

# FURTHER STUDIES OF LINKAGE IN THE SWEET PEA.

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(With Two Text-figures.)

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## INTRODUCTION.

IN 1927 I published a brief note pointing out that the experimental work carried out for many years past on the sweet pea was in accordance with the chromosome theory. For the nineteen characters investigated fell into five linkage groups and two unassociated characters—a result in harmony with the fact that the haploid number of the chromosomes in *Lathyrus odoratus* is seven. The object of this paper is to present in more detail the evidence upon which the statement of 1927 was based.

## CHARACTERS INVESTIGATED.

The characters made use of during the investigation have, with two exceptions, been already described in the earlier publications (1923, 1925) summarising our genetical knowledge of the sweet pea to date. The two additional characters referred to in 1927 are mauve flower colour and flaking of the petals, each of which calls for a few remarks.

*Mauve* ( $g_3$ ), or “lavender” as it is more generally described in horticultural lists, behaves as a simple recessive to purple, and there are various shades of mauve corresponding to the various shades of purple. In its paler form of lavender it is characteristic of such varieties as the old “Countess Radnor” and the more modern “Robert Felton.” Mauve flowers have a marked tendency to deepen in colour as the flower ages.

Thus in one family (53/1924) the newly opened flowers were of the "purplish lilac" of Ridgway's Pl. XXXVII, and on ageing turned to the "violet purple" of Pl. XI. The corresponding red is of a rosy pink shade, and also deepens on ageing. A peculiar feature of the mauve flower colour is that it is associated with small shrivelled seed, though the germinating power of this is unimpaired. It is a curious fact that the corresponding red (= rosy pink) does not show these shrivelled seeds. The character seems only to develop when  $A_1$  is also present, but it would probably repay further investigation<sup>1</sup>.

*Flaking* of the petals is characteristic of a few well-known horticultural varieties such as "Senator" (purple) and "America" (red). At the time of publication of the 1927 note it was supposed that flaking behaved as a recessive to self-colour, and that the factor concerned was located in the **D** chromosome. Subsequent experiment has shown that the matter is more complicated. Actually, flaking is a member of the allelomorphous series self—flaked—*C*—white, behaving as recessive to the first and dominant to the last form. There is, however, good reason for presuming the existence of a factor which, in the heterozygous state, greatly darkens the flaking, and, when homozygous, turns it into a self-coloured flower. This modifying factor is closely linked with the tendril-acacia pair ( $D_1-d_1$ ), and it was this circumstance that led me to the erroneous supposition that the factor for flaking itself was located in the **D** chromosome (cf. p. 102). The character is at present the subject of fresh experiment and will not be further dealt with here.

#### CROSSING RESULTS.

A summary of the data is given in Table VII at the end of this paper (p. 109). In compiling this table only  $F_2$  families were used in which the nature of the cross was definitely known to be either of the coupling ( $XY \times xy$ ) or of the repulsion ( $Xy \times xY$ ) type. In so far as was possible both linkage types were made use of in each cross. The characters used and the crosses made between them are schematised in Fig. 1 on p. 99. Each linkage group is denoted by a letter, and a number is added for each character falling into the group. Thus the three pairs, purple—red flower colour, long—round pollen, and erect—hooded standard, which are known to be linked with one another, are denoted respectively as  $A_1-a_1$ ,  $A_2-a_2$ ,  $A_3-a_3$ . There are five such linkage groups, viz. **A**, **B**, **D**, **F**, **G**; and there are two further pairs, tall—short (**E**—**e**) and clamped—open keel (**H**—**h**), in which there is no evidence for postulating either linkage with

<sup>1</sup> There is the possibility that the character may be very closely linked with purple ( $A_1$ ).

one another or with any member of the five groups. Hence the number of linkage groups and independent factors does not exceed seven, which is the haploid number of chromosomes in *Lathyrus odoratus*.

It is, of course, conceivable that **E** and **H** are located in the same chromosome but so far apart as to render detection of any linkage practically impossible without the addition of some other factor. Conceivably also either **E** or **H** might be located in chromosome **F** for which only two loci are at present known. Since at least three separate loci are

	A <sub>1</sub>	A <sub>2</sub>	A <sub>3</sub>	B <sub>1</sub>	B <sub>2</sub>	B <sub>3</sub>	D <sub>1</sub>	D <sub>2</sub>	D <sub>3</sub>	D <sub>4</sub>	D <sub>5</sub>	E	F <sub>1</sub>	F <sub>2</sub>	F <sub>3</sub>	G <sub>1</sub>	G <sub>2</sub>	G <sub>3</sub>	H		
A <sub>1</sub>																				A <sub>1</sub> =Purple—red	
A <sub>2</sub>																					A <sub>2</sub> =Long—round
A <sub>3</sub>																					A <sub>3</sub> =Erect—hood
B <sub>1</sub>	⊗	⊗	⊗																		B <sub>1</sub> =Dark—light
B <sub>2</sub>	⊗	•	⊗																		B <sub>2</sub> =Fertile—sterile
B <sub>3</sub>	⊗	•	×																		B <sub>3</sub> =Normal—cretin
D <sub>1</sub>	⊗	×	+	⊗	⊗	⊗															D <sub>1</sub> =Tendrill—acacia
D <sub>2</sub>	⊗	×	+	⊗	⊗	•															D <sub>2</sub> =Bright—dull
D <sub>3</sub>	⊗	×	⊗	⊗	⊗	•															D <sub>3</sub> =Hairy—smooth
D <sub>4</sub>	⊗	×	⊗	⊗	⊗	•															D <sub>4</sub> =Deep—picotec
D <sub>5</sub>	⊗	⊗	⊗	⊗	⊗	×															D <sub>5</sub> =Tall—cupid
E	⊗	•	⊗	⊗	⊗	•	×	×	×	×	×										E=Colour—R-white
F <sub>1</sub>	•	+	+	•	×	•	×	+	×	•	•										F <sub>1</sub> =Procumbent—bush
F <sub>2</sub>	⊗	+	⊗	⊗	×	•	⊗	×	⊗	+	×										F <sub>2</sub> =Self—marbled
F <sub>3</sub>	×	×	+	⊗	×	•	⊗	+	⊗	⊗	⊗										F <sub>3</sub> =Colour—C-white
G <sub>1</sub>	•	⊗	⊗	×	⊗	×	×	×	×	⊗	⊗	•	⊗	×							G <sub>1</sub> =Purple—copper
G <sub>2</sub>	×	•	⊗	⊗	×	×	×	×	⊗	•	⊗	•	•	×							G <sub>2</sub> =Full—mauve
G <sub>3</sub>	+	×	+	+	⊗	•	⊗	•	×	×	×	×	•	×	×						H=Normal—Spencer (=clamped—open keel)
H	⊗	×	⊗	⊗	⊗	•	×	×	×	×	×	⊗	×	×	×	⊗	×	×	×		

