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THE GENETICS OF *PRIMULA SINENSIS*.

II. SEGREGATION AND INTERACTION OF FACTORS IN THE DIPLOID.

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(With Plates I–XIII.)

THE genetical analysis of *Primula sinensis* was begun in 1903 by W. Bateson and R. P. Gregory. The main results of their work with the diploid were communicated by Gregory (1911) and Gregory, de Winton and Bateson (1923). In this paper we shall deal only with the diploid and confine ourselves to a description of the individual factors, their interaction and segregation. Linkage and related problems will be dealt with in a later paper. A description of the genetics of the tetraploid will also be given later[1]. The results here given include those by Bateson and Gregory. It will be necessary to recapitulate some parts of the former papers for the sake of completeness and also because earlier results have sometimes received a new interpretation.

Genetical analysis has so far revealed 25 pairs of allelomorphic factors, and two sets of three allelomorphs. In addition three other factor pairs are suspected in the diploid, but analysis is not yet complete. In the tetraploid seven of the well-known allelomorphic pairs are present, and also one pair from each of the sets of three allelomorphs, while a tenth factor pair, not represented in the diploid, is suspected.

We shall first deal with the effects of the factors one at a time. The results can be expressed in two ways. In the first place we may describe the action of each dominant factor, in terms of Bateson and Punnett's presence and absence theory. This theory may require modification in so far as a recessive factor is often an inactive rather than an absent gene, but it accounts for dominance, and describes the function of factors in physiological terms. Secondly, we may describe the effects, on the presumed original type of plant, of a change in its factorial basis involving one factor at a time. This is the method used by Morgan and his colleagues to describe the mutants in *Drosophila*. It is clearly

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[1] See also Sverdrup-Sömme (1930).

applicable in that case, and as clearly inapplicable to a domestic animal such as the hen, whose "wild" type is not known, as it is possibly derived from several species. *Primula sinensis* occupies an intermediate position. The wild form is not known, but the plants brought over in 1820–5 only varied in respect of the factors **Ch**, **S** and possibly, though not very probably, **I**. As Gregory, de Winton and Bateson point out, **Ch** causes a type of flower unknown elsewhere in the genus *Primula*, and there is therefore reason to suppose that the original plant lacked the factor **Ch**. On the other hand, like many other species of *Primula*, it was presumably polymorphic for **S** (short style). It probably possessed **I**, but the loss of this factor produces so slight an effect that this is not quite certain. In what follows we take a type possessing **S** and **I**, but lacking **Ch**, as our original wild type, though realising that this is a somewhat arbitrary procedure (Pl. XIII).

Table I gives a brief account of the known factors. Where the Mendelian behaviour has not yet been conclusively established the factor is queried, but there is every reason to think that at least **C** and **Z** will behave in a normal manner[1]. The factors are arranged in linkage groups. The linkage between **R** and **N** is still somewhat uncertain, and the order in the group **M Y H K** quite uncertain. **F**, $\mathbf{f^s}$, $\mathbf{f^l}$ and **A′**, **A**, **a** are multiple allelomorphs. The factors **Ch**, **D** and **A′**, which are italicised, are dominants over the wild type. The remaining mutant types are recessive, but **J j** plants are intermediate in some respects. The second column of Table I describes the factors in Bateson and Punnett's terminology, the third in Morgan's.

All of these factors except **Ep** segregate in the diploid, and **s**, **b**, **g**, **f** (probably $\mathbf{f^l}$), **Ch**, **D**, **y**, **v**, **a** and **ep** are found in the tetraploid, while **x** was formerly found in it.

We have provisionally divided the factors into eight groups, according to their most conspicuous effects:

1. Factors intensifying anthocyanin. **V**, **J**, **K**, **E**, **H**.
2. ,, inhibiting anthocyanin. **G**, **D**, **I**, **L**, **B**.
3. ,, altering anthocyanin. **R**.
4. ,, inhibiting flower plastids and flattening the edge of leaves and petals. **F** (3 allelomorphs), **A** (three allelomorphs), **P** (**Sp**).
5. ,, affecting flower structure. **S**, **X**, **M**, **Ch**, **N**, (**Ep**).
6. ,, ,, leaf structure. **Y**, **O**, **T**, **Mp**, **C**, **Z**.

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[1] Since writing the above the new crop has germinated, and claw (**z**) plants are coming in F_2 in approximately normal ratios.

7. Factors affecting both flower and leaf structure. **W**, **Iv**.
8. ,, ,, habit. **Q**, (**U**).

Of these **U**, **Sp** and **Ep** are still doubtful. In addition there is an extra-nuclear "factor" or plasmon affecting the chloroplasts of the leaves.

TABLE I.

Linkage group	Factor	Action of factor	Appearance of mutant
I	**S**	Shortens style, lengthens anthers	"Pin," long style, short anthers (probably present in nature)
	B	Blues anthocyanin, increases flavone	Red flowers
	X	Converts extra petals into stamens, etc.	Sterile double flowers
	G	Suppresses anthocyanin in flower centre	Red stigma, dark centre to flowers
	L	Partly suppresses anthocyanin in stem and leaf	Dark purple stems and leaves
II	**P**	Restricts eye, flattens petals	"Peculiar" large eye, rolled petals
	F	Suppresses growth of leaf edge	— —
	f^s	— —	"Sutton's" moderately crimped leaf, normal eye
	f^l	— —	"Lee's" intensely crimped leaf, large eye
	Ch	Increases flower growth, shortens stem	"Sinensis," fringed petals, 10 calyx teeth
III	*D*	Suppresses anthocyanin in flowers, especially at edge	White flowers
	E	Spreads anthocyanin over petals	Flaked petals
IV	**M**	Suppresses extra whorl of petals	Fertile double flowers
	Y	Shortens leaves	"Fern" leaf
	H	Makes petal colour and size uniform	"Harlequin" flowers
	K	Oxidises pink anthocyanin to darker type	"Coral" stems, pale or white flowers
V	**O**	Joins leaflets	"Oak" incised leaves
	Mp	Lengthens hairs, alters leaf edge	"Maple" leaf, semi-glabrous
VI	**R**	Acidifies petal sap	Blue flowers
	N	Inhibits overgrowth of calyx and bracts	Leafy bracts and large calyces
	V	Makes anthocyanin	Green stems, white—pale pink flowers
	J	Makes anthocyanin	Green stems, "Sirdar" flowers
	I	Slightly dilutes anthocyanin	Deeply coloured flowers
	A′	Suppresses plastids of eye	"Alexandra" white eye in flower
	A	Restricts plastids of eye	— —
	a	— —	Large "Primrose Queen" eye, very short style
	Sp?	Intensifies plastids of eye	"Ghost" eye
	Ep?	Restricts petal number	Extra petals
	T	Makes leaves rounder, and incises them	"Tongue" triangular leaves
	C?	Increases vigour of plant	"Cup" leaves, small unhealthy plants
	Z	Expands leaf, suppresses dorsal comb, etc.	"Claw" leaves, rolled up
	Iv	Makes leaf margins crenate	"Ivy" leaf, reduced flowers
	W	Increases vigour of plant	"Feeble-minded," stunted plants
	Q	Causes open growth	Rosetted habit
	U?	Reduces leaf number and stem size	Umbellated, often fasciated habit

The above classification is quite provisional. Thus to a bee, to which red appears as black, **R**, which converts slaty blue into red, would appear to belong to group 1. Again **Ch** and **N** have a decided effect on habit as well as on flower structure, and **O**, **T** and **Mp** have a certain slight influence on flower as well as leaf structure, even in the absence of **Ch**.

