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SOME PHYSIOLOGICAL VARIATIONS OF PLANTS, AND THEIR GENERAL SIGNIFICANCE[1]

IN a survey of the domain of the biological sciences in recent years, one of the most significant facts is found in the extent to which physiology has invaded those fields of this domain which, in the earlier stages of development, seemed entirely apart from and independent of physiological relations. When species of plants were supposed to have been created at the beginning just as we find them to-day, and to transmit their original characters unchanged to their remotest possible descendants, there was no physiological question as to the variations within species, and none as to the relation of species to each other nor as to the origin of new species. In that view there could be no origin of new species. They were all created at the beginning, and then the Creator rested.

When botany first began to be a science it was merely an attempt to classify plants, that is, to discover the characters of species as they were originally created, to group together those that were most alike and to separate those that were unlike. The characters used in the first attempts at classification were more or less superficial, and systematic botany was merely a study in formal external morphology.

But a change has come; and this change began with the general acceptance, among biologists, of the view that species are not

[1] Presidential address delivered before the Michigan Academy of Science at Ann Arbor, Mich., March 28, 1907.

entities with *necessarily fixed characters.* Even though *some* species of plants have persisted with constant characters ever since their earliest records were inscribed upon the rocks, no biological theory has received more certain confirmation in recent work than the theory that species are even now in process of creation. The creative power is not resting, never has rested. Species are appearing before our eyes. We have only to open them and see. In short, nature has been caught in the act of originating new species.

I refer, of course, to the work of de Vries, who has found among the evening primroses species which, every year, are giving rise to forms among their offspring sufficiently different from their immediate parents to be regarded as elementary species. With some of these new forms the characters which distinguish them from their parents are constant when propagated by seed. This is not to be regarded as the inheritance of characters acquired by the parents of these new elementary species, but rather as the appearance of new characters in the race, not by a gradual modification of parental characters, but by a sudden transformation to which de Vries has given the name *mutation.* These new characters can not be ascribed to the direct influence of external factors on the adult or developing forms in which the new characters appear, since they appear and persist in the same conditions of life in which the parental type is continued. De Vries offers no explanation as to how these new characters are produced, but following his work, MacDougal has succeeded in producing new modifications by artificial means, using as the subject of his experiments species which are closely related to those with which de Vries obtained his notable results. MacDougal injected various substances, radium preparations, sugar solutions, calcium nitrate and zinc sulphate, into the capsules of the plants experimented upon, before the eggs were fertilized by the nuclei from the pollen grain. From the many capsules used, a few furnished seeds which, on planting, produced plants notably different from the type of the parent plant. The flowers of the new type were closely guarded to prevent cross fertilization, and their seeds when planted gave a few plants which conformed in every particular to the new type.

If there is no mistake about MacDougal's results, and I see no reason for supposing there is, at least one very important conclusion seems to be well founded, namely, that in an early stage of development of the plant egg, before it has been fertilized, it may be so profoundly modified that the adult plant resulting from it is decidedly different from what it would have been had the egg not been so modified, and the modifications thus produced are transmitted to the next generation through the seeds. Taking the results of both de Vries and MacDougal, we may conclude that the necessary modification of the egg is sometimes produced in nature, and may also be induced by means under the control of the experimenter.

There is one question which will probably be both affirmed and denied by different biologists for some time in the future. It is this: Are the new types which appear by sudden leaps to be considered new species or only varieties of the parent species. The debate on this question will be all the more acrid and prolonged because of the impossibility of giving a satisfactory definition of the term species.

