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I. On Hybridism considered as a cause of variability in Vegetables.

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The changes of form in the species of the vegetable kingdom are very properly considered at the present moment one of the phenomena which are most worthy of attracting the attention of observers. The subject of the variability of species, which was put aside amongst questions of secondary consideration, has within a short time assumed an unexpected importance; and without mentioning the philosophical deductions to which it has given rise, it may be asserted that it forces itself on our notice at the very commencement of all our descriptive works. For the last ten years I have devoted to it all my attention, and though duly estimating the facts in this direction observed by my predecessors, it is nevertheless to my own experiments I have looked especially for enlightenment on this obscure subject. I do not pretend to have solved all the difficulties which it involves, but I think that I have arrived at results which, I hope at least, will throw some light upon points in the biology of vegetables which have been hitherto perplexed.

In a memoir which I had the honour of presenting to the Academy two years ago I established this fact, confirmed since by new experiments, that, setting out from the second generation, hybrid vegetables, when they are fertile, revert very frequently to one of the two species from whence they were derived. This

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reversion to forms authorized by nature is not universal; nothing is more common, in fact, than to find in hybrids of the same origin and of the second generation, or of a generation more advanced, in company with individuals which revert to the form of the parent species, a more or less numerous residue of individuals, which do not retrograde, or which even differ more from these last, than they differ from hybrids of the first generation. What sort of physiognomy do these refractory hybrids present, and what are their descendants? This is the question which I purpose to examine in the present memoir.

In 1862 I made numerous crosses, all of them successful, between *Datura lævis*, *ferox*, *Stramonium*, and *quercifolia*, four species perfectly distinct, between which there are no known intermediates, and which moreover do not appear susceptible of variation. Nevertheless, though very distinct, these species are sufficiently closely related to admit of reciprocal impregnation, and to give rise to hybrids, which, though sterile at first, become very fertile at a more advanced period. They were then in the most favourable condition for the object which I proposed—the observation of their hybrids during at least two consecutive generations.

In order to apprehend properly the facts which follow, I ought to state that the species of *Datura* of the subgeneric group to which these four species belong, may be divided into two groups, one in which the plants have green stems and white flowers, the other in which the stems are more or less brown, or blackish purple, and the flowers violet. For brevity I shall call them the white and violet groups. *D. Stramonium*, *lævis*, and *ferox* belong to the first; *D. Tatula*, *quercifolia*, and some others to the second.

As I have just remarked, I have made numerous crosses between these species, all of which have succeeded, and under such conditions of insolation that I could have no doubt of the results which I obtained. I will not speak here of all these experiments, which I reserve for a more extended memoir; I wish only at present to lay before the Academy the very remarkable phenomena of variation which have been elicited by these crosses, and to point out the consequences which appear to me to result from them.

Datura lævis and *ferox*, the two species which differ the most in the white group, having been fecundated the one by the other, and in both directions, I was able in 1863, by help of the seeds derived from this double intercrossing, to raise sixty individuals of *Datura lævi-ferox*, and seventy of *D. feroci-lævis*, in all 130 hybrid plants, derived from the same parents, which had alter-

nately acted the part of father and mother. All these plants attained the most complete development, and were so perfectly like each other that the two sets might easily have been regarded as one. This is a new confirmation of what I have already announced in the memoir cited above—that there is not a sensible difference between reciprocal hybrids of two species, and that in the first generation the hybrids of the same origin resemble each other as much as the individuals of pure species from the same sowing. In this first generation, I repeat, the entire collection of hybrid individuals of the same origin, however numerous they may be, is as homogeneous and as uniform as a group of individuals of an invariable species, or of a pure and neatly-defined race would be.

But these 130 hybrids presented a fact which was quite new to me: if they perfectly resembled each other, they differed strangely from the two species from which they were derived. They had neither the stature, the habit, the flowers, nor the fruit of their parents; there was not even anything intermediate between their forms which were so well known and so decided. Any one who did not know the origin of these hybrids, would not have hesitated to make a new species of them, and what is worth notice, would have classed them in the violet series, for all had the flowers of this colour and brown stems. Notwithstanding, as I said above, the two parent species belong to the group characterized by green stems and white flowers.

