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THE CONTRIBUTION OF CARL FRIEDRICH VON GÄRTNER TO THE HISTORY OF PLANT HYBRIDIZATION

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In the beginning of the nineteenth century, the question of the sexuality of plants was still undergoing a certain amount of disputation, despite Koelreuter’s investigations; the history of which episode is sufficiently traceable through the writings of Schelver and Henschel. In order to assist in the settlement of the matter, the Royal Prussian Academy of the Sciences at Berlin, made public announcement in 1819 of an offer of a prize for the solution of the question—"Does hybrid fertilization exist in the plant kingdom." No response having been evoked, the Academy extended the competition period, and doubled the amount of the prize offered. On July 3, 1826, the prize was awarded, although not in its entirety, since the Academy did not consider the solution adequate, to Dr. A. F. Wiegmann, of Braunschweig.

In January, 1830, the question was propounded anew by the Dutch Academy of the Sciences at Haarlem, in the following language:

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 others, and what economic and ornamental plants can be produced and multiplied in this way.

Since, by the termination of the contest period, January 1, 1834, no response had been received, the period was extended to January 1, 1836. In October, 1835, Carl Friedrich von Gärtner of Calw, son of a distinguished botanist, Joseph Gärtner, formerly professor at the universities of Tübingen and St. Petersburg, and who for a
considerable period of years had been conducting experiments of his own in hybridization, became aware of the offer of the Dutch Academy. Thus far, only brief reports of his work had appeared at Tübingen and Paris.

On account of the shortness of the time available, Gärtnert sent to the academy merely a preliminary report of his experiments, accompanied by one hundred and fifty mounted specimen sheets of his different plant hybrids, which elicited a favorable response, and induced the academy to grant an extension of the time for sending in the completed work to December 30, 1836. The interesting resolution of the committee runs in part as follows:

That, in view of the number of new results, which could only have been obtained through very manifold investigations over many years, the service of the author be acknowledged.

The requirements of the committee having been compiled with, the award was formally conferred on May 20, 1837. The thesis appeared in Dutch translation, as a document of 202 pages, in the Proceedings of the Academy for 1838. In 1849, a revised and greatly enlarged edition, "the fruit of unbroken, zealous, almost twenty-five years' work," was published in German at Stuttgart.

The writer has found nowhere in current literature any adequate presentation of this seldom read, and little referred-to work, and yet it contains not only much interesting information of a concrete nature, but a great deal of speculative philosophical insight in dealing with problems in hybridization, that shows a scientific mind of distinct value.

Sachs says of the writings of Gärtnert (3), "The two works together, are the most thorough and complete account of experimental investigation into sexual relations in plants which had yet been written. They are a brilliant termination of the period of doubt with respect to sexuality in plants, which succeeded to the age of Koelreuter." "And thus it was," says Sachs further,—"in two small cities of Württemberg, that the foundations of the sexual theory were laid, and the theory itself perfected, so far as it could be, by experiment only, by three of the most eminent of observers, Camerarius of Tübingen, Koelreuter and K. F.
Gärtner of Calw, who contributed so largely to the empirical establishment of the theory, that all that was done by others would seem of small importance” (p. 427).

As Focke says ((1) p. 437), “In numbers of experiments, he has probably been surpassed by no other hybridizer.”

An idea of the sheer laborious work which Gärtner’s operations involved, may be obtained from the mere statement that he performed close to ten thousand separate experiments in crossing, involving nearly seven hundred different species belonging to eighty different genera, and from which some two hundred and fifty hybrid plants were produced.

From such a large mass of detail as Gärtner’s memoir involves, it is difficult to derive a concise series of statements of the experimental results. In endeavoring to group the phenomena of hybridization upon a scientific basis, Gärtner undertook to classify hybrids into three divisions, according to their external habit: (1) “intermediate types,” (2) “commingled types,” and (3) “decided types,” although, as he says (p. 277):

There exists no exact delimitation among them, but they go variously over into one another, so that it is not seldom very doubtful to which of these forms, this or that hybrid should, with the greater right be assigned.

In regard to the intermediate types, Gärtner follows Koelreuter’s view that, as in the fertilization of pure species, so also with hybrid breeding in the case of simple hybrids, a complete balance occurred of both fertilizing materials, either in respect to mass or activity. In this assumption he was still further strengthened through the similarity of types from reciprocal crossing. He believed further, that in the later generations of simple hybrids, and in the further grades of hybridization, where no such regular process of hybridization occurs, the inclination of types either toward the father or the mother, proceeded from the not quite complete balance, or the slight overbalance of the one or the other fertilization materials (p. 277).

