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*SOME RECENT IDEAS ON THE EVOLUTION OF PLANTS.**

THERE is endless dissimilarity in nature. No two plants and no two animals are exactly alike. There are more plants and animals than can find a place in which to live and thrive. There results a struggle for existence. Those animals or plants which, by virtue of their individual differences or peculiarities, are best fitted to the conditions in which they are placed, survive in this struggle for existence. They are 'selected' to live. Those that survive propagate their peculiarities. By virtue of continued variation, and of continual selection along a certain line, the peculiarities may become augmented; finally the gulf of separation from the parental stem becomes great and what we call a new species has originated.

This, in epitome, is the philosophy of Darwin in respect to evolution of organic forms. It contains the well-known postulate of natural selection, the principle that we know as Darwinism. This principle has had more adherents than any other hypothesis of the process of evolution. All recent hypotheses in some way relate to it. A number of them modify it, and some cut across it. The most pronounced counter-

* Address before the Society for Plant Morphology and Physiology, Washington, December 29, 1902.

hypothesis is also the newest. It is that of Professor De Vries, botanist, of Amsterdam, who denies that natural selection is competent to produce species, or that organic ascent is the product of small differences gradually enlarging into great ones. According to De Vries's view, species-characters arise suddenly, or all at once, and they are ordinarily stable from the moment they arise.

I. VARIATION: DE VRIES.

De Vries conceives that variations, or differences, are of two general categories: (1) Variation proper, or small fluctuating, unstable differences peculiar to the individual (only partially transmitted to offspring), and (2) mutations, or differences that are usually of marked character, appear suddenly and without transition to other forms and are at once the starting-points of new races or species. The variations proper may be due to the immediate environment in which the plant lives. The mutations are due to causes yet unknown, although these causes are considered to be physiological.

Natural selection works on both variations and mutations by eliminating the forms that are least adapted to persist. It is conceived to be a destructive, not a constructive or augmentative, agency. It merely weeds out.

We may first consider selection with reference to variations proper. Among variations, or individual fluctuations, there may be a slight cumulative effect of selection, but it is incompetent ever to enlarge the differences into stable characteristics; and when natural selection ceases to act, the so-called variety falls back into its original form or splits up into other forms. Varieties of this kind are notably indefinable and unstable. It is impossible to 'fix' them in any true sense; selection only preserves them, and when it is removed they perish as varieties. They are relatively only temporary and have no effect on phylogeny. Many of the minor adaptations of plants to the particular conditions in which they chance for the time being to be placed are of this category. Much of the variation which results in acclimatization belongs here. The fluctuating horticultural varieties, and gardeners' 'strains,' are of this kind. This discussion of the effect of cessation of selection recalls Weismann's panmixia, a name proposed to designate the breaking up of varietal or specific characteristics when natural selection ceases to act. Panmixia is not of itself an original force or an agency; it is merely a name for the results of all the forces or energies which are allowed to assert themselves when the restricting force of natural selection is removed. In De Vries's view, the progress made by selection must be maintained by selection.

We may next consider selection with reference to mutations. The mutations are practically stable or 'fixed' the moment they arise. Of course there may be individual fluctuations, or variations proper, amongst plants that have sprung from a mutated individual; but the main characteristics of the mutations are heritable. An organism is a complex of organs and attributes. Each attribute is a unit. From any unit a new unit may arise by mutation. The origination of a new unit constitutes at once a full and important character and marks the organism that possesses it as a new physiological species. Not only one unit, but any number of units, may give rise to mutations; and any one of these new mutations may give rise to other mutations. But the point is that these mutations, be they great or small, arise by steps, are full-formed when they arise, and do not grow or enlarge into other mutations. The mutations are multifarious (*all-seitig*), occurring apparently at random and in diverse directions, and without regard to fitness. They may be either quantitative or qualitative. Variations proper arise mostly in a definite line. Now, natural selection may weed out mutated individuals as it does mere variant individuals; and thus breaks may arise in the chain, and we have left what we know as taxonomic species.

Natural selection, with survival of the fittest, is, therefore, of two distinct categories,—that which operates within the species and results in the formation of local minor races, and that which operates between species and results in the formation of a line of ascent.

Everywhere and always plants are variable. Now and then and relatively rarely, plants are mutative. Any man who sees two plants, sees variation; there are no two plants alike. Only he who studies and observes critically, sees mutation. One must examine a hundred or a thousand or ten thousand individuals. In De Vries's extended experiments with *Œnothera*, only 1.5 per cent. of the plants were mutative, and mutation is undoubtedly more common in cultivation than in the wild, and the mutated individuals are more likely to persist. The investigator should employ only statistical methods of comparison. He should contrast unit-characters, rather than individuals as a whole. Moreover, not only are the numbers of mutating individuals relatively uncommon, but the species may not now be in a mutative epoch.

