LINKAGE IN THE SWEET PEA (*LATHYRUS ODORATUS*).

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(With Six Text-figures and Plate III.)

CONTENTS.

INTRODUCTION.

THE data discussed in this paper have accumulated in the past 19 years. During the earlier part of this period, 1904–1909, Mr Bateson and I were working more especially upon what we then termed "coupling and repulsion" in sweet peas. The discovery of groups of characters shewing this phenomenon of linkage suggested that a further study of the subject was likely to be of interest in connection with the much discussed possibility of the location of genetic factors in the chromosomes. Though we failed to devise any explanation of linkage in terms of chromosomes, and eventually put forward the hypothesis of "reduplication," we felt nevertheless that a thorough analysis of the sweet pea ought to be undertaken. The object of this analysis was to decide whether the number of characters, or groups of characters, shewing independent inheritance was greater, equal to, or less than the haploid number of the chromosomes.

At the time we decided to undertake this analysis we had, in addition to the characters belonging to the two linkage groups already found, several others of which the simple recessive nature had been demonstrated. And we knew also of further characters which promised to be of assistance in the undertaking. Moreover we had ascertained from Mr R. P. Gregory that the haploid number in *Lathyrus* was almost certainly 7, a point eventually confirmed by Winge in 1918. In 1909 Mr Bateson left Cambridge, and the continuation of the sweet pea work devolved upon me. Soon after this the advent of *Drosophila* brought a definite answer to the question we had set out to attack. The brilliant researches of Morgan and his colleagues shewed beyond a doubt that the number of the linkage groups was in this case the same as the haploid number of the chromosomes. Though for many the matter appeared to be finally settled, I decided to carry on with the programme of the sweet pea work, especially as it seemed at one time not unlikely that the number of independent groups of characters might prove to be greater than that of the chromosomes. But during the past summer several fresh linkages were discovered, and although the number of apparently independent groups at present stands at 8, the data available are not in all cases sufficient to preclude the possibility of a low grade of linkage* between certain of them. Some of these I expect to test further in the near future; and I have also started experiments with other characters which I hope to work into the general scheme. Some years must, however, elapse before I can accumulate the necessary data, and I feel that the present juncture is a convenient one for taking stock of the position. Though the question we set out to answer cannot be regarded as finally settled, I have nevertheless come to the opinion that the number of linkage groups in *Lathyrus* will eventually be found to correspond to the haploid number of the chromosomes.

Material.

The account given below deals with seventeen pairs of characters shewing normal Mendelian inheritance, of which ten have already been described in earlier papers. In the following notes on these characters I have adopted a system of symbols differing from that previously used. The factors in the same linkage group are now denoted by the same letter, the separate factors being distinguished by a numeral. Thus **A**^{1}, **A**^{2}, **A**^{3} are three distinct factors shewing linkage with one another, while **B**^{1}, **B**^{2}, **B**^{3} are also three factors in the same linked system. But, so far as is known, no member of the **A** series shews linkage with any member of the **B** series. In each case the dominant character of the pair is given first.

(1) Purple, **A**^{1}—Red, **a**^{1} (= **B**—**b** of earlier papers). This was one of the first pair of characters worked with. There are, of course, numerous

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* I.e. where the number of the crossovers is nearly as great as the number of the non-crossovers.

shades of purples, corresponding to each of which is a shade of red. Owing to the fact that some of the other factors used are modifiers of flower colour I have rarely made use of any but deep colours. In these the dominance of purple, as judged by the eye, is complete, and it is not possible by inspection to distinguish the homozygous from the heterozygous individuals.

(2) Long pollen, A^2—round pollen, a^2 (= L—l of earlier papers).

(3) Erect standard, A^3—hooded standard, a^3 (= E—e of earlier papers).

(4) Dark axil, B^1—light axil, b^1 (= D—d of earlier papers). Though usually quite distinct and easily classified, the dark axil is relatively pale where the flower colour is blue or blue-red. With care, however, I have not found these cases to present any difficulty.

(5) Fertile anthers, B^2—sterile anthers, b^2 (= F—f of earlier papers).

(6) Normal flower, B^3—cretin flower, b^3 (= N—n of earlier papers).

(7) Tall, E—Cupid e (= T—t of earlier papers).

(8) Colour, F^1—*R*-white f^1 (= C—c of earlier papers). This is the white originally found in Emily Henderson with round pollen. That association was, doubtless, accidental. In our explanation of the appearance of the reversionary purples from a cross between the white Emily Henderson with round pollen, and the white Emily Henderson with long pollen, we denoted the two postulated complementary factors by C and R. Hence the use of the terms "*R*-white" and "*C*-white" (cf. (10) below). For by "*R*-white" we denoted the white which carried the factor R, and by "*C*-white" the white, viz. Emily Henderson with long pollen, which carried the factor C.

(9) Procumbent, F^2—bush, f^2 (= P—p of earlier papers).

(10) Colour, G^1—*C*-white, g^2 (= R—r of earlier papers).

All of the above ten pairs of characters have already been described in one or other of Reports I—IV of the Evolution Committee to the Royal Society. The remaining seven pairs, of which brief notes are now given, have not hitherto been mentioned in the course of this work.

(11) Hairy, C—glabrous, c. This glabrous form I owe to the kindness of Mr T. H. Dipnall, who found it in his cultures and was good enough to send me some seed. The stems are quite smooth, lacking the short stiff hairs which give a rough feel to the stem of the normal sweet pea. The difference is most noticeable in the very young pods, which, in this variety, are devoid of the silky hairs so characteristic of the

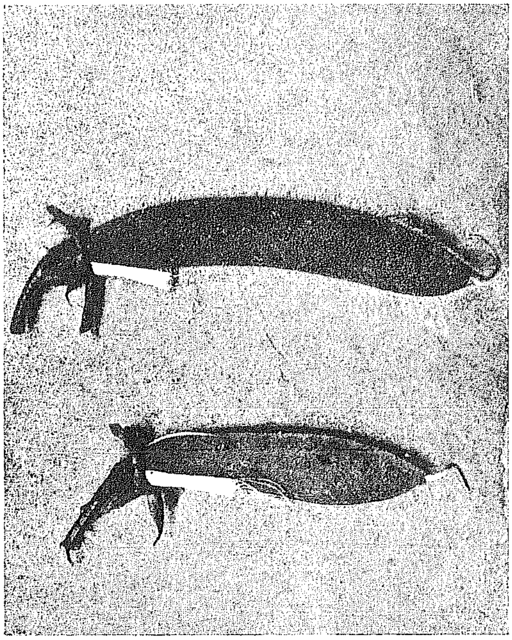

Fig. 1. Two immature pods, the upper hairy, and the lower glabrous.