In the face of this unexpected result, one might have been tempted to believe that two species, intermarrying, might impart to their progeny characters which they do not possess themselves; but such a conclusion was too paradoxical to be accepted without a reexamination. I resolved therefore to recommence the experiment the following year, observing at the same time more closely not only the hybrids, but also the species from whence they were derived.

This year (1864) I have sown afresh *D. lævi-ferox* and *ferox-lævis*, and by their side *D. ferox* and *D. lævis* in a state of purity. Thirty-six new plants of *D. lævi-ferox*, and thirty-nine of *ferox-lævis* reproduced all the identical features of their brethren of the preceding year. They had the same brown stems, the violet flowers, and thorny fruit. But what I had not previously remarked, in *D. ferox* of a pure strain the stem at the moment of germination is of a deep purplish violet. This vivid tint extends from the root to the cotyledons, where it suddenly ceases, giving

place to the clear green tint; but it remains during the whole existence of the plant on the part which it occupies, and where it traces a coloured circle. From this moment all was clear: if the hybrids of *D. ferox*, allied to another species of the white group, have brown stems and violet blossoms, it is because *D. ferox* itself possesses the germ of this colouring. In the pure species, the colouring remains in a rudimentary state, occupying only the small interval which extends from the commencement of the root to the cotyledons; in the hybrid it acquires an enormous increase, extending over all parts of the plant, and manifesting more especially its action on the flower. Here then is a first mode of variation induced by the crossing of two species, and which produces its effects on the first hybrid generation. The second generation is about to offer us variations of another kind, and still more remarkable.

All these hybrids, though sterile at the first seven or eight dichotomies, were very fertile in those which were developed later. Their seeds, sown last spring, gave me in the second generation nineteen plants of *D. feroci-lævis*, and twenty-six of *lævi-ferox*. The two sets still resembled each other, but by a character diametrically opposite to that which was the prominent trait of the preceding generation. The most astonishing diversity of feature succeeded the former great uniformity, a diversity of such an extent, that out of the forty-five plants of which the two sets were composed, no two were found which precisely resembled each other. They differed in stature (in the proportion of one to four), in habit, in the form of the leaves, the colouring of the stem and flowers, the degree of fertility, the size of the fruit, and the degree of aculeation. With the exception of a single individual of the *lævi-ferox* set, which had completely reverted to *D. lævis*, with this slight difference that there was still at the base of the stem a circle of purplish violet, not one of these plants had sensibly approached this species, and there was only a very small number in which one could recognize faint resemblances to *D. ferox*; the greater part even more closely resembled *D. Stramonium* and *D. quercifolia*, with which they had no relationship, than the species from which they descended. Some had white flowers and green stems, either self-coloured or tinted with purple at the base, while others had violet flowers of various shades, and stems more or less brown, sometimes even of a purplish black as deep as that of *D. Tatula*, which is the most perfect type of the violet group; the fruit was of all sizes, from that of a filbert to

that of a large walnut, and some of them were very spiny, while others were covered with tubercles, or almost destitute of spines; certain individuals bore fruit at the first fork, while others were fertile only towards the last, and finally there were some which set only a single fruit. On the whole, the forty-five plants of the two sets constituted, so to speak, as many individual varieties, as if, the bond which ought to unite them to the specific types being broken, their vegetation had wandered in every direction. This is what I call irregular variation, in opposition to another very different mode of sporting, of which I shall speak presently.

I could bring forward many other examples of the excessive variability which arises in consequence of crossing. Not being able to give to this note all the space which the subject demands, I shall confine myself to the following examples, which have likewise been furnished by my experiments.

In 1863 I received from an horticultural amateur a full-grown plant of *Mirabilis longifloro-jalapa* of the first generation, the issue, as the name implies, of the common Marvel of Peru, with purple flowers, fecundated by *M. longiflora*. A seed obtained from the first cross of the two species accompanied the plant, which was destined to give me a second hybrid individual, equally of the first generation. The two plants, cultivated side by side, became enormous. Intermediate in the same degree between the parent species, which they far surpassed in stature, they resembled each other as exactly as possible, which might be expected, as they both belonged to the first generation. They were moderately fertile, and out of the many thousand flowers which they expanded in the course of nearly three months, they produced some hundreds of perfectly similar seeds.