In other words, there are epochs in the history of the plant when mutations occur. These are the 'mutation-periods' of De Vries. There are epochs of non-mutations, when no progress seems to be making. It may be conceived that some force is then withholding or restraining the mutative impulse. This force is what we are in the habit of calling heredity. When heredity is overcome, there arises a 'premutation-period,' in which the mutations are beginning to express themselves; and eventually the full mutation-period may appear. Heredity and non-heredity, these are the ever-opposing and ever-contrasting forces of organic life, the one resulting in the survival of the like, the other resulting in the survival of the unlike. One is heredity; the other is variation. One makes for continuity; the other for evolution. No hypothesis of the energy of evolution is perfect that does not account for both. A theory of heredity, or continuity, must also account for the opposite of itself. It is not easy to construct an hypothesis or a metaphor that will accomplish this.

The phenomena of continuity and discontinuity are well contrasted by Korschinsky. These phenomena, he conceives, are the results of two antagonistic tendencies. Under normal or usual conditions heredity is the stronger force. The tendency to vary is always present, being predisposed by environment but not caused by it; when it gathers the necessary energy it overbreaks the power of inheritance and sudden variations or sports arise, and these sports are the starting-points of evolution. This sudden appearing of new forms is called by him heterogenesis.

The conceptions of *per saltum* variations of Korschinsky and De Vries seem to be practically identical. De Vries has carried his work further, into the realm of actual experimental investigation. He studied many species of plants in the hope of finding one or more that might be in its mutation-period. Finally, he chose the common evening primrose, *Œnothera Lamarckiana*, and by continual sowing of seeds and raising of great numbers of plants he discovered several truly mutative forms. These forms reproduce themselves by means of seeds as accurately as accepted species do. He has given them specific names. The full experimental history of them is given in the first volume of his brilliant work, 'Die Mutationstheorie.' These forms, he contends, are true elementary species. That is, they have new specific characters. These characters are heritable. It does not matter whether these characters are large or small—they become phylogenetic. These plants having the new specific characters may not be species in the Linnæan or historic or morphological sense, but they are real entities. We must give up the historical view of species when we study the evolution of organic forms. Historic or Linnæan species are taxonomic conceptions; the evolutional or elementary species are physiological conceptions.

The different categories of species, as respects their origin, are given as follows by De Vries:

A. Origin by means of formation of new characters, or progressive species-origin.

B. Origin without formation of new characters.

1. By the becoming latent (*latentwerden*) of present characteristics, or retrogressive species-origin. Atavism in part belongs here.
2. By the becoming active (*activirung*) of latent characteristics, or degressive species-origin.
   (*a*) Taxonomic anomalies.
   (*b*) Real atavism.
3. By means of hybrids.

It will now be seen that the mutation theory of De Vries, which is in some respects a rephrasing and an extending of the old idea of sports, does not of itself introduce any new theory of the dynamics of evolution. It is not a theory of heredity nor of variation. His hypothesis of 'intracellular pangenesis' carries the explanation of these phenomena one step farther back, however. The plant cells give off pangenes. Each of these pangenes divides into two. Ordinarily, these two resemble the parent; but now and then one of them takes on a new character—the two become unlike—and gives rise to a mutation. This hypothesis, like Darwin's pangenesis, is useful as a graphic basis for discussion, whether or no it has real physiological foundation.

The most emphatic points of the mutation theory, as they appeal to me, are these: (1) It classifies variation into kinds that are concerned in evolution and kinds that are not; and thereby it denies that all adaptation to environment makes for the progress of the race. (2) It denies the power of natural selection to fix, to heap up or to augment differences until they become truly specific. (3) It separates the results of struggle for existence and survival of the fittest into two categories, only one of which has an effect on phylogeny. (4) It asserts that evolution takes place by steps, small or great, and not by a gradual unfolding or evolving of one form into another. (5) It enforces the importance of critical comparative study of great numbers of individual plants or animals. (6) It challenges the validity of the customary conception of species as competent to elucidate the method of evolution.

