THE FOUNDERS OF THE ART OF BREEDING—III

Pre-Mendelian Breeders of the Nineteenth Century

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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?" and this, despite the fact that as far back as 1761, Koelreuter, in the preface to his published work, had flattered himself with the hope that now "even the most stubborn doubter of the truth of the sexuality of plants would be completely convinced." "If, contrary to all conjecture," he says, "there should be such a one, who after a rigid examination, still maintained the contrary, it would astonish me as greatly as though I heard someone on a clear mid-day maintain that it was night." Fifty-six years after this utterance, however, the Prussian Academy still sought light in the darkness that Koelreuter had flattered himself to have dispelled.

On the third of July, 1826, the Academy's prize was conferred upon Dr. A. F. Wiegmann, physician of Braunschweig. Since the investigation did not, in the Academy's opinion, furnish a complete solution to the question, but half instead of the whole of the prize was granted. The award was made in the following language: "The author has described the results of his investigation with appropriate brevity. These results are in part completely convincing, and in part not," the reason being given that certain of Wiegmann's hybrid specimens submitted scarcely showed evidence of being of a hybrid character. Since, on the other hand, Wiegmann's results completely confirmed and extended those of Koelreuter, and especially by reason of his determination of the fact that self-fertilized hybrids may bear fertile seeds, it was decided to grant an award.

Wiegmann, through forty years of observation, including the fact of having actually produced two geranium crosses as early as his sixteenth year, was already predisposed toward the affirmative of the question submitted. His investigations, begun in 1822, were finally published in 1828. In order to overcome all possible criticisms from the opponents of the idea of sexuality in plants, which he considered might be directed against what he refers to as "an unnatural handling of plants in pots," he conducted his operations in the open ground, in connection with which he alludes to the several hindrances he was obliged to undergo, "weak sight, a trembling hand, and painful bending and kneeling" (p. 2).

Wiegmann refers to the many failures encountered, including the attempted repetition of a number of Koelreuter's experiments, as being probably due in part to having attempted crosses between different genera, "since many stigmas, according to my numerous experiments, take the pollen of too distant genera either not at all, or with extreme difficulty" (p. 2). "Plants which together are to produce hybrids," he says (p. 26), "must have some relationship with one another, as Koelreuter has already remarked. The nearer the parent plants are related to one another, the more easily will hybrid fertilization succeed; most easily in the case of different sub-species or varieties; then different species of the same genus; less easily in the case of plants of different genera."

Wiegmann, however, was completely free from any rigid dogmatic attitude on the species question. His views in this regard are completely modern.

Continuing the above, he says, "Yet at the same time, one needs indeed pay less attention to differences based on artificial generic characters. Genera like *Pisum* and *Vicia*, *Ervum* and *Vicia*, *Lychnia* and *Cucubalus*, are in their nature so related that hybrids can arise from them, as Koelreuter and I have demonstrated" (p. 27). "So much the more I dispute his opinion," he says of Koelreuter (p. 25), "respecting the falsely derived difference between true 'species' and 'variety' from the fertility or infertility of the hybrid plants."

CHANCE CROSSING IN NATURE

Wiegmann in fact 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 (p. 26), "that many species, or constant subspecies, e. g., *Pisum arvense*, *Vicia leucosperma*, *Vicia faba* (red-seeded), 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 gardens, through the proximity of a few related plants, and which have remained constant."

Wiegmann sums up the matter of the bearing of degree of relationship upon crossing as follows (p. 27): "Mainly it comes to the point that the different plants do not vary from one another greatly in their natural constitution, and that their secretions are not too heterogeneous, since otherwise the pollinating substance would not be absorbed by the stigma. "In general," he says, "foreign pollen takes hold of the stigma with much greater difficulty than does its own, and in order to obtain complete fertilization, one must often deposit it several times, even when the foreign pollen is from a plant of the same species" (p. 3).

Wiegmann's experiments covered a list of thirty-six crosses, using the following species and cultivated varieties:

Allium (onion, etc.), 2 species.

Brassica (cabbage, etc.), 4 race-species.

Dianthus (pink), 3 species.

Ervum (lentil), 1 species.

