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THE PLANT INDIVIDUAL IN THE LIGHT OF EVOLUTION.*

THE PHILOSOPHY OF BUD-VARIATION, AND ITS BEARING UPON WEISMANNISM.

I.

WHILST the animal and vegetable kingdoms originate at a common point and are not clearly distinguishable in a number of

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the lower groups or organic beings, they nevertheless diverge rapidly and they finally become very unlike. I believe that we shall find that this divergence into two coördinate branches of organic nature is brought about by the operation of at least two fundamentally distinct laws. There is a most unfortunate tendency, at the present time, to attempt to account for all phenomena of evolution upon some single hypothesis which the observer may think to be operative in the particular group of animals or plants which he may be studying. For myself, I cannot believe that all forms of life are the results of any one law. It is possible that all recent explanations of evolution contain more or less truth, and that one of them may have been the cause of certain developments, whilst others have been equally fundamentally important in other groups of organisms. If I were a zoölogist, and particularly an entomologist, I should hold strongly to the views of Lamarck; but, being a horticulturist, I must accept largely, for the objects which come within the range of my vision, the principles of Darwin. In other words, I believe that both Lamarckism and Darwinism are true; and, in this connection, it is significant to observe that Lamarck propounded his theory from studies of animals, whilst Darwin was first led to his theory from observations of plants. I am willing to admit, also, at least for the sake of argu-

ment, that Weismannism, or the Neo-Darwinian philosophy, may be true for some organisms, but it is wholly untenable for plants.

There is one feature of this difference between the animal and the plant to which I wish to call your attention on this occasion. It is the meaning of individuality in the two. I must say, at the outset, that when I speak of a plant or an animal I refer to those higher forms which the layman knows by these names, for it is not my purpose to discuss the original causes of divergence so much as those phenomena of individuality which are most apparent to the general observer. The animal may be said to have complete autonomy. It has a more or less definite span of life. It grows old and dies without having been impaired by decay, and the period of death may have no immediate relation to environment. It has a definite number of parts, and each part or organ is differentiated and performs one function, and this function serves the whole animal and not the organ itself. If any part is removed the animal is maimed and the part cannot be supplied, and the severed portion has no power to reproduce either itself or the animal from which it came. The only means by which the animal can multiply is by a union of sexes. The plant, on the contrary, has no perfect or simple autonomy. It has no definite or pre-determined proximate span of life, except in those instances when it is annual or biennial, and here duration is an evident adaptation to environment. The plant frequently dies as the result of decay. It has not a definite number of parts, and each part of the plant may perform a function for itself, and the part may be useful to the remainder of the plant or it may not. One part is like what all other parts are or may be. If one portion is removed the plant may not be injured; in fact, the plant may be distinctly benefited. And the severed portion may not only have

the power of reproducing itself, but it may even reproduce an organism like that from which it came. In other words, plants multiply both with and without sex. Potentially, every node and internode of the plant is an individual, for it possesses the power, when removed and properly cared for, of expanding into what we call a plant, and of perfecting flowers and seeds and of multiplying its kind.

Those of you who are botanists now recall the contention of Gaudichaud concerning the plant unit or phyton. He proposed that the leaf, with its connecting tissues, is the vegetable individual and that the plant is a colony of these individuals. Gaudichaud offered this theory as an explanation of the morphology and physiology of plants, and the hypothesis really has no place in the present discussion; but, inasmuch as I have borrowed the word which he proposed for the plant unit, it is no more than fair that I should explain his use of it; and this explanation may serve, incidentally, to illustrate some of the problems of individuality to which I shall recur. Gaudichaud, while recognizing that a cell which develops into a bud is itself an individual, nevertheless considered that the leaf, with its dependent tissues, represents the simple vegetable unit. Each of these units has an aerial or ascending part and a radicular part. The ascending part has three kinds of tissues or merithals—the stem merithal, petiolar merithal and the limbic merithal. Now, each phyton fixes itself upon the trunk or upon an inferior phyton, in the same manner as a plant fixes itself in the soil, and, sending its vascular threads downwards between the bark and the wood, is enabled to support itself upon the plant colony; and, at the same time, the extension of these threads produces the thickening of the stem, and the superposition of phytons increases the height of the plant. This mechanical theory of the morphology

of plants was not original with Gaudichaud, but he greatly enlarged it and gave it most of its historic value, and, what is more to our purpose, he used the word *phyton*, which, in lieu of a better one, I shall use as a convenient expression for that asexual portion of any plant which is capable of reproducing itself. Gaudichaud's fanciful hypothesis was not completely overthrown until the exact studies of Von Mohl upon the vegetable cell established a rational basis of morphology and physiology.

