PART I

PANGENESIS

A. The Nature of Hereditary Characters

CHAPTER I

THE MUTUAL INDEPENDENCE OF HEREDITARY CHARACTERS

§ 1. *The Combination of Specific Characters Out of Hereditary Characters*

Among the many advantages which have lent such a prominent significance to the theory of descent in the investigation of living nature, the shattering of the old conception of species occupies an important place. Formerly every species was regarded as a unit and the totality of its specific attributes as an indivisible concept. Even the latest theories on heredity accept this concept as one that does not require any further analysis.

But if the specific characters are regarded in the light of the theory of descent it soon becomes evident that they are composed of single factors more or less independent of each other. One finds almost every one of these factors in numerous species, and their varying groupings and combinations with less common factors causes the extraordinary diversity in the organic world.

Even the most cursory comparison of the various organisms leads, in this light, to the conviction of the composite nature of specific characters. The power to produce chlorophyll and, by means of this, in light, to decompose carbon dioxide, is evidently to be regarded as a property which, in great measure lends to the botanical world its peculiar stamp. This power, however, is lacking in many groups throughout the system, and therefore is by no means inseparably connected with the other factors of plant nature.

Other factors are the predispositions *(Anlagen)* which enable many species to produce definite chemical compounds. First of all, the red and blue coloring matter of flowers, then the different tannic acids, the alkaloids, etherial oils, and numerous other products. Only a few of these are limited to a single species, many recur in two or more species, which are often systematically far apart. There is no reason for supposing that, in every individual case there is a different mode of origin for the same compound; rather it is obvious that essentially the same chemical mechanism underlies the same process, wherever we find it.

In a similar manner we must also accept as possible the analysis of the morphological characteristics of the species. It is true that morphology is not by any means so far advanced that such an analysis could be carried out in every individual case. But the same leaf-form, the same leaf-edge, coarsely or delicately notched, recur in numerous species, and even the customary terminology teaches us that the configurations of all the various leaf-forms are composed of a comparatively small number of simple characters.

It would be superfluous to accumulate instances which are easily accessible to every one, and it is only a question of thoroughly familiarizing one's self with these ideas, so that the synthesis of the whole out of its component parts is clearly recognized. It will then be seen that the character of each individual species is composed of numerous hereditary qualities, of which by far the most recur in almost innumerable other species. And even if, in the building up of any single species, such a large number of these factors is necessary that we almost shrink from the consequences of an analysis, it is clear, on the other hand, that, for the building up of the sum total of all organisms, there is required a rather small number of individual hereditary characters in proportion to the number of species. Regarded in this way, each species appears to us as a very complex picture, whereas the whole organic world is the result of innumerable different combinations and permutations of relatively few factors.

These factors are the units which the science of heredity has to investigate. Just as physics and chemistry go back to molecules and atoms, the biological sciences have to penetrate to these units in order to explain, by means of their combinations, the phenomena of the living world.

Phylogenetic considerations lead to the same conclusions. Species have gradually been evolved from simpler forms, and this has taken place by the addition of more and more new characteristics to those already existing. The factors which compose the character of a single species are, therefore, in this sense, of unequal age; the characteristics of the larger groups being in general, older than those of the smaller systematic divisions. But the very consideration that the characteristics have been acquired singly or in small groups, shows us again from another side their mutual independence.

It is a striking, yet by far insufficiently appreciated fact that frequently, in distant parts of the genealogical tree, the same character has been developed by wholly different species. Such "parallel adaptations" are extremely numerous, and almost every comparative treatment of a biological peculiarity shows us examples thereof. The insect-eating plants belong to the most varied natural families, yet they all possess the power of producing from their leaves the necessary mixture of an enzyme, and of an acid which is needed for dissolving protein bodies.[1] The agreement, emphasized by Darwin, of this mixture with the gastric juice of the higher animals justifies even the supposition that those plants and the animal kingdom have some hereditary qualities in common.