There will arise confusion, in the forthcoming discussions of the theory of discontinuity, as to what is a species; but this confusion is not new. There are two conceptions of species: (1) As taxonomic groups, more or less arbitrarily made for purposes of classification; (2) as real things, marked by recordable differences, however small or great, and conceived to be the actual steps in the phylogeny of the race. These categories are so distinct that they would not be confounded except for the unfortunate circumstance that we use one word (species) for the two. There has been a growing conviction that the two classes must be sharply separated when evolution questions are discussed. Nearly ten years ago I endeavored to combat the species-dogma from the garden point of view, as, in differing ways, others had done before ('Survival of the Unlike,' Essay IV.). The confusion of the two conceptions expresses itself in the terminology of plant-breeding. Some writers define hybrid, for example, as a cross between species; this is the classificatory idea. Others define it to be any cross. The former use of the word is the more proper merely because it is the historic use, originating as a systematist's concept. The latter idea should have been expressed by a new word. It is for this reason that I have held to the old or systematic definition of hybrid; but there is no appeal against usage, so, while still proclaiming the righteousness of my cause as an easement of my conscience, I strike my colors and henceforth use the word hybrid for a cross of any kind or degree. How often does mere language confuse us!

From an argumentative point of view, it will be difficult to determine, in a given case, just what are variations and what mutations, for these categories are separated not by any quantitative or qualitative characters—the 'step' from one to the other may be ever so slight—but by the test that one kind is fully heritable and the other only partially so. If a mutation is to be defined as a heritable form, then it will be impossible to controvert the doctrine that evolution takes place by mutation, because the mutationist can say that any form that is inherited is by that fact a mutation. This will be equivalent to the position of those who, in the Weismannian days, denied the transmission of acquired characters, but defined an acquired character to be one that is not transmissible. However, it is to be hoped that the discussion of the mutation theory will not degenerate into a mere academic debate and a contention over definitions. Professor De Vries has himself set the direction of the discussion by making actual experiments the test of the doctrine. There will be confusing points, and times when we shall dispute over particular forms as to whether they are variations or mutations; but every one who has studied plants from the evolution point of view will be prepared to believe that species do originate by mutation. For myself, I am a Darwinian, but I hope that I am willing to believe what is true, whether it is Darwinian or anti-Darwinian. My own belief is that species do originate by means of natural selection, but that not all species so originate. De Vries's work will have a profound and abiding influence on our evolution philosophies.

II. HEREDITY: MENDEL.

De Vries made a thorough search of the literature of plant evolution. In an American publication he saw a reference to an article on plant hybrids by G. Mendel, published in 1865 in the proceedings of a natural history society of Brünn in Austria. On looking up this paper he was astonished to find that it discussed fundamental questions of hybridization and heredity and that it had remained practically unknown for a generation. In 1900 he published an account of it; and this was soon followed by independent discussions by Correns, Tschermak and Bateson. In May, 1900, Bateson gave an abstract of Mendel's work before the Royal Horticultural Society of England; and later the society published a translation of Mendel's original paper. It is only within the present year, however, that a knowledge of Mendel's work has become widespread in this country. Perhaps the two agencies that have been most responsible for dissemination of the Mendelian ideas in America were the instruction given by Webber and others in the Graduate School of Agriculture at Columbus last summer, and the prolonged discussion before the International Conference on Plant-Breeding at New York last fall. Lately, several articles on the subject have appeared from our scientific press.

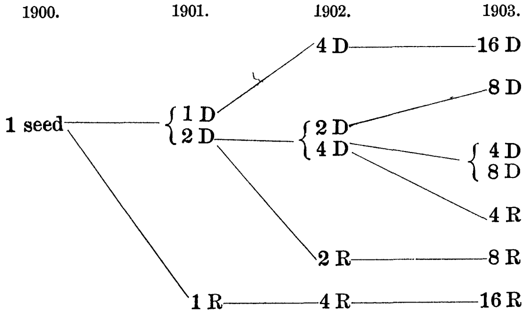
Mendel's work is important because it cuts across many of the current notions respecting hybridization. As De Vries's discussions call a halt in the current belief regarding the gradualness and slowness of evolution, so Mendel's call a halt in respect to the common opinion that the results of hybridizing are largely chance and that hybridization is necessarily only an empirical subject. Mendel found uniformity and constancy of action in hybridization; and to explain this uniformity he proposed a theory of heredity.

One of the most significant points connected with Mendel's work is the great pains he took to select plants for his experiments. He believed that hybridism is a complex and intricate subject, and that, if we are ever to discover laws, we must begin with the simplest and least complicated problems. He was aware of the general belief that the most diverse and contradictory results are likely to follow any hybridization. He conceived that some of this diversity may be due to instability of parents rather than to the proper results of hybridizing. He also saw that he must exclude all inter-crossing in the progeny. Furthermore, the progeny must be numerous, for, since incidental and aberrant variation may arise in the plants, it is only by a study of averages of large numbers that the true effects of the hybridizing are to be discovered. Moreover, the study must be more exact than a mere contrasting and comparing of plants: character must be compared with character.

