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Fred C. Werkenthin
Iowa State College

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FRED C. WERKENTHIN

The paper by Prof. Werkenthin on History of Plant Breeding was one of the assigned topics in the course given at Iowa State College on the History of Botany. The subject matter is so admirably treated that it has seemed wise to publish this as a posthumous paper. It was the last paper prepared by him, finished only a few weeks before he was taken sick. — L. H. Pammel.

Since there is a close relation between the mode of reproduction and the method of breeding a plant, a knowledge of sexuality was, therefore, almost a necessity before it was possible to develop the art of breeding.

Existence of fruit-bearing and sterile trees of the date palm was known to the people of Egypt and Mesopotamia in early times and records of artificial pollination as early as 700 B.C have been found. *Kazwini,* the Arabic writer on natural history, says of the date, "It is created out of the same substances as Adam, and is the only tree that is artificially fertilized. The seeds of the date produce about half and half, male and female trees." Kazwini, who died about 682 A.D., says plainly in his book, "Of the marvels of nature, and of the singularities of creating things," "the date has a striking resemblance to man, through the beauty of its erect and slender figure, its division into two distinct sexes and the property, which is peculiar to it, of being fecundated by a sort of union."

BEGINNING OF A NEW ERA

On the 25th of August, 1694, in his laboratory in the University of Tübingen, in South Germany, *Rudolph Jacob Camerer,* Professor of Natural Philosophy, better known to science under his latinized name of *Camerarius,* finished the writing of an extremely long letter to his friend, Professor Michael Bernhard Valentin, of the University of Giessen. This letter, which fills some fifty printed pages, is entitled "De Sexu Plantarum Epistola" (Letter concerning the sex of plants).

Camerarius was the first botanist to discover by actual experiments that the pollen is indispensable for fertilization in flowers, and that the pollen-producing flowers or plants are therefore male, and the seed bearing ones female in nature. Camerarius conducted his experiments with spinach, hemp, and hops, in which the pollen and seed-bearing plants are distinct and also with Indian Corn.

He was the first botanist to discover, two hundred years after maize had been introduced into Europe from America, that on removing the pollen-bearing flowers from the tassel of an isolated corn plant, the seeds on the ears remained unfertilized.

On page 28 of his book, Camerarius comes to this conclusion regarding sex in plants: "They behave indeed to each other as the male and female, and are otherwise not different from one another." On page 49 he goes on to say: "The difficult question which is also a new one, is whether a female plant can be fertilized by a male of another kind, the female hemp by the male hop; the castor bean from which one has removed the staminate flowers through pollination with the pollen of Turkish wheat (maize); and whether, in what degree altered, a seedling will arise therefrom."

Camerarius, however, seems never himself to have attempted the artificial crossing of plants, and it was a full hundred years before his discovery regarding sex in plants received any recognition whatsoever, and before we find the first recorded instance of an actual experiment in hybridization.

MISCELLANEOUS EXPERIMENTS REGARDING SEX IN PLANTS

It is of interest to know that the first person who is reported to have actually crossed plants artificially, was an Englishman named *Thomas Fairchild* who, according to Bradley, crossed two kinds of pinks in *1719*. The cross in question was known still to gardeners, one hundred years later, as "Fairchild's Sweet William."

In 1731, *Philip Miller,* in the first edition of his "Gardener's Dictionary" reported his own repetition of Bradley's experiment with seedlings. Miller also grew male and female plants of spinach apart, and found that the latter bore seeds which contained no embryos.

Eight years later, in 1739, *James Logan,* an American citizen of Irish birth, and at that time governor of Pennsylvania, published in Latin an account of his experiments with Indian corn, entitled "Experimenta et maletamata de plantarum generatione" (Experiments and considerations on the generation of plants).

In 1751, *Gleditsch,* Director of the Berlin Botanical Garden, published an account of an experiment in crossing a species of palm (Chamaerops humilis) entitled "Essai d'une fécondation artificielle fait sur l'espece de palmier qu'on nomme Palma dactylifera folio flabilliformi." According to Sach's History of Botany "This treatise, in point of scientific tone and learned handling of the question, is the best that appeared between the time of Camerarius and that of Koelreuter."

KOELREUTER, THE FIRST SCIENTIFIC PLANT BREEDER

These were the words of *Joseph Gottlieb Koelreuter*: "From the 25th of August, 1694, when Camerarius wrote his letter concerning his experiments upon sex in plants, until September 1, 1761, there has been no real progress in the scientific knowledge which underlies plant breeding." On this latter date, however, appeared Koelreuter's "Preliminary Report of some Experiments and Observations concerning Sex in Plants." This report, with three additional papers on the same subject, which were published in 1763, 1764 and 1766, records the results of 136 distinct experiments in the crossing of plants.