Fig. 3. Small plant of form intermediate between tendrillar and acacia forms.

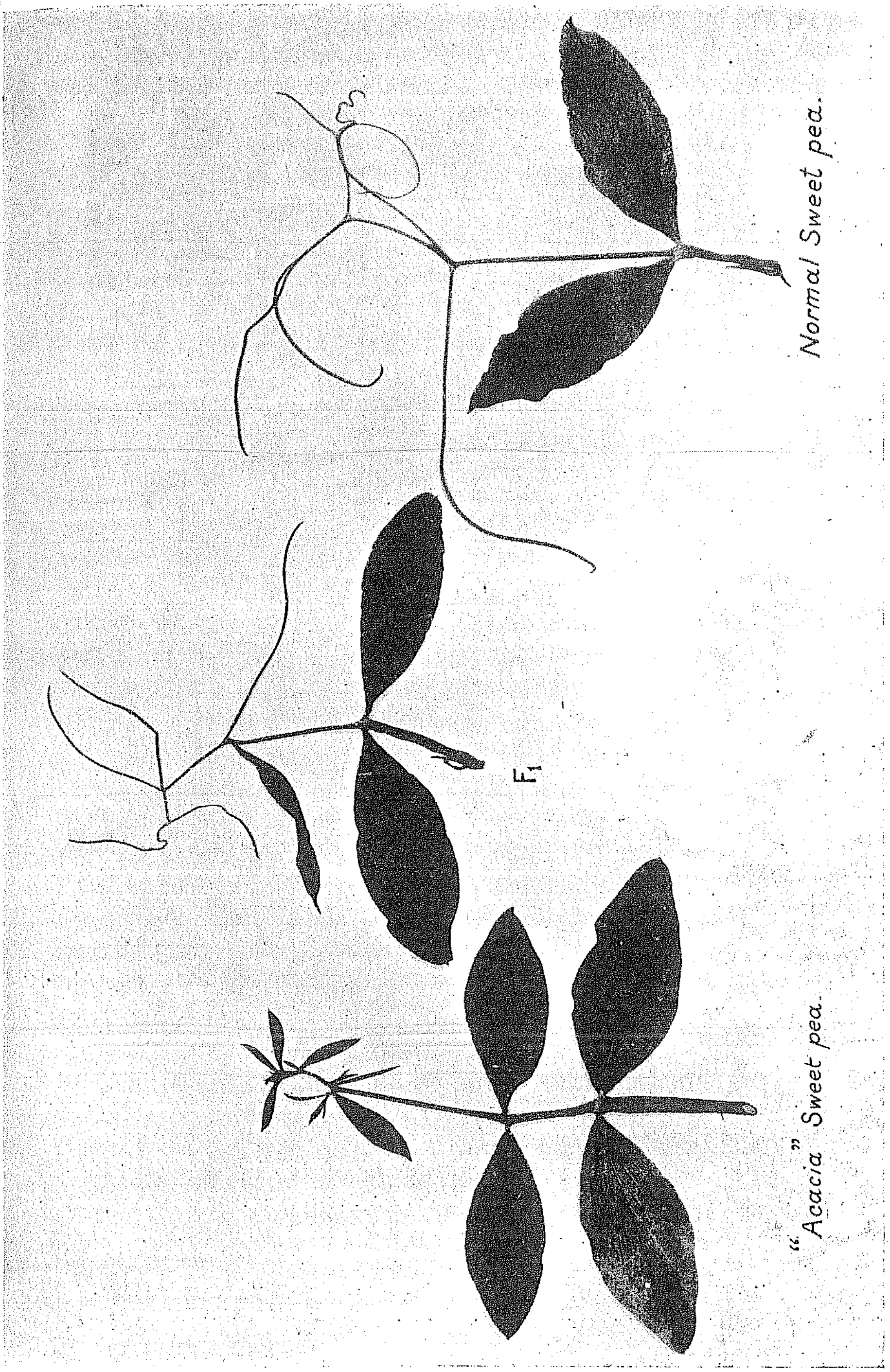

Fig. 2.

normal form. The glabrous character of the pod remains a striking feature throughout its growth (cf. Fig. 1). Glabrousness proved to be a simple recessive, and, being a structural feature, has proved of great service in the experiments.

(12) Tendril, D^1—acacia, d^1. The acacia-leaved sweet pea was originally found by Mr Unwin, the well known expert on sweet peas, and was first grown by us in 1909 from seed which he kindly gave us. As illustrated in Fig. 2 its peculiar feature consists in the place of the tendrils being taken by leaflets. So far as my experience goes, the lack of tendrils is complete, for I have examined considerably over a thousand of these plants without finding any that shewed a tendril. The case is of some interest as being one of the few found in *Lathyrus* in which dominance is generally incomplete. F_1 plants from acacia × tendril have always shewn an occasional leaflet replacing a tendril (cf. Fig. 2), while in F_2, besides normal tendrils and acacias, intermediates of various grades generally occur. But in all of these various intermediates I have never seen any of the tendrils beyond the basal pair transformed into leaflets. In a low grade intermediate, such as a normal F_1 plant, only an occasional basal tendril is transformed: in a high grade intermediate most of the pairs of basal tendrils throughout the plant are transformed into leaflets (cf. Fig. 3). Such high grade intermediates I have found always to be heterozygotes, throwing tendrillar plants, high grade intermediates and acacias in the ratio 1 : 2 : 1. In such families the tendrillar plants nearly always shew an occasional extra leaflet. From this, and from other experiments, I think it probable that in this case we are probably concerned with two factors. Where we have the clear cut 1 : 2 : 1 ratio we may suppose that we are concerned with a factor T, Tt plants being high grade intermediates, and tt plants acacias. To explain the other grades of intermediates we may postulate the existence of a factor, I, which intensifies the tendrillar character when T is present, but has no effect upon the acacia itself. Normal pure tendrillar plants contain both T and I. Hence the low grade intermediates in F_1, as well as the range of intermediates in F_2. At this stage, however, I do not wish to insist upon this interpretation. The point of importance here is that the full acacia is always unmistakeable, and always behaves as a simple recessive, whatever the grade, or grades, of the accompanying intermediate heterozygous forms.