Regarding the so-called “commingled” types, Gärtner says as follows (p. 282):
The second kind of types, frequently occurring among hybrids, is that with commingled parental characters, insofar as 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.

Under the third class of hybrid types, Gärtner considers those—

Among which the resemblance of a hybrid to one of its parents, either to the father or to the mother, is so marked and preponderating that the agreement with the one or with the other is unquestioned, and strikes one at once (p. 285).

Regarding the behavior of plant hybrids in the first hybrid or $F_1$ generation, as compared with their behavior in the second generation, Gärtner’s remarks are interesting, although not based on numerical data.

Among plants, by far the greater number of the normal and regular types of the hybrids from the first cross, as compared with the exceptions and varieties, testifies against the operation of . . . external influences, and proves rather the inner necessity of a regular formative development according to law on the part of pure species in general as well as of hybrids (p. 275).

Regarding this supposed formative force (Bildungskraft), Gärtner arrived at a conception of the inner nature of the phenomenon occurring in hybridization, which is scientifically interesting, although amounting to a theory, and not to a conclusion directly derived from experiment.

The foundation and the determination of the types of hybrids, might therefore be discoverable, not so much in the mass and the relationship of the germinal materials, as in a vital modification of the formative force of the one or the other fertilization material (p. 270).

As we now know from Mendel’s experiments, however, it is this modification of the “sexual material” itself which pre-determines the direction in which the formative force may run. In Gärtner’s day, the abstract conception of a relative potency of the one or the other parent in hybridization, was a prevalent one, and this statement above is a philosophical conception, which
Mendel’s data made it possible to precipitate into a definite morphological theory. Gärtner went so far, however, as to attempt to measure this “potency” in a definite manner, by means of the number of viable seeds produced in reciprocal crosses.

That this relation of the factors of the fertilization forces in the case of species of plants capable of hybridization, is definite and according to law, we assume from the fact that from such a hybrid combination come more or fewer good seeds to be sure, according to the favorableness or otherwise of the incidental circumstance, but that, however, in the case of every such hybrid combination, it is never able to produce over a certain maximum of viable seeds, which maximum is peculiar to each combination of that kind (p. 206).

Gärtner goes so far as to say:

The inequality in the strength of sexual affinity (Wahlverwandtschaft), in the case of the reciprocal combination of species, is a general phenomenon occurring in plants, and will therefore lead in time to the disclosure of the relations, and to a closer determination of the value in respect to magnitude of the individual factors of sexual affinity. This inequality establishes a scale of sexual affinity peculiar to each species, which lies in the difference in the relationship of the strength of the two factors. In this singular characteristic of plants, the peculiar nature of the species is most plainly recognized,—much more, in fact than in its external form (p. 200).

Those species which are able in crossing, to exert a preponderating influence upon other species, Gärtner calls “generic types.”

Just as such generic types in hybrid breeding, are able, as it were, to gain the upper hand over the type of other species, so is the strength and form of these species broken and overmastered by others (p. 290).

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 there can be no question there of any balance of factors. To be sure in mixed hybrids, the relationship of the formative forces of the two sexual substrata appears to be tolerably alike; however, in them likewise, in this or that part of the hybrid, now the character of the one, now that of the other factor is more plainly expressed (p. 290).

Gärtner seems to see in this dominance of type in
species, a way of evolution which leads to the establishment of dominant family types.

The generic types appear to have their analogue in the natural family types, and, since the origin of family types has occurred according to certain laws, so will type-formation of hybrids, since it is not at random, but is constant, follow the same laws, according to which plant forms in general are formed and have developed (p. 291).

This brings Gärtnér to a further statement regarding the possibility of recreating ancestral types, which is especially interesting as a pre-Darwinian view upon evolution. Referring to species of Lobelia, Lychnis, Dianthus, etc., he says:

If these nearly related species had once come from a common ancestral type, or had become separated from one another through the subsequent development of the one or the other individual, then it appears to be highly improbable that they would not again unite in their ancestral form through reciprocal crossing, or prove themselves to be analogous types in hybrid breeding (p. 163).

Gärtnér then arrives at one of the most striking conclusions in the older literature on the then so much mooted species question, and which is the more interesting because it takes the physiological rather than the morphological point of view. He says:

The essential nature of a species, therefore, consists in the definite relation of its sexual forces to other species, which relationship, taken together with the specific form, is a characteristic, individual and constant one; for every species, form and essence in this regard are one (p. 163).

