

THE FOUNDERS OF THE ART OF BREEDING—IV

Pre-Mendelian Breeders of the Nineteenth Century—Concluded

HERBERT F. ROBERTS

Kansas State Agricultural College

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, "*Considérations sur la production des hybrides, des variantes et des variétés en général, et sur celles de la famille des Cucurbitacées en particulier*," which appeared in 1826 in the *Annales des Sciences Naturelles*, Vol. 18.

SAGERET ON SEGREGATION

Sageret made some discoveries that clearly anticipate 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 representative of its kind. In stating the results of the cross, Sageret for the first time, so far as the writer knows, 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)

1. Flesh white.
2. Seeds white.
3. Skin smooth.
4. Ribs slightly evident.
5. Flavor sugary, and very acid at the same time.

Cantaloupe (male)

1. Flesh yellow.
2. Seeds yellow.
3. Skin netted.
4. Ribs strongly pronounced.
5. Flavor sweet.

Sageret remarks: "The assumed product of the crosses made ought to have been intermediate: (1) Flesh very pale yellow, (2) seeds very pale yellow, (3) netting light, (4) sides slightly marked, (5) flavor at once sweet and sprightly, but the contrary was the case."

As a matter of fact, 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

1. Flesh yellow.
2. Seeds white.
3. Skin netted.
4. Ribs rather pronounced.
5. Flavor acid.

Second hybrid

1. Flesh yellowish.
2. Seeds white.
3. Skin smooth.
4. Ribs wanting.
5. Flavor sweet.

In the further support of his conclusions regarding the descent of characters in unitary fashion, he remarks upon the inheritance of human hair and eye color in the mating of a brunette with a blonde type. He comments upon the fact that these two hybrids are types of which he had "several times obtained the analogues or their equivalents." While there is fusion here and there, he says, "one sees here a much more marked distribution of their different characters, without any mixture between them." He 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 expectation 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 ascendants consisted, not in an 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*." (Italics inserted.)

Here we meet again, for the first time in the literature of hybridization, the phrase "distribution of characters" now so familiar. "These facts," Sageret remarks, "have been confirmed by a multitude of my experiments." It is evident from the following statement that Sageret appraised his discovery of the dominance of characters in crossing at its proper value: "The ideas which I present," he says, "have appeared remarkable to me; they seem to me to be of a very great importance."

In addition to his melon crosses, Sageret secured a hybrid between a black radish and a cabbage, of which he says: "The fruits, instead of being intermediate, were like either cabbage or radish on the same inflorescence. Each silique bore a single seed, analogous to its pod," to which he makes reference in a further comment upon "*the distribution among hybrids, of the characters of their ascendants without fusion of these characters*," a point of view with regard to the results of hybridization that needs little to make it modern. It is, however, a matter of further interest that Sageret was able to derive the natural scientific conclusion from the facts of unit-character inheritance as he found them, with respect to the reappearance of old or the appearance of new "species." The hybrids "often reproduced for me,"

he says, "varieties which had long ago disappeared."

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, which develops or not according to circumstances, and possibly that which we call a new species, in which develop organs, ancient but forgotten, of which the germ existed, but which the development had not yet 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 (Chap. 9) 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 offspring were sterile, they were thereby proved to be distinct "species." If they freely intercrossed, or if their offspring 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, Gartner 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 recognizable 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 . . . (p. 14). 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 an union. The hybrids, moreover, produced from reciprocal crosses often differ in fertility" (p. 16).

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 (p. 14). 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" (p. 4).

Darwin finally summarizes the evidence 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" (p. 44).

In 1861 the Paris Academy of the Sciences proposed the following problem to receive the grand prize in the physical sciences: "To study 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 pistil 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 at 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 fécondité et de la perpétuité ou non-perpétuité de leurs caractères.*" His paper is chiefly devoted 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 forms 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."

Godron remarks that the same fact has been observed by Lecoq in the fertile hybrids of stocks, by Naudin in the fertile hybrids of tobacco, and by several observers in primula and in petunia. From these experiments, then, he concludes the proof of the final return of fertile hybrids to their parental forms to be established. Godron was a victim of the rigid idea of species, which held, that because so many hybrids between different "species," so called, were sterile, that therefore any hybrid which proved fertile must necessarily, *ipso facto*, prove the parents not to be of different species but to be merely varieties of the same species.