Koelreuter was born April 27, 1733, in the Swabian village of Sulz, in the Black Forest region of southwest Germany. He conducted his experiments partly in his native village, partly in the garden of a physician in the town of Calw in Wurttemberg, and partly in Petrograd, Berlin, and Leipzig. From 1764, until his death in 1806, he was Professor of Natural History in the University of Karlsruhe. At Sulz, in 1760, Koelreuter produced the first plant hybrid ever obtained in a scientific experiment by crossing *Nicotiana paniculata* and *Nicotiana rustica*. Some twenty of these hybrids came to maturity, but unfortunately, these hybrids were completely sterile.

Koelreuter made, besides other crosses between species of Nicotiana, crosses between species of Kedmia, pink (Dianthus), stocks (Matthiola), black henbane (Hyoscyamus) and Verbascum.

He ascertained the fact, that in general only nearly related plants, and not always even these, can be crossed. He determined experimentally the fact that if the stigmas of flowers are pollinated at the same time by their own and by pollen from another species, that fertilization is effected by the former, which would account for the comparative rarity of "species hybrids" in nature. Koelreuter also made the discovery, the explanation of which was not furnished until much later, that the continued self-pollination of hybrids finally results in re-appearance of the original parental forms.

THE SIGNIFICANCE OF SPRENGEL'S DISCOVERY TO PLANT BREEDING

Christian Konrad Sprengel (1750-1816) published in 1793 an epoch-making book "The Newly Revealed Secret of Nature in the Structure and Fertilization of Flowers." It was Sprengel's chief contribution to discover the fact of insect pollination. His conclusion, that nature in most cases intended that flowers should not be fertilized by their own pollen and that the peculiarities of flower structure can be understood only when studied in relation to the insect world, was revolutionary for his time.

The significance of Sprengel's discovery to plant breeding lies in the fact that in general most flowering plants with definite floral envelopes are naturally cross-fertilized. It means simply this, that the bringing together of new combinations of parental characters is the rule rather than the exception in nature, and that, therefore, the breeding of new types in the plant world may be said to be going on all the time.

PRE-MENDELIAN BREEDERS OF THE NINETEENTH CENTURY

At the beginning of the nineteenth century there began to appear in England the first signs of the application of the science of hybridization to the practical art of breeding, in the work of *Thomas Andrew Knight* and *William Herbert*.

Knight was a country gentlemen by occupation, born August 12, 1759, and educated at Oxford. He early began to interest himself, on his estate at Elton in Herefordshire, in experiments in the raising of new varieties of fruits and vegetables. In 1841, three years after his death, a collection of eighty-two of his papers was published by the botanists Bentham and Lindley. Knight's principal work of crossing was carried out with currants, grapes, apples, pears, and peaches, to the end of producing hardier and superior fruits. One of his discoveries of genetic interest was that, in crosses of varieties of red upon white currant, by far the greater number of the hybrids produced red fruit, i.e., the dominance of red. A conclusion formulated by Knight on the basis of his experience, and afterwards confirmed by Darwin, and since called the Knight-Darwin law, was that, "new varieties of every species of fruit will generally be better obtained by introducing the farina (pollen) of one variety of fruit into the blossom of another, than by propagating from one single kind. However, the work of Knight that attracts the most attention from the standpoint of genetics is his experiment with peas. The paper in question, read before the Horticultural Society, June 3, 1823, was entitled, "Some remarks on the Supposed Influence of the Pollen in Cross-breeding, on the color of the seed-coats of plants and the Qualities of their Fruits."

In the particular experiment in question, Knight determined that, in crossing a pea with grey seed-coats upon one with white seed-coats, no immediate change took place, but that the resulting hybrid seeds produced plants the next year which bore grey seeds, as well as having the purple-colored stems and flowers of the male parent.

He further discovered the fact that by crossing plants grown from these (heterozygous) grey seeds, with pollen from what he calls a "permanent" white variety, plants of two types appeared, one bearing grey and the other white seeds.

The work of *William Herbert* was to a considerable extent contemporary with that of Knight. Born January 12, 1778, son of the Earl of Carnarvon, educated at Eton and Oxford, he was trained for the bar which he finally left for the church, entering orders and finally becoming Dean of Manchester. Herbert worked largely on the improvement of florists' flowers, but also conducted experiments with some agricultural plants. He was engaged for a considerable time upon his own experiments, before he came upon the work of Koelreuter, which he immediately assimilated and estimated at its true value. Herbert's experimental work was animated by the connection of the fact which he felt himself to have established, that the then current botanical dogma was wrong, which regarded the existence of sterile offspring from a cross, as evidence that the two parents were of different "species." His views were contrary to those held at the time by Knight, in common with many botanists, that the production of a fertile cross was proof that the two parents were of the same species, "assuming, as a consequence" that the sterile offspring were nearly conclusive evidence that they were of different species, and this dictum was advanced without suggesting any alteration in the definition of the term "species," but leaving it to imply what it had before universally signified in the language of botanists.