What I wish now to show is that the evolution of the vegetable kingdom cannot be properly understood until we come to feel that the *phyton*, or each portion of the plant, which, when removed, has the capability of reproducing itself and its parent, is in reality a potential autonomy. In doing this I shall not forget that the plant also has an individuality as a whole, but as this feature is quite aside from my argument and is the conception of the plant which is everywhere accepted, I shall necessarily confine my remarks to the individual life of the *phyton*. The mere fact that the *phyton* may reproduce itself is not the most important point, but, rather, that each part of the plant may respond in a different manner or degree to the effects of environment and heredity. Before proceeding to this matter, I should say that there is no doubt about the capability of every plant to be propagated asexually. It is true that all plants have not been so propagated, but there is every reason to suppose that the gardener can acquire the requisite skill to grow oaks and hickories from cuttings were it worth his while to do so. At present there are cheaper modes of multiplying these plants. But certain pines and spruces, which do not seed under cultivation, are propagated by cuttings, and the tissue of these trees is as little adapted to such use as that of any plants with which I am acquainted. The fact that plants are

not grown from cuttings does not prove that they cannot be so propagated, for we know that the essential structure of all of them is very similar, and that each node and internode—or each *phyton*—does or may produce branches and flowers and seeds when it is borne upon its parent plant. And I should remind you that those plants which are not readily multiplied by cuttings are generally propagated by grafting, which, for illustration, amounts to the same thing, for we only substitute the stock of another plant for the soil. Plants of the most various kinds are readily multiplied by graftage. Even tuberous herbaceous stems, which are not commonly associated with the art of the grafter, unite with ease. One of the latest investigators in this field is a Frenchman, Daniel, and his conclusions upon the physiology of grafted plants show that the physiological modifications in these plants are largely such as arise from physical causes, showing that the parts still preserve their essential autonomy.

Now, if every plant varies in the number of parts, or *phytons*, of which it is composed, it follows that this number must be determined by agencies which act immediately upon the given plant itself. We all know that the number of these parts is determined very largely by environment. A dozen plants springing from the same capsule may vary immensely in the numbers of their branches, leaves and flowers, and this variation is generally obviously correlated with amount of food, amount of space which the plant is allowed to occupy, and other physical conditions which affect its welfare. But we not only find that no two plants have the same number of parts, but that no two branches in the same plant are alike. One part grows longer, one more erect, one has greener leaves, one bears more fruit. So, too, there may be different forms of flowers on the same plant, a subject to which Darwin has devoted an entire

volume. We know, also, that this variation amongst the sisterhood or colony of branches is determined by very much the same conditions which determine variation in independent plants growing in soil. I believe that the primary and most important determinant of this variation is the variation in food supply, the same which Darwin believed to be the most potent factor in the origination of variations in general. That branch or phyton which receives the most food, because of its position or other incidental circumstance, is the one which grows the largest, has the heaviest and greenest leaves, and, in the end, is the most fruitful. I use the word food to designate not only the supply of nutriment which is derived from the soil, but also that obtained from the air and which is most quickly and thoroughly elaborated in the presence of the brightest sunlight. Thus the uppermost branches of the tree, whilst farthest from the root, are generally the strongest, because they are more freely exposed to light and air and their course is least impeded. Many branches in the interior of tree tops are undoubtedly parasites upon the plant colony, taking from it more than they return.

If the number of the plant units is determined by circumstances peculiar to that plant, and if there is variation amongst these units in any plant, then it follows that there must be struggle for existence between them. And this struggle differs from the conflict between independent plants in the complex battle for life only in the circumstance that it is more intense or severe, from the fact that the combatants are more closely associated. There are weak branches and strong branches, and the survival of the fittest is nature's method of pruning. The strong terminal branch, shooting upwards towards air and sunlight, makes the bole of the tree, whilst the less fortunate or side branches perish and fall. The leaf surface

of any tree or large plant is always pushing outwards towards the periphery, which is only another way of saying that the anterior branches die. I often find fruit growers who refuse to prune their trees because they believe it to be unnatural, while at the same time their tree tops are full of dead limbs, every one a monument to the stupidity of the owner!