Nicotiana (tobacco, etc.), 2 species.

Phaseolus (bean), 2 varieties.

Pisum (pea), 2 species.

Vicia (vetch), 1 species.

The general conclusions Wiegmann draws from his experiments are most interesting. The most important are those which relate to the possible vigor of new species (p. 3): . . . "My experiments sufficiently prove," he says, "that the fertilization of different subspecies, *inter se*, is a source of manifold running-out of species in the plant kingdom, and that insects, especially bees and humblebees, as well as little beetles and flies, play a much more important rôle in the fertilization of plants than one has lately been inclined to allow them, but of which I have the most indubitable proofs."

"Even though the structure of the corolla in the case of leguminous plants," he says again (p. 26), "scarcely appears to admit of the access of insects and foreign pollen, yet the plants obtained from the seed of experimental plants show such a striking alteration in their specific characters, especially in the form of the seed and its envelopes, that an influence of foreign pollen on the ovules will scarcely be able to be denied. I myself have numberless times convinced myself of the fact that humblebees, bees and small insects from the orders of flies and beetles, can fertilize the flowers of the Leguminosae in the manner stated by Sprengel. It is therefore necessary in agriculture to give heed to this matter, if one wishes to keep plants that are to be cultivated, in their quality and integrity."

With respect to observations of a more special nature, Wiegmann's memoir contains much of interest. Regarding the breaking up of the progeny of hybrids, he says, speaking of Koelreuter's observations: "I have found his observation well founded, that the plants produced from one seed and from one capsule of hybrid plants often differ from one another in respect to fertility, and especially in the struc-

ture of certain parts, now approximating more to the father, now to the mother" (p. 25).

Wiegmann's independence of traditional authority is witnessed in his contradiction of the view of "the great Linnaeus," that hybrids resemble the mother in the fertilization apparatus and the father in foliage and habit. Instead, he says: "the change through the foreign fertilizing pollen shows itself in very different parts in different plants; in the anther filaments, . . . in the inflorescence, in the form, color, and odor of the corolla, in the height of the stem and its divisions, in the form and outside covering of the leaf" (p. 23).

Referring to the then general assumption that hybrids (of the F_1 generation, as we should say) occupy a mid-position, with respect to their characters, between the two parents, he says: ". . . in many cases this does not occur, but either the color of the father or that of the mother shows itself alone dominant (herrshend) in the hybrid. The same also obtains among animal hybrids; the two colors may, through mingling, give an intermediate one, but in just as many cases the one only prevails. Plant hybrids therefore unite in themselves in part the peculiarities of the father, in part those of the mother, whereby they approach now the maternal, now the paternal form" (p. 21).

THE QUESTION OF DOMINANCE

Regarding the matter of dominance, Wiegmann further incidentally remarks upon the case of the crossing of two species of *Dianthus*, where "the form of the father has almost entirely suppressed that of the mother" (p. 22).

To the present-day geneticists, one of the most interesting points in Wiegmann's report is his discussion of the immediate effect of the pollen in the case of peas. According to his statement, that there occurs, "even immediately after fertilization, an alteration arising in the form and color of the seed, and in the form and size of the pods, is especially unmistakable in the case of the leguminous plants, although

otherwise all fruits and seeds of hybrid plants from other families, have never shown themselves to me to be different from those of the mother plants" (p. 23). And again, "The principle expressed by Gärtner, that the influence of foreign pollen changes nothing in the form and external character of the fruits and seeds of the mother plant, should, according to my investigations, undergo a modification in the case of the *Diadelphina* (Leguminosae), since, in the case of these, the foreign pollen exerts an immediate effect upon the form, color, and other characters of the fruits and seeds" (p. 29).

In the case of *Phaseolus* (common bean), he says; "Previous experiments have taught me that *Phaseoli* of one species, but of two kinds of flowers and seeds, when placed together, bear differently colored seeds, and, in the second generation, also differently colored flowers" (p. 23).

Wiegmann carried on some field experiments with beans, vetches, oats, and cabbage, in which adjoining rows of plants were allowed to freely cross-pollinate through the agency of wind and insects, from which he concluded: "It appears further, from the behavior of the Leguminosae and of cabbage, that agronomists and gardeners cannot be careful enough in the arrangement of their fields, in order not to suffer from the great damage through hybrid fertilization occurring even the first year" (p. 36).

