

**GREGOR MENDEL'S LETTERS TO CARL
NÄGELI. 1866-1873**

(Gregor Mendel's Briefe an Carl Nägeli. 1866-1873)

*Translated by Leonie Kellen Piternick and George Piternick
Department of Zoology, University of California
Berkeley, California*

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GREGOR MENDEL'S LETTERS TO CARL NÄGELI. 1866-1873

*Translated by Leonie Kellen Piternick and George Piternick
Department of Zoology, University of California, Berkeley, California*

I

HIGHLY ESTEEMED SIR:

The acknowledged pre-eminence your honor¹ enjoys in the detection and classification of wild-growing plant hybrids makes it my agreeable duty to submit for your kind consideration the description of some experiments in artificial fertilization.

The experiments, which were made with different varieties of *Pisum*, resulted in the offspring of the hybrids forming curious series, the members of which, in equal measure resembled the two original types. The presence of non-variant intermediate forms, which occurred in each experiment, seems to deserve special attention. In the developmental series for two and three differentiating characters, discussed in the monograph² (pp, 17-18), the notations for the constant forms have been placed first, since the terms are arranged according to

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- ¹ The German term "Ew. Wohlgeboren" has been translated "your honor" throughout, although the terms are not strictly equivalent. Trs.
 - ² Mendel, Gregor, *Versuche über Pflanzenhybriden*, Verh. des Naturf. Vereines in Brünn 4, 1866. In this translation the page numbers cited will refer to the translation of the paper by the *Royal Horticultural Society of London*, reprinted in 1948 by the Harvard University Press.

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their coefficients; but they receive a more correct position when the terms are placed according to their natural relationship to the two parental types, whereby that term which represents a hybrid in all characters and has, at the same time, the highest coefficient, will be placed exactly in the center.

The results which Gärtner obtained in his experiments are known to me; I have repeated his work and have re-examined it carefully to find, if possible, an agreement with those laws of development which I found to lie true for my experimental plant. However, try as I would, I was unable to follow his experiments completely, not in a single case! It is very regrettable that this worthy man did not publish a detailed description of his individual experiments, and that he did not diagnose his hybrid types sufficiently, especially those resulting from like fertilizations. Statements like: "Some individuals showed closer resemblance to the maternal, others to the paternal type," or "the progeny had reverted to the type of the original maternal ancestor," etc., are too general, too vague, to furnish a basis for sound judgment. However, in most cases, it can at least be recognized that the possibility of an agreement with *Pisum* is not excluded. A decision can be reached only when new experiments in which the degree of kinship between the hybrid forms and their parental species are precisely determined, rather than simply estimated from general impressions, are performed.

In order to determine the agreement, if any, with *Pisum*, a study of those forms which occur in the first generation should be sufficient. If, for two differentiating characters, the same ratios and developmental series which exist in *Pisum* can be found, the whole matter would be decided. Isolation during the flowering period should not present many difficulties in most cases, since we are dealing only with few plants; those plants whose flowers are being fertilized and a few hybrids which have been selected for seed production. Those hybrids which are collected in the wild can be used as secondary evidence only, as long as their origin is not unequivocally known.

Hieracium, *Cirsium*, and *Geum* I have selected for further experiments. In the first two, manipulation in artificial pollination is very difficult and unreliable because of the small size and peculiar structure of the flowers. Last summer I tried to combine *H. Pilosella* with *pratense*, *praealtum*, and *Auricula*; and *H. murorum* with *umbellatum* and *pratense*, and I did obtain viable seeds; however, I fear that in spite of all precautions, self-fertilization did occur. The appearance of the young plants hardly suggests the desired result. *Hieracium* species can easily be grown in pots, and set abundant seed, even if they are confined in a room or a greenhouse during the flowering period.

In *Cirsium*, the dioeciously blooming *arvense* was fertilized by *oleraceum* and *canum*. The flowers were protected against visits of insects by coverings of bolting cloth, this protection appears to be sufficient for *Cirsium* species. Furthermore, the fertilization of *C. canum* and *C. lanceolatum* by *C. oleraceum* was attempted simply by transmission of pollen, without removing the anthers from the flowers of the former two. Whatever can be accomplished in the wild by insects should ultimately be possible by human hands, and among a great number of seedlings one should obtain a few hybrids. I plan to use the same procedure next summer with *Hieracium* as well.

The hybrid *Geum urbanum+rivale* deserves special attention. This plant, according to Gärtner, belongs to the few known hybrids which produce nonvariable progeny as long as they remain self-pollinated. To me it does not seem quite certain that the hybrid which Gärtner obtained was actually *G. intermedium* Ehrh. Gärtner calls his plant an intermediate type; this designation can not be applied without qualification to *G. intermedium*. In the transformation of *G. urbanum* into *rivale*, Gärtner states explicitly that, by fertilization of the hybrid with the pollen of *rivale*, only homogeneous offspring, which definitely resemble the paternal type, were obtained. However, we are not informed as to where this resemblance lies, and to what degree characters of *G. urbanum* were suppressed by each successive fertilization, until finally the pure *rivale* type emerged. It can hardly be doubted that this gradual transformation obeys a definite law, which, if it could be discovered, would also give clues to the behavior of other hybrids of this type. I hope to be able to get this artificial hybrid to flower next summer.

The surmise that some species of *Hieracium*, if hybridized, would behave in a fashion similar to *Geum*, is perhaps not without foundation. It is, for instance, very striking that the bifurcation of the stem, which must be considered a transitional trait among the piloselloids, may appear as a perfectly constant character, as I was able to observe last summer on seedlings of *H. stoloniflorum* W. K.

In the projected experiments with species of *Cirsium* and *Hieracium* I shall be entering a field in which your honor possesses the most extensive knowledge, knowledge that can be gained only through many years of zealous study, observation, and comparison of the manifold forms of these genera in their natural habitat. For the most part I lack this kind of experience because the press of teaching duties prevents me from getting into the field frequently, and during the vacations it is too late for many things. I am afraid that in the course of my experiments, especially with *Hieracium*, I shall encounter many difficulties, and therefore I am turning confidently to your honor with

the request that you not deny me your esteemed interest when I need your advice.

With the greatest esteem and respect for your honor,

I subscribe myself,
GREGOR MENDEL
Monastery capitular and
teacher in the high school.

Brünn, 31 December 1866

II

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 honor 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 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 honor 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 a 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 (p. 13). Of the varieties which bred true (pp. 15-18) 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 descendent 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*:

<i>B.</i> albumen yellow	<i>b.</i> albumen green
<i>C.</i> seed-coat grayish-brown	<i>c.</i> seed-coat white
<i>D.</i> pod inflated	<i>d.</i> pod constricted
<i>G.</i> axis long	<i>g.</i> 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 color (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 with seed-coats of a pure white color, 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 honor 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 this 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 honor'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 color and has taken up the yellow color. 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 color; *b*, green color 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 color of the seeds is changed, the pollen was taken from.....*aB*
 If both shape and color 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

<i>AB</i>	produce pollen of the type	<i>AB</i>
<i>ABb</i>	“ “ “ “ “	<i>AB</i> and <i>Ab</i>
<i>AaB</i>	“ “ “ “ “	<i>AB</i> and <i>aB</i>
<i>AaBb</i>	“ “ “ “ “	<i>AB</i> , <i>Ab</i> , <i>aB</i> , and <i>ab</i>

Fertilization of ovules occurs:

I.	Ovules <i>ab</i> with pollen	<i>AB</i>
II.	“ <i>ab</i> “ “	<i>AB</i> and <i>Ab</i>
III.	“ <i>ab</i> “ “	<i>AB</i> and <i>aB</i>
IV.	“ <i>ab</i> “ “	<i>AB</i> , <i>Ab</i> , <i>aB</i> , and <i>ab</i>

The following varieties may be obtained from this fertilization:

I.	<i>AaBb</i>
II.	<i>AaBb</i> and <i>Aab</i>
III.	<i>AaBb</i> and <i>aBb</i>
IV.	<i>AaBb</i> , <i>Aab</i> , <i>aBb</i> , and <i>ab</i>

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
one half round and green
- III. one half round and yellow
one half angular and yellow
- IV. one quarter round and yellow
one quarter round and green
one quarter angular and yellow
one quarter angular and green

Furthermore, since the numerical relations between *A B*, *ABb*, *A aB*, *A aBb* 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

vellow 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.