Now, the effect of this struggle for existence allows of mathematical measurement. Each bud should produce a branch or a cluster of fruit. A seedling peach tree may be two feet high the first year, producing thirty leaves, and in every axil a bud. Each of these buds should produce a branch, which should again produce thirty buds. The third year, therefore, whilst the tree is only six or eight feet high, it should have 900 branches, and in the fourth year 27,000! Yet a peach tree twenty years old may not have more than 1,000 branches! That is, many millions of possible branches have been suppressed or have died. I once made an actual observation of such a battle and counted the dead and wounded. A black cherry tree came up near my door. The first year it made a straight shoot nineteen inches high which produced twenty-seven buds. It also sent out a branch eight inches long which bore twelve buds. The little tree had therefore enlisted thirty-nine soldiers for the coming conflict. The second year twenty of these buds did not grow. Nineteen of them made an effort, and these produced 370 buds. In two years it made an effort, therefore, at 409 branches, but at the close of the second year there were only twenty-seven branches upon the tree. At the close of the third year the little tree should have produced about 3,500 buds or branch-germs. It was next observed in July of its fourth year, when it stood just eight feet high; instead of having between 3,000 and 4,000 branches, it bore a total of 297, and most of them were only weak

spurs from one to three inches long. It was plain that not more than twenty, at the outside, of even this small number could long persist. The main stem or trunk bore forty-three branches, of which only eleven had much life in them, and even some of this number showed signs of weakness. In other words, in my little cherry tree, standing alone and having things all its own way, only one bud out of every 175 succeeded in making even a fair start towards a permanent branch. And this struggle must have proceeded with greater severity as the top became more complex, had I not put an end to its travail with the axe!

II.

I am now ready to say that I believe bud-variation to be one of the most significant and important phenomena of vegetable life, and that it is due to the same causes, operating in essentially the same way, which underlie all variation in the plant world. As some of you may not be familiar with the technical use of the term, I will explain that a bud-variety is an unusual or striking form or branch appearing upon a plant; or, as Darwin put it, bud-variation is a term used to "include all those sudden changes in structure or appearance which occasionally occur in full-grown plants in their flower-buds or leaf-buds." A classical example is the origination of the nectarine from a branch of a peach tree; and one often hears of Russet apples upon a certain branch of Greening apple tree, of weeping, variegated or cut-leaved shoots on otherwise normal trees, or of potatoes that 'mix in the hill.' Now, this matter of bud-variation has been a most puzzling one to all writers upon evolution who have touched upon it. It long seemed to me to be inexplicable, but I hope that you will now agree with me in saying that it is no more unintelligible than seminal variation of plants, for I have already shown that there is abundant asex-

ual variation (of which bud-variation is itself the proof), and that this variation takes place as readily when the phyton is growing upon a plant as when it is growing in the soil. The chief trouble has been, in the consideration of this subject, that persons have observed and recorded only the most marked or striking variations, or those which appear somewhat suddenly (although suddenness of appearance usually means that the observer had not noticed it before), and that they had therefore thought bud-variation to be rare and exceptional. The truth is, as I have said, that every branch or phyton is a bud-variety, differing in greater or lesser degree from all other phytons on the same plant. These differences, even when marked, may arise in every part of the parent plant, as on stems aerial and subterranean, from bulbs and tubers, or even from the adventitious buds of roots; and the characters of these varieties are as various as those originating from seeds. The nurseryman knows that branches differ amongst themselves, for he instructs his budders to cut buds only from the top-most shoots of the nursery rows in order that he may grow straight, vigorous trees; and every farmer's boy knows that the reddest and earliest apples grow on the uppermost branches, and his father will always tell him that he should never select cions from the center or lower part of a tree. Every skilful horticulturist will tell you that the character of the orchard is determined very largely by the judgment of the propagator in selecting cions. To select out the extreme forms of these variations and to attempt to explain bud-variation by them is exactly like selecting the extreme types of seminal variations, and, by ignoring the lesser ones and the intermediates, to attempt to build thereon a theory of the variation of plants. If you ask me why it is that the nectarine was produced upon a branch of a peach

