The birth of genetics [by] Mendel, De Vries, Correns [and] Tschermak in English translation.

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GENETICS

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THE BIRTH OF GENETICS

MENDEL

DE VRIES—CORRENS—TSCHERMAK

In English Translation

SUPPLEMENT

TO

GENETICS

A PERIODICAL RECORD OF INVESTIGATIONS

BEARING ON HEREDITY AND EVOLUTION

Published bi-monthly at Menasha, Wisconsin

By the Brooklyn Botanic Garden, Brooklyn 25, New York, U. S. A.

1950

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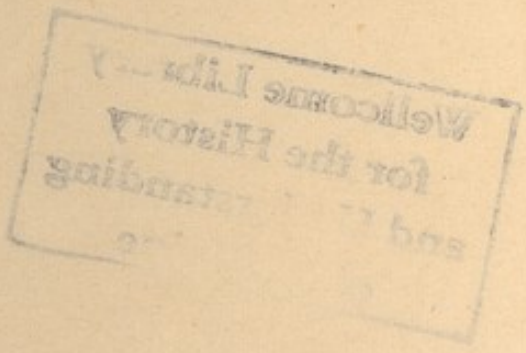

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FOREWORD

GENETICS celebrates the fiftieth anniversary of the rediscovery of MENDEL'S work by offering herewith English translations of the first papers in which DE VRIES, CORRENS, and TSCHERMAK announced their findings. Preceding the translations of these historic contributions the letters of MENDEL to NÄGELI, written between 1866 and 1873, are also reproduced in English. Together with the well known translations of MENDEL'S two genetic papers* all important documents centering around the birth of modern genetics are thus made available to the English speaking world. A study of these writings permits an insight into the origin and development of a great scientific concept in the minds of different individuals.

THE EDITORS OF GENETICS

* (1) "Versuche über Pflanzenhybriden" (1866), translated in Journal of the Royal Horticultural Society **26:** 1–32 (1901). Reprinted in W. BATESON, 1909, MENDEL'S Principles of Heredity. Cambridge University Press. Available separately as: GREGOR MENDEL, Experiments in plant hybridisation. Harvard University Press. 41 pp. (1948).

(2) "Über einige aus künstlicher Befruchtung gewonnene Hieracium Bastarde" (1869), translated in W. BATESON (l.c.).

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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

I

HIGHLY ESTEEMED SIR:

The acknowledged pre-eminence your honor[1] 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 monograph[2] (pp. 17–18), the notations for the constant forms have been placed first, since the terms are arranged according to 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 be 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

* Abhandlungen der Mathematisch-Physischen Klasse der Königlich Sächsischen Gesellschaft der Wissenschaften **29**: 189–265, 1905. Reprinted in "CARL CORRENS, Gesammelte Abhandlungen zur Vererbungswissenschaft aus periodischen Schriften" 1899–1924. (FRITZ V. WETTSTEIN ed.) Berlin, Julius Springer, 1924. pp. 1237–1281.

[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.

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 then 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 diffculties, 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:*

B. albumen yellow	*b*. albumen green
C. seed-coat grayish-brown	*c*. seed-coat white
D. pod 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 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

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

Fertilization of ovules occurs:

I.	Ovules	ab	with	pollen	AB
II.	"	ab	"	"	AB and Ab
III.	"	ab	"	"	AB and aB
IV.	"	ab	"	"	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
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 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.

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 Prenanthoidea (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, I 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 *Tropaeoleum majus*+*T. minus* (1st generation) must also be mentioned.

For the current year exploratory experiments with Veronica, Viola, Po-

tentilla, 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 *Tropaeoleum 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 75^2 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, $6\frac{1}{2}$ 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 phoeniceum*+*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. auriculaeforme,* and *aurantiacum,* and also *H. pulmonarioides* 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. praenanthoides. 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. praealtum* 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]

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.

[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. 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. 18. 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*+*H. 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 (mirrow 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. vulgatum* 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. amplexicaule, 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

Brünn 18/11 1873

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

CONCERNING THE LAW OF SEGREGATION OF HYBRIDS

(SUR LA LOI DE DISJONCTION DES HYBRIDES)*

HUGO DE VRIES

Translated by ALOHA HANNAH

Department of Zoology, University of California, Berkeley, California

According to the principles which I have expressed elsewhere (Intracelluläre Pangenesis, 1889), the specific characters of organisms are composed of separate units. One is able to study, experimentally, these units either by the phenomena of variability and mutability or by the production of hybrids. In the latter case one chooses in preference hybrids from parents which are distinguishable from each other by only a single character (the monohybrids) or by a small number of well delimitated characters, and for which one considers only one or two of the units and leaves the others aside.

Ordinarily the hybrids are described as exhibiting simultaneously the characters of the father and the mother. In my opinion, one must admit, in order to understand this result, that the hybrids have some of the simple characters from the father and other equally simple characters from the mother. But when the father and the mother are distinguishable only by a single point, the hybrid could not be in the middle, since the simple character must be considered as one non-divisible unit.

Otherwise the study of simple characters of the hybrids can furnish the most direct evidence of the stated principle. The hybrid always shows the character of one of the two parents and that in all of its force. The character of one parent is always separated from the other, it is not present reduced by one half.

The table which follows gives some examples. Ordinarily it is the character of the species which prevails over that of the variety, or the most ancient character prevails over that which is the younger. But I observed diverse exceptions to this rule.

In the hybrid the simple differential character from one of the parents is accordingly visible or *dominant* while the antagonistic character is in the latent condition or *recessive*.[1]

The antagonistic characters ordinarily remain combined during all of the vegetative life, one dominant, the other latent. But in the generative period, they are segregated. Each grain of pollen and each oosphere receives only one of the two.

For the monohybrids, one has therefore the thesis *that their pollen and their ovules are no longer hybrid*, so that they have the pure character of one of the parents. And the same proposition can be supported for the others (di- and polyhybrids), when one considers only a single character at a time.

* Comptes Rendus de l'Academie des Sciences (Paris) **130**: 845–847, 1900.

[1] In this article I was only concerned with the true hybrids and omitted the *false hybrids* of MILLARDET.

By this principle one is able to deduce almost all of the rules which govern the distribution of characters in the descendents of hybrids. I have tested a portion by experiment, but shall restrict myself here to summarizing the experiments which establish the principle of the laws.