A PRECURSOR OF MENDEL

Besides the work of Knight and Herbert, an experiment from the first half of the nineteenth century, which has elicited considerable interest, because of its suggestion of the later discoveries of Mendel, is that of *John Goss* of Hatherleigh, in Devonshire, England, with garden peas. In the summer of 1820, Goss pollinated flowers of the Blue Prussian variety with pollen of a dwarf pea known as Dwarf Spanish, obtaining, as the result of the cross, three pods of hybrid seeds. In the spring of 1821, when he opened these pods for planting, he was surprised to find that the color of the seeds instead of being a deep blue like those of the female parent, was yellowish white like those of the male. However, the parents growing from these seeds in that season "produced some pods with all blue, some with all white, and many with both blue and white peas in the same pod." Here was evidently a plain discovery of the fact of segregation, according to what later became known as Mendel's law. The following spring (1822) he separated the blue peas from the white, sowing the seeds of each in separate rows. He found that the blue seeds, which we should now call the "recessive," produced in turn only blue seeds; while the white seeds, or "dominants" as they are now called, "yielded some pods with all white, and some with both blue and white peas intermixed." Here, then, is the typical case of the segregation of the heterozygotes or hybrid dominants.

In 1819 the Physical Section of the Royal Prussian Academy of the Sciences offered a prize for an answer to the question — "Does hybrid fertilization occur in the plant kingdom?" On the third of July, 1826, the Academy's prize was conferred upon *Dr. A. F. Wiegman,* physician of Braunschweig. Wiegman regards chance crossing in nature, between species or sorts of plants, as having given rise to new agricultural races. "It appears from my experiments," he says, "that many species, or constant subspecies, e.g., *Pisum arvense, Vicia leucosperma, Vicia faba,* as well as the most of the varieties of cabbage and the cereals, whose origin is unknown, possibly are hybrid plants, which have been produced upon our fields and in our garden, through the proximity of a few related plants, and which have remained constant." Regarding the matter of dominance, Wiegman incidentally remarks upon the case of crossing of two species of *Dianthus,* where "the form of the father has almost entirely suppressed that of the mother." According to Wiegman's statements "there occurs even immediately after fertilization, an alteration in the form and color of the seed, and in the form and size of the pods, which is especially unmistakable in the case of the leguminous plants, although otherwise the fruits and seeds of hybrid plants from other families, have never shown themselves to be different from those of the mother plants."

In the valley of the Nagold, in the Black Forest region of Württemberg, some forty miles southwest of Stuttgart, the capital, lies the village of Calw. Here Koelreuter, whose home was in Sulz, did some of his work on hybridization, in the garden of a local physician. By a curious coincidence, in the same village of Calw lived and died *Carl Friedrich von Gärtner,* who for twenty-five years conducted experimental work in hybridization. An idea of the amount of labor expended by Gärtner during the twenty-five years of his hybridization experiments may be obtained by the statement that he carried out nearly ten thousand separate experiments in crossing, among about seven hundred species, belonging to eighty different genera of plants, and obtained in all some two hundred and fifty hybrid plants as the total result. Gärtner, recognized, as did the other hybridizers of his day, that there was always a difference between the first and the succeeding generations, the former being uniform, the later ones variously splitting up. Gärtner did not fail to recognize the fact of unusual vigor in hybrids, although he does not distinguish as to the generation. Gärtner derived, from his long experience, a certain philosophy concerning the nature of hybrids which is noteworthy. He recognized an inequality in the influence or the "potency" as he termed it, of one parent over another in a cross, which potency was maintained, whichever way the cross was made. Gärtner, not having the knowledge which has come since and in consequence of Mendel's investigations, sought a theoretical explanation for this phenomenon of dominance and gave it the designation of "sexual affinity" in the crossing of species, the magnitude of which he considered could be measured by the number of viable seeds produced in the cross. Gärtner did not realize, in spite of Sageret's experiments, that some individual characters of a parent might be found to dominate in a cross and others not. Gärtner's work is noteworthy, not only for the remarkable number of species with which he experimented but for the scrupulous care which he exercised in his operations.

During the time of the prosecution of the work of Knight and Herbert, appeared the results in hybridization obtained by *Sageret* in France. Sageret's experiments in crossing were largely confined to the Cucurbitaceae, and his results were published in a memoir entitled: "Considerations sur la production des hybrides, des variantes et des variétés en général, et sur celles de la famille des Cucurbitacees en particulier," which appeared in 1826 in the Annales des Sciences Naturelles, Vol. 18.