(13) Bright flower colour, D^2—dull flower colour, d^2. To the bright series belong the normal purples and reds, those of the corresponding

recessive dull series being blues and blue-reds. In the deeper colours the bright and dull series are perfectly distinct. A blue such as "Lord Nelson[*]" is the dull form of the deep purple recorded in our earlier experiments as "Duke of Sutherland[†]," which itself is the hooded form of *Ppw*[‡] (= purple with purple wings). Among the reds the two series are equally distinct, the bright red formerly known as "Miss Hunt[§]" being represented in the dull series by the type shewn on Pl. III, fig. 5. It should be mentioned that this pinkish mauve colour can be closely matched by plants which are genetically purples For instance the F_1 ex "Countess Radnor" × "Barbara" is not dissimilar, though both of these belong to the bright series, and "Countess Radnor" is genetically a purple. But such cases of resemblance are only to be found among the paler forms of purple: in the deeper colours, which alone have been made use of in these experiments, the distinction between the bright and the dull series is never in doubt.

(14) Self-coloured, F^3—marbled, f^3. Corresponding to each self-coloured form is a recessive one in which the colour is broken up by finely divided white "marbling." The general appearance of these marbled forms is well shewn on Pl. III, figs. 1—4, which represent the marbled forms of blue, red, deep purple, and blue-red respectively. The blue marbled (Fig. 1) corresponds closely with the horticultural variety known as "Helen Pierce," in which form the marbled character was originally introduced into these experiments. The marble form must not be confused with the flaked sweet peas such as "Senator" or "America." The older flowers on a marbled plant often display coarser and more blotchy markings, which can be closely paralleled by flowers from the flaked varieties. There is however a constant point of difference between the two, for in a marbled form the keel and the under surface of the wings are white, while in a flaked form these structures always shew some colour, at any rate in the darker shades with which alone I have worked.

Another peculiar feature of the marbled form is that it always shews the light axil. It can, however, carry the dark axil, as I have proved by a series of appropriate crosses. In this respect it resembles the two forms of white ((8) and (10)).

An interesting feature in the genetics of marbled is its relation to

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[*] Figured in *Journal of Genetics*, Vol. XII. Pl. XXI, fig. 3.

[†] Figured in Bateson's *Mendel's Principles of Heredity*, Pl. V, fig. 8.

[‡] Figured in *Mendel's Principles of Heredity*, Pl. V, fig. 7.

[§] Figured in *Mendel's Principles of Heredity*, Pl. V, fig. 9.

R-white. The three forms, self-coloured, marbled, and *R*-white must be regarded as forming an allelomorphic series. Marbled × *R*-white has always given a marbled F_1, even when the *R*-white used came from a family in which all the coloured members were self-coloured. Again, self-coloured plants that throw *R*-whites do not throw marbled, while those that give marbled do not give any *R*-whites. It is the only example of what has been termed a multiple allelomorphic series that I have hitherto met with in the sweet pea.

When crossed with *C*-white, extracted from self-coloured, the marbled form gives a self-coloured F_1, and the F_2 generation contains both marbled and whites. A further point of interest is found here, in that the marbled which throws *C*-white is paler than the homozygous marbled form. This would appear to be another instance of a definite heterozygous form in the sweet pea (cf. p. 106).

(15) Purple, G^2—red-purple, g^2. This pair of characters has been dealt with at length in an illustrated account recently published in Vol. XII. of this Journal. Some further notes in connection with it are given under (17) below.

(16) Clamped keel, H—open keel, h. The clamped keel is the ordinary form (Fig. 4*a*) found in the wild sweet pea and in all forms with the non-waved type of standard, whether it be erect or hooded.

(*a*) (*b*)

Fig. 4. Diagrammatic representation of clamped keel (*a*), and open keel (*b*).

The open keel is characteristic of the more modern type of flower with the waved or "Spencer" standard. It is markedly less curved (Fig. 4*b*) than in the clamped type; its free edges are rather waved, and not in close contact with one another; and, finally, it does not press closely against the stigma along its curvature, as is the case in the clamped form. The distinction between the clamped and open keel is in reality that between the non-waved and the waved standard. The waving of the standard is however subject to a great deal of variation, and it is not always easy to distinguish the waved from the non-waved by the appearance of the standard alone. I have, however, never found any difficulty in the case of the keels, the distinction between open and clamped being quite sharp in the flower that is fully out.

(17) Purple, B^4—maroon, b^4. The type of maroon referred to here is that found in the variety "Dobbie's maroon," which was exhibited as a seedling at the Chelsea Show of 1919. In my experience it behaves as a recessive to deep purple. It is of interest in connection with the Purple-red-purple pair, as will appear from the following notes. After I had obtained a pure strain of red-purple, I crossed it among other things with "Robert Sydenham," to test for possible linkage in the shape of the keel. In the F_2 generation, in 1918, appeared the "Spencer" form of red-purple. It was a novel and striking form, and I decided to fix it in the normal way, by growing on an F_3 generation in 1919. It was therefore interesting to find Messrs Dobbie and Co. bringing out as a novelty in that year what appeared to be a form identical with that which had arisen in the course of my experiments. In 1920 I grew "Dobbie's Maroon" side by side with my own Spencerised red-purple. The growth in "Dobbie's Maroon" was a trifle more free, the stems, pedicels, and foliage a shade less dusky, and the flower-colour not quite so fiery. But the differences were slight, and the two forms would almost certainly have been regarded by experts as "too much alike" varieties. Yet genetically they are totally distinct, though I did not find this out until later. In 1920 a cross was made between "Dobbie's Maroon" and violet*, which is the dull (or "blue") form of red-purple. Had "Dobbie's Maroon" been genetically similar to red-purple, this cross should have given a red-purple in F_1, and in F_2 red-purples and violets in the ratio 3 : 1. Actually the F_1 plants were normal purples, though with a distinctly reddish hue. In F_2 appeared, besides red-purples and violets, various shades of purple, including some like the F_1 plants, and some ordinary hooded purples similar in shade to the old-fashioned "Duke of Sutherland." There also appeared some normal blues. The F_2 generation was a small one, some 50—60 plants only, and the analysis has not been pushed further. It is clear however that maroon and red-purple, though practically identical in appearance, differ from the normal purple in distinct factors. I have also found that from "Dobbie's Maroon" × R-white some creams appear in F_2, though I have never met with these from red-purple crossed with either C-white or R-white. Maroon is probably rather a duller form than red-purple, but in "Dobbie's Maroon" the yellow plastids of the cream basis brighten it up, so that it comes to look

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* Illustrated on Pl. XXI, fig. 2 in Vol. XII. of this Journal.

very like a red-purple with colourless plastids. The genetical distinction between maroon and red-purple is further emphasised by the fact that they belong to different linkage systems. For red-purple shews linkage relations with the *C*-white, while maroon is linked with axil-colour.

