FURTHER DATA ON THE SELF- AND CROSS-INCOMPATIBILITY OF VERBASCUM PHOENICEUM

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A research into the genotypical nature of self- and cross-incompatibility of *Verbascum phoeniceum* was begun in 1913 and had led to some preliminary conclusions which I published in 1917. This species is a very favourable one for the study of incompatibility; flowers are formed in abundance; the period of flowering is a rather long one; the capsules contain a great many seeds; castration and handling the pollen is very easy; the plant is a perennial, it can be propagated vegetatively and can reach an age of more than fifteen years, so that a comparison of results in succeeding years and in doubtful cases repetition of the same cross on a larger scale is very well possible.

Pseudofertility, i.e. end-season-self-compatibility, as observed by EAST in *Nicotiana*, does not occur in *Verbascum*; only very young buds, immediately after the opening of the flower, can be self-pollenized with any sort of success; so that if one takes care not to use flowers, which are younger than one day, every possibility of selffertilization is excluded.

In my earlier paper (1917), some statements were derived from the behaviour of an F_1-generation, consisting of 46 plants which was the offspring of one pair of self-incompatible parents; they may be summarized as follows:

Crosses between different plants give in most cases a positive result; a number of plants, however, showed to be cross-incompatible.

Reciprocal crosses generally give the same result, but in a rather great number of cases differences between the crosses may be observed, the one pollination being successful, the reciprocal one however unsuccessful.

The constitution of the F_1-generation is very complicated; a classification into groups of individuals, the behaviour of which was identical, could not be made. No two individuals were found, which gave the same results in their crosses with the other plants of this F_1-generation.

Among the F_1-plants there seemed to be some individuals (numbers 1 and 22), which when used as male parents, gave positive pollinations only in exceptional cases, while as female parents these plants were compatible to their sibs in a great number of successful pollinations. Inversely, other plants (numbers 19 and 29) used as males were more compatible to the remaining F_1-individuals, while a great many times they failed to fruit as female parents.

These conclusions were rather controversial to those of other writers; the regularities observed by CORRENS a.o. could not be corroborated. The simple mendelian interpretation which he gave, consequently did not appear to be the right one. My own data, however, were rather incomplete, as they were derived from the F_1-generation only. Both in CORRENS's studies and in my experiments there were moreover a number of doubtful cases; the same pollination of four flowers for instance, gave now two positive and then again two negative results so that a decision as to their real character was very difficult. A further study of the question was therefore desirable.

A very great difficulty, met with in the F_1 was the practical impossibility to make all combinations between the 46 individuals on a satisfactory number of flowers. From these 46 plants therefore twenty were selected, and with these twenty plants all the possible crosses and selfings were made on four flowers. When the results of these 4 pollinations were the same, they allowed of a decision as to the character of these pollinations; when however one or two pollinations turned out to differ from the others, the pollination was repeated, in some cases even on as many as ten flowers, The character of practically all combinations could so be determined; in the later generations, however, some crosses remained doubtful even when the number of pollinations was increased to 10, these were then described as „slight success". The perennial nature of the plants was a very favourable circumstance in such cases; every combination that could not be made in the first year, or gave a doubtful result, could be repeated in later years.

Since my first publication, the work has been extended until the seventh generation, each of which consisted of twenty plants; the F_1 was grown in 1915 and the next generations in the following years: F_2 1916; F_3 1917; F_4 1918; F_5 1919; F_6 1920 and F_7 1921. Until 1924 crosses between these individuals were made; for the sake of other researches the experiments have now been discarded. I therefore wish to publish here the data in full; the conclusions, drawn from these results will be added very summarily, as I shall discuss the main points in connection with the results of other workers in another paper (1926*a*).

The complete results of the F_1-generation (Table I) seemed to corroborate my previous conclusions; the numbers 1 and 22 indeed gave more positive results when used as females than they produced as male parents; the numbers 19 and 29 behaved themselves inversely (cf. Table XI). From these the plants 1 and 19 were selected as parents for one F_2-generation (Table II); here again the same irregularity was observed; no two plants turned out to be identical, while some of them (11 and 17) seemed to possess a stronger „male", others a more distinct „female" (14 and 18) character. Another F_2-generation (Table III), also consisting of 20 plants, was obtained by crossing 19 with 22; the results were again the same. On the whole a mass of complicated irregularities; one plant (number 8) gave more positive results when used as a female parent, another (number 11) was more productive as a male parent.

One F_3-family was obtained by crossing these extreme individuals, and as is shown in Table IV here again the same state of things was found; a lack of any regularity stood in the way of the interpretation of the phenomena along mendelian lines. In this F_3-family, however, such characteristic extreme forms, as found in the first two generations, were absent; the most distinct „female" plant was number 19, which used as a female, gave 13 positive results of the twenty possible ones, as a „male" parent 8 successful combinations.

