Introduction

In the late 1860s Mendel wrote a series of letters to Carl Nägeli, one of the leading experts on plant hybridization at the time. We reproduce an english translation of one of these letters below, in which Mendel explains his interpretation of his experimental results, and makes predictions about the kinds and proportions of offspring one might expect from certain crosses and also tries to address some doubts that Nägeli, who really did not understand the significance of Mendel's work, had earlier raised. Mendel's notation is different from that commonly used now in genetics: he uses single letters of the alphabet to designate phenotypes (e.g. the phenotype *bcDg* in Mendel's notation would today be written as the genotype *bbccD_gg)*, and double letters (e.g. *Aa*) to designate phenotypes intermediate between the parents. The letter exemplifies Mendel's essentially modern approach to his scientific work, an approach involving observation, hypothesis making and the designing of experiments to test predictions made from the hypothesis.

# *Letter to Carl Nägeli*

Highly Esteemed Sir:

My most cordial thanks for the printed matter you have so kindly sent me! The papers "die Bastardbildung im Pflanzenreiche," "über die abgeleiteten Pflanzenbastarde", "die Theorie der Bastardbildung," "die Zwischenformen zwischen den Pflanzenarten", "die systematische Behandlung der Hieracien rücksichtlich der Mittelformen und des Umfangs der Species," especially capture my attention. This thorough revision of the theory of hybrids according to contemporary science was most welcome. Thank you again!

With respect to the essay which your honour had the kindness to accept, I think I should add the following information: the experiments which are discussed were conducted from 1856 to 1863. I knew that the results I obtained were not easily compatible with our

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contemporary scientific knowledge, and that under the circumstances publication of one such isolated experiment was doubly dangerous; dangerous for the experimenter and for the cause he represented. Thus I made every effort to verify, with other plants, the results obtained with *Pisum*. A number of hybridizations undertaken in 1863 and 1864 convinced me of the difficulty of finding plants suitable for an extended series of experiments, and that under unfavorable circumstances years might elapse without my obtaining the desired information. I attempted to inspire some control experiments, and for that reason discussed the *Pisum* experiments at the meeting of the local society of naturalists. I encountered, as was to be expected, divided opinion; however, as far as I know, no one undertook to repeat the experiments. When, last year, I was asked to publish my lecture in the proceedings of the society, I agreed to do so, after having re-examined my records for the various years of experimentation, and not having been able to find a source of error. The paper which was submitted to you is the unchanged reprint of the draft of the lecture mentioned; thus the brevity of the exposition, as is essential for a public lecture.

I am not surprised to hear your honour speak of my experiments with mistrustful caution; I would not do otherwise in a similar case. Two points in your esteemed letter appear to be too important to be left unanswered. The first deals with the question whether one may conclude that constancy of type has been obtained if the hybrid $Aa$ produces a plant $A$, and this plant in turn produces only $A$.

Permit me to state that, as an empirical worker, I must define constancy of type as the retention of the character during the period of observation. My statements that some of the progeny of hybrids breed true to type thus includes only those generations during which observations were made; it does not extend beyond them. For two generations all experiments were conducted with a fairly large number of plants. Starting with the third generation it became necessary to limit the numbers because of lack of space, so that, in each of the seven experiments, only a sample of those plants of the second generation (which either bred true or varied) could be observed further. The observations were extended over four to six generations. Of the varieties which bred true some plants were observed for four generations. I must further mention the case of a variety which bred true for six generations, although the parental types differed in four characters. In 1859 I obtained a very fertile descendant with large, tasty, seeds from a first generation hybrid. Since, in the following year, its progeny retained the desirable characteristics and were uniform, the variety was cultivated in our vegetable garden, and many plants were raised every year up to 1865. The parental plants were *bcDg* and *BCdG*.

| | |
|---|---|
| *B*. albumen yellow | *b*. albumen green |
| *C*. seed-coat grayish brown | *c*. seed-coat white |
| *D*. pot inflated | *d*. pod constricted |
| *G*. axis long | *g*. axis short |

The hybrid just mentioned was *BcDG*.

The color of the albumen could be determined only in the plants saved for seed production, for the other pods were harvested in an immature condition. Never was green albumen observed in these plants, reddish-purple flower colour (an indication of brown seed-coat), constriction of the pod, nor short axis.