The indigenous creeping and climbing plants, the tropical lianas, the tuberous and bulbous plants, the fleshy, leafless stems of the Cactaceæ and Euphorbiaceæ, the pollinia of the Orchidaceæ and Asclepiadaceæ, and numberless other instances show us parallel adaptations. Very beautiful pictures are furnished on the one hand by the desert plants, which all have to protect themselves in some way against the disadvantages of evaporation, and whose anatomical relations have been so thoroughly described by Volkens.[2] On the other hand are the ant-plants, into the adaptations of which to harmful and useful species of ants Schimper has given us an insight.[3]

Everywhere we see how one and the same hereditary character, or definite small groups of the latter, can combine with other most diverse hereditary characters, and how, through these exceedingly varied combinations, the individual specific characters are produced.

[1]This statement is now known to hold true only in the case of *Nepenthes* (Vines, *Ann. Bot.* **11**: 563. 1897. **12**: 545. 1898) and of *Drosera* (see Fr. Darwin's articles). Schimper found no proteolytic enzyme secreted by Sarracenias. (*Bot. Zeit.* **40**: 225. 1882). His results were confirmed by Miss Robinson, but she demonstrated the secretion, by *Sarracenia purpurea,* of a starch-digesting enzyme. (*Torreya* **8**: 1908). *Tr.*

[2]Volkens, G. *Die Flora der Aegyptisch-Arabischen Wüste.*

[3]Schimper, A.F.W. Die Wechselbeziehungen zwischen Pflanzen und Ameisen im tropischen Amerika. *Bot. Mittheil. aus den Tropen.* Band I, Heft 1, 1888.

§ 2. *The Similarity of the Differences Between Species and Between Organs*

The comparison of species with the organs of a single individual leads us to quite similar conclusions as does the comparison of species with each other, for the differences between the organs can be traced back, in the same way, to various combinations of individual hereditary qualities.

Even the simplest observation teaches us this. Just as chlorophyll is lacking in some species it is also lacking in single organs and tissues of higher plants. The red coloring matter of flowers is limited to certain plant species, and in these again to definite organs. Tannic acid, etherial oils, and like substances, where present, show a local distribution. Calcium oxalate is lacking in most ferns and grasses, and on the other hand in the roots of many species rich in calcium. The same is true, apparently, of morphological attributes. I need not cite examples, for it will certainly be granted that a very close agreement exists between the manner in which the organs of a single plant differ from each other and the distinction between different species. Both depend upon varying combinations and a varying selection from a great range of given factors.

A series of phenomena, which we may summarize under the name *dichogeny*, leads to similar conclusions. I mean all those cases where the nature of an organ is not yet decided during the early stages of its development, but may yet be determined by external influences. Thus, under normal conditions, the runners of the potato-plant form at their tips the tubers, but on being exposed to light, or when the main stem has been cut off, they develop into green shoots. By severing the stems, the rhizomes of *Mentha, Circaea,* and many other plants, can be made into ascending stems, and the transformations which the thick almost resting rhizomes of *Yucca* undergo after such treatment are remarkable. In a similar manner Goebel has succeeded in causing the rudiments of bracts to develop into green leaves,[4] and Beyerinck[5] observed even the transformation of young buds of *Rumex Acetosella* into roots.

In such cases it is clear that the possibility of developing in either of two different directions is dormant in the young primordia. For this very reason I should like to apply the name *dichogeny* to this phenomenon. And it evidently depends upon external influences what direction is taken. Therefore a selection must take place from among the available hereditary characters of the species, and this selection may be influenced by artificial interference. For the theory of hereditary characters such experiments are therefore of the highest interest.

Here are naturally included the phenomena of bud-variation. Many of these are cases of atavism. Let us select an example. In plants with variegated leaves one frequently observes single green branches. Since the variegated plant is descended from green ancestors, this case is regarded as a reversion. The variegated individual evidently still possessed the characteristics of the green ancestor, though in a latent condition. During the bud-formation it split its entire character, but in such a way

[4]Goebel, K. Beiträge zur Morphologie und Physiologie des Blattes. *Bot. Zeit.* **40**: 353. 1882.