As the selection of extreme „male" and „female" individuals from the former generations seemed to give a most complicated offspring, the method of selecting parents for F_4-generations was now changed; two F_4-generations were grown from the numbers 5 and 13 from the F_3-generation in both reciprocal ways. Regarding the „male" or „female" character, both these F_3-plants seemed to be indifferent: number 5 had given, as a male, 12, as a female 11 successful combinations out of the twenty possible ones; number 13 produced as a male 10, as a female 12 positive results. The constitution of these F_4-families can be seen from Tables V and VI. In the first F_4-generation, family 1918. 3 21, there appeared 2 groups of identical individuals; one consisting of 3 individuals (numbers 3, 13 and 18), the other of two plants (numbers 5 and 6). The identity of these individuals appeared not only in their crosses with the other plants of the same family, but also in backcrosses with both parents. Regarding their behaviour towards the individuals of both these groups, the remaining 15 plants could be grouped again in two classes, but in intercrosses these plants showed again the same irregularities, as observed in the previous generations.

In the second F_4-generation, family 1918. 322 again two groups of identical individuals were observed, each consisting of two plants. The remaining 16 plants when crossed with individuals of these two groups, gave all the same results, but in intercrosses again a mass of confused data were found.

As it seemed probable, that the constitution of the individuals, which belonged to the separate groups, would be a simpler one than that of the irregular plants, I selected two parents from these groups (family 1918. 321, numbers 3 and 5) for breeding a fifth generation, grown as family 1919. 44 (Table VI). A clearer insight in their behaviour was thus obtained: among the twenty plants of this F_5-generation three distinct groups, each of 3 individuals, could be found, while the remaining eleven plants again produced rather irregular results. The crosses between plants of these three groups were, however, especially important, as they brought to light, that the difference in reciprocal crosses is not an individual phenomenon, but a character of whole groups. All the plants of group 5 etc. used as males in pollinating those of group 8 etc. gave positive results, while all the reciprocal crosses turned out to be negative.

As parents for breeding the F_6-generations, one plant from each of these three groups was selected: two F_6-generations were grown, one from plant 9 as a female and number 5 as a male, and one from 9 as a seedparent with 10 as a pollenparent.

Both these F_6-families, 1920. 547 and 549, turned out to consist of four sharply distinguishable groups, each containing only self-incompatible and intra-incompatible individuals, while the intercrosses between plants belonging to different groups behaved differently. These different results can be seen from tables VIII and IX: in family 547 there were two cases out of 6, of differences between reciprocal group-crossings, and two cases also of differences between the eight possible reciprocal backcrosses of these groups with the F_5-parents. In family 549 this difference was more prominent still; out of six reciprocal combinations between these groups, five gave different results; out of the eight backcrosses with the F_5-parents, four of them behaved inversely in the reciprocal crosses. Almost all the crosses gave doubtless results, so that the division into groups in these F_6-generations was a very clear one. There remained, however, a few cases of slight success, while one cross (family 549:6 female×4 male) produced ten unsuccessful pollinations, while a positive result should have been expected.

A seventh generation was grown to get still more certainty on this point; as F_6-parents the numbers 8 and 3 of family 549 were chosen, and this F_7-generation was grown as family 1921. 129. The case was so much the more interesting, as the reciprocal crosses between these F_6-parents were different; 8 male × 3 female gave no successful pollinations, while the seed used was obtained from the reciprocal cross 3 male × 8 female.

The composition of this F_7-generation (Table X) was somewhat different from that of the family 549, from which the parents were selected; two backcrosses with the parents showed reciprocal differences while the other six behaved identically in both directions; two intercrosses between the four groups were reciprocally inverse, while the other four produced the same reciprocal results.

The continuation of the experiments has thus produced the important result, that the irregularities observed in the first three generations have been removed by the selection of favorable plants, while from the F_4-generation on, a distinct classification dawned. In the sixth generation all the individuals could be grouped into four classes of intra-incompatible nature, while the intercrosses between plants belonging to different classes could produce positive as well as negative effects. The differences between reciprocal crosses were established to be a character of groups, not of individuals.

On the whole, the data obtained in the sixth and seventh generations, are wholly in accord with the hypothesis of oppositional factors, as supposed first by PRELL (1921) and since adopted by EAST and MANGELSDORF (1925). This hypothesis has the following leading thought: In every diploid organism, which is self-incompatible, there are two oppositional factors, let us say s_1 and s_2, which in the style inhibit the growh of pollen-tubes possessing one of these factors. Consequently flowers from a plant with the formula s_1s_2 can only be fertilized by pollengrains, which either do not possess any s-factors at all, or if they do so, others than s_1 or s_2, so for instance s_3 or s_4. Self-fertilization is thus out of the question, and cross-fertilization only possible with organisms, which are not also s_1 s_2.

A slight extension however of this hypothesis is necessary; the supposition is not sufficient for an explanation of the differences between the reciprocal crosses, and these differences may now be considered to exist really. EAST thinks, that he may assume for instance in an s_1s_2-plant the growth of s_1-pollen by way of exception, from which homozygous s_1s_1-plants are produced. Such s_1s_1-plants crossed with s_1s_2-individuals show a difference in reciprocity; s_1s_1 as a male with s_1s_2 as a female is incompatible, inversely the cross is compatible.

In my opinion however another solution is more probable; namely the supposition, that for instance s_1-pollen is incompatible not only in an s_1-style, but also in an s_2-style, while inversely s_2-pollen can function in an s_1-style.

The schemes, added to the tables VIII-X, show that this theoretical explanation is wholly in accord with the experimental data obtained in the sixth and seventh generations, so that in principle the hypothesis of PRELL-EAST and MANGELSDORF can be accepted as the right one.