Linkage Groups.

So far five different linkage groups have been definitely detected, and the evidence for their existence may now be given.

A. Under this letter are collected the three pairs of characters: Purple-red (A^1), long-round pollen (A^2), and erect-hooded standard (A^3), for the linkage relations of which evidence has already been given in earlier papers*. That between A^1 and A^3 is very close, in the neighbourhood of 1 °/$_0$ of crossovers. The number of crossovers between A^1 and A^2 is about 12 °/$_0$ (cf. Haldane, 1919, p. 294). Though there is little evidence one way or the other, it seems probable from such as exists, that A^1 lies between A^2 and A^3 on the chromosome†.

B. In this chromosome are found the factors for the dark (B^1) and light axil pair, for the fertile (B^2) and sterile anther pair, and for the normal shaped flower (B^3) and cretin pair. The data for these linkages have already been given elsewhere (*Journal of Genetics*, III. pp. 84 *seq.*), and it is probable that B^2 and B^3 are about 25 units apart on the chromosome, while B^1 lies about 6 units from B^2, between the latter and B ‡. That the purple-maroon pair is also found in this chromosome is evident from the following data. Maroon with light axil was crossed with *R*-white carrying purple and dark axil. F_1 was dark axilled purple, and the F_2 generation (No. 50/22) consisted of

Purple dark axil	99
„ light axil	19
Maroon dark axil	9
„ light axil	28
White	48

The figures point clearly enough to a linkage between maroon and light axil, but the numbers are too scanty and irregular to fix its value. Further experiments, too, are required before it is possible to fix the position of maroon in the B chromosome.

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[*] The most recent statement of this case will be found in *Journal of Genetics*, Vol. VI. p. 185 *seq.*

[†] See Bridges, 1914, p. 528, and Punnett, 1917, p. 189.

[‡] Bridges (1914) arrives at rather different values, but the point is here immaterial.

D. In 1919–20 a number of families from the cross between bright flowered acacia (d^1D^2) and dull (blue) flowered tendril (D^1d^2) gave bright flowered tendrils in F_1. The F_2 generation comprised a number of families distributed as follows among the four expected classes:

Bright flowered tendril ...	847
Dull " " ...	298
Bright flowered acacia ...	300
Dull " " ...	49

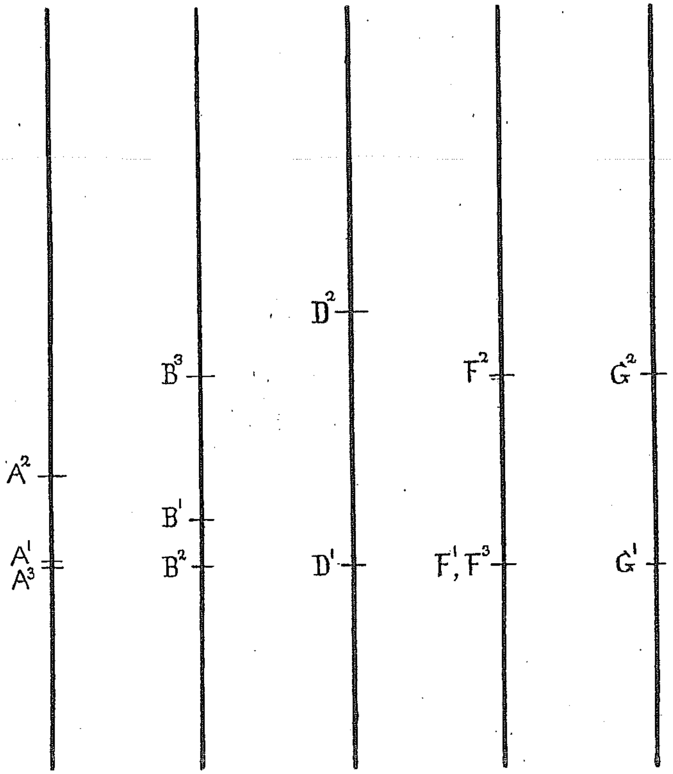

Fig. 5. Provisional map of the chromosomes for the five linkage groups hitherto identified. The figure shews only the relative, not the actual position on the chromosomes. B^2 for example may be either near the middle, or at the extreme end of the chromosome. Further data are required before the positions can be fixed more accurately.

The deficiency of the dull acacias suggested the possibility of a linkage between bright colour and acacia. Accordingly the reciprocal cross between bright tendril and dull acacia was made. F_1 was bright tendril as before, but F_2 consisted of

Bright tendril ...	424
Dull „ ...	99
Bright acacia ...	102
Dull „ ...	91

Evidently there is linkage, and the figures suggest that the number of crossovers is somewhere in the neighbourhood of 33 °/ₒ.

F. That R-white and marbled must, on the chromosome hypothesis, occupy the same locus, has already been pointed out. There is also evidence of linkage between R-white and bush. In 1905 a cross was made between the bush sweet pea and the ordinary procumbent cupid, both being white flowered. As recorded elsewhere (*Reports to the Evolution Committee of the Royal Society*, IV. p. 6), F_1 was tall purple. In F_2 appeared the expected segregation, bush cupids appearing as well as bush talls, while the ratio of coloured to whites was 9 : 7. Other experiments shewed that of the two parents the bush was to be regarded as the C-white, and the cupid as the R-white. The cross was therefore of the nature $\mathsf{g}^1\mathsf{F}^1\mathsf{f}^2$ (bush) × $\mathsf{G}^1\mathsf{f}^1\mathsf{F}^2$ (cupid). The F_2 generation consisted of the four following classes:

Coloured procumbent ...	130
„ bush	53
White procumbent ...	89
„ bush	24

The bush plants formed more than a quarter of those with coloured flowers—less than a quarter of those with white flowers.