INTERACTION OF THE FACTORS.

With the nuclear factors and extra-nuclear factor available in the diploid, the possible number of homozygous genotypes is $2^{25} \times 3^2$, or 301,989,888, besides a very much larger number of heterozygous genotypes. Not all these types would be distinguishable. For example the majority would have white flowers. Needless to say only a few thousand have been made up, and it is possible that hitherto quite unexpected interactions will be revealed later on. Such interactions as those of **A** and **f**^{1}, or **L** and **R** warn us of this possibility. In what follows we shall deal with the colour and structure of different parts of the plant separately, the following being considered: stem and leaf colour; gynaecium colour; petal sap colour; flower plastids and leaf and petal edge; leaf structure, and correlated variations of flower structure; flower structure; bract form.

Stem and leaf colour.

The factors concerned are **V**, **J**, **K** and **L**, though in a few cases **G**, **E** and **Ch** appear to have a slight effect. Two types of anthocyanin are found in the stem. Plants carrying **K** all appear to possess the same pigment, shown by Scott-Moncrieff to be a monoglucoside of petunidin. The quantity however varies from a large amount to a barely perceptible trace. The following table gives the types arising from interaction of **V**, **L** and **J** in presence of **K**. The types are numbered from the lightest (1) to the darkest (7).

TABLE II.

Genotype	Grade	Description
V JJ L	6	Purple, evenly distributed
V J j L	5	Light purple, stems almost as dark as "wild," leaves and bracts nearly green
V jj L	4	Green, but much colour in base of older leaves
V JJ ll	7	Dark purple
V J j ll	6	Light purple, calyx and bracts green, leaf backs fairly dark
V jj ll	5	Light purple, calyx and bracts green
vv JJ L	2	Green, slight colour in young petioles and flower stalks
vv J j L	1–2	Green
vv jj L	1	Green, no anthocyanin visible
vv JJ ll	3	Dark green, considerable colour in young petioles and flower stalks
vv J j ll	?1–3	Green, not yet separated from other types
vv jj ll	?1–3	Green, not yet separated from other types

The classification of stem colour at first caused considerable trouble. There is hardly ever any difficulty in distinguishing **K** from **kk** plants. This only arises when owing to the presence of recessives, *e.g.* **vv jj**, the stems are green and the flowers white. If any appreciable amount of pigment is present in stems or flowers the distinction is easy. The interaction of **V** and **J** was worked out by Gregory, and our **J** corresponds to his **F**, our **V** to his **Q**. We do not, however, find it necessary to postulate two other factors, which he used to explain his stem-colour results. As regards the interaction of **V** and **J** we have a large number of results in which the classes were incompletely separated. The following families illustrate the segregation observed when four of these classes are scored separately. The figures given are sums of six F_2 families derived from selfing the F_1's of **vv JJ** × **VV jj** and **VV JJ** × **vv jj**. As **V** and **J** are not linked they can legitimately be grouped.

Grade	6	5	4	2–1
Phenotype	**JJ V**	**J j V**	**jj V**	**vv**
Found	131	255	122	198
Expected	132·4	264·7	132·4	176·5

In the **vv** class it was rarely possible to distinguish between grades 1 and 2 with certainty, but the pure greens, when tested by mating to **VV JJ** or **VV jj**, proved to be **vv jj**, those with most colour being **vv JJ**.

In the case of **V** and **L** the cross between Etna (**VV ll**) and Queen of the Pinks (**vv LL**) and similar crosses has been made several times. Up to 1929 the distinction between **vv L** and **vv ll** was not clear. The latter has a considerable amount of anthocyanin, and the leaves are of a dark green. Mr Stone finds that under certain circumstances the chlorophyll may be dissolved out, leaving a little anthocyanin behind. **vv ll** plants often bear numerous flowers, and give very good pollen, but out of 80 tested, both by selfing and crossing with various types, none has ever produced a seed. They are in fact sterile on the female side. Recent work by Mr Afify shows that the ovules of these plants do not develop, though pollen tubes grow normally down to them. Their leaves have a characteristic shape, the sinuses being less acute than usual. Moreover in certain families dwarfs have appeared only among the **vv ll** plants.

The genetic constitution of these plants has been fully confirmed by crossing them with **vv LL** and **VV ll**. The numbers obtained are:

F_2 from **VV ll** × **vv LL** *and reciprocal. Seven families.*

V L	**V ll**	**vv L**	**vv ll**
303	123	111	30

F_2 from **VV LL** × **vv ll**. *Four families.*

V L	**V ll**	**vv L**	**vv ll**
112	21	39	11

From **v L V l** × **vv ll.**

V L	**V ll**	**vv L**	**vv ll**
75	61	51	70

The first one suggests linkage between **V** and **L**, but this has not been confirmed by recent work. A further complication in these families is due to the influence of **G**. **vv L G** plants are pure green, but **vv L gg** may have an appreciable amount of colour in the petioles and flower-stem bases. However their leaves are light green, so they are not likely to be mistaken for **vv ll**.