Speaking generally, he says further (p. 30): "It is not entirely improbable that that which exhibited itself to me thus far, as being peculiar to the Leguminosae alone, may take place also among other plant-families, and the clearing up of this matter remains very desirable for botany, as well as for agriculture in particular" (p. 30).

Wiegmann's work, as a whole, impresses one as the work of a man without scientific prepossessions, willing to investigate for himself, to dispute freely the authority of other investigators such as Linnaeus, Koelreuter, and Gärtner, and, withal, a man with a practical bias and a sympathy for agriculture.

In the valley of the Nagold, in the Black Forest region of Württemberg, some 40 miles southwest of Stuttgart, the capital, lies the village of Calw. Here Koelreuter, whose home was in Sulz, a little way to the south in the Neckar valley, lived for a time, and did some of his work on hybridization, in the garden of a local physician. By a curious coincidence, in the same village of Calw in which Koelreuter had previously worked, and but 40 miles north of Sulz, where also Koelreuter had formerly obtained the first hybrid plant ever produced in a scientific experiment, lived and died Carl Friedrich von Gärtner, who for twenty-five years conducted extensive experimental work in hybridization. He was a son of the distinguished botanist Joseph Gärtner, Professor at Tübingen and St. Petersburg, and author of an authoritative work on the seeds and fruits of plants, in which figured the morphology of more than a thousand species. The introductions to the volume for 1788 contain, in the words of Sachs, "valuable reflections on sexuality in plants."

In 1830, two years after the appearance of Wiegmann's memoir, the Dutch Academy of Sciences at Haarlem, propounded the riddle of hybridization anew in the following words: "What does experience teach regarding the production of new species and varieties, through the artificial fertilization of flowers of the one with the pollen of the other, and what economic and ornamental plants can be produced and multiplied in this way?" No reply was received by the end of the time for which the prize was offered (January 1, 1833), and the offer was accordingly renewed for another three years (until January 1, 1836).

In October, 1835, Gärtner learned of the prize offer and was able to present a brief résumé of his work up to that time, which, indeed, prompted a further extension of time on the part of the Academy. Gärtner finally presented the Academy with a memoir of two hundred pages, and with herbarium mounts of one hundred and fifty different sorts of hybrid plants produced by hand pollination. On May 20, 1837, this memoir received the prize and was later (April 20, 1849), published in revised and extended form, together with an extensive list of the experimental material, and with the obtained results arranged in tabulated form.

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.

Among the prominent genera worked with were *Althaea*, *Avena*, *Campion*, *Columbine*, *Currant*, *Datura* (Jimson weed, etc.), *Fox-glove*, *Fuchsia*, *Gladiolus*, *Larkspur*, *Lobelia*, *Maize*, *Mallow*, *Mullein*, *Nicotiana* (Tobacco, etc.), *Oenothera* (Evening Primrose), *Pink*, *Poppy*, *Primrose*, *Snapdragon*, *St. Johnswort*, and *Stocks*.

The following brief table, giving some of the numerical data, in crosses involving a few of the principal genera, will afford a conception of Gärtner's labors; yet these constitute but one-tenth of the total number of his crosses.

<i>Genus</i>	<i>No. of species used in the crosses</i>	<i>No. of attempted combinations</i>	<i>No. of hybrid plants obtained</i>
<i>Nicotiana</i> (tobacco, etc.)	23	432	85
<i>Dianthus</i> (Pink)	20	349	87
<i>Lychnis</i> (Campion)	..	137	18
<i>Verbascum</i> (Mullein)	14	118	97
<i>Lobelia</i>	4	97	20
<i>Digitalis</i> (Foxglove)	9	59	14
<i>Datura</i> (Jimson weed, etc.)	8	55	16
<i>Oenothera</i> (Evening Primrose)	19	52	6
<i>Aquilegia</i> (Columbine)	9	33	23
	107	1332	366

Gärtner undertook to classify hybrids for convenience into three types: (1) intermediate, (2) commingled, and (3) decided. The first included those in which "a complete balance occurred of both fertilizing materials, either in respect to mass or activity" (p. 227). Commingled types are those in which "now this, now that part of the hybrid approaches more to the maternal or to the paternal form, whereby, however, the characters of the parents, in their transference to the new organism, never go over pure, but in which the parental characters always suffer a certain modification" (p. 282). Under the third class of hybrids, Gärtner places those "among which the resemblance of a hybrid to one of its parents, either to the father or the mother, is so marked and preponderating that the agreement with the one or with the other is unquestioned" (p. 285).