This peculiar distribution was confirmed in the F_3 generation, where 4 families from parents heterozygous for both of the colour factors gave the following results:

		Coloured procumbent	Coloured bush	White procumbent	White bush
1908	No. 133	83	57	101	17
	,, 135	161	70	141	36
	,, 139	66	26	42	9
	,, 159	57	21	60	9

If it be supposed that bush and R-white shew linkage, and that the number of crossovers is about 25 °/ₒ (= repulsion on a 3 : 1 basis between

F^1 and F^2), then we should expect the four classes to appear in the ratio 99 : 45 : 93 : 19. For the F_2 and F_3 results the combined figures are:

	Coloured procumbent	Coloured bush	White procumbent	White bush
	497	227	433	85
Expectation	*485*	*218*	*447*	*92*

and they are evidently in close accord with linkage of the value suggested.

In addition to the four F_3 families recorded above, in which the ratio of coloured : white was 9 : 7, there were four others in which the ratio was 3 : 1, viz.:

		Coloured procumbent	Coloured bush	White procumbent	White bush
1908	No. 128	29	8	6	3
	,, 129	20	3	2	2
	,, 158	48	17	23	1
	,, 161	174	66	69	6

In the last two families (Nos. 158 and 161) we again meet with the phenomenon of an excess of bush plants among the coloureds, and a deficiency among the whites. If we suppose that these F_2 parents were heterozygous for *R*-white, and homozygous for the other colour factor, and at the same time were produced by the gametic union $F^1f^2 \times f^1F^2$, the numbers are close to what would be expected on a 25 % crossover basis, as the following figures shew:

	Coloured procumbent	Coloured bush	White procumbent	White bush
158 161	222	83	90	7
Expectation	*208*	*94*	*94*	*6*

The other two families (Nos. 128 and 129) are probably of a different nature, for they shew neither excess of coloured bush, nor deficiency of white bush. It is reasonable to suppose that the whites here are *C*-whites, for there is an equal chance of the two kinds of white being found in F_3 families, which throw coloured and white in the ratio 3 : 1. If so, of course we should look for a normal 9 : 3 : 3 : 1 ratio.

Further experiments have been started in connection with the linkage relations of the factors F^1, F^2 and F^3. Meanwhile we may assume that F^1 and F^3 occupy the same locus, and that F^2 is about 25 units distant from this locus.

G. In 1920 a red-purple was crossed with a strain of *C*-white known to be homozygous for normal purple. F_1 plants were normal purples, and in 1922 an F_2 generation was raised from 14 similarly bred F_1 plants. In respect of the two pairs purple—red-purple and colour—*C*-white, the distribution of the characters in the F_2 generation was

Purple ...	156
Red-purple ...	78
White ...	80

The red-purple class was half the size of the normal purple class instead of forming only one quarter of the coloured plants. Since the cross was of the nature $G^1g^2 \times g^1G^2$, this result is readily explicable on the assumption that linkage occurs. On these data alone however it is not possible to form any trustworthy estimate of the value of the linkage. For the following reason, however, I am inclined to think that it is not very close. As stated elsewhere (*Journal of Genetics*, XII. p. 256) the red-purple differs in habit from the corresponding normal purple, being smaller, and at the same time "duskier" in appearance. Though of course the duskiness is absent in whites, I have noticed that in an F_2 generation from *R*-white × red-purple, some of the whites recall the red-purple habit. The foliage is of a rather darker green, and in well-grown plants it is possible, with care, to separate the two kinds. The F_2 generation from *C*-white × red-purple was not well grown, owing to the late germination of most of the seeds, and I did not attempt to distinguish "red-purple" *C*-whites from the rest. Nevertheless I noticed several plants which gave me the impression of belonging to the "red-purple" class. As the total F_2 generation comprised only 314 plants, the presence of 5 such plants would indicate a crossover value of about 25 °/₀. I am inclined to think therefore that it lies somewhere about here, but until further experiments, now in progress, have matured, the point must remain unsettled. I do not however feel any doubt of the existence of linkage between these two pairs of characters.

The linkage-testing data.

Of the pairs of characters used in this work, three, viz. C, E, and H, appear to stand outside the 5 linkage systems hitherto identified; and we may now consider the evidence for this, as well as for the independence of the 5 linkage systems themselves. Back-crosses of the doubly heterozygous individual on to the double recessive, such as have been used with such success in *Drosophila*, are impracticable in *Lathyrus*, owing to the great amount of time and labour involved in obtaining reasonably large numbers. For deciding the question whether linkage does or does not occur between two given pairs of characters, the only practicable method is to make the cross both ways and to examine the F_2 generation in each case. By making the cross "both ways" is of course meant that the crosses are of the nature $\mathsf{XY} \times \mathsf{xy}$, as well as of the nature $\mathsf{Xy} \times \mathsf{xY}$, when X and Y represent the factors corresponding to the two dominant characters of the pairs whose relations are being investigated. During the past 12 years an attempt has been made to cross nearly every one of the 16 pairs of characters given on page 116 with nearly every other one, and, so far as was possible, to make the cross both ways. The number of crosses undertaken, from which an F_2 generation was raised, is shewn graphically on Fig. 6: the actual data are given in condensed form in Table I, pp. 119—122. In some cases the cross between two characters was not made because the evidence already obtained shewed it to be unnecessary. In other cases again the cross was made, but no results were obtained, either because it failed, or because the F_1 plants died prematurely through disease or drought. In some cases also the F_2 figures are, for similar reasons, smaller than might reasonably have been expected.

In the majority of the crosses given in Table I the figures are clearly opposed to the idea of any linkage. Some of them taken by themselves may suggest that linkage occurs, but when considered in connection with other crosses, involving other members of the same linkage groups, it will become evident that such figures are due to what may be termed accidental irregularities. To take an example—the cross $\mathsf{A}^2 \times \mathsf{F}^3$, which was made in the manner $\mathsf{A}^2\mathsf{f}^3 \times \mathsf{a}^2\mathsf{F}^3$, gave in F_2 the expected four classes in the proportion 330 : 90 : 116 : 22. Here the fourth term is well below expectation, as would be expected if there were a low grade of linkage involved. But F^1 is situated at the same locus as F^3, and if there were linkage we should look for this to be reflected in the F_2 results from the cross $\mathsf{A}^2\mathsf{F}^3 \times \mathsf{a}^2\mathsf{f}^3$. The actual F_2 numbers here however are exceedingly close to the expectation on a 9 : 3 : 3 : 1 basis. Moreover, various other crosses between the A and F groups, viz. $\mathsf{A}^1 \times \mathsf{F}^2$ (both ways), $\mathsf{A}^1 \times \mathsf{F}^3$, $\mathsf{A}^3 \times \mathsf{F}^1$, and $\mathsf{A}^3 \times \mathsf{F}^3$, give no indication of any linkage. Yet if linkage really existed between A^2 and F^3 we should expect to find it reflected in some of these other crosses. From the fact that it is not evident, we must conclude that the deficiency of the fourth term in the F_2 generation from the cross $\mathsf{A}^2\mathsf{f}^3 \times \mathsf{a}^2\mathsf{F}^3$ is due rather to some accident (such, perhaps, as a higher mortality among marbled plants with round pollen) than to any linkage.

