular behavior of the hybrids between elementary species which are very difficult to classify. Crosses between *Œnothera nanella* and *O. rubrinervis,* for instance, the one a retrograde variety of *Lamarckiana* and the other a distinct elementary species, gave very variable results, with splittings in the first and succeeding generations in very inconstant ratios, and the occasional production of blends which bred fairly true. We have here a curious combination of the characteristics of unisexual and bisexual crosses.

It would not be difficult to bring forward many other cases which refuse to fall within the scheme of classification propounded by De Vries. There are many kinds of variations which are inherited in many kinds of ways. The pangen theory of the celebrated botanist has proved a deceptive guide and has led its author to do scant justice to many classes of facts which do not fall in line with it. Hypotheses about paired and unpaired pangens have determined De Vries's classification of the different kinds of variations and profoundly influenced his interpretation of his extensive and valuable researches. The doctrine of intracellular pangenesis has never received the logical development that characterizes Weismann's theory of the germ plasm and is considerably inferior to the latter as a scholastic production. The explanation it affords of the alleged distinction between varieties and elementary species is, as we have seen, practically no explanation at all. The theory may be consistent with the facts of Mendelian inheritance and the supposed independent variability of parts, but why it should lead one to anticipate that elementary species differing from the parent throughout their organization originate by a single sudden leap is not so clear. Rather it would lead one to expect that organisms would be modified, a part here and a part there, corresponding to the independently variable elements determined by particular pangens, of which there are numerous kinds, until the whole was slowly transformed. De Vries, however, is careful to explain that a single pangen may be responsible for certain characters found in various parts of the organism, such as the color of leaves, flower and fruit, and that pangens are supposed to influence each other's manifestation so that a variation in a single pangen may have a far-reaching effect. In a chapter on the association of characters in his recent book on Plant Breeding a great deal of emphasis is laid upon the value of a study of the correlation of the different parts of the plant. He says:

> We come to the conception of a general interdependency of all parts, organs and qualities of an organism. They are governed more or less by the same laws which cause them to undergo corresponding changes when subjected to the same influences.

It seems to me that the author is here upon treacherous ground. Through the assumption of manifold correlations De Vries attempts to account for a change in a single pangen which has to do primarily with one independently variable part of the organism producing a modification of the organism as a whole, but in so doing he is taking the foundation away from the argument upon which the justification of the pangen assumption rests.

To the extent that the organism is a whole of interdependent parts, to just that extent it gives evidence of not being a piece of mosaic work and hence removes the necessity for a hypothesis of discrete germinal units. De Vries even goes so far as to say that "in order to be correlated the characters must begin by being independent entities which through some later means may come into relation with others." At one time it is argued that the existence of pangens is proved by the fact that the parts of the organism are independently variable; and now it is said that we must assume that pangens must exist to account for the parts being correlated; that is, for the fact that they are not independently variable!

The most salient feature of the mutation theory is that the process of evolution is conceived to take place by sudden steps of considerable magnitude. This has been heralded with *éclat* as enabling us to get rid of certain difficulties inherent in the Darwinian theory, such as the assumed absence of intermediate forms between existing and fossil species and even the contention that the geological history does not afford time enough for the process of evolution as it was formerly conceived to take place. But it is not correct to say that a mutation is necessarily a large variation. Mutations may be very small steps, falling far within the limits of ordinary fluctuating variability, as is especially emphasized by De Vries in his later writings.

> In groups (such as brambles, roses, buttercups, willows and many others) where large numbers of species are closely allied, the differences between any two of them become smaller, and the number of distinct forms increasing, the distinction in the end may become reduced to a single differential mark for each two neighboring types. Such differences must be assumed to be produced each by a single mutation.