The older of these two plants having already borne fruit the preceding year, and some of its seeds having been sent to me by the donor, I obtained the same year (1863) six other hybrid plants of the second generation. None of them acquired the large stature of the hybrids of the first generation; none, moreover, resembled them. Of these six plants, there were two which seemed to be the image of each other, so slightly did they differ: this was an exception; they flowered abundantly, but though well developed and very vigorous, they remained entirely sterile. A third almost reverted to the normal form of *Mirabilis jalapa*, of which it possessed the stature, the leaves, the flowers, and the fertility; it differed only in a slightly more expanded habit, and the tube of the corolla being more elongated. The three last were

plants of low stature, more or less deformed, as different from each other as from the hybrids of the first generation; besides, like the two first, they were sterile, or at the most yielded only a few fruits, in which the seeds were only incompletely developed. Three new plants of the second generation, cultivated in 1864, presented the same diversities of physiognomy; they no more resembled those of the former year than the first hybrids. One of these, which approached *M. jalapa* very sensibly, was extremely fertile; the two others flowered very unequally, and did not yield a single seed. What results from this second experiment is still the irregular variation of the offspring of a hybrid plant, when it does not resume the livery of the species from which it descends.

It may be asked whether this propensity of hybrids to vary continues to the third and following generations, when they preserve their fertility. My answer to this question is as follows:—

I observed in 1863 and 1864 the sixth and seventh generations of a hybrid which I have kept for several years, *Linaria purpureo-vulgaris*, both represented by some hundreds of individuals. A good number of these last reverted, some completely, the others partially, to the form of *Linaria vulgaris* with yellow flowers, a small number to those of *Linaria purpurea* with purple flowers. Others, still very numerous, inclined, so to speak, towards neither the one nor the other, but nevertheless did not resemble the hybrid of the first generation. There were all possible kinds of variation; tall or dwarf stature, broad or narrow leaves, the corolla deformed in various ways, discoloured, or exhibiting unusual tints, and out of all these combinations there did not result two individuals which were perfectly alike. It is very clear that we have to do here with irregular variation, which engenders only individualities, and that uniformity is not established between the descendants of hybrids, except on the condition that it resumes the normal livery of the parent species.

Similar facts, to which all the attention which they merited has not been paid, have been produced, and are produced daily in the practice of Floral Horticulturists. Here is a well-known and well-authenticated instance: there exist in gardens two species of *Petunia* perfectly defined, the one (*P. nyctaginiflora*) has white flowers, the other (*P. violacea*) has purple flowers, neither of which at present has varied, but intercrossing easily and yielding hybrids as fertile as themselves. In the first generation, all the hybrids are alike; in the second they vary in the most remarkable degree, some reverting to the white species, others to the purple, and a

large residue showing all the shades between the two. When these varieties are fecundated artificially by each other, as is the practice of some gardeners, we obtain a third generation still more parti-coloured, and continuing the process we arrive at extreme variations, sometimes at monsters, which the prevailing fashion regards as so many marks of perfection. The essential point is, that these varieties are purely individual, and without any persistence. Their seeds when sown yield new forms, which have no greater resemblance amongst each other than they have to the plants which produced them.

Were we to review other groups of ornamental plants, where at the commencement of their cultivation there existed two or more species sufficiently alike in organization to give rise to fertile hybrids, we should discover the same facts of individual, and not collective variability, such as I have just noticed. Primroses and roses, not to bring forward other instances, are memorable examples. Intercrossed a thousand times, either intentionally by horticulturists, or accidentally by insects, the species of these two genera have given birth to varieties so numerous, that we can scarcely reckon them up, and that the primitive types of the species, merged in this confused and ever-changing multitude, have scarcely more than a conventional existence. Whatever the variety may be of rose or of the garden-primrose, so well named *Primula variabilis*, whose seeds we sow, we may be sure beforehand that it will not be identically reproduced, and that we shall see almost as many new variations as individuals spring up from the seed.