Gärtnér frequently returns to a philosophical contemplation of the nature of the fertilization process in hybridization, characteristically as follows:

Not external resemblance in form and habit of species, but the harmony of the inner nature, gives the capacity for hybrid fertilization; both are not always harmoniously bound together (p. 186).

For an actual hybrid combination, a certain harmony in both sexual elements is, however, necessary, and precisely in this harmony lies the capacity for the union of two otherwise heterogeneous species (p. 110).

Only a harmony of the inner nature, on which the relationship of the germinal materials rests, which indeed is ordinarily accustomed to be associated with the external generic characters, but is not necessarily
bound up with concordance in external structure, determines the presence of the capacity for hybrid fertilization (p. 142).

In the following discussion, more or less in the same manner, Gärtner shows an intellectual freedom from the fetish of morphological species, and clearly demonstrates the possession of a physiological temper and attitude of mind.

Our investigation concerning harmony of forms in families and genera, have shown that we have to consider two different kinds of relationship among plants, an external and an internal: the former rests upon conformity in habit, i.e., in growth, in the shape and form of the leaves, and in the harmony of the flowers and the organs of pollination: these, however, in their greater or lesser inclination to sexual combination of species in hybrid fertilization. The former might be identified with the morphological, the latter closely with the physical relationship. Now, since both are not infrequently met with in combination, for that reason, our predecessors have not clearly distinguished both kinds of relationship from one another, but have held both as identical, or rather, have regarded the inner relationship as an immediate consequence of the external, and assumed this as a law, so that the agreement of species in habit, not only favored, not merely the existence, but also the strength of the sexual attraction, and indeed likewise conditioned it (p. 166).

From the agreement of the external form and habit of species of plants it may not therefore be inferred, that the sexual powers and relationships must also agree therewith, as experience indeed teaches, that many plants, however congruent they otherwise are in form, and even in organs of fertilization, nevertheless possess little or no inclination to unite in hybrid fertilization. One of the best-known examples of this is Pyrus and Malus, which, despite their near relationship in habit and sex organs, from the testimony of other observers also, do not admit of fertilization on the one side or the other (p. 167).

In the following passage, the morphological and the physiological points of view are well contrasted:

The systematic genera are artificial syntheses, which are not united according to absolute laws, but according to arbitrary external characters, which indeed often harmonize with the inner nature of the species, but likewise not seldom differ from this, if indeed it is not to be questioned, that even these characters proceed from the inner organism, and are determined through it (p. 139).

Gärtner, no more than any other investigator in the field of hybridization of his day, with the possible excep-
tion of Sageret, had any conception of the idea of unit characters operating as such, and capable of being analyzed separately. The then prevalent idea was one of "potency" and "pre-potency," in the case of the hybrid types that Gärtnert called "decided," i. e., in which the dominance of the one or the other parent was plainly evident. A species in a cross was supposed to function as a whole as such. An idea of this older point of view is obtained from the following:

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).

Gärtnert did not regard Sageret's case of segregation of characters to be the normal result of hybrid fertilization. While it is true that Gärtnert recognized in a certain sense the fact that parental characters often behave in a more or less unitary manner, he was led by the nature of his mind, as well as by the results of his observations, to take a synthetic rather than an analytical view of the hybrid organism.

The explanation of the origin and development of the forms of the hybrids from the elements and characters of the parents, is as important for plant physiology as for systematic botany (p. 25), and further,—

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 interrelationship. 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).

However, Gärtnert's most fundamental view upon the question whether the plant as a whole, or its individual characters considered as such, determine the nature of the hybrid offspring, is expressed in the following clear manner.
In the formation of simple hybrids, as in sexual propagation in general, two factors are functional; this inequality of activity flowing out of the specific difference of species, expresses itself in the more marked or the more feeble emergence of the individual paternal characters in the different parts of the hybrid. Whether the species nature in its entirety and its formative impetus, determines the direction and form of the type, or whether also the individual parts of plants have a special influence upon modifications, can only be determined through further investigations (p. 257).

In the absence of what he deemed sufficient evidence to the contrary, Gärtner conservatively adhered to the view that the parent organism entered into the cross as a whole, rather than as a congeries of character-units, behaving in a manner separately, although often linked together.

Regarding the recognized instability of hybrids, Gärtner simply says, without distinguishing as to the generation:

Variability in the progeny of hybrids is a principal character of hybridity (p. 518).

So far as any distinction as between the first and second generation is concerned, Gärtner merely says:

The general laws of development of the parts of plants, hence appear to undergo through hybridization no change perceptible to the senses, but all the developments and changes of the hybrid plant body appear to follow the same laws as in pure species, the organs of reproduction, and the material ground materials of the cross alone excepted.