One ought to ask pardon perhaps for quoting *authority* in science, but a high botanical authority has said that he believes no better definition of species has ever been invented than this: "A species is a perennial successon of like individuals.'' An equally high botanical authority has said that a species is a judgment. And this also is true. Species and other categories of classification are more or less arbitrary distinctions, made for convenience in classification of our knowledge. Hence in a given case, the question whether two different forms are to be regarded as two different species or not, is in part a matter of individual judgment. If Darwin's view is correct, that new species may originate by the gradual accumulation of exceedingly minute differences, there could be no line of demarcation between species provided we could have all the transitional forms. Only where the transitional forms had disappeared, or the new forms had migrated to a new region, could we have sharp lines of distinction between species. Even in the case where the new form had migrated to a region not occupied by the old, the transitional forms would be disclosed on studying the species in all its range. Distinctions of species in such a case must necessarily be more or less a conventional matter. But if species originate by the sudden production of entirely new characters, that is by mutations, as de Vries believes, then there are no transitional forms connecting the new to the old. The condition in nature in this case would be similar to that in which there has been an extinction of the transitional forms between two different types derived from a common ancestor by gradual modifications. In either case there is room for individual judgment in the delimitation of species, according as the differences between the two types are greater or smaller. We say, ''A species is a perennial succession of like individuals.'' But how nearly alike must they be? No two individuals are exactly alike, and the extreme differences possible between two individuals of the same species may be greater than those between two individuals of different species. In other words, the differences within the species may be greater than the differences between species, as de Vries has pointed out. How then are we to decide whether two individuals comparatively different from each other, and yet alike, belong to the same or different species? It has been found that for any given character the variations within the species may be expressed numerically by an average with deviations, both above and below that average. For instance, the average height of the stem in a given species of plants may be two feet. Most of the plants composing the species may vary only slightly from this average, say from one to three feet. But the greater the number of individuals examined and measured the more certain it becomes that we shall find a few individuals which differ far more widely from the average. In our supposed case we might find that the extreme limits of size were six inches to ten feet, while the average was only two feet. These deviations from the average of the species are called the fluctuating variations. They are largely determined by the external conditions in which the species grows. Professor George Klebs has shown that when plants are subjected to extremes of variation in the external conditions of light, heat, moisture and food supply, the deviations from the average of the fluctuating variations become far greater than are usually found in a state of nature. Klebs's results with Sempervivum were truly remarkable. He produced variations that are not found in a state of nature in the species with which he worked, changes in the color, size and shape of the flower, great variations in length of the stem and its mode of branching, the size, shape and arrangement of the leaves. As the result of this kind of work, carried on for a considerable number of years, Klebs has given us a definition of a species which expresses the dependence of the form of the plant upon the environment. According to Klebs we must say: "To a species belong all individuals which, propagated vegetatively or by self-fertilization, under like external conditions, show the same characters through many generations." If two plants under these conditions show a noticeable difference, they are to be regarded as belonging to two species, even though they have descended from a common ancestor. Gaston Bonnier has shown by experiment that plants transplanted from the region of Fontainebleau near Paris to Toulon in the Mediterranean region show in a few years adaptations both of external form and internal structure which cause them to resemble the species characteristic for the Mediterranean region. The same investigator found similar results on transplanting from the plains to Alpine regions. Knowing the origin of such widely variant forms we do not call them two species, but merely extremes in the fluctuating variations of the species. It is conceivable, however, that nature might perform this same experiment on such a scale and in such ways as to make it difficult or impossible to recognize the common origin of two such different types. In that case the botanical collector or systematist, finding the two types in widely separated regions, would describe them as two species of plants. If the distribution of the species was continuous from one of these extreme regions to the other the connecting intermediate forms would show that we had to do merely with extreme fluctuating variations brought about by extremes in soil, moisture, heat and light. If, however, the geographical continuity of the species had been interrupted in any way, it would be impossible to determine by observation alone that the two extreme types were only fluctuating variations of one species. That could be determined by the experimental method as followed by Klebs and Bonnier. Plant the two types in the same region, grow them under exactly the same conditions, and if after many generations they continue to exhibit constant differences they are to be regarded as two species. On the contrary, if they show the same characters under the same conditions, they are one species. Such a method of determining whether one has a new species or not involves an enormous amount of labor, and a great deal of time. It is not in favor with the systematists who work with the higher plants. Nevertheless, there is an increasing recognition among botanists of the necessity of physiological work even in those fields of research that have in the past been dominated by morphology alone.

Such experiments might help to decide the question whether the so-called alpine species have been constant since the glacial period, as de Vries supposes they must have been, or whether, as seems possible, similar combinations of climatic conditions, operating in widely separated regions such as the alpine region of central Europe and the high latitude of Norway, have produced species of similar form. It does not even seem necessary to assume that the parent species of the alpine forms has been the same in these widely separated regions. De Vries has pointed out that species sometimes overlap by what he calls *transgression variations.* Klebs has shown that in one species of Sempervivum he could produce nearly all the characters found in the other species of the genus. Is it not therefore possible that the continuation of conditions of soil, temperature, moisture and light characteristic of the alpine regions, could produce a type varying about a new average, which lies near one of the extremes of the fluctuating variations of the parent species.