To the vain purpose of settling this verbal controversy, as to whether such and such plants were to be regarded as separate "species," or merely as varieties of the same species, many of the most ardent endeavors of hybridists, both before and since Mendel's time, have been conscientiously and duly devoted. A sample of this method of reasoning in a circle so vigorously combated by Herbert, and characterized by Sageret as "fighting the air," is exemplified in a sentence of Godron which typifies the then general view. He says: "*To admit that two distinct species have produced hybrids which, from the very first have become very fertile, would constitute a very grave exception to the law which has its sanction in the numerous experiments which, for a century past, have been made by Koelreuter, Wiegmann, C. F. Gartner, etc., and by M. Naudin himself, that simple hybrids are sterile or but little fertile.*" (Italics inserted.)

Considering the fact, however, that

hybrids between confessedly distinct species are so frequently sterile, it is not surprising that, in view of the then greater interest in the species question itself, that hybridizers should have turned systematic botanists and have made the sterility of the hybrid offspring a criterion of species distinction. Besides his competing memoir before the Paris Academy, Godron was the author of several other contributions to the literature of plant hybridization, including that of the then celebrated question as to the possible origin of cultivated wheat from the wild plant *Aegilops ovata*.

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 (6c) 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" (p. 129).

"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*" (p. 129).

UNIT CHARACTERS

An essential feature in Naudin's paper, of high importance from our present standpoint, is the independent behavior of characters in a cross, and referred to by the Academy committee as follows: "Not content with responding by numerous experiments to the questions propounded by the Academy, the author . . . has sought to throw light upon several points, some obscure, others not yet studied, in the

history of hybrids. He has confirmed that which Sageret already knew, that in a hybrid the characters of the two parents are often shown, not blended but approximated, in such fashion that the fruit of a *Datura* hybrid, born of two species, the one with a smooth, the other with a spiny capsule, *presents smooth places in the midst of a surface generally spiny*. This disjunction, as it is called, is explained according to him by the presence in the hybrid of two specific essences, which tend to be separated more or less rapidly the one from the other. He even sees in this disjunction the true cause of the return of fertile hybrids to the types from which they came" (p. 131). (Italics inserted.)

It is further of great interest to note that the seeds gathered from the smooth side of the capsule reproduced only the smooth-capsule form, *Datura laevis*, while those taken from the spiny side gave rise only to the spiny form, *Datura stramonium*. In Verlot's paper, yet to be discussed, further instances of this vegetative segregation, as it may be called, will be found.

Naudin stated, more clearly and definitely than others had hitherto done, the fact of the general uniformity of the hybrid offspring of the first generation (the F_1 generation), as we should say, and the diversity of form, with partial reversion to, or, as we would now put it, the reappearance of, the parental types in the second hybrid (or F_2 generation). His language is as follows: "Finally, one may say that the hybrids of the same cross resemble one another in the first generation as much, or almost as much, as the individuals which come from a single legitimate species."

In contradiction to the results derived by Sageret from his particular set of experiments, Naudin asserts the generally intermediate nature of the first generation hybrids: "All the hybridologists are in accord in recognizing that the hybrids (and it is always the question of the hybrids of the first generation) are mixed forms, intermediate between those of the two parent species. This is, in fact, what takes place in the immense majority

of cases; but it does not follow therefrom that these intermediate forms are always at an equal distance from that of the two species." He goes on to remark upon the vagueness with which this relative approximation is determined, resting as it does, largely upon a basis of opinion. He also calls attention to the fact that sometimes the hybrids resemble one of the two parents in certain parts and the other in other parts. Regarding segregation in the second hybrid generation he says: "Very often, to the so perfect uniformity of the first generation, there succeeds an extreme medley of forms, some approaching the specific type of the father, the others that of the mother It is, as a matter of fact, in the second generation that this dissolution of the hybrid forms commences in the great majority of cases. . . . Among several of these hybrids of the second generation, there is a complete return to one or the other of the two parental species, or both, and diverse degrees of approach to these species."