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. He made no distinction between the second and the other following generations, and simply says that the fundamental ground material of which the hybrid is made "behaves differently in the second and in the further stages of breeding, where, on account of the different nature of the two factors of the hybrid in the succeeding fertilizations, an altered, shifting, variable direction in type-formation enters into the arising varieties" (p. 572).

He further says, concerning variability in hybrids of the second and succeeding generations: "Other hybrids, and in fact the most of them which are fertile, present from the seeds of the second and further generations, different forms, *i. e.*, varieties, varying from the normal types, which in part are unlike the original hybrid mother, or deviate from the same, now more, now less" (p. 422).

Gärtner's most definite statement, however, regarding what we call "seg-

regation" in the second hybrid generation, is as follows: "Among many fertile hybrids, this change in the second and succeeding generations affects not only the flowers but also the entire habit, even to the exclusion of the flowers, whereby the majority of the individuals from a single cross ordinarily retain the form of the hybrid mother, a few others have become more like the original mother parent, and, finally, here and there an individual more nearly reverted to the original father" (p. 422).

Gärtner did not fail to recognize the fact of unusual vigor in hybrids, although he does not distinguish as to the generation: "The marked increase in the size of the flowers is a phenomenon not seldom occurring among hybrids" (p. 295); and "one of the most marked and general characters of plant hybrids is the luxuriance of all their parts, since, among very many of them, an exuberance of growth and development of roots, branches, leaves and flowers manifests itself, which is not encountered among the parents, even under careful cultivating" (p. 526).

PRACTICAL POSSIBILITIES

Gärtner recognized at once the possibilities for agriculture in this fact of the increased vigor of hybrids, although, of course, he did not realize the fact that this increased vigor belonged to the first or hybrid generation, properly so called: "Among the characters of hybrids worthy of recommendation for agriculture, their tendency toward luxuriance in stalks and leaves and their extraordinary capacity for tillering is related above. With respect to the raising of forage, agriculture could, without doubt, make great use of this characteristic" (p. 634).

Gärtner derived, from his long experience, a certain philosophy concerning the nature of hybrids which is noteworthy. He recognized an inequality in the influences 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. As we now understand it, it

means the relative dominance of one or more factors or character-units of the parents. 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" (*Wahlverwandschaft*) 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 seems to confuse the matter by appearing to indicate that there might possibly be a different number of seeds produced by the reciprocals of reciprocal crosses, thus presumably indicating a possible "prepotency," so called, of one of the parents in the cross. In other places he simply seems to mean the relative influence, so to speak, of such and such species when crossed with others. This appears to be the meaning in the following:

"This manifestation of generic types, according to which one species acts in a predominant manner over several other species in hybrid breeding, is a further uncontradictable proof that the relationship of the forces, through which the union of two pure species takes place, must be unlike, and that thereby there can be no question of any balance of factors" (p. 290).

It will be seen that Gärtner's view of hybridization was that "species" was crossed with "species" as such, each species as a whole exerting its own relative power or potency in the cross—the hybrid being regarded as the resultant, so to speak, of the contest for supremacy of the two competing natures in the compound. This view is well enough expressed in the following passage: "Thus, just as there are species in a natural genus, which possess a prepotent fertilizing power upon several other species of their genus, so there are also species which exert upon several others such a typical predominating effect, not to an equal extent, to be sure, but still of such a nature that their operation, in all combinations, is to be recognized by a character in common.

Both of these forces are, however, of

different kinds and follow different laws" (p. 289).