There remains however another problem, not yet solved sufficiently. The regularities, as explained by the hypothesis of oppositional factors, did not appear before the F_4-generation, and even the explanation of the data, found in this generation and those of the F_5 cannot be given along the lines indicated. In the earlier generations there must be a series of other oppositional factors, which are combined in pairs in every diploid organism, but the probability must be accepted, that each diploid organism in these generations had formed a number of genotypically different gametes, each possessing another oppositional factor, or combination of factors.

So we may suppose:

1. that these factors were present in the individuals of the earlier

generations as a series of multiple factors and that by means of loss-mutations the continuous sib-mating has expelled most of them, while one pair of such factors only is left, or

2. that the original parents of the earlier generations possessed one pair only, and that this pair of factors has produced after segregation a series of multiple allelomorphs, differing quantitatively, while by the selection of favourable individuals, only plants possessing a pair of very little differing factors were used to breed the sixth and seventh generations.

In my opinion this last suggestion has more probability than the first one. A further discussion of this antithesis of multiple allelomorphs versus multiple factors will be given in an other paper (1926*b*).

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TABLE I.

VERBASCUM PHOENICEUM

F_1-generation. Family 1914. 1022.
+ successful pollinations.
— unsuccessful pollinations.
s slight success.

Ma

Females	A	B	1	2	4	5	6	8	11	12	15	19	22	24	28	29	33	34	38	40	41	42
A	—	+	—	+	—	+	—	+	+	+	+	+	—	+	—	+	+	—	—	+	+	+
B	+	—	—	—	+	+	—	+	+	+	—	+	—	—	+	+	+	+	—	+	+	+
1	+	+	—	+	+	+	+	+	—	+	+	+	—	+	+	+	—	+	+	+	+	+
2	+	—	—	—	+	+	—	+	—	+	+	+	—	+	+	+	+	—	—	+	—	—
4	+	+	—	+	—	—	—	+	+	+	+	+	—	+	+	+	—	+	+	—	+	—
5	+	—	+	—	+	—	—	+	—	—	+	+	—	—	—	—	—	+	+	+	+	+
6	—	+	—	+	—	+	—	—	—	+	+	+	—	+	+	+	+	+	—	+	—	+
8	—	—	—	+	—	—	+	—	—	+	—	+	—	+	+	—	—	+	+	—	—	+
11	—	+	—	+	—	—	+	—	—	+	—	+	—	+	—	+	+	+	+	—	+	—
12	+	+	+	+	—	+	+	—	+	—	+	+	+	—	+	+	—	+	+	—	+	+
15	+	+	—	—	+	—	+	—	+	+	—	—	—	+	+	+	—	—	+	—	+	—
19	—	—	—	—	—	—	—	—	+	—	—	—	+	—	+	+	—	—	—	+	—	—
22	+	+	+	+	+	+	+	+	+	+	+	+	—	+	+	—	+	—	+	+	+	+
24	+	+	—	+	+	+	—	—	+	+	+	+	—	—	—	+	+	+	—	—	—	+
28	+	—	—	—	+	+	+	—	+	—	—	+	—	+	—	+	+	—	+	+	+	+
29	—	—	—	—	+	—	—	—	—	—	—	—	—	—	+	—	—	—	—	—	—	—
33	—	+	—	+	—	+	+	—	—	—	—	+	—	—	—	+	—	+	+	+	+	+
34	+	—	—	+	+	—	—	+	+	—	+	+	+	+	—	+	+	—	—	+	—	+
38	—	—	+	+	+	+	+	—	—	+	+	+	—	+	—	+	+	+	—	—	+	+
40	+	+	—	—	+	+	+	—	+	—	—	—	—	+	+	—	+	+	+	—	+	+
41	+	+	—	+	—	—	—	+	—	—	+	+	—	+	+	+	+	+	+	+	—	+
42	+	+	—	+	+	+	+	—	+	+	+	—	—	+	+	—	+	+	+	+	+	—
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1913. 90. 1 × 90. 4.

les.

3	7	9	10	13	14	16	17	18	20	21	23	25	26	27	30	31	32	35	36	37	39	43	44	45	46	
+	−	−	−	+	+		+	−		+		+	−		+	−	−	+		+		+	−	+	+	A
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												−										−				43
				−							+						+		−				−			44
						−		+																−		45
																		+							−	46

TABLE II.

VERBASCUM PHOENICEUM. 1914. 1022. 1 × 1022. 19.

F_2-generation. Family 1916. 31.
+ successful pollinations.
— unsuccessful pollinations.
s slight success.