I have all the piloselloid *Hieracia* which your honor recommends for the experiments; also *H. murorum* and *H. vulgatum* of the Archieracia; *H. glaucum* *H. alpinum*, *H. amplexicaule*, *H. prenanthoides*, and *H. tridentatum* do not occur in this vicinity. Last summer I found a withered Hieracium, which has the seed color of *Prenanthis* (Fries: *Achaenia typice testaces [pallida]*), but did not resemble any of the herbarium specimens of this type very closely; finally our botanist declared it to be a hybrid. The rootstock has been transplanted to the garden for further observations, and the seeds have been planted. On the whole, this area is poor in *Hieracia*, and probably has not been sufficiently searched. Next summer I hope to have the time to roam the sandy lignite country which extends eastward from Brünn for several miles to the Hungarian frontier. Several other rare plants are known from this region. The Moravian plateau also is probably terra incognita as far as the *Hieracia* are concerned. If I should find anything noteworthy during the summer, shall hurry to send it to your honor. At the moment permit me to include with the seed packets the plant just mentioned, albeit in a rather defective condition, together with another Hieracium. Last year I found at least 50 specimens of it on an old garden wall. This plant is not found in the local herbaria; its appearance suggests both *H. praealtum* and *H. echioides*, without being one or the other. *H. Praealtum* does occur in the environs of the city, *H. echioides* does not.

Several specimens of the hybrid *Geum urbanum*+*G. rivale* (from last year's hybridization) wintered in the greenhouse. Three are now flowering, the others will follow. Their pollen is fairly well developed, and the plants should be fertile, just as Gärtner states. It seems strange that all the plants now flowering are of the exceptional type mentioned by Gärtner. He says: "*Geum urbano-rivale*, mostly with large flowers, like *rivale*, and only a few specimens with small yellow flowers like *urbanum*." In my plants the flowers are yellow or yellow-orange, and about half the size of those of *G. rivale*; the other characters correspond, as far as can be judged at present, to those of *G. intermedium* Ehrh. Could it be that the exceptional type has an earlier flowering season? To judge from the buds, however, the other plants do not have large flowers either. Or could it be that the exception has become the rule? I believe I have good reasons for considering my

parental species pure. I obtained *G. urbanum* in the environs of the city, where neither *G. rivale*, nor any other species of the genus occurs; and I got *G. rivale* in a damp mountain meadow, where *G. urbanum* certainly does not occur. This plant has all the characteristics of *G. rivale*; it is being maintained in the garden, and seedlings have been produced from self-fertilization.

The *Cirsium arvense*+*C. oleraceum* hybrids, sown in the fall, have died during the winter; one plant of the *C. arvense*+*C. canum* hybrid survived. I hope the spring seedlings will do better. Two other *Cirsium* hybrids have wintered well in the greenhouse. Last summer I observed, on a flowering plant of *C. praemorsum* M. (*olerac.+rivulare*), that in those heads which develop first and last on the stems, no pollen is formed, and thus they are completely sterile; on the others (about one half of the total heads) some pollen and fertile seed is formed. Fertilization experiments were conducted with two of the late-developing heads; pollen of *C. palustre* was transferred to one, pollen of *C. canum* to the other. Viable seeds were obtained from both, the resulting plants survived the winter in the greenhouse, and are now developed to a stage at which the success of the hybridization is evident. Some seedlings of *C. praemorsum*, others of a hybrid (probably in the group *C. canum+palustre* and those of a third one, probably *C. rivulare+palustre* have survived the winter in the open quite well. The same may be said of the autumn seedlings of the hybrids *Aquilegia canadensis+vulgaris* *A. canadensis+A. atropurpurea*, and *A. canadensis+A. Wittmaniana*. However, fall seedlings of some *Hieracia* which were grown to test constancy of type have suffered considerable damage. In this genus it is preferable to sow in the early spring, but then it is doubtful that the plants will flower in the same year. Nevertheless, Fries has made this statement concerning the division *Accipitrina*: “*Accipitrina*, praecocius sata, vulgo primo anno florent.”

I have obtained luxuriant plants of *Linaria vulgaris*+*L. purpurea*; I hope they will flower in the first year. The same may be said of *Calceolaria salicifolia* and *C. rugosa*. Hybrids of *Zea Mays major* (with dark red seeds)+*Z. Mays minor* (with yellow seeds) and of *Zea Mays major* (with dark red seeds)+*Zea Cuzko* (with white seeds) will develop during the summer. Whether *Zea Cuzko* is a true species or not I do not dare to state. I obtained it with this designation from a seed dealer. At any rate it is a very aberrant form. To study color development in flowers of hybrids, cross-fertilizations were made last year between varieties of *Ipomoea purpurea*, *Cheiranthus annuus* and *Antirrhinum majus*. An experiment with hybrids of *Tropaeolum majus*+*T. minus* (1st generation) must also be mentioned.

For the current year exploratory experiments with Veronica, Viola, Potentilla, and Carex are planned. Unfortunately, I have only a small number of species.

Because of lack of space the experiments can be started with a small number of plants only; after the fertility of the hybrids has been tested, and when it is possible to protect them sufficiently during the flowering period, each in turn will receive an extensive study. Thus far the three Aquilegia hybrids mentioned above and *Tropaeolum majus*+*T. minus* are suitable, although the latter has only partial fertility. It is hoped that *Geum urbanum*+*G. rivale* can be included in the group of suitable plants.

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

III

HIGHLY ESTEEMED SIR:

My project of studying the Hieracia of this locality in their natural environment has, unfortunately, been carried out to only a very limited extent. Lack of time is chiefly to blame for this, and I am no longer very fit for botanical field trips, for heaven has blessed me with an excess of avoirdupois, which becomes very noticeable during long travels afoot, and, as a consequence of the law of general gravitation, especially when climbing mountains. If it is thus not possible to send a

collection of wild-growing Hieracia, as I should have liked to do, permit me to submit for your gracious attention some material from my garden instead.

First in importance as a Hieracium hybrid: *H. praealtum*+*H. stoloniflorum* (Autorum). I inclose the two parental plants for your critical examination, since I do not trust myself to make an accurate determination in this genus. It should be mentioned that this *H. praealtum* (perhaps var: *obscurum* Rchb.) occurs frequently in somewhat damp localities such as meadows etc., in the vicinity of Brünn, and that it frequently grows more luxuriantly than does the cultivated specimen. Twenty-eight seedlings of the current year showed no variation. Runners are always absent. *H. stoloniflorum* also occurs locally, but only sporadically. I have raised this form from seeds obtained in Breslau from a herbarium specimen, to which the following note was added: "Occurs commonly, and is not a hybrid." I can only state that the local plant is identical with that from Breslau, that last year's seedlings (2nd generation) have shown no deviations, and that they are all completely fertile.

In addition to other experiments which I performed last year in order to achieve artificial fertilization in Hieracia, I also tried to inhibit pollen development in the above mentioned *H. praealtum*, or, at least, to prevent it from reaching the stigma. To this end, more than half the involucral bracts of a young, incompletely developed head were cut off, and the small flower buds, except for 10-12 removed; the latter were slit open in several places with a fine needle so as to expose the style completely. Fertilization with pollen of *H. stoloniflorum* was performed immediately and was repeated later on. In spite of this drastic treatment, four well developed seeds were obtained, which, when sown in the spring, produced as many plants. Three were completely like *H. praealtum*, whereas the fourth showed considerable divergence, and doubtless represents the hybrid form *H. praealtum*+*H. stoloniflorum*. Thus at least once in four cases, self-fertilization had been prevented by the procedure described; the latter seems to be useful, although it is most complicated, and strains and tires the eye. Since, to judge from leaf formation in the young plant, fertilization of *Cirsium canum* with *C. oleraceum* was achieved in the same way last year, I have used the same procedure in all fertilizations among Hieracia this summer.