NAUDIN'S EXPLANATION

Naudin now comes to what he regards as the philosophical explanation of these facts: "All these facts are naturally explained by the disjunction of the two specific essences, in the pollen and in the ovules of the hybrid. A hybrid plant is an individual in which are found united two different essences, having their respective modes of development and final direction, which mutually counter one another, and which are incessantly in a struggle to disengage themselves from one another." "The hybrid," he says, "in this hypothesis would be a living mosaic, in which the eye would not discern the discordant elements as long as they remained intermingled; but, if in consequence of their affinities, the elements of the same species mutually approximating one another, agglomerate in rather considerable masses, there may result therefrom parts discernible to the eye, sometimes entire organs, etc."

Naudin concludes that the pollen and the ovules, and the pollen especially,

"are the parts of the plant where the specific disjunction takes place with the most energy." He goes on to suppose, and here, perhaps he comes closest to a statement of Mendel's view, "that in the hybrids of the first generation the disjunction takes place at the same time in the anther and in the contents of the ovary; that some of the grains of pollen belong totally to the species of the father, and others to the species of the mother; that in others the disjunction has not occurred or has just commenced; let us grant again that the ovules are, in the same degree, segregated toward the side of the father and toward the side of the mother. . . . If the tube from a grain of pollen, approximated to the species of the male parent, encounters an ovule segregated in the same direction, there will be produced a plant entirely reverted to the paternal species. The same combination being accomplished between a grain of pollen and an ovule, both segregated in the direction of the female parent of the hybrid, the product will return in the same way to the species of the latter; if, on the contrary, the combination is effected between an ovule and a grain of pollen segregated in a direction contrary the one to the other, there will result a true cross-fertilization like that which has given birth to the hybrid itself, and there will result therefrom a form intermediate between the two specific types."

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, chief among which he enumerates 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" (p. 4).

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" (p. 30); 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" (p. 38).

We now know at least that the increased variation manifested by wild plants, when brought into cultivation, is probably due to the removal of the restrictive influences of competition rather than to any actual increase in the range of heritable variability itself.

Verlot cites, as examples of the changes supposedly wrought by culture, the changes brought about in the roots of such plants as beet and parsnip, in the production of dwarf plants, in various modifications in general habit, such as fastigate, pyramidal and weeping variations in trees; in the appearance of variations with lacinate or otherwise modified leaves; in varieties with leaves colored white, yellow, red or brown; in the arrangement of the leaves, as in the sudden appearance on an ordinary alternate-leaved plant of *Rosa alba*, of a shoot with opposite leaves, propagated as *Rosa cannabifolia*. From the evidence he concludes that cultivation sets up within the plant a condition of instability, which gives rise not only to seed variation but to variation within the plant itself—what we would call bud-variation or somatic segregation—

as in the case just cited, the case of a chrysanthemum reported which bore at the same time yellow and rose-colored flowers, and of a citrus fruit half-and-half orange and lemon. Another case cited by Verlot is that of a variegated *Camellia imperialis* which, for twelve years, had constantly given brilliant white flowers set off with rose-colored striations and variegations, and upon which a small branch appeared one year bearing three flowers, in a group of a uniform rose color, the same in tint as that of the striations and variegations of the other flowers.

"It is evident, in these cases," says Verlot, "that the colorations disjoin and that this variation returns by disjunction to its colored types, as we have indicated for certain plants of hybrid origin. (p. 67). As we see," he says, "by the sole fact that a plant is cultivated, it is forced to vary. The instability of a cultivated plant is even evident in certain cases in such a way that it does not only manifest itself in the direct descendants of the plant, but also in the plant itself. Thus, while the generality of the branches of a plant bear leaves, flowers and fruits of definite forms or colors, a branch is sometimes produced in which the leaves, flowers, and fruits present completely different characters. We recognize that culture has been and is still the essential cause of the variation of plants, and that thereby man has, so to speak, compelled them to re-clothe themselves with new forms appropriate to his needs or to his caprices" (p. 5).