For the interrelations between the five groups A, B, D, F, G the figures may be left to speak for themselves. The evidence is, I think

	A¹	A²	A³	B¹	B²	B³	C	D¹	D²	E	F¹	F²	F³	G¹	G²	H
A¹																
A²																
A³																
B¹	× ×	×	× ×													
B²	× ×	·	× ×													
B³	× ×	·	×													
C	×	×	×	×	×	·										
D¹	× ×	·	×	×	×	× ×	×									
D²	×	×	×	× ×	·	·	× ×									
E	× ×	·	×	×	×	·	×	×	×							
F¹	·	×	×	×	×	·	×	×	×	·						
F²	× ×	·	·	×	·	·	×	×	·	×						
F³	×	×	×	×	·	·	×	×	×	×						
G¹		× ×	× ×	·	× ×	×	×	·	×	×	·	× ×	·			
G²	×	·	×	× ×	·	×	× ×	·	×	× ×	·	·	×			
H	× ×	·	·	× ×	×	·	×	×	×	×	×	·	×	·	×	

A¹ Purple—red.
A² Long—round pollen.
A³ Erect—hooded standard.

B¹ Dark—light axil.
B² Fertile—sterile anthers.
B³ Normal—cretin flower.

C Hairy—glabrous.

D¹ Tendril—Acacia.
D² Bright—dull flower colour.

E Tall—cupid.

F¹ Colour—*R*-white.
F² Procumbent—bush.
F³ Self colour—marbled.

G¹ Colour—*C*-white.
G² Purple—red-purple.

H Clamped—open keel.

Fig. 6. Scheme illustrating the various crosses made between 16 pairs of characters. The actual data will be found in Table I. In none of these crosses was there any definite indication of linkage. × × signifies that the cross was made both ways, *i. e.* that both of the combinations XY × xy, and Xy × xY were made. × signifies that the cross was only made either in one way or in the other.

sufficient to convince the critic that these five linkage groups are independent of one another; and that the factors concerned must, on the chromosome hypothesis, be regarded as situated in different chromosomes.

There remain for consideration the factors C, E, H, and these may be considered separately in connection with the figures in Table I*.

(1) The factor C.

A × C. If C were about 50 units distant from A^1 and A^3, which are close together, then if it is on the same side of the chromosome as A^2, it should shew about 38 °/o of crossovers with A^2. The figures for the $A^2 \times C$ cross are 311 : 96 : 121 : 33, where expectation on the 38 °/o crossing over basis would be 301 : 120 : 120 : 20. The actual figures lie on the whole between this expectation and the figures based on absence of linkage, and the question must at present remain undecided, though the evidence is, perhaps, more against linkage than for it.

B × C. The results from $B^1 \times C$ might be construed as representing a linkage near 50 °/o; for both end terms are rather below, and both middle terms rather above normal expectation. The $B^2 \times C$ figures are irregular, and suggest rather that there is a higher mortality among the smooths, both fertile and sterile, than any linkage. On the whole, linkage here is unlikely though the matter cannot be regarded as settled until results have been obtained from the $B^3 \times C$ cross.

C × D. The evidence here affords no grounds for supposing that linkage occurs.

C × E. The numbers, though small, give no indication of linkage. But, of course, a crossover value in the region of 50 °/o is not ruled out.

C × F. In the $C \times F^3$ cross the fourth term is low. But on the other hand the middle terms are also below normal expectation instead of above it, as they should be if there were linkage. And the first term is well above normal expectation instead of being below it. On the whole, the figures are more in accordance with a higher mortality among the marbled classes. The results of the crosses with F^1 and F^2 offer no clear grounds for assuming the existence of linkage.

C × G. The numbers seem to point clearly to there being no linkage here.

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* Some years ago we suggested the possibility of linkage between the purple-red and the dark-light axil pairs (cf. Bateson and Punnett, 1906, p. 36). The figures then obtained were not, however, conclusive; and since that date the point has been more fully investigated. The data obtained since 1906 are given in Table I, and tell conclusively against the existence of such a linkage.

C × H. The numbers, though small, are in close accordance with normal expectation, though here again a crossover value of 50 °/₀ is not ruled out.

(2) The factor E.

A × E. The figures afford no indication of linkage; but since A_1 and A_3, which alone were used, are close to one another, the possibility of a 50 °/₀ crossover is not ruled out.

B × E. The fourth term in the numbers from B^1 × E is much larger than on normal expectation. If this be taken as indicating low grade linkage, the locus of E must be about 50 units from B^2, on the side on which B^1 lies.

D × E. Though the numbers are irregular the facts are against linkage. For D^1 and D^2 are so far apart that if E shewed 50 °/₀ linkage with either one it would have to shew much closer linkage with the other*.

E × F. Since F^2 and F^3 are some 25 units apart, and since E shews no clear indication of linkage with either, it may be taken as fairly certain that the locus of E is not in the F chromosome.

E × G. Though there is some irregularity in the numbers, there is no indication of linkage.

E × H. The numbers of the cross made do not point to linkage, but the possibility of a 50 °/₀ crossover value is not ruled out.

(3) The factor H.

A × H. Though there is irregularity in the middle terms in the reciprocal crosses, the end terms in each case are close to expectation. The possibility of a 50 °/₀ crossover value is not ruled out.

B × H. Since B^1 and B^2 are only about 6 units apart the possibility of a crossover value of about 50 °/₀ is not entirely ruled out.

D × H. Since D^1 and D^2 are about 35 units apart, it is improbable, in view of the figures obtained, that the locus for H is in chromosome D.

F × H. In the absence of data relating to F^2 the possibility of a 50 °/₀ crossover value is not ruled out.