tree I will answer that nectarines have also been produced from peach seeds. The answer to one answers the other. It is true that bud-variations, if we use that term, as we logically must, to denote all variations between phytons, are commonly less marked than seed-variations, but this is only because the conditions of origin and environment of the phyton are less varied than those of the seedling. The phytons originate from one parent, not from two; and they all grow in very like conditions. But I am convinced that, when we consider the plant individual in the light of evolution, the bugbear of bud-variation vanishes.

A good proof that bud-variation and seed-variation are one in kind is afforded by the fact that selection can be practiced for the improvement of forms originating by either means. Darwin was surprised, as he says, to "hear from Mr. Salter that he brings the principle of selection to bear on variegated plants propagated by buds, and has thus greatly improved and fixed several varieties. He informs me that at first a branch often produces variegated leaves on one side alone, and that the leaves are marked only with an irregular edging, or with a few lines of white and yellow. To improve and fix such varieties he finds it necessary to encourage the buds at the bases of the most distinctly marked leaves and to propagate from them alone. By following, with perseverance, this plan during three or four successive seasons a distinct and fixed variety can generally be secured." This practice, or similar ones, is not only well known to gardeners, but we have seen that nature selects in the same manner, through the operation of the same struggle for subsistence which Darwin so forcibly applied to all other forms of modification. Once given the three fundamental principles in the phylogeny of the phyton, the variation amongst themselves, the struggle for existence, the capability of perpetuating themselves—an in-

disputable trinity—and there can no longer be any doubt as to the fundamental likeness of the bud-variety and the seed-variety.

Yet I must bring another proof of this likeness to your mind. It is well known that the seedlings of plants become more variable as the species is cultivated; and it is also true that bud-varieties are more frequent and more marked in cultivated plants. Note, for example, the tendency of cultivated plants to bear variegated or cut-leaved or weeping shoots, and the fact that the colors and doubleness of flowers often vary greatly upon the same plant. Many of our best known roses, carnations, chrysanthemums, violets and other garden plants originated as bud-sports. This fact is so well known that critical gardeners are always on the alert for such variations. In any house of 200 roses, all grown from cuttings, the grower will expect to find more than one departure from the type, either in color or freedom of bloom or in habit of plant. Every gardener will recall the 'sporting' tendencies of *Perle des Jardins* rose, and the fact that several commercial varieties have sprung from it by bud-variation. As early as 1865 Carrière gave a descriptive list of 154 named bud-varieties, and remarked at length upon their frequency amongst cultivated plants. This fact of greater bud-variability under cultivation was fully recognized by Darwin, and he regarded this as one of the strongest proofs that such variation, like seed-variation, is "the direct result of the conditions of life to which the plant has been exposed."

In order to extend the proofs of the essential ontogenetic likeness of bud and seminal variations, I will call to your remembrance the fact that the characters of the two phytons may be united quite as completely by means of asexual or graft hybridism as by sexual hybridism. I do not need to pursue this subject, except to say that we now believe that graft-hybrids are rare

and exceptional chiefly because the subject has received little experimental attention. Certainly the list given by Focke, and the anatomical researches of Macfarlane, show that such hybrids may be expected in a wide variety of subjects and with some frequency. It is now stated positively by Daniel, as the result of direct experiment, that the seeds of cions of certain cultivated herbs which are grafted upon a wild plant give offspring which show a marked return to the wild type. I should also add that the breaking up of seminal hybrids into the characters of either parent may take place, as Darwin has shown, through either seed- or bud-variation. You are all no doubt aware that hybrids generally tend to revert to the types from which they sprung, and this sometimes occurs even in hybrid offspring which is propagated exclusively by buds or cuttings.

