PISUM-CROSSES. II [1]

by

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Page

I. INTRODUCTION 337

§ 1. *Scope of experiments; Methods,* 337; § 2. *Materials,* 338.

II. SINGLE CHARACTERS 339

§ 1. *Bloom,* 339; § 2. *Texture of pod,* 341; § 3. *Length of the internodes,* 342; § 4. *Hilum-colour,* 342; § 5. *Marbling of the seed-coat,* 343; § 6. *Location of the seeds in the ripe pod,* 344.

III. INTERRELATION OF FACTORS 344

§ 1. *Cross 7, factors* A_1—$\underset{\smile}{Gp}$—P—V, 344; § 2. *Cross 25, factors* R—$\underset{\smile}{Bl}$—W—S, 346; § 3. Cross *37, factors* R—$\underset{\smile}{Bl}$—W—$\underset{\smile}{Le}$, 350.

IV. ANALYSIS OF SOME SPONTANEOUS CROSSES 353

§ 1. *Spont. cross I, factors* A_1—B—$\underset{\smile}{Pl}$—M_2, 353; § 2. *Spont. cross II, factors* A_1—P_1, 356.

V. SUMMARY 357

LITERATURE CITED 360

APPENDIX: TABLES OF THE TOTAL F_2-RESULTS OF THE CROSSES 361

I. INTRODUCTION

§ 1. *Scope of experiments; Methods*

In this paper the results of some new artificial Pisum-crosses will be dealt with. In considering these crosses we will follow the same plan as in „Pisum-Crosses I", with the restriction, however, that we consider the genetical basis of the single characters only then, when some new

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[1] Continued from Genetica VII, 1925, p. 1—64.

results have been obtained, or when such characters are described for the first time by the author. If all the factors involved in a cross have already been described before, such a cross will be considered only in the chapter on the interrelation of genetic factors.

In chapter IV, moreover, we will deal with the analysis of two spontaneous Pisum-crosses.

§ 2. *Materials* [1]

The following pure varieties were used in the crosses, described in this paper:

No.	Name	Characteristics studied
P_1	Belle de Châtenay	smooth cotyledons; little bloom; long internodes.
P_{15}	Johnson's British Empire	wrinkled cotyledons; no bloom; seeds free in the ripe pod; short internodes.
P_{16}	Pois à brochettes	smooth cotyledons; little bloom; seeds adherent in the ripe pod („chenille").
P_{20}	Mangetout tardif à cosse jaune	white flower-colour; yellow pod-colour; no pod-membrane.
P_{21}	Pois Géant sans parchemin (= Groote grijze Reuzenpeul)	purple flower-colour; green pod-colour; thin pod-membrane.

The results of the following crosses will be dealt with:

No.	Cross	Number of individuals		Characters studied
		F_1	F_2	
7	$P_{20} \times P_{21}$	2	151	flower-colour; pod-colour; pod-membrane.
25	$P_{15} \times P_{16}$	3	189	form of cotyledons; bloom; location of seeds in the ripe pod.
37	$P_{15} \times P_1$	3	167	form of cotyledons; bloom; length of internodes.

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[1] Mr. A. R. ZWAAN, a seed-grower at Voorburg–The Hague, has kindly drawn my attention to the fact, that some of the varietal names, used in "Pisum-Crosses I",

Details as to the composition of the F_2-generations of these crosses, as well as such of the F_2-generations obtained from the spontaneous hybrids, will be found in the appendix, p. 361. The frequency numbers, ascertained in these experiments, which have served as a basis for the calculations in the following chapters, will be found in these tables.

II. SINGLE CHARACTERS

§ 1. *Bloom*

On p. 14 of „Pisum-Crosses I" the hypothesis of a bifactorial basis for the bloom-character was advanced. It was supposed that the factor $\underset{\smile}{Bl}$, if present alone, caused but little bloom, while the addition of $\underset{\smile}{W}$ to $\underset{\smile}{Bl}$ caused the production of much bloom, the plant then becoming glaucous. Factor $\underset{\smile}{W}$, if present alone, was supposed to be inactive. The F_2-generations of the crosses 25 and 37 tend to confirm this hypothesis.

Cross 25. Johnson's British Empire (no bloom) × Pois à brochettes (little bloom).

F_1: much bloom (glaucous).

F_2:		102 much bloom:	33 little bloom:	54 no bloom.
theor. expect.				
[(9) : (3) : (4)]		(106.4)	: (35.4)	: (47.2)
	s	±6.8	±5.3	±5.9
	d	—4.4	—2.4	+6.8

From this F_2-ratio the following 3 : 1 ratios can be derived:

a) (much + little bloom): no bloom =		135	:	54
theor. expect. [(3) : (1)]		(141.75)	:	(47.25)
	s	±5.9		
	d	∓6.75		

b) If we leave the no-bloom group out of consideration we get for the ratio:

much bloom: little bloom =	102	:	33
theor. expect. [(3) : (1)]	(101.25)	:	(33.75)

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have synonyms which are more generally known than the dutch names. "Haarsteegsche" is synonymous with "Express", "Groote grijze Reuzenpeul" with "Pois Géant sans parchemin", "Slierpeul" with "Ramshorn" or "Corne de Bélier", "Krombekdoperwt" with "White Scimitar" or "Serpette d'Auvergne".

Cross 37. Johnson's British Empire (no bloom) × Châtenay (little bloom).

F_1: much bloom (glaucous).

F_2:	92 much bloom :	33 little bloom :	42 no bloom.
theor. expect.			
[(9) : (3) : (4)]	(94.0)	: (31.3)	: (41.7)
s	±6.4	±5.0	±5.5
d	—2.0	+1.7	+0.3

From this F_2-ratio we can derive the following 3 : 1-ratios:

a) (much + little bloom) : no bloom =	125	:	42
theor. expect. [(3) : (1)]	(125.25)	:	(41.75)
b) Leaving again the no-bloom group aside, we find:			
much bloom : little bloom =	92	:	33
theor. expect. [(3) : (1)]	(93.75)	:	(31.25)
	s ± 4.8		
	d ∓ 1.75		

These results may be accounted for by assuming the no-bloom varieties to be $\underset{\smile}{bl}\,\underset{\smile}{bl}\,WW$, the little-bloom varieties $\underset{\smile}{Bl}\,\underset{\smile}{Bl}\,ww$. The monofactorial difference between (much + little) bloom and no bloom points to the action of $\underset{\smile}{Bl}$, that between much bloom and little bloom (leaving no bloom out of consideration) to the action of W.