Having cultivated several hundreds of individuals from seeds of different hybrids, with which I took care in assuring a pure cross pollination, I have found for the products the following proportion of individuals presenting the recessive character:

Parent having the dominant character	Parent having the recessive character	Proportion of hybrids with the recessive character
Agrostemma Githago	*A. nicaeensis*	24 per 100
Chelidonium majus	*C. laciniatum*	26 " "
Coreopis tinctoria	*C. brunea*	25 " "
Datura Tabula	*D. Stramonium*	28 " "
Hyoscyamus niger	*H. pallidus*	26 " "
Lychnis diurna (red)	*L. vespertina* (white)	27 " "
Lychnis vespertina (hairy)	*L. glabra*	28 " "
Œnothera Lamarckiana	*Oe. Brevistylis*	22 " "
Solanum nigrum	*S. chlorocarpum*	24 " "
Trifolium pratense	*T. album*	25 " "
Veronica longifolia	*V. alba*	22 " "

One sees that the proportion of the hybrids with the recessive character is always close to 25 per 100.

The culture of a further generation permits the study of a distinction among the 75 per 100 individuals presenting the dominant character. I cite as an example a cross of a poppy having basal black spots on the petals with one having white spots.

If one grows the hybrid seeds from the two varieties, calling N the plants with black spots, and B the plants with white spots, one obtains as for the preceding:

75 per 100 N and 25 per 100 B

But a second culture of seeds contributed by the self pollinated N plants, the seeds arising from each plant grown in a separate plot, gives for 25 of the 75 plants a pure progeny with black petals and for the 50 others a mixture of plants with black petals and plants with white petals in the proportion of 37.5 N to 12.5 B.

One has therefore, in short, by assembling the results of the two successive cultures:

100 hybrid seeds of N and of B

75 N		25 B
25 N	50 B	25 B
25 N	37.5 N+12.5 B	25 B

I have also studied two other successive generations of these same hybrids. Each time they have repeated the same phenomena of segregation.

I have obtained the same results with the hybrids of sugary corn and starchy corn, within which the endosperms are visibly hybrid at the same time as the embryo.

One can unify the whole of these results by supposing that the two antago-

nistic qualities, dominant and recessive, are distributed [mutually exclusively] in equal parts to the pollen just as to the ovules.

If one calls D the grains of pollen or the ovules having a dominant character and R those which have the recessive character, one can represent the number and the nature of the hybrids by the following representative formula in which the numbers of D and R are equal:

$$(D+R)(D+R) = D^2+2DR+R^2$$

This repeats the statement that there will be 25 per 100 of D, 50 per 100 of DR and 25 per 100 of R.

The D individuals will have the pure dominant character, having inherited it from father and mother. In the same fashion the R individuals will have the pure recessive character, while DR will be the hybrids. The latter bear the dominant visible character and the recessive latent character.

One will only be able to distinguish the 25 per 100 D, from the 50 per 100 DR by a second culture.

The totality of these experiments establishes the law of segregation of hybrids and confirms the principles that I have expressed concerning the specific characters considered as being distinct units.

G. MENDEL'S LAW CONCERNING THE BEHAVIOR OF PROGENY OF VARIETAL HYBRIDS

(G. MENDEL'S REGEL ÜBER DAS VERHALTEN DER NACHKOMMENSCHAFT DER RASSENBASTARDE)*

CARL CORRENS

Translated by LEONIE KELLEN PITERNICK
Department of Zoology, University of California, Berkeley, California

THE latest publication of HUGO DE VRIES: Sur la loi de disjonction des hybrides[1] which through the courtesy of the author reached me yesterday, prompts me to make the following statement:

In my hybridization experiments with varieties of maize and peas, I have come to the same results as DE VRIES, who experimented with varieties of many different kinds of plants, among them two varieties of maize. When I discovered the regularity of the phenomena, and the explanation thereof—to which I shall return presently—the same thing happened to me which now seems to be happening to DE VRIES: I thought that I had found *something new.*[2] *But then I convinced myself that the Abbot* GREGOR MENDEL *in Brünn, had, during the sixties, not only obtained the same result through extensive experiments with peas, which lasted for many years, as did* DE VRIES *and I, but had also given exactly the same explanation, as far as that was possible in 1866.*[3] Today one has only to substitute "egg cell" or "egg nucleus" for "germinal cell" or "germinal vesicle" and perhaps "generative nucleus" for "pollen cell." An identical result was obtained by MENDEL in several experiments with Phaseolus, and thus he suspected that the rules found might be applicable in many cases.

MENDEL's paper, which although mentioned, is not properly appreciated in FOCKE'S "Pflanzenmischlingen," and which otherwise had hardly been noticed, is among the best that has ever been written about hybrids, in spite of some objections which one might raise with respect to matters of secondary importance, e.g. terminology.

At the time I did not consider it necessary to establish my priority for this "re-discovery" by a preliminary note, but rather decided to continue the experiments further.

In the following I shall limit myself to an account of the experiments with varieties of peas.[4] Inter-varietal hybrids of maize show identical behavior in

* Berichte der Deutschen Botanischen Gesellschaft **18:** 158–168. Reprinted in: CARL CORRENS Gesammelte Abhandlungen zur Vererbungswissenschaft aus periodischen Schriften 1899–1924. (FRITZ V. WETTSTEIN, ed.) Berlin, Julius Springer, 1924, pp. 9–16.

[1] Compt. rend. de l'Acad. des Sciences, (Paris), **130,** 1900, 26. mars.

[2] See the postscript. (footnote added later).

[3] GREGOR MENDEL, Versuche über Pflanzen-Hybriden. Verh. des Naturf. Vereines in Brünn, **4.** 1866.

[4] The names of the varieties given in this paper are those which I received from HAAGE and SCHMIDT in Erfurt.

all essential points, but are more difficult to experiment with, and I have not yet elucidated to my satisfaction several points of secondary importance. They will be discussed somewhere else.

Varieties of peas are invaluable for the problem which interests us here, as MENDEL had emphasized correctly, since the flowers are not only autogamous, but are very rarely fertilized by insects. On the basis of experiments on the formation of xenia—which, in the case of peas yielded only negative results—I came across this material. When I realized, that the rules here are much clearer than they are in maize, where I had first discovered them, I continued the observations.

The *characters* which differentiate the varieties of peas, can, as in all other cases, be grouped into *pairs*, each member having an effect on the same trait, one in one and the other in the other one of the varieties e.g. the color of the cotyledons, the color of the flower, the color of the seed coat, the hilum of the seed, etc. In many pairs one character, or rather the anlage thereof is so much stronger than the other character, or its anlage, that the former alone appears in the hybrid plant, while the latter does not show up at all. This one may be called the *dominant*, the other one the *recessive* anlage. MENDEL named them in this way, and, by a strange coincidence, DE VRIES now does likewise. For example the yellow color of the cotyledons is dominant over the green color, and red flower color over white flower color.