The garden pea seemed to fulfill all the requirements. Mendel chose well-marked horticultural races or varieties. These he grew two years before the experiment proper was begun, in order to determine their stability or trueness to type. When the experiments were finally begun, he used only normal plants as parents, throwing out such as were weak or aberrant. Peas are self-fertile. It is to be expected that under such conditions the hybrid offspring would show uniformity of action; and it did.

In order to study the behavior of the hybrids, it was necessary to choose certain prominent marks or characters for comparison. Seven of these characters were selected for observation. These marks pertain to seed, fruit, position of flowers and length of stem, and they may be assumed to be representative of all other characters in the plant. These characters were paired (practically opposites) as long-stem *vs.* short-stem, round-seed *vs.* angular-seed, inflated-pod *vs.* constricted-pod. They were 'constant' and 'differentiating.' Of course every parent plant possessed one or the other of every pair of contrasting characters, but in order to facilitate his studies Mendel chose a different set of parents for each character, studying seed-shape in one set of hybrids, seed-color in another, pod-shape in another; in this way he avoided much complication in the results. Since it is not my purpose to discuss Mendel's work in detail, but only the general significance of its results, as they appeal to me, I need not describe these characters here. It will be sufficient for my purpose if I choose only one, the shape of the seed.

The seed-shape characters were roundness and angularity—the former being the 'smooth' pea of gardeners, and the latter the 'wrinkled' pea. Let us suppose that twenty-five flowers on round-seeded plants were cross-pollinated in the summer of 1900 with pollen from angular-seeded plants, or *vice versa,* and that an average of four seeds formed in each pod. With the death of the parent plants the old generation ended, and the 100 seeds that matured in 1900—the year in which the cross was made—began the next generation; and these 100 seeds were hybrids. Now, all these 100 seeds were round. Roundness in this case was 'dominant.' (Dominance pertaining to the vegetative stage of the plant of course would not appear until 1901, when the seeds 'grow.') These seeds are sown in the spring of 1901. If each seed be supposed to give rise to four seeds—or 400 in all—this next generation of seeds (produced in 1901) will show 300 round and 100 angular seeds. That is, the other seed-shape now appears in one fourth of all the progeny; this character is said to have been 'recessive' in the first hybrid generation. If the 100 angular seeds, or recessives, are sown in 1902 it will be found that all the progeny will be angular-seeded or will 'come true'; and this occurs in all succeeding generations, providing no crossing takes place. If the 300 round seeds, or dominants, are sown in the spring of 1902, it will be found that 100 of them produce dominants only, and that 200 of them behave as before—one fourth giving rise to recessives and three fourths to dominants; and this occurs in all succeeding generations, providing no crossing takes place. In other words, the three fourths of dominants in any generation are of two kinds,—one third that produce only dominants and two-thirds that are hybrids. That is, there is constantly appearing from the hybrids one fourth part that are recessives, one fourth part that are constant dominants, and one half part that are dominants to all appearances, but which in the next generation break up again into dominants and recessives. This one half part that breaks up into the two characters consists of the true hybrids; but they are hybrids only in the sense that they hold each of the two parental characteristics—roundness and angularity—in their purity and not as blends or intermediates; and these two characteristics reappear in all succeeding generations in a definite mathematical ratio. Proportionally, these facts may be expressed as follows:



It will be seen that two thirds of the dominants break up the following year into one fourth constant dominants, one fourth recessives, and one half that again break up, the half that break up being the hybrids. This formula for the hybrids is Mendel's law. In words, it may be expressed as follows: Differentiating characters in plants reappear in their purity and in mathematical regularity in the second and succeeding generations of hybrid offspring of these plants; the mathematical law is that each character separates in each of these generations in one fourth of the progeny and thereafter remains true. In concise figures it is expressed as follows:

$$1D:2DR:1R.$$

$1D$ and $1R$ come true, but DR breaks up again into dominants and recessives in the ratio of 3 to 1.

Mendel found that this law holds more or less for the other characters that he studied in the pea, as well as for the seed-shape. He did not conclude, however, that it holds good for all plants, but left the subject for further investigation. He himself found different results in *Hieracium*. It will be seen at once that it will be a very difficult matter to follow this law when many characters are to be contrasted, particularly when the characters are merely qualitative and grade into each other. The dominant characters pertain to either parent: some of them may come from the mother and some from the father.

When this roundness is dominant from the male parent, it falls under the denomination of what we commonly know as xenia, or the immediate effect of pollen; when it is from the female parent, there is no xenia. In the case of the pea, the seed-content is embryo and we are not surprised if there is xenia. In those plants in which the embryo is embedded in endosperm, however, it would seem to be difficult to account for xenial dominance, unless there is double fecundation, as appears to be the case in Indian corn, as pointed out by De Vries, Webber* and others. It looks as if the question of dominance would introduce a new point of view into the study of xenia. There is now a strong tendency, however, to use the word xenia to designate only those effects occurring outside the embryo.