The above statement excellently presents the older point of view regarding variation. Such cases as the rose, chrysanthemum and orange, and the famous hybrid *Cytisus Adami* (*purpureus* × *laburnum*), Verlot accounts for under the guise of Naudin's conception of "disjunction": "It is by disjunction that, in these last cases, the specific forms thus reappear in hybrid plants, and it is with woody plants, it will be noticed, that this fact presents itself; individuals, that is to say, which, persisting for long years, must achieve all the phases of existence of a hybrid plant.

an existence of which this disjunction would be the last term" (p. 14). He then refers to Naudin's case of disjunction in *Datura*, which is elsewhere discussed. Verlot's expression of views on the matter of methods of selection is so thoroughly typical of the thought of his time, *i. e.*, that variation is in consequence of the "breaking up" of the "type," and that selection, *ipso facto*, intensifies the variation in the direction selected for, that it is a matter of interest to present here the view expressed. "If a variation is produced in a direction other than that toward which one tends, it ought not to be abandoned for that; one will have more chance of obtaining new variations in sowing a deviation from the type, even in a diametrically opposite direction, than in sowing anew the type itself. In the deviation there is already a tendency toward perturbation, and toward the beginning of the destruction of atavism" (p. 31).

Another interesting example of the older empirical point of view regarding plant improvement is Vilmorin's opinion, quoted by Verlot, and which is here reproduced to show how thoroughly the primary idea of "breaking up the type" in order to bring about "variation" entered into the thought and operations of pre-Mendelian breeders.

"To obtain from a plant not yet modified, varieties of a kind determined in advance, I will first set myself to making it vary in some direction or other, choosing for the reproducing factor, not that one of the accidental varieties which would most nearly approach the form which I have proposed to myself to obtain but simply that which would most differ from the type. In the second generation, the same care would make me choose a deviation, the greatest possible at first, the one most different, in a word, from that which I would have chosen in the first place. Following this direction for several generations, there necessarily ought to result, in the products obtained, an extreme tendency to vary; there then results again, and that is the principal point according to me, that the force of

atavism, exerting itself counter to very divergent influences, will have lost a great part of its power, or, if one ventures to make use of this comparison, it will exert it always in a broken line" (p. 28).

Man's relation to the fixation of characters in new races of plants is stated by Verlot in the usual manner prevalent in the days before Mendelian analyses: "In brief, gardeners have remarked with reason that a plant newly introduced is very susceptible to vary. This fact, it is conceived, has nothing surprising about it. It confirms that which we have previously said, that a variety, whatever it might be, had need, in order to become fixed, of being cultivated for a greater or less length of time, until one had finally come to maintain with it the tendency not to depart from being that which he had made it" (p. 70).

In other words, the idea then prevalent, and more or less incoherently expressed, was that, in some unknown manner, man, by continued selection, succeeds in impressing upon a "variety" the stamp of a certain type, and, through repeated and continuous selection in the same direction, finally "fixes" it, so that the variety becomes, as it were, stabilized. Analyzed in a modern way, it simply means that, by continuous selection of some certain type, those individuals are usually isolated which are homozygous for the character-units thus represented, and which become "fixed," because no heterozygous factors are left to split apart.

We have here, in other words, an unscientific sensing through practical experience of the fact which the breeder of today would define as the selection of a heterozygote having dominant characters differing from those of the species. Being of hybrid nature, such a plant would break up and hence yield new types, whereas the plants resembling the type are more apt to be homozygous and less liable to vary in their progeny. He emphasizes the view just set forth still more emphatically in the following words: "If two variations are produced, of which the one differs little

from the type, but is placed upon the line which leads in the desired direction, and the other is placed in an opposite direction, but departing considerably from the type, we shall not neglect nevertheless to follow this latter, because with it the breaking-up of atavism is more advanced" (p. 31).

The necessity of fixing upon some single individual plant as the basis of selection is referred to by Verlot in the following terms: "We ought, then, to recognize that it is necessary to take account for the choice of the seed-bearers, not only of the external characters but even of the idiosyncrasy of each one of them. Now since this does not manifest itself except by its effects, we shall, if a variation seems to present some difficulties in becoming fixed, have to examine separately the products of each of the seed parents and make our choice bear upon those which present, in the least pronounced degree, atavism, or the tendency to return to the primitive type" (p. 32).

Verlot's experience with and observations upon hybrid plants, as coming from an experienced horticulturist, are interesting, and, to the practical plant breeder, valuable. Regarding the now well-understood fact of the gradual disappearance of the hybrid forms through segregation, he says: "Their fertility is of short duration, through the more or less rapid return of their products to the types which have given them birth" (p. 25).