⊕ = coupling series.      × = repulsion series      ⊗ = both series.

Fig. 1.

known in the other four chromosomes it is unlikely, on the evidence in Table IV, that either **E** or **H** is located in any of these.

It will be noticed that in many cases the figures in Table VII are decidedly irregular as compared with a normal 9 : 3 : 3 : 1 ratio. Such irregularities, however, would appear most often to be due to a deficiency of one or other of the recessive characters entering into the cross. In a very few cases, e.g. **A**<sub>1</sub> × **D**<sub>4</sub>, **A**<sub>1</sub> × **D**<sub>5</sub> and **A**<sub>1</sub> × **B**<sub>1</sub>, the irregularities are such as might be expected from a very loose linkage; but if we take into account the evidence from the reciprocal cross, as well as the general evidence from the table as a whole, there can be little doubt

that we are dealing with "chance" irregularities. In some cases the irregularities are evidently due to a deficiency of one of the recessive characters, and this is most clearly the case for "marbled" ( $f_3$ ). Where this character is concerned the 2nd and 4th terms are, in the majority of the crosses, below normal expectation, suggesting that in most combinations marbled plants are less viable than the corresponding self-coloured ones (see later, p. 104).

In view of these irregularities I have used Kappert's method of calculating the "ideal" series which the actual numbers may be supposed to represent. It will be seen that in almost all cases the two series are sufficiently near to preclude the likelihood of linkage.

Before dismissing the question of irregularities I may allude briefly to a case which is not without interest. In 1928 I raised an unusually large and well-grown family (7/1928) from an  $F_1$  plant *ex* purple sterile (carrying white)  $\times$  blue picotee fertile. The seeds, thoroughly mixed in a single packet, were sown in three parallel rows 4 ft. apart, and germination was exceptionally good. Eventually 388 plants flowered, and the three rows were recorded separately. The result is given in Table I.

TABLE I.

Row	Fertile					Sterile					Total
	Pur.	Blue	Pic.	Blue pic.	White	Pur.	Blue	Pic.	Blue pic.	White	
1	38	12	10	9	21	16	1	7	—	4	118
2	55	16	12	4	27	15	6	7	2	5	149
3	38	11	11	4	24	9	8	3	2	11	121
Totals	131	39	33	17	72	40	15	17	4	20	388

If, omitting the whites, we consider the relative distributions of the bright—dull flower colour ( $D_2-d_2$ ) and the fertile—sterile ( $B_2-b_2$ ) pairs we obtain the following figures for the three rows:

Row	$B_2D_2$	$B_2d_2$	$b_2D_2$	$b_2d_2$
1	48	21	23	1
2	77	20	22	8
3	49	15	12	10
Totals	174	56	57	19

The cross was of the repulsion type, viz.  $b_2D_2 \times B_2d_2$ , and if the results of row 1 alone had been recorded the observer would have had good grounds for suspecting the existence of linkage. The figures for row 3, however, are such as we should expect in a case of coupling; while those of row 2 are close to a normal 9 : 3 : 3 : 1 distribution. The total of the three rows is very close indeed to a normal distribution with independent

assortment. I can think of nothing apart from pure chance which could serve to account for this peculiar distribution, and I only mention it as suggesting how desirable it is to have considerable numbers in work of this kind.

The numbers given in Table IV are, of course, a summary of all the families where any two given pairs of characters entered into a cross in either of the two possible ways (*i.e.*  $\mathbf{XY} \times \mathbf{xy}$  or  $\mathbf{Xy} \times \mathbf{xY}$ ). The number of families used for the different crosses varies very considerably. In some cases only three or four families were procured, whereas in others there were ten or a dozen times as many. Thus for the cross  $\mathbf{B}_1 \times \mathbf{D}_4$  (repulsion series) 42 families were available. The complete records are of course in the original note-books, to which an index, facilitating reference, has been prepared. For the present they are preserved in the Genetics Institute at Cambridge.

#### THE D GROUP.

The tendril-acacia ( $\mathbf{D}_1$ ) and the bright—dull flower colour ( $\mathbf{D}_2$ ) pairs were shown in 1923 to be linked together. To these two pairs must now be added two further pairs, *viz.* hairy—smooth ( $\mathbf{D}_4$ ) and deep—picotee flower colour ( $\mathbf{D}_5$ ). A summary of the accumulated data for these four pairs is given in Table II.

TABLE II.