The Hieracium hybrid mentioned is a healthy, luxuriant plant. Early in July it developed simultaneously several vertical stems; runners were absent at the time. When the first heads were about to open, the plant with all its roots and surrounding earth was transplanted to a pot, and isolated while blooming. Only after withering of all heads did a short, thick, sterile runner appear, and soon root. The plant was

later returned to the ground, and here it started to bloom a second time, at about the end of September; the stems, however, remained much shorter and weaker. Soon afterwards, a creeping, sterile stolon developed, which bore five vertical heads.

The hybrids *H. Pilosella*+*H. Auricula* and *H. Pilosella*+*H. praealtum*, produced by Fr. Schultz using artificial fertilization, were described as sterile. Since the hybrid *H. praealtum*+*H. stoloniflorum* furnished a number of good seeds, it deserves some attention. 1044 flowers were counted in a total of 14 heads; of these 624 furnished seeds good to all appearances; the majority, however, were not viable, since only 156 plants developed from them (about 15%). These have rooted well, and should flower next year. Whether they will retain the characteristics of the hybrid type, or whether they will show variations, will be determined by next year's observations.

I should like to add some remarks on those characters of the hybrids which are rather difficult to determine in the dried plants.

The leaves are covered in the same fashion as those of *H. stoloniflorum*, but the bristles, especially those of the lower surface, are much less numerous; the stellate hairs are less dense. The stem is covered with stellate hairs, a few grayish-white bristles, and glandular hairs (in *H. praealtum* the base of the bristles is brown, the glandular hairs absent). Bracts of the involucre and flower stalks are densely covered with stellate and glandular hairs (bristles are lacking, as in *H. praealtum*). The sheath of the withered heads is only slightly inflated toward the stem; the marginal flowers are unicolored. On the average, the number of flowers per head is (according to 14 different counts) 39 in *praealtum*, 145 in *stoloniflorum*, and 75 in the hybrid. The latter number thus does not represent the mean, which should be 92; it is, however, almost the exact geometric mean; since 752 is approximately 39×145 .

The plant will be observed again next year. Of this year's fertilizations among *H. Pilosella*, *stoloniflorum*, *Auricula*, and *praealtum* on the one hand, and among *H. murorum*, *vulgatum*, *rigidum*, *boreale*, and *umbellatum* on the other hand, I also hope to obtain more hybrids for further study.

Unfortunately I lack other species, necessary for my experiments. The seeds of the fertilized piloselloids were sown shortly after they matured, and the plants were transplanted to the garden, where they have developed rather well. To judge from the appearance of the basal rosette of leaves, the combination of *H. praealtum* (var. *Bauhini*) with *H. aurantiacum* may be considered successful. Planting of the *Archieracia* will take place next spring; they bloom 5-6 months after being sown.

Also included among the experimental plants was that species with pale brown seed of which I sent you a withered specimen last spring. The plant grows in the Punkwa Valley in the foothills of the Moravian mountains, on a lime-containing substrate, and is not uncommonly found on cut over lands, in association with *H. murorum*, *H. vulgatum*, and *H. boreale*. In August I have found it starting to wither. In dry, infertile soil, the plant appears sparsely developed, and the lateral branches are poorly or not at all developed; in locations rich in humus, on the other hand, one can hardly recognize it as the same plant. I am inclosing the most luxuriant specimen I have found. Plants raised from seed in the garden show no variation, but grow even larger and more vigorously, although they will grow in unfertilized, sandy, soil, just as do other *Hieracia*.

Also included is a *Hieracium* (probably *praealtum*) whose seeds had a lighter color than is the case in the varieties of *H. praealtum* which are known to me. I collected the plant in the vicinity of Tscheitscher Lake, where it grows in abundance. On a sunny slope among low bushes I also found bifurcate types, which are probably of hybrid origin, in association with *H. praealtum* and *H. Pilosella*. I am inclosing some of them. The *H. praealtum* appears to be very close to *H. cymigerum* Rchb. The luxuriant specimen was collected in a somewhat damp location; the other on dry, stony, soil.

From last year's hybrid *Cirsium praemorsum+canum*, only two plants were obtained, and they bloomed this summer. I am sending leaves and flowers of both plants, which are designated as I and II respectively. The pinnatifid radical leaves of plant II were completely destroyed by snails; the inclosed leaves of this plant are cauline leaves at various levels. I must also mention that both plants were very luxuriantly developed, especially plant I. (Height, 6 feet, circumference of the stem at ground level, 6½ inches.) The lower cauline leaves were only slightly recurved, the upper ones not at all. Numerous branches develop from close to the base of the stem. The corollas, which are originally white, soon assume a yellowish-white color; and when withering, a straw-yellow color, while the styles gradually turn red to appear at last strongly crimson. In plant I, the lower half of the stem, the ribs of the radical leaves, and also parts of those of the cauline leaves, were of a dark red color; in plant II, this coloration was absent. Plant I bloomed early in July, plant II a whole month later. Plant I is of average fertility, plant II is nearly sterile. The roots can not be examined until next spring without damaging the plants. The striking differences in leaf formation and position of flowers may be recognized in the dried specimens. About 50 progeny of each parental plant are available from this year's spring sowing. Their development next

summer will show whether or not variants do appear following self-fertilization, and what kinds, and what relation they bear to the differences between the two hybrids.

Fertilization of *C. praemorsum* with *C. canum* was repeated in order to obtain several hybrids for further comparisons.

Geum urbanum+*G. rivale* (from last year's hybridization) looks like *G. intermedium* Ehrh. The varieties with reddish-yellow flowers and those with half-size flowers do not occur among my hybrids. Not all of them had equal fertility, but none of the plants was completely sterile. Fertilized for further experiments were:

G. urbanum with the hybrid
G. rivale with the hybrid
 the hybrid with *G. urbanum*
 the hybrid with *G. rivale*

Plants obtained from these fertilizations, and those produced by self-fertilization from the hybrid were planted in the garden at the beginning of August.

The hybrid *Linaria vulgaris*+*L. striata* bloomed during the first year. I received the latter plant under the designation *Linaria purpurea* (*Antirrhinum striatum*); it seems to be none other than *Linaria striata* DC. The hybrid is intermediate between the parental species as regards position of leaves and flowers, and size and shape of flowers; the fruits, however, are like those of *L. striata*; the inflated, wrinkled capsule form of *L. vulgaris* is not apparent in them. Flower color and shape of seed are peculiar. The bluish-violet striations of the upper lip especially is that of *L. striata*, the orange colored palate spot, that of *L. vulgaris*; the ground color of the flowers was pale yellow in 33 out of 55, pale violet in 21, and one plant produced both colors, but on separate flower stems. I am sending both flowers of the latter, dried in sand, as well as those of *L. striata* and *G. urbanum*+*G. rivale*. When flowers are dried between papers, much becomes indistinguishable.

The seeds of *L. vulgaris* are known to be flat and lenticular, with a rough surface, and equipped with a circular, broad, wing margin; those of *L. striata* are oval, sharply triangular, the surfaces wrinkled and pitted, and without wings. The seeds of the hybrid show considerable variation. While individual ones resemble those of *L. striata* very closely, being distinctly triangular, and lacking wings, the intermediate condition is suggested in the majority by an expansion of one of the three surfaces, while the opposite edge becomes rounded off, is merely suggested, or completely disappears in some seeds. In the latter case, the seeds get a plano-convex or concave-convex shape, and are

equipped with a very narrow wing margin. Wrinkles and pits are always present, but less densely than in *L. striata*. Reciprocal fertilizations were undertaken in the same manner as in the Geum hybrid.