I can not understand why DE VRIES assumes that in all pairs of characters which differentiate two strains, one member must always be dominant.[5] Even in peas, where some characters completely conform to this rule, other character pairs are also known, in which neither character is dominant, as for instance the color of the seed coat, being either reddish-orange or greenish-hyaline.[6] In this case the hybrid may show all transitions, (this is true especially for the seed coat of peas), or it shows either more of one or of the other character (for example in hybrids of stocks; here a certain hybrid may be *just barely* distinguished from one parental form by its hardly noticeable slighter covering of hairs, although with some care, separation is always possible, while it is *highly distinct* from the other, i.e., the glabrous parental type).

The following holds only for pairs of characters which have a dominant and a recessive member; there is no reason to believe that it may not hold for other types of pairs of characters as well, but at present we know of no example.[7] Let us first consider a single pair of characters. It is immaterial whether the

[5] For instance "D'autre part, l'étude des caractères simples des hybrides peut fournir la preuve la plus directe du principe énonce. *L'hybride montre toujours le caractère d'un des deux parents, et cela dans toute sa force;* jamais le caractère d'un parent, manquant a l'autre, ne se trouve réduit de moitié." (l.c. paragraph 3, italics mine).

[6] The color of the hilum on the other hand (whether black, brownish etc.) represents a dominant character.

[7] In the meantime I have found an example (Footnote added later).

varieties to be crossed are only differentiated by this one pair, or by others as well. The specific pair of characters we may select is the *color of the embryo, either yellow or green.* It is very easy to obtain large numbers for this trait.

The facts, which MENDEL found, I can fully confirm. They also agree with the findings of DE VRIES for his experimental objects. They are as follows:

1. In the *first* generation, all hybrid individuals are uniform and only the *dominant* character appears. In our special case the cotyledons are yellow.

2. When these seeds with yellow embryos are sown, plants are obtained, whose pods, which were produced by self-fertilization, contain seeds with *yellow* embryos and seeds with *green* embryos, (the second generation) and on the average, there are *three* yellow ones for each green *one*. If there are four or more seeds in each pod, one containing a green embryo will usually be among them.

3. When the seeds with a *green* embryo are sown, plants are obtained, whose pods, which were produced by self-fertilization, contain *only* seeds with *green* embryos, (the *third* generation). These, in turn, produce only seeds with *green* embryos, (the *fourth* generation), etc. With respect to this character, the *recessive* one, they behave like the *pure* variety, which carries it.

4. If the seeds with *yellow* embryo are sown, plants are produced which may be grouped into *two classes*,

Class A, those plants, whose pods, which were obtained by self-fertilization, contain *only* seeds with *yellow* embryos (the *third* generation) and

Class B, those plants, whose pods, which were produced by self-fertilization, contain seeds with *yellow* as well as seeds with *green* embryos (the *third* generation). Numerically, there are again on the average *three* seeds with *yellow* embryos for each *one* with a *green* embryo, just as in the second generation (see paragraph 2).

The *number of individuals* in classes A and B is approximately *one* to *two*.

Let me emphasize again, that *embryos* of Class A do not differ in their *appearance* in any way from those in Class B, only after the pods which were produced by self-fertilization, have been harvested, can it be decided to which one of the classes the seed belonged.

5. Seeds with *yellow* embryos, which descended from plants of *Class A* (paragraph 4), produce plants, whose pods, which originated by self-fertilization, again contain *only* seeds with *yellow* embryos (the *fourth* generation). Plants which develop from them in turn produce *only* seeds with *yellow* embryos etc. As regards this character, the *dominant* one, they behave like the *pure* variety which carries it.

6. The seeds with *green* embryos, which are obtained from plants of *Class B* (paragraph 4, B) produce plants, whose pods, which originated by self-fertilization again contain only seeds with *green* embryos (the *fourth* generation). Plants which develop from them in turn produce *only* seeds with *green* embryos, (the *fifth* generation) etc.;—just as did the green embryos of the *second* generation (paragraph 3).

7. The seeds with *yellow* embryos, which are obtained from plants of *Class B* (paragraph 4, B) again produce, just as it was described in paragraph 4, *two*

types of plants, in the ratio *one* to *two*, whose seeds behave in the same way as described in paragraphs 5 and 6 and so forth.

The following table explains and summarizes the results discussed above, it also gives the numerical ratios.

TABLE 1

PARENTS	HYBRID					
	I. GEN.	II. GEN.	III. GEN.	IV. GEN.	V. GEN.	VI. GEN.
green		1 green...	∞ green...	∞ green...	∞ green..	∞ green
			1 green...	∞ green...	∞ green..	∞ green
				1 green...	∞ green..	∞ green
					1 green..	∞ green
					2 yellow	1 green
	∞ yellow	2 yellow	2 yellow	2 yellow	3	3 yellow
		3	3	3	1 yellow..	
						∞ yellow
				1 yellow...	∞ yellow..	∞ yellow
			1 yellow...	∞ yellow...	∞ yellow..	∞ yellow
yellow		1 yellow...	∞ yellow...	∞ yellow...	∞ yellow..	∞ yellow

The sign ∞ indicates that all of the seeds of the progeny in this group contained like embryos.

The two following tables show the results obtained in two of my experimental series. The generations are given in vertical sequence. The upper *figure in bold face* denotes in each generation the *number of embryos obtained*, the *figure in light face* the *number of individuals*, which were raised from these embryos and produced fruits; ye- yellow, gr- green. The rest is self-explanatory.