In the light of experiments made at Svalof, De Vries now concludes that "ordinary varieties of cereals are built up of hundreds of elementary forms which with few exceptions have hitherto escaped observation. The high variability which is commonly attributed to our ordinary varieties of cereals consists only in the differences among the constituents of the mixtures." Much of the improvement of grains that was formerly obtained by continued selection De Vries ascribes to the unconscious selection of elementary species and the gradual improvement of an originally mixed stock. Rimpau's rye, a stable race obtained by gradual selection, is thus accounted for, but the burden of proof is here on the part of the mutationists. It is apparently not so easy to test the rôle of mutations *versus* fluctuations in the improvement of species, because if one should secure a stable race by the usual process of selection, the mutationist might urge that, after all, amid the confusion of seemingly fluctuating variability, there were some mutations which escaped notice, and, through the unconscious selection of these and their offspring, the stock was gradually purified and converted into an improved stable form.

Where ordinary varieties include "hundreds of elementary forms," separated by characters which in many cases are so small that they "may be scarcely perceptible to the inexperienced eye," how is one to tell whether he is dealing with mutations or ordinary fluctuations? The latter may be much greater in extent, and, as we have seen, there is no structural criterion by which a mutation may be recognized. Crossing experiments give us no certain test and we have therefore to fall back upon the criterion of stability and class as mutations those variations which breed true from their first appearance. Here the opportunities for begging the question are excellent. If by the ordinary process of selection a stable race is produced we can of course ascribe it to the unconscious choice of one or more undetected mutations. To be sure, stable races can be produced only on the basis of stable variations, and if this is all that the mutation theory necessarily implies its divergence from Darwin's teaching is not very wide.

If now it should turn out that stability is a matter of degree the last distinguishing feature of the mutation theory would be destroyed. This is a question upon which we are sadly in need of light. Some of De Vries's own mutations are, however, quite inconstant and show a strong tendency to revert to the parent species. *Œnothera scintillans,* when self-pollinated, produced from 8 per cent. to 52.9 per cent. of *Lamarckianas* and 34 per cent. to 69 per cent. of its own kind and a variable number of other mutants. *O. elliptica* and *O. linearis* repeat their kind in still smaller ratios. The reversion of these mutants like their origin is sudden, but it shows an unstable condition of their germ plasm and it may be questioned if this reversion is essentially different from the slower reversion which often follows the cessation of the selection of ordinary fluctuations.

That the differences between mutations and fluctuations are not so fundamental as the pangen theory implies is indicated by several facts, some of the most suggestive of which have been furnished by De Vries's own experiments. For a number of years De Vries carried on a series of experiments on the corn-marigold *Chrysanthemum segetum,* with the purpose of creating a double-flowered variety. De Vries chose a garden variety of this form, *grandiflorum,* and raised several generations, selecting the seed each time from heads which contained 13 rays florets. After four years of propagation, when he was satisfied of the purity of the isolated strain, De Vries began to discard all plants with less than 21 rays in the terminal head. The selection was continued for a number of generations when a plant appeared which seemed to form a promising one for the production of a double variety.

It was not remarkable for its terminal head, which exhibited the average number of rays of the 21-rayed race. Nor was it distinguished by the average figure for all the heads. It was only selected because it was the one plant which had some secondary heads with one ray more than all the others. This indication was very slight, and could not have been detected save by the counting of the rays of thousands of heads. But the rarity of the anomaly was exactly the indication wanted, and the same deviation would have had no significance whatever had it occurred in a group fluctuating symmetrically around the average figure. On the other hand, the observed anomaly was only an indication, and no guarantee of future developments.

From this slight indication De Vries selected for three years more and found that the

average number of rays increased rapidly and with it the maximum of the whole strain. The average came up from 21 to 34. . . . The largest numbers determined in the succeeding generations increased by leaps from 21 to 34 in the first year, and thence to 48 and 66 in the two succeeding summers.

Up to this time, while there was a great increase in the number of ray florets, there was no trace of doubling, but in a few of the best heads "the new character suddenly made its appearance." If sudden, the step was certainly a very modest one. A single plant was found in which careful inspection revealed "three young heads with some few rays in the midst of the disk." "Had the germ of the mutation," asks De Vries, "lain hidden through all this time? Had it been present, though dormant, in the original sample seed? Or had an entirely new creation taken place during my continuous endeavors? Perhaps as their more or less immediate result?" It is stated that "The new variety came into existence at once"—but when? While certain that a mutation must have appeared, De Vries is uncertain when and where it appeared. "The leap," he says, "may have been made by the ancestor of the year 1895, or by the plant of 1899 which showed the first central rays, or *the sport may have been gradually built up during these four years*" (italics mine).