		Males																					
		1022		31..........																			
		1	19	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Females	1022. 1	—	+	+	—	+	+	+	+	+	—	+	+	+	+	+	—	+	+	—	—	+	+
	19	—	—	—	—	+	+	+	—	—	—	—	+	+	+	—	—	—	+	—	—	+	+
	31. 1	+	—	—	+	+	+	—	+	+	+	+	+	+	+	+	+	—	+	+	+	—	+
	2	—	+	+	—	+	+	+	+	+	+	+	—	+	+	+	—	+	+	+	—	+	+
	3	+	+	+	+	—	+	+	—	+	+	+	+	—	+	+	—	+	+	—	+	+	+
	4	—	+	+	+	—	—	+	+	+	—	+	+	—	+	+	—	+	+	+	—	+	+
	5	—	+	+	—	+	+	—	+	+	+	—	+	+	—	+	—	+	+	+	—	+	—
	6	—	+	+	—	+	—	+	—	+	+	+	—	+	+	—	—	+	+	+	—	+	+
	7	+	—	+	+	+	+	+	+	—	+	+	+	+	—	+	—	+	+	+	—	+	+
	8	—	+	—	+	+	+	—	+	+	—	—	+	+	+	+	+	+	—	+	+	+	—
	9	+	+	+	+	—	+	+	+	—	+	—	—	—	+	+	—	+	+	—	+	—	+
	10	—	+	+	—	—	+	+	+	+	+	—	—	+	+	+	—	+	—	+	+	—	+
	11	—	—	—	—	—	—	—	+	+	—	+	+	—	—	—	—	—	—	—	—	+	—
	12	+	+	+	+	+	+	—	+	+	—	+	+	—	—	+	+	+	+	+	—	+	+
	13	—	+	+	+	—	+	+	—	+	—	+	+	+	+	—	—	+	+	+	+	—	+
	14	+	—	+	+	—	+	—	+	+	—	+	+	—	+	+	—	—	+	+	—	+	+
	15	—	+	+	—	+	+	—	+	+	—	+	+	+	+	+	—	—	+	+	—	+	+
	16	+	+	+	+	—	+	+	+	+	+	—	+	+	+	+	—	+	—	+	+	—	+
	17	—	—	+	—	—	—	—	—	—	+	—	—	—	—	+	—	+	—	—	+	—	—
	18	+	—	—	+	+	+	—	+	+	+	+	+	+	+	—	+	+	+	—	—	+	+
	19	—	+	+	+	+	+	+	—	+	+	—	+	+	—	+	+	+	—	+	+	—	—
	20	—	+	+	+	—	+	+	+	—	+	+	+	+	+	—	+	+	—	+	—	+	—

TABLE III.

VERBASCUM PHOENICEUM. 1022. 19 × 1022. 22.

F_2-generation. Family 1916. 32.
+ successful pollinations.
— unsuccessful pollinations.
s slight success.

Males

	1022 19	1022 22	32. 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1022. 19	—	+	+	—	+	+	+	+	—	+	+	+	—	+	+	+	+	—	+	+	+	+
	+	—	+	+	+	+	+	+	+	+	+	+	—	+	+	+	+	+	+	—	+	—
Females 32. 1	+	—	—	+	+	+	—	+	+	+	+	+	—	—	+	+	+	—	+	+	—	+
2	+	—	+	—	—	+	+	+	+	+	—	+	—	+	+	+	+	+	—	+	+	+
3	+	—	+	+	—	+	+	+	+	+	+	—	+	+	+	+	—	+	+	+	—	+
4	—	—	+	+	+	—	+	+	+	+	+	+	—	+	+	—	+	+	+	+	—	+
5	+	—	—	+	+	+	—	+	—	+	+	+	—	+	+	+	+	+	—	+	+	+
6	—	+	+	+	+	+	+	—	+	+	—	+	+	+	+	+	+	+	—	+	—	—
7	+	—	+	+	+	+	+	—	—	+	+	+	—	+	+	—	+	+	+	—	+	+
8	+	—	—	—	+	—	—	—	—	—	+	—	—	—	—	—	—	—	—	+	+	—
9	+	—	+	+	+	+	+	+	+	+	—	+	—	+	+	+	+	—	—	+	+	—
10	+	+	+	—	+	+	+	—	—	+	+	—	—	+	+	+	—	+	+	—	+	+
11	+	+	+	+	+	+	+	+	—	+	+	+	—	+	+	—	+	+	+	+	—	+
12	+	—	+	+	+	—	+	+	+	+	—	—	—	—	+	+	+	+	+	—	+	—
13	+	—	+	—	—	+	+	+	+	+	+	+	—	+	—	+	+	—	+	—	+	+
14	—	—	—	+	—	+	+	+	—	+	+	—	+	+	+	—	+	—	—	—	—	+
15	+	—	+	+	—	+	+	+	+	+	—	+	—	+	+	+	—	+	+	+	+	—
16	+	+	+	—	+	—	+	+	+	+	—	+	—	+	+	+	—	—	—	—	+	+
17	+	—	—	+	—	+	+	+	—	—	+	+	—	+	—	+	+	+	—	+	—	+
18	—	—	+	+	+	+	—	—	—	+	—	+	—	+	+	+	—	+	+	—	—	+
19	+	+	—	+	—	—	+	+	+	+	—	+	—	+	+	+	—	+	+	+	—	—
20	+	+	+	—	—	—	+	—	+	+	+	—	—	+	+	+	—	—	—	+	+	—

TABLE IV.

VERBASCUM PHOENICEUM. 1916. 32. 11 × 32.8.

F_3-generation Family 1917. 58.
+ successful pollinations.
— unsuccessful pollinations.
s slight success.

Males.