Still another proof of the similarity of bud-varieties and seed-varieties is the fact that the seeds of bud-varieties are quite as likely to reproduce the variety as the seeds of seed-varieties are to reproduce their parents. Darwin and others have recorded this seminal transmission of bud-sports. "Notwithstanding the sudden production of bud-varieties," Darwin writes, "the characters thus acquired are sometimes capable of transmission by seminal reproduction. Mr. Rivers has found that moss-roses [which are bud-varieties] generally reproduce themselves by seed; and the mossy character has been transferred by crossing from one species to another." This general fact that bud-sports may reproduce many of their essential acquired characters by seeds is so well grounded in the minds of gardeners that the most critical of them make no distinction, in this respect, between varieties of bud and seed origin when selecting parents for making crosses. And if we can prove the similarity of bud and seed variations by showing that both bear

the same relation to transmission of characters by means of seedage, we can demonstrate it equally well by the converse proposition—that both bear the same relation to the perpetuation of their features by cuttings. Some seed-varieties will not 'come true' by cuttings, and there are also some bud-sports which will not, as every gardener of experience knows. I will cite a single case of 'sporting' in bud offspring. One winter a chance tomato plant came up in one of my greenhouses. I let it grow, and it bore fruit quite unlike any other variety which I ever saw. There was no other tomato plant in the house. I propagated it both by seeds and cuttings. I had two generations of cuttings. Those taken directly from the parent plant, 'came true' or very nearly so; then a lot of cuttings from these cutting-grown plants was taken, making the second asexual generation from the original seedling. While most of the seeds 'came true,' few of these second cuttings did, and, moreover, they 'sported' into several very unlike forms—so much unlike that I had both red and yellow fruits from them. In respect to transmission of characters, then, bud- and seed-varieties are alike, because either class may or may not transmit its marks either by seeds or buds.

Finally, let me say, in proof of the further similarity of bud- and seed-variations, that each class follows the incidental laws of external resemblance which pertain to the other class. For instance, there are analogous variations in each, giving rise to the same kinds of variegation, the same anomalies of cut and colored foliage, of weeping branches, party-colored fruits and the like; and the number of similar variations may be as great for any ameliorated plant in the one class as in the other. The most expert observer is not able to distinguish between bud-varieties and seed-varieties; the only way of distinguishing the two is by means

of the records of their origins, and because such records of any varieties are few we have come to overlook the frequency of bud-variation and to ascribe all progressive variability in the vegetable kingdom to seeds or sex.

Whilst it is not my purpose to discuss the original sources of bud-variations, I cannot forbear to touch upon one very remarkable fact concerning reversions. It is a common notion that all bud-varieties are atavistic, but this position is untenable if one accepts the hypothesis, which I have here outlined, of the ontogenetic individuality of the phyton, and if he holds, at the same time, to the transforming influence of environment. It is also held by some that bud-varieties are the effects of previous crossing, but this is controverted by Darwin in the statement that characters sometimes appear in bud-varieties which do not pertain to any known living or extinct species; and the observations which I am about to recite also indicate the improbability of such influence in a large class of cases. The instances to which I call your attention are, I think, true reversions to ancestral types. Those of you who have observed the young non-blooming shoots of tulip-tree, sassafras and some other trees will have noticed that the leaves upon them often assume unusual shapes. Thus the leaves of sassafras often vary from the typical oval form to three-lobed and mitten-shaped upon the strong shoots. There are the most various forms on many tulip-trees, the leaves ranging from almost circular and merely emarginate to long-ovate and variously lobed; all of them have been most admirably illustrated and discussed recently by Holm in the proceedings of the National Museum. Holm considers the various forms of these *liriodendron* leaves to be so many proofs of the invalidity of the fossil species which very closely resemble them. This may be true, for there are probably no

specific names of organisms founded upon so fragmentary and scant material as those applied to fossil plants; and yet I cannot help feeling that some of these contemporaneous variations are reversions to very old types. I was first led to this opinion by a study of the sports in ginkgo leaves, and finding them suggestive of Mesozoic types. "This variation in leaf characters," I wrote at the time, "recalls the geologic history of the ginkgo, for it appears to be true that leaves upon the young and vigorous shoots of trees are more like their ancestors than are the leaves upon old plants or less vigorous shoots, as if there is some such genealogical record in leaves as there is in the development of embryos in animals." Subsequent observation has strengthened my belief in the atavistic origin of many of these abnormal forms, and this explanation of them is exactly in line with the characters of reversions in animals and in cultivated plants. It would, of course, be futile to attempt any discussion of the merits of the specific types proposed by palæobotanists, but in those cases, like the ginkgo, where the geologic types are fairly well marked, constant and frequent, and where the similar contemporaneous variations are rare, there is apparently good reason for regarding contemporaneous forms as fitful recollections of an ancient state; and this supposition finds additional support in the ginkgo, because the species is becoming extinct, a fact which also applies to the tulip-tree, which is now much restricted in its distribution. I am further reinforced in this view by Ward's excellent study of the evolution of the plane-tree, for, in this instance, it seems to be well determined that the geologic type has fairly well marked specific characters, and the auricular or peltate base upon contemporaneous leaves, which records the connection between the two, is sufficiently rare to escape comment. Various writers have remarked upon the