It must be remembered that in „Pisum-Crosses I", p. 14, Pois à brochettes was said to be absolutely free of bloom. It was subsequently found however, that this variety develops a little bloom at a somewhat later stage in its development than the one in which it had been observed in former years. About ten days before the flowering begins, a thin coating of wax distinctly develops. Therefore DE VILMORIN'S (8) ¹) cross Emereva (little bloom) × Pois à brochettes (little bloom), which gave much bloom in F_1 followed by a 9 : 7 F_2-segregation, is not in agreement with the bifactorial hypothesis proposed above. DE VILMORIN'S cross Emereva (little bloom) × Johnson's British Empire (no bloom), on the other hand, is.

A closer observation of a number of emerald varieties has shown that

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¹) The figures between brackets after the names of the authors refer to "Literature cited", p. 360.

a division into two classes „no bloom'' and „little bloom'' is not sufficient since varieties with „very little bloom'' and with „somewhat more than little bloom''may also be rather definitely distinguished. These types show that very probably more than two factors cause the differences discussed here. New crosses having been made in order to investigate this question we will postpone the discussion until the results of these will have been obtained. The bifactorial hypothesis, however, fits the crosses 25 and 37, as described above.

§ 2. *Texture of pod*

For the character „texture of pod'' a bifactorial hypothesis was proposed, quite analogous to the one for „bloom''. Here we assumed a factor *P*, which by itself produces a thin membrane, and a factor *V* which causes together with *P* the production of a strong membrane („parchmented pea''), but which remains inactive if alone present. (Cf. „Pisum-Crosses I'', p. 28).

The following cross gives an example of no membrane × thin membrane — *pp VV* × *PP vv* — which, according to the above hypothesis, should give strong membrane in F_1, followed by a 9 : 3 : 4 segregation in F_2.

Cross 7. Mangetout tardif à cosse jaune (no membrane) × Pois Géant sans parchemin (thin membrane).

F_1: strong membrane.

F_2: 87 strong : 22 thin : 42 no membrane.
theor. expect. [(9) : (3) : (4)] (85.0) : (28.3) : (37.7)
s ±6.0 ±4.8 ±5.3
d +2.0 —6.3 +4.3

From this segregation we can derive the following 3 : 1 segregations:

a) (strong + thin membrane): no membrane =
= 109 : 42
theor. expect. [(9) : (3) : (4)] (113.25) : (37.75)
s ±5.3
d ∓4.25

b) If we exclude the no-membrane group we have:
strong membrane : thin membrane =

= 87 : 22
theor. expect. [(3) : (1)] (81.75) : (27.25)
s ±4.5
d ±5.25

Consequently this analysis has given exactly the same results as those of the cross strong membrane × no membrane (*PPVV* × *ppvv*) — cf. „Pisum-Crosses I", p. 27 —, results which we could expect on the strength of the theory.

The hybrid Mangetout tardif à cosse jaune (no membrane) × Pois sans parchemin beurre (thin membrane), which also had a strong membrane in F_1, gave but uncertain results in the F_2-generation, as a great number of the plants were destroyed by leather jacquets (*Tipula*). We therefore will postpone the further consideration of this cross until new data will be at hand.

§ 3. *Length of the internodes*

A distinct difference in the manner of growth between the two parental types of cross 37 was observable. A closer inquiry showed this difference to be caused by a difference in the length of the internodes. The following data were collected.

Cross 37. Johnson's British Empire (short internodes) × Châtenay (long internodes).

F_1: long internodes.
F_2: 127 long : 40 short.
theor. expect. [(3) : (1)] (125.25) : (41.75)
s ±5.6
d ±1.75

This monofactorial difference is apparently due to the action of the factor $\underset{\smile}{Le}$ which was first described by KEEBLE and PELLEW (3). Therefore Johnson's British Empire may be represented by $\underset{\smile}{le}\,\underset{\smile}{le}$, Châtenay by $\underset{\smile}{Le}\,\underset{\smile}{Le}$.

§ 4. *Hilum-colour*

The F_1 of the spontaneous cross I differed from the motherplant in having a black hilum, while that of the motherplant was colourless. In F_2 a segregation was observed in

153 black hilum : 44 colourless hilum.
theor. expect. [(3) : (1)] (147.75) : (49.25)
s ± 6.0
d ± 5.25

The monofactorial segregation observed in this cross with regard to this character has been observed by many other investigators [Cf. WELLENSIEK (10, p. 382—384)]. The black colour of the hilum is due to the action of the factor *Pl*.

§ 5. *Marbling of the seed-coat*

A segregation with regard to the factor M_2, responsible for marbling of the seed-coat was observed in the spontaneous cross I. LOCK (4) was the first who found that such marmoration is caused by a factor, which is active only, in case the groundfactor for flower-colour A_1[1]) — or a factor absolutely linked to A_1 — is also present. In the absence of A_1 a „ghost-marbling" may be produced on the colourless testa.

The F_1 of the cross in question had marbled seeds while those of the motherplant showed no pattern at all. Among the F_2-plants with coloured flowers there were

105 marbled : 36 not marbled.
theor. expect. [(3) : (1)] (105.75) : (35.25)

Among the F_2-plants with white flowers — the seeds of which had a colourless testa, because the groundfactor for flower-colour and that for seed-coat-colour are absolutely coupled — there were

26 ghost-marbled : 30 without any marbling.
theor. expect. [(3) : (1)] (42) : (14)
s $\pm$ 3.2
d ∓ 16

The deviation from a 3 : 1-ratio might be explained by assuming that the factor for marbling does not always manifest itself as a ghost-marbling on the colourless seed-coat. Apparently environmental circumstances also play a part [cf. KAPPERT (2, p. 21)].

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[1]) Cf. the additional note, p. 359.

§ 6. *Location of seeds in the ripe pod*

In most Pisum-varieties the seeds lie free in the ripe pod. In the „Pois-chenille" or „Pois à brochettes", however, the seeds adhere to one another in the ripe pod. The chenille-characteristic is highly modifiable, though apparently F_2-plants from a cross of these two types can be sharply separated into „free" and „chenille". From PH. DE VILMORIN's results (9) we may conclude that a difference of but one factor exists between free and chenille and that free dominates over chenille. The results of the following cross confirm this conclusion.