During the next two years improvement by selection was kept up.

The average number of rays which had already risen from 13 to 34 now at once came up to 47 and 55. . . . The maximum numbers came as high as 100 in 1900 and even 200 in 1901. . . . Real atavists or real reversionists are seen no more after the first purification of the race.

A variety which is pronounced "permanent and constant" was produced whose lower limit of the number of rays was raised to about 34, "a figure never reached by the *grandiflora* parent."

The unbiased reader who has carefully followed the account of the production of this double flower can scarcely escape the feeling that the interpretation of the facts according to the mutation theory is at times somewhat strained. The starting point of the whole process is the selection of fluctuations. Now and then the selection of a somewhat more pronounced variation was made; but the so-called mutations had very small and weak beginnings, and De Vries is uncertain just where they occurred and even suggests that they may have been built up gradually! The selection of fluctuations seems to have had the effect of inducing variations of greater stability, if not greater extent, in the same direction. It is not unreasonable to suppose that the appearance of florets with ligulate corolla on the disk is due to the same factors which cause the increase in the number of ray florets, and the variation may be in reality not so discontinuous as it seems. In fact we are ignorant of the stability or the real discontinuity of many of the steps in advance towards the production of the double flower. If a mutation can make its appearance as an extra ray floret in one case, and by the occurrence of two or three ligulate corollas on the disk of a few flowers of the plant in another, and if both these characters can be increased by selection until they reach a stable condition that is far more highly developed than their original one, the facts do not lend much support to a theory of the saltatory origin of species. Rather they would indicate that species have been formed along lines determined by selective processes much in the same way as Darwin conceived them to be.

By a similar method of selection Burbank has produced a scarlet variety of the California poppy, *Eschscholtzia californica*. He noticed one flower with a fine scarlet line on one petal. From the seed of this plant other poppies with scarlet lines were produced, but only to a slight extent. After selection was practised for some years a race of pure scarlet poppies was finally obtained with no indication of their yellow ancestor. This case is cited by De Vries as one of mutation, but certainly it required more than one mutation to bring about the result.[1]

Discontinuity may often be more apparent than real, the discontinuous variations in the soma being the outcome of continuous variability instead of abrupt changes in the germ. Let us consider from this point of view the occurrence of digital anomalies such as polydactylism, cleft hand, etc., which are frequently cited as illustrations of discontinuous variability. These anomalies are often strongly inherited, but in most cases which have been fully studied, the inheritance, while partly alternative, is not Mendelian. In the race of polydactylous guinea pigs which Castle has produced and bred for a number of generations the anomaly appeared in different individuals in various stages of completeness. The parent of the group, a male, bore an imperfectly developed toe on his left hind foot. The extra toe contained a claw and probably the phalanges, but it was loosely attached and hung limply down on one side. This male produced 27 young, of which 15 were polydactylous. Of the latter some had an extra digit on both hind feet, others had it on but one, and in a few individuals the digit was more fully developed than in the father. In subsequent generations the anomaly appeared in very different degrees of development, some animals having a fully developed digit, others having a loosely hanging toe with or without a nail, while in extreme cases there was only a fleshy bag of skin without bones or claw which often shriveled up and disappeared a few days after birth. The variation, when appearing on one side alone more frequently was limited to the left side (l. 630, r. 589), and when unequal on the two sides the left one was usually the better developed. Normal and polydactylous individuals did not segregate in Mendelian ratios. In some instances the normal condi-

[1] See also the experiments of MacCurdy and Castle in relation of continuous and discontinuous variation in rats. Publications of the Carnegie Institution, No. 70, 1907.

tion gave evidence of being recessive, but this was not borne out by many other cases in which crosses between normal individuals produced polydactylous young. Crosses of normal individuals both of which were of polydactylous ancestry yielded a much higher per cent. of polydactylous young than did crosses in which one individual came from a normal breed, thus showing a certain tendency in the blood towards polydactylism even when it did not manifest itself by any outward mark. Different males of the same amount of polydactylous ancestry often showed great variation in the potency with which they were able to transmit the anomalous character.