The interaction of **J** and **L** is shown in derivatives from crosses of Etna (**JJ ll**) with Sirdar (**jj LL**) and a green-stemmed white-flowered plant (**jj LL ee**) obtained from the late Mr Elwes. In the derivatives of the latter the **ee** plants had slightly lighter stems than **E**, moreover it was possible to classify **ee** plants into **JJ**, **J j** and **jj** on the basis of their flower colour. Until 1929 it was not possible to separate all the six types of stem. This has been done in an F_2 from Sirdar (**jj LL**) × Etna (**JJ ll**) and in one from **J j LL ee** × Etna. In the latter case the male parent was a derivative of Elwes' white (**jj LL ee**) and the F_1 were of grades 5 (**J j L l**) and 6 (**JJ L l**). One of the former was selfed to give an F_2. The totals for the two F_2s were:

	JJ L	**J j L**	**jj L**	**JJ ll**	**J j ll**	**jj ll**
Found	54	82	45	14	30	18
Calculated	45·6	91·1	45·6	15·2	30·4	15·2

In two earlier F_2's from **JJ ll** × **jj LL** the pooled numbers were:

Stem-colour grade	7	6	5	4
Genotypes	**JJ ll**	3 **JJ L** + 2 **J j ll**	6 **J j L** + 1 **jj ll**	3 **jj L**
Found	12	83	69	45
Calculated	13	65	91	39

There was an excess of grade 6 and shortage of grade 5, probably because the **L l** plants were sometimes scored in too high a grade. The notes at the time read "The intermediate stem colour classes grade into each other, and it is quite impossible to sort them correctly." This has since become possible, owing to the isolation of plants from the above crosses. It was found that while some of the grade 6 plants bred true, others when selfed gave approximately 1 grade 7 (**JJ ll**) : 2 grade 6

(**J j ll**): 1 grade 5 (**jj ll**). The actual numbers obtained from five such plants were:

	JJ ll	**J j ll**	**jj ll**
Found	65	99	44
Calculated	52	104	52

but one such plant, from natural seed, gave

	JJ ll	**J j ll**	**jj ll**
Found	43	64	23
Expectation	32·5	65	32·5

The **JJ ll** derivatives bred true and behaved like normal **JJ ll** in all crosses, the **J j ll** crossed with **JJ LL** gave 78 grade 6 (**JJ L l**) and 52 grade 5 (**J j L l**) in five families. The **jj ll** bred true and gave all grade 5 (**J j L l**) when crossed with **JJ LL**.

The grade 5 plants from the F_2 of **JJ ll** × **jj LL** occasionally bred true (**jj ll**) but usually on selfing gave a variety of grades, explicable by the fact that they were either **J j LL** or **J j L l**.

Finally **J**, **V** and **L** all segregated in two F_2 families from crosses of Snowdrift (**jj vv LL**) × Etna (**JJ VV ll**). These gave a range of all the stem-colour grades, and were classified as follows:

	JJ V L	**JJ V ll**	**J j V L**	**J j V ll**	**jj V L**	**jj V ll**	**JJ vv L**	**JJ vv ll**	Other green stems
Found	18	7	31	11	13	1	7	1	12
Calculated	14·2	4·7	28·4	9·5	14·2	4·7	4·7	1·6	18·9

Considering the difficulty of classification the agreement is not bad. The classification was, of course, assisted by the fact that **J** and **V** affect flower colour, and **L** is closely linked with **G**, which does so. A plant which on these grounds was taken to be **vv jj ll** was roughly of stem-colour grade 4.

kk plants possess a different anthocyanin, which Scott-Moncrieff regards as a derivative of pelargonidin. It is a yellowish pink substance, and stems can easily be distinguished from **K** of about the same depth. The effects of **J**, **V** and **L** are much the same on **kk** as on **K** stems, even the lower grades of colour have definitely perceptible pigment. Indeed **jj kk** seems to have rather more anthocyanin in the collar than **jj KK**. It is quite easy to distinguish the colour grades given by **J**, **V** or **L** alone on **kk** stems. We have a few cases of more complex segregation, involving *e.g.* **J**, **V** and **K**, but it was not possible to separate all the stem-colour classes.

G, **E** and **Ch** have no visible effect on the darker stem colours, but may in some cases appreciably affect the lighter. Thus **vv G** plants have very little anthocyanin, **vv gg** have somewhat more in the young petioles and flower stalks, but not as much as grade 3, nor are their leaves of as dark a green. In four families from **J j** × **jj** and reciprocally, in which **E** and **Ch** were also segregating, it was observed that both **J j** and **jj** stems were lighter on **ee** and **chch** plants than on the corresponding dominants. However the two recessives together did not make **J j** plants as light as **jj**, *i.e.* depress grade 5 to grade 4. These effects of **G**, **E** and **Ch** are only noticeable when the plants are grouped for these factors. The slightly different average colour then becomes apparent. But even under the most favourable conditions it would not be possible to score **G**, **E** or **Ch** by their effect on stem colour. In all probability other factors, and environmental conditions, have slight effects on stem colour.

Gynaecium colour.

This is mainly controlled by **G**, but **R**, **V** and **K** may have a slight effect. All **G** plants have green stigmas, capsules and ovules, the stigma turning yellowish with age. The effects of the other factors are given in Table III.

TABLE III.

Genotype	Stigma	Capsule and ovules
G	Green	Green
gg R V	Red	Red
gg rr V	Purple	Red
gg R vv	Yellow	Very pale red
gg rr vv	Yellow	Very pale red

Thus **R** probably has some effect on the *p*H of the stigmas, little on that of the capsules and ovules. The effect of **gg** on **vv** stigmas is rather inconstant. In some years it has been possible to distinguish **gg** from **G** on **vv** stems with certainty. In other years this has not been possible. On the whole the effect of **G** is most marked on the ovules. **kk** gynaecia are somewhat paler than **K**.

Petal sap colour.

The main factors affecting flower colour qualitatively are **K**, **B** and **R**. **V**, **J**, **D** and **G** have a marked effect on its intensity, **I** and **L** a less effect. **E** and **H** affect the distribution, but the most fully coloured parts of **ll** and **bb** plants are as dark as those of **E** and **H**. We may divide the factors according to whether they intensify or inhibit pigmentation:

Intensifiers **V**, **J**, **K**, **E**, **H**.
Inhibitors **D**, **G**, **I**, **L**, **B**.

R cannot be placed in either class. We can best appreciate the nature of the interaction by studying the interaction of **B**, **R**, **V** and **K**, in presence of all the other dominants except **D** and **G**. Their effects are given in Table IV. It will be seen that there is no doubt about the appearance of the four **V K** genotypes. But in **V kk** and **vv K** plants the effects of **B** and **R** are not so certain, and there is some overlap between the different phenotypes. Tables V and VI give details of the analysis. In each case a number of **V kk** or **vv K** plants appearing in F_2, F_3 or elsewhere were crossed to slaty, **V K bb rr**, and the progeny in the subsequent year noted. If even a single blue or red-flowered plant appeared in the progeny, the tested plant was known to carry **B** or **R**

TABLE IV.

Genotype	Petal colour
V K B R	Magenta
V K B rr	Blue
V K bb R	Red
V K bb rr	Slaty
V kk B R	Nearly white—pale coral pink
V kk B rr	Nearly white
V kk bb R	Coral pink
V kk bb rr	Very pale pink—pale coral pink
vv K B R	White—pale pink, and picotee
vv K B rr	White
vv K bb R	Very pale pink—pink
vv K bb rr	White—pale pink
vv kk	White—very pale pink

TABLE V.