Cross 25. Johnson's British Empire (seeds free) × Pois à brochettes (seeds „chenille"-like).

F_1: seeds free.

F_2:	143 free	:	46 chenille.
theor. expect. [(3) : (1)]	(141.75)	:	(47.25)
s	± 5.9		
d	± 1.25		

Consequently we can represent Johnson's British Empire by *SS*, the Pois à brochettes by *ss*.

III. INTERRELATION OF FACTORS

In our account of the interrelation of the factors, which manifest themselves in each cross by segregation, we shall deal in the first place with the segregation of these single characteristics, which have not been considered in the preceding chapter. The relations we shall treat in the same way as in „Pisum-Crosses I", p. 33—48.

§ 1. *Cross 7. Mangetout tardif à cosse jaune* × *Pois Géant sans parchemin* ; $a_1a_1\, \underbrace{gp}\, \underbrace{gp}\, pp\, VV \times A_1A_1\, \underbrace{Gp}\, \underbrace{Gp}\, PPvv$

Single factors.

(1) A_1: coloured flowers (in the present cross: purple).

a_1: white flowers.

F_2:	110 coloured	:	41 white.
theor. expect. [(3) : (1)]	(113.25)	:	(37.75)
s	± 5.3		
d	∓ 3.25		

(2) $\underset{\smile}{Gp}$: green pods.
$\underset{\smile}{gp}$: yellow pods.
F_2: 111 green : 40 yellow.
theor. expect. [(3) : (1)] (113.25) : (37.75)
s ±5.3
d ∓2.25

(3) P: membrane in the pod, strong or thin.
p: no membrane in the pod.
V: strong membrane in the pod } in the presence of P.
v: thin membrane in the pod } in the presence of P.
For F_2-ratios see p. 341.

Interrelations.

(1) A_1—$\underset{\smile}{Gp}$.

	$A_1\underset{\smile}{Gp}$	: $A_1\underset{\smile}{gp}$	: $a_1\underset{\smile}{Gp}$	: $a_1\underset{\smile}{gp}$
	75	: 35	: 36	: 5
theor. expect. [(9) : (3) : (3) : (1)]	(85.0)	: (28.3)	: (28.3)	: (9.4)
s	±6.0	±4.8	±4.8	±2.9
d	—10.0	+6.7	+7.7	—4.4

(2) A_1—P.

	A_1P	: A_1p	: a_1P	: a_1p
	76	: 34	: 33	: 8
theor. expect. [(9) : (3) : (3) : (1)]	(85.0)	: (28.3)	: (28.3)	: (9.4)
s	±6.0	±4.8	±4.8	±2.9
d	—9.0	+5.7	+4.7	—1.4

(3) A_1—V. If we exclude the no-membrane group we get:

	A_1V	: A_1v	: a_1V	: a_1v
	59	: 17	: 28	: 5
theor. expect. [(9) : (3) : (3) : (1)]	(61.4)	: (20.4)	: (20.4)	: (6.8)
s	±5.1	±4.0	±4.0	±2.5
d	—2.4	—3.4	+7.6	—1.8

(4) $\underset{\smile}{Gp}$—P.

	$\underset{\smile}{Gp}P$	: $\underset{\smile}{Gp}\,p$	: $\underset{\smile}{gp}\,P$	: $\underset{\smile}{gp}\,p$
	80	: 31	: 29	: 11
theor. expect. [(9) : (3) : (3) : (1)]	(85.0)	: (28.3)	: (28.3)	: (9.4)
s	±6.0	±4.8	±4.8	±2.9
d	—5.0	+2.7	+0.7	+1.6

(5) $\underset{\smile}{Gp}$—V. If we exclude the no-membrane group we have:

	$\underset{\smile}{Gp}V$	$\underset{\smile}{Gp}\,v$	$\underset{\smile}{gp}\,V$	$\underset{\smile}{gp}\,v$
	67	13	20	9
theor. expect. [(9) : (3) : (3) : (1)]	(61.4)	(20.4)	(20.4)	(6.8)
s	±5.1	±4.0	±4.0	±2.5
d	+5.6	—7.4	—0.4	+2.2

(6) *P—V*. That *P* and *V* are transmitted independently from one another has already been shown on p. 341.

Conclusion.

From the foregoing data the independent inheritance of A_1—$\underset{\smile}{Gp}$—*P*—*V* follows. Independent inheritance of the four factors in question has been found also in other crosses (cf. „Pisum-Crosses I", p. 49).

§ 2. *Cross 25. Johnson's British Empire × Pois à brochettes;* $rr\ \underset{\smile}{bl}\,\underset{\smile}{bl}\ WW\ SS \times RR\ \underset{\smile}{Bl}\,\underset{\smile}{Bl}\ ww\ ss$

Single factors.

(1) *R*: smooth cotyledons.
r: wrinkled cotyledons.

F_2:	223 smooth	62 wrinkled.
theor. expect. [(3) : (1)]	(213.75)	(71.25)
s	±7.3	
d	±9.25	

All these seeds were sown, but only from 154 smooth ones and from 35 wrinkled ones full-grown plants were obtained; consequently 30.9 % of the smooth seeds and 43.5 % of the wrinkled ones failed to germinate or gave rise to plants that died prematurely.

F_3-seed-generation:

a) The F_2-plants, grown from 35 wrinkled seeds yielded wrinkled seeds only.

b) The F_2-plants, grown from 105 smooth seeds, yielded smooth seeds as well as wrinkled ones, those from 49 smooth seeds yielded smooth ones only.

Actual numbers:	105 segregating	49 constant.
theor. expect. [(2) : (1)]	(102.7)	(51.3)
s	±5.8	
d	±2.3	

(2) $\underset{\smile}{Bl}$: bloom (little or much).
$\underset{\smile}{bl}$: no bloom.
W: much bloom } in the presence of $\underset{\smile}{Bl}$.
w: little bloom }
For F_2-ratios, see p. 339.

(3) S: seeds free in the ripe pod.
s: seeds adherent in the ripe pod.
For F_2-ratio, see p. 344.

Interrelations.