The evidence goes to show that we are dealing here with a tendency which, whatever may be its basis, varies continuously and not abruptly, although producing variations which, taken alone, would naturally be classed as mutations. The extra toe is a new character, but the polydactylous breed behaves neither like an elementary species nor like a retrograde variety. The character fluctuates to the vanishing point and even beyond (as shown by crossing experiments with individuals of different ancestry) and shows varying degrees of fidelity of transmission in different strains. Do we not have a condition intermediate between the abrupt discontinuous variations which breed true with great fidelity and ordinary fluctuations? It might be said that we have to do with a mutation which fluctuates to an unusual degree, although it originally depended upon a sudden change in the germ plasm; but the assertion would have no evidence to rest upon. It might be said, on the other hand, that the variation is dependent on the undue activity of some of the factors of normal development, an expression, for instance of increased growth tendency in the part at a certain period, and that this tendency is kept from definite expression until it reaches a certain strength, when it manifests itself as a sudden variation. This conclusion is warranted, I believe, not only by the great variability of the anomaly, but by the fact already cited that normal individuals of abnormal ancestry are more apt to produce abnormal offspring than are normal individuals of another strain.

The studies of Lewis and Embleton and of Pearson on the inheritance of split hand and split foot in man yield results in many respects similar to the preceding. Although the normal condition seems to be recessive, segregation does not occur in Mendelian ratios. Often both hands and both feet were abnormal, but frequently not in the same way, and in many cases there were marked differences in the variations on the two sides of the body. As Pearson remarks, it is difficult to specify in such cases what the unit character may be. With this, that or the other bone present in some individuals and absent in others and represented in very varying degrees of development, the inheritance gives little evidence of definite units of any kind. What is inherited appears to be a condition which manifests itself in varying ways and degrees and which can not be accounted for by any theory of the sharp segregation of characters.

Why certain germinal variations are strongly inherited and others not is a problem of much interest, but the solution of it may lie, not in the supposed behavior of distinct morphological entities representing certain parts, but in the physiological relations of the basis of the variation to the organized structure of the germ plasm. The sex cells are organisms as well as the bodies that arise from them; they have the same capacity for self regulation; and it is not at all probable that all kinds of variations that may arise in response to the various influences to which they are subjected should be retained to the same degree. Weismann has made the suggestive comparison between the variations of an organism and the oscillations of a polyhedron on one of the faces upon which it rests. If the oscillations are small the body tends to come to rest in the same situation as before; if they are larger it may topple over upon a new face about which it may oscillate as around a new center of equilibrium. Weismann postulates a self-regulating power in the germ plasm which keeps numerous minor fluctuating variations from producing any essential modification of the stock. If, however, a certain variation forms a new center of stability it may be permanent. The various mutants of *Œnothera lamarckiana*,[2] most if not all of which contain the potency of giving rise to any of the others and which present very different degrees of stability, may be due to more or less stable forms which the germ plasm may assume rather than the creation of new kinds of germinal units. The stability of a variation may be due, however, not so much to its extent as the analogy with the polyhedron might lead us to expect as to its kind. Variations which are physiologically congruent with the organized structure of the germ plasm form stable races; those which are not tend to become reduced sooner or later to the norm through the regulatory activity of this substance.

The germ plasm may be conceived to exercise, in regard to its variations, a kind of selective activity which may manifest itself as a proneness of the organism to vary along certain lines. It is well known that there are particular types of variation which crop out independently and more or less frequently and may be faithfully perpetuated. Polydactylism, split-hand and split-foot, albinism and melanism, the appearance of races of hairless animals and glabrous plants, the development of nectarines from peaches and peaches from nectarines, the origin of peloric flowers, etc., have occurred many times in independent