Analysis of **V kk** *plants* (*all* **gg**).

Flower colour of plant tested	Genotype found			
	B R	**B rr**	**bb R**	**bb rr**
Full coral pink **L**	0	0	2	0
Dark stemmed "brick" **H**	0	0	5	0
"?Coral" and "Near coral" **L**	6	0	1?	1 + 2?
Dark stemmed "pale brick" **H**	3	0	0	1
"Coral white" **L** and **H**	8	10	0	0

TABLE VI.

Analysis of **vv K** *plants* (*all* **G**).

Flower colour of plant tested	Genotype found			
	B R	**B rr**	**bb R**	**bb rr**
Pink	0	0	8	0
Pale pink	3	0	2	1
Picotee	13	0	1?	0
Opening white, later pale pink	16	1?	4	0
White	2	2	1?	3

respectively, if a magenta, both. However, in the case of small families giving only recessive forms, there was a doubt as to the genotype of the plant tested. Such plants are queried in the tables. The genotypes of the 39 **V kk** plants so tested are given in Table V. In addition two pure lines of full coral pink plants are known to be of composition **VV kk bb RR**. On light stems we can distinguish three types of flower, full coral pink, paler pinks, and plants which are coral pink in the bud, and later turn out white or a very pale pink. On dark stems the pigment is generally concentrated in patches, which may be rather darker than the petals of **L** corals. Two types of coloured flowers, and more rarely whites, can be distinguished on 11 plants.

The "coral" and "near coral" plants which are queried gave families of 1, 1 and 2 only. On the other hand the **bb rr** plant gave a family of 12, and examination of a number of **kk** plants derived from **K k bb rr** selfed and **K k bb rr** × **kk bb rr** leave no doubt that **kk bb rr** plants, though generally paler than **kk bb R**, have a certain amount of colour. Indeed in some though not all families pure for **bb** but segregating for **K** and **R**, **R** can be scored in the **kk** plants. The range of colour shown by **kk B R** plants is not due to incomplete dominance of **B** or **R**. It is partly due to temperature, since the pale-flowered **kk** plants become paler in heat, and probably in part to the factor **I**.

The genotypes of 57 **vv K** plants similarly tested by crossing with **V K bb rr** are given in Table VI. The three doubtful plants gave families containing 1, 1 and 2 **V** only, and it is likely that all of them were really **B R**. A number of other plants gave confirmatory results. Thus Sutton's "Queen of the Pinks" is **vv bb RR**, and it will be seen that plants of this composition are generally pink, and rarely, if ever, white. The variation in the colour is partly due to the factor **I**, and **G** has also a slight inhibitory effect. **G** was present in all the plants tested in Table VI. **vv gg** plants have somewhat more pigment than their **vv G** sisters, and in particular generally have a flush round the eye. It is doubtful whether a picotee flower would be possible on a **gg** plant, but we do not know the lowest degree of colour compatible with a yellow stigma, as no **K vv B rr gg** plants have been studied. It will be seen that both among **kk V** and **K vv** plants **bb R**, corresponding to red, are the darkest, and **B rr**, corresponding to blue, white or nearly so, while the forms corresponding to magenta (**B R**) and slaty (**b r**) are intermediate.

The following provisional account of the chemistry of the interaction of these factors can be given. It is based on work performed by Miss

Scott-Moncrieff, working for one of us with a grant from the Department of Scientific and Industrial Research, but must not be taken to represent her opinions. She hopes shortly to publish an account of her chemical investigations, and we must thank her for permission to summarise certain of them.

The main pigment found in all types of **V K** flowers (magenta, red, blue and slaty) is primulin, or malvidin 3-monoglucoside (Scott-Moncrieff, 1930). The yield, however, is comparatively low from blue and slaty flowers, and owing to slight colour differences in the crude extracts, she suspects the presence in these **rr** plants of a second anthocyanin along with primulin.

kk flowers, when they contain any pigment at all, yield an anthocyanin which may be identical with that in their stems and leaves, and certainly resembles it in being a pelargonidin derivative. The coral pigment is quite clearly distinguishable from any of the types of pink found in **K** plants. Its colour is the *Carmin saumoné* of the *Répertoire des couleurs* of the *Société française des Chrysanthémistes*. Thus pure lines of **W kk bb RR** have been described commercially as "Orange King" and "Salmon King." Gregory's Fig. 3 is quite inadequate. **V kk** flowers are always pink in the bud, even when they become white on opening. Thus **kk** plants appear to be incapable of performing a certain oxidation, or less probably, of performing an abnormal reduction. Whether the factor **K** is responsible for the methylation of the malvidin is of course uncertain. There are no phenolic groups in positions available for methylation in pelargonidin derivatives, and we do not know whether **kk** plants could methylate them were they available. Thus the factor **k** is analogous to the recessive factor for alcaptonuria in man (Garrod, 1923) or to those for white and yellow hair in the rabbit (Onslow, 1915). In each case the recessive form seems to be incapable of carrying out an oxidation.

Nothing is known concerning the chemical nature of the pigment in **K vv** flowers. But the pink of the deepest such flowers might be taken for that of **G I K V** flowers, and it is very possible that it is due to primulin. While **kk V** flowers are pink in the bud, **K vv** flowers, even when subsequently pink, are white in the bud. **kk vv** flowers are generally white, but may have a faint tinge of coral pigment.

B has four manifest effects. It turns red into magenta and slaty into blue. It inhibits pigmentation in **vv** and **kk** plants. It also has a more general effect, discovered by Miss Scott-Moncrieff. It produces flavone which, though invisible, turns a bright yellow in ammonia. The effect is best seen on whites which lack anthocyanin owing to the presence of **D** and **gg**, or on the white parts of flaked (**ee**) flowers. In all these cases flowers known to be carrying **B** turn a bright yellow, **bb** flowers a pale dun. It is thus possible to score **B** with certainty in a number of cases where this was not formerly practicable. The reaction is equally clear on **kk** plants, whose anthocyanin disappears in ammonia vapour, so that **B** can be scored by this means. On the other hand **vv** plants, even when of composition **BB**, never give a bright yellow. Reds and slaties turn blue in ammonia vapour, while magentas and blues give a dark green, due to a mixture of blue anthocyanin and yellow flavone. Another effect of **B** is shown by the fact that **bb rr** (slaty) flowers always, and **bb RR** (red) occasionally, contain solid crystals of anthocyanin which give them a somewhat matt appearance to the naked eye.