If this new average should be established within the limits of the transgression variations of two species one of which existed in northern Europe and the other in central Europe, we should have the production of similar types, the alpine and arctic type, in widely separated regions and from different parent species. The characters of the new type are not 'fixed' in the sense of being due to inheritance, but only in the sense that they are a response to a particular combination of external factors, and this combination is constant in the given regions. Such a view of the origin of alpine types is not merely of theoretical interest, since the application of the physiological method gives the means of reaching more or less definite conclusions.

De Vries and others have pointed out that the species of the manuals and the systematic botanists are in large part composite or collective species and not simple or elementary species. In his view the latter differ from their parent species by *new* characters, not by modifications of old ones. The new characters are inheritable as soon as they appear, and are not regulated by the external conditions in which the adult plant lives.

If MacDougal's work stands the test of repetition, physiological experiment may open up a new field in investigating the *origin* of species. One method of applying physiological experiment to determining the *limits* of species has just been discussed. But other applications of this method are possible. It is well known that cross fertilization generally takes place only between closely related species of plants, rarely between genera. When attempts are made to cross species remotely related, either the pollen does not grow upon the stigma of the strange species, or fertilization of the egg does not take place, or if seeds develop the resulting hybrid is sterile, not being able to produce seeds for its propagation. What lies at the basis of these physiological differences is still obscure. It is probable that enzymes, toxins or other chemical substances play a part. But whatever the explanation, the fact may be used in determining the nearness or remoteness of the relationship between forms. This possibility has been recognized by many investigators, and biologists have proposed using the degree of fertility of hybrids as the means of distinguishing genera, species, and varieties. Though this has been found not to be reliable in all cases, de Vries has suggested it as a means of distinguishing his elementary species from varieties. If on crossing two forms the resulting hybrid is constant in regard to a given character, when guarded against further crossing, the two forms were different species. But if, on crossing, the descendants of the resulting hybrid followed Mendel's law of hybrids, according to which one fourth of the offspring of the hybrid in each succeeding generation resembled one parent in respect to a given character, one fourth resembles the other parent as regards the corresponding character, while half are like the original hybrid, then the parent forms of the hybrid were one and the same species.

Whatever the limitations of this method in its practical application, the significant fact is the extent to which physiological conceptions have invaded a realm that was purely morphology. We may use the experimental method in studying the origin of new species and varieties. We may apply physiological methods in determining the range of the fluctuating variations within the species. We may use physiological affinities as the test of the degree of relationship existing between different forms found in nature.

The foregoing discussion has had special reference to the higher plants. But among the lower forms of plant life physiological methods are far more applicable, indeed necessary, in determining the characteristics of species. In all that group of plants known as bacteria, species can be distinguished only by physiological means. These organisms are so simple in structure, their morphological characters are so few, it is utterly impossible to classify our knowledge of them even from a systematic point of view without using physiological means as the basis of species distinctions. The most important relations which the bacteria bear to the organic world in general, and to the human race in particular, are physiological in their nature. Some of them have the power of invading the animal body and producing there substances which we call toxins, and which may be so exceedingly poisonous that the result may be fatal in an extraordinarily short time. Fortunately the animal body has the power to vary its ordinary physiological processes in such a way as to produce antitoxins which neutralize the action of the toxins. A given organism may vary in its virulence at different times. An epidemic due to an organism in the so-called attenuated state, produces a mild form of the disease. A given animal or plant may be especially resistant to the toxin of one species of bacteria, as the horse is to diphtheria toxin, or it may be very susceptible to a given toxin, as the human body is to the toxin of tetanus, or lockjaw. Also the same organism shows different powers of resistance, or immunity, at different periods. It is well known that any conditions of life that produce a low state of vitality in a given individual, make that individual far more susceptible to disease, that is, to the toxins of other organisms. Not only are plants and animals susceptible to the toxins produced by other plants and animals, but each organism produces substances which are toxic to itself. This is true not only for the lower organisms, but at the present time a discussion is being carried on as to whether the necessity of the so-called rotation of crops of higher plants is more dependent upon the partial exhaustion of the soil in elements necessary for a given crop, or upon the gradual accumulation in the soil of substances detrimental to the kind of plants that produced them. The physiological variations of organism, and the physiological relations of one kind of organism to another, form a series of the most fascinating as well as the most difficult of biological problems. The small size of the bacteria and the rapidity with which they multiply make them very favorable subjects for experiment along the line of the fundamental biological processes. An organism that requires several hundred years to complete its life cycle is obviously not a favorable subject for an experiment that requires the study of several generations. But if, as in the case of some of the bacteria, a new generation may be produced every fifteen minutes, it is possible to obtain within a few hours hundreds of generations and millions of individuals.