	Coupling series				Approx. cross- over value	Repulsion series				Approx. cross- over value
	$\mathbf{XY}$	$\mathbf{Xy}$	$\mathbf{xY}$	$\mathbf{xy}$		$\mathbf{XY}$	$\mathbf{Xy}$	$\mathbf{xY}$	$\mathbf{xy}$	
$\mathbf{D}_1$ - $\mathbf{D}_2$	194	61	41	41	37	1828	668	696	91	41
$\mathbf{D}_1$ - $\mathbf{D}_4$	2980	664	667	472	35	214	88	112	23	38
$\mathbf{D}_1$ - $\mathbf{D}_5$	—	—	—	—	—	2457	871	869	219	45
$\mathbf{D}_2$ - $\mathbf{D}_4$	1437	424	375	138	48	1149	353	374	102	49
$\mathbf{D}_2$ - $\mathbf{D}_5$	1293	387	380	150	46	476	162	133	43	50
$\mathbf{D}_4$ - $\mathbf{D}_5$	164	42	43	33	41	2356	940	921	125	35

In certain cases, notably in that of  $\mathbf{D}_2 \times \mathbf{D}_4$  and of  $\mathbf{D}_2 \times \mathbf{D}_5$ , the cross-over value approaches 50 per cent., and were these figures taken alone there would be no reason for bringing  $\mathbf{D}_2$  into this linkage group. Yet there can be no question about its belonging here, since both  $\mathbf{D}_2$  and  $\mathbf{D}_4$  are obviously linked with  $\mathbf{D}_1$ , while  $\mathbf{D}_4$  and  $\mathbf{D}_5$  are no less obviously linked with one another.

With so many high cross-over values it has not been found possible to obtain a satisfactory picture of the way in which the loci of these

four factors are located relatively to one another in the chromosome. The question is, however, being further studied in connection with a fifth factor,  $D_3$ . Recent results (cf. p. 98) have indicated that this factor is a modifier of the flaked flower, such as occurs in the well-known variety "Senator." In the heterozygous condition  $D_3$  turns the normal flaking into a very dark flake; in the homozygous condition it turns it into a self-coloured flower. The flaked character itself is a member of the allelomorphous series self—flaked—*C*-white. Present results point to  $D_3$  being closely linked with  $D_1$ , the cross-over value being about 8 per cent. The relations of  $D_3$  to the other members of the  $D$  group are not yet adequately determined. It is possible that when this has been done the data will enable us to obtain a clearer picture of the way in which the five members of this group are related to one another along the chromosome.

#### THE F GROUP.

It was shown in 1923 that marbled and *R*-white are multiple allelomorphs of full-colour, and it was further pointed out that certain early experiments accorded with the supposition that linkage existed between the colour—*R*-white and the procumbent—bush pairs. The rather scanty data suggested a cross-over value of about 25 per cent. (1923, p. 112), but in view of the fact that they were complicated by the simultaneous presence of the two visibly indistinguishable types of white this value was necessarily but a rough approximation. To avoid this complication crosses were made to determine the cross-over value between the procumbent—bush and the self-coloured—marbled pairs; for the intensity of the linkage should be the same here as between the procumbent—bush and the self-coloured—*R*-white pairs. When the nature of the cross was  $F_2f_3 \times f_2F_3$  the  $F_2$  figures were:

Tall self	...	...	...	...	497
Tall marbled	...	...	...	...	163
Bush self	...	...	...	...	185
Bush marbled	...	...	...	...	23

As is usually the case the marbled plants are in deficiency. If they are brought up to one-third of the total of the self-coloured and distributed *pro rata* among the tall and bush plants the figures so corrected are 497 : 199 : 185 : 28, and these correspond to a cross-over value of about 37 per cent.

In the coupling series ( $F_2F_3 \times f_2f_3$ ) six families grown in 1928 gave

Tall self	...	...	...	295
Tall marbled	...	...	...	42
Bush self	...	...	...	57
Bush marbled	...	...	...	36

When corrected for deficiency of marbled as above these figures become 295 : 63 : 57 : 54, and correspond to a cross-over value of about 32 per cent.

In a further series of four families grown in 1929 the figures were:

Tall self	...	...	...	74
Tall marbled	...	...	...	16
Bush self	...	...	...	16
Bush marbled	...	...	...	15

There is here no deficiency of marbled and the cross-over value works out at about 32 per cent.

Taken together these data suggest that the cross-over value of 25 per cent. put forward in 1923 on the *R*-white data was too low, and that truer value for this linkage lies somewhere about 30–35 per cent.

#### THE G GROUP.

Reasons were given in 1923 (pp. 113–114) for supposing that linkage existed between the purple—copper and the coloured—*C*-white pairs. Further data have confirmed this supposition and have also shown that the purple—mauve pair is linked with these two pairs. The data are briefly given in Table III.

TABLE III.

	Coupling series				Repulsion series			
	$\mathbf{XY}$	$\mathbf{Xy}$	$\mathbf{xY}$	$\mathbf{xy}$	$\mathbf{XY}$	$\mathbf{Xy}$	$\mathbf{xY}$	$\mathbf{xy}$
$\mathbf{G}_1 \times \mathbf{G}_2$	366	74	148		156	78	80	
$\mathbf{G}_1 \times \mathbf{G}_3$	—	—	—	—	322	118	148	
$\mathbf{G}_2 \times \mathbf{G}_3$	—	—	—	—	606	203	211	34

In the case of  $\mathbf{G}_1 \times \mathbf{G}_2$  the cross-over value is about 27 per cent. in the coupling series, and about 25 per cent. in the repulsion series. For  $\mathbf{G}_1 \times \mathbf{G}_3$  the cross-over value is about 45 per cent., and for  $\mathbf{G}_2 \times \mathbf{G}_3$  about 41 per cent. Owing to the fact that the  $\mathbf{xY}$  and  $\mathbf{xy}$  classes cannot be distinguished in three cases these values are but rough approxima-

tions, but so far as they go they accord with the supposition that  $G_2$  lies between  $G_1$  and  $G_3$ . The data are, however, sufficient to make it certain that these three pairs of characters form a linkage group.