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. "The laws of hybrid types orient themselves, not toward the individual organs of plants—do not apply to a single part, *e. g.*, stems, leaves, etc.—but are applicable rather to the inner nature of species. The organs which determine the types of hybrids must therefore be investigated and compared in their totality and in their mutual inter-relationship. For the most part, the individuality of a hybrid expresses itself in its entire habit, but in this respect the flower, above other parts of the plant, is most frequently and plainly distinguished" (p. 251).

Gärtner made some crosses with corn and with peas to determine the question of the immediate influence of the pollen upon the character of the seed. In corn he got no results, because of crossing white corn with red, in which latter the color, being due to the skin or pericarp, does not show until the seeds of the following season ripen. In peas he crossed four varieties. In certain crosses, *e. g.*, Paris Wax (yellow) × Sugar Pea (greenish-yellow), Early Green Brockel (green) × Paris Wax (yellow), and Sugar Pea (greenish-yellow) × Dwarf Creeping (yellow), the yellow color dominates over the green in the hybrid seeds.

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, if we may judge from his own statements; as, for instance, the following:

"For complete assurance of the purity and reliability of the products of hybrid breeding, and for testing the conclusions derived therefrom, we have repeated most of the experiments, especially the doubtful cases, not once only, but several times, and put them to the test through crossing of the same species, for even with the most scrupulous foresight and precision, individual

rare instances have still occurred in these tedious and wearisome investigations, where the suspicion had made itself felt, of a mistake or error having crept in, either in pollination or emasculation, since such results stood in direct contradiction to the usual experiences, and on a repetition of the experiments, made itself incontrovertibly evident as an error. We believed it possible to attain no higher degree of certainty in this branch of natural science, and to be able to bring the conclusions derived therefrom to no higher proof, than through the precise coincidence of the forms of the products, by repetition under the same conditions with the same species, but with different individuals, and at different times" (p. 675).

THE ENGLISH BOTANISTS

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.

THE WORK OF KNIGHT

Knight was a country gentleman by occupation, born August 12, 1759, and educated at Oxford, and who 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 1795 his work as a horticulturist first became known through some papers read at the sessions of the Royal Society. He was an organizer of the Horticultural Society of London, founded 1804, of which he was president from 1811 until his death in 1838. He was an annual contributor to its "Transactions" and was the author of upwards of one hundred papers. In 1841, three years after his death, a collection of eighty-two of his papers was published by the botanists Bentham and Lindley. Of Knight's published papers, forty-six are enumerated in the Royal Society's Catalogue. Knight was not a scientific man, but a practical horticulturist with scientific

instincts, who proceeded on the principle that the improvement of plants depended upon the same scientific laws as the improvement of animals, and that cross-breeding was the key to the origination of new and improved sorts. His 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." This paper is really, in part, a reply to certain phases of the experiments of John Goss upon the same plant. Knight's introductory statement, which follows, is a curious reminder, in point of form, of Mendel's own introduction to his report upon his experiments with peas nearly half a century later:

"The numerous varieties of strictly permanent habits of the pea, its annual life, and the distinct character in form, size and color of many of its varieties induced me, many years ago, to select it for the purpose of ascertaining, by a long course of experiments, the effects of introducing the pollen of one variety into the prepared blossoms of another. My chief object in these experiments, was to obtain such information as would enable me to calculate the prob-

able effects of similar operations upon other species of plants, and I believe it would not be easy to suggest an experiment of cross-breeding upon this plant, of which I have not seen the result, through many successive generations."

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 uniformly 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—in other words, the result of the cross of a recessive white upon a hybrid dominant grey, as we should say nowadays. No numbers are reported, so that a scientific basis of ratios, as later found by Mendel, was not laid. Despite the fact that Focke says (p. 436) "he has contributed more to our knowledge of hybrids than any other writer during the first half of the nineteenth century"—a statement which may well be seriously disputed—it is nevertheless true that Knight was the first experimenter to apply the science of plant hybridization to plant improvement. Although endowed with scientific insight of no mean order, his chief claim to recognition lies in the fact that he possessed a practical instinct for getting improved orchard fruits into existence.

The following examples will serve to illustrate the nature of his results. Of his currant crosses, he says: "Five varieties, three red and two white. out of about two hundred, appeared to me to possess considerably greater merits than either of their parents, and one of the red will, I believe, prove larger than any red currant now in cultivation."