When studying the interrelations of the factors R, $\underset{\smile}{Bl}$, W and S in this cross, it is not quite correct, as far as the factor R is concerned, to work with the four-group-ratios, as was done in the analysis of the foregoing cross, because the 3 : 1 ratio of the segregation into smooth and wrinkled cotyledons has been disturbed by the perishing of relatively more wrinkled seeds than smooth ones. We shall, therefore, consider the distribution of the pairs of characteristics in the group, grown from smooth seeds, and in the one, grown from wrinkled seeds, separately. If in each case the actual numbers agree with a 3 : 1 segegration, linkage does not exist. (Cf. „Pisum-Crosses I", p. 37, § 6).

(1) R—$\underset{\smile}{Bl}$.

a) 154 F_2-seeds[1]) with smooth cotyledons gave	112 $\underset{\smile}{Bl}$	:	42 $\underset{\smile}{bl}$
theor. expect. [(3) : (1)]	(115.5)	:	(38.5)
s	±5.3		
d	∓3.5		
b) 35 F_2-seeds with wrinkled cotyledons gave	23 $\underset{\smile}{Bl}$	:	12 $\underset{\smile}{bl}$
theor. expect. [(3) : (1)]	(26.25)	:	(8.75)
s	±2.5		
d	∓3.25		

(2) R—W. If we exclude the no-bloom group we find:

a) 112 F_2-seeds with smooth cotyledons gave	84 W	:	28 w
theor. expect. [(3) : (1)]	(84)	:	(28)
b) 23 F_2-seeds with wrinkled cotyledons gave	18 W	:	5 w
theor. expect. [(3) : (1)]	(17.25)	:	(5.75)

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[1]) The expression "F_2-seeds" stands for: "seeds produced by the F_1-plants, containing F_2-embryos".

(3) R—S.

a) 154 F_2-seeds with smooth cotyledons gave	113 S	:	41 s
theor. expect. [(3) : (1)]	(115.5)	:	(38.5)
s	±5.3		
d	∓2.5		
b) 35 F_2-seeds with wrinkled cotyledons gave	30 S	:	5 s
theor. expect. [(3) : (1)]	(26.25)	:	(8.75)
s	±2.5		
d	∓3.75		

We may conclude, in all these cases, to independent inheritance. Further we have:

(4) $\underset{\smile}{Bl}$—W. The independent transmission of these two factors follows from the data, considered on p. 339.

(5) $\underset{\smile}{Bl}$—S.	$\underset{\smile}{Bl}\ S$	:	$\underset{\smile}{Bl}\ s$	:	$\underset{\smile}{bl}\ S$	:	$\underset{\smile}{bl}\ s$
	101	:	34	:	42	:	12
theor. expect. [(9) : (3) : (3) : (1)]	(106.4)	:	(35.4)	:	(35.4)	:	(11.8)
s	±6.8		±5.3		±5.3		±3.3
d	—5.4		—1.4		+6.6		+0.2

This is already a sufficient agreement, and if we consider the progenies of only two of my three F_1-plants, we even find a perfect harmony between actual and theoretical numbers, to wit:

	53	:	17	:	19	:	6
theor. expect [(9) : (3) : (3) : (1)]	(53.5)	:	(17.8)	:	(17.8)	:	(5.9)

(6) W—S. If we exclude the no-bloom group we have:

	WS	:	Ws	:	wS	:	ws
	100	:	2	:	1	:	32
theor. expect. [(9) : (3) : (3) : (1)]	(76,0)	:	(25.3)	:	(25.3)	:	(8.4)
s	± 5.7		± 4.5		± 4.5		±2.8
d	+24.0		—23,3		—24.3		+23.6

The deviations point to linkage and a perfect agreement is obtained, if we assume a 40 : 1 linkage. On this assumption the theoretical expectation is:

(99.2) : (2.1) : (2.1) : (31.6)

We may therefore conclude to a rather strong linkage between W and S, the crossing-over percentage being about 2.4 %.

Conclusions and discussion.

From the foregoing data we may conclude that the factors R, $\underset{\smile}{Bl}$ and W are transmitted independently from one another. This is also the case for R and S as well as for $\underset{\smile}{Bl}$ and S, whereas W and S are linked. When we put the linked factors between square brackets the conclusion can be represented in this way: R—$\underset{\smile}{Bl}$—[W—S].

As the relation of the chenille-factor to the bloom-factors has been subject to much discussion, it may be of value to give a brief review of the literature on this matter.

In 1911 Ph. de Vilmorin (9) was the first to publish results of crosses, in which the Pois Chenille was involved. He did not, however, enter into a detailed interpretation of these results, concluding only to "une corrélation évidente entre la couleur du feuillage et la fréquence de l'adhérence des grains" (9, p. 371). There are some circumstances which may account for the difficulties de Vilmorin met with in the interpretation of his results. In the first place he did not begin with the study of the segregation of the single factors; in the second place he did not study the relation of pairs of factors separately. Furthermore it must have been a drawback to him, that he as yet could not distinguish the two bloom-factors from one another.

In 1914 Mr. and Mrs. Hagedoorn (1, p. 175) advanced the hypothesis that the two bloom-factors, when they happen to be present in the same plant, will cause the seeds to be more disconnected, but that neither has, if present alone, any appreciable effect. The authors did not, however, discuss the reasons, that led them to this supposition.

Three years later Orland White (12, pp. 574, 582) gave an interpretation of de Vilmorin's results, which, indeed, is far more attractive. He concluded to linkage between one of the bloom-factors and the chenille-factor. It could not be decided from the data, which of the two bloom-factors, $\underset{\smile}{Bl}$ or W, was linked to S. The reasons that led him to assume — when discussing the interrelation of Pisum-factors (13, p. 173, 177, 189) — that $\underset{\smile}{Bl}$ was linked to S, were not discussed by White.

Meunissier (5, p. 11) writes: "les plantes "chenillées" sont donc toujours émeraudes", and four years later, in 1922, he says (6, p. 295): "le caractère Pois chenille se montra ...... toujours corrélatif du caractère émeraude". From this statement it would follow that glaucous plants never have chenille-seeds, and this led Miss Pellew and Miss Sverdrup (7, p. 128 footnote) to consider the linkage, supposed by White, as unproved. Wellensiek (10, p. 441), when discussing the literature on this subject drew attention to the fact that in DE VILMORIN's crosses the combination glaucous-chenille occurred six times, a fact that Miss PELLEW and Miss SVERDRUP overlooked. Besides, even if this combination should not occur, this might be accounted for by assuming that presence of bloom on the seeds mechanically prevents them from clinging together.