#### RECESSIVE RATIOS.

As already pointed out (p. 99), irregularities in the proportions of the four forms occurring in  $F_2$  ratios are generally due to a deficiency of one or other or both of the recessives involved, and this naturally led to an examination of the figures from the point of view of specific lethal factors. Were we concerned with this phenomenon we might expect the families relating to a given cross to fall roughly into two groups, viz. those in which the recessive was markedly below 25 per cent., and those in which the proportion of dominant to recessive was approximately normal. Examination of the figures for the various families has, however, failed to reveal any marked distinction of the kind. Where a recessive is deficient in the sum total the deficiency runs in varying degree through most of the families concerned. As an example we may take the case of "marbled" ( $f_3$ ). In Table IV are given the figures for all  $F_2$  families containing more than 100 individuals where marbled was recessive. In the 29 families the  $D/R$  ratio varies from 2.48 to 6.21, the average being 3.58. Fig. 2 shows the distribution of these ratios graphically. There is some slight clumping about 4, and it might conceivably be argued that two groups are present, viz. one varying on either side of 3 and another varying on either side of about 4—the former representing the families with a normal 3 : 1 ratio, and the latter those in which there occurs a lethal loosely linked with marbled.

There is, however, a consideration which seems to me to tell against the idea of a specific lethal. It is clear that if Fig. 2 is interpreted in terms of a hypothetical lethal we must suppose that at least half the families, and probably rather more, contain the lethal. This means that the marbled parent used in crossing must always have been heterozygous for the lethal. Now the marbled parent used for the  $F_2$  families raised in 1919 was the well-known variety "Helen Pierce," originally brought out in 1905, and subsequently propagated by self-fertilisation. Three separate plants, viz. 100<sup>1</sup>, 100<sup>2</sup> and 100<sup>3</sup>, were used for crossing in 1917, and the  $F_2$  families derived from these are shown separately in Table V. If we suppose that families with a low proportion of recessives contain a lethal factor it is evident that all of the three plants of "Helen Pierce" used in 1917 must have been heterozygous. But when we consider the rapidity with which the proportion of heterozygotes drops in a strain of

TABLE IV.

Ref. no.	F <sub>3</sub>	f <sub>3</sub>	Ratio
1919, 2	202	49	4.08 : 1
3	113	33	3.42 : 1
6	83	21	3.95 : 1
8	109	32	3.40 : 1
11	83	21	3.95 : 1
12	109	31	3.51 : 1
72	120	32	3.75 : 1
124	102	25	4.08 : 1
1920, 36	133	45	2.96 : 1
37	104	42	2.48 : 1
39	75	28	2.68 : 1
56	93	21	4.43 : 1
1921, 74	88	21	4.19 : 1
1922, 71	118	19	6.21 : 1
87	184	46	4.00 : 1
88	112	28	4.00 : 1
89	140	34	4.12 : 1
1923, 30	109	31	3.52 : 1
1926, 34	143	44	3.25 : 1
35	199	51	3.90 : 1
37	73	27	2.70 : 1
58	232	56	4.14 : 1
1927, 57	237	66	3.59 : 1
58	434	139	3.13 : 1
63	114	34	3.35 : 1
64	103	34	3.03 : 1
65	143	48	2.98 : 1
75	104	24	4.33 : 1
1928, 1	93	22	4.23 : 1

No. of F<sub>3</sub> = 3952 } Total 5056  
 ,, f<sub>3</sub> = 1104 }

Ratio in total = 3.58 : 1

No. of families = 29

Average per family = 174

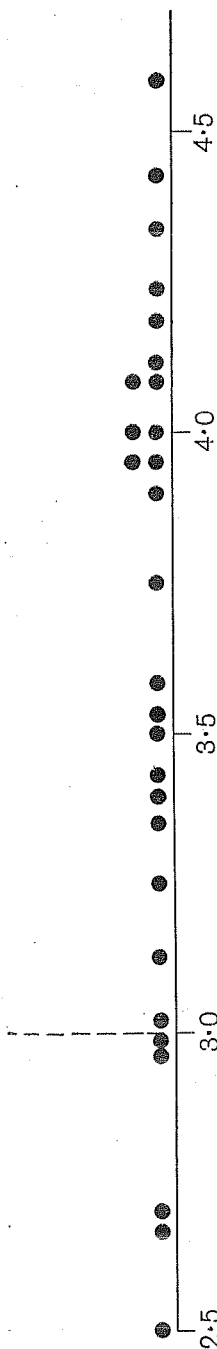


Fig. 2. Showing the distribution of the D/R ratios for the "marbled" families given in Table IV. Family 71 of 1922, with a ratio 6.21 : 1, has been omitted.

self-fertilised plants in which the recessive is automatically eliminated, we must suppose that the row of "Helen Pierce" raised in 1917 was derived in direct line from the plant in which the mutation appeared—a most unlikely supposition having regard to the normal practices of seedsmen. Moreover, an examination of Table V lends no support to the view that the families fall into two groups with respect to the proportion of recessives. With two exceptions these proportions are all low, though in varying degree. So far as the facts go I do not think we can say more than that, for some unknown reason, the marbled plants were less viable in the conditions under which they were grown. I have frequently noticed that in  $F_2$  families where the plants tend to be crowded the smaller and later flowering ones show a proportion of recessives above

TABLE V.

Ref. No.	$Ex\ 100^1$			Ref. No.	$Ex\ 100^2$			Ref. No.	$Ex\ 100^3$		
	$F_3$	$f_3$	$D/R$		$F_3$	$f_3$	$D/R$		$F_3$	$f_3$	$D/R$
72	120	32	3.75	8	109	32	3.40	2	202	49	4.08
73	58	11	5.27	9	43	12	3.58	3	113	33	3.42
124	102	25	4.08	10	87	26	3.35	4	58	11	5.36
131	66	23	2.87	11	83	21	3.95	5	76	17	4.47
132	20	7	2.86	12	109	31	3.51	6	83	21	3.95
133	29	8	3.62	66	43	14	3.07	7	25	6	4.17
				67	42	9	4.66	69	71	22	3.23
				68	36	4	9.00	71	39	9	3.33

the normal. This is especially the case with marbled ( $f_3$ ), smooth ( $d_4$ ) and Spencer ( $h$ ). It suggests that the recessive is in some cases, and for some unknown reason, inherently weaker, but at present we can attach nothing precise to the statement.