[5]Beyerinck, M. W. Beobachtungen und Betrachtungen über Wurzelknospen und Nebenwurzeln. *Veröffentl. Akad. Wiss.* Amsterdam, pp. 41-41. 1886. Cf. also Tafel I, Fg. 9.

that in one branch the variegated combination predominated, in the other one the green color.

As a further illustration of bud-variation, I may mention the nectarines. These are hairless peaches, which originated in several varieties, and in some of them repeatedly through bud-variation. This fact can be explained only by saying that the possibility of producing hairy fruit can become lost in single branches, easily and independently from all other characters, or at least become latent.

The characteristics which originate through bud-variation are usually preserved by propagation by means of grafts, cuttings, et cetera, and, in isolated cases, are even constant from seed. New varieties may therefore be produced in this manner. And, since we regard varieties as incipient species, this consideration is further evidence of an accordance in the differences between species and between organs.

Naturally included with bud-variations is the consideration of monoecious plants, for the latter agree with the former in the fact that different branches allow different qualities to develop. In the young plant the sexes are not yet separated, and frequently for a long time the possibility of producing both is retained. If this process, however, is started, it is accomplished by a kind of separation: one bud develops into a staminate, the other into a pistillate flower. Or staminate and pistillate inflorescences are produced, or whole branches are predominantly pistillate and others staminate. The specific character was therefore present in the young plant as a whole, but in a latent state, and, in order to manifest itself, it had to split into its two chief parts.

The formation of organs, bud-variation, and the production of staminate and pistillate branches in monoecious plants are therefore due to a kind of splitting. The potentialities, united in the young plant, separate from each other in order to be able to unfold. And the grouping of the hereditary characters in the separate branches and organs shows a very great agreement with the combination of such characters to form the various specific marks of related organisms.

§ 3. *The Similarity Between Secondary Sexual Characters and Specific Attributes*

Continuing in a similar manner as in the previous paragraph we will now take into consideration the secondary sexual characters, for they lead to exactly the same conception of a specific character.

This is most clearly seen in those cases where the two sexes of one species, upon being first discovered have been described as different species.[6] But otherwise, too, the secondary differences between the individuals of both sexes are of the same order as the differences between the various species in the same and in allied genera.

It is the same with those plants which bear flowers on various individuals, the sex-organs of which exhibit constant differences, the so-called cases of heterostyly. In the Primulaceæ we distinguish one form with long and another with short style; in some species of flax there occur three different forms of flowers in different individuals.

Although here the individuals belonging to two or three different groups of the same species are different

[6]*Catasetum tridentatum* has three different forms of flowers, which were formerly considered to belong to three different genera: *Catasetum, Monachanthus* and *Myanthus.* de V., 1909.

neither according to sex nor to generation, nevertheless they are distinguished by attributes which are as constant and of the same order as the specific attributes taken from the same organs in allied genera.

In the way of a supplement I will consider, in this connection, the alternation of generations, because here also the differences between the physiologically non-equivalent individuals, belonging to different generations, are of the same order as the specific characters. This we are taught by the Uridineæ and the Cynipideæ, and all those cases where the presence of an alternation of generations was discovered only after the single forms had been described as species, and had been classified with different genera and families of the system. And even to-day it is impossible to prove morphologically that two forms belong together; experimental cultures alone can decide this question. The successive alternating generations cannot be reduced to the same primary form, for each of them compounds its characters by means of a different selection from the available hereditary endowments of the species.

In summing up the result of this paragraph and the two preceding ones, we find that every thorough consideration of a specific character, and every comparison of this with other characters, leads us to regard the former as a mosaic, the component parts of which can be put together in various ways.

§ *4. The Variation of the Individual Hereditary Characters Independently of One Another*

A comparative consideration of the organic world convinced us that the hereditary characters of a species, even if connected with each other in various ways, are yet essentially independent entities, from the union of which the specific characters originate. Now let us see whether or not this conclusion is supported by experiment.