Sageret made some discoveries that clearly anticipated our modern knowledge of segregation, and he was able to furnish what was, for the time, a fairly satisfactory scientific explanation for the reappearance of ancestral characters. The experiment upon which his conclusions were primarily based was a cross in which a muskmelon was the female and a cantaloupe the male parent. Each plant was regarded as a relatively pure or type representation of its kind. In stating the results of the cross, Sageret for the first time in the history of plant hybridization, aligned the characters of the parents in opposing or contrasting pairs after Mendel's fashion forty years later. Following is the list of contrasting parental characters as Sageret gives them.

Muskmelon (female)	Cantaloupe (Male)
1. Flesh white	1. Flesh yellow
2. Seeds white	2. Seeds yellow
3. Skin smooth	3. Skin netted
4. Ribs slightly evident	4. Ribs strongly pronounced
5. Flavor sugary and very acid at the same time.	5. Flavor sweet

In the two hybrid fruits reported upon, the characters were not blended or intermediate at all, but were clearly and distinctly those of the one or the other parent.

First hybrid	Second hybrid
1. Flesh yellow	1. Flesh yellowish
2. Seeds white	2. Seeds white
3. Skin netted	3. Skin smooth
4. Ribs rather pronounced	4. Ribs wanting
5. Flavor acid	5. Flavor sweet

Sageret even uses, for the first time in the literature of plant hybridization, the word "dominate" with reference to characters in crossing, in the following words. Speaking of the inheritance of flavor in various melon crosses, he says, "The acid flavor of the muskmelon is encountered in the forms of the cantaloupe and the snake-melon, in others, the form of the cantaloupe dominated."

Summing up the results of his experiments in a general conclusion, he says, with regard to the natural explanation that in a hybrid there will be a complete or partial fusion of the parental characters, that "this fusion of characters may take place in certain cases, but it has appeared to me that, in general, things did not take place in this way"; and again, "it has appeared to me that, in general, the resemblance of the hybrid to its two parents consisted, not in any intimate fusion of the diverse characters peculiar to each one of them in particular, but rather in a distribution, equal or unequal, of the same characters."

He finally concludes: "To what, then, does this faculty belong, which nature has, of reproducing upon the descendants such or such a character which had belonged to their ancestors? We do not know. We are able, however, to suspect that it depends upon a type, upon a primitive mould, which contains the germ which sleeps and awakens, and which develops or not according to circumstances, and possibly that which we call a new species is a case in which develop organs, ancient but forgotten, which have existed in the germ but have not had their development favored."

Darwin on Hybrids.—On November 24, 1859, appeared the first edition of Darwin's epoch-making book, "The Origin of Species," in which he briefly reviewed the results and conclusions regarding hybrids and hybridization up to his time. In reading Darwin's chapter, one is strangely struck by the persistence of the species-variety question.

Is this a "species," or is it merely a "variety"?—a question which crossing was expected to answer. If two organisms would not cross, or if their offsprings were sterile, they were thereby proved to be distinct "species." If they freely intercrossed, or if their offsprings were fertile, then ipso facto, they were "varieties" of the same species. Darwin's thesis—that "species," so called, grew out of "varieties" so called, by natural selection, caused him to review the evidence which the work of the hybridists, especially Koelreuter, Gärtner and Herbert, afforded. Regarding the matter of the relation of hybrids to species-affinity, Darwin writes with his usual conservative wisdom:

"No one has been able to point out what kind or what amount of difference, in any recognized character, is sufficient to prevent two species crossing. It can be shown that plants most widely different in habit and general appearance, and having strongly marked differences in every part of the flower, even in the pollen, in the fruit and in the cotyledons, can be crossed. The facility of making a first cross between any two species is not always governed by their systematic affinity or degree of resemblance to each other. This latter statement is clearly proved by the difference in the result of reciprocal crosses between the same two species, for according as the one species or the other is used as the father or the mother, there is generally some difference, and occasionally the widest possible difference in the facility of effecting a union. The hybrids, moreover, produced from reciprocal crosses often differ in fertility."

Again he says: "There is often the widest possible difference in the facility of making reciprocal crosses. Such cases are highly important, for they prove that the capacity in any two species to cross is often completely independent of their systematic affinity, that is, of any difference in their structure or constitution, excepting in their reproductive systems. It can thus be shown that neither sterility nor fertility affords any certain distinction between species and varieties. The evidence from this source graduates away, and is doubtful in the same degree as is the evidence derived from other constitutional and structural differences."

Darwin finally summarizes the evidences as follows: "First crosses between forms, sufficiently distinct to be marked as species, and their hybrids, are very generally, but not universally sterile. The sterility is of all degrees and is often so slight that the most careful experimentalists have arrived at diametrically opposite conclusions in ranking forms by this test."