The evident deficiency of recessives in certain cases led me to tabulate the data for the eighteen pairs of characters used, and these are given in Table VI. In three cases ( $a_1$ ,  $b_1$ ,  $g_1$ ) the recessives are in slight preponderance; in three other cases ( $a_2$ ,  $d_5$ ,  $f_1$ ) the figures accord almost exactly with the expected 3:1 ratio; and in the remaining twelve the proportion of dominants ranges from 3.07 to 3.57. When these proportions are considered in connection with the ages of the recessives involved a point of some interest emerges. Though in most cases we cannot fix the exact date at which a given recessive was first recorded we have evidence for a rough classification of the order of appearance. Of those used in these experiments, red ( $a_1$ ) and whites ( $g_1$ ,  $f_1$ )<sup>1</sup> are

<sup>1</sup> Probably the earliest white was the *C*-white ( $g_1$ ), but we know that Emily Henderson ( $f_1$ ) was certainly grown last century.

among the earliest known varieties, being recorded before 1750. Also we know that the light axil ( $b_1$ ) occurs in the wild state (Bateson and Punnett, 1908, p. 16). Picotee ( $d_5$ ) again is among the earliest of the colour varieties. Round pollen ( $a_2$ ) is in all probability a fairly early mutation, since it was in the old white variety, "Emily Henderson," that it was first found (Bateson and Punnett, 1905, p. 80). In other words, of the six cases where the proportion of recessives is highest, four, viz.  $a_1$ ,  $b_1$ ,  $g_1$ ,  $d_5$ , are the oldest mutations in the series, while the other two ( $a_2$ ,  $f_1$ ) are certainly as old as, and possibly older than, any of the rest used.

We may now turn to those mutations which are known to be of recent origin. Two of these originated in the Cambridge experiments, viz. copper ( $g_2$ ) (about 1905) and cretin ( $b_3$ ) in 1907. Acacia ( $d_1$ ) was

TABLE VI.

	Recessive	Total	D	R	Ratio D/R	No. of families	Av. per family
$A_1-a_1$	Red	17,400	12,980	4420	2.93 : 1	167	104
$A_2-a_2$	Round	8,767	6,592	2175	3.03 : 1	114	77
$A_3-a_3$	Hood	11,978	9,036	2942	3.07 : 1	119	100
$B_1-b_1$	Light	18,594	13,906	4688	2.97 : 1	157	118
$B_2-b_2$	Sterile	18,924	14,235	4689	3.03 : 1	140	135
$B_3-b_3$	Cretin	1,934	1,493	441	3.38 : 1	20	96
$D_1-d_1$	Acacia	13,192	9,983	3209	3.11 : 1	108	121
$D_2-d_2$	Blue	8,373	6,351	1972	3.22 : 1	80	104
$D_4-d_4$	Smooth	11,779	8,969	2810	3.19 : 1	98	120
$D_5-d_5$	Picotee	11,181	8,394	2787	3.01 : 1	67	167
E-e	Cupid	5,179	3,908	1271	3.07 : 1	59	88
$F_1-f_1$	White	3,582	2,689	893	3.01 : 1	67	53
$F_2-f_2$	Bush	5,555	4,234	1321	3.20 : 1	52	107
$F_3-f_3$	Marbled	7,305	5,735	1570	3.57 : 1	74	99
$G_1-g_1$	White	9,557	7,101	2456	2.89 : 1	112	85
$G_2-g_2$	Copper	2,919	2,240	679	3.30 : 1	47	62
$G_3-g_3$	Mauve	4,790	3,668	1122	3.27 : 1	32	149
H-h	Spencer	4,978	3,832	1146	3.34 : 1	64	78

given to us in 1908 by Mr Unwin, the well-known raiser, while smooth ( $d_4$ ) was sent to me in 1912 by the late Mr T. H. Dipnall soon after he had found it. "Spencer" (h) was first shown in 1901 (Sydenham, 1910), and "Helen Pierce" ( $f_3$ ) in 1905. Of these six most recent mutations in Table VI four (viz.  $b_3$ ,  $f_3$ ,  $g_2$ , h) show the lowest proportion of recessives in the whole series, while the proportions for the other two ( $d_1$  and  $d_4$ ) are also on the low side.

The remaining six mutations ( $a_3$ ,  $b_2$ ,  $d_2$ , e,  $f_2$ ,  $g_3$ ) probably all originated between 1880 and 1899, and in certain cases the data collected by Sydenham (1910) enable us to fix the dates rather more precisely. "Waverley," a hooded form ( $a_3$ ), is recorded as having come out about 1886. The first real blue, "Navy Blue" ( $d_2$ ), made a sensational appearance

in 1899. "Cupid" first appeared in California in 1893, while one of the earliest lavenderes ( $g_3$ ), "Countess of Radnor," was brought out by Eckford in 1890. Steriles ( $b_2$ ) were first recorded in the Cambridge experiments in 1903 when they appeared as a normal recessive after a cross between Emily Henderson and Lady Penzance (Bateson and Punnett, 1905, p. 91). The origin of this mutation doubtless goes back to last century, but how far back it is impossible to say. I have been able to find no definite dated record of the first appearance of the bush sweet pea ( $f_2$ ), but it was certainly no novelty when we first grew it at Cambridge in 1905. As a group we may say that these six mutations come between the other two groups in point of time as they also do in respect of the proportion of recessives, which is lower than that of the earlier group, but higher than that of the later one.

Though the data as a whole certainly suggest that the viability of a recessive may be correlated with its age they are too few to make this more than a suggestion. I have brought the case forward in the hope that other workers with comparable data may find the point worth further investigation.

#### SUMMARY.

Extensive data are given on the crossing of eighteen pairs of characters in *Lathyrus odoratus*. As a result these eighteen pairs arrange themselves into five linkage groups and two unassociated characters. Since the haploid number of the chromosomes is seven, the data are in accordance with the chromosome theory. Attention is drawn to the frequency of deficiency of recessive characters in the  $F_2$  generation, and it is suggested that the degree of deficiency may possibly be correlated with the age of the recessive mutation in question, the youngest mutations showing the most marked deficiencies, and *vice versa*.