Experiment I

Hybrid between the "*green late* [*variety*] *Erfurter Folgererbse*" with *green* embryos and the "[*variety*] *Kneifelerbse with purple-violet pods*," having *yellow* embryos.[8]

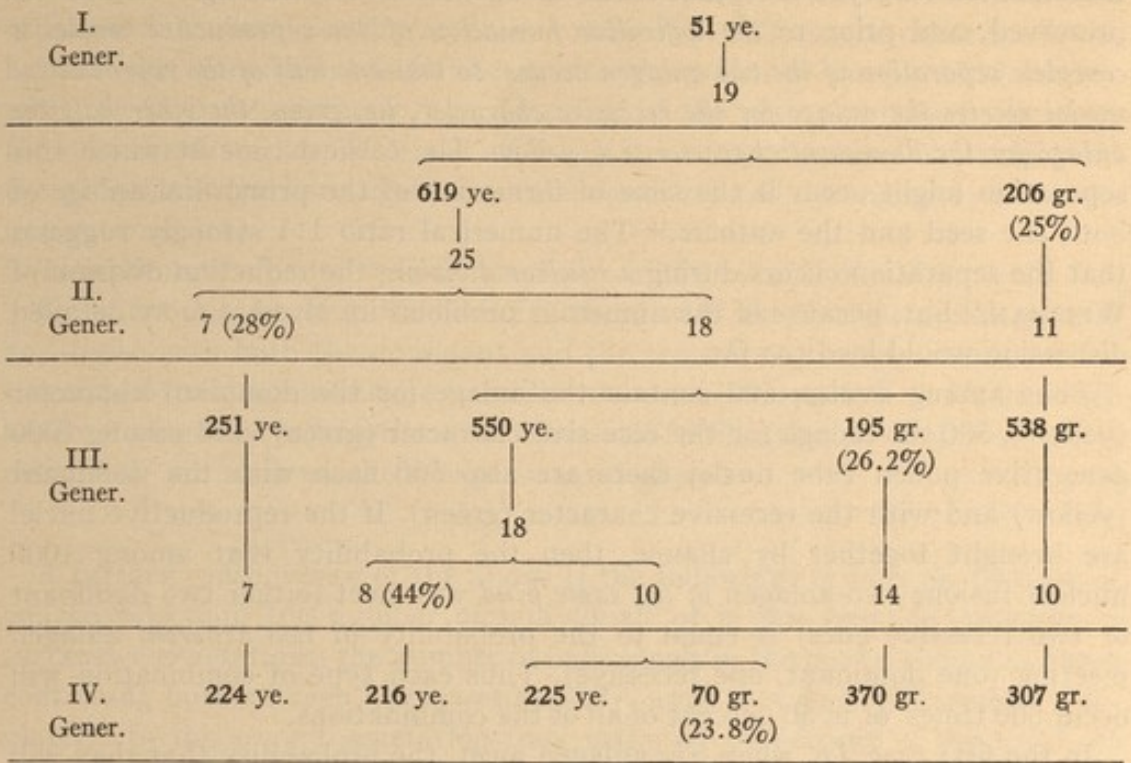
Experiment II.

Hybrid between the "*green, late* [*variety*] *Erfurter Folgererbse*," with *green* embryos and the [*variety*] "*Bohnenerbse*," with *yellow* embryos.

The numerical ratios of yellow embryos to green embryos are quite variable in individual plants. In experiment I the smallest percentages for green being 14.9 and 7.7 and the largest ones 44.2 and 40.0.—It is of no importance whether the dominant character was introduced by the paternal or by the maternal plant; in *all* varieties, which possess a specific pair of characteristics the latter behaves in the same manner.

[8] Under identical conditions the plants produced an average of 43.3, 47.7, and 28.8 seeds in successive generations; this is a good example to show the consequences of self-fertilization, and also furnishes an explanation of the "giant growth" of some hybrids (footnote added later).

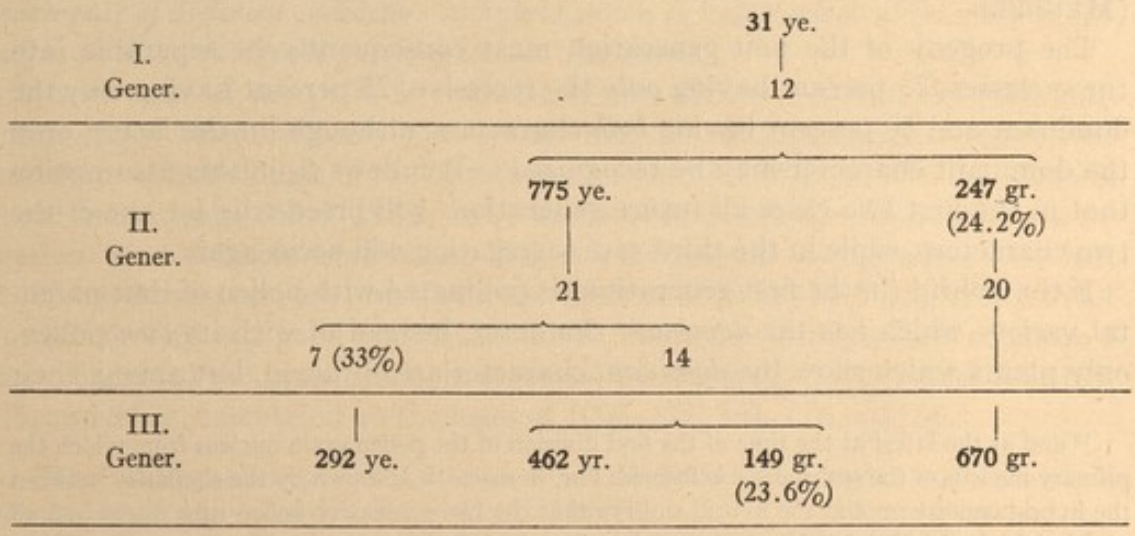
TABLE 2



Experiment II. shows by chance the exact numerical ratios between the two classes of individuals which are produced by seeds with yellow embryos (7:14=1:2), while this ratio can be determined only from the mean of generations III and IV in experiment I: 15 [=7(III)+8(IV)] individuals in one class as opposed to 28 [=18(III)+10(IV)] of the other (34.9:65.1 instead of 33.3:66.6).

In order to *explain* the facts, one must assume (as did MENDEL) that following fusion of the reproductive nuclei,[9] the anlage for one character, the recessive

TABLE 3



[9] MENDEL, of course, does not mention nuclei, but only "germinal cells" and "pollen cells."

one, (*green* in our case) is suppressed by the other character, the dominant one, therefore all embryos are *yellow*. The anlage, however, although "latent" is preserved, and prior to *the definitive formation of the reproductive nuclei a complete separation of the two anlagen occurs, so that one half of the reproductive nuclei receive the anlage for the recessive character, i.e. green, the other half the anlage for the dominant character, i.e. yellow*. The earliest time at which this separation might occur is the time of formation of the primordial anlage of both the seed and the anthers.[10] The numerical ratio 1:1 strongly suggests that the separation occurs during a *nuclear division*, the reduction division of WEISMAN,[11] but, because of the numerous problems involved, a more detailed discussion would lead too far.