similarities of these occasional leaves to geologic types, but, so far as I recall, they regard them as remnants or vestiges of the ancient types rather than as reversions to them. There is this important difference between a remnant and a reversion. A remnant or rudiment is more or less uniformly present under normal conditions, and it should give evidence of being slowly on the decline; whilst a reversion is a reappearance of wholly lost characters under unusual or local conditions. Now, my chief reasons for considering these sports to be reversions is the fact that they occur upon the sterile and verdurous shoots, the very shoots which are most likely to vary and to revert because they receive the greatest amount of food supply, as Darwin has shown to be the case with independent plants. And I am therefore able to make still another analogy between phytons and plants, and to illustrate again the essential sameness of bud-variations and seed-variations.

III.

I now wish to recall your attention more specifically to the subject of asexual variation. I have shown that no two branches are alike any more than are any two plants. I have also cited the frequent occurrence of differences so marked that they are called bud-varieties or sports. Carrière enumerated over 150 of them of commercial importance in France, and, as nearly as I can estimate, there are no fewer than 200 named horticultural varieties grown at the present moment in this country which had a like origin. It is also known that there are a number of species in which seeds are practically unknown, and yet which run into many varieties, as the pineapple, banana and bread-fruit; and note, if you will, the great variations in weeping willows, a tree which never fruits in this country. In our gardens there are three or four varieties of

the common seedless 'top' onion, and I have been able, by treatment, to vary the root of the horse-radish, a plant which rarely, if ever, produces viable seeds in this climate; and there are variable seedless plants in our greenhouses. I might also cite the fact that most fungi are sexless, so far as we know, and yet they have varied into innumerable species. You will be interested in a concrete case of the apple. The Newtown Pippin, which originated upon Long Island, New York, has been widely disseminated by graftage. In Virginia it has varied into a form known as the Albemarle Pippin, and a New York apple exporter tells me that it is a poorer shipper than the Northern Newtown and is not so long-keeping. In the extreme Northwestern States the Newtown, while it has not been rechristened there, is markedly unlike the Eastern fruit, being much longer and bearing distinct ridges about the apex. Finally, in New South Wales, the ridges are more marked and other characters appear, and the variety is there known as the Five-crowned Pippin. This is not an isolated case. Most Northeastern varieties of apples tend to take on this elongated form in the Pacific Northwest, to become heavy-grained and coarse-striped in the Mississippi Valley and the Plains, and to take other characteristic forms in the higher lands of the South Atlantic States. This asexual variation is sometimes very rapid. An illustration came directly under my own observation (and upon which I have once reported) in the case of the Chilean strawberry. Within two years this plant, growing in my garden, varied or departed from its wild type so widely as to be indistinguishable from the common garden strawberry, which has been regarded by many botanists to be specifically distinct from the Chilean berry. This remarkable departure, which has enabled me, as I believe, to reconstruct the evolution of the garden strawberry, was one in

which no seedling plants were concerned. If all the common garden strawberries owe their origin to a like source—as I cannot doubt—then we have here a most instructive case of sexless evolution, but one in which the subsequent generations reproduce these characters of sexless origin by means of seeds.