B probably produces a blueing "co-pigment" similar to that described by Robinson and Robinson (1931) which changes the colour of primulin, regardless of the *p*H (cf. Scott-Moncrieff, 1932). This substance may or may not be identical with the flavone, but we regard their identity as probable. Secondly it appears that on the whole plants with **B** contain less anthocyanin than corresponding plants lacking it. This is most obvious in the **vv** and **kk** series, but dark reds also appear to be darker than the darkest magentas, and may contain more pigment. This is in harmony with the fact that solid anthocyanin is found in some **bb**, but no **B** plants.

From the point of view of pure genetics, the main results of these chemical investigations are that in families which are all **bb**, **kk bb R** and **kk bb rr** plants can generally be distinguished with certainty. **B** can also be distinguished from **bb** on **D gg** whites, flakes and **kk** plants. On the other hand little help is afforded in the analysis of **vv** plants, and we cannot always be sure of the distinction between **kk B R** and **kk B rr**, both of which may have very little anthocyanin.

The action of **R** is not so clear. Robinson and Robinson (1931) have made the suggestion that the difference in colour between magenta and blue flowers can be accounted for by co-pigment action. The blue flowers, they think, contain less anthocyanin, and hence the action of the same amount of co-pigment is greater.

This suggestion can, we think, provisionally be rejected on three grounds. While a light blue such as "Reading Blue" has rather little anthocyanin owing to inhibition by **G**, a dark **gg ii** blue appears to contain more anthocyanin than a light **G I** magenta. Secondly the effect of **R** is quite clear on **bb** plants, which do not contain the only co-pigment so far known in *Primula sinensis*. The Robinsons' explanation would thus require the presence of a second co-pigment. This is not of course impossible, but we do not care to postulate it. Finally, as Scott-Moncrieff (1932) has shown, factors altering the colour of anthocyanin do not always act by means of a co-pigment, but may produce changes in the anthocyanin molecule.

Miss Scott-Moncrieff takes the view that **rr** plants contain appreciable quantities of a bluer anthocyanin along with primulin. In this case the blue *Primula sinensis* would be analogous to the recessive blue *Primula acaulis*. This theory, however, does not offer a very clear explanation of the absence of pigment in **kk rr** plants.

A third possibility, which we think should be kept open, is that **R** acts by causing an increase in the acidity of the petal cell sap, as compared with **rr**. Blue (**V K B rr**) flowers placed in acetic acid vapour become magenta, slaty blue (**K V bb rr**) becoming red. The pale **V kk bb rr** flowers become coral pink in acetic acid vapour, while equally pale **V kk B R** flowers do not. Again, while red flowers turn blue in ammonia vapour, coral flowers lose their colour almost completely, in correspondence with the fact that **V kk bb rr** has much less colour than **V kk bb R**, though the hue is similar. Blue and slaty flowers are purplish in the bud, becoming bluer in the winter, a process which could be compared with the loss of acidity by fruit during ripening. But during the summer they never turn fully blue, remaining purple.

The facts seem, therefore, consistent with the view that **R** acts by producing an acid in the petal sap. It might act by producing some other substance which alters the state of ionisation of the anthocyanin molecule in the same way as do hydrogen ions. Such an action would be analogous to the well-known "protein error" and "salt error" of indicators. It is hoped that further chemical data will be available in 1934 which will make a decision as to the nature of the action of **R** possible.

So far we have only described **JJ** plants. **J j** flowers are similar but much paler when young. **jj** flowers open almost white, but later develop the peculiar white-edged pattern known as "Sirdar." The central part of the flower is almost as deeply coloured as in **JJ** plants, and both anthocyanin and flavone pigments seem to be the same. There is rarely any difficulty in distinguishing magenta from red, or blue from slaty. Both **J j** and **jj** are generally distinctly paler when grown at about 70° F. than when grown at about 50° F., but this effect does not always occur. **jj kk** flowers are sometimes a pale coral pink, but all **jj vv** flowers so far observed have been pure white. The white fern-leaved "Snowdrift" variety with which much work was done in the past, especially by Gregory, was **jj vv**, and its analysis proved difficult.

D and **G** may be considered together. Both are inhibitors of anthocyanin, but not of flavone. **G** inhibits anthocyanin completely in the stigma and tube, and makes the centre of the flower very pale. Its inhibitory effect extends to the periphery, which is always paler in **G** than in **gg** flowers. It has much the same effects on **vv**, **jj** and **kk** plants, but in view of the small and uncertain amount of colour in **vv** and **kk**, it could not always be detected by examination of the petals only. **D** is a somewhat stronger inhibitor than **G**, but its effect is greatest at the periphery, and diminishes inwards, having no effect at all on the stigma. Thus **DD gg** plants are magenta-centred whites, and **dd G** white-centred magentas. **D** appears to exert its full effect on **vv**, **jj** and **kk** plants. **G** is fully dominant in the diploid, but **D** is incompletely so in presence of **gg**. **D d gg** plants are magenta with a darker centre and a flush of colour extending to the edge. **DD gg** is known commercially as "Duchess," and **D d gg** was at one time sold as "General Buller." **D** and **G** together give a pure white, between them inhibiting all colour. **D** appears to be completely dominant in presence of **G**. However in some families **D G** plants may have a very pale flush. It is not known with certainty whether in these families **DD G** flowers are paler than **D d G**.

We can give a provisional account of the biochemical action of these factors, as follows:

V increases the yield of anthocyanin throughout the plant, and of flavone in the flowers.

J has a similar action to **V**, but less marked in the centre of the flowers.

B increases the yield of flavone and of a blueing substance which may be identical with flavone, at the expense of anthocyanin.

K completes the oxidation of anthocyanin or its precursor. It has no action on flavone.

R increases the acidity of the petal sap.

D inhibits anthocyanin (but not flavone) peripherally.

G inhibits anthocyanin (but not flavone) centrally.

I has been very little investigated, and it is not even known with certainty that the factor described as **I** is the same in all cases. It has a moderate effect in presence of **B**, but much more marked on **bb**. Plants carrying it have lighter flowers than those without, but the depth of colour seems to be equally affected in all regions. The lightening effect is best seen on reds (**V K bb**), green-stemmed pinks (**vv K bb**) and corals (**V kk bb**). All the commercial varieties of the latter two types, such as "Queen of the Pinks" (**vv KK bb**) and "Coral" (**VV kk bb**) prove to be of composition **ii**. If they are crossed with a pale red (**VV KK bb II**) about one-quarter of the reds appearing in F_2 are deep red (**V K bb ii**) and three-quarters of the green-stemmed or coral-stemmed F_2 are paler than the corresponding grandparent, owing to the presence of **I**. **I** can be scored (with some difficulty) even in presence of **B** on normal stems, but in **vv** and **kk** plants this is impossible. In presence of **V** and **K** it can be scored on **rr** plants (blue and slaty).