Thus among ovules, 500 contain the anlage for the dominant character (yellow), 500 the anlage for the recessive character (green), and among 1000 generative pollen tube nuclei there are also 500 each with the dominant (yellow) and with the recessive character (green). If the reproductive nuclei are brought together by chance, then the probability that among 1000 nuclear fusions two anlagen *of the same kind* will meet (either two dominant or two recessive ones) is equal to the probability of *two different* anlagen meeting (one dominant, one recessive). Thus each type of combination will occur 500 times, or in 50 percent of all of the combinations.

In the first case, i.e. when *like* anlagen meet, the probability that they will be two *recessive* ones is as great as that they will be two *dominant* ones, again one half, or each one will occur 250 times or in 25 per cent of all combinations. For the pair of characters under investigation, the result is here the same, as if two reproductive nuclei of either one of the pure varieties would unite.

In the second case—when *different* anlagen are combined the result of self-fertilization must be the same as that found in hybrids of the first generation, which were produced by experiment. The dominant anlage suppresses the recessive one, but later, preceding definitive formation of the reproductive nuclei, the two anlagen separate again, as was described for the artificially produced hybrid. "There occurs, accordingly a repeated hybridization" (MENDEL).

The progeny of the first generation must consequently be separable into three classes, 25 percent having *only* the recessive, 25 percent having *only* the dominant and 50 percent having *both* characters, although [in the latter] only the dominant character may be recognized.—It follows from this assumption that in the first two cases all future generations will breed true for one of the two characters, while in the third case segregation will occur again.

If the hybrid (in the first generation) is pollinated with pollen of that parental variety which has the *dominant* character, instead of with its *own* pollen, only plants which show the *dominant* character are obtained, but among their

[10] and at the latest at the time of the first division of the pollen grain nucleus from which the primary nucleus of the embryo sac is formed. For, in maize, it is shown by the similarity between the hybrid endosperm and the hybrid embryo that the two generative pollen tube nuclei and all of the eight nuclei of the embryo sac contain only one of the two anlagen. (Footnote added later).

[11] See also "Keimplasma" p. 392 ff.

progeny *one half* will in turn produce *only* individuals with the *dominant* character, while *the other half* produces some plants with the *dominant* and others with the *recessive* character, in a ratio of 3:1. If, on the other hand, the hybrid (first generation) is fertilized with the pollen of the parental variety with the *recessive* character, then *one half* of the plants obtained will show the *recessive* character, while the *other half* shows the *dominant* character, and the progeny of the *latter* again show the *dominant and* the *recessive* characters in a ratio of 3:1.

This theoretically derived rule also holds in the hybrids of maize.

Since two classes of individuals i.e. those with the dominant anlage only and those with both the dominant and the recessive anlagen, cannot be distinguished from one another externally, the correct numerical ratios can only be determined by *self-fertilization*. Since self-fertilization normally occurs in peas, they are such excellent experimental objects.

A further consequence of the above is the following: as long as, because of chance selection, the number of individuals of a plot remains constant in successive generations, the number of individuals in the modal class, *i.e.*, those containing both anlagen, decreases steadily, until they finally disappear completely. In the second generation they make up 50 percent of the total, 25 percent in the third generation, 12.5 in the fourth, 6.25 in the fifth and $100/2^{n-1}$ percent in the nth generation. This numerical decrease of the modal class had already been derived by MENDEL.[12]

Thus far we have considered only the behavior of those pairs of characters in which one member is dominant. The case of two or more differentiating characters also was discussed *theoretically* and tested *experimentally* by MENDEL. It was shown that all possible combinations occur as frequently as they are expected on the basis of the laws of probability, assuming that their production is due to chance. "It is demonstrated at the same time, *that the relation of each pair of different characters in hybrid union is independent of the other differences in the two original parental stocks.*" (MENDEL)[13]

In the case of *two* pairs of characters, *nine* different classes of individuals may occur. However, only *four groups* may be distinguished *externally*, the numbers of individuals in the classes must occur in a ratio of 9:3:3:1. Among 1000 individuals, 562.5, 187.5, 187.5 and 62.5 respectively will be grouped together. In a suitable experiment MENDEL did obtain the numbers 315, 101, 108, and 32 respectively, which on the basis of 1000 are as 566.6, 181.6, 194.4 and 57.6. This is a good approximation to the ratio. With hybrids of maize I have obtained the same result, in one case, for instance, the numbers 308, 104, 96, and 37 or, calculated on the basis of 1000, 565, 191, 176, and 68.

[12] One hardly needs to point out, how important this behavior is in regard to the question of species formation from hybrids. (Footnote added later).

[13] There are again exceptions to this rule; strains with linked characters exist. (Footnote added later).

MENDEL concludes "*that the pea hybrids form egg and pollen cells which, in their constitution, represent in equal numbers all constant*[14] *forms which result from the combination of the characters when united in fertilization.*" We may say in the terms used in this paper: *In the hybrid reproductive cells are produced in which the anlagen for the individual parental characteristics are contained in all possible combinations, but both anlagen for the same pair of characters are never combined. Each combination occurs with approximately the same frequency.*—If the parental strains differ only in *one* pair of characters (2 characters: *A*, *a*) the hybrid will form only *two types* of reproductive nuclei (*A*, *a*) which are like those of the parents. Each type is 50 percent of the total. If the parents differ in *two* pairs of characters (4 characters: *A*, *a; B*, *b*) *four types* of reproductive nuclei will be formed, (*AB*, *Ab*, *aB*, *ab*) and 25 percent of the total will be of each type. If the parents differ in *three* pairs of characters (6 characters: *A*, *a; B*, *b; C*, *c*) *eight types* of reproductive nuclei will be formed (*ABC*, *ABc*, *AbC*, *Abc*, *aBC*, *aBc*, *abC*, *abc*), and 12.5 percent of the total are of each type.[15]

This I call MENDEL'S *law*. It includes the "loi de disjonction" of DE VRIES, also. Everything else may be derived from this law.

At present, however, this law is applicable only to a certain number of cases, i.e. those where one member of a pair of characters is dominant,[16] and probably only to hybrids between varieties. It seems impossible that all pairs of characters of all hybrids should behave according to this law. Some hybrids of peas bear this out.

In the *first* generation of the combination of the "green, late [variety] Erfurter Folgererbse" with an almost colorless seed coat, and the "[variety] Kneifelerbse with purple-violet pods," or the "[variety] Pahlerbse with purple pods" both having a solid-color, orange-red seed coat, which turns brown on aging, the seed coats within the same pod were sometimes colorless, sometimes intensely red, *but usually more or less tinted with orange*, and also speckled to a variable degree with purplish-black spots. Thus, in addition to a *dilution* of one of the characters, an (apparently) *new* character had originated. In the second generation, however, the seeds which show the two extremes of coloration, i.e. those with orange red, and those with almost colorless seed coats will again produce the extreme types and all of the transitions between them. The speckling was sometimes unchanged, sometimes not present at all or very slight and sometimes somewhat increased. Size and shape of the seed and texture of the seed surface behaved in a similar way.