In 1861 the Paris Academy of Sciences proposed the following problem to receive the grand prize in the physical sciences: "To study the plant hybrids from the point of view of their fecundity, and of the perpetuity or non-perpetuity of their characters. The production of hybrids among plants of different species of the same genus is a fact determined a long time since, but many precise researches still remain to be made in order to solve the following questions, which have an interest equally from the point of view of general physiology, and of the determination of the limits of species, of the extent of their variations.

"1. In what cases of hybrids are they self-fertile? Does this fecundity of hybrids stand in relation to the external resemblances of the species from which they come, or does it testify to a special affinity from the point of view of fertilization, as has been remarked regarding the ease of production of the hybrids themselves?"

"2. Do self-sterile hybrids always owe their stability to the imperfection of the pollen? Are the pistils and the ovules always susceptible of being fecundated by a foreign pollen, properly selected? Is an appreciable imperfect condition sometimes observed in the pistil and the ovules?"

"3. Do hybrids which reproduce themselves by their own fecundation sometimes preserve invariable characters for several generations, and are they able to become the type of constant races, or do they always return, on the contrary, to the forms of their ancestors after several generations, as recent observations seem to indicate?"

The Ideas of Godron. — The two chief competitors under the Academy's offer were *Charles Naudin* of the Museum of Natural History at Paris, and *D. A. Godron* of the University of Nancy, the prize being awarded to the former. The papers of both appeared in Vol. 19 of the Annales des Sciences Naturelles (Botanique), 4 me. Serie (1863).

The title of Godron's thesis was "Des hybrides végétaux, considérées au point de vue de leur féconditè et de la perpetuité ou non-perpetuité de leurs charactéres." His paper is devoted chiefly to the solution of the question as to whether "hybrids reproducing by self-fertilization sometimes keep their characters invariable during several generations, and whether they are able to become the types of constant races, or whether, on the contrary, they always return to the forms of one of their ancestors at the end of several generations, as recent observations seem to indicate." In answer to this query, he says: "We have determined, upon hybrids of *Linaria* that the hybrid form may become very fertile, and that a certain number of individuals, from the second generation, return respectively to the two primitive types, when they grow in company with their parents, and this return movement manifests itself much more in the following generations."

Naudin's conclusions. — The general conclusions of importance for his time, at which Naudin arrived, are as follows — in the language of the award committee of the Academy — and which are quoted in their own words to show the point of view of science at that time: "The first, and the most important of all, is that the singular beings which result from the cross-fertilization of two different types, far from being condemned to absolute sterility, are frequently endowed with the faculty of producing seeds capable of germination."

"The second consequence of major interest which proceeds from the numerous experiments in the same memoir is that fertile hybrids have a manifest tendency to return to the forms that produced them, and that without other action than that of their own proper pollen, under such conditions that the pollen of the parents is not able to exercise the influence to determine this return."

In 1864 Naudin communicated a second report to the Academy, in which he confirmed his previous results as to uniformity in the first generation crosses, the identity of reciprocal crosses, and the "disorderly variation," as he calls it, of the hybrids of the second and succeeding generation. In neither of the two papers is there any numerical classification of the hybrid types.

Naudin's memoir is often referred to as amounting virtually to a statement of Mendel's law of the disjunction of hybrids. In Naudin's case, however, the statement was of a speculative nature and consisted in the proposition of a scientific hypothesis; in Mendel's case, his "law" was a scientific conclusion derived as the result of experiment. Naudin propounded, in 1863, a well-reasoned theory of probable truth; Mendel, in 1868, formulated a statement of ascertained fact.

The work of Verlot.—in 1865, *B. Verlot,* of the Jardin des Plantes at Paris, published a brief memoir which in 1862 had received a prize from the Imperial and Central Horticultural Society, the thesis of which was as follows: "To demonstrate the circumstances which determine the production and fixation of varieties in ornamental plants." The memoir is of interest as thoroughly and typically embodying the general point of view of the day concerning hybridization and the origin of new varieties, while affording at the same time much matter of interest from the standpoint of practical horticulture. Verlot presented the view that, while the causes of variation are unknown, they arise under definable circumstances, and the ones which he enumerates are prolonged cultivation, removal from one set of climatic and soil conditions to another, and hybridization.

The thought of the time did not clearly distinguish a difference between the nature of the changes brought about by the external environment and those arising from sexual fertilization. Both were generally assumed to be equally heritable. Cultivation long continued was considered to have been especially potent in bringing about variation. In Verlot's words: "It is especially with plants cultivated for a great number of years, with those the introduction of which is so ancient that it is lost in the night of time, that one finds profound and multiplied modifications."