By crossing the "Noblesse" peach (female) by "Nutmeg," (male), he

obtained about twenty seedlings, of which three "appeared better peaches than I previously possessed." Of one of these he says: "Its fruit has attained a more uniform degree of perfection than I have ever witnessed in any other variety. The trees have also been free from every vestige of mildew, in the situation where the disease is very prominent, and have entirely escaped the attacks of insects."

As to the result of his crosses of apple varieties with the Siberian Crab, with the object of producing fruits that would ripen in cold and exposed situations, he says: "The plants thus produced seem perfectly well calculated in every respect to answer the object of the experiment, and possess an extraordinary hardiness and luxuriance of growth."

WILLIAM HERBERT

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. Fond of outdoor life and sport, he possessed also, in addition to literary talent, an instinct for plant studies. 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, as the following comment indicates:

"The first experiments, with a view to ascertain the possibility of producing hybrid vegetables (plants) appears to have been made in Germany, by Koelreuter, who published reports of his proceedings in the Acts of the Petersburg Academy between fifty and sixty years ago. *Lycium*, *Digitalis*, *Nicotiana*, *Datura*, and *Lobelia* were the chief plants with which he worked successfully, and as I have found nothing in his reports, to the best of my recol-

A PIONEER IN THE STUDY OF HEREDITY

Thomas Andrew Knight (1758-1838)

An English horticulturist who published in 1795 his views on the inheritance of diseases among fruit-trees, which attracted much attention. (Fig. 20.)

lection, opposed to my own general observations, it is unnecessary to state more concerning his mules, than the fact that he was the father of such experiments. They do not seem to have been at all followed up by others, or to have attracted the attention of cultivators or botanists as they ought to have done; and nothing else material on the subject has fallen under my notice of earlier date than Mr. Knight's report of his crosses of fruit trees, and my own of ornamental flowers, in the Transactions of the Horticultural Society of London. Those papers attracted the public notice, and appear to have excited many persons, both in this country and abroad, to similar experiments."

Herbert's experimental work was animated by the conviction 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 was 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 has 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

pod 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 (*i. e.*, of the cotyledons), instead of being a deep blue like those of the female parent, was yellowish-white like that of the male. Here was evidently a case of complete dominance of yellow-white over blue cotyledons. However, the plants 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 color in separate rows. He found that the blue seeds, which we should now call the "recessives," 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.

Although Goss in this experiment undoubtedly made evident the facts of dominance and of segregation, he did not recognize them as such, nor did he, apparently, sow the seeds of his different plants separately, or make counts of the number of seeds of the two colors found on each separate plant, as did Mendel in his experiments. Goss was chiefly interested in the question of the possibility of the "new variety" having superior value as an edible pea, and yet remarked that, in case it possessed no superior merit, that there yet might be "something in its history that will emit a ray of physiological light." However, the "physiological light" did not appear until after the rediscovery of Mendel's papers in 1900. The paper of John Goss was read before the Horticultural Society, October 15, 1822. At the meeting of the 20th of August preceding, a communication was read on the same subject from Alexander Seton. Seton had pollinated the flowers

of the Dwarf Imperial, a grey-seeded pea, with the pollen of a tall white-seeded variety. One pod with four peas was produced, all of which were green, *i. e.*, the dominance of green cotyledon color over its absence (white). The plants growing from the four peas (F_1 seeds, as we should call them) were intermediate in size between the two parents, and the pods, on ripening, "instead of their containing peas like those of either parent, or of an appearance between the two, almost every one of them had some peas of the full green color of the Dwarf Imperial and others of the whitish color of that with which it had been impregnated, mixed indiscriminately and in undefined numbers; *they were all completely either of one color or the other, none of them having an intermediate tint.*" (Italics inserted.)

Here again were recorded the phenomena of dominance and of segregation, but owing to the fact that the numbers of seeds of each color of each plant were not counted and recorded separately, the results were not available for scientific purposes, nor would they have aroused attention any more than those of Goss, except for Mendel's later work with the same kind of plants.

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(To be continued)