From these considerations it is clear that for the 3 factors C, E, H there are many possibilities of a very low grade linkage, in the neighbourhood of 50 °/₀. If only one of these should be proved the number of independent groups would be reduced from 8 to 7, which is the

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* But see p. 111.

haploid number of the chromosomes. But in order to settle this point there is need for the utilisation of further characters. The greater the number of characters dealt with, the more surely can be assigned to each its peculiar chromosome and locus. The number of workable characters in *Lathyrus* hitherto unexploited is small; for the finer shades of flower colour present difficulties in classification which render their use undesirable. Structural features are the most satisfactory to use; and I should be most grateful for assistance in the shape of seeds from any novelty, however undesirable horticulturally, that readers of this paper may happen to come across.

In conclusion I wish to express my thanks to the Director of the John Innes Horticultural Institution for facilities freely afforded for growing sweet peas at Merton, and for the beautiful drawings reproduced on Plate III, which were made by Mr Osterstock. Especially, too, am I grateful to those who have helped me, both at Cambridge and at Merton, in the labour of recording the many thousands of plants which were grown for the data in this paper.

TABLE I*.

	Type of Mating $XY \times xy$				Type of Mating $Xy \times xY$			
$A_1 \times B_1$	1363 *1318·5*	393 *439·5*	438 *439·5*	150 *146·5*	3251 *3345*	1112 *1116*	1148 *1116*	438 *372*
$\times B_2$	3894 *3895*	1220 *1299*	1390 *1299*	422 *433*	511 *525*	186 *175*	167 *175*	69 *58*
$\times B_3$	308 *296*	84 *99*	108 *99*	27 *33*	421 *454·5*	126 *151·5*	195 *151·5*	66 *50·5*
$A_2 \times B_1$	1442 *1368*	458 *462*	399 *462*	167 *154*	493 *492*	160 *165*	170 *165*	54 *55*
$A_3 \times B_1$	203 *195*	63 *66*	70 *66*	13 *22*	409 *430*	164 *143*	142 *143*	49 *48*
$\times B_2$	241 *236*	75 *78*	77 *78*	25 *26*	691 *680*	239 *226*	217 *226*	60 *75*
$\times B_3$	—	—	—	—	145 *142*	42 *47*	45 *47*	20 *16*
$A_1 \times C$	—	—	—	—	584 *626*	211 *208*	245 *208*	71 *69*
$A_2 \times C$	—	—	—	—	311 *316*	96 *105*	121 *105*	33 *35*
$A_3 \times C$	405 *375*	112 *125*	119 *125*	31 *42*	—	—	—	—

* The figures in italics shew the expectation on a 9 : 3 : 3 : 1 basis.

TABLE I—*continued.*

	Type of Mating $XY \times xy$				Type of Mating $Xy \times xY$			
$A_1 \times D_1$	1270 *1261*	381 *420*	448 *420*	142 *140*	602 *599*	207 *199*	187 *199*	67 *66*
$\times D_2$	—	—	—	—	1778 *1780*	552 *593*	636 *593*	197 *197*
$A_2 \times D_2$	—	—	—	—	369 *356*	109 *119*	115 *119*	40 *39*
$A_3 \times D_1$	526 *528*	179 *176*	174 *176*	59 *58*	—	—	—	—
$\times D_2$	399 *404*	149 *134*	129 *134*	39 *44*	—	—	—	—
$A_1 \times E$	110 *104*	26 *34*	39 *34*	8 *11*	189 *189*	62 *63*	66 *63*	19 *21*
$A_3 \times E$	96 *86·5*	21 *28·5*	26 *28·5*	10 *9·5*	—	—	—	—
$A_1 \times F_2$	228 *238*	73 *79*	93 *79*	28 *26*	322 *311*	102 *103*	95 *103*	32 *34*
$\times F_3$	—	—	—	—	1288 *1222*	340 *408*	412 *408*	134 *136*
$A_2 \times F_1$	618 *616*	205 *205*	204 *205*	67 *68*	—	—	—	—
$\times F_3$	—	—	—	—	330 *313*	90 *105*	116 *105*	22 *35*
$A_3 \times F_1$	203 *198*	68 *66*	57 *66*	24 *22*	—	—	—	—
$\times F_3$	447 *402*	99 *134*	133 *134*	35 *44*	—	—	—	—
$A_1 \times G_2$	—	—	—	—	86 *85·5*	32 *28·5*	25 *28·5*	9 *9·5*
$A_2 \times G_1$	1206 *1212*	437 *414*	406 *414*	129 *138*	307 *279*	89 *93*	78 *93*	22 *31*
$A_3 \times G_1$	1158 *1185*	422 *396*	398 *396*	131 *132*	311 *313*	120 *104*	98 *104*	27 *35*
$A_3 \times G_2$	117 *117*	39 *39*	62 *58·5*	16 *19·5*	—	—	—	—
$A_1 \times H$	150 *159*	65 *53*	48 *53*	19 *17*	556 *553·5*	160 *184·5*	208 *184·5*	60 *61·5*
$B_1 \times C$	—	—	—	—	1107 *1118*	381 *373*	390 *373*	110 *124*
$B_2 \times C$	—	—	—	—	524 *498*	139 *166*	178 *166*	44 *55*
$B_1 \times D_1$	784 *778*	273 *259*	249 *259*	76 *86*	—	—	—	—
$\times D_2$	319 *331*	134 *111*	95 *111*	42 *87*	99 *90*	24 *30*	33 *30*	4 *10*
$B_2 \times D_1$	—	—	—	—	573 *573*	196 *191*	175 *191*	74 *63*
$\times D_2$	—	—	—	—	477 *469*	158 *157*	139 *157*	61 *52*
$B_3 \times D_1$	94 *76·5*	25 *25·5*	15 *25·5*	2 *8·5*	385 *373*	130 *124*	105 *124*	42 *41*