He further voices the then prevailing view regarding the relation between culture and variation: "If we compare," he says, "a species in its spontaneous condition with the same species cultivated, transported, that is to say, most often into conditions of climate, soil, etc., completely different from those where it lived before, we shall be struck by seeing that in our gardens this latter will show deviations of type more numerous than in the wild state. We shall derive from this fact the consequence that the faculty of varying, which is proper to the plant, augments with culture. If we observe, then, that the plants cultivated in our gardens which have varied the most — as, for example, the dahlias, the roses, the camellias, the rhododendrons, the potato, etc. — are not borrowed for the most part from our flora, nor from one of the neighboring floras, but on the contrary, come from distant countries, where they grow under conditions often absolutely different from those in which we cultivate them, we shall conclude that the more a species is depatriated, the more it will easily vary;" and again: "The more plants are cultivated, the greater their variations are, and, by the same token, the easier they are to fix. We will possibly be contradicted, but we do not hesitate to consider, once more, long-practiced culture as one of the most favorable antecedents to the rapid fixation of variations."

Verlot's Summary. — Verlot summarizes his views upon hybrids in the following words, which are worth reproducing because they fairly well represent the general knowledge of the time, as follows: (1) "Hybrid fecundation is not able to produce anything but variations which will be able, it is true, to multiply themselves mechanically, but which will not be fixable, and which consequently cannot be brought to constitute races or varieties, the products which arise from them being sterile, or if they are fertile, having only a fertility limited to a few generations, or disappearing after a certain time by the disjunction of the types. (2) One of the characters of the hybrids is also a great development of the vegetative organs, coincident with less abundant flowering. They are in general intermediate between the species types, but often approach more the father. (3) The hybrid, self-fertilized, returns more or less rapidly to the parents. (4) The hybrid, fertilized by a parent, returns also promptly to the parent. (5) Crossing — that is to say, reciprocal fertilization of varieties or races of the same species — will serve for obtaining new variations, intermediate between the parents, very fertile, and which can be fixed more or less rapidly, and constitute new varieties or races."

Reviewing this list of statements in the light of present knowledge, we can see that they constitute a more or less correct non-scientific formulation of the truth. For example, the more or less rapid return of hybrids — that is to say, heterozygotes — to the parental forms, is well established today as a fact of segregation according to Mendelian ratios, which, if there is a single pair of allelomorphs in question, goes on, on a 1.2.1 basis in each successive generation. The more or less rapid return to its parents of the hybrid fertilized by parent is simply the splitting off of 50 per cent dominants or recessives as the case may be, and which are the parental types in the case of simple ratios.

Wichura's Work. — In 1865 there appeared *Wichura's* memoir on the hybridization of plants, "Die Bastardbefruchtung im pflanzenreich, erläutert an den Bastarden der Weiden, Breslau, 1865" based upon experiments in the crossing of willows, which had occupied him from 1852 to 1858 inclusive. A brief preliminary report had appeared in Flora in 1854, and also within the same year in the report of the Schlesische Gesellschaft.

Taken as a whole, Wichura's work dealt, not with the investigations of individual specific characters but with species taken entire and crossed as such. As was the general custom, he regarded a "species" as an integral whole that could be crossed in its entirety. With this exception he made what he called "binary," "ternary" and "quaternary" crosses, i.e., crosses: (1) between two species; (2) between a species and a hybrid; and (3) crosses between two hybrids. Besides the smaller list of Wichura's successful crosses, he published a much longer one of his failures, which stand as evidence both of the considerable amount of crossing work that was done and of the scientific integrity of the experimenter. Of the ordinary, or as he calls them, "binary" crosses, Wichura made, in all, thirty-five successful crosses and combinations of crosses (of which ten were "binary," i.e., simple crosses in the ordinary sense) between twenty-one different species of willows.

Although, as has been stated, Wichura, no more than most of the other hybridists of his day, paid attention to the crossing of characters as such, he remarks upon the evidence of individual characters being inherited as such: "It was of interest," he says, "to observe how the unusual narrowness of the leaves in the experiment, utilizing *Salix purpurea x viminalis,* remained still recognizable in the following generation; a proof that, even in hybrid fertilization, individual characteristics of the parent plants can be inherited."

This closes the account of the work in the field of hybridization from the time of Koelreuter to the time of Gregor Mendel, 1760-1866. Mendel's investigations, however, did not become generally known until 1900, so that very little change occurred in the methods pursued in the study of hybrid phenomena until after the date last mentioned. Comparatively few students of plant breeding, however, realize the historical value of the work of the earlier hybridists, in whose experiments lie the germs of our present knowledge.