There is another group of organisms about which I wish to speak, not so simple as the bacteria in structure, but far inferior in that respect to the highest plants. I refer to the filamentous fungi, and I wish to call your attention to some facts that again have to do with the question: What is a species? As in the case of higher plants, the first attempts to classify these organisms were upon a purely morphological or structural basis. But a deeper knowledge of their life histories and physiological variations makes it more and more apparent that here, as among the bacteria, it is necessary to use physiological means of distinguishing, shall we say species? For the present we can avoid making the decision, and say forms or races, yet at the same time we can hold our minds open to evidence as to whether these forms or races are not, after all, incipient species. Two groups of these fungi especially force themselves upon our attention from the point of view we are considering. One of the groups has been called the Uredineæ or rust fungi, and the ordinary rust of cultivated cereals is a typical example. The other group is known commonly as the mildews, or more technically the family Erisyphaceæ. The rose mildew and the grape mildew are common examples. In both of these groups it has been found necessary to distinguish what have been called biologic forms or races, distinguished from each other only by the fact that they differ in capacity to infect different species or genera of the host plant. Working with the wheat rust, which was formerly supposed to be the same on any of the cultivated cereals and wild grasses, Eriksson has found that there are numerous races adapted more or less closely to the species of single genera, and they are able to infect species of other genera either with difficulty or not at all. Their forms can not be distinguished morphologically, and yet the infection experiments show that physiologically they are decidedly different from each other. In trying to conceive the origin of these forms, there seem to be three possibilities. First, these biologic forms may have had an origin from different species growing on a narrowly limited group of host plants. There seems to be little evidence for this view. Second, they may have been derived from one species, by sudden physiological changes in the fungus alone, without any influence of the host. This would be similar to the origin of elementary species by mutation, as found by de Vries among the evening primroses. There seems to be no direct evidence for this view. Third, a group of biological forms which can not be distinguished morphologically may have originated from one species which at first grew on a wide range of host plants, but when a strain or race is propagated continuously on the same species of host, there is a special adaptation of the fungus to that species of host, and it becomes able to infect that one more readily, and others less readily, and at last not at all. For this view there is some direct evidence. A form of rust which was capable of growing on four genera of host plants, was propagated for ten years continuously on only one of the four. At the end of the ten-year period it could infect that one genus strongly and the other three weakly or with uncertainty. If this experiment indicates the way in which the biological forms have come into existence, they have originated, not by mutation, but by adaptation. The differences they exhibit have come about by the gradual accumulation of imperceptible modifications.

Among the mildews there has been found an adaptation of forms even closer than among the rusts. Experiments of Salmon on the mildews of grasses disclosed the fact that adaptation is not only to one or few genera, but in many cases actually to one or a few species within the genus. The mildews exhibit the phenomena of adaptation carried much farther than it is carried among the rusts.

The question remains, can these biologic forms or adaptive races ever rise to the dignity of true species? Again the direct evidence is lacking. But if these fungi are as variable in their morphological character as Klebs found even the flowering plants to be under different physiological conditions, we might expect the same causes which bring about the physiological adaption to be able to produce morphological differences as well. But even if no morphological differences appear, are we not justified in making physiological characters the basis of species among the fungi as is already done among the bacteria? The speaker is inclined to answer this question in the affirmative. It seems certain that, for practical purposes at least, it is becoming absolutely necessary in other groups of fungi, as well as in the rusts and mildews, to make distinctions on physiological grounds, not to the exclusion of morphology, but in addition to it. Whether you call the groups of individuals so distinguished species or not, matters very little. The important thing is that the distinction must be made.