I will discuss these points at a later time.

Tübingen, 22, April, 1900.

Postscript (added in proof)

In the meantime DE VRIES has published in these proceedings (No. 3 of this year) some more details concerning his experiments. There he refers to

[14] MENDEL calls a type constant, if it no longer contains the two different anlagen of a pair of characters.

[15] If the pollen grains of the two parental strains differ externally, one may, if MENDEL'S law holds, expect the hybrid to form two externally different types of pollen grains. That this is true was first observed by FOCKE.

[16] See footnote 6 p. 34.

MENDEL'S investigations, which *were not even mentioned in the "Comptes rendus."* I must emphasize again:

1. *that in many pairs of characters there is no dominant member* (p. 34),
2. *that* MENDEL'S *law of segregation cannot be applied universally.* (p. 39).

Tübingen, 16, May, 1900.

CONCERNING ARTIFICIAL CROSSING IN PISUM SATIVUM

(UEBER KÜNSTLICHE KREUZUNG BEI PISUM SATIVUM)*[1]

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STIMULATED by the experiments of DARWIN on the effects of cross- and self-fertilization in the plant kingdom, I began, in the year 1898 to make hybridization experiments with *Pisum sativum*. The group to which *Pisum sativum* belongs was especially interesting to me because in it are found exceptional results from the generally accepted principle of the advantageous effect of crossing different individuals and different varieties in contrast to self-fertilization. In most of the species with which DARWIN worked (57 against 26 respectively 12), the seedlings from a cross between individuals of the same species almost always exceeded the competing individuals produced by self-fertilization in height, weight, vigor and frequently also in fertility, while in the case of the pea the amount of difference in height of plant produced by hybridization to those which were products of self-fertilization was as 100:115. DARWIN believed that the reason for this behavior in peas was the result of many generations of repeated self-fertilization in the northern lands. Considering the limited material which DARWIN observed (only four pea plant pairs were measured and observed) it appears to me, especially, since DARWIN never emasculated the flowers, that these experiments should be repeated on a larger scale and with greater accuracy.

I also made artificial crosses between different varieties of *Pisum sativum*. The purpose was to study the immediate influence of the foreign pollen upon the constitution (form and color) of the seeds thus produced, and also to follow, in the next generation of hybrids, the inheritance of the constant, differentiating characters of the parental types used in the hybridization. In the second year of experiment, the behavior of the hybrids in respect to growth (especially height), seed production, and change in color and form of seeds and pods was compared with the corresponding characters of the descendents obtained from self-fertilization of the parents. Pollinations with two different pollen types (so called double pollinations) were performed on several flowers to determine whether there occurs a simultaneous action of both or whether there is predominance of one of them. Crossing the hybrids with their parental varieties—or pure varieties with hybrids—gave regular results. Finally, by making the necessary numerous weight determinations of individual peas, it was possible for me to draw conclusions regarding the position of the heaviest kernel in the pod.

* Berichte der Deutsche Botanischen Gesellschaft **18**: 232–239, 1900.

[1] The detailed paper will be published in: Zeitschrift für das landwirthschaftliche Versuchswesen in Oesterreich, **3** (5), 1900.

METHODS

When the flowers were in the early bud stage, they were opened with a slender lancette, and the anthers were extracted by means of a hooked forceps. For pollination I employed ordinary writing pen-points. The advantage over the camel's hair brush usually employed is that the mass of pollen accumulated at the tip of the pen-point can be distributed over the stigma with much greater certainty. This has been proven to be true especially in my double fertilization experiments. In addition it is possible, after every pollination to cleanse the pen-point rapidly and completely with a rag. Covering the flowers to protect them against unwanted foreign pollination is, as the results of my experiments have shown, not at all necessary, since the blade vane and keel, even after emasculation has taken place, still fit together so closely that they form a natural protective covering against the entrance of large insects. Nevertheless, I have, as a precaution, protected many flowers, especially those which served for double fertilization experiments, by a small, close meshed bag of gauze whose edges were turned under and sewn together and whose opening could be drawn shut or opened again by means of a drawstring. In the year 1898, the experiments had primarily the aim to produce material by self-fertilization as well as by crossing in order to repeat, next year, the competition experiments discussed by DARWIN.

The plants grew in pots in a closed room under the most uniform conditions possible. In the year 1899, competing plants from seeds of equal weight were also grown in pots in a covered place. Concurrently, parallel experiments were also made by growing plants in the open. Crosses of nine different pea varieties were carried out between flowers of the same plant (geitonogamy), between flowers of the same variety but from different individuals (isomorphic xenogamy) and between flowers of different varieties. The seeds of the latter were distinct from one another either in regard to their form or by color or both characters (heteromorphic xenogamy).

RESULTS

The several pollination types generally produced no decisive difference in relation to the absolute number of the mature seeds, or in relation to the proportion of the mature seeds of the number of the potentially seed setting ovules. Neither could a definitive influence of hybridization as compared to self-fertilization, with respect to the weight of the peas, be detected. The proportional heights in the case of the descendents from self-fertilization and from geitonogamy was on the average 94:100, in the case of the competing ones from self-fertilization and from isomorphic xenogamy 95:100.

This result thus agrees with the former experiments of DARWIN. In the competition experiments between descendents from self-fertilization and those from heteromorphic xenogamy (hybrids), only certain hybrid forms showed increased growth over the self-fertilized plants. Other combinations, however, lacked such an "advantage" as a result of crossing against self-fertilization. The relative strength of the hybrid as compared to the self-fertilized maternal variety, for example, a hybrid from a cross of a relatively short

variety with a relatively tall one, should usually be interpreted simply as an inheritance from the father rather than an "advantage" resulting from the cross, as such, in comparison to the self-fertilization. An interpretation in the later sense is justifiable only in such cases in which a hybrid exceeds, in height, the descendents of self-fertilization not only of the maternal variety but also of the paternal variety. The taller type always has the greater influence, regardless of whether it characterized the maternal or paternal variety. The descendants of a relatively short type after pollination with the pollen of a relatively tall one, appear relatively greatly increased in height, as ANDREW KNIGHT has already observed; in the reverse case the hybrids are only slightly dwarfed, if at all.