		32		58............																			
		11	8	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	32. 11	—	+	—	+	+	+	+	+	+	+	+	—	+	+	+	+	+	—	—	—	+	+
	8	—	—	—	—	—	—	—	—	—	+	+	—	—	—	—	+	—	+	+	—	—	—
	58. 1	—	+	—	+	+	—	+	+	+	+	—	+	+	—	+	+	+	—	—	—	—	+
	2	—	+	+	—	—	—	—	+	+	—	—	—	—	—	+	—	+	+	—	—	—	—
	3	+	+	—	+	—	+	+	—	+	+	+	+	+	—	—	+	+	+	+	+	—	+
	4	—	+	+	+	+	—	—	+	—	—	+	+	—	+	—	+	+	—	+	+	+	—
F	5	+	+	+	+	+	—	—	—	—	+	—	+	+	+	+	—	—	—	+	+	—	+
e	6	—	+	—	—	+	+	+	—	+	+	+	—	—	+	+	—	+	+	—	+	+	+
m	7	+	—	+	—	—	+	—	+	—	+	+	—	+	+	—	+	—	—	—	—	+	—
a	8	—	+	+	+	—	+	+	—	+	—	+	—	+	+	—	+	+	+	—	+	+	—
l	9	—	+	—	+	—	+	+	—	+	+	—	+	—	—	+	+	—	+	+	—	—	+
e	10	—	+	+	—	+	—	+	+	—	+	—	—	+	—	+	+	—	+	—	+	+	—
s	11	+	—	+	—	+	+	+	—	+	—	—	+	—	—	+	—	+	+	+	—	—	—
	12	—	+	+	—	—	—	—	+	+	—	—	—	+	—	—	+	—	—	—	—	—	+
	13	—	+	+	—	+	+	+	—	+	—	—	+	+	—	—	+	—	+	+	+	—	+
	14	+	—	—	+	+	—	—	—	+	+	+	—	+	—	+	—	+	—	—	+	+	—
	15	—	+	+	—	+	—	+	—	+	+	+	—	+	—	+	—	—	+	—	+	—	—
	16	—	+	—	+	+	—	+	—	+	+	—	+	—	—	+	—	+	—	+	—	+	—
	17	—	+	+	—	+	+	+	+	—	+	+	+	—	—	—	+	+	—	—	+	—	+
	18	—	—	+	—	—	—	—	+	+	+	—	+	+	—	—	+	+	—	+	—	+	—
	19	—	+	—	+	+	+	—	+	—	+	+	+	—	+	—	+	+	—	+	+	—	+
	20	+	+	+	—	+	+	+	—	—	+	—	+	—	+	—	+	+	—	+	+	—	—

TABLE V.

VERBASCUM PHOENICEUM. 1917. 58.5 × 58.13.

F_4-generation Family 1918. 321.
+ successful pollinations.
— unsuccessful pollinations.
s slight success.

		Males																					
		58		321																			
		5	13	1	2	7	8	9	12	14	15	16	17	20	4	10	11	19	3	13	18	5	6
	58. 5	—	+	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	+	+	+	+	+
	13	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	321. 1	—	+	—	+	+	—	+	—	—	+	—	+	+	+	+	—	—	+	+	+	—	—
	2	—	+	+	—	+	+	—	+	+	—	+	—	+	+	+	—	—	+	+	+	—	—
	7	—	+	—	—	—	+	+	—	+	—	—	+	—	+	+	—	+	+	+	+	—	—
	8	—	+	+	+	—	—	+	+	+	+	—	—	—	—	—	+	+	+	+	+	—	—
	9	—	+	—	—	+	+	—	—	+	—	+	—	+	+	—	—	—	+	+	+	—	—
	12	—	+	+	+	+	—	+	—	—	—	—	+	—	+	+	+	+	+	+	+	—	—
F	14	—	+	s	—	—	+	—	+	—	—	+	—	+	—	—	—	—	+	+	+	—	—
e	15	—	+	+	+	+	+	+	+	+	—	+	+	+	+	+	+	—	+	+	+	—	—
m	16	—	+	—	—	+	+	+	—	+	+	—	+	—	—	—	+	+	+	+	+	—	—
a	17	—	+	—	—	+	—	—	—	+	+	+	—	+	+	+	+	—	+	+	+	—	—
l	20	—	+	—	+	s	—	+	+	+	—	+	+	—	—	+	—	+	+	+	+	—	—
e	4	+	+	—	+	—	—	+	—	+	—	—	—	+	—	—	+	+	—	—	—	+	+
s	10	+	+	+	+	+	+	+	+	—	+	—	+	—	+	—	—	+	—	—	—	+	+
	11	+	+	—	—	+	—	—	+	+	+	—	+	+	—	+	—	—	—	—	—	+	+
	19	+	+	—	+	—	+	+	—	+	—	+	—	+	—	—	—	—	—	—	—	+	+
	3	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	+	+
	13	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	+	+
	18	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	+	+
	5	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—
	6	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—

TABLE VI.

VERBASCUM PHOENICEUM. 1917. 58. 13 × 58. 5.

F_4-generation. Family 1918. 322.
+ successful pollinations.
— unsuccessful pollinations.
s slight success.