TABLE I—*continued.*

	Type of Mating $XY \times xy$				Type of Mating $Xy \times xY$			
$B_1 \times E$	442	134	155	60	—	—	—	—
	446	*148*	*148*	*49*				
$B_2 \times E$	—	—	—	—	88	22	30	11
					86	*28*	*28*	*9*
$B_1 \times F_1$	—	—	—	—	225	—	73	—
					224		*74*	
$\times F_2$	144	37	38	12	—	—	—	—
	131	*43*	*43*	*14*				
$\times F_3$	—	—	—	—	602	—	232	—
					625·5		*208·5*	
$B_2 \times F_1$	—	—	—	—	225	74	78	28
					228	*76*	*76*	*25*
$\times F_3$	—	—	—	—	472	122	157	30
					438	*147*	*147*	*49*
$B_1 \times G_2$	189	58	59	16	240	81	109	29
	182	*60*	*60*	*20*	*258*	*86*	*86*	*29*
$B_2 \times G_1$	725	218	180	68	151	61	63	18
	671	*223*	*223*	*74*	*165*	*55*	*55*	*18*
$B_3 \times G_1$	—	—	—	—	32	10	13	4
					35	*11*	*11*	*4*
$\times G_2$	—	—	—	—	54	16	26	4
					56	*19*	*19*	*6*
$B_1 \times H$	51	14	13	4	812	224	274	72
	47	*15*	*15*	*5*	*778*	*259*	*259*	*86*
$B_2 \times H$	—	—	—	—	537	162	166	51
					515	*172*	*172*	*57*
$C \times D_1$	—	—	—	—	148	51	80	18
					167	*56*	*56*	*18*
$\times D_2$	405	112	134	43	331	108	96	25
	394	*130*	*130*	*43*	*315*	*105*	*105*	*35*
$C \times E$	—	—	—	—	54	17	23	6
					56	*19*	*19*	*6*
$C \times F_1$	—	—	—	—	314	105	91	28
					303	*101*	*101*	*33*
$\times F_2$	—	—	—	—	130	41	52	8
					131	*43*	*43*	*14*
$\times F_3$	—	—	—	—	729	194	222	49
					672	*224*	*224*	*74*
$C \times G_1$	—	—	—	—	590	159	160	60
					545	*182*	*182*	*60*
$\times G_2$	336	103	97	24	174	59	63	15
	315	*105*	*105*	*35*	*176*	*58*	*58*	*19*
$C \times H$	—	—	—	—	67	18	19	6
					63	*20*	*20*	*7*

TABLE I—*continued.*

	Types of Mating $XY \times xy$				Types of Mating $Xy \times xY$			
$D_1 \times E$	—	—	—	—	118 *122*	38 *40*	42 *40*	17 *13*
$D_2 \times E$	—	—	—	—	212 *204·5*	80 *67·5*	48 *67·5*	22 *22·5*
$D_1 \times F_1$	—	—	—	—	163 *176*	68 *58*	60 *58*	20 *19*
$\times F_2$	—	—	—	—	95 *93*	28 *31*	34 *31*	8 *10*
$\times F_3$	427 *403*	96 *134*	155 *134*	38 *45*	766 *732*	229 *244*	229 *244*	77 *81*
$D_2 \times F_1$	195 *201*	70 *67*	92 *89*		—	—	—	—
$\times F_3$	1868 *1768·5*	552 *589·5*	554 *589·5*	170 *196·5*	—	—	—	—
$D_2 \times G_1$	—	—	—	—	426 *410·5*	142 *136·5*	161 *182*	
$\times G_2$	—	—	—	—	526 *501*	157 *167*	155 *167*	52 *55*
$D_1 \times H$	—	—	—	—	244 *201*	43 *67*	53 *67*	17 *22*
$D_2 \times H$	—	—	—	—	67 *61*	20 *21*	18 *21*	5 *7*
$E \times F_2$	—	—	—	—	521 *475*	122 *158*	151 *158*	50 *53*
$\times F_3$	70 *62*	14 *20*	18 *20*	7 *7*	—	—	—	—
$E \times G_1$	—	—	—	—	360 *360*	127 *120*	104 *120*	49 *40*
$\times G_2$	77 *59*	12 *19*	10 *19*	4 *6*	46 *47*	18 *16*	11 *16*	9 *5*
$E \times H$	—	—	—	—	330 *311·5*	85 *103·5*	109 *103·5*	29 *34·5*
$F_2 \times G_1$	108 *118*	40 *40*	49 *40*	14 *13*	139 *138·5*	52 *46·5*	40 *46·5*	16 *15·5*
$F_3 \times G_2$	—	—	—	—	413 *377*	121 *126*	107 *126*	30 *42*
$F_1 \times H$	—	—	—	—	132 *136*	50 *45*	46 *45*	13 *15*
$F_3 \times H$	—	—	—	—	33 *31*	7 *10*	11 *10*	3 *3*
$G_1 \times H$	—	—	—	—	20 *21·4*	7 *7·1*	8 *7·1*	3 *2·4*
$G_2 \times H$	—	—	—	—	132 *143*	53 *48*	55 *48*	15 *16*

EXPLANATION OF PLATE III.

Fig. 1. Marbled form of blue.
Fig. 2. Marbled form of deep red (*e.g.* Miss Hunt).
Fig. 3. Marbled form of deep purple.
Fig. 4. Marbled form of blue red (Fig. 5).
Fig. 5. Blue-red, being the "dull" form of "Miss Hunt" in the "bright" series.

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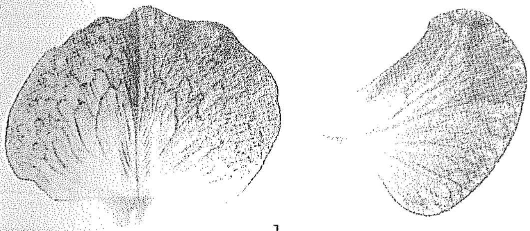

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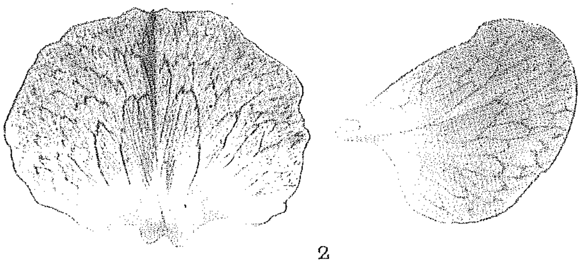

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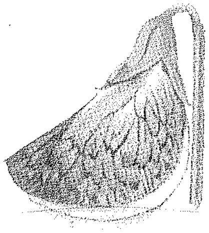

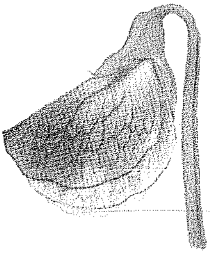

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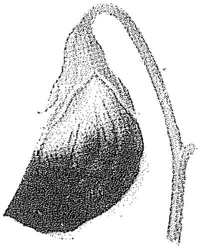

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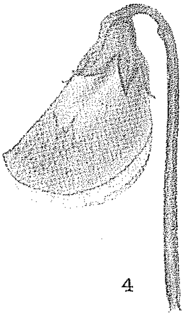

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