Which characters will be dominant in any species we cannot determine until we perform the experiment; that is, there is no mark or attribute which distinguishes to us *a priori* a dominant or a recessive character. However, the mere fact as to whether the one or the other character is dominant is relatively unimportant, for constant dominance is no more a regular behavior than recessiveness is. In various subsequent experiments it has been found that even when marked dominance is not shown in the first product, the hybridization may follow the law in essential numerical results. The really important points are two: (1) that the characters typically remain pure or do not bend, (2) and that their reappearance follows a numerical order.

After finding such surprising results as these, Mendel naturally endeavored to discover the reasons why. The product of his speculations is the theory of gametic purity (to use our present-day terminology), which is a partial theory of heredity. Every plant is the product of the germ cell fertilized by the sperm cell. When constant progeny is produced, it must be because the two cells, or gametes, are of like character. When inconstant progeny is produced, it must be because the sperm cell is of one character and the germ cell of another. When these unlike gametes come together, they will unite according to the law of mathematical probabilities, one fourth of those of each kind coming together and one half of those of both kinds coming together. If A and B represent the contrasting parental characteristics, they would combine as

$$\begin{aligned} A + A &= A^2 \\ A + B &= AB \\ B + A &= BA \\ B + B &= B^2 \end{aligned}$$

A^2 and B^2 are equivalent only to A and B. Since both of the opposed or contrasted characters can not be visible at the same time, we have the following:

$$\begin{array}{c} A \\ A^b \\ A^b \\ B \end{array}$$

in which small b represents the character that for the time being is not able to express itself, or is recessive, and large B represents the same character fully expressed.

* 'Bull. 22, Div. of Veg. Phys. and Path.,' U. S. Dept. Agric., 1900.

In these gametes, the unit characters of the plants that bear them are pure. Even in hybrid plants, the pollen grains and the egg cells are not hybrids. According to this hypothesis of gametic purity, therefore, hybrids follow natural and numerical laws; but these laws are always obscured by new crossing. True intermediate characters do not occur. If new characters appear, it is because they have been recessive or latent for a generation or because the plant has varied from other causes: they are not the proper results of hybridization. Possibly new characters that appear because of effect of environment or other cause may be impressed on the gamete and thereby be perpetuated. The results of hybridization, then, according to the Mendelian view, are not fundamentally a mere game of chance, but follow a law of regularity of averages; but the results are so often masked that it is sometimes impossible to recognize the law.

Mendel's law of heredity is recently stated as follows by Bateson and Saunders: 'The essential part of the discovery is the evidence that the germ-cells or gametes produced by cross-bred organisms may in respect of given characters be of the pure parental types, and consequently incapable of transmitting the opposite character; that when such pure similar gametes of opposite sexes are united together in fertilization, the individuals so formed and their posterity are free from all taint of the cross; that there may be, in short, perfect or almost perfect discontinuity between these germs in respect of one of each pair of opposite characters.'

This, in barest epitome, is the teaching of Mendel. This teaching strikes at the root of two or three difficult and vital problems. It presents a new conception of the proximate mechanism of heredity, although it does not present a complete hypothesis of heredity, since it begins with the gametes after they are formed, and does not account for the constitution of the gametes nor the way in which the parental characters are impressed upon them. This hypothesis will focus our attention along new lines, and I believe will arouse as much discussion as Weismann's hypothesis did; and it is probable that it will have a wider influence. Whether it expresses the actual means of heredity or not, it is yet much too early to say; but this hypothesis is a greater contribution to science than the so-called 'Mendel law' as to the numerical results of hybridization; the hypothesis attempts to explain the 'law.'*

One great merit of the hypothesis is the fact that its basis is a morphological unit, or at least an appreciable unit, not a mere imaginary concept. This unit should be capable of direct study, at least in some of its phases. It would seem that the Mendelian hypothesis would give a new direction to cytological research.†

It is yet too early to say how far Mendel's law applies. We shall need to restudy the work that has been done and to do new work along more definite lines. There are relatively few results of experiments that can be conformed to Mendel's law, because the data are not complete enough or not made from the proper point of view. We should expect the fundamental results to be masked when the plants with which we work are themselves unstable, when cross-fertilization is allowed to take place, or when the pairs of contrasting characters are very numerous and very complex. Marked numerical results

* This, I take it, is also the opinion of Bateson, the leading interpreter of Mendel in English; for he calls his new book on the subject (1902) 'Mendel's Principles of Heredity,' as if the heredity idea were greater than the hybridization idea.