L has a slight diluting effect on the colour of **R** flowers, though less marked than that of **I**, so that it would not be possible to score **L** by its effect on the intensity of flower colour. In presence of **G** it also slightly contracts the coloured area, so that small white patches appear between the yellow eye and the peripheral area in which the sap is coloured. The effect is much more marked on **rr** flowers. The pigment is here irregularly distributed so as to give a quite characteristic mottled effect[1]. The effect on **kk bb R** flowers is also quite characteristic. In presence of **ll** their pigment is concentrated in the peripheral part of the petals, which are rather darker than in sister plants carrying **L**. **kk ll** plants are definitely less healthy than **K ll** or **kk L**. They germinate normally, and can be scored by their characteristic stem colour, but tend to "damp off" during the flowering period.

e is an unstable factor, occasionally mutating back to **E**. If **ee** plants are selfed, a proportion which may reach 1 per cent. in certain families are fully coloured, and of composition **E e**. The remainder are flaked. On normal stemmed plants (*i.e.* **V JJ K**) the flakes may be magenta, red, blue or slaty according to the factors carried. The number and size of the flakes is greatly influenced by **G**. **gg ee** plants have numerous flakes, ranging from small areas up to whole petals, or occasionally whole flowers. **G ee** may at first sight be pure white, though a careful search over several flowers will generally reveal a few small flakes. But **G** is not the only factor determining the degree of flaking. It is not yet known whether the differences between the different **G ee** plants are determined by modifying factors, or by the presence of several allelomorphs of **e**. The flavones appear to be normal in the white parts of **ee** flowers, the effect of **B** being clearly marked.

ee plants show clear flaking in presence of **kk**, and on **jj gg**, though

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[1] See Plate XI, *Journ. Gen.* **13**, No. 2.

ee jj G is nearly white. But a strain of plants obtained from the late Mr Elwes of composition **jj gg ee** generally has white flowers, though when first obtained it had a faint colour. It would appear that some unanalysed factor is suppressing the pigment in this case. **vv ee** plants are generally white flowered, but very occasionally a flake can be seen.

E is possibly allelomorphic with **D**. So far all attempts to obtain **D d ee** plants by crossing **gg D E . d e** and **gg d e . d e** have failed. This may be due to very intense linkage. If it is due to allelomorphism the relation of the factors is unique. By analogy with other plants, and with *Drosophila* (Demereč, 1928) one would expect **e** to be allelomorphic with a recessive rather than a dominant white.

hh plants[1] have the two or three outer petals much paler than the inner. Especially in older plants the pale petals tend to be small (see Gregory, de Winton and Bateson[2]).

Flower plastids and leaf and petal edge.

It will be seen that many of the factors affecting the plastids also affect the edge of the petal and leaf, and conversely. Some of them have other effects which will be considered separately. Further, some of the factors mainly affecting leaf shape may alter the degree of serration of the petals. These also will be considered later.

The four main sets of allelomorphs concerned are **Ch–ch**, sinensis-stellata, **P–p**, normal eye–peculiar eye, $\mathbf{F}$–$\mathbf{f^s}$–$\mathbf{f^l}$, flat-Sutton's crimp–Lee's crimp, **A′–A–a**, white eye–normal eye–large eye. The interactions of these factors, apart from **A′**, are set out in Table VII. In addition **Y** has a slight effect on the eye. **Ch** never affects the size of the eye, its only effect on the leaf edge is to intensify the crimping due to $\mathbf{f^s}$ and $\mathbf{f^l}$. It has a very marked effect on the petal edge, both by itself and in conjunction with other factors. **P** on the other hand has its main effect on the eye, a slight effect on the petal edge, and none on the leaf edge. The **F** group of allelomorphs affects all three characters, but the effect of $\mathbf{f^s}$ on the leaf and petal edge in **chch** plants is very slight. **A′** inhibits the eye, but has so far had no effect on structure. The main effect of **aa** is to produce a large eye. The leaves are generally flat, but in some F_2 families the **aa** plants have had very slightly crimped leaves. It is not known what other factors are responsible for this effect. On the other hand **aa** has the curious effect of increasing the crimping of the leaves and petals of $\mathbf{Ch\ f^sf^s}$ plants to that characteristic of $\mathbf{ch\ f^lf^l}$.

A few further details are as follows. The **pp** flower has a slightly

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[1] See Plate XII, *Journ. Gen.* **13**, No. 2.

[2] *Ibid.* p. 229.

larger and greener eye than **P**. The amounts both of plastids and anthocyanin in the tube are increased. There is sometimes a small effect on the flower shade. The tube is more constricted at the bottom, and opens more gently at the top. In **Ch ch** and **chch** plants the petals are rolled back (Fig. 5), but this is not so in **ChCh** (Fig. 4). Occasionally a single petal may be quilled in **P p** plants. The tube and back of the petals are distinctly more hairy in **pp**.

TABLE VII.

Genotype	Eye		Degree of crimping of leaf edge		Flower edge	
Ch P F A	Normal	1	None	0	Serrated	2
ch P F A	,,	1	,,	0	Smooth	0
Ch p F A	Peculiar	3	,,	0	Deeply serrated (**Ch ch** quilled)	3
ch p F A	,,	3	,,	0	Smooth (quilled)	0
Ch P f^{s} A	Lobed	2	Slight	1	Serrated	2
ch P f^{s} A	,,	2	Very slight	0–1	Smooth-slight fringe	0–1
Ch p f^{s} A	Peculiar	3	Slight	1	Deeply serrated	3
ch p f^{s} A	?		?		?	
Ch P f^{l} A	Large	4	Very crimped	3	Very serrated	4
ch P f^{l} A	,,	4	Crimped	2	Fringed	1–2
Ch p f^{l} A	Large and green	6	Very crimped	3	Very deeply serrated (deformed)	5
ch p f^{l} A	,, ,,	6	Crimped	2	Fringed and quilled	1–2
Ch P F a	Primrose Queen	5	Generally flat	0–1	Serrated	2
ch P F a	,,	5	,,	0–1	Smooth	0
Ch p F a	Primrose Queen peculiar	6	,,	0–1	Deeply serrated	3
ch p F a	,,	6	,,	0–1	Smooth (quilled)	0
Ch P f^{s} a	Primrose Queen	5	Crimped	2	Serrated	3
ch P f^{s} a	?		?		?	
Ch p f^{s} a	?		?		?	
ch p f^{s} a	?		?		?	
Ch P f^{l} a	Primrose Queen large	7	Very crimped	3	Very serrated	4
ch P f^{l} a	,,	7	Crimped	2	Fringed	1–2
Ch p f^{l} a	?		?		?	
ch p f^{l} a	?		?		?	