[2] It is of course possible that the mutations of *Œnothera Lamarckiana* result from the impurity of the stock. The species has been for a long time cultivated as an ornamental flower, and we have nothing but conjecture regarding its origin. Should it turn out to be derived from a mixture of two or more forms the mutation theory would be deprived of some of its best evidence, but there would still remain a considerable number of mutations from pure ancestry. In *Œnothera gigas* the interesting fact has been discovered that there is double the normal number of chromosomes. Whether this is the cause or the effect or merely one instance of the differences between this mutant and the type is unknown.

strains. These phenomena may be compared to various anomalies which take their origin in the soma. The embryo in its development is liable to certain accidents resulting in the production of teratological phenomena such as hare-lip, double formations, anencephaly and many others. These anomalies fall into certain classes and in many cases can be attributed to particular defects of development. The germ plasm also may be regarded as liable to certain classes of accidental modifications which produce heritable variations of more or less clearly defined types. No one would think of attributing anomalies of somatic origin to the development of a new kind of organic unit. If the same mutation appears time after time, would it not be more reasonable to suppose that it arose after the fashion of somatic anomalies than that it depended upon the creation each time of the same kind of a new pangen? The fact that mutations can be induced through the influence of the environment certainly favors such a view. Tower found that in Leptinotarsa certain variations or mutations arose repeatedly in independent strains and that by subjecting the beetles to unusual conditions during the period of active development of their germ cells the proportion of these sudden variations could be very greatly increased. The variations thus produced belonged to a few well-marked types, and while it would be hazardous to set bounds to the possible number of mutants the species may produce, it is probable that the number is subjected to a certain limitation imposed by the peculiar organization of the germinal substance.

The selection of variations by the germ plasm may be illustrated by some observations of Jennings upon inheritance in Protozoa. In a few specimens of Paramœcium it was noticed that the body was furnished with a spine-like excrescence. During fission the spine was transmitted to but one of the individuals, the acquired peculiarity not arising on the other. In one case the spine was transmitted through twenty-one generations, when the strain disappeared. In other cases the spine was gradually diminished during successive divisions and ultimately disappeared. Other anomalies such as crookedness, blunt ends, bent tip of body and various abnormalities, provoked by artificial mutilation, while persisting for a variable number of generations, were eventually regulated out, leaving a normal strain.

In like manner we may imagine that through environmental changes the germ plasm becomes affected by modifications which in the course of a few generations become regulated out, thereby causing a reversion to the primitive stock. Reversion may thus be conceived as but a manifestation of form regulation. Variations to be permanent must be accepted by the organized structure of the germ cells, so that they may be included instead of excluded by the processes of functional equilibration to which these cells like other parts of the organism are continually subjected. The congruity of the variation is the important thing; whether the variation be large or small, sudden or slow, is of much less consequence.

After all, it may be asked, granting that variations may be interpreted in the manner here set forth, do not the phenomena of Mendelian inheritance, showing as they do that characters may be separated and combined in many different ways prove that these characters must be borne by some sort of units in the germ plasm? This is a conclusion which is adopted by a large number of Mendelians, but, plausible as it seems, it is, I believe, a totally erroneous view. In the first place it is open to question if the assumed purity of the gametes is a fact even in typical cases of Mendelian inheritance, but, granting that there is an absolute separation of ancestral tendencies, it by no means follows that there is any sorting of individual unit characters apart from the complex of tendencies which make for the production of the organism as a whole. Hereditary anlagen may perhaps be shuffled and sorted as wholes, but if the germ plasm were composed of discrete parts representing the unit characters of the individuals, the result would probably be utter confusion instead of orderly development. We might assume that albinism is dependent upon the peculiar properties of a single chromosome, that length of hair is dependent upon the constitution of a second chromosome, that a short tail is associated with a third, and so on. These characters may not be represented by any kind of structural element; they may have their basis in the general chemical constitution of the chromosome and be produced during development in a purely epigenetic fashion. Chromosomes probably have their individual peculiarities of chemical constitution as might be expected from the fact that the chromatin content of an individual represents contributions from many different ancestors. Each chromosome or even a small constituent of the chromosome may have a relation to the inheritance of the whole body, but the peculiarities of one chromatic element may dominate in one part, those of another chromatic element in another. When albinism is eliminated it does not mean that this character alone is separated, but *the anlage of an albino organism.* Even if it is shown that the number of separate characters which Mendelize is greater than the number of chromosomes of the variety, Mendelian phenomena can be explained on the basis of sorting out ancestral tendencies as wholes instead of unit characters. The facts of Mendelian inheritance at present known do not necessarily give any support to the theory of discrete bearers of unit characters, or the theory of the independent variability of parts as conceived by De Vries and Weismann. This is a point which, I believe, needs to be emphasized on account of the uncritical acceptance of these views by so many writers on heredity and variation. The presence or absence of certain characters may be independent of the presence or absence of certain others, but this fact may very readily be accounted for without having recourse to a particulate theory of inheritance.