† See, for example, 'A Cytological Basis for the Mendelian Laws,' *Bull. Torr. Bot. Club*, 29, 657 (1902), by W. A. Cannon.

have been found by various workers in different fields, in this country notably by Spillman in hybrid wheats. Mendel was able to discover the numerical law because he eliminated nearly all of the confusing contingencies. In the discussion of every bold new hypothesis, we are in danger of becoming partisans, taking a stand either for it or against it. The judicial attitude is also the scientific one. We want to know.

Two processes are now going forward in the discussion of Mendel's law—one the explaining away of 'exceptions,' the other the endeavoring to find the true place of the law in the scheme of evolution. The one is primarily an effort to uphold the law; the other is primarily a desire to adjudge it. One is an effort to apply it universally; the other to determine whether it is universal. Already so many adjustments have been made of the Mendelian principles that it is becoming difficult to determine what Mendelism is. These cases are typical of the discussions on almost every vital question connected with evolution. At the hard places we make a supposition and modify the hypothesis in the face of a fact. We can prove anything by supposing.

The results of Mendel's work have two important bearings on current evolution discussion: (1) on the part that hybridization plays under natural conditions in the evolution of the forms of life, and (2) the part that it plays in plant-breeding. In the former category, Mendel's work gives a hint of definiteness to the rôle of hybridization in the origination of new combination-forms. In the latter category, it is difficult as yet to measure its importance, since extended applications to practice have not been made and since, also, the Mendelian principles have been so much extended and redefined within the past two years that it is difficult to determine just what is Mendelism and what is an endeavor to make the Mendelian suggestions fit our present-day knowledge. In discussing the application of Mendel's work to plant-breeding, I desire to keep in mind the work that he did with peas, upon which the 'Mendel law' chiefly rests.

III. APPLICATION TO PLANT-BREEDING.

The wildest prophecies have been made in respect to the application of Mendel's law to the practice of plant-breeding, for the mathematical formulæ express only definiteness and precision. Unfortunately, the formulæ can not express the indefiniteness and the unprecision which even Mendel found in his work. My own feeling is that the greatest benefit of Mendel's work to the plant-breeder will be in improving the methods of experimenting. We can no longer be satisfied with mere 'trials' in hybridizing: we must plan the work with great care, have definite ideals, 'work to a line,' and make accurate and statistical studies of the separate marks or characters of plants. His work suggests what we are to look for and new ways of attacking difficult problems.

Beyond this, I do not see how the original Mendelian results will greatly modify our plant-breeding practice. The best breeders now breed to unit characters, for this is the significance of such expressions as 'avoid breeding for antagonistic characters,' 'breed for one thing at a time,' 'know what you want,' 'have a definite ideal,' 'keep the variety up to a standard.' In certain classes of plants the Mendelian laws will be found to apply with great regularity, and in these we shall be able to know beforehand about what to expect. The number of cases in which the law, or some modification of it, applies is being extended daily, both for animals and plants (see, for example, Bateson and Saunders' report to the Royal Society on heredity);

but in practice we shall probably find many more exceptions to the formulæ than confirmations of them, even though the exceptions can be explained, after we find them, by Mendel's principle of heredity.