The latter behaves differently in the second generation and in the succeeding stages of hybrid fertilization, where, on account of the different nature of the two factors of the hybrid in the succeeding zygoses, an altered, shifting, variable direction in type-formation enters into the varieties thus originating (p. 572).

Concerning variability in hybrids of the second and succeeding generations, he says:

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 type, which in part are unlike the original hybrid mother, or deviate from the same, now more, now less (p. 422).

Perhaps the most definite allusion describing the con-
dition in general terms, of what we term segregation in the second generation, is the following:

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).

Regarding the matter of unusual vigor in hybrids, Gärtner remarks, giving examples, although again without referring to any particular 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 luxurance 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 cultivation (p. 526).

Gärtner did not omit to apprehend the possible value of this fact to agriculture, although, of course, he did not recognize the first hybrid generation as a special phenomenon.

Among the characters of hybrids worthy of recommendation for agriculture, their tendency toward luxurance 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).

So far as genetics from the present technical standpoint is concerned, Gärtner’s data of course are not of special interest, because his crossing was made upon species as units, and not upon the character-unit basis, and no records were made of the numbers of the different types secured from his crosses. It is of interest to note, however, that Gärtner’s methods in his hybridization operations partially anticipated the rigorous methods of to-day, regarding the purity of parental types.

In order to judge with certainty concerning the nature of the types which have arisen, and in order to obtain entirely reliable results, it is
above all necessary that one be in advance in complete certainty concerning the species with which the experiments shall have been instituted, that they be specifically correctly determined, and that no doubt prevail concerning their purity (p. 252).

Finally, Gärtner’s investigations upon color inheritance, which cover thirty pages of text, while not of genetic value from the modern standpoint, are interesting and valuable as a summary of the then existing knowledge on the subject. One observation upon intensification of color deserves mention:

Red with red, not seldom gives a heightened brilliancy of color, as is especially plainly shown in the flame-colored flowers of Lobelia cardinalis, fulgens and splendens (p. 315).

One of the matters of genetic interest is the fact that Gärtner experimented in the crossing of corn, with a view to determining the matter of change of color in the seeds due to crossing, as reported by Sageret. Unfortunately for Gärtner’s experiment, however, he crossed a dwarf yellow corn without pericarp color, with corn having colored pericarp (“of red, gray and striped color”), instead of with colored endosperm. In consequence, of course, the seeds borne the first year, “differed neither in size nor in color in the least from the natural seeds of Zea Mays nana of the earlier sowings” (p. 322).

The following year, however, instead of getting complete color dominance, he obtained from one ear a ratio of 224 with non-colored pericarp, to 64 with pericarp colored. The other ear gave 104 seeds without pericarp color to 39 colored. He carried the seeds through to the next generation, but gives no numbers for them. Gärtner also crossed Lychnis diurna with reddish or dark-brown seeds, and Lychnis vespertina with ashy-gray seeds, finding no change occurring as the result of crossing, but obtaining what we should call dominance of ashy-gray in the first hybrid generation. From Gärtner’s observations, therefore, he felt justified in stating as a law—

That the influence of the foreign pollen in hybrid fertilization, alters nothing in the forms and external characters of the fruits and seeds
peculiar to the mother plant, but produces in the embryo only, the capacity of bringing forth a mixed product from both concurrent factors, through the germination and the further development of the new plant (p. 327).

In an earlier paper of Gärtner's (2b), he cites Mauz's case of modifications in the character of different fruits on a pear tree, through pollination from various varieties of pears, whereby he was said to have obtained, "a great number of fruits different in form and colors" (p. 138).

His interest aroused by the phenomenon reported in maize, he undertook a series of crossing experiments to determine "whether foreign pollen exercises or does not exercise an immediate influence on the external character of the fruits and seeds which are the result of these fertilizations," but with entirely negative results. No change whatsoever was observed in the color or external characteristics of the fruits arising from crossing.

The influence of the foreign pollen does not then change anything in the external forms peculiar to the mother plant, or in the external qualities of the fruits, the seeds and even the embryo. This influence only gives to the latter the faculty of producing, through germination and through the ulterior development of the new plant, an intimate combination of the form of the members of the two species which have united in its production (p. 139).

One of the most interesting matters, of course, is that which concerns the alteration in the character of hybrid seeds or fruits due to the immediate effect of foreign pollen. Gärtner reviews in detail the previous work of Knight, Goss and Seton with peas. In 1829, he started a selfed and a crossed series of peas, using four varieties (pp. 81–85).