The mixing up and separation of characters in inheritance, far from proving the independent variability of parts, is just what renders the proof of this theory exceedingly difficult. The alleged independent variability of parts is Weismann's strongest proof of his doctrine of determinants. If a pit in the ear or a white tuft of hair on the head can be transmitted for several generations without involving any other change in the organism, we are forced to assume, according to Weismann, that there is a small part of the germ plasm varying independently of the rest which forms the basis or determinant of this character. But the contention particularly difficult of proof is that the characters really do appear in independence of the other parts of the organism. A variation may conceivably depend upon a general change in the constitution of the substance of heredity, although manifesting itself most conspicuously in a single part. A pit in the ear may be the most obvious sign of the very slight constitutional differences between two individuals. It is common to find two closely allied species or varieties differing markedly in one or two features and much less conspicuously in numerous other parts of their structure. Peculiarities of horns are sometimes associated with less noticeable characteristics of the hair, thus pointing to a common origin of these features in some general modification of the ectoderm which in turn may result from some change affecting the germ plasm as a whole. Albinism which is so often cited as a unit character is a peculiarity of far reaching correlations, being often associated with impaired sight or hearing, diminished fertility, and even lessened power of resistance to disease.

To establish the independent variability of parts requires a much closer study of possible correlations than has yet been made. The task is rendered particularly difficult by the varied combination and segregation of ancestral tendencies, which we have just considered. If we can account for the independence of certain characters on the ground of combining and sorting ancestral tendencies as wholes, one has to disprove the possibility of applying this explanation of the appearance of a particular variation before the latter can be regarded as giving evidence of a corresponding determinant. The burden of proof is on the shoulders of the upholders of the doctrine of determinants and it is a far heavier one than the champions of this doctrine commonly appreciate. Let us suppose that among the various sets of hereditary tendencies that find expression in the organization of an individual one should include the production of a particular variation in a single small part. The constitutional differences which may go along with this peculiarity and of which it may be regarded as one expression may be modified or kept from becoming manifest by other and rival sets of hereditary tendencies thereby rendering it almost impossible to detect the correlations that really exist, and giving the character the delusive appearance of independence. The question of the independent variability of parts is a crucial one for the particulate theories of inheritance, but it is one so beset with practical difficulties that a final answer may not soon be forthcoming.

In the preceding discussion the attempt has been made to show that the various categories of variations recognized by De Vries and others are not sharply separable either on morphological grounds or by their behavior when subjected to crossing experiments. The attempt was made also to show that neither the facts of variability nor those of Mendelian inheritance give any support to the doctrine of pangens, determinants, or other assumed bearers of unit characters, and that unit characters, as elements than can enter or depart from the complex of tendencies that make up an organism probably have no existence. It is evident that variations differ in their stability, but the explanation of this fact may lie in the physiological relations of the variation rather than in some hypothetical representative unit. Whether the variations of the discontinuous type have been influential, in any marked degree, in shaping the course of evolution is a question upon which we need much more evidence. Mutations, as we have seen, may be very small affairs.