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TABLE VII.

The figures in italics represent the "ideal" series calculated by Kappert's method.

	Coupling series				Repulsion series			
	XY	Xy	xY	xy	XY	Xy	xY	xy
$A_1 \times B_1$	2514	776	775	313	3351	1109	1158	438
	<i>2472</i>	<i>818</i>	<i>817</i>	<i>271</i>	<i>3321</i>	<i>1139</i>	<i>1188</i>	<i>408</i>
$A_1 \times B_2$	4667	1467	1589	511	511	186	167	69
	<i>4660</i>	<i>1474</i>	<i>1596</i>	<i>504</i>	<i>506</i>	<i>191</i>	<i>172</i>	<i>64</i>
$A_1 \times B_3$	332	88	112	29	421	126	195	66
	<i>332</i>	<i>88</i>	<i>112</i>	<i>29</i>	<i>417</i>	<i>130</i>	<i>199</i>	<i>62</i>
$A_1 \times D_1$	1481	440	530	162	602	207	187	67
	<i>1478</i>	<i>443</i>	<i>533</i>	<i>159</i>	<i>601</i>	<i>208</i>	<i>188</i>	<i>66</i>
$A_1 \times D_2$	499	140	139	36	1798	552	636	197
	<i>501</i>	<i>138</i>	<i>137</i>	<i>38</i>	<i>1797</i>	<i>553</i>	<i>637</i>	<i>196</i>
$A_1 \times D_4$	721	220	184	71	621	223	261	79
	<i>712</i>	<i>229</i>	<i>193</i>	<i>62</i>	<i>629</i>	<i>215</i>	<i>253</i>	<i>87</i>
$A_1 \times D_5$	1936	577	629	258	625	221	184	50
	<i>1896</i>	<i>617</i>	<i>669</i>	<i>218</i>	<i>634</i>	<i>212</i>	<i>175</i>	<i>59</i>
$A_1 \times E$	110	26	39	8	189	62	56	19
	<i>111</i>	<i>25</i>	<i>38</i>	<i>9</i>	<i>189</i>	<i>62</i>	<i>56</i>	<i>19</i>
$A_1 \times F_2$	228	73	93	28	522	144	142	45
	<i>229</i>	<i>72</i>	<i>92</i>	<i>29</i>	<i>518</i>	<i>148</i>	<i>146</i>	<i>41</i>
$A_1 \times F_3$	—	—	—	—	1288	340	412	134
	—	—	—	—	<i>1273</i>	<i>355</i>	<i>427</i>	<i>119</i>
$A_1 \times G_2$	—	—	—	—	86	32	25	9
	—	—	—	—	<i>86</i>	<i>32</i>	<i>25</i>	<i>9</i>
$A_1 \times G_3$	216	54	72	30	—	—	—	—
	<i>209</i>	<i>61</i>	<i>79</i>	<i>23</i>	—	—	—	—
$A_1 \times H$	150	65	48	19	779	227	282	88
	<i>151</i>	<i>64</i>	<i>47</i>	<i>20</i>	<i>776</i>	<i>230</i>	<i>285</i>	<i>85</i>
$A_2 \times B_1$	2063	709	610	250	493	160	170	54
	<i>2040</i>	<i>732</i>	<i>633</i>	<i>227</i>	<i>494</i>	<i>159</i>	<i>169</i>	<i>55</i>
$A_2 \times D_1$	—	—	—	—	877	287	296	103
	—	—	—	—	<i>874</i>	<i>290</i>	<i>299</i>	<i>100</i>
$A_2 \times D_2$	—	—	—	—	369	109	115	40
	—	—	—	—	<i>366</i>	<i>112</i>	<i>118</i>	<i>37</i>
$A_2 \times D_4$	—	—	—	—	997	329	345	112
	—	—	—	—	<i>998</i>	<i>328</i>	<i>344</i>	<i>113</i>
$A_2 \times D_5$	1076	364	364	133	332	122	110	37
	<i>1071</i>	<i>369</i>	<i>369</i>	<i>128</i>	<i>334</i>	<i>120</i>	<i>108</i>	<i>39</i>
$A_2 \times F_1$	1406	462	440	141	—	—	—	—
	<i>1408</i>	<i>460</i>	<i>438</i>	<i>143</i>	—	—	—	—
$A_2 \times F_2$	677	242	232	71	—	—	—	—
	<i>683</i>	<i>236</i>	<i>226</i>	<i>77</i>	—	—	—	—
$A_2 \times F_3$	—	—	—	—	514	137	164	31
	—	—	—	—	<i>522</i>	<i>129</i>	<i>156</i>	<i>39</i>
$A_2 \times G_1$	1327	477	456	145	307	89	78	22
	<i>1337</i>	<i>467</i>	<i>446</i>	<i>155</i>	<i>307</i>	<i>89</i>	<i>78</i>	<i>22</i>
$A_2 \times G_3$	—	—	—	—	124	42	47	16
	—	—	—	—	<i>124</i>	<i>42</i>	<i>47</i>	<i>16</i>
$A_2 \times H$	—	—	—	—	109	24	41	13
	—	—	—	—	<i>107</i>	<i>26</i>	<i>43</i>	<i>11</i>
$A_3 \times B_1$	792	258	260	68	1478	547	497	173
	<i>801</i>	<i>249</i>	<i>251</i>	<i>77</i>	<i>1485</i>	<i>540</i>	<i>490</i>	<i>180</i>
$A_3 \times B_2$	1289	408	428	127	1100	388	356	101
	<i>1294</i>	<i>403</i>	<i>423</i>	<i>132</i>	<i>1114</i>	<i>374</i>	<i>342</i>	<i>115</i>
$A_3 \times B_3$	—	—	—	—	145	42	45	20
	—	—	—	—	<i>141</i>	<i>46</i>	<i>49</i>	<i>16</i>

TABLE VII (cont.).