For this purpose let us turn to experiments on the formation of varieties, especially to those which have been made on a large scale by plant breeders. They teach us that almost every character may vary independently from the others. Numerous varieties differ from their ancestral form, in only one attribute, as, for example, the white sports of red-flowered species. The red color changes in the corolla through all gradations, into white; it may be lacking or it may be present not only in the blossoms, but also in the stems and leaves, and can be developed to every conceivable degree, without any other hereditary quality being necessarily involved in the variation. In the same way the hairiness, the arming with thorns and spines, the green color of the leaves, may each vary by itself, and even disappear completely while all other hereditary characters remain quite unchanged. Frequently some characters that belong together vary in groups without exercising any influence on the other groups. Thus an increase in the number of petals is not rarely accompanied by a petal-like development of the calyx or the bract-leaves, while otherwise the plant remains normal. I have cultivated a *Dipsacus sylvestris,* which offers all conceivable diversities in the arrangement of the leaves, and which is otherwise constant in thousands of specimens. The *Papaver somniferum polycephalum* deviates only in the transformation of numerous stamens into carpels. It is the same for the cultivated *Sempervirum tectorum.* Such instances are so numerous, in the plant kingdom as well as in the animal kingdom, that the independent varying of single characteristics forms the rule, while the combined variation of several of them is the exception. It is true that in most cases it cannot be decided whether the given attribute is determined by a single hereditary character or by a small group of them.

On the other hand an accumulation of several variations in one race can easily be accomplished, and it occurs quite commonly in cultures as well as in nature. But the cases which were sufficiently well controlled and described, usually show that the single variations have not evolved simultaneously, but one after another, and this is sufficient to prove their independence.

Such an hereditary character, isolated from the rest, can now become the object of experimental treatment. Through suitable selection it may be gradually strengthened or weakened, and at the will of the breeder it may be brought into a certain relation to the other unchanged characters. The red color of the copper-beech has been so much intensified that even the cell-sap in the living cells of the wood became intensely red. The doubling of flowers frequently leads to a complete disappearance of the sexual organs. And in numerous instances only those organs change which are subjected to selection while the others remain unaffected by it. The adaptation of the cultivated plants of agriculture to the needs of man, and of the horticultural ones to his æsthetic sense, demonstrates this to us in the clearest manner.

Experimental treatment further leads to the study of the influence of external circumstances on the unfolding of hereditary characters. Here again these prove themselves to be factors of which each may vary independently from the others. Young varieties especially are objects for study, and all those which have not as yet been sufficiently fixed, and in which, therefore, external influences will still play a prominent part in answering the question as to whether a given seed will produce a true or an atavistic individual. Rimpau and others have taught that with a given kind of seed disturbances and interruptions of growth exercise a powerful influence on the number of specimens that bear seed in the first year.[7] And in horticultural and teratological literature one finds scattered numerous data from which the importance of external influences generally is clearly evident. To the experimental investigator there is here opened a large and almost untrodden field. Theoretically the chief task will consist in isolating as much as possible the variations of the hereditary characters in order to obtain, in this way, a knowledge of the individual factors of the respective character.

The variations which we observe in nature frequently appear to us as if they had suddenly sprung into existence, and the same is true of cultures on a small scale, or when the single indivduals are not completely under control.

However, experience with cultivated plants, during the first years after the beginning of their cultivation, teaches us that the deviations often develop but slowly, and that the modifying influences, as a rule, have to operate through several generations before they can accumulate their effect in such a manner that it becomes evident.[8] The facts with reference to this, collected by Darwin, give the impression that the new characters at first arise only in a latent state, and in this condition grad-

[7]Rimpau, A. W. Das Aufschiessen der Runkelrüben *Landwirtschaft. Jahrbücher.* **9**: 191. 1880.