The results of my cross 25, as stated above, clearly show, that $\underset{\smile}{Bl}$ and S are transmitted independently from one another, but that W and S are linked. Furthermore stress must be laid on the occurrence of two Ws-plants, combining the characteristics glaucous and chenille.

WHITE assumed that the other factor for bloom $\underset{\smile}{Bl}$ is linked with S. We must therefore conclude, that WHITE, who had no facts at his disposal, allowing him to choose between W and $\underset{\smile}{Bl}$, supposed the wrong factor to be linked to S, for very probably the monofactorial difference between glaucous and emerald in DE VILMORIN's cross, the results of which have been interpreted by WHITE, has been due to the factor W. This results from the fact, that we had to represent Pois à brochettes by $\underset{\smile}{Bl}\ \underset{\smile}{Bl}\ ww$ and Pois de Momie, the other parental from in DE VILMORIN's cross, being glaucous, by $\underset{\smile}{Bl}\ \underset{\smile}{Bl}\ WW$. The only remaining difference between WHITE's interpretation and my results, is the degree of linkage. WHITE surmised a 8 : 1 linkage, while my results may be accounted for by the assumption of a 40 : 1 linkage. As in many other cases, the degree of linkage seems to be variable.

§ 3. *Cross 37. Johnson's British Empire × Châtenay;*
$rr\ \underset{\smile}{bl}\ \underset{\smile}{bl}\ WW\ \underset{\smile}{le}\ \underset{\smile}{le} \times RR\ \underset{\smile}{Bl}\ \underset{\smile}{Bl}\ ww\ \underset{\smile}{Le}\ \underset{\smile}{Le}$

Single factors.

(1) R: smooth cotyledons.
r: wrinkled cotyledons.

F_2:		181 smooth	:	49 wrinkled.
theor. expect. [(3) : (1)]		(172.5)	:	(57.5)
	s	±6.5		
	d	±8.5		

All these seeds were sown, but only 148 smooth ones and 19 wrinkled ones developed into full-grown plants; consequently 18.2 % of the smooth seeds and 61.2 % of the wrinkled ones either failed to germinate or gave rise to plants that died prematurely, an analogy to the facts described for cross 25 on page 346.

The F_3-generation has not been studied, as the plants were cleared away after the degree of development of bloom and the length of the internodes had been noted.

(2) $\underset{\smile}{Bl}$: bloom, little or much.
$\underset{\smile}{bl}$: no bloom.

$$\left.\begin{array}{l} W\text{: much bloom} \\ w\text{: little bloom} \end{array}\right\} \text{in the presence of } \underset{\smile}{Bl}.$$

For the F_2-ratio, see p. 340.

(3) $\underset{\smile}{Le}$: long internodes.
$\underset{\smile}{le}$: short internodes.
For the F_2-ratio, see p. 342.

Interrelations.

In our study of the interrelations of R and the other factors involved in this cross, we shall follow the same method as in cross 25, p. 347.

(1) R—$\underset{\smile}{Bl}$.

a) 148 F_2-seeds with smooth cotyledons gave	113 $\underset{\smile}{Bl}$	:	35 $\underset{\smile}{bl}$
theor. expect. [(3) : (1)]	(111)	:	(37)
s	±5.2		
d	±2.0		
b) 19 F_2-seeds with wrinkled cotyledons gave	12 $\underset{\smile}{Bl}$	:	7 $\underset{\smile}{bl}$
theor. expect. [(3) : (1)]	(14.25)	:	(4.75)
s	±1.8		
d	∓2.25		

(2) R—W.

If we leave the no-bloom group out of consideration we find:

a) 113 F_2-seeds with smooth cotyledons gave	83 W	:	30 w
theor. expect. [(3) : (1)]	(84.75)	:	(28.25)
s	±4.6		
d	∓1.75		
b) 12 F_2-seeds with wrinkled cotyledons gave	9 W	:	3 w
theor. expect. [(3) : (1)]	(9)	:	(3)

(3) R—$\underset{\smile}{Le}$.

a) 148 F_2-seeds with smooth cotyledons gave	112 $\underset{\smile}{Le}$	:	36 $\underset{\smile}{le}$
theor. expect. [(3) : (1)]	(111)	:	(37)
s	±5.2		
d	±1.0		

b) 19 F_2-seeds with smooth cotyledons gave	15 *Le*	:	4 *le*
theor. expect. [(3) : (1)]	(14.25)	:	(4.75)

As no deviations of significance from the expected numbers have been found, we may conclude that the pairs of factors considered are transmitted independently from one another. Furthermore we have to consider:

(4) *Bl*—*W*. The independent transmission of these factors follows already from the data, stated on p. 340.

(5) *Bl*—*Le*.

		Bl Le	*Bl le*	*bl Le*	*bl le*
		95	30	32	10
theor. expect. [(9) : (3) : (3) : (1)]		(94.0)	(31.3)	(31.3)	(10.4)
	s	±6.4	±5.0	±5.0	±3.1
	d	+1.0	—1.3	+0.7	—0.4

(6) *W*—*Le*. If we exclude the no-bloom group we find:

		W Le	*W le*	*w Le*	*w le*
		66	26	29	4
theor. expect. [(9) : (3) : (3) : (1)]		(70.4)	(23.4)	(23.4)	(7.8)
	s	±5.5	±3.3	±3.3	±2.7
	d	—4.4	+2.6	+5.6	—3.8

The agreement between the numbers actually found and the theoretical ones is sufficient. Yet the possibility of linkage is not excluded, for if we suppose a 1 : 1.5 linkage, we find for the theoretical expectation:

	(67.5)	(26.25)	(26.25)	(5.0)
s	±5.5	±4.5	±4.5	± 2.1
s	—1.5	—0.25	+2.75	— 1.0

The agreement with these numbers is far better, but the material at hand is not sufficient to decide wether linkage between *W* and *Le* exists or not. It may be by a mere coincidence that the deviations in the first and fourth groups, as well as those in the second and third ones run paralell, and that this alone is the reason that the actual numbers agree better with the expectation, when we assume linkage.