Lamarck (1774-1829), the noted French naturalist, taught that all living things have been derived from pre-existing forms, that the effects of use and disuse caused changes in bodily structure; that these changes were inherited and accentuated from generation to generation. According to Lamarck, in plants and animals, whenever the conditions of habitat, exposure, climate, nutrition, mode of life, et cetera, are modified, the characters of size, shape, relations between parts, coloration, consistency are modified proportionately: some of the arguments against the validity of Lamarckism are: (1) that no one has ever been able to prove by experiment or otherwise, that the effects of use, the so-called "acquired characters" are inheritable, while innumerable facts indicate that they are not; (2) the hypothesis could apply only to the animal kingdom, since plants in general have no nervous and muscular activities like those of animals. A hypothesis of organic evolution, to be valid, must apply equally to both plants and animals.

The question of the method of evolution continued to be debated, with no satisfactory solution in sight, *until 1859 when Charles Darwin* published the greatest book of the nineteenth century, and one of the greatest in the world's history, the "Origin of Species." This book was the result of over twenty years of careful observations and thought. It consisted of the elaboration of two principal theories: (1) that evolution is the method of creation, (2) that natural selection is the method of evolution, based upon inheritance, variation, fitness for environment, struggle for existence, and survival of the fittest.

The theory of heredity which was chiefly responsible for replacing pangenesis was proposed by *Weismann* who was born at Frankfort on the Main in 1834 and died in 1914. In 1893, he published "The Germ-Plasm, A Theory of Heredity," a treatise which elicited much discussion. The main features of Weismann's Theory of Continuity of Germ plasm are as follows:

(1) The germ plasm has had unbroken continuity from the beginning of life; owing to its impressionable nature, it has an inherited organization of great complexity.

(2) Heredity is accounted for on the principle that the offspring is composed of some of the same stuff as its parents. The body-cells are not inherited.

(3) There is no inheritance of acquired characters.

(4) Variations arise from the union of the germinal elements, giving rise to varied continuations and permutations of the qualities of the germ-plasm. The purpose of amphimixis is to give rise to variations. The direct influence of environment has produced variations in unicellular organisms.

(5) Weismann adopts and extends the principle of natural selection. Germinal selection is exhibited in the germ-plasm.

GREGOR MENDEL (1822-1884)

One of the most important contributions ever made to biological science, was made by a teacher who studied plants as a pastime because he loved to do it. This man was *Gregor Mendel,* a monk in the monastery at Brünn, Austria, where he finally became abbot.

In his garden he made many experiments upon the inheritance, particularly in peas, of color and of form; and through these experiments he demonstrated a law of inheritance which was one of the greatest biological discoveries of the nineteenth century. He published his papers entitled "Experiments in Plant-Hybridization" in 1866, but since the minds of naturalists at that time were very much occupied with the questions of organic evolution, raised through the publication of Darwin, the ideas of Mendel attracted very little attention.

The discovery by Mendel of alternation inheritance will rank as one of the greatest discoveries in the study of heredity. The fact that in cross-breeding the parental qualities are not blended, but that they retain their individuality in the offspring, has many possible practical applications, both in horticulture and in the breeding of animals.

In planning his crossing experiments, Mendel adopted an attitude which marked him off sharply from the earlier hybridizers. He realized that their failure to elucidate any general principle of heredity from the results of cross fertilization was due to their not having concentrated upon particular characters or traced them carefully through a sequence of generations. That source of failure he was careful to avoid and throughout his experiments he crossed plants presenting sharply contrasted characters, and devoted his efforts to observing the behavior of these characters in successive generations. Thus in one series of experiments he concentrated his attention on the transmission of the characters tallness and dwarfness, neglecting, in-so-far as these experiments were concerned, any other characters in which the parent plants might differ from one another. For this purpose he chose two strains of peas, one about six feet in height, and another of about one and one-half feet. Previous testing had shown that each strain bred true to its peculiar height. These two strains were artificially crossed with one another, and it was found to make no difference which was used as the pollen parent and which was used as the ovule parent. In either case the result was the same. The result of crossing tall with dwarf was in every case nothing but talls, as tall as or even a little taller than the tall parent. For this reason Mendel termed tallness the *dominant* and dwarfness the *recessive* character. The next stage was to collect and sow the seeds of these tall hybrids. Such seeds in the following year gave rise to a mixed generation consisting of talls and dwarfs but *no intermediates*. By raising a considerable number of each plant, Mendel was able to establish the fact that the number of talls which occurred in this generation was almost exactly *three times* as great as the number of dwarfs. As in the previous year, seeds were carefully collected from this, the second hybrid generation, and in every case the seeds from each individual plant were harvested separately and separately sown in the following year. By this respect for the individuality of the different plants, however closely they resembled one another, Mendel found the clue that had eluded the efforts of all his predecessors. The seeds collected from the dwarf recessive bred true, giving nothing but dwarfs. And this was true for every dwarf tested. But with the talls it was quite otherwise. Although indistinguishable in appearance, some of them bred true, while others behaved like the original tall hybrids, giving a generation consisting of talls and dwarfs in the proportion of three of the former to one of the latter.