It has been said that we shall soon be able, as a result of Mendel's discoveries, to predict varieties in plant-breeding. Before considering this question, we must recall the fact that a cultural variety is a succession of plants that have characters sufficiently marked and uniform to make it worth cultivating in place of some older variety. Now and then it may be worth while to introduce some new energy or new trend into a general lot of offspring by making wholesale crosses, not expecting ever to segregate any particular variety or strain from the progeny; but these cases are rare, and the gain is indefinite and temporary. So far as our knowledge at present goes, I see no warrant for the hope that we can predict varieties with any degree of exactness, at least not beyond a very narrow effort. Following are some of the reasons that seem to me to argue against the probability of useful prophecy of varities, so far as the Mendelian results are concerned: (1) We do not know what plants will Mendelize until we try. (2) Even in plants that do Mendelize, only half of the offspring have stable characters. But we can not predict for even this half, for it is impossible to determine beforehand which seeds showing dominant characters (and these are three fourths of the offspring) will 'come true.' Dominance, as we have seen, is of two kinds in respect to its behavior in the next generation—constant and hybrid; and the hybrid dominance, which is twice as frequent as the other, breaks up into constant dominance, hybrid dominance and recessiveness. (3) Mendel's law deals primarily with mere characters, not with a variety or with a plant as a whole. Every plant is a composite of a thousand characters, and from the plant-breeder's point of view there may be as many undesirable characters as desirable ones. No plant is perfect; if it were there would be no need of plant-breeding. The breeder wants to preserve the desirable characters or traits and eliminate the undesirable ones, but under the strict interpretation of Mendelism this is difficult. The one germ gamete and the one sperm gamete that unite to make the new plant each contain all the alternative characters; these characters are bound to reappear in the offspring, and all that the breeder gains is a new combination or arrangement of characters, and undesirable attributes may be as troublesome as before. (4) The breeder usually wants wholly new characters as well as recombinations of old ones, or he wants augmented characters. For example, a carnation grower wants a four-inch flower, but he has only three-inch flowers to work with, and augmentation of characters is no part of the original Mendelian law. Perhaps these augmented and new characters are to be got by means of ordinary variation and selection, or other extra-crossing means; but we know, as a matter of fact, that augmented characters do sometimes appear in hybrids. (5) New and unpredictable characters are likely to arise from the influence of environment or other causes, and these may be recorded in the gametes and vitiate the final results. (6) Variability itself may be a unit character, and therefore pass over. There is probably such a thing as a 'tendency to vary,' wholly aside from the fact of variation. (7) Many of the plants with which we need most to work in plant-breeding are themselves eminently variable, and the results, even if there is true Mendelism, may be so uncertain as to be wholly unpredictable. (8) Many plants with which we must work will not close-fertilize. Some of them are monœcious or diœcious. Even if there is gametic purity in such plants, the probability is that the fact can be discovered only by a long line of scientific experimenting for that particular purpose, and not by the work of the man who desires only to breed new plants. (9) A cultural variety, in any true acceptation of the term, is a series of closely related plants having a pedigree. It runs back to one individual plant, from which propagation has been made by seeds or asexual parts. Now, one can never predict just what combination of characters any plant will have, even though it be strictly Mendelian. A person might have a thousand plants of peas of which no one plant shows any of the characters in the proportion of 3 to 1, let alone all the characters as 3 to 1; and yet the total average numerical results might conform exactly to the Mendelian law. Mendel's law is a law of averages. The very fact that one must employ such large numbers to secure the numerical results shows that we can not predict as to individuals. For example, in ten plants of pea, Mendel found the following ratios in respect to seed-shape and seed-color:

Shape.	Color.
3.75:1	2.27:1
3.37:1	4.57:1
3.43:1	2.80:1
1.90:1	2.59:1
2.91:1	1.85:1
4.33:1	3.33:1
3.66:1	2.43:1
2.20:1	4.88:1
4.66:1	3.57:1
3.57:1	2.44:1

Mendel reports one instance in which the ratio in seed-shape was 21 to 1, and another of 1 to 1. He also reports instances of seed-color of 32 to 1 and 1 to 1. It has been said that, because of Mendel's work, we shall be able to produce hybrid varieties with the same certainty that we produce chemical compounds. Now, a plant is made up of many combinations of many units, and these combinations are the results of mathematical chance or probability. Chemical compounds are specific entities, in which the parts combine by mathematical definiteness. The comparison, as it appeals to me, is fallacious and the conclusions unsound.

We must remember that there are whole classes of cases of plant-breeding that do not fall under hybridization at all. Granting the De Vriesian view that selection is incompetent to produce species from individual fluctuations, it is, nevertheless, well established (and admitted by De Vries) that very many of our most useful cultural varieties have been brought to their present state of perfection by means of selection; and by selection they are maintained in their usefulness. Selection will always be a most important agency in the hands of the gardener—none the less so now that we have challenged its rôle in the evolution of the plant kingdom. For the time being, the new discussions of hybridization are likely to overshadow all other agencies in plant-breeding; but selection under cultivation is as important now as it was in the days of Van Mons and Darwin.

IV. INTERPRETATION OF HYBRIDISM.

I believe that the clearest insight into this whole new question of hybridization is to be got by following the work of De Vries. The concluding parts of the second volume of his 'Mutationstheorie,' a volume devoted wholly to hybridization, is on the press at this moment. The Mendelian laws are fully discussed in this volume, but the summary conclusions may be presented here. De Vries had been working at hybridization long before he discovered Mendel, and had arrived at practically the same results; he had also arrived at other results that are not Mendelian. De Vries denominated the law of numerical segregation as the 'law of separation of characters in crosses.' Like Mendel, he had found that merely to cross 'varieties' or 'species' is of no avail in the study of fundamental problems; for the varieties and species that we know are mere systematic groups with characters of all kinds and degrees. We must cross characters or units, not species.

Now, every unit character he conceives to be represented in the germ by a pangene. This pangene may be active, in which case the character appears in the plant; or it may be dormant, in which case the character is not visible, or for the time being is lost. Active pangenes may at any time become latent, or latent ones may become active.