	Coupling series				Repulsion series			
	XY	Xy	xY	xy	XY	Xy	xY	xy
$A_3 \times D_1$	1865 <i>1845</i>	599 <i>619</i>	593 <i>613</i>	225 <i>205</i>	—	—	—	—
$A_3 \times D_2$	399 <i>404</i>	149 <i>144</i>	129 <i>124</i>	39 <i>44</i>	—	—	—	—
$A_3 \times D_4$	1589 <i>1577</i>	476 <i>488</i>	484 <i>496</i>	165 <i>153</i>	682 <i>686</i>	236 <i>232</i>	228 <i>224</i>	71 <i>75</i>
$A_3 \times D_5$	1591 <i>1580</i>	509 <i>520</i>	524 <i>535</i>	187 <i>176</i>	1173 <i>1142</i>	396 <i>427</i>	396 <i>427</i>	144 <i>113</i>
$A_3 \times E$	96 <i>93.5</i>	21 <i>23.5</i>	26 <i>28.5</i>	10 <i>7.5</i>	325 <i>330</i>	106 <i>101</i>	105 <i>100</i>	25 <i>30</i>
$A_3 \times F_1$	203 <i>200</i>	68 <i>71</i>	57 <i>60</i>	24 <i>21</i>	—	—	—	—
$A_3 \times F_2$	176 <i>178</i>	69 <i>67</i>	76 <i>74</i>	27 <i>29</i>	676 <i>678</i>	235 <i>233</i>	233 <i>231</i>	78 <i>80</i>
$A_3 \times F_3$	628 <i>622</i>	140 <i>146</i>	184 <i>190</i>	50 <i>44</i>	—	—	—	—
$A_3 \times G_1$	1158 <i>1166</i>	422 <i>414</i>	398 <i>390</i>	131 <i>139</i>	1193 <i>1214</i>	467 <i>446</i>	402 <i>381</i>	119 <i>140</i>
$A_3 \times G_2$	117 <i>119</i>	39 <i>37</i>	62 <i>60</i>	16 <i>18</i>	490 <i>495</i>	152 <i>147</i>	154 <i>149</i>	40 <i>45</i>
$A_3 \times G_3$	648 <i>648</i>	194 <i>194</i>	198 <i>198</i>	60 <i>60</i>	—	—	—	—
$A_3 \times H$	36 <i>37</i>	20 <i>19</i>	13 <i>12</i>	5 <i>6</i>	168 <i>161</i>	32 <i>39</i>	45 <i>52</i>	19 <i>12</i>
$B_1 \times D_1$	1037 <i>1043</i>	345 <i>339</i>	335 <i>329</i>	100 <i>106</i>	1138 <i>1137</i>	369 <i>370</i>	397 <i>398</i>	130 <i>129</i>
$B_1 \times D_2$	1148 <i>1147</i>	403 <i>404</i>	390 <i>391</i>	138 <i>137</i>	99 <i>101.5</i>	24 <i>21.5</i>	33 <i>30.5</i>	4 <i>6.5</i>
$B_1 \times D_4$	243 <i>242</i>	82 <i>83</i>	81 <i>82</i>	29 <i>28</i>	2821 <i>2834</i>	915 <i>902</i>	988 <i>975</i>	298 <i>311</i>
$B_1 \times D_6$	1759 <i>1761</i>	580 <i>578</i>	650 <i>648</i>	211 <i>213</i>	2337 <i>2332</i>	773 <i>778</i>	774 <i>779</i>	261 <i>256</i>
$B_1 \times E$	442 <i>435</i>	134 <i>141</i>	155 <i>162</i>	60 <i>53</i>	441 <i>436</i>	132 <i>137</i>	130 <i>135</i>	48 <i>43</i>
$B_1 \times F_2$	763 <i>756</i>	250 <i>257</i>	280 <i>287</i>	104 <i>97</i>	447 <i>448</i>	151 <i>150</i>	142 <i>141</i>	47 <i>48</i>
$B_1 \times F_3$	182	—	56	—	569	—	196	—
		(+56 marbled)				(+229 marbled)		
$B_1 \times G_1$	—	—	—	—	486	(white)	156	(white)
$B_1 \times G_2$	189 <i>190</i>	58 <i>57</i>	59 <i>58</i>	16 <i>17</i>	940 <i>938</i>	283 <i>285</i>	339 <i>341</i>	106 <i>104</i>
$B_1 \times G_3$	1274 <i>1288</i>	418 <i>404</i>	435 <i>421</i>	118 <i>132</i>	—	—	—	—
$B_1 \times H$	118 <i>118</i>	33 <i>33</i>	39 <i>39</i>	13 <i>13</i>	1198 <i>1197</i>	335 <i>336</i>	393 <i>394</i>	111 <i>110</i>
$B_2 \times D_1$	200 <i>204</i>	75 <i>71</i>	62 <i>58</i>	16 <i>20</i>	1889 <i>1875</i>	636 <i>650</i>	668 <i>682</i>	250 <i>236</i>
$B_2 \times D_2$	485 <i>480</i>	128 <i>133</i>	153 <i>158</i>	48 <i>43</i>	543 <i>534</i>	175 <i>184</i>	155 <i>164</i>	66 <i>57</i>
$B_2 \times D_4$	689 <i>679</i>	209 <i>219</i>	216 <i>226</i>	82 <i>72</i>	2154 <i>2131</i>	643 <i>666</i>	748 <i>771</i>	264 <i>241</i>
$B_2 \times D_5$	1162 <i>1154</i>	367 <i>375</i>	348 <i>356</i>	123 <i>115</i>	1297 <i>1320</i>	473 <i>450</i>	465 <i>442</i>	127 <i>150</i>
$B_2 \times E$	39 <i>39</i>	11 <i>11</i>	10 <i>10</i>	3 <i>3</i>	800 <i>790</i>	255 <i>265</i>	238 <i>248</i>	93 <i>83</i>
$B_2 \times F_1$	—	—	—	—	225 <i>223</i>	74 <i>76</i>	78 <i>80</i>	28 <i>26</i>

TABLE VII (cont.).