This is the extent of my experience. I cannot judge whether these findings would permit a decision as to constancy of type; however, I am inclined to regard the separation of parental characteristics in the progeny of hybrids in *Pisum* as complete, and thus permanent. The progeny of hybrids carries one or the other of the parental characteristics, or the hybrid form of the two; I have never observed gradual transitions between the parental characters or a progressive approach toward one of them. The course of development consists simply in this; that in each generation the two parental characteristics appear, separated and unchanged, and there is nothing to indicate that one of them has either inherited or taken over anything from the other. For an example, permit me to point to the packets, numbers 1035-1088, which I sent you. All the seeds originated in the first generation of a hybrid in which brown and white seed-coats were combined. Out of the brown seed of this hybrid, some plants were obtained white seed-coats of a pure white colour, without any admixture of brown. I expect those to retain the same constancy of character as found in the parental plant.

The second point, on which I wish to elaborate briefly, contains the following statement: "You should regard the numerical expressions as being only empirical, because they can not be proved rational."

My experiments with single characters all lead to the same result: that from the seeds of the hybrids, plants are obtained half of which in turn carry the hybrid character ($Aa$), the other half, however, receive the parental characters $A$ and $a$ in equal amounts. Thus, on the average, among four plants two have the hybrid character $Aa$, one the parental character $A$, and the other the parental character $a$. Therefore $2Aa+A+a$ or $A+2Aa+a$ is the empirical simple, developmental series for two differentiating characters. Likewise it was shown in an empirical manner that, if two or three differentiating characters are combined in the hybrid, the developmental series is a combination of two or three simple series. Up to this point I don't believe I can be accused of having left the realm of experimentation. If then I extend this combination of simple series to any number of differences between the two parental plants, I have indeed entered the rational domain. This seems permissible, however, because I have proved by previous experiments that the development of any two differentiating characteristics proceeds independently of any other differences. Finally, regarding my statements on the differences among the ovules and pollen cells of the hybrids, they also are based on experiments. These and similar experiments on the germ cells appear to be important, for I believe that their results furnish the explanation for the development of hybrids as observed in *Pisum*. These experiments should be repeated and verified.

I regret very much not being able to send your honour the varieties you desire. As I mentioned above, the experiments were conducted up to and including 1863; at that time they were terminated in order to obtain space and time for the growing of other experimental plants. Therefore seeds from those experiments are no longer available. Only one experiment on differences in the time of flowering was continued; and seeds are available from the 1864 harvest of the experiment. These are the last I collected, since I had to abandon the experiment in the following year because of devastation by the pea beetle, *Bruchus pisi*. In the early years of experimentation this insect was only rarely found on the plants, in 1864 it caused considerable damage, and appeared in such numbers in the following summer that hardly a 4th or 5th of the seeds was spared. In the last few years it has been necessary to discontinue cultivation of peas in the vicinity of Brünn. The seeds remaining can still be useful, among them are some varieties which I expect to remain constant; they are derived from hybrids in which two, three, and four differentiating characters are combined. All the seeds were obtained from members of the first generation, i.e., of such plants as were grown directly from the seeds of the original hybrids.

I should have scruples against complying with your honour's request to send these seeds for experimentation, were it not in such complete agreement with my own wishes. I fear that there has been partial loss of viability. Furthermore the seeds were obtained at a time when *Bruchus pisi* was already rampant, and I cannot acquit this beetle of possibly transferring pollen; also, I must mention again that the plants were destined for a study of differences in flowering time. The other differences were also taken into account at the harvest, but with less care than in the major experiment. The legend which I have added to the packet numbers on a separate sheet is a copy of the notes I made for each individual plant, with pencil, on its envelope at the time of harvest. The dominant characters are designated as *A, B, C, D, E, F, G* and as concerns their dual meaning please refer to p.11. The recessive characters are designated *a, b, c, d, e, f, g*; these should remain constant in the next generation. Therefore, from those seeds which stem from plants with recessive characters only, identical plants are expected (as regards the characters studied).

Please compare the numbers of the seed packets with those in my record, to detect any possible error in the designations – each packet contains the seeds of a single plant only.

Some of the varieties represented are suitable for experiments on the germ cells; their results can be obtained during the current summer. The round yellow seeds of packets 715, 730, 736, 741, 742, 745, 756, 757, and on the other hand, the green angular seeds of packets 712, 719, 734, 737, 749 and 750 can be recommended for this purpose. By repeated experiments it was proved that, if plants with green seeds are fertilized by those with yellow seeds, the albumen of the resulting seeds has lost the green colour and has taken up the yellow colour. The same is true for the shape of the seed. Plants with angular seeds, if fertilized by those with round or rounded seeds, produce round or rounded seeds. Thus, due to the changes induced in the color and shape of the seeds by fertilization with foreign pollen, it is possible to recognize the constitution of the fertilizing pollen.