Regarding the general aspects of plant hybrids, he adds: "All their characters, of whatever nature they may be, with the exception of a more considerable development of the organs of vegetation, are, in general, intermediate between those of the parents, but always limited by them" (p. 25). Regarding the matter of the bounds or limits of the hybrid characters he remarks elsewhere: "Let us call attention to a circumstance always constant in the hybrids, which we have to consider, that is, the absence in the products of colors other than those, or a combination of those of the parents. We shall insist upon this characteristic,

because we shall have occasion to recur to it; it will serve us to establish the fact that up to now the facts prove that, by hybrid fecundations, one will obtain, in whatever part of the plant they present themselves, the variations of color only, limited to those of the parents" (p. 18).

Since Verlot's view regarding the nature of a hybrid was the conventional one that it consists of a cross between what are commonly called distinct species, he was led to notice the very common fact of comparative sterility in these cases. Noting the well-known characteristic of augmented vegetative growth in hybrids, he is led to ascribe the seed sterility to the latter, a conclusion easily if naively arrived at from the well-known inverse relation between undue vegetative luxuriance and seed reproduction. As an instance of intermediacy, Verlot alludes to the matter of height: "In crossing an almost dwarf species with the pollen of a taller species . . . the seeds of this cross will undoubtedly produce individuals taller than was their mother" (p. 44).

Regarding intermediateness in size in flowers, he says: "In crossing a species *parviflora* by its variety *grandiflora* we shall be able . . . to obtain individuals with flowers larger than those of their mother . . . by crossing one is able then to create a race or a variety in which the size of the flowers will be augmented" (p. 47). With regard to the same matter in respect to earliness and lateness, he says: "Supposing one crosses a very early plant with its very late variety, or *vice versa*, one will only be able to obtain varieties intermediate between the parents in earliness or lateness" (p. 50).

Regarding fragrance he mentions the case of a cross between *Rhododendron ciliatum* (odorless) and *R. Edgeworthii* (very fragrant), the hybrid being less intensely fragrant than the pollen parent (p. 31). In the matter of color intermediateness he makes the statement: "Once obtained, white coloration is able to serve, either by crossing or by hybridization, in the production of new variations, ordinarily intermediate

between it and the color from which it has proceeded" (p. 59); in other words, as we should say today, dilution through the presence of but a single dose of the color factor.

The most interesting portion of Verlot's memoir is his discussion of the practical results achieved with ornamental plants in the field of hybridization. Regarding dwarfing he cites McNab (p. 42), to the effect that the best dwarf varieties of rhododendron are obtained by the use of pollen taken from the small stamens, "the products of which," he says, "I am able to certify, are very different from those obtained by the use of the pollen of the large stamens." Regarding breeding for winter hardiness, he mentions the case of the cross of *Amaryllis brasiliensis*, a delicate species impossible to winter out of doors, by *Amaryllis vittata*, a much hardier plant, whereby hybrids were produced which, with light covering, would support the climate of Paris. Likewise *Rhododendron arboreum*, which cannot resist more than 2 to 3 degrees of cold, gave, when crossed by *R. catawbiense* (a much hardier form, though with inferior inflorescence), hybrids which inherited the hardiness of the female plant.

Verlot did not recognize the phenomenon of dominance in the first generation of the hybrids, but he mentions the case of a white *Gloxinia* crossed by pollen from a blue-flowered variety, in which out of one thousand seedlings "all bore nothing but perfectly blue flowers, not a single one of them being white, nor a single one variegated" (p. 65). Likewise the crossing of the same plant by a red-flowered variety gave the same result, "all the plants coming from sowings of seeds thus produced had entirely blue flowers" (p. 65).

Regarding the inheritance of variegations it may be of simple interest to note that the following species are mentioned in which the variegated form breeds true from the seed. *Alyssum maritimum*, *Barbarea vulgaris*, *Celtis australis*, *Cheiranthus cheiri*. With these are to be included the variegated ferns *Pteris argyraea* and *P. aspericaulis* var. *tricolor*.

He remarks upon an interesting fact

that the variegations do not appear upon the first leaves of a variegated variety. Regarding the heredity of double flowers, he reports no crosses, but simply remarks upon cases of double-flowered peach and apple which came true from the seed (p. 83).