Linaria vulgaris may fairly easily be fertilized by the pollen of other *Linaria* species; among five attempts made this summer, four were successful. Among them is the combination with the beautiful *L. genistifolia*; this hybrid is reported to grow in the wild around Brünn. *L. vulgaris* could not be fertilized with *L. triphylla*.

To conclude, let me report an observation which I made last summer on a *Verbascum* hybrid. I undertook hybridizations among several species of *Verbascum* in 1864. The hybrids raised in the garden were completely sterile; not even a single seed was obtained. By accident one plant of the cross *Verbascum phoenicium*+*V. Blattaria* was left in the seed bowl, and remained therein in a corner of the garden without any care throughout the summer. This very stunted plant was discovered in the autumn and planted in the open ground, along with its luxuriantly developing siblings. Although it became fairly vigorous during the following year, it did not bloom, and wintered for the second time, whereas its siblings died as two year old plants, after having bloomed. This summer the plant made up for everything it had missed, for from June to September it flowered continuously, and produced more than 100 well-formed seeds. It might winter for a third time, since a complete leaf rosette developed after flowering.

I am impatiently awaiting the coming summer, because several fertile hybrids will exhibit their progeny in flower for the first time. Care has been taken that they may appear in large numbers, and I only hope that they will reward my anticipation, with much information about their life history.

With greatest respect I sign myself your honor's

Sincere admirer,
GREGOR MENDEL

Brünn, 6 Nov. 1867.

IV

HIGHLY ESTEEMED SIR:

After having in the past two years collected some experience in the artificial fertilization of Hieracia, I intend to perform some systematic experiments with this genus, experiments which will be limited to crosses between the main types. I have, with few exceptions, the typical species of the piloselloids, but I lack almost all of the Archieracia. I should like to purchase the missing material, but where? That is the question I can not answer. In this predicament I dare to appeal to your honor's kindness, hoping to obtain the desired information.

The species which I should like to have are: *H. cymosum* (*genuinum*), *H. alpinum*, *H. amplexicaule*, *H. glanduliferum*, *H. piliferum*, *H. villosum*, *H. glaucum*, *H. porrifolium*, *H. humile*, *H. tridentatum*, *H. praenanthoides*, *H. albidum*.

H. glaciale, *H. alpicola*, and *H. staticifolium* would also be very welcome. I am very anxious to receive seeds, plants, or both, of the species enumerated. One might still expect plants to flower this summer from seeds sown now.

Repeating my request, I gladly add my promise to send dried or living specimens of the hybrids if the experiments should succeed.

With greatest respect for your honor, I sign myself,

G. MENDEL
(AltBrünn, Monastery of St. Thomas)

Brünn, 9 February 1868.

V

HIGHLY ESTEEMED SIR:

Accept my most cordial gratitude for the Hieracium seeds, which arrived in good condition. How grateful I am for this kind shipment, and how much I do appreciate your kindness in promising also a shipment of living plants. I shall do my utmost to produce all the possible hybrids among the species, and if they should be fertile, their progeny will be observed for several generations. I must ask you to

please charge the expenses of purchase and transportation, and any others, to my account.

I have received the news of your accident of May 1, esteemed Sir, with the greatest regret, and I am sincerely happy that the mishap was not accompanied by any worse consequences.

Recently there has been a completely unexpected turn in my affairs. On March 30 my unimportant self was elected life-long head, by the chapter of the monastery to which I belong. From the very modest position of teacher of experimental physics I thus find myself moved into a sphere in which much appears strange to me, and it will take some time and effort before I feel at home in it. This shall not prevent me from continuing the hybridization experiments of which I have become so fond; I even hope to be able to devote more time and attention to them, once I have become familiar with my new position.

On the whole the plants have wintered well in the experimental plots, and their development has progressed fairly well; most of the piloselloids and some of the Archieracia already show flower buds. The hybrids *H. Auricula*+*H. Pilosella*, *H. praealtum (bauhini)*+*H. aurantiacum*, and probably also *H. Pilosella*+*H. Auricula* may be considered to have been successfully produced. About 100 of the autumn seedlings of last year's hybrid *H. praealtum*+*H. stoloniflorum* (Autor.) have survived the winter. Up to now these plants (still very small) are uniform in the structure and the hairy covering of the leaves, and resemble the hybrid seed plant. I am awaiting their further development with some suspense.

With the assurance of my deepest esteem I sign myself,

Your devoted friend,
GREGOR MENDEL
Abbot and Prelate of the
Monastery of St. Thomas

Brünn, 4 May 1868

VI

HIGHLY ESTEEMED FRIEND:

Forgive me for being so tardy in expressing my most sincere gratitude for the species of *Hieracium* which you sent me. I received the little box on May 12. Since I had to start a long tour of inspection on the same day, I could not find the time necessary to thank you in writing. The gardener received instructions to handle the plants with great care, to pot one specimen of each, and plant the rest in the garden. When I returned a few days ago, I found to my great regret, that half of the potted plants had died, probably the consequence of excessive watering. The garden plants were well preserved, with few exceptions; they must be sorted, however, for the gardener neglected to add the names. The plants so lost include the piloselloids, with the exception of *H. flagellare*, *H. auriculæforme*, and *aurantiacum*, and also *H. pulmonariodes* and *H. albidum*. I hope, however, that none of the species was lost in its entirety.

Of the seeds which you kindly sent me, the following have germinated: *H. amplexicaule*, *H. elongatum*, *H. alpinum*, *H. gothicum*, *H. tridentatum*, *H. praeanthoides*, *H. villosum*, *H. albidum*, and *H. glaucum* did not germinate.

The first generation of last year's hybrid *H. praealtum*+*H. flagellare*, consisting of 112 plants, is flowering. As far as I am able to judge, all plants are alike in the essential characteristics, and they differ from the hybrid seed plant, which is now flowering, only to the extent of having weaker, shorter, and less branched stems. This is not remarkable in view of the greater age and strength of the seed plant. Fertility, as far as it can be judged at this time, is complete in all. The less favorable result obtained last year with the hybrid seed plant in this respect, might be explained by the fact that the latter was while flowering removed from the ground and transplanted to a pot; this must result in injury to the roots, and a weakening of the plant at the time of seed formation.

Five other piloselloid hybrids were obtained from last years fertilizations:

1. *H. praealtum (Bauhini)*+*H. aurantiacum* This hybrid is about intermediate between the parental species. The upper sides of the ray flowers are striped with orange, the lower sides striped with purple, the other flowers are golden or light yellow; the styles are yellow, the stigmas rusty brown. It was transplanted before starting to flower, therefore perhaps, poorly fertile for that reason. I obtained another aberrant type from the same hybridization, but only two heads are opened thus far. In formation of leaves and stolons it resembles *H. traealtum* much more closely, and the stigmas are yellow; the stem, however, is bristly, and the flowers are definitely of hybrid color!

2. Another hybrid: *H. praealtum* (?) + *H. aurantiacum* has just started to flower. One of the parent plants appears to be intermediate between *H. praealtum* and *H. echioides*. The hybrid is of intermediate type, the flower color is as in the preceding plants; the stigmas are rusty brown.

3. *H. Auricula* + *H. Pilosella*, having the characteristic bifurcation of the stem, is also flowering. The heads are strikingly large, much exceeding the average, but this might be due only to the very luxuriant development of this plant.

4. *H. praealtum* (*Bauhini*) + *H. Pilosella*, and also *H. Auricula* + *H. aurantiacum* are just about to start flowering.

Plants from the spring sowing are not yet developed far enough to say anything about the success of the hybridization, but some success should have been obtained with them. They are mostly *Archieracia*.

Next spring my greatest concern will be to send you, as living specimens, all hybrids along with their respective parental species.