[8]On this point compare Darwin, *The Variation of Animals and Plants under Domestication.* Ed. 2. **2**: 39. 1875.

ually gain in strength, until they finally reach the stage necessary to make them visible. Here again it must therefore be assumed that every hereditary character is miscible to any extent with the others.

The independence of the hereditary characters is most beautifully shown in atavism. A character may remain latent through a number of generations while all the others unfold normally. From time to time it appears again, mostly without exercising any kind of influence on the other characters. We do not know what external circumstances condition this reappearance; in all probability they do not act simply on the atavistic individuals, but we must conceive that the given potentiality is always latent in the others, only it is very fluctuating in its strength. To us only the crests of the highest waves are visible.

To all appearance such qualities can be transmitted through a long series of generations, from one generation to another. Their existence can be reckoned by millenniums in those cases where they are at least as old as the species itself. I mean the cases of reversion to the ancestors of the species, of which the zebra-like stripes of the horse form such a well-known instance.[9] We have a similar illustration in the *Primula acaulis* var. *caulescens*, which occurs from time to time in the field as a quite isolated specimen among thousands of non-umbellate plants, and then forms an inflorescence quite similar to that of the most nearly allied umbellate species. Cultivation has taken possession of this more richly flowering variety, and has put it on the market in many nuances of color.

I should not close this section without having pointed

[9]Darwin, *loc. cit.* 1: 59.

out one phenomenon which greatly complicates the study of hereditary characters. I refer to the circumstance, already repeatedly alluded to, of their being commonly united in smaller and larger groups which behave like units, the single members of the groups usually appearing together. We see this in the staminate and pistillate flowers and inflorescences of monoecious plants, in the described cases of bud-variation and dichogeny. The sexual characters of various individuals and the difference between the alternating generations of the same species teach us the same thing.

This combination of the individual characters into groups is therefore quite general, although it occurs in all degrees, and although some hereditary characters, as for instance the power of assuming a red color, do not unite, as a rule, into a group with certain others. It is recognized most clearly in those cases of the formation of groups of green bracts instead of flowers, caused by aphids, phytopters, and other parasites, where the stimulus calls forth a whole series of characters that ordinarily develop in other parts of the plant.

Every theory of heredity has to take into account this combination of the hereditary characters into larger and smaller groups, and different authors, like Darwin and Nägeli have strongly emphasized this point. But right here lies a great difficulty which interferes with a working out of the theory in detail, for in many cases it will obviously be extremely difficult to decide whether one is dealing with a single hereditary character or with a small group of them. There is here a large field for morphological analysis which awaits working up.

§ 5. *The Combination of Hereditary Characters*

Hereditary characters can be combined to any extent and in any proportion. This is shown in variegated leaves and striped flowers, where the result of this combination, after corresponding splitting, is almost directly demonstrated to us. Almost endless is the diversity of pattern of variegated leaves, frequently on the same plant, or at least on the different individuals of one and the same crop. Striped flowers, according to Vilmorin, arise through partial atavism from old white-flowering varieties of red or blue species.[10] Young varieties usually revert by leaps to the ancestral form, while the older ones do so by steps, through the appearance of isolated stripes of the original color on the white back-ground. It is as if the color potentialities were already too much weakened to tint the whole corolla in one effort. The descendents of the first striped flowers, however, soon form broader stripes, and finally return, after a few generations, [at least in some specimens,[11]] to the uniform color of the ancestral form.

Extremely peculiar are those cases where hereditary potentialities, which in the active state necessarily exclude each other, occur together in a latent state. Instead of giving a long enumeration of many cases, I prefer to describe a well-known case of variability, and select for the purpose the arrangement of leaves in whorls.

Two-ranked whorls, the leaves of which stand crosswise over each other on the successive nodes, belong to the best and most constant characteristics of entire natural families. Less frequent are the cases of three- and more-ranked whorls. Quite frequently, however, one

[10]Vilmorin, L. Lévêque de. *Notices sur l' améliorations des plantes par le semis*. pp. 39-41. 1886. (According to modern views the stripes are due to a separate character. de V. 1909.)