Females	Males 58		322																			
	13	5	1	2	3	4	5	6	8	9	10	11	12	14	15	17	18	20	7	16	13	19
58. 13	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	+	+	+	+	—	—
5	+	—	+	—	+	+	+	+	—	+	+	—	+	+	+	—	+	+	+	+	+	+
322. 1	+	+	—	+	+	+	—	—	+	+	+	—	—	+	—	—	+	+	+	+	+	+
2	+	—	+	—	—	+	+	+	—	+	+	+	—	+	+	—	+	+	+	+	+	+
3	—	—	+	+	—	—	—	—	—	+	+	+	—	+	+	—	—	—	+	+	+	+
4	—	+	+	+	+	—	+	—	+	+	—	+	+	—	+	+	+	+	+	+	+	+
5	+	+	—	+	+	—	—	+	+	+	+	—	+	+	—	+	—	+	+	+	+	+
6	+	—	—	—	+	+	—	—	+	—	—	+	+	+	+	—	+	+	+	+	+	+
8	+	—	+	—	+	—	+	+	—	+	+	+	—	+	—	+	+	—	+	+	+	+
9	—	—	+	—	—	—	—	—	+	—	—	—	—	+	—	—	+	+	+	+	+	+
10	—	+	+	—	+	+	+	+	—	—	—	+	—	+	+	—	+	—	+	+	+	+
11	—	—	—	+	—	—	+	+	—	+	—	—	+	+	+	—	+	+	+	+	+	+
12	+	+	+	+	—	+	+	+	—	+	+	—	—	+	+	+	+	—	+	+	+	+
14	+	+	+	—	+	+	—	—	—	+	+	+	+	—	—	—	—	+	+	+	+	+
15	+	+	—	+	—	+	+	+	—	+	—	+	+	+	—	+	—	+	+	+	+	+
17	+	+	+	—	+	+	—	+	+	—	—	+	+	—	+	—	+	—	+	+	+	+
18	—	—	—	+	—	—	—	—	+	+	+	—	—	+	—	+	—	+	+	+	+	+
20	+	—	—	+	+	+	+	—	—	+	+	—	+	+	+	—	—	—	+	+	+	+
7	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	+	+
16	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	+	+
13	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—
19	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—

TABLE VII.

VERBASCUM PHOENICEUM. 1918. 321. 3 × 321. 5.

F_5-generation. Family 1919. 44.
+ successful pollinations.
— unsuccessful pollinations.
s slight success.

Females \ Males	321. 3	321. 5	44. 1	2	4	7	13	14	18	3	11	12	19	5	6	20	8	10	15	9	16	17
321. 3	—	+	+	+	+	+	+	+	+	—	—	—	—	—	—	—	+	+	+	+	+	+
5	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
44. 1	+	—	—	+	+	—	+	+	—	+	—	+	+	+	+	+	—	—	—	+	+	+
2	+	—	—	—	+	+	—	+	+	—	+	+	+	+	+	+	—	—	—	+	+	+
4	+	—	+	+	—	+	—	+	—	+	—	+	+	+	+	+	—	—	—	+	+	+
7	+	—	+	+	—	—	+	—	+	—	—	+	—	+	+	+	—	—	—	+	+	+
13	+	—	+	—	+	+	—	+	—	+	+	+	—	+	+	+	—	—	—	+	+	+
14	+	—	—	—	+	—	—	—	—	+	—	—	—	+	+	+	—	—	—	+	+	+
18	+	—	+	+	+	+	+	—	—	—	+	+	+	+	+	+	—	—	—	+	+	+
3	—	+	+	+	+	—	+	+	—	—	+	+	—	—	—	—	+	+	+	—	—	—
11	—	+	—	—	+	+	+	—	—	+	—	+	—	—	—	—	+	+	+	—	—	—
12	—	+	+	—	+	—	+	+	+	+	—	—	+	—	—	—	+	+	+	—	—	—
19	—	+	+	+	+	—	+	+	+	—	+	+	—	—	—	—	+	+	+	—	—	—
5	—	+	+	+	+	+	+	+	+	—	—	—	—	—	—	—	+	+	+	+	+	+
6	—	+	+	+	+	+	+	+	+	—	—	—	—	—	—	—	+	+	+	+	+	+
20	—	+	+	+	+	+	+	+	+	—	—	—	—	—	—	—	+	+	+	+	+	+
8	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	—	—	—
10	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	—	—	—
15	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	—	—	—
9	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	+	+	+	—	—	—
16	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	+	+	+	—	—	—
17	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	+	+	+	—	—	—

TABLE VIII.

VERBASCUM PHOENICEUM. 1919. 44.9 × 44.5.

F_6-generation. Family 1920. 547.
+ successful pollinations.
— unsuccessful pollinations.
s slight success.