Your kind offer of supporting and augmenting my experimental flora in the future evokes my warmest gratitude, and inspires me, at the same time, to make the best possible use of the offered materials.

With the assurance of my deepest respect I sign myself,

Your devoted friend,
GREGOR MENDEL

Brünn, 12 June 1868

VII

HIGHLY ESTEEMED SIR AND FRIEND:

I am sending you as promised some hybrids of *Hieracium*, *Cirsium*, *Geum*, and *Linaria* which I have obtained by artificial fertilization. The catalogue is enclosed; the numbers correspond to those written on the labels tied to the plants.³

³ The following enumeration did not appear in the original letter. It was written on the letter by Nägeli, presumably using a list which Mendel sent along with the specimens. (vide Correns) Trs.

- No. 1 was fairly fertile; the plants raised from seed thus far do not differ from each other morphologically. This hybrid, as well as Nos. 2, 5, 8, 9 are last year's and were raised in pots.
- No. 2 was obtained from the same hybridization as No. 1, but is morphologically quite distinct and was quite infertile.
- Nos. 3 and 4 are the two parental species.
- No. 5 bloomed prolifically, but produced only four viable seeds.
- Nos. 6 and 7 are the two parental species of the preceding hybrid.
- No. 8 was completely sterile. The two parental species are Nos. 4 and 6.
- No. 9 was completely fertile. The progeny which are still young, are uniform in their leaf formation.
- No. 10 is the parent of the preceding species. It grows on the wall of our monastery garden; thus far I know of no other location where it occurs.
- No. 11. Was only partially fertile when raised in a pot, but completely so when raised in the open ground.
- Nos. 12 and 13 are the two parental species.
- No. 14. All of last year's seedlings (there were 112) resembled the hybrid seed plant No. 11. All of them were fertile.
- No. 15. This is a vigorous, beautiful plant of medium fertility. Another irregular form was obtained from the same fertilization; it was sterile and died last summer.
- Nos. 16 and 17 are the two parental types.
- No. 18. I have already reported on the interesting progeny of hybrid No. 15 in my last letter. To my regret I must state today that I am only able to send four specimens, because the others, although they appeared to be vigorous and bloomed plentifully throughout the summer, died during the winter contrary to all expectations. I regret this the more, because, counting on a longer life span, I neglected to dry branches for the herbarium. It is hoped that the damage will be repaired, since the seed plant is healthy and vigorous. Considering the great hardiness of perennial *Cirsia*, it is remarkable that more than two thirds of the vigorous and luxuriant plants were lost after the first bloom. Were they destined by their composition to live only for two years? Or would they have lived longer under more favorable circumstances?
- No. 19 is a very beautiful plant of average fertility. Although the seedlings are still young, their leaf formation leads me to expect as much variability as in the case of No. 19. Hybrids of *Hieracium* show, strangely enough, a very different behavior in the production of their

progeny, than do those of *Cirsium*. *Cirsium* would be an excellent experimental plant for the study of variable hybrids, if it required less space.

Nos. 17 and 20 are the parental species of the preceding hybrid.

No. 21. Several hybrids from the same fertilization varied somewhat in flower size and were of unequal fertility.

Nos. 22 and 23 are the parental types.

Nos. 24, 25, 26 will flower for the first time this year. Nos. 27 and 28 produced some incomplete flowers last year. According to Gärtner, progeny of this *Geum* hybrid show no variation.

No. 29. With respect to flower Color two different types of hybrids were obtained from the same fertilization; 33 hybrids had a rather yellowish, 21 a more purplish coloration, and one plant showed both colors. Fertility is low and the progeny show variation.

No. 31. A beautiful and vigorous hybrid, also of low fertility.

I have one specimen of the interesting hybrid *Mirabilis Jalappa*+*M. longiflora*. A few plants were obtained from the small number of seeds which it bore last summer; they are, however, still too delicate to stand transportation. The same is true of the hybrids:

H. cymosum+*H. Pilosella*

H. Auricula+*H. pratense*

(*H. praealtum*+*H. aurantiacum*)+*H. aurantiacum*

(*H. praealtum*+*M. aurantiacum*)+*H. praealtum*

(*H. Auricula*+*H. Pilosella*)+*H. Auricula*

Antirrhinum vulgare+*A. rupestre*

Lynchnis diurna+*L. vespertina*

which were produced during last year's fertilization experiments.

I have not yet succeeded in producing hybrids of *Archieracia*, but I hope that this year's sowing will yield results. Of the species which you so kindly sent me I was able to use only *H. humile*, *H. Sendtneri*, *H. picroides*, *H. prenanthoides*, *H. hispidum*, and *H. canescens* last summer. Since they, as well as the other species, have wintered well, I shall be able to extend my experiments. This shall be done exactly according to the plan which you, honored friend, were kind enough to send me.

For weeks we have been enjoying the most wonderful spring weather. As compared to several year's average, the vegetation is 13 days earlier than usual; almost everything has come into leaf already.

In gladly taking this opportunity to express to you, my most esteemed friend, my sincere respect and admiration and to commend myself to your continued benevolence, I sign myself,

Yours always respectfully,
GREGOR MENDEL

Brünn, 15 April 1869

VIII

HIGHLY ESTEEMED FRIEND:

Please do not be vexed with me for being so tardy in expressing my gratitude for the living *Hieracia*, all of which arrived safely, and are growing splendidly. Building operations on some remote dairy farms and other business matters have occupied me exclusively for many weeks, and when I returned to Brünn on Whitsunday, I found urgent and time-consuming tasks there also. I have been master of my own time for only a few days now, and in a position to resume my favorite occupation, which I had to discontinue about the end of June of last year, because of an eye ailment.

I found myself in serious danger of having to renounce my hybridization experiments completely, and this due to my own carelessness. Since diffuse daylight was not adequate for my work on the small *Hieracium* flowers, I had recourse to an illumination apparatus (mirror with convex lens), without suspecting what damage I might have done with it. After having occupied myself a good deal during May and June with *H. Auricula* and *H. praealtum*, a peculiar fatigue and exhaustion of the eyes appeared and reached a serious degree in spite of my immediately sparing my eyes as much as possible. It made me incapable of any exertion well into the winter. Since then the affliction has luckily been almost completely lost, so that I am again able to read for long stretches at a time, and can undertake the fertilization experiments in *Hieracium* as well as can be done without artificial illumination.

With today's letter I am sending some living *Hieracium* hybrids; where necessary the parental forms are also inclosed.

The results of the experiments thus far may be termed trifling, and are too incomplete to draw any final conclusions. Some experiences

have been gathered, however, and I take the liberty to mention briefly what seems to me to be of some importance.

I must mention first that I have not yet succeeded in obtaining, by fertilization with foreign pollen, even a single hybrid in some species of piloselloids, in spite of numerous attempts. This is true, for instance, for *H. aurantiacum*. In this species I have not been able thus far, to overcome the influence of its own pollen. *H. Pilosella* and *H. cymosum* also cause difficulties. In others, for instance, in the varieties of *H. praealtum*, fertilization with foreign pollen succeeds more easily with the same treatment, and I have repeatedly convinced myself that *H. auricula* is a completely reliable experimental plant, if some care is employed. Last year I fertilized more than 100 heads of this species with pollen of *H. Pilosella*, *cymosum*, and *aurantiacum*; although about one half of them dried up because of injuries suffered, and only 2-6 seeds were obtained from each of the remaining plants, the plants raised from them are without exception hybrids. The tiny plants of *H. Auricula+H. Pilosella*, and *H. Auricula+H. cymosum* were, with few exceptions, unfortunately browsed upon by snails in the hothouse, but those of *H. Auricula+H. aurantiacum* were preserved; 98 of them have been planted in the garden. They should flower next month.

Still another type seems very suitable for experiments. I inclose it in the shipment under the designation No. XII, since I can neither name nor classify it. I have found it in large numbers on cut over lands. The one attempt at fertilization I made using it and the pollen of *H. Pilosella* was completely successful; all of the 29 plants obtained are hybrids.