A direct influence of the foreign pollen on the seeds could be determined in certain cases of artificial crossing of different varieties of peas. Certain specific combinations yielded this effect with regularity. The characters which were taken into consideration to recognize such an influence, related to the form of the seeds and the color of the storage tissue. The peas of the varieties used were either round and smooth or only slightly wrinkled, or they were more or less cubical (*Pisum quadratum*) and at the same time deeply wrinkled. The color of the storage tissue was either many shades of yellow or green.[2] My experiments showed the fact that the above mentioned differences of the same entity, i.e., the characteristic "trait" of the individual varieties were found not to be equivalent in regard to their inheritance. Quite regularly one of the characters (in question) from either the paternal or the maternal plant (the dominating character according to MENDEL) is developed exclusively while the recessive character of the other parental plant is not developed. The latter one, nevertheless, will reappear at least in part in the seeds of the hybrid plant. In agreement with MENDEL'S data[3] the round smooth form shows dominance over the cubical deeply wrinkled one, and the yellow color of the storage tissue over the green color. This is equally true whether the seed or pollen (of the parental plants) carried the character (in agreement with MENDEL). The appearance of the dominating or the recessive character is not an all or none phenomenon. In individual cases I was sometimes able to establish, with certainty, a simultaneous appearance of both, i.e. transition stages. The principle, established by the investigator above, of the regular non-equivalence of characters in inheritance, is confirmed by my experiments on *Pisum sativum*. Likewise the observations of KÖRNICKE, CORRENS and DE VRIES on *Zea Mays* as well as those made by DE VRIES in his species crosses[4] completely corroborate it. It proves to be of the highest significance for the study of inheritance in general. A possible modification of the seed coat in the direction of the pollen plant as a result of crossing needs to be interpreted in a very different way from that in the storage tissue, respectively the endosperm. The seed coat is a purely maternal product, but the endosperm (according to

[2] "Die Farbe des Speichergewebes war entweder gelb oder grün in mannigfachen Nuancen." [Original German text.]

[3] G. MENDEL in Verhandl. des naturf. Ver. Brünn, Vol. **4**: 1, 1865. [Publ. 1866. Tr.]

[4] Vol. **18** (3), 1900 this publication.

the investigations of NAWASCHIN and GUIGNARD) a derivitative of the embryo sac, which was fertilized by the (heteromorphic) pollen, in other words a product of the fusion of the second pollen tube nucleus with the so called embryo sac nucleus or the endosperm double nucleus. The storage tissue consists, on the other hand, apparently of products of the ovule. While in both of the latter cases we are dealing with hybrid- or crossing-effect, in the first case, a change in a product or part of the maternal organism would be involved in consequence of an action of the hybrid egg, i.e., we would have here an indirect effect of the heteromorphic pollen. Only in this way would possible effects on the seed coat as well as effects on the pod and the mother organism at large be at all understandable on the basis of contemporary knowledge. I denote such cases as "xeniodochien." The hypothesis of direct action on the somatic cells of the mother plant by the pollen cells without the intermediary of the hybrid egg cell (or respectively an embryo sac) appears not to be tenable (the hybrid egg cell, could die very early).[5] On the other hand the possibility of a direct effect by the pollen cells on the somatic cells, especially of the stigma, in the sense of a release of further development of the ovary in the typical direction may well be possible.

In certain cases of form- (and also in part color-) differences in the parental varieties where there was an indication of intermediacy in the hybrids, each of the parental varieties showed relatively more influence on the character (especially the form) of the hybridization-products when it furnished the ovule than when it furnished the pollen.

In the seeds obtained by self-fertilization of the first generation hybrids, the characters yellow and smooth appeared to have a higher value or hereditary potency than the characters green and wrinkled exactly as in the cross pollinated seeds of the mother plant. However, while in the artificial production of products of heteromorphic xenogamy, the first named characters are almost without exception dominant, and the latter "recessives" appear in pure form or as admixtures only in a very few cases, in the seeds of the first hybrid generation, the former characters are expressed in pure form in a majority of cases only, and the recessive character appears in pure form in a minority. In the first case an almost absolute dominance exists, in the second a mere prepotency (in a fixed proportion). Combinations of both character groups are also here rare, but perhaps less rare than in the former case. The ratio of seeds carrying the dominant, prevailing character to those carrying the recessive is about 3:1. A comparison of the progeny obtained from reciprocal crosses of different varieties showed, in agreement with the results analogous to those reported above for the products of reciprocal pollination, that in certain experimental cases the egg cell appears to be a more effective transmitter of the dominating color character than the pollen cell. Further experiments, however, are required to make a definite statement. The combination of two dominant or recessive characters in one parental type results in the seed production of the hybrid having a behavior similar to that of the respective isolated characters.

[5] Contrary to DARWIN, "The Variations of Animals and Plants under Domestication," Vol. 1, Chap. 11.

An alteration in the potency as, for instance, an increase in the dominance thus is not produced.

Interesting results which are of unexceptional regularity were obtained by pollination of emasculated hybrids with parental pollen. Pollination of the hybrid by the parental type with the dominating character, regardless of whether it is the paternal or maternal variety, produces exclusively seeds with the dominating character. When fertilized by the parental type with the recessive character, the number of bearers of the recessive character are increased over that of self-fertilization of the hybrid. The influence of the character "yellow" in the seeds in the hybrid was in this case reduced by 57 per cent, while that of the character "green" was reduced by 43.5 percent.

In addition flowers of the pure varieties were pollinated with hybrid pollen. If the former had a recessive seed character, a mixture of seed types always appeared, however if they had the so-called dominant seed character then pollination with hybrid pollen did not change the typical uniform seed type showing the dominant character. Thus the reproduction products of the hybrid pollen with pure varieties bearing the recessive character are just as polymorphic as those of the pollen of pure recessively marked parental types with a hybrid. This is not surprising since we are simply dealing with products of recriprocal crosses.