Conclusions.

In the F_2-generation of the present cross the factors *R*, *Bl* and *W* are evidently transmitted independently from one another, thus confirming the results of cross 25, p. 348. Independent transmission has also been found for R and $\underset{\smile}{Le}$ [confirmation of WHITE's (13, p. 175, 188) and KAPPERT's (2, p. 7, 23, 28) results] as well as for $\underset{\smile}{Bl}$ and $\underset{\smile}{Le}$. In the case of W—$\underset{\smile}{Le}$, however, though independent transmission is probable, the possibility of linkage is not entirely excluded.

IV. THE ANALYSIS OF SOME SPONTANEOUS CROSSES

In 1924 Professor A. M. SPRENGER showed me some pea-plants, which differed from their motherplants and from their sisters in one or more characteristics. He supposed that these plants had arisen by spontaneous cross-fertilisation. This could be tested by a study of their progeny, while, if it should turn out, that segregation did take place, one might possibly be able to trace the form or forms the pollen of which had caused the cross.

The seeds of the aberrant plants were collected and progenies of some of them were grown in 1925; two of these gave satisfactory results. These were called: spontaneous cross I and spontaneous cross II and will be considered here.

§ 1. *Spontaneous cross I*

Two abnormal plants, found in a line extracted from the cross Châtenay × Express (= Haarsteegsche) differed from their ancestry in having purple flowers 1), a black hilum and a marbled seed-coat, while in the original type these characteristics are respectively white, colourless and non-marbled. The following segregation was observed in the progeny of the deviating plants.

Single characters.

(1) *Flower colour.*		105 purple	: 36 pink	: 56 white.
theor. expect. [(9) : (3) : (4)]		(110.9)	: (36.9)	: (49.2)
	s	±6.9	±5.4	±6.0
	d	—5.9	—0.9	+6.8

---

1) As in all other hybrids a coloured leaf-axil and a coloured seed-coat were always correlated with coloured flowers.

We can derive from these data the following 3 : 1 segregations:

a) Coloured: white =		141	: 56
theor. expect. [(3) : (1)]		(147.75)	: (49.25)
	s	± 6.0	
	d	∓ 6.75	

b) Among the plants with coloured flowers we find:

purple: pink =	105	: 36
theor. expect. [(3) : (1)]	(105.75)	: (36.25)

From these data we may conclude that the aberrant plants — which we shall in future designate as F_1 — may be represented by $A_1a_1\ Bb$. Since the egg-parent is white-flowered, the cross may have been either $a_1a_1\ BB \times A_1A_1\ bb$ or $a_1a_1\ bb \times A_1A_1\ BB$; in the first case the pollen-parent would have been pink-flowered, in the second case purple-flowered. The material at hand allows no choice between these two possibilities; the first one however is the more probable of the two, as all white-flowered varieties, studied so far, possessed the factor B cryptomerically.

(2) *Hilum-colour and marbling of the seed-coat.*

The monofactorial segregation of the present cross as to hilum-colour and marbling of the seed-coat has already been discussed on p. 342—343; the facts point to the presence of $\underset{\smile}{Pl}$ and M_2 in the pollen-parent.

Conclusion. We may therefore conclude that our "spontaneous cross I" must have been either $a_1a_1\ BB\ \underset{\smile}{pl}\ \underset{\smile}{pl}\ m_2m_2 \times A_1A_1\ bb\ \underset{\smile}{Pl}\ \underset{\smile}{Pl}\ M_2M_2$ or $a_1a_1\ bb\ \underset{\smile}{pl}\ \underset{\smile}{pl}\ m_2m_2 \times A_1A_1\ BB\ \underset{\smile}{Pl}\underset{\smile}{Pl}\ M_2M_2$. Among the varieties that in 1923 — the year that the crossing is supposed to have occurred — were grown in the neighbourhood of the line that yielded the hybrids, there was none that answers to the formula $A_1A_1\ BB\ \underset{\smile}{Pl}\underset{\smile}{Pl}\ M_2M_2$, but there was one variety, "*Pisum thebaicum*" [1]), with pink flowers, a black hilum and a marbled seed-coat, which may be represented by $A_1A_1\ bb\ \underset{\smile}{Pl}\ \underset{\smile}{Pl}\ M_2M_2$,. and therefore in all probability has acted as the pollen-parent.

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[1]) This variety, grown in Professor SPRENGER's Experimental gardens, differs from the *Pisum thebaicum*, used by KAPPERT (2), in having a normal, non-fasciated stem.

Interrelations.

As in the present cross segregation for the factors A_1, B, $\underset{\smile}{Pl}$ and M_2 occurred, the interrelations of these factors may be studied exactly in the same way as has been done in the case of artificial hybrids.

(1) A_1—B. The independent transmission of these two factors has been stated on p. 353.

(2) A_1—$\underset{\smile}{Pl}$.

	$A_1\,\underset{\smile}{Pl}$	$A_1\,\underset{\smile}{pl}$	$a_1\,\underset{\smile}{Pl}$	$a_1\,\underset{\smile}{pl}$
	107	34	46	10
theor. expect. [(9) : (3) : (3) : (1)]	(110.9)	(36.9)	(36.9)	(12.3)
s	±6.9	±5.4	±5.4	±3.2
d	—3.9	—2.9	+9.1	—2.3

(3) A_1—M_2.

	A_1M_2	$A_1\,m_2$	$a_1{}^{M_2}_{m_2}$
	105	36	56
theor. expect. [(9) : (3) : (4)]	(110.9)	(36.9)	(49.2)
s	±6.9	±5.4	±6.0
d	—5.9	—0.9	+6.8

It is of course a mere coincidence that the numbers actually found are precisely identical with those found in the segregation for flower-colour, p. 353. Since plants occur which combine purple flower-colour with either marmorated or non-marmorated seed-coat, as well as such which combine pink flower-colour with either of these kinds of seed-coat, there is no reason to suppose that B and M_2 are identical.