Mendel's law results from an interchange of contrasting characters. True physiological or elementary species differ from each other by new unit characters. They have arisen by progressive mutation. The characters are not contrasting or differentiating. One species has one kind of pangene, another species another kind of pangene. On combining these there can be no interchange of characters, and therefore no Mendelism. There is nothing for one character to exchange against the other. In the case of true progressive mutations, therefore, upon which the progress of the plant race depends, there can be no Mendelizing. Hybrids of these cases are intermediates, or else follow only one or the other of the parents.

Now, varieties differ from true mutative species in the fact that they have contrasting characters. These characters are represented by their special kinds of pangenes. The pangene may be active or passive. That is, the variety may be a variety because one or more of its characters has become latent (retrogressive) or because characters have become active (degressive). When these characters are crossed, there is an interchange of the pairs. Both parents bear the same unit character, but this character is active in the one and dormant in the other. The hybrid receives an active pangene from one parent and a similar but inactive pangene from the other. When these two units unite, the calculus of chance determines that there shall reappear in the second generation equal numbers of both the parental units, and half of the whole that are still hybrids and break up in the same ratio in the third generation. That is, true Mendelism is confined to crossings of retrogressive and degressive varietal characters.

There are, therefore, two general classes of hybrid formation—the isogons, giving rise to crosses in which two antagonistic parental characters reappear in numerical order (Mendelian cases); anisogons, giving rise to crosses in which two antagonistic sometimes separate unequally, but ordinarily do not separate at all. When only one parent is represented in the offspring, we have the 'unisexual crosses' of Macfarlane or the 'false crosses' of Millardet. These are cases in which there are no true contrasting characters. Spillman has recently explained the false hybrids by supposing that the plants in this case are self-fertile and sterile with other pollen. That is, *A* is fertile with *A*, *B* with *B*, but *A* is not fertile with *B* nor *B* with *A*; there results, therefore, no true crossing. This hypothesis should be capable of experimental proof or disproof.

The isogon hybrids are of all degrees of complexity, and classification of them will at once show how far we have already got away from the old systematic idea of variety-hybrids and species-hybrids. Hybrids between plants that differ only in one unit-character are monohybrids. These are the ones in which the numerical results are most clearly traced, but they are also exceedingly rare. Those in which two unit characters are concerned are dihybrids. In these the combination series gives four different kinds of offspring. So there are trihybrids, giving eight possible combinations, tetrahybrids, and so on to polyhybrids; and in every succeeding grade the difficulties of statistical and comparative studies increase. Of how many characters is a plant composed?

V. CONCLUSION.

Now, in conclusion, what are the great things that we have learned from these newer studies? (1) In the first place, we have been brought to a full stop in respect to our ways of thinking on these evolution subjects. (2) We are compelled to give up forever the taxonomic idea of species as a basis for studying the process of evolution. (3) The experimental method has finally been completely launched and set under way. Laboratory methods, comparative morphology, embryological recapitulation, life history studies, ecological investigations—all these means are likely to be overshadowed for a time by experiments in actually growing the things under conditions of control. (4) We must study great numbers of individuals and employ statistical methods of comparison. (5) The doctrine of discontinuous evolution is now clearly before us. (6) We are beginning to find a pathway through the bewildering maze of hybridization.

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THE SOCIETY FOR PLANT MORPHOLOGY AND PHYSIOLOGY.

The sixth regular annual meeting of this society was held, in conjunction with the meetings of the American Society of Naturalists and the American Association for the Advancement of Science, at Washington, December 30 and 31, 1902, under the presidency of Professor Volney M. Spalding. A large part of the members were in attendance, and the meeting was in all ways most successful and pleasant. New members were elected as follows: Messrs. W. A. Cannon, of the New York Botanical Garden; Judson F. Clark, of Cornell University; G. P. Clinton, of the Connecticut Agricultural Experiment Station; W. C. Coker, of the University of North Carolina; C. C. Curtis, of Columbia University; E. J. Durand, of Cornell University; J. E. Kirkwood, of Syracuse University; W. A. Orton, of the United States Department of Agriculture, and K. M. Wiegand, of Cornell University. The following officers were elected for the ensuing year:

President—Roland Thaxter, of Harvard University.

Vice-President—Conway MacMillan, of the University of Minnesota.

Secretary-Treasurer—W. F. Ganong, of Smith College.

The chief item of business of general interest was the discussion upon the practicability and desirability of the new Central Bureau 'for the obtaining and distribution of material for investigation and demonstration' proposed by the Association Internationale des Botanistes. An expression of opinion taken after the discussion showed a unanimous opinion against the plan. Suggestions were formulated towards securing further improvements in the *Botanisches Centralblatt,* and a committee was appointed to draw up and publish in Science and elsewhere a statement to American botanists of the desirability of giving their full support to the *Centralblatt,* and of declining to support a competing journal.

The social features of the meeting were of unusual attractiveness. The society joined with the other societies in the vari-