About the only criterion by which they may be recognized is their stability, and even that gives some evidence of being a matter of degree. No limit has been discovered to the minuteness of the stable modifications that may occur, and it may happen that further study will reveal the comparatively frequent appearance of very slight variations of this kind. In fact, considerable progress has even now been made in this direction by the study of grains; and the number of more or less stable modifications that are likely to be discovered threatens to overwhelm systematists with the labor of naming and describing them. In many organisms not propagated by self-fertilization the detection of these small steps is no easy task and the attempt to describe them all would undoubtedly prove a futile effort. Among human beings, for instance, what are we to designate as elementary species? We meet with all grades of differences from well-marked family traits to those which separate the Caucasian from the negro. Are we to regard the Hapsburg lip which was transmitted with fidelity for many generations as the mark of an elementary species? It was apparently a new character and therefore presumably dependent upon a new pangen or determinant. The Celts, Teutons, Slavs, etc., differ by more or less constant characters which are constitutional and not confined to single parts, and the same may be said of the various subdivisions of these groups. The Aryan stock to which these groups belong is separated by still greater differences from the other subdivisions of the Caucasian race, and the latter in turn differs still more widely from the negroes and Mongolians. One has considerable difficulty in disposing of these groups either as varieties or elementary species. They can not from De Vries standpoint be considered the results of fluctuating variability on account of their constancy even under very varied external conditions. If the small divisions have arisen by slow changes, as everything indicates, there is no logical halting place short of admitting that the greater ones may have done the same. In fact a survey of the racial differences of man in their varying degrees and kinds and their correlation with geographical distribution shows us pretty clearly that these differences have been slowly acquired by the summation of very small variations. These groups are not related as the so-called retrograde or digressive varieties are, but they are based on differences in general constitution affecting the shape of the skull, the characteristic complexion, the general temperament, and many other traits too numerous to specify. They may have arisen by minute, discrete, stable variations, but to call each step in advance an elementary species seems absurd, and to talk of the immutability of species still more so. We gain little by characterizing as elementary species the small steps of which there may be a dozen or more separating a German from a Frenchman.

Students of geographical distribution as a rule set little store by the theory of mutation. The relation of variation and species-forming to distribution as illustrated by the work of Gulick and Hyatt on the Achatinnelidæ, the Sarasins on the snail fauna of Celebes, of Plate on the mollusca of the Bahamas, and of many students of the mammals, birds and fishes of North America indicate that the steps concerned in species-forming have been very modest ones. If sudden mutations of considerable magnitude have been a not uncommon source of varieties of domesticated animals and cultivated plants it does not follow that the selection of comparatively small variations has not been the predominant method of species-forming in a state of nature.

After fifty years from the publication of Darwin's "Origin of Species" we are still debating, and more lively than ever, the central problem of that epoch-making book; but it is not improbable the views of its sagacious author will prove more nearly correct than those of most of his modern critics. Much remains to be done before the problem is finally solved, and there are few fields before the investigator that are more fruitful and alluring.[3]

[3] *Mendelism and Unit Characters.*—Since this article on the Categories of Variation was sent in for publication several articles have appeared whose contents would have been referred to had they been published somewhat earlier. One of these is a short paper by W. J. Spillman in "The Nature of Unit Characters," in the April number of this journal, in which an interpretation of so-called unit characters is given which is, in many respects, similar to my own. Reference to Mr. Spillman's views would naturally be expected in an article appearing later than his in the same journal, so that it may be well to state that the proof of my paper was returned to the publishers in the first part of February, and that no modification of the paper has since been made. I am glad to find myself in agreement with Mr. Spillman at least to the extent that the facts of Mendelian inheritance do not compel us to adopt a particulate theory of heredity. That Mendelian inheritance can be explained by the sorting process which is supposed to take place in the reducing divisions of the germ cells I feel by no means assured; there are grave difficulties in the way of such an interpretation. But if this explanation prove to be the correct one it would be far from justifying the commonly accepted doctrine of unit characters with all its evolutionary implications.

Reference might also be made to some recent articles by De Vries, especially one on the crosses of *Oenothera nanella* (Ueber die Zwillingsbastarde von *Oenothera nanella.* Ber. Bot. Ges. 26, p. 667, '08), inasmuch as the experiments reported tend to strengthen further the contention of the present writer that no sharp line can be drawn from the results of crossing experiments between elementary species and so-called retrograde varieties.