Let *B* designate yellow colour; *b*, green colour of the albumen.
Let *A* designate round shape; *a*, angular shape of the seeds.

If flowers of such plants as produce green and angular seeds by self-fertilization are fertilized with foreign pollen, and if the seeds remain green and angular, then the pollen of the donor plant was, as regards the two characters ............................ *ab*

If the shape of the seeds is changed, the pollen was taken from .................. *Ab*

If the colour of the seeds is changed, the pollen was taken from ................ *aB*

If both shape and colour is changed, the pollen was taken from ................ *AB*

The packets enumerated above contain round and yellow, round and green, angular and yellow, and angular and green seeds from the hybrids *ab+AB*. The round and yellow seeds would be best suited for the experiment. Among them (see experiment p. 15) the varieties *AB, ABb, Aab,* and *AaBb* may occur; thus four cases are possible when plants, grown from green and angular seeds, are fertilized by the pollen of those grown from the above mentioned round and yellow seeds, i.e.

I. $ab + AB$
II. $ab + ABb$
III. $ab + AaB$
IV. $ab + AaBb$

If the hypothesis that hybrids form as many types of pollen cells as there are possible constant combination types is correct, plants of the makeup

| | |
|---|---|
| $AB$ | produce pollen of the type $AB$ |
| $ABb$ | produce pollen of the type $AB$ and $Ab$ |
| $AaB$ | produce pollen of the type $AB$ and $aB$ |
| $AaBb$ | produce pollen of the type $AB$, $Ab$, $aB$ and $ab$ |

Fertilization of ovules occurs:

| | |
|---|---|
| I. | Ovules $ab$ with pollen $AB$ |
| II. | Ovules $ab$ with pollen $AB$, and $Ab$ |
| III. | Ovules $ab$ with pollen $AB$, and $aB$ |
| IV. | Ovules $ab$ with pollen $AB$, $Ab$, $aB$ and $ab$ |

The following varieties may be obtained from this fertilization:

| | |
|---|---|
| I. | $AaBb$ |
| II. | $AaBb$ and $Aab$ |
| III. | $AaBb$ and $aBb$ |
| IV. | $AaBb$, $Aab$, $aBb$ and $ab$ |

If the different types of pollen are produced in equal numbers, there should be in

| | |
|---|---|
| I. | All seeds round and yellow |
| II. | one half round and yellow<br>one half round and green |
| III. | one half round and yellow<br>one half angular and yellow |
| IV. | one quarter round and yellow<br>one quarter round and green<br>one quarter angular and yellow<br>one quarter angular and green |

Furthermore, since the numerical relations between *AB, ABb, AaB, AaBb are* 1:2:2:4, among any nine plants grown from round yellow seed there should be found on the average *AaBb* four times, *ABb* and *AaB* twice each, and *AB* once; thus the IVth case should occur four times as frequently as the Ist and twice as frequently as the IInd or IIIrd.
If on the other hand, plants grown from the round yellow seeds mentioned are fertilized by pollen from green angular plants, the results should be exactly the same, provided that the ovules are of the same types, and formed in the same proportions, as was reported for the pollen.

I have not performed this experiment myself, but I believe, on the basis of similar experiments, that one can depend on the result indicated.

In the same fashion individual experiments may be performed for each of the two seed characters separately, all those round seeds which occurred together with angular ones, and all the yellow ones which occurred with green seeds on the same plant are suitable. If, for instance, a plant with green seeds, was fertilized by one with yellow seeds, the seeds obtained should be either 1) all yellow, or 2) half yellow and half green, since the plants originating from yellow seeds are of the varieties *B* and *Bb*. Since, furthermore, *B* and *Bb* occur in the ratio of 1:2, the 2nd fertilization will occur twice as frequently as the 1st.

Regarding the other characters, the experiments may be conducted in the same way; results, however, will not be obtained until next year....

As must be expected, the experiments proceed slowly. At first beginning, some patience is required, but later, when several experiments are progressing concurrently, matters are improved. Every day, from spring to fall, one's interest is refreshed daily, and the care which must be given to one's wards is thus amply repaid. In addition, if I should, by my experiments, succeed in hastening the solution of these problems, I should be doubly happy.

Accept, highly esteemed Sir, the expression of most sincere respect from

Your devoted
G Mendel

(Altbrünn, Monastery of St. Thomas
Brünn, 18 April, 1867).