Another interesting piece of information given is that, in the case of double camellias, the full round seeds produced plants with very double flowers, while the more elongated seeds produced plants with single or but slightly doubled flowers (p. 87). Among color variations in plants, few are more interesting than the red or copper-leaved forms of ordinary green-leaved types. It may be of interest here to note Verlot's citations of such color varieties as are homozygous for the color, and which hence come true to type, among the recorded instances being the purple beech and the purple-leaved barberry.

One of the most interesting matters recorded in Verlot's paper, is his citation of Bridgmann's investigations on the inheritance of leaf variation in ferns. Many species of ferns show various degrees of leaf lacination, the latter becoming often many times compounded. In the case of several species of *Scolopendrium* with crisped or lacinate leaves, spores were separately sown from the modified and from the unmodified leaves, with the result that the resulting plants, although derived from the same original plant as a parent, inherited the characteristics of the particular leaves or parts of leaves from which the spores were taken.

"The spores from the deformed part of the frond were collected and sown separately. . . . The result was that all the plants which came from them reproduced the crisped form of the individual mother plant, and some of them even in a higher degree" (p. 98).

"The spores from the normal part of the frond, which had furnished the first sowing, were collected with the same care, and sown under identical conditions. There originated in the same way thousands of young plants, but it was scarcely possible in the

quantity of them for one to find a dozen which showed, even to a feeble degree, the irregularities of form so characteristic of the first lot. The two sowings were so different from one another that, if one had not known their derivation, one would never have been able to believe that they were such near relatives. The great majority here were perfectly normal; as to the small number of those which showed traces of the maternal monstrosity, this monstrosity was limited to fronds bi-lobed or tri-lobed at the top, with the edges more or less sinuous or a little slashed; yet this alteration most often did not reach more than one or two fronds on the same individual" (p. 98).

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 a 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 (10), 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 conception 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.*, simply 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 (p. 27), "to observe how the unusual narrowness of the leaves in the experiment, utilizing *Salix purpurea* \times *viminialis*, remained still recognizable in the following generation; a proof that, even in hybrid fertilization, individual characteristics of the parent plants can be inherited." (*Italics inserted.*)

Wichura noted in willows, as others had done in other plants, the fact of a higher degree of sterility on the part of hybrids obtained between species of more distant specific relationship. The greater amount of vegetative vigor of hybrids was remarked upon by Wichura in the following words (p. 40): "Not only in the reproductive organs, but also in their vegetative behavior, hybrids show many phenomena whereby they are more or less strikingly distinguished from true species. According to the corroborating observations of Koelreuter and Gärtner, a larger part of the hybrids obtained by them by hand crossing, were distinguished by luxuriance of growth. The plants grew to a greater height than the parents, spread out farther laterally by virtue of an increased capacity for sprouting, had a longer life-period, were able to withstand cold longer, and had more abundant, larger and earlier flowers than the parents. . . . Among the willow hybrids, similar phenomena occur, but the examples of luxuriant growth by no means constitute the rule."

Wichura further observed that: "Even the most sterile hybrids fall behind the parents in their productiveness. A certain deficiency in the parts set aside for reproduction must therefore also occur with them, and if we associate this in reverse relation with the excess of their vegetative development, it stands in complete harmony with the facts otherwise demonstrated. We shall therefore have to say, in order to express the relationship correctly, that in the case of very vigorous hybrids the weak-

ness of the sexual parts brings out an increased development of the vegetative growth, whereas it is not the case with others which are too weak for such a reaction" (meaning crosses between too distant species) (p. 43).

Wichura concluded from his observations that hybrids were intermediate in respect to the differing parental characters. Cases of dominance do not seem to have come under his hand. "Among the numerous artificial and natural willow hybrids observed by me," he says, "I have throughout verified but one apparent exception to the principle of intermediateness. . . . Even the time of flowering of hybrids holds the mean between the time of flowering of the two parents" (p. 47). "The leaf-form of *Salix caprea* \times *viminialis*, for example, holds so completely the mean between the linear-lanceolate leaves of *S. viminialis* and the round-ovate leaves of *S. caprea*, that they in fact appear to represent the mathematical mean between the curves for the outlines of paternal and the maternal leaves" (p. 47). With regard to what we should call absence of dominance, he has to say (p. 50): "As rich in species as the genus of the willows is, and as numerous combinations of hybrid fertilizations as it has to show, nevertheless I have never yet verified anything of a preponderant influence in any one of its species, but rather always found that their hybrids always hold the mean between the constant characters of the parents"; and again (p. 86): "In hybrid fertilization, if unlike factors unite, there arises an intermediate formation, etc."