	Males	44		547																			
Females		9	5	5	7	10	12	14	6	11	18	2	8	9	13	16	17	20	1	3	4	15	19
44.	9	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	5	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
547.	5	+	+	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	7	+	+	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	10	+	+	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	s	+	+	+	+
	12	+	+	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	s	+
	14	+	+	—	—	—	—	—	+	+	+	+	s	+	+	+	+	+	+	+	+	+	+
	6	+	+	+	+	+	+	+	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+
	11	+	+	+	+	+	s	+	—	—	—	+	+	+	+	s	+	+	+	+	+	+	+
	18	+	+	+	+	+	+	+	—	—	—	+	s	+	+	+	+	+	+	+	+	+	+
	2	—	+	—	—	—	—	—	+	+	+	—	—	—	—	—	—	—	+	+	+	+	+
	8	—	+	—	—	—	—	—	+	s	+	—	—	—	—	—	—	—	+	+	+	+	+
	9	—	+	—	—	—	—	s	+	+	+	—	—	—	—	—	—	—	+	+	+	+	+
	13	—	+	—	—	—	—	—	+	+	+	—	—	—	—	—	—	—	+	+	+	+	s
	16	—	+	—	—	—	—	—	+	+	+	—	—	—	—	—	—	—	+	+	+	+	+
	17	—	+	—	—	—	—	—	+	+	+	—	—	—	—	—	—	—	+	+	+	+	+
	20	—	+	—	—	—	—	—	s	+	+	—	—	—	—	—	—	—	+	+	+	+	+
	1	—	+	+	+	+	+	+	—	—	s	+	+	+	+	+	+	+	—	—	—	—	—
	3	—	+	+	+	+	+	+	—	—	—	+	+	+	+	+	+	+	—	—	—	—	—
	4	—	+	+	+	+	+	+	—	—	—	+	+	+	+	+	+	+	—	—	—	—	—
	15	—	+	+	+	+	+	+	—	—	—	+	+	+	+	+	+	+	—	—	—	—	—
	19	—	+	+	+	+	+	+	—	—	—	+	+	+	+	+	+	+	—	—	—	—	—

TABLE VIII (continued).

THEORETICAL EXPLANATION

F_5-parents 44.9 s_1s_2 and 44.5 s_5s_6
F_6-generation $s_1s_5 + s_1s_6 + s_2s_5 + s_2s_6$
s_1-pollen incompatible in s_1- and in s_2-styles

Males

		44.9 s_1s_2	44.5 s_5s_6	5 etc. s_1s_5	6 etc. s_1s_6	2 etc. s_2s_5	1 etc. s_2s_6
	44.9 s_1s_2	—	+	+	+	+	+
F	44.5 s_5s_6	+	—	+	+	+	+
e m	5 etc. s_1s_5	+	+	—	+	+	+
a l	6 etc. s_1s_6	+	+	+	—	+	+
e s	2 etc. s_2s_5	—	+	—	+	—	+
	1 etc. s_2s_6	—	+	+	—	+	—

TABLE IX.

VERBASCUM PHOENICEUM. 1919. 44. 9 × 44. 10.

F_6-generation. Family 1920. 549.
+ successful pollinations.
— unsuccessful pollinations.
s slight success.

	Males	44		549																		
		9	10	8	13	14	15	20	2	9	10	18	19	1	6	12	17	3	4	5	7	11	16
	44. 9	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	10	+	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	549. 8	+	+	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	13	+	+	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	14	+	+	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	15	+	+	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	20	+	+	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	s	+	+	+
	2	×	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+
F	9	+	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+
e	10	+	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+
m	18	+	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+
a	19	+	—	—	s	—	—	—	—	—	—	—	—	+	s	+	+	+	+	+	+	+	+
l	1	—	+	—	—	—	—	—	+	+	+	+	+	—	—	—	—	+	+	+	+	+	+
e	6	—	+	—	—	—	—	—	+	+	+	+	+	—	—	—	—	+	—	+	+	+	+
s	12	—	+	—	—	—	—	—	+	+	+	+	+	—	—	s	—	+	+	+	+	+	+
	17	—	+	—	—	—	—	—	+	+	+	+	+	—	—	—	—	+	+	+	+	+	+
	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	s	—	—	—
	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	s	—	—	—	—	—	—	—
	11	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE IX (continued).

THEORETICAL EXPLANATION

F_5-parents 44.9 s_1s_2 and 44.10 s_3s_4
F_6-generation $s_1s_3 + s_1s_4 + s_2s_3 + s_2s_4$
s_1-pollen incompatible in s_1- and in s_2-styles
s_3-pollen incompatible in s_3- and in s_4-styles.

Males

		44.9 s_1s_2	44.10 s_3s_4	8 etc. s_1s_3	2 etc. s_1s_4	1 etc. s_2s_3	3 etc. s_2s_4
Females	44.9 s_1s_2	—	+	+	+	+	+
	44.10 s_3s_4	+	—	+	+	+	+
	8 etc. s_1s_3	+	+	—	+	+	+
	2 etc. s_1s_4	—	+	—	—	+	+
	1 etc. s_2s_3	—	+	—	+	—	+
	3 etc. s_2s_4	—	—	—	—	—	—

TABLE X.

VERBASCUM PHOENICEUM, 1920. 549. 8 x 549. 3.

F_7-generation. Family 1921. 129.
+ successful pollinations.
— unsuccessful pollinations.
s slight success.