[11]Matter in the body of the text in brackets has been introduced anew into the translation by the author of the original. *Tr.*

species will change from its normal type into another form of whorl, and in numerous plants with decussate leaves, single branches with three- and more-ranked whorls have been observed. The Fuchsias and the Weigelias of our gardens, are common examples. The transitions from one number in the whorls to the other usually take place by leaps, in such a way that the whole shoot springing from one bud is alike in this respect; however, branches with another number in their whorls will frequently develop from its terminal bud or its lateral buds. More rarely a shoot will change, during its development, from one number to another, as is the rule, for example, in *Lysimachia vulgaris.* Intermediate forms between two- or three- and four-ranked whorls are exceedingly rare, although from our present knowledge, they may develop quite readily, and have actually been observed from time to time in most plants with whorled leaves.[12] I mean those whorls in which one leaf is more or less deeply split at its apex, while the mid-vein forks. This splitting occurs in all conceivable degrees and leads to a complete doubling in those leaves which bear two blades on one cleft petiole. Consideration of numerous examples gives the impression that the single whorl-forms are antagonistic to each other, and that each tries to exclude the other. It is rare that they do not succeed in this effort, and then we get the above mentioned leaves with the forked mid-vein, the complete series of transition of which, from one leaf to two leaves has been figured and described by Delpino.[13]

Therefore, even such qualities, which in the developed plant exclude each other, are miscible, apparently

[12]Cf. Delpino, F. Teoria generale della Fillotassi. *Atti R. Univ. Genova* 4: 197. 1883.

[13]*Loc. cit.* p. 206, Taf. LX, Fig. 60.

without difficulty, in the latent state. In truth, the principle illustrated by this example holds good also in the phenomena of monoecism and dioecism, of the di- and trimorphism of flowers, and indeed, throughout the entire range of organ-formation. Everywhere we find characteristics which cannot exist simultaneously in the same organ, and yet must be associated in a latent state during its youth.

In summarizing briefly what has been said, we see that experiments and observations on the origin and fixing of variations teach us to recognize hereditary characters as units with which we can experiment. They teach us further that these units are miscible in almost every proportion, most experiments really amounting merely to a change in this proportion.

The above considerations are verified in a striking manner by experiments in hybridization and crossing. In no other connection does the concept of a species as a unit made up of independent factors stand forth so clearly. Everyone knows that the hereditary characters of two parents may be mixed in a hybrid. And the excellent experiments of many investigators have taught us how, in the descendents of hybrids, an almost endless variation can usually be observed, which is essentially due to a mixing of the characteristics of the parents in a most varied manner.

The hybrids of the first generation have quite definite characteristics for each pair of species. If one produces a hybrid of two species, which previous investigators have already succeeded in crossing, he can, as a rule, rely on the description given of it tallying exactly with the newly produced intermediate form. If the hybrid is fertile without the help of its parents, and if its progeny are grown through a few generations in thousands of specimens, one can almost always observe that hardly any two are alike. Some revert to the form of the pollen-parent, others to that of the pistil-parent; a third group occupies a central position. Between these are placed the others in the most motley variety of staminate and pistillate characteristics and in almost every gradation of mutual inter-mixture.

Many and prominent authors have pointed out the *significance of hybrids for establishing the nature of fertilization.* With the same right we may use them in trying to penetrate into the mystery of specific character. And then they clearly prove to us that this character is fundamentally not an indivisible entity. The characteristics of a hybrid (of the first generation) are as sharply defined and as constant, and on the whole of the same order as those of the pure species, and the frequent specific name, *hybridus,*[14] might go to prove that even the best systematists felt this agreement.

Kölreuter, Gärtner, and others have combined in one hybrid two, three, and more species, and there is no reason why any other than a purely practical limit should be put to this number, and that, in fact, there should not be combined in one hybrid characteristics which have been taken from an unlimited series of allied species. But this is of small importance, the chief point being the proposition that the character of a pure species like that of hybrids, is of a compound nature.