The latter passage appears to be the first occasion where the term "factor" has been used in the literature of plant breeding, although here the factors referred to are the parents as a whole which participate in the cross, and not the character-forming elements of those parents. His general conclusion is (p. 46): "Constant characters, through which the parent species are distinguished from one another . . . go half over to the hybrid, so that it holds the middle position between them."

Two observations of Gärtner's were verified by Wichura—the identity of reciprocal crosses (pp. 51 and 186), and the fact of "variation" in hybrid progeny.

The question was as to the relative importance of the egg or the pollen in the result of fertilization. Wichura says (p. 57): "One sees the question is still far removed from having been brought to light, but from Gärtner's and my own observations it appears at least determined that the products of hybrid pollen in breeding are more various than those of the pollen of true species."

From the generally admitted identity of reciprocal crosses, Wichura draws the following conclusion (p. 86): "We have found that the products which come from reciprocal crossing, unlike the well-known experiments made in the animal kingdom, completely coincide with each other. *From this it follows, however, with mathematical necessity, that the pollen cell must have exactly the same share in the conformation of the fertilization product as the egg.*" (Italics inserted.)

Sofar as the writer knows, this is the first complete categorical statement in the literature of breeding of such a conclusion as to the behavior of the sex cells in amphimixis. One is completely impressed, in reading Wichura's work, with the scrupulous care, accuracy and precision with which his hybridization experiments were carried out. One or two passages in point are interesting. Referring to a case of Gärtner's, where exceptional types appeared in the midst of "a greater number of hybrid plants of completely similar hybrid types," he says (p. 53): "To judge concerning the here-mentioned exceptional types without myself having seen them is scarcely possible. From the relatively limited number of my experiments, which have not yielded the like, I cannot, to be sure, deny its possibility, but here likewise, as above in the case of reversions, the suspicion of a complete disturbance of the experiment, whether that the protection had not been complete, or the pollen utilized for fertilization not pure, or the seeds sown not free from foreign

admixture. Whoever knows from his own experience how much care must be observed in order to keep an experiment clean becomes skeptical respecting all results of an experiment which vary from the usual rule, of the correctness of which one has not achieved conviction through his own observation."

Regarding these and other so-called anomalies as the result of crossing, he again says (p. 89): "That concerning all these points and many other disputable questions . . . we know so little, has indeed its basis in part in the method hitherto of artificial cross-fertilization, which suffers from the double deficiency that the care requisite to the correctness of the experiment, through the exclusion of foreign pollen, has not been taken in the first place, and second, that although many experiments have been instituted in very different families, nevertheless the individual hybrids have not been bred and observed in sufficient number. However, this is imperative throughout for attainment of general results: Only when one has at hand the same hybrid in hundreds of cases, partly from the same, partly from different parents, repeated through different years, only then will one be in position to separate the essential phenomena of hybridization from the more accidental ones."

Finally (p. 92), Wichura remarks, expressing the hope that a learned society or an individual with means might repeat his own experiments on a larger scale: "The most scrupulous exactness in such case would be indispensable. Failing this, and especially if the possibility of the access of foreign pollen is not completely excluded, then all experiments, the more extensively they are undertaken, only contribute so much the more to the confusion of the matter. This must be taken to heart."

Regarding the possibility of securing, in any given case, a cross, Wichura remarks (p. 84): ". . . only such species can be united in a hybrid which agree in relatively many characters, and correspondingly in many life conditions. Experience teaches the same thing in the familiar rule, that hybrid combinations

only occur between species of the same genus, or though different, yet nearly related genera." This statement represents a point of view resembling that held by Gärtner, as we have seen. He comes to a generalization of genetic value in the following statement (p. 85): "It is known that families die out, after a few generations, whose members carry in themselves the germ of a disease, and who marry only among themselves; and variety breeders know very well that all diverging characters of animal and plant species may be intensified, when, in successive fertilization, the precaution is taken that only similarly divergent individuals mate with one another."

This closes the account of the work in the field of hybridization from the time of Koelreuter to the time of Gregor Mendel, 1760 to 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.

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