		Males																					
		549		129																			
		8	3	1	3	8	12	15	18	2	5	11	16	4	7	9	14	20	6	10	13	17	19
Females 549.	8	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
129.	1	+	+	—	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	3	+	+	—	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	8	+	+	—	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	12	+	+	—	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	15	+	+	—	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	18	+	+	—	—	—	—	—	—	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	2	—	+	+	+	+	+	+	+	—	—	—	—	+	+	+	+	+	—	—	—	—	—
	5	—	+	+	+	+	+	+	+	—	—	—	—	+	+	+	+	+	—	—	—	—	—
	11	—	+	+	+	+	s	+	+	—	—	—	—	+	+	+	+	+	—	—	—	—	—
	16	—	+	+	+	+	+	+	+	—	—	—	—	+	+	+	+	+	—	—	—	—	—
	4	—	+	—	—	—	—	—	—	+	+	+	+	—	—	—	—	—	+	+	+	+	+
	7	—	+	—	—	—	—	—	—	+	+	+	+	—	—	—	—	s	+	+	+	+	+
	9	—	+	—	—	—	—	—	—	+	+	+	+	—	—	—	—	—	+	+	+	+	+
	14	—	+	—	—	—	—	—	—	+	+	+	+	—	—	—	—	—	+	+	+	+	+
	20	—	+	—	—	—	—	—	—	+	s	+	+	—	—	—	—	—	+	+	+	+	+
	6	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	—	—
	10	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	—	—
	13	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	—	—
	17	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	—	—
	19	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	—	—	—	—	—

TABLE X (continued).

THEORETICAL EXPLANATION

F_6-parents 549.8 s_1s_3 and 549.3 s_2s_4
F_6-generation $s_1s_2 + s_1s_4 + s_2s_3 + s_3s_4$
s_1-pollen incompatible in s_1- and in 2_2-styles
s_3-pollen incompatible in s_3- and in s_4-styles

Males

Females	549.8 s_1s_3	549.3 s_2s_4	1 etc. s_1s_2	2 etc. s_1s_4	4 etc. s_2s_3	6 etc. s_3s_4
549.8 s_1s_3	—	+	+	+	+	+
549.3 s_2s_4	—	—	—	—	—	—
1 etc. s_1s_2	+	+	—	+	+	+
2 etc. s_1s_4	—	+	+	—	+	—
4 etc. s_2s_3	—	+	—	+	—	+
6 etc. s_3s_4	+	+	+	+	+	—

TABLE XI.

SUCCESSFUL POLLINATIONS WITH ALL THE PLANTS OF THE SUCCESSIVE GENERATIONS, USED AS MALES AND AS FEMALES.

F_1 1022			F_2 31			F_2 32			F_3 58			F_4 321		
	m	f		m	f		m	f		m	f		m	f
1	4	16	1	16	16	1	14	14	1	13	12	1	10	11
2	13	11	2	13	16	2	14	15	2	9	6	2	13	12
4	12	12	3	10	15	3	12	16	3	13	14	7	14	12
5	11	10	4	16	14	4	14	16	4	10	12	8	13	11
6	11	12	5	11	13	5	16	15	5	12	11	9	16	9
8	7	9	6	15	13	6	14	15	6	9	13	12	12	12
11	10	10	7	16	16	7	12	15	7	13	9	14	16	7
12	11	14	8	13	14	8	18	4	8	14	13	15	11	16
15	12	9	9	13	12	9	12	15	9	9	11	16	12	11
19	15	5	10	15	13	10	14	13	10	12	11	17	13	11
22	3	17	11	13	5	11	3	16	11	11	10	20	14	11
24	14	11	12	14	15	12	17	13	12	7	6	4	13	8
28	13	12	13	15	14	13	17	14	13	10	12	10	13	12
29	14	2	14	6	13	14	15	11	14	13	10	11	11	9
33	11	10	15	16	14	15	12	15	15	13	10	19	12	8
34	13	12	16	13	15	16	13	12	16	9	10	3	13	17
38	13	14	17	15	5	17	11	12	17	10	12	13	13	17
40	11	11	18	9	15	18	13	12	18	12	10	18	13	17
41	12	12	19	13	14	19	11	12	19	8	13	5	7	18
42	13	14	20	14	14	20	13	10	20	9	11	6	7	18
	223	223		266	266		265	265		216	216		247	247

TABLE XI (continued).

F_4 322			F_5 44			F_6 547			F_6 549			F_7 129		
	m	f		m	f		m	f		m	f		m	f
1	13	13	1	16	13	5	8	15	8	0	15	1	9	14
2	13	15	2	15	13	7	8	15	13	0	15	3	9	14
3	13	11	4	18	13	10	8	15	14	0	15	8	9	14
4	13	16	7	14	11	12	8	15	15	0	15	12	9	14
5	12	14	13	16	13	14	8	15	20	0	15	15	9	14
6	12	13	14	16	8	6	12	17	2	9	10	18	9	14
8	11	14	18	13	14	11	12	17	9	9	10	2	16	11
9	16	9	3	12	10	18	12	17	10	9	10	5	16	11
10	13	13	11	11	8	2	13	8	18	9	10	11	16	11
11	13	13	12	15	10	8	13	8	19	9	10	16	16	11
12	12	15	19	11	11	9	13	8	1	10	11	4	15	9
14	17	12	5	13	10	13	13	8	6	10	10	7	15	9
15	13	14	6	13	10	16	13	8	12	10	11	9	15	9
17	10	13	20	13	10	17	13	8	17	10	11	14	15	9
18	14	11	8	7	17	20	13	8	3	14	0	20	15	9
20	14	13	10	7	17	1	15	12	4	13	0	6	11	15
7	18	18	15	7	17	3	15	12	5	14	0	10	11	15
16	18	18	9	13	17	4	15	12	7	14	0	13	11	15
13	18	18	16	13	17	15	15	12	11	14	0	17	11	15
19	18	18	17	13	17	19	15	12	16	14	0	19	11	15
	281	281		256	256		242	242		168	168		248	248