	Coupling series				Repulsion series			
	XY	Xy	xY	xy	XY	Xy	xY	xy
$B_2 \times F_2$	—	—	—	—	774	210	248	70
					772	212	250	68
$B_2 \times F_3$	—	—	—	—	1313	326	444	127
					1303	336	454	117
$B_2 \times G_1$	813	246	201	76	444	161	157	54
	806	253	208	69	446	159	155	56
$B_2 \times G_2$	—	—	—	—	676	199	215	68
					675	200	216	67
$B_2 \times G_3$	2426	771	813	234	142	39	39	15
	2440	757	799	248	140	41	41	13
$B_2 \times H$	335	71	122	31	978	284	286	93
	332	74	125	28	972	290	292	87
$B_3 \times D_1$	94	25	15	2	385	130	105	42
	95	24	14	3	381	134	109	38
$B_3 \times D_5$	—	—	—	—	249	71	75	36
					240	80	84	27
$B_3 \times G_1$	—	—	—	—	32	10	13	4
					32	10	13	4
$B_3 \times G_2$	—	—	—	—	54	16	26	4
					56	14	24	6
$D_1 \times E$	—	—	—	—	177	56	56	24
					173	60	60	20
$D_1 \times F_1$	—	—	—	—	163	68	60	20
					165	66	58	22
$D_1 \times F_2$	297	67	96	34	1119	377	358	113
	290	74	103	27	1123	373	354	117
$D_1 \times F_3$	1978	513	651	173	766	230	229	72
	1975	516	654	170	764	232	231	70
$D_1 \times G_1$	—	—	—	—	1519	539	480	168
					1520	538	479	169
$D_1 \times G_2$	—	—	—	—	80	18	31	11
					78	20	33	9
$D_1 \times G_3$	355	102	114	36	588	177	184	55
	355	102	114	36	588	177	184	55
$D_1 \times H$	—	—	—	—	463	117	111	38
					457	123	117	32
$D_3 \times E$	—	—	—	—	392	126	91	35
					389	129	94	32
$D_3 \times F_1$	195	(white)	70	(white)	—	—	—	—
$D_3 \times F_2$	—	—	—	—	193	43	52	12
					193	43	52	12
$D_3 \times F_3$	1958	576	573	177	—	—	—	—
	1953	581	578	172	—	—	—	—
$D_3 \times G_1$	—	—	—	—	647	(white)	217	(white)
$D_3 \times G_2$	—	—	—	—	624	173	168	64
					613	184	179	53
$D_3 \times H$	—	—	—	—	67	20	18	5
					67	20	18	5
$D_4 \times E$	—	—	—	—	214	63	86	19
					217	60	83	22
$D_4 \times F_1$	—	—	—	—	314	105	91	28
					315	104	90	29
$D_4 \times F_2$	44	8	18	2	1327	427	448	131
	45	7	17	3	1334	420	441	133
$D_4 \times F_3$	1105	331	352	84	861	219	270	58
	1118	318	339	97	867	213	264	64
$D_4 \times G_1$	—	—	—	—	1046	350	295	111
					1039	357	302	104

TABLE VII (cont.).

	Coupling series				Repulsion series			
	XY	Xy	xY	xy	XY	Xy	xY	xy
D <sub>4</sub> × G <sub>2</sub>	1116 1119	333 330	360 357	102 105	174 178	59 55	63 59	15 19
D <sub>4</sub> × G <sub>3</sub>	—	—	—	—	1182 1190	367 359	392 383	108 116
D <sub>4</sub> × H	—	—	—	—	168 163	45 50	44 49	20 15
D <sub>5</sub> × E	—	—	—	—	188 190	53 51	69 67	17 19
D <sub>5</sub> × F <sub>2</sub>	1494 1498	504 500	500 496	161 165	—	—	—	—
D <sub>5</sub> × F <sub>3</sub>	314 319	105 100	103 98	25 30	528 519	133 142	154 163	53 44
D <sub>5</sub> × G <sub>1</sub>	391	(white)	154	(white)	416	(white)	134	(white)
D <sub>5</sub> × G <sub>3</sub>	—	—	—	—	452 451	138 139	146 147	46 45
D <sub>5</sub> × H	—	—	—	—	133 134	24 23	45 44	7 8
E × F <sub>2</sub>	—	—	—	—	581 568	135 148	158 171	58 45
E × F <sub>3</sub>	70 68	14 16	18 20	7 5	57 57	10 10	20 20	3 3
E × G <sub>1</sub>	332 338	129 123	126 120	38 44	360 353	127 134	104 111	49 42
E × G <sub>2</sub>	77 75	12 14	10 12	4 2	46 43.5	18 20.5	11 13.5	9 6.5
E × G <sub>3</sub>	—	—	—	—	666 674	220 212	235 227	64 72
E × H	426 428	128 126	129 127	36 38	413 411	111 113	140 142	41 39
F <sub>1</sub> × H	—	—	—	—	132 134	50 48	46 44	13 15
F <sub>2</sub> × G <sub>1</sub>	108 110	40 38	49 47	14 16	428 432	147 143	123 119	35 39
F <sub>2</sub> × G <sub>3</sub>	—	—	—	—	314 318	103 99	103 99	27 31
F <sub>2</sub> × H	—	—	—	—	152 155	36 33	61 58	10 13
F <sub>3</sub> × G <sub>1</sub>	—	—	—	—	102	(white)	29	(white)
F <sub>3</sub> × G <sub>2</sub>	—	—	—	—	501 500	142 143	130 131	38 37
F <sub>3</sub> × G <sub>3</sub>	—	—	—	—	599 596	176 179	173 176	56 53
F <sub>3</sub> × H	—	—	—	—	33 33	7 7	11 11	3 3
G <sub>1</sub> × H	178 172	31 37	35 41	15 9	86 89	34 31	34 31	8 11
G <sub>2</sub> × H	—	—	—	—	172 174	66 64	61 59	20 22
G <sub>3</sub> × H	—	—	—	—	646 635	185 196	192 203	74 63