A morphological account of the crimped leaf, with its enormous overdevelopment of hydathodes, is given by Gregory, de Winton and Bateson (1923, p. 223). **Ch f^{l}f^{l}** and **Ch f^{l}f^{l} aa** flowers are so seriously deformed as to cause a good deal of sterility. The calyx is much enlarged, the number of teeth rising to as many as a hundred; the flower is large in **Ch f^{l}f^{l}**, but **Ch f^{l}f^{l} aa** is generally small, and falls off at an early stage. It is almost wholly covered by the eye, so that the sap colour can only be scored with difficulty.

Dominance is generally complete throughout the group, with the exceptions noted, but **F f^{s}** and **F f^{l}** can sometimes be picked out. **A′ A F** has a small "ghostly" eye; **A′ a F**, **A′ A f^{l}f^{l}** and **A′ a F pp** large ghostly eyes. The few plastids remaining are arranged in lines radiating outwards from the tube over the area which they would cover in the absence of **A′**.

A fourth factor affecting eye size possibly exists. In a family in 1930 from **A a** selfed one **aa** plant had a "ghost" eye, in which the pigment was faint over the whole large eye, instead of in lines as in **A′ a**. The plant bred true, and the condition disappeared on crossing, but very few came back in F_2. It is being investigated further.

The effect of this group of factors on bracts, stigma and habit will be discussed later.

Leaf structure, and correlated variations of flower structure.

Apart from $\mathbf{f}^{s}$ and $\mathbf{f}^{l}$, leaf shape is affected by the five well-studied factors **Y**, **O**, **T**, **Mp**, **Iv** and two which have only recently appeared, namely **C** and **Z**. Other factors affect it slightly, and the above leaf-shape factors may affect petals, calyx, bracts and general habit. These five factors were present in the original plants, the abnormal forms being recessive. **iv** has unfortunately been lost. The other six can form 64 homozygous combinations, of which only a minority have yet been made. In addition certain heterozygous types are distinguishable.

yy (fern, Fig. 44) plants are described by Gregory, de Winton and Bateson (1923). The leaf is longer than in **Y**, there being about eight lateral lobes on each side, shorter than the normal type, and the general type being pinnatifid. The general effect of **Y** is much the same in all combinations, and there has never been any doubt in scoring it. Dominance is generally complete in the diploid, but heterozygotes sometimes have a small extra lobe at the base of one or more leaves. The genetics of this phenomenon are under investigation. **yy** does not affect petal shape, but renders the eye slightly more angular.

oo (oak, Fig. 41), also described by Gregory, de Winton and Bateson, has deep sinuses. There are generally one apical and two lateral lobes, the posterior lobes being almost separated to form independent leaflets. Scoring is always easy, and dominance nearly complete except in the presence of **tt**. However the heterozygotes on the whole have a rather deeper sinus than **OO**. But the difference is not sufficient to make separation of **OO** and **O o** possible. **oo** flowers are abnormal only in presence of **Ch** (see p. 16) when the petals are deeply serrated, and the calyx enlarged.

tt (tongue, Fig. 39) is the "ivy" of commerce. By itself it has less effect on the leaf than the other factors here considered. The leaf has an unusually broad base, and the individual lobes are more serrated and less pointed. A small basal lobe is sometimes partly separated from the main leaf. This separation is often more marked on one side of the leaf than the other, so that the leaf as a whole is asymmetrical. Scoring is easy and dominance very nearly complete. **tt** flowers are only abnormal in presence of **Ch**, when the petals are elongated and the calyx teeth reduced.

mpmp (maple, Fig. 38) leaves are semi-glabrous, the sinuses between the lobes are generally deeper and always less sharp, so that the lobes stand out more clearly. The cuticle appears to differ from the normal, and the veins are more easily visible. Possibly as a result of their lack of hair, maple leaves are commonly attacked by aphids under circumstances when other varieties are free from them. Dominance is very nearly complete. In presence of **Ch** the calyx has an abnormal shape.

iviv (ivy, Gregory, 1911) leaves were characterised by an absence of serration, and a general leaf shape not unlike **tt**. The flowers were much reduced, and seed rarely set before the second year. Unfortunately it was lost before it had been crossed with any leaf shape except **yy** (fern). We do not know, therefore, whether it may not have been an extreme allelomorph of **t**, to mention one possibility. The original **iviv** was proved by breeding to be **chch**, and in F_2 it was not possible to distinguish **iviv Ch** from **iviv chch**, which suggests effects on habit.

cc (cup, Fig. 11) has only recently appeared, but seems to be behaving as a recessive. The margins of the leaves are usually upturned, but the shape is otherwise normal. Growth is poor, and the plants may not flower, but when they do so the flowers, though rather small, are of normal shape whether **Ch** be present or not.

zz (claw, Fig. 12) appeared in an F_2 from an X-rayed plant, and may be an induced mutant. It appears to be a normal recessive. The sinuses are very deep, and the leaves are rolled up with concavity downwards, giving the impression of a hand with claws. The dorsal surface of the leaves may show a curious crest. Floral structure is nearly normal.

Neither **c** nor **z** has yet been combined with **y**, **o**, **t** or **mp**. Thirteen of the 16 possible combinations of **y**, **o**, **t** and **mp** are now known, besides heterozygous forms. A probable linkage between **O** and **Mp** has for the moment delayed progress. All the nine combinations of **y**, **o** and **t** are known. **yy oo T Mp** and **yy O tt Mp** are as expected. The leaves are long and narrow as in fern (**yy O T Mp**), and the main effect of **oo** or **tt** is on the shape of the lobes and the depth of the sinuses (Figs. 48 and 49). **Y O o tt Mp** occasionally differs markedly from **Y OO tt Mp**, the leaves being much more dissected, but not all such heterozygous plants are abnormal. The reasons for this fact are under investigation. **Y oo tt Mp** has very abnormal leaves (Fig. 53), the leaf consisting of a number of irregular narrow lobes, and its total surface being a good deal reduced. On the other hand **yy oo tt Mp** (Fig. 46) has leaves of a much more normal appearance, the general shape being fern, and the lobes being well separated (effect of **oo**) and pointed (effect of **tt**) but not much reduced in size. The effect of **yy** on **oo tt** is thus to restore a physiological balance.

yy O T mpmp (Fig. 51) is as expected, a semi-glabrous fern with well-separated lobes. **Y oo T mpmp** (Fig. 47) combines the oak and maple characters, the general shape of the leaf being oak, but the pattern is somewhat simplified. **Y O tt mpmp** (Fig. 52) has semi-glabrous leaves with rather little serration. They tend to curve downwards, as if the dorsal surface grew faster than the ventral. **yy OO tt mpmp** (Fig. 54) has the same type of leaf, but longer and narrower. **yy oo T mpmp**, **Y oo tt mpmp** and **yy oo tt mpmp** have not yet been obtained. The effect of these factors on the flower is on the whole additive.

yy, **oo**, **tt**, **mpmp** and some of their combinations have been combined with **f^lf^l** (Lee's crimp) and some also with Sutton's crimp. Fern crimp (Fig. 45) and tongue crimp call for no comment, but **oo ff** (Fig. 42) and **mpmp f^lf^l** (Fig. 50) differ from the corresponding **F** forms rather by overgrowth of the leaf than by actual crimping. The deepness or broadness of the sinus gives the different lobes and serrations an opportunity to overlap with relatively little folding of the leaf.