(4) B—$\underset{\smile}{Pl}$. If we exclude the white-flowered plants we find:

	$B\,\underset{\smile}{Pl}$	$B\,\underset{\smile}{pl}$	$b\,\underset{\smile}{Pl}$	$b\,\underset{\smile}{pl}$
	78	27	29	7
theor. expect. [(9) : (3) : (3) : (1)]	(79.4)	(26.4)	(26.4)	(8.8)
s	±5.8	±4.6	±4.6	±2.8
d	—1.4	+0.6	+2.6	—1.8

(5) B—M_2. If again we exclude the white-flowered plants we have:

	$B\,M_2$	$B\,m_2$	$b\,M_2$	$b\,m_2$
	78	27	27	9
theor. expect. [(9) : (3) : (3) : (1)]	(79.4)	(26.4)	(26.4)	(8.8)
s	±5.8	±4.6	±4.6	±2.8
d	—1.4	+0.6	+0.6	+0.2

(6) $\underset{\smile}{Pl}$—M_2. If once more we exclude the white-flowered plants we find:

	$\underset{\smile}{Pl}M_2$	:	$\underset{\smile}{Pl}\,m_2$	:	$\underset{\smile}{pl}\,M_2$	:	$\underset{\smile}{pl}\,m_2$
	74	:	33	:	31	:	3
theor. expect. [(9) : (3) : (3) : (1)]	(79.4)	:	(26.4)	:	(26. 4)	:	(8.8)
s	±5.8		±4.6		±4.6		±2.8
d	—5.4		+6.6		+4.6		—5.8

Conclusions.

From the foregoing data we can conclude that A_1—B—$\underset{\smile}{Pl}$—M_2 are transmitted independently from one another. KAPPERT (2), when studying the same interrelations, came to analogous results.

§ 2. *Spontaneous Cross II*

One plant in a line, extracted from the cross Bliss Abundance × Express (= Haarsteegsche) was distinghuished from the normal type of that line by purple flowers and violet pods, whereas the line itself is characterized by white flowers and green pods. 75 seeds of the aberrant plant were sown and showed the following segregation.

Single characters.

(1) *Flower-colour.*	56 purple	: 19 white.
theor. expect. [(3) : (1)]	(56.25)	: (18.75)

(2) *Pod-colour.*	41 violet	: 34 green.
theor. expect. [(9) : (7)]	(42.2)	: (32.8)
s	±4.2	
d	∓1.2	

If we exclude the white-flowered individuals, which were without exception green-podded, we find for the pod-colour

	41 violet	: 15 green.
theor. expect. [(3) : (1)]	(42)	: (14)
s	±3.2	
d	∓1.0	

Conclusion. From the segregation of the flower-colour we may conclude that the hybrid must have been A_1a_1; furthermore B must have been present in both parents as the hybrid and many of the F_2-plants had purple flowers while $A_1{}^{A_1}_{a_1}\,bb$ individuals (pink-flowered) did not occur in F_2. The segregation as to pod-colour shows, that the hybrid was P_1p_1 (because it as well as part of the F_2-plants had violet pods), while $\underset{\smile}{Gp}$, necessary for the development of violet pod-colour must have been present in both parents as $\underset{\smile}{gp}\ \underset{\smile}{gp}$-individuals did not occur in F_2 (Cf. „Pisum-Crosses I'', p. 21, 22).

Consequently the cross has been $a_1a_1\ BB\ \underset{\smile}{Gp}\ \underset{\smile}{Gp}\ p_1p_1 \times A_1A_1\ BB\ \underset{\smile}{Gp}\ \underset{\smile}{Gp}\ P_1P_1$. There are two varieties answering to the formula $A_1A_1\ BB\ \underset{\smile}{Gp}\underset{\smile}{Gp}\ P_1P_1$, namely "Pois à cosse violette" and "Amsterdamsche Blauwschok Capucijner", so that either of them may have been the pollen-parent, but which of these two really acted as such, cannot be stated.

Relation of A_1—P_1.		A_1P_1	: A_1p_1	: $a_1{}^{P_1}_{p_1}$
		41	: 15	: 19
theor. expect. [(9) : (3) : (4)]		(42.2)	: (14.0)	: (18.8)
	s	±4.2	±3.3	±3.7
	d	—1.2	+1.0	+0.2

These numbers point to independent transmission of the factors A_1 and P_1 as was also found in previous experiments (Cf. „Pisum-Crosses I'', p. 38, 40, 44, 45).

V. SUMMARY

1. In some artificial Pisum-crosses both the segregation of the separate factors and their interrelation has been studied. Moreover two spontaneous hybrids have been analysed. One of these evidently was arisen from the cross of a $a_1a_1\ BB\ \underset{\smile}{pl}\underset{\smile}{pl}\ m_2m_2$ plant with a $A_1A_1\ bb\ \underset{\smile}{Pl}\underset{\smile}{Pl}\ M_2M_2$ one, the other from that of $a_1a_1\ BB\ \underset{\smile}{Gp}\underset{\smile}{Gp}\ p_1p_1$ plant with a $A_1A_1\ BB\ \underset{\smile}{Gp}\ \underset{\smile}{Gp}\ P_1P_1$ one.
2. The bifactorial hypotheses for the characters bloom and for texture of the pod, advanced in „Pisum-crosses I'', have been confirmed by the following crosses:
   (1) no bloom ($\underset{\smile}{bl}\ \underset{\smile}{bl}\ WW$) × little bloom ($\underset{\smile}{Bl}\ Bl\ ww$) which gave much bloom ("glaucous") in F_1, followed by a 9 : 3 : 4 F_2-segregation.
   (2) no membrane ($pp\ VV$) × thin membrane ($PP\ vv$) which gave a strong membrane ("parchmented pea") in F_1, followed by a 9 : 3 : 4 F_2-segregation.
3. The following four factors had not been considered previously by the author:

   (1) $\underset{\smile}{Le}$: long internodes vs. $\underset{\smile}{le}$: short internodes. (Confirmation of the results of Keeble and Pellew).
   (2) $\underset{\smile}{Pl}$: Black hilum vs. $\underset{\smile}{pl}$: colourless hilum. (Confirmation of the results of Lock a.o.).
   (3) M_2: causes marbling of the seed-coat in the presence of A_1; in the absence of A_1 the factor M_2 may cause the appearance of a "ghost-marbling", the development of which seems to be influenced by external circumstances. (Confirmation of the results of Lock).
   (4) S: seeds free in the ripe pod vs. s: seeds clinging together "caterpilar"-like in the ripe pod. (Confirmation of the results of Ph. de Vilmorin).
4. As to the interrelation of the factors involved in the crosses, the following results have been obtained:
   (1) Independent transmission of the factors A_1—$\underset{\smile}{Gp}$—P—V in cross 7 is evident. (Confirmation of earlier results).
   (2) In cross 25 W and S are rather strongly linked, the crossing-over percentage being about 2.4 %. There is independent transmission of [W—S], R and $\underset{\smile}{Bl}$. The literature on this problem, which has been subject to much discussion, has been briefly discussed.
   (3) R—$\underset{\smile}{Bl}$—W in cross 37 are transmitted independently from one another (confirmation of the results of cross 25), as well as R—$\underset{\smile}{Le}$ (confirmation of White's and Kappert's results) and $\underset{\smile}{Bl}$—$\underset{\smile}{Le}$. As to the relation of W and $\underset{\smile}{Le}$ it has been shown that though the assumption of linkage is not necessary to explain the observed segregation, a better agreement between actual and theoretical numbers is obtained, if we assume the existence of linkage between these two factors.
   (4) In spontaneous cross I independent transmission of the factors A_1—B—$\underset{\smile}{Pl}$—M_2 has been found. (Confirmation of Kappert's results).
   (5) In spontaneous cross II the factors A_1 and P_1 are transmitted independently from one another. (Confirmation of earlier results).

The author is indebted to Mr. A. Meunissier of Verrières-le-Buisson for the supply with most of the varieties used in these crosses, to Pro-

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Wageningen, Sept. 23d, 1923.

Additional notes.

In a recent paper (Hereditas 7, 1925, 102—108, see p. 104—105), which came under my notice after this paper had gone to the press, Hans and Olof Tedin suggest that their flower-colour factor, symbolized by me as A_1, is identical with the factor A used by White (12). This is, however, only partially true, for both factors are groundfactor for flower-colour, but A_1 gives in itself light-purple while A by itself gives pink. I therefore feel justifted in keeping the symbol A_1.

In „Genetics", vol. 10, 1925, p. 197—210, Orland E. White describes in details a number of crosses between *Pisum* races with straight or sligtly curved pods on the one side, and a race with strongly curved pods on the other side. The first-named races had broader fruits than the latter. A monofactorial difference between the two characteristics was found, with imperfect dominance of the straight or slightly curved broad type. White designates the factor in question as S_s.

This factor is the same as the one described by the present author (10, p. 417; 11, pp. 22—24) and symbolized by $\underset{\smile}{Cp}$. As, however, White's publication is dated accurately one month previously to that of the present author, the symbol S_s has the right of priority.

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APPENDIX

THE TOTAL F_2-RESULTS OF THE CROSSES

Cross 7. Mangetout tardif à cosse jaune × *Pois Géant sans Parchemin*

Characteristics studied.

	Manget. tard. c. jaune	F_1	P. Géant s. parch.
flower-colour	white	purple	purple
pod-colour	yellow	green	green
pod-membrane	absent	strong	thin

Composition of F_2-generation of Cross 7.

Characteristics			F_2-groups [1]		total
flower-colour	pod-colour	pod-membrane	7—1	7—2	
purple	green	strong	21	20	41
		thin	7	2	9
		absent	11	14	25
	yellow	strong	8	10	18
		thin	4	4	8
		absent	6	3	9
white	green	strong	9	17	26
		thin	2	2	4
		absent	4	2	6
	yellow	strong	1	1	2
		thin	1	0	1
		absent	0	2	2
		total	74	77	151

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[1] Each group refers to the progeny of 1 F_1-plant.

Cross 25. Johnson's British Empire × Pois à brochettes

Characteristics studied.

	J.'s Br. Emp.	F_1	P. à broch.
cotyledons	wrinkled	smooth	smooth
bloom	absent	much	little
location of seeds in the ripe pod	free	free	chenille

Composition of F_2-generation of Cross 25.

Characteristics			F_2-groups			total
cotyledons	bloom	location of seeds	25—1	25—2	25—3	
smooth	much	free	30	16	36	82
		chenille	0	1	1	2
	little	free	0	0	1	1
		chenille	7	6	14	27
	absent	free	5	8	17	30
		chenille	1	5	6	12
		total	43	36	75	154
wrinkled	much	free	1	6	11	18
		chenille	0	0	0	0
	little	free	0	0	0	0
		chenille	2	1	2	5
	absent	free	3	3	6	12
		chenille	0	0	0	0
		total	6	10	19	35

Cross 37. Johnson's British Empire × Châtenay

Characteristics studied.

	J.'s Br. Emp.	F_1	Châtenay
cotyledons	wrinkled	smooth	smooth
bloom	absent	much	little
internode-length	short	long	long

Composition of F_2-generation of Cross 37.

Characteristics			F_2-groups			total
cotyledons	bloom	internode-length	37—1	37—2	37—3	
smooth	much	long	28	11	20	59
		short	14	6	4	24
	little	long	13	5	8	26
		short	2	2	0	4
	absent	long	10	7	10	27
		short	5	2	1	8
		total	72	33	43	148
wrinkled	much	long	5	1	1	7
		short	1	1	0	2
	little	long	1	1	1	3
		short	0	0	0	0
	absent	long	2	3	0	5
		short	2	0	0	2
		total	11	6	2	19

Spontaneous Cross I

Characteristics studied.

	mother (unnamed)	F_1	father (probably Pisum thebaicum)
flower-colour	white	purple	purple
hilum	colourless	black	marbled
seed-coat	unmarbled	marbled	marbled

Composition of F_2-generation of Spont. Cross I

Characteristics			F_2-groups		total	
flower-colour	hilum	seed-coat	I—1	I—2		
purple	black	marbled	26	28	54	
		unmarbled	14	10	24	
	colourless	marbled	16	8	24	
		unmarbled	2	1	3	
pink	black	marbled	12	8	20	
		unmarbled	4	5	9	
	colourless	marbled	3	4	7	
		unmarbled	0	0	0	
white	black	ghost-marbled	8	11	19	46
		unmarbled	5	22	27	
	colourless	ghost-marbled	6	1	7	10
		unmarbled	2	1	3	
		total	98	99	197	

Spontaneous Cross II

The total F_2-composition of this cross has already been given on p. 357.