It is impossible to apply de Vries's test for species and varieties among the fungi. For most of them there can be no such thing as cross-fertilization. For many there is no fertilization at all, and even where present, it is generally strictly self-fertilization. Naegeli long ago pointed out that where plants were propagated only vegetatively or by self-fertilization and it may be added parthenogenetically, individual peculiarities were perpetuated in the descendants, while with open or cross-fertilization the peculiarities of one individual may be modified in the next generation by mingling with another line of inheritance representing peculiarities of another individual opposed to those of the first. Open or cross-fertilization therefore tends to keep the species homogeneous by neutralizing extreme individual variations. While in those plants which are propagated by parthenogenesis, that is where the eggs develop without fertilization, or by self-fertilization, or by non-sexual spores, or by vegetative means, the species tend to become heterogeneous. They are made up of many lines of descent which are never mingled, individual peculiarities tend to become extreme, and species limits are particularly difficult to determine. Among flowering plants the hawkweeds furnish an example of the results of reproduction by parthenogenesis. In this genus, *Hieracium*, it is said that of two noted men who had made a special study of the species of this genus, neither could identify the species by the other's descriptions. The same result is apparent among the fungi, in the development of the biologic forms or adaptive races.

Individual adaptation to a given host is not neutralized by fertilization from a plant with a different adaptation, but is continually accentuated. The practical importance of many of these adapted forms compels us to recognize them as distinct entities, and to give them names. For practical purposes then they are species, even though they can be distinguished only physiologically.

This capacity for physiological variation or adaptation on the part of fungi is significant in another direction. It is certain that among the fungi as well as among the bacteria, forms that for the most part live only on dead organic matter, that is, as saprophytes, may under certain special conditions become adapted to a parasitic life. They thus become the producers of new diseases. Though for the most part supposed new diseases are only a wider distribution of old diseases, it is entirely possible for new diseases actually to originate by physiological adaptation. This has been proved in the production of plant disease experimentally.

But if this kind of variation has its somber side, there is also an obverse side. Physiological variation enables us in many cases to select and propagate cultivated plants that are particularly resistant, and sometimes completely immune, to a given disease. The same phenomenon may be observed here as in the human family. In any given epidemic there are always certain individuals who never contract the disease. They have a certain natural immunity to that particular disease, and this immunity is due to some physiological peculiarity. So in a field of rusted or mildewed wheat some individual plants show themselves more resistant than their fellows to the species of rust fungus found upon that species of host. By selecting and propagating these immune individuals we may develop an immune race or strain. The problem is not always so simple as here stated. It may happen that a race immune to one disease may be very susceptible to another, or immunity may be accompanied by other qualities altogether undesirable. One might be led to suppose, on reading certain popular articles intended to show how new forms of plants are produced, that it is only necessary to imagine an ideal plant and then set to work to create it. Nothing is farther from the truth than this. Nature does sometimes produce something new, as a stoneless plum, or a nectarine on a peach tree. But man must take the materials furnished by nature, combine them in new ways, or modify them within limits which are usually soon reached. He can not create a wheat plant immune to rust, nor a watermelon resistant to the wilt fungus. But if nature furnishes a few individuals with the desired qualities, man can propagate the individuals possessing those qualities, and by rigid selection maintain the qualities to a high degree. If it is possible to cross the plants with other species or with varieties of the same species, he may be able to combine in the same individual a number of desirable qualities. Having obtained these qualities in one individual, he can best conserve them by vegetative propagation, such as by grafts, cuttings, bulbs or tubers, according to the habit of the plant propagated. He may care nothing whatever about the limits of species or varieties except in so far as their physiological relations help or hinder his combinations. Following MacDougal's method, it may be possible to produce in plants some new characters. But even if it were possible to produce in this way really new species, it is hardly within the range of possibility that we could choose beforehand the kind of a species we would produce. It would be a case of 'cut and try.' If the result be a form with desirable qualities, let it be preserved, but if it be worthless, let it die. Nature has repeated this experiment ten thousand times. If we would imitate her we must search out her secrets in the physiological realm. She conceals them well, but is not unwilling to reveal them to him who questions her with a hearing ear, a seeing eye, and a thinking brain, tools which she herself has given him.

JAMES B. POLLOCK
UNIVERSITY OF MICHIGAN

A PLEA FOR THE STUDY OF THE HISTORY OF MEDICINE AND NATURAL SCIENCES[1]

FOR a number of years a new current of thought has been gradually coming to the front in the minds of scientific thinkers of the times. The nineteenth century, the mental development of which is now assured, has of late been severely criticized for its unhistorical character, and perhaps not without reason. Over this inheritance from the preceding generation a certain dissatisfaction is being more and more keenly felt in the most diverse branches of science. The main trend of the last century was naturalistic and economic to a marked degree; so much so, that the new methods discovered in natural science, and

[1] Read before the American Anthropological Association, at the meeting of the American Association for the Advancement of Science, December 31, 1906.