Crossings of varieties of the same species belong, especially in horticultural practice, to the most common operations. Ordinarily the object pursued is simply that of producing intermediate forms. Not infrequently,

[14]E. g. *Papaver hybridum* L., *Trifolium hybridum* L.

however, one desires to impart single definite qualities to one variety and he derives these from another variety, sometimes even from another species. Hardening against winter-frost has frequently been transmitted in this manner from one form to another. Carriére[15] cites instances of Begonias which, through crossing with a variety of another species with variegated leaves, have been made varigated without having their other qualities changed. The conviction is really quite general in horticultural practice that, by crossings, one may combine the characters of varieties at will, and thus improve his races according to his needs in many as well as in individual desirable points.

§ 6. *Cross- and Self-fertilization*

In addition to the arguments dealt with in the preceding paragraph, which gives us the results of experiments in crossing and hybridization, we will now consider normal fertilization and see to what extent, in this domain, the facts support our conception of the mutual independence and miscibility of hereditary characters.

To fathom the meaning of fertilization is one of the most difficult problems of biology. The numerous adaptations of this process to the most varied conditions of life, and the powerful influence which it has exercised on the differentiation of species, especially through the development of the secondary sexual characters, threaten always to mislead us, and to make us mistake its essential nature through its later acquired significance. Here, as in so many cases, the conditions in the plant kingdom are clearer

[15]Carrière, E. A. *Production et fixation des variétés,* p. 22. 1865. Other examples are given by Verlot, *Sur la production et la fixation des variétés.* pp. 46 and 65. 1865. Cf. also Darwin, *loc. cit.* **2**: 73.

and simpler than in the animal kingdom, in which especially the exclusive limitation of propagation of the higher animals to the sexual method makes us only too easily over-estimate the significance of this process. To this must be added the fact that, for the vegetable kingdom, quite an unexpected light has been thrown on the nature of this process through the exhaustive comparative study of the significance of cross- and self-fertilization, for which we are indebted to Darwin.

Darwin's experiments have taught us that the essence of fertilization consists in the mixing of the hereditary characters of two different individuals.[16] Self-fertilization, which takes place so readily in the vegetable kingdom, and is so easily accomplished experimentally, has not by any means the same significance. From seeds obtained in the last named manner the individuals produced were always weaker in Darwin's experiments than those obtained in a crop from crossed flowers. The first ones were smaller, with less profuse branching, flowering less abundantly and less constantly, and accordingly they bore less seed. Crossing two flowers of the same plant was more deterimental than the pollination of the flowers with their own pollen.

Even the crossing of different individuals was not sufficient to keep the species normal when it was cultivated year after year in the same bed, and protected from being fertilized by specimens of a different origin. The whole colony deteriorated steadily and distinctly in the course of a few years; not only did the plants become smaller and weaker, but their individual differences decreased so much that they resembled each other almost completely. A

[16]Darwin, *Origin of Species.* 6 Ed., pp. 76-79, and *Cross and Self Fertilization in the Vegetable Kingdom.* 1876.

single cross, however, of such a colony with individuals of another origin restored the original vigor.

The process of fertilization, in its essence, does not consist, therefore, in the union of two sexes, but in the *mixing of the hereditary characters of two individuals of* different origin, or at least of such as have been subjected to different external conditions. Therefore, a difference in hereditary characters is obviously a condition for attaining the full advantage of fertilization; this difference, however, must have been acquired in the last instance through a life under different influences.

Let us regard the individual hereditary factors as independent units, which can be combined with each other in different proportions into the individual character of a plant. Let us further assume that their relative increase or decrease depends on external influences. Evidently there is then a great probability that, under similar external conditions, the same factors will deteriorate in different individuals, while under different conditions this fate will befall other factors in every individual. Thus, *on crossing the plants of the same bed only, the individual* deviations of the same kind are strengthened; the weakened factors are therefore made still weaker. But if we cross individuals of the most different culture possible, the differences in the individual factors are clearly balanced, at least in part; and this the more so, the more numerous the specimens which deviate from each other, and which are used for the crossing.