This asexual modification is not confined to domesticated plants. Any plant which is widely distributed by man by means of cuttings or other vegetative parts may be expected to vary in the same manner, as much experiment shows; and if they behave in this way when disseminated by man they must undergo similar modification when similarly disseminated by nature herself. I need only cite a few instances of habitual asexual distribution of wild plants to recall to your attention the fact that such means of distribution is common in nature, and that in some cases the dispersion over wide areas is quite as rapid as by means of seeds; and some plants, as various potamogetons, ceratophyllums and other aquatics, are more productive of detachable winter buds and other separable vegetable organs than they are of seeds. The brittle willows drop their twigs when injured by storms of ice or wind, or by animals, and many of these cuttings take root in the moist soil, and they may be carried far down streams or distributed along lake shores; the may-apple and a host of rhizomatous plants march onward from the original starting point; the bryophyllum easily drops its thick leaves, each one of which may establish a new colony of plants; the leaves of the lake-cress (*Nasturtium lacustre*) float down the streams and develop a new plant while they travel; the house-leeks surround themselves with colonies of off-shoots, the black raspberry travels by looping stolons, and the strawberry by long runners; the tiger-lily scatters its bulb-like buds, and all bulbiferous plants spread quite as easily by their fleshy

parts as by seeds. Now all these vegetative parts, when established as independent plants, produce flowers and good seeds, and these seeds often perpetuate the very characters which have originated in the asexual generations, as we have seen in the case of many bud-varieties; and it should also be remarked that these phytons usually transmit almost perfectly the characters acquired by the plant from which they sprung. Or, to put the whole matter in a convenient phrase, there may be, and is, a progressive evolution of plants without the aid of sex.

Now, where is Weismann's germ-plasm? One of the properties of this material—if an assumption can receive such designation—is its localization in the reproductive organs or parts. But the phyton has no reproductive parts; or, if it has them, they are developed after the phyton has lived a perfectly sexless life, and possibly after generations of such life, in which it and its progeny may either have remained comparatively stable or may have varied widely, as the circumstances may have determined. If any flower, therefore, contains germ-plasm it must have derived it out of the asexual or vegetative or soma-plasm. And I will ask where the germ-plasm is in ferns. These plants are fertilized in the prothallial stage, and one brief sexual state is all that the plant enjoys, after which the sex-organs die and wholly disappear. The fern, as the layman knows the plant, is wholly asexual, and the spores are as sexless as buds; yet these spores germinate and give rise to another brief prothallial or sexual stage, and if there is any germ-plasm at all in these fleeting sexual organs it must have come from the sexless spores. It is interesting to note, in this connection, this bud-variation is as frequent in ferns as in other plants. Or, if the Weismannians can locate the germ-plasm in all these instances, pray tell us where it is in the myriads of sexless fungi! There is no such thing as continu-

ous localization of germ-plasm in plants. Weismann himself admits that the germ-plasm must be distributed in 'minute fraction' in all 'somatic nuclei' of the begonia leaf, because that leaf is capable of giving rise to new plants, by means of cuttings, and all the plants may produce good flowers, which, if they are sexual at all, are so only by virtue of containing some of this elusive germ-plasm. There is no other way for these plants to get their germ-plasm, except from the somatic leaf from which they came. It would seem that this admission undermines the whole theory of the localization of the germ-plasm in plants, for one exception in the hypothesis must argue that there are others. But not so! There are no insurmountable difficulties before the Weismannians. It is the begonia which is the exception, for it is abnormal for plants to propagate by any such means! The answer which has been made to this statement is that very many plants are propagated asexually by horticulturists, and that all plants can probably be so propagated if there were any occasion for the effort. This answer is true; but the philosophical answer is that every phyton is an autonomy, and that the mere accident of its growing on the plant, in the soil, or in a bottle of water, is wholly aside from the point, for wherever it grows it lives at first a sexless life, it has an individuality, competes with its fellows, varies to suit its needs, and is capable, finally, of developing sex.

Another fundamental tenet of Weismannism is the continuity of the germ-plasm; the passing down from generation to generation of a part or direct offspring of the original germ-plasm. Now, if there is any continuity in plants, this ancestral germ-plasm must be inextricably diffused in the soma-plasm, as I have said, for every part or phyton of these plants, even to the roots and parts of the leaves, is able to produce sexual parts or germ-plasm. And if

this germ-plasm is inextinguishably associated with every cell of the plant body, why does it not receive and transmit all incident impressions upon the plant? Why should acquired characters impress themselves upon the soma-plasm and not upon the germ-plasm when this latter element is contained in the very nuclei, as Weismann admits, of somatic cells? If the theory of the continuity of the germ-plasm is true for plants, then acquired characters *must* be transmitted! The only escape from this position is an arbitrary assumption that one plasm is impressionable and that the other is not; and, now, that we can no longer relegate the germ-plasm to imaginary deep-seated germ-cells, such an assumption is too bold, I think, to be suggested.