I venture to state here that I have, thus far, used only a single form of *H. Pilosella* for fertilizations. Since, however, an adjacent type of *Pilosella* invaded the territory of my experimental plant, as I noticed later, at the time of flowering, I am not certain that a mistake was not made in last year's shipment, and I am inclosing the plant again, designated as *H. Pilosella* (Brünn). I do not dare to state an opinion as to whether this form stands in any kind of relationship to *H. echioides* or not, but will mention that it commonly occurs here, whereas the next known locality of *H. echioides* is about five miles away. The plant which I sent you under the designation of *H. praealtum* (?), was found there in association with *H. echioides* and *H. praealtum*; thus it is beyond doubt that the assumption of it belonging to the *H. echioides-praealtum* group was correct. A comparison with the parental species shows that it resembles *H. echioides* more closely.

I would be very grateful, honored friend, if you should give me, when convenient, your opinion on *Hieracium No. XII*. This plant, and *H. Auricula*, are among the best experimental plants, because a fairly

large number of hybrids may rather easily be obtained from them. This condition is important, because the variations occurring among hybrid individuals can only be interpreted in cases where a fairly large number of hybrids is obtained from the same fertilization.

As a matter of fact, variants appeared in all those cases in which several hybrid specimens were obtained. I must admit to having been greatly surprised to observe that there could result diverse, even greatly different forms, from the influence of the pollen of one species upon the ovules of another species, especially since I had convinced myself, by growing the plants under observation, that the parental types, by self-fertilization, produce only constant progeny. In *Pisum* and other plant genera I had observed only uniform hybrids and therefore expected the same in *Hieracium*. I must admit to you, honored friend, how greatly I was deceived in this respect. Two specimens of the hybrid *H. Auricula*+*H. aurantiacum* first flowered two years ago. In one of them, the paternity of *H. aurantiacum* was evident at first sight; not so in the other one. Since, at the time I was of the opinion that there could be only one hybrid type produced by any two parental species, and since the plant had different leaves and a totally different yellow flower color, it was considered to be an accidental contamination, and was put aside. Thus, in last year's shipment I inclosed only the specimen which closely resembled *H. aurantiacum* in flower color. But when three specimens, each of the same hybrid produced from the fertilization in 1868, and also the hybrid *H. Auricula*+*H. pratense* (var.) later flowered, as three different variants, the correct circumstances could no longer escape recognition.

As I see from your treasured letter that the specimen of *H. Auricula*+*H. aurantiacum*, and the parental species *H. Auricula* which I sent you, have died, I am replacing them, and also include the long misunderstood hybrid twin *H. Auricula*+*H. aurant.* 868b. Last year's three specimens are designated 869 c, d, e. The variant c is completely fertile.

During the winter, one variant of the hybrid *H. Auricula*+*H. pratense*, and the parental species *H. pratense*, have died. The latter was not a typical *H. pratense*, since it carried some stellate hairs on the leaves. The two specimens made available to me through your kindness died during the first year in the garden; one became stunted without having flowered, the other during the flowering period. I have not yet been able to find the pure species in this vicinity.

The hybrid *H. No. XII*+*H. Pilosella* (Brünn) has just started to wither. Very striking variations are seen among the 29 specimens available. Although they represent all transitional types from one parental species to the other, no one would take them for siblings if he

found them growing in the wild. I shall send you the whole collection, as soon as the runners have rooted sufficiently; this should be the case in a few weeks. At that time I hope to be ready to report on this year's major experiment with *H. Auricula*+*H. aurantiacum*; because of the fairly large number of specimens I hope to get some information from it.

Hieracium No. XII has now been fertilized with *H. Pilosella vulgare* (München), and next year the comparison between the two hybrid series *H. No. XII*+*H. Pilosella* (Brünn) and *H. No. XII*+*H. Pilosella vulgare* (München) should not be without interest. *H. Auricula* has also been hybridized with *H. Pilosella vulgare* (M.) and *H. Pilosella* (Br.), shortly it will also be done with *H. Pilosella niveum* (M.). I have only seen one flower of *H. Pilosella incanum* as yet; it is hoped that others will appear.

Twenty-five plants of the hybrid *H. praealtum* (*Bauhini*?) + *H. aurantiacum* of which I sent you two specimens last year, will come into flower soon. Differences between them exist, as far as may be observed at present. Of two specimens raised in pots, and already long past flowering, one is completely fertile, while the other is almost completely sterile. Both total sterility and complete fertility occur in the series of *H. Auricula*+*H. aurantiacum* hybrids. The second generation of the hybrids *H. praealtum* (?) + *H. aurantiacum* and *H. praealtum* (*Bauhini*?) + *H. aurantiacum* has flowered, as has the third generation of *H. praealtum*+*H. flagellare*. Again the hybrids do not vary in these generations. On this occasion I cannot resist remarking how striking it is that the hybrids of *Hieracium* show a behavior exactly opposite to those of *Pisum*. Evidently we are here dealing only with individual phenomena, which are the manifestation of a higher, more fundamental, law.

If one wants to follow the development of those hybrids having only partial fertility, it is necessary to protect the plants most carefully from the influence of foreign pollen; since individual ovules, which would normally remain unfertilized because of the predominantly poor quality of the pollen from the same plant, are readily fertilized by the pollen from other plants. I am sending at the same time some double hybrids, obtained from *H. praealtum* (*Bauhini*?) + *H. aurantiacum* this plant being left to bloom and wither among plants of *H. Pilosella* (Brünn) but removed from other *Hieracia*. The hybrid should therefore, be designated as (*H. praealtum* (*Bauh.*?) + *H. aurantiacum*) + *H. Pilosella* (Brünn). In more than one respect they are very interesting types.

If, in flowers of partially fertile hybrids, the stigmas are covered with the pollen of other, not too distantly related species, they always

produce more seed than when kept isolated and dependent upon self-fertilization; that this is due exclusively to the action of the foreign pollen, can easily be demonstrated by cultivation of the seeds. Careful isolation is, however, not necessary for completely fertile hybrids. Experiments with *H. praealtum?*+*H. aurantiacum* have shown that foreign pollen, even that of the two parental species, may be put upon the stigmas in quantity, without interfering with self-fertilization. All seeds produce the original hybrid form. I am adding the hybrid *H. cymosum* (München)+*H. Pilosella* (Brünn) to the shipment. It is the only hybrid of *H. cymosum*, thus far obtained, although I have tried to fertilize this species many times.

In the Archieracia it is very difficult to prevent self-fertilization. Thus far only two hybrids have been obtained. The seed plant of one is that species with light brown seeds which I sent you once, as a dried specimen; the pollen was taken from a narrow-leaved *H. umbellatum*. The hybrid and the parental plants are inclosed. Among this year's seedlings, fertilization of a form of *H. valgatum* with the above mentioned *H. umbellatum* can be recognized as having been successful. In vain I am looking for an Archieracium which might serve as, well within its group as do *H. Auricula* and *Hieracium No. XII* among the piloselloids.

Of the Archieracia which I owe to your special kindness, all except *H. glaucum* have been subjected to experiments. They are the following: *H. mplexicaule*, *pulmonarioides*, *humile*, *villosum*, *elongatum*, *canescens*, *hispidum*, *Sendtneri*, *picroides*, *albidum*, *prenanthoides*, *tridentatum*, and *gothicum*. The artificially fertilized heads have always withered in *H. amplexicaule* and *H. albidum*. I do not have *H. alpinum*. From the seeds marked Breslau and München which you kindly sent me, *H. nigrescens* and one other species were obtained, that one, however, is not *H. alpinum*.

At this opportunity let me say that all my Archieracia are growing well. *H. albidum* is somewhat delicate when potted, especially during the winter, but it keeps well in the open ground. The same is true of the piloselloids, with the exception, however, of *H. pratense* and *H. Hoppeanum*; the latter died during the first winter in the open ground as well as in pots.