In order to determine the effect of double-pollination with its own pollen as well as with that of another variety upon the seeds themselves, it was necessary to select as the seed plant a variety with a so called recessive character and to take the pollen, for the heteromorphic xenogamy, from a variety with the dominant character. Several pods with different colored seeds, yellow and green, were gathered, as well as those with all seeds exhibiting either the recessive or dominant character. The seeds with the recessive character must, with great probability, be due to self-fertilization. Those with the dominant character must with certainty, be due to cross-fertilization. Possible exceptions within the first group, in which in spite of cross-fertilization by a variety with a dominant character the recessive character of the seed plant still manifests itself, could of course be recognized in plants which had been grown from those seeds and been left to self-fertilization. A modification of growth in comparison to the mother form (in case of divergent types of growth of the father) as well as the occurrence of differently colored or shaped seeds, especially in one and the same pod, would in such cases disclose the hybrid character and the origin of the seeds from self-fertilization would be excluded. On the contrary if the product obtained resulted from self-fertilization, then naturally, the adult plants grown from these seeds would precisely copy the mother variety in the type of growth and in the type of seeds produced by self-pollination. In the case of all seeds exhibiting the recessive characters, it is therefore highly probably that only self-fertilization operated. In the case of differences (dominant and recessive characters) of seeds in the same pod—a case which occurred extremely rarely in heteromorphic xenogamy of emasculated flowers—a partial effectiveness of the foreign pollen is certain, and that of [additional] self-fertilization is very likely. In any case my experiments, in

agreement with the results of FRITZ MÜLLER[6] on *Ruellia silvicola* and *formosa*, makes it impossible to support the statement made by DARWIN[7] and later by SACHS[8]—which has been pronounced generally and has been adopted in many text books—that, upon simultaneous application of two different kinds of pollen on the same stigma, only one of them will effect fertilization. At least for pollination between varieties of one species this statement is not valid.

Likewise in double fertilization of the hybrids with their own pollen, or with pollen of the same kind, and with pollen from one of the parental varieties both can act; by no means is one kind of pollen excluded by the other in the fertilization or prevails over it regularly. The same is true for double fertilization of a parental kind with its own and with hybrid pollen.

An orderly relationship between the absolute weight of the specific pea and their arrangement in the pod has been denied by some observers.[9] Both authors gave no consideration to the aborted seed anlage, and this accounts probably for their results of an "irregular change in position of the heaviest seed." Numerous weighings made by me gave the result that in incompletely filled pods the heaviest seed lies on the average approximately in the center. If, in my tables, one adds the number of funiculi and divides the result by the sum of the respective number (counted as funiculi) of the heaviest kernels, one finds that the proportional number is 1.7 (159:94) not 2 which would be the midpoint of funiculi number. As, with complete wholly intact pods, this calculation results in the same proportional number, I believe that the conclusion is justified that the position of the heaviest kernel is not essentially dependent upon the number and arrangement of the fully formed or aborted seed, but rather is determined, primarily, already before further development of the anlagen, and lies generally somewhat above the middle of the sequence.

POSTSCRIPT

CORRENS[10] has just published experiments which also deal with artificial hybridization of different varieties of *Pisum sativum* and observations of the hybrids left to self-fertilization through several generations. They confirm, just as my own, MENDEL'S teachings. The simultaneous "discovery" of MENDEL by CORRENS, DE VRIES[11] and myself appears to me especially gratifying. Even in the second year of experimentation, I too still believed that I had found something new.

[6] Abhandlungen des naturf. Ver zu Bremen, Vol. **12**, page 379.

[7] The Effects of Cross and Self Fertilization in the Vegetable Kingdom: "It is a much more remarkable fact that pollen from another individual of the same variety surpasses the pollen of the same plant."

[8] Pflanzenphysiologie, 1882, page 957.

[9] FRUWIRTH, Über den Sitz des schwersten Kornes in den Fruchtständen bei Getreide und in den Früchten der Hülsenfrüchte, in WOLLNY'S Forschungen, Vol. **15**: 49, and FELDMANN, Beiträge zur Kenntniss der Individualität des Saatkornes. 1897.

[10] G. MENDEL'S Regel über das Verhalten der Nachkommenschaft der Rassenbastarde. Ber. der Deutschen Bot. Gesellsch., **18** (4): 158–168, 1900.

[11] Das Spaltungsgesetz der Bastarde. Ber. der Deutschen Bot. Gesellsch. **18** (3): 83, 1900.

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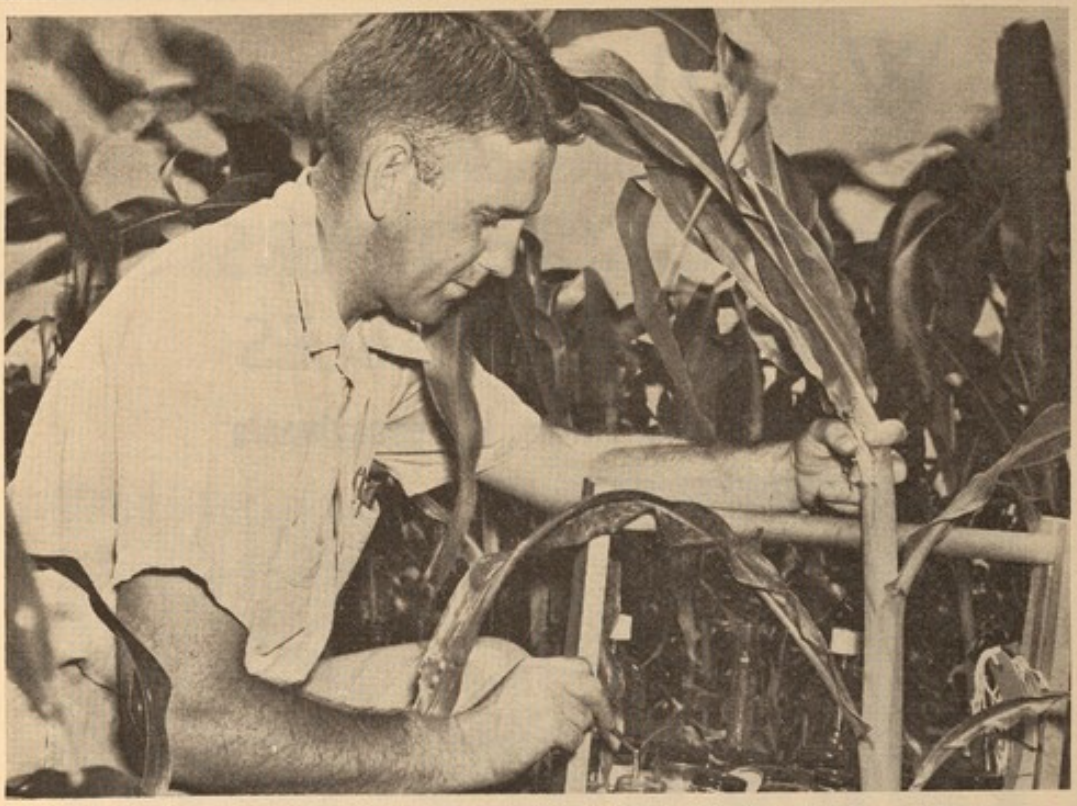

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