Mendel is also known to have made experiments with many other plants, and a few of his results are incidentally given in his series of letters to Nägeli the botanist. The only other published work that we possess dealing with heredity is a brief paper on some crossing experiments with the hawkweeds (*Hieracium*), a genus that he chose for working with because of the enormous number of forms under which it naturally exists.

By crossing together the more distinct varieties, he evidently hoped to produce some of these numerous wild forms, and so throw light upon their origin and nature. In this hope he was dissappointed. Instead of giving a variety of forms in the F_2 generation, they bred true and continued to do so as long as they were kept under observation. More recent research has shown that this is due to a peculiar feature known as parthenogenesis and not to any failure of the characters to separate clearly from one another in the gametes. Mendel, however, could not have known of this, and his inability to discover in *Hieracium* any indication of the rule which he had found to hold good for both peas and beans must have been a source of considerable disappointment. Whether for this reason or owing to the utter neglect of his work by the scientific world, Mendel gave up his experimental researches during the later part of his life. His closing years were shadowed with ill health and embittered by a controversy with the Government on a question of the rights of his monastery. He died of Bright's disease in 1884. Mendel's experiments, published in 1866, remained unnoticed until the facts were rediscovered in 1900 by *DeVries, Correns* and *Tschermak.*

THE MUTATION-THEORY OF DEVRIES

Hugo DeVries, director of the Botanical Garden in Amsterdam, has experimented widely with the growth of plants, especially the evening primrose, and has shown that different species appear to rise suddenly. The sudden variations that breed true, and thus give rise to new forms, he called mutations, and this indicates the source of the name applied to his theory.

In his "Die Mutations theorie," published in 1901, he argues for the recognition of mutations as the universal source of the origin of species. Although he evokes natural selection for the perpetuation and improvement of variations, and points out that his theory is not antagonistic to that of natural selection, it is nevertheless directly at variance with Darwin's fundamental conception — that slight individual variations "are probably the sole differences which are effective in the production of new species" and that "as natural selection acts solely by accumulating slight, successive, favorable variations; it can produce no great or sudden modifications." The fundamental idea of DeVries' theory is that "species have not arisen through gradual selection, continued for hundreds or thousands of years, but by sudden leaps and bounds.

The work of Devries is a most important contribution to the study of the origin of species, and is indicative of the fact that many factors must be taken into consideration when one attempts to analyze the process of organic evolution. One great value of his work is that it is based on experiments and that it has given a great stimulus to experimental studies.

NILSSON'S DISCOVERY OF THE ELEMENTARY SPECIES OF AGRICULTURAL PLANTS (1890)

During the last twenty years, experiments in the breeding of cereals and other agricultural crops have been conducted on an unusually large scale at the Swedish Experiment Station of Svalof under the leadership of Dr. Hjalmar Nilsson, Director of the Station. Nilsson's principle for all breeding purposes is to derive his strains from single mother plants. Only such strains give pure breeds. A second discovery made at Svalof, and equally valuable for practice and for science was that of the almost astonishing richness in elementary species among our agricultural crops. Every cultivated species seems to embrace something like a hundred of them, and the cereals were found to include even several hundred in each of the older species. By carful search of the field in almost every case a plant may be found which complies with the ideal sought for. From such a plant a pure and constant one may be derived without other means than that of isolating and multiplying its progeny. On the basis of these facts, Nilsson has founded an elaborate method of selecting original plants for his pedigree-cultures and of comparing their value for practical purposes. Meanwhile, variation was being studied from a new point of view, which we may call *biometry*. *Francis Galton* (1889) was the founder of biometry but its full development has been due chiefly to the valuable work of *Karl Pearson*. The underlying idea in biometry is to apply to the study of evolution the precise quantitative method followed in the study of physics and chemistry with such signal success.

Biometry is the statistical study of variation and heredity. Biometry is best adapted to deal with continuous variations. Its ideal, to make biological investigation more accurate and comprehensive, is wholly commendable.

JOHANNSEN'S CONCEPTION OF HEREDITY

The conception that inheritance, as previously noted, is not the transmission of external characters from parent to offspring, but the reappearance, in successive generations, of the same organization of the protoplasm with reference to its character-units, was first developed by Johannsen, of Copenhagen, Denmark, in 1909, and published in his book "Elements der Exakten Erblichkeitslehre (Elements of the teaching of exact heredity). Johannsen proposed the term "genes." The sum total of all the genes in a gamete or zygote is a genotype. Inheritance is the appearance, in successive generations, of the same genotypical constitution of the protoplasm.

This conception of heredity is diametrically opposed to the older and popular conception but is much more closely in accord with the facts revealed by recent studies of plant and animal breeding.

Department of Botany
Iowa State College.

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