Because of my eye ailment I was not able to start any other hybridization experiments last year. But one experiment seemed to me to be so important that I could not bring myself to postpone it to some later date. It concerns the opinion of Naudin and Darwin that a single pollen grain does not suffice for fertilization of the ovule. I used *Mirabilis Jalappa* for an experimental plant, as Naudin had done; the result of my experiment is, however, completely different. From

fertilizations with single pollen grains, I obtained 18 well-developed seeds, and from these an equal number of plants, of which ten are already in bloom. The majority of the plants are just as vigorous as those derived from free self-fertilization. A few specimens are somewhat stunted thus far, but after the success of all the others, the cause must lie in the fact that not all pollen grains are equally capable of fertilization, and that furthermore, in the experiment mentioned, the competition of other pollen grains was excluded. When several are competing, we can probably assume that only the strongest ones succeed in effecting fertilization.

Besides, I want to repeat the experiment; and it should also be possible to prove directly by experiment whether or not two or more pollen grains can participate simultaneously in the fertilization of the ovule in *Mirabilis*. According to Naudin, at least three are needed!

Of the experiments of previous years, those dealing with *Matthiola annua*. and *glabra*, *Zea*, and *Mirabilis* were concluded last year. Their hybrids behave exactly like those of *Pisum*. Darwin's statements concerning hybrids of the genera mentioned in "the variation of animals and plants under domestication," based on reports of others, need to be corrected in many respects.

Two experiments are still being continued. I have about 200 uniform specimens of the hybrid of *Lychnis diurna* and *L. vespertina*. The first generation should flower in August.

The color experiments with *Matthiola* have lasted now for 6 years, and will probably still go on for several years. With the data already obtained, I hope finally to get to the bottom of the problem. Lack of a reliable color chart has hindered the experiments greatly. Although I had ordered from Erfurt an assortment of *Matthiola annua* in 36 named colors, it proved unsuitable for my purposes. I have given my special attention to this experiment, and I shall take the liberty to report on it as soon as the inspection of the 1500 specimens of this year's culture has been completed. It will be done at the same time as the shipment of the hybrid series *H. No. XII+H. Pilosella*.

In thanking you again, esteemed friend, for your kindness in making the shipment, I sign myself, with the expression of greatest respect,

Your devoted,
GR. MENDEL

Brünn, 3 July 1870

IX

HIGHLY ESTEEMED SIR AND FRIEND:

Together with this letter I am sending the 29 hybrids of *H. No. XII* (*H. cymigerum*)+*H. Pilosella* (Var. of Brünn) which I promised. The Hieracium designated No. XII (already sent you) is still an enigmatic form to me; might it perhaps be *H. poliotrichum* Wim.?

Eighty-four specimens of the hybrid *H. Auricula*+*H. aurantiacum* have flowered, some have died, others have not yet flowered. Variation among them was considerable. Each hybrid characteristic appears in a certain number of variants which represent different transitional stages between one ancestral character and the other. It seems that the variants of the different characteristics may occur in all possible combinations. This seems probable because in the available hybrid plants the assortment of variants of the characters is exceedingly diverse, so as hardly to be the same in any two instances. If this assumption is correct, many hundreds of possible hybrid types should result because of the large number of characters which differentiate *H. Auricula* from *H. aurantiacum*. The observed number of hybrid types is too small in the case of parental species as distant as these to determine the true facts. Success should be obtained more easily with the hybrid *H. Auricula*+*H. Pilosella vulgare*; I hope to obtain 200 specimens of it next year. *H. Auricula*+*H. Pilosella niveum* and *H. Auricula*+*H. Pilosella incanum* is completely sterile, and could not be fertilized with the pollen of the same *H. Auricula*.

I should like to mention that about one quarter of the hybrid types of *H. Auricula*+*H. aurantiacum* may be called completely fertile, one half partially fertile and one quarter sterile. The degree of fertility appears to be independent of the type of the hybrid.

If it should accord with your wishes, esteemed friend, I will send you the whole collection next spring. Of this season's seedlings of Archieracia only a small portion has bloomed in this persistently cold and rainy weather; to date not a single specimen of *H. humile*, which I like to use as an experimental plant. The seedlings of the hybrid *H. ?*+*H. umbellatum*, which I have already sent you, are not yet blooming either; they might still do so, however, if the autumn weather proves favorable. Thus far no differences among them are detectable. I would like to classify the doubtful parental species as *H. racemosum*, if

the pale brown color of the seeds, shown thus far to be constant, were not present.

The experiment designed to solve the question whether or not a single pollen grain suffices for fertilization, was repeated with *Mirabilis Jalapa*, with the same results as last year. Plants obtained from last year's fertilizations using a single pollen grain cannot be distinguished in any way from those produced by self-fertilization. In the beginning it seemed as if individual plants might lag behind in development; later, however, they completely made up the loss.

Under way is another experiment with *Mirabilis*, designed to find out also whether two pollen grains may simultaneously participate in fertilization. The varieties with crimson red, yellow, and white, flowers, respectively are constant when raised from seed, as I know from experience, and the hybrids which first result from the crosses crimson+yellow and crimson+white show no variations in their characteristic coloration. Both fertilizations succeed equally well and thus no differences in the degree of relationship [among the three varieties] is apparent. In the crimson variety a fairly large number of fertilizations was undertaken in such a way that two pollen grains were simultaneously put on each stigma, one of the yellow, and one of the white variety. Since the resultant flower colors of the crosses crimson+yellow and crimson+white are known, it will be shown next year whether in addition to the hybrid colors still a third color will appear, one explainable by joint action of the two pollen grains.

In the latter case, development of the progeny should also be different from that in the two simple color hybrids. These behave like *Pisum*, and half of the first generation again produces the hybrid color, while the other half receives the two parental colors in equal parts, and remains constant in the next generation. Those offspring of the hybrid crimson+yellow, which received the parental colors in the first generation, have also proved themselves to be constant as regards color in the second generation raised from seeds. Both colors re-appear in pure form, as though they had never been in hybrid combination. Darwin and Virchow have pointed to the high degree of independence that is typical for individual characters and whole groups of characters in animals and plants. The behavior of plant hybrids indisputably furnishes an important proof of the correctness of this point of view.

The color experiments with *Matthiola annua* have made only minor progress this year in spite of the great number of experimental plants. According to experiences thus far, an agreement with *Pisum* appears probable. Certain phenomena concerned with the intensity of coloration cause difficulties. Instead of the expected color there frequently appears a higher or lower octave of color, if I may express it

thus, or both appear jointly; and this happens not in isolated cases, but in a whole series of specimens. Thus sorting becomes very unreliable, because it is easy to put together what should be separated, or make the opposite error. The numbers thus obtained for the frequency of the different color variants are useless for the derivation of the developmental series. Recently a new group of experimental plants has been studied; perhaps I will succeed in obtaining a simpler series with them.

Finally, let me report on a curiosity in the numerical ratios in which the male and the female plants of the hybrid *Lychnis diurna*+*L. vespertina* occur. I fertilized three flowers of *L. diurna* and planted the seeds of each capsule separately. They produced:

Capsule I.	74 plants	54 female	20 male
“ II.	58 “	43 “	15 “
“ III.	71 “	54 “	17 “
203		151	52

Is it chance only that the male plants occur here in the ratio 52: 203 or 1: 4, or has this ratio the same significance as in the first generation of hybrids with varying progeny? I should doubt the latter, because of the strange conclusions which would have to be drawn in this case. On the other hand the problem can not be so easily dismissed if one considers that the anlage for the functional development of either the pistil alone or of the anthers alone, must have been expressed in the organization of the primordial cells from which the plants developed, and that this difference in the primordial cells could possibly be due to the ovules as well as the pollen cells being different as regards the sex anlage. Therefore I do not want to dismiss the matter completely.