It is well known to plant breeders that luxurious conditions which are varied as much as possible lead to an accumulation and increase of individual differences, while simple and uniform circumstances make them disappear gradually, and thus further the uniformity of all specimens. The first method is applied in improving races, the latter in fixing newly acquired varieties.

To maintain a species with the required proportion of all its hereditary factors, only an occasional crossing is necessary. It need not precede every generation. Where sexual generations alternate with asexual ones, as in the gall-fly, and even where the latter occur in the majority, as in many aphids, this is clearly seen.

With bees the fertilized eggs become females, the unfertilized ones males. But since every male descends necessarily from a female that originated through fertilization, it evidently profits sufficiently by the advantages of an occasional crossing. The aphids, in which the male as well as the female originate parthenogenetically, teach us that here we have to do not with fundamental relations, but with special adaptations.

The never-opening, so-called cleistogamous flowers, the numerous devices for insuring self-fertilization in flowers in case they are not visited by insects, and the almost unlimited use of vegetative multiplication in plants, all serve to teach us that an occasional fertilization is all that is necessary for the normal preservation of the species. That in higher animals every individual originates in the sexual way, is therefore obviously only a special adaptation.

In summarizing the result of these considerations, we may say that the true essence of fertilization consists in mixing the hereditary characters of the different individuals of a species. Hybrids have taught us how we are to conceive this co-mingling. There is no doubt that the process of mixing is, in principle, the same in both cases. And just as Wichura[17] succeeded in producing hybrids

[17]Wichura, Max. *Bastardbefruchtung im Pflanzenreich erläutert an den Bastarden der Weiden.* Breslau, 1865.

from six different kinds of willows, so should it be possible to combine, by crossing, the hereditary qualities of several individuals into one.

In the preceding paragraphs we have seen how the single hereditary characters occur as independent units in the experiments of hybridization and crossing, and how they can be attained in almost every degree. In the same way, evidently, must we think of those units as independent in the ordinary process of fertilization as well.

§ 7. *Conclusion*

Seemingly elementary, the specific character is actually an exceedingly complex whole. It is built of numerous individual factors, the hereditary characters. The more highly differentiated the species, the higher is the number of the component units. By far the most of these units recur in numerous, many of them in numberless organisms, and in allied species the common part of the character is built up of the same units.

On trying to analyze species into these individual factors, we are confused by their number, which, in the higher plants and animals reaches probably into the thousands. If, however, we regard the entire world of organisms as the subject of our analysis, then the total number of hereditary characters which is needed for the building up of all living beings, is indeed large in itself, but, in relation to the number of species it is small. In that limited sphere our method of investigation leads apparently only to complications, but, on the whole, it evidently leads the way towards a very considerable simplification of the problems of heredity.

The hereditary factors, of which the hereditary characters are the visible signs, are independent units which may have originated separately as to time, and can also be lost independently from one another. They can be combined with each other in almost every proportion, every individual character from complete absence through all gradations being capable of attaining the highest development. Frequently the conditions are so unfavorable for some of them that they cannot manifest themselves at all, and so remain latent. In this condition, they may either persist for thousands of generations, or they may appear in every generation during the development of the individual from the fertilized egg, in which they are nearly all latent.

The hereditary factors compose the entire specific character; there is no separate basis to which they are attached.

Although independent to the degree that each, of itself, can become weaker and even disappear completely, they are yet, as a rule, united into smaller and larger groups. And the condition is such that, when external influences, such as a stimulus to gall-formation, bring a definite character into dominance, the entire group to which it belongs is usually set into increased activity.

Independence and miscibility are therefore the most essential attributes of the hereditary factors of all organisms.

To find a hypothesis which will make these characteristics more comprehensible to us, is, according to my opinion, the chief problem of every theory of heredity.