1. Paris Wax (yellow seeds).
2. Dwarf Creeping (white flowers, yellow seeds).
3. Sugar peas (red flowers, wrinkled greenish-yellow seeds).
4. Early Green Brockel (white flowers, green seeds).

The results as to the immediate effect of the cross on the seeds were as follows:
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<th>Parents</th>
<th>Hybrid Seeds</th>
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<tr>
<td>Paris Wax (yellow) × Sugar Peas (greenish yellow) . . . . . yellow.</td>
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<tr>
<td>Paris Wax (yellow) × Early Green Brockel (green) . . . . . greenish-yellow.</td>
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<tr>
<td>Sugar Pea (greenish yellow) × Dwarf Creeping (yellow) . . . dirty-yellow.</td>
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<td>Dwarf Creeping (yellow) × Early Green Brockel (green) . . . greenish-yellow.</td>
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<td>Early Green Brockel (green) × Dwarf Creeping (yellow) . . . . . yellow.</td>
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As the above results show, the same dominance of yellow over green in the hybrid seed appears as in the experience of Knight, Goss and Seton.

Respecting identical results obtained as the result of reciprocal crosses, Gärtnert makes the following unqualified statement:

The most important and the most interesting phenomenon in the crossing of plants in hybrid breeding, is the complete similarity of the two products; since the seeds produced from the one as from the other fertilization, give rise to plants of the most complete similarity, so that their different origin and derivation, upon the most careful investigation of both kinds of hybrids, does not show the least difference in respect to their form and type; and even the most practiced specialist with a hybrid species, is not in position to distinguish the origin of the hybrid with respect to the sex of the parents (p. 223).

Gärtnert’s work is not only noteworthy for its remarkable extent with respect to the number of species experimented upon, but with regard to the care which he exercised in his operations, he says:

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, using different individuals of that 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 emasculature, 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).

Again, in another place, he makes substantially the
same statement with respect to testing what he refers to
as "selective affinity."

In order to gradually get as close as possible to the true selective
affinity relation among the species of plants, it is necessary not only that
a greater number of experiments be instituted with the same species of
plants, but also that the same experiments be repeated with different
individuals and at different times, because as well in the female organs
of a plant, as in the pollen of another species, a basis for different
results may be concealed (p. 214).

Gärtnér was not behind in realizing the practical utility
of hybridization in agriculture and horticulture. The
following somewhat extended extract shows his keen
sense of interest to the possibilities latent therein, al-
though his own scientific efforts did not lead him into
economic experiments.

The heightened fruiting capacity of hybrids and variety crosses, de-
serves the most marked attention in respect to orchard, vineyard, and
the whole of garden culture. The striking fertility of several orchard
and vineyard varieties may find its explanation herein. It is, to be
sure, to be surmised that this capacity does not reside in an equal degree
in all variety crosses, and that this character would incline toward the
peculiarity of the species; nevertheless it is to be expected with tolerable
certainty, that with many valuable orchard and vineyard varieties, an
increased yield might be able to be attained through crossing with other
varieties. Improved sorts with weak or weakened vegetative power,
united with other species of more vigorous growth, would promise an
improved product with a longer life duration and a stronger structure
of the plant body. As already many admirable stone, pome and vine-
yard varieties have been raised from seeds which had originated through
chance crossing, so, through intentional artificial crossing of varieties,
still many other sorts might be very easily produced. But to get definite
results, and to be able to determine the outcome exactly, for the advan-
tage of science as a whole, fertilization should not be committed to
mere chance, but an exact and scrupulous procedure must be observed,
with careful records of the varieties combined.

Of still more extended utility is hybrid breeding for æsthetic botany;
for the latter, artificial fertilization opens a wide field for activity, en-
joyment and achievement. For the fancier of ornamental plants, the
ease with which many hybrids are able to be produced, is an inexhaustible source of satisfaction and profit. He recognizes that he is in possession of materials with which he can busy himself, and he deliberates over the way and manner he can best and most profitably combine them; in that, he gives attention to the characters wherein each species characterizes itself, whether in the splendor of the colors of the flowers, the fineness of their delineation; fragrance, growth, form, quantity of flowers; whether endurance of the severity of our climate in this or that combination is to be taken into special consideration;—he will attempt to calculate provisionally with some probability the possible appearance of the hybrids, and he will finally be surprised at getting a plant which had never before existed in nature (pp. 638–639).

This concludes the matter of general interest in Gärtner’s memoir. The writer believes that it should be carefully read by every plant breeder, not only for the details of practical and historical value therein contained, but because of the philosophical spirit underlying Gärtner’s scientific attitude upon the nature of the hybrid organism.

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