This leads me naturally to glance at our fruit-trees, our apples and pears especially, whose varieties are counted by hundreds, and I might say by thousands, if we kept all those which we have seen arise from seeds. Well-informed cultivators of seeds are unanimous in allowing that these varieties are individual, and without permanence, and that grafting them is absolutely necessary to preserve them and propagate them, of which M. Decaisne has recently given experimental proof*. Must we conclude that these varieties are the result of crossing between distinct species and races? The direct proof is wanting, but I dare affirm that it is really the cause, and that under all this multitude of unstable forms, several types, primitively specifically distinct, are concealed, to which it is no longer possible to assign their true characters.

* A translation of M. Decaisne's memoir will be found in another part of this Journal.

Further, whatever opinion we may form in this respect, we must allow that these forms, not transmissible by way of generation, want in this very respect the essential character of species and true races, which is to perpetuate themselves faithfully by seed and to increase. We may say strictly that these varieties are no longer represented sometimes after ages of duration, save by a single individual, always the same, and always renewed by grafting, that is to say, by the indefinite division of its branches.

But if crossings have produced these phenomena of irregular variability in cultivated plants, would it not be possible that the same cause had made them arise in plants remaining in a wild state? One is led to believe, when we cast our eyes on certain generic groups, as those of *Salix*, *Potentilla*, *Rubus*, &c., where species well characterized at first sight are connected nevertheless with one another by intermediate forms so numerous and so well graduated, that at last we do not know where to place the limits of these species; thus, in spite of the most laborious studies, these genera have remained a matter of dispute amongst botanists. What renders this supposition probable is, that the species of these different groups are precisely those which occur under physical conditions the most calculated to favour crossing. But it is sufficient here that two species, when crossing, give place to fertile hybrids which do not all revert to the specific types, in order that the irregular variability should come into play, and induce, after some generations, that chaos of undecided forms in the face of which all the efforts of botanical describers miscarry*.

After having related how hybrids vary, it is time to examine how pure species behave themselves, when their forms are modified. Let us state first, that in respect of variability they are very unequally gifted. There are some which we never see varying, at least in the sense which we attach to this word; there are others which vary, and sometimes within extremely wide limits. We know not what causes determine these variations; it is nevertheless allowable to believe that emigration and cultivation are not without influence, for we see many remarkable varieties spring up in their course. But species, when they vary in consequence of their innate tendency to do so, do it in a very different manner from

* The translator of this memoir was peculiarly struck three years since with the infinite variety of forms of *Salix* which occur along the course of the Dee. It really seemed as if every bush possessed some character of its own, and in consequence a neighbouring botanist, who set out with the intention of collecting every variety of willow in Aberdeenshire, gave up the matter in despair.

that which we have demonstrated amongst hybrids. While in these last the form dissolves, from one generation to another, into individual and unpersistent variations, in the pure species, on the contrary, the variation has a tendency to perpetuate itself and to increase. When it is produced, one of two things takes place, either it disappears with the individual in which it took rise, or it is transmitted without alteration to the following generation, and from thence, if circumstances are favourable, and no crossing with the type of the species or with another variety disturbs it in its evolution, it passes into the condition of a definite race, and impresses its seal on an unlimited number of individuals. It is thus that I explain the formation of those well-marked races of economical vegetables, so homogeneous and so stable, of which cultivation has beheld the origin, and which it preserves with so much care. If we consider only the regularity of their progress, we should take them for real species; but their instability, when they are submitted to the chance of crossing, testifies their real nature. They are not species in the botanical sense of the word, they are categories in a larger species, or, if you will, confraternities of individuals similar in organization, and having a uniform livery. This homogeneousness and fixity of character are the distinctive mark of true races, as diversity and want of permanence are the mark of agglomerations arising from half-blood or hybridity. The latter, tainted with illegitimacy, are the fruit of irregular variation, the former of the regulated and normal variation of the species. I could even say more willingly that they are the species itself adapting itself to new media and new finalities.

I know not if facts analogous to those which I have just reported have been observed in the animal kingdom; but I should not be surprised if we came some day to recognize that there also crossings between definite races are a cause of variability perfectly individual, and that they are impotent to create new races, that is to say, uniform fellowships, and capable of enduring infinitely. It would certainly not be without interest, if, when intermarrying, races perfectly distinct should melt into a new mixed but homogeneous race; or if, as in plants, the crossing should have the effect of infinitely diversifying physiognomies and temperaments. But it is a subject for which I am not competent, and which I hasten to leave to professional zoologists.