The entire Weismannian hypothesis is built upon the assumption that all permanent or progressive variation is the result of sexual union; but I have shown that there is much progressive variation in the vegetable kingdom which is purely asexual, and, for all we know, this type of modification may proceed indefinitely. There is no doubt of the facts; and the only answer to them which I can conceive the Weismannian to make is that these progressive variations arise because of the latent influence of ancestral sexual unions. In reply to this I should ask for proofs. Hosts of fungi have no sex. I am not convinced but that there may be strains or types of some species of filamentous algæ and other plants in which there has never been sexual union, even from the beginning. And I should bring, in rebuttal, also, the result of direct observation and experiment to show that given hereditary asexual variations are often the direct result of climate, soil or other impinging conditions. As a matter of fact, we know that acquired characters may be hereditary in plants; if the facts do not agree with the hypothesis, so much the worse for the hypothesis. Unfortunately,

the hypothesis is too apt to be capable of endless contractions and modifications to meet individual cases. I sometimes think that we are substituting for the philosophy of observation a philosophy of definitions.

I have, therefore, attempted to show :

1. That the plant is not a simple autonomy in the sense in which the animal is.

2. That its parts are virtually independent in respect to (a) propagation (equally either when detached or still persisting upon the parent plant), (b) struggle for existence amongst themselves, (c) variation, (d) transmission of their characters, either by means of seeds or buds.

3. That there is no essential difference between bud-varieties and seed-varieties, apart from the mere fact of their unlike derivation; and the causes of variation in the one case are the same as those in the other.

4. That all these parts are at first sexless, but finally may or may not develop sex.

5. That much of the evolution of the vegetable kingdom is accomplished by wholly sexless means.

There is, then, a fundamental unlikeness in the ultimate evolution of animals and plants. A plant, as we ordinarily know it, is a colony of potential individuals, each one of which, save the very first, is derived from an asexual parent, yet each one may, and usually does, develop sex. Each individual is capable also of receiving a distinct or peculiar influence of the environment and struggle for existence, and is capable, therefore, of independent permanent modification. It is not possible, therefore, that there is any localization or continuity of a germ-plasm in the sense in which these conceptions are applied to animals; nor is it possible for the plant as a whole to make a simple functional adaptation to environment. If there is a continuity of germ-plasm in plants this element must of necessity be intimately associated with every par-

ticle of the plant body, even to its very periphery, and it must directly receive external impressions; and this concept of Weismann—the continuity of the germ-plasm—becomes one of the readiest means of explaining the transmission of acquired characters. All these conclusions prove the unwisdom of endeavoring to account for the evolution of all the forms of life upon any single hypothesis; and they illustrate with great emphasis the complexity of even the fundamental forces in the progression of organic nature.

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CURRENT NOTES ON PHYSIOGRAPHY (III.).

WOODWARD'S SMITHSONIAN GEOGRAPHICAL TABLES.

'THE average geographer,' to whose needs Professor Woodward has attempted to suit the recent volume of *Geographical Tables* issued by the Smithsonian Institution, should certainly feel highly complimented by this tribute to his quality. The volume contains, among many other matters, tables of coördinates for the projection of polyconic maps, lengths of a degree on parallels and meridians at different latitudes, areas of latitude-and-longitude, quadrilaterals of different dimensions and at different latitudes, adopted dimensions of the earth's spheroid, value of gravity at the earth's surface, and salient facts of physical geodesy. The latter heading includes the area of the earth, of oceans and continents, and the average heights of continents and depths of oceans, taken from Helmert's *Geodäsie*. For areas the continents are given 51,886,000, and the oceans 145,054,000 square miles. The mean depth of the oceans is placed at 3,440 meters. The mean heights of the continents are given as follows: The earlier results of Humboldt's, still often quoted, and the later ones of Penck (*Morphologie der Erdoberfläche*, 1894) being added for comparison.