In commending myself, esteemed Sir and friend, to your treasured consideration, I sign myself, with the expression of greatest respect,

Yours very devotedly,
GR. MENDEL

Brünn, 27 September, 1870

X

HIGHLY ESTEEMED SIR AND FRIEND:

Despite my best intentions I was unable to keep my promise given last spring. The *Hieracia* have withered again without my having been able to give them more than a few hurried visits. I am really unhappy about having to neglect my plants and my bees so completely. Since I have a little spare time at present, and since I do not know whether I shall have any next spring, I am sending you today some material from my last experiments in 1870 and 1871. If, because of the late season, the plants can no longer be put in the open ground, they will winter easily in the greenhouse, covered by moderately damp earth or sand.

I am sending you:

1. *H. praealtum* (München)+*H. Pilosella incanum* (München)
2. *H. Auricula*+*H. Pilosella vulgare* (München)
3. *H. Auricula*+*H. Pilosella vulgare* (Brünn)
4. *H. Auricula*+*H. Pilosella niveum* (München)
5. *H. Auricula*+*H. aurantiacum* (Brünn)

In the following notes I must rely upon my records of 1871.

- ad. 1 1 hybrid, completely sterile.
 ad. 2 84 hybrids, all sterile, hardly any differences among them.
 ad. 3 25 do. all fertile, all uniform.
 ad. 4 35 “ all sterile, all uniform.
 ad. 5 circa 90 “ partially fertile, very variable.

The inflorescences in 1-4 are frequently simple, as in the parental species *H. Pilosella*.

The name following the hybridization symbol + refers in all cases to that species from which the pollen was taken. Thus the + sign has the meaning: fertilized with the pollen of . . .

All the hybrids listed under each number were placed in isolated beds, one for each number, and thus did not disturb each other by growth of their stolons. All the hybrids of one group grew in the same bed, and intermingled to such an extent while they were without care and supervision, that sorting them is difficult, at times even impossible. For shipment I have selected only such specimens as I can assume with some certainty to have originated from separate hybrid seedlings. Only in No. 5 (*H. Auricula*+*H. aurantiacum*) was separation no longer possible, since extremely luxuriant specimens, which cover the bed like a carpet, occur in this hybrid. I am sending three completely fertile variants of this hybrid, which I had transplanted to a separate bed for a

future experiment in the first summer after their seeds had matured. Two of them, which are closer to *H. aurantiacum*, have intermingled in the new location as well, and cannot be distinguished with certainty. Under No. 5, plants of both are found, I hope, in the envelope designated with a. The envelope b contains plants, of the third variant, which resembles the parental species *H. Auricula* more closely.

Since the three hybrid variants just mentioned were shown to be completely fertile, they were to serve for studies of later generations, but these experiments were not executed. It can probably be assumed as rather certain that the progeny originating from self-fertilization of these variants will not be subject to the same variation shown in the original hybrids. At least the plants which were raised as a sample from those seeds formed by the variants, growing in the open ground without any protection, and among all the other hybrids, completely and without exception resemble the seed plant. *H. aurantiacum* was also flowering in the vicinity, and at the same time as the hybrid variants mentioned, without any influence of its pollen having been discernible.

Gärtner has proved the prepotency of the parental pollen over the pollen of hybrids in several species of plants. I have performed a single experiment with Hieracium, the result of which, although representing an isolated case, seems to deserve a brief report. The hybrid *H. praealtum*+*H. aurantiacum* was used as the experimental plant; it is only partially fertile so that only one fourth to one third of the flowers of each head developed good seeds.

The experimental plant was raised in a pot at the window. After several heads had finished flowering, all those still flowering were removed, and only two of the heads still unopened were selected for the experiment. As soon as their first florets opened, the stigmas emerging from the anther tubes were immediately and thoroughly covered with pollen of *H. aurantiacum*. This was continued for three or four days until all florets had opened and all stigmas had been covered. At the time of maturation it became evident that each of the two artificially fertilized heads had formed considerably more seeds than had the other heads, which had been left to self-fertilization. The seeds of the latter were counted and the average number for each head was determined.

In the following year two types of plants were obtained from the seeds of the artificially fertilized heads, those completely resembling the hybrid seed plant, and others which were much closer to *H. aurantiacum*. Furthermore, numerical comparison showed that the number of those seedlings which had not deviated from the hybrid seed plant, and thus had originated by self-fertilization, was almost as great as it should have been, according to the determined average, if the two heads had been left to self-fertilization alone.

The pollen of *H. aurantiacum* is therefore effective only in those florets which would have remained sterile without interference, but it was unable to replace the hybrid pollen.

I want to emphasize here that I gave the utmost attention possible to this experiment which was, by the way, easily performed; that I never missed the hours of 7-9 in the morning, at which time daily a new zone of florets opens from the periphery of each flower disc toward the center, and that very fresh pollen of *H. aurantiacum* was transmitted to the stigma as soon as it made its appearance.

Far be it from me to interpret the result of this experiment as showing that Gärtner is wrong when he claims the pollen of the hybrid to be ineffectual in competition with the parental pollen. No proof to the contrary may be deduced from this experiment-, the exception which Hieracium seems to make in this respect must find a natural explanation in the peculiar structure of the florets and the reaction of the organs of fertilization.

I suspect that free competition is excluded in this genus, as long as self-produced pollen is well developed and of good fertilizing ability, since then the foreign pollen would always come too late and could contend only unsuccessfully due to this fact. I have had frequent occasion to convince myself that, in the Hieracia, the anthers open within the bud, and transfer the pollen to the stigma, which they surround closely, so that the latter emerges from the tube already covered with pollen when the bud opens. In *H. aurantiacum*, *H. murorum*, and others I have many times, at least a day before flowering, carefully severed the anther tube at its base and pulled it over the style without slitting it open on the side, and used all additional precautions possible, after which I covered the stigma repeatedly with the foreign pollen destined for the fertilization, and still have never raised anything except *H. aurantiacum* or *H. murorum* out of the obtained seeds.

On the basis of this experience I consider it likely that fertilization with foreign pollen can occur only if self-fertilization fails, as long as the ovule remains capable of fertilization; this seems not infrequently to be the case in this genus.

It is known that unfavorable changes in environmental conditions may result in reduced reproduction, therefore they may cause a sexual weakening or complete sterility, wherein the male organs always suffer first, as in animals in captivity. It should not be otherwise in plants. *H. Pilosella incanum* can not adapt itself very well to the local climate. In the summer the air here seems to be too dry, perhaps also too warm for this plant. In 1870 the May and June flowers were completely sterile, partially fertile in the following year, and toward autumn individual

heads appeared to be completely fertile. Presumably the reason for this sterility was to be found, in the case of the summer flowers, in the poor quality of their own pollen, since I could not successfully fertilize *H. Auricula* with it either, while at the same time fertilization with the pollen of other *Pilosella* varieties caused no difficulties. Toward the end of August, however, fertilization with the pollen of *H. Pilosella incanum* was successful. Gärtner was also convinced by his experiments that the male principle (as he puts it) is always affected first.

If this were actually the case, the naturally-occurring hybridizations in *Hieracium* should be ascribed to temporary disturbances, which, if they were repeated often or became permanent, would finally result in the disappearances of the species involved, while one or another of the more happily organized progeny, better adapted to the prevailing telluric and cosmic conditions, might take up the struggle for existence successfully and continue it for a long stretch of time, until finally the same fate overtook it.

Species of which numerous hybrids have been shown to exist I would consider decrepit or would at least assume that they were well past their prime. (*H. Auricula*, *H. praealtum*).

I cannot yet give a report on the success of the collection of Moravian hybrids of *Hieracium* initiated by Prof. Niessl. Shipments from the corresponding members of our society are expected not sooner than this winter.

With the expression of my greatest admiration and esteem I sign myself,

Yours very respectfully,
GR. MENDEL

Brünn 18/11 1873