Finally the leaves of **ll vv** are slightly abnormal. They are unusually small, though the petioles may be of normal length. Also the sinuses are somewhat more open than usual. As pointed out above, such plants are always female-sterile, and dwarfism is not uncommon.

Flower structure.

The effects of the factor **S** and **s** are fully discussed by Gregory. Other factors affecting flower structure are **Ch**, **f^s**, **f^l**, **p**, **m**, **a**, **o**, **t**, **mp**, **w**, **iv** and **n**. Those of **f^s**, **f^l**, **p**, **t**, **mp** and **iv** have been described. **SS** and **S s** plants have short styles and long stamens (thrum), while **ss** (pin) have long styles and short stamens. The relation of **S** and **s** to fertility is still obscure. The difference in fertility between **ss** × **ss** (or **ss** selfed), **S s** × **ss**, **ss** × **S s**, and **S s** × **S s** (or **S s** selfed) is not very marked. Darwin found considerable differences in favour of the "legitimate," *i.e.* pin × thrum and thrum × pin. The fact that for many years no thrums have been grown by English horticulturists may have caused an accumulation of modifying factors favouring the fertility of **ss** × **ss**. One important fact however is that all attempts to establish a pure line of **SS** plants have failed. Such plants exist and will produce offspring when selfed. But lines derived from them have always developed sterility.

xx plants are sterile doubles, described by Gregory, de Winton and Bateson (1923). All the stamens are converted into petals, and the gynaecium is generally split open. So far five viable seedlings have been obtained from such plants. Three of these were diploids, from a cross with a diploid. The character behaved as a normal recessive. In addition two fertile, and therefore presumably tetraploid, seedlings were obtained with tetraploid pollen. One of these plants was thought by Gregory, de Winton and Bateson to have been a diploid. As, however, it set good seed with tetraploids, and failed with diploids, it was clearly a tetraploid.

mm plants (described by Gregory) typically possess an extra whorl of petals, set in the throat of the tube. These are reversed, *i.e.* the external side resembles the outside of the normal petals. In **mm ss** plants the style is long, but the anthers are attached near the opening of the tube. This is a much more constant character than the extra petals. In plants proved to be **mm** the extra petals may almost disappear late in the season, or more rarely, may never appear except as rudiments. Such plants are homostyled, with typical **ss** pollen. If regard is paid to the position of the anthers, there is never any difficulty in scoring **m** on **ss** plants. The effect of **mm** on the position of the anthers in **S** plants is less marked. Dominance is rarely complete, a small extra petal occurring on one or more flowers of a heterozygote.

Ch, besides causing fringing and enlargement of the petals, increases the number of calyx teeth from five to ten or more (unless counteracted by **tt** or **mpmp**) and gives the whole plant a more compact habit, the heterozygote being intermediate in this respect (cf. Gregory). As pointed out, it intensifies the effects of many other factors.

aa plants have a shorter style than the corresponding **AA** or **A a**. In fact the effect of **A** on style length is more marked than that of **S**. Thus in a group of comparable sister plants the following lengths in millimetres were found:

S A	5 – 6·5	Average	5·8	Thrum
ss A	10·5–12	,,	11·3	Pin
S aa	2 – 3	,,	2·5	Thrum
ss aa	3·5– 4	,,	3·6	Homostyle

In addition the stigma and ovary in **aa** plants tend to be pointed instead of flat-topped (see Fig. 1), but these characters are not very constant, even among the flowers of the same plant. On the other hand the position of the anthers is unaffected by the presence or absence of **A**, and depends entirely on **S**. In consequence **ss aa** plants are homostyle, whilst **S aa** are not obviously different in structure from ordinary thrums, except as regards the shape of the stigma and ovary. **A′** has no definite effect on flower structure.

oo chch flowers are normal save for a slight bulging of the calyx, but **oo Ch** flowers are always different from **O Ch**[1]. The petals are generally much incised, and may be split to the base. They are generally smaller than normal, and may resemble **O chch** petals. Their bases never overlap, as in **O Ch**. The calyx is enlarged; the number of teeth exceeds ten. It may tend to close tightly round the ripening capsule, or it may be everted (Fig. 2). The genetical basis of this difference is under investigation. The effect of **oo** on the petals is greatly augmented by **pp** provided **Ch** is present. But **oo** has little effect on **chch pp** flowers.

tt chch flowers are nearly normal, but **tt Ch** (Fig. 17) have typical elongated petals, the serration being reduced. The number of calyx teeth is also reduced, and in **Ch ch** plants may fall as low as four to six, but the individual teeth are serrated. The calyx is conical and the bracts simplified. On the whole the effect of **tt** is a partial neutralisation of the effects of **Ch** on the flower, however the elongated petals are characteristic. While **pp tt chch** flowers are like those of **pp T ch**, the petals of **pp tt Ch** are abnormal (Fig. 18), being long and narrow.

mpmp flowers have short pedicels, but otherwise are only abnormal in presence of **Ch**. In the **mpmp Ch** plant the number of calyx teeth is often less than ten, and the calyx has a peculiar inflated appearance, being broad at the base, and opening with some difficulty.

Though **yy** and **yy oo** flowers are normal, the petals of **yy oo Ch pp** are divided into a series of lobes not unlike those of the "oak" leaf (Fig. 24). So far this is the only combination in which **yy** has much effect on flower structure.

tt oo chch flowers are nearly normal, but **tt oo Ch** resemble those of **T O chch**, though they are set farther apart, so that there are large gaps between them. The eversion of the calyx often found in **T oo Ch** is exaggerated in them. The presence of **oo**, and even **O o**, exaggerates the abnormality of **pp tt Ch** petals, and those of **pp tt oo Ch** resemble

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[1] See Plate XVI, fig. 33, Gregory, de Winton and Bateson (1923).

the leaves of the oak tree in shape (Fig. 7). They are one of the most aberrant petal types so far obtained.

tt mpmp flowers combine the effects of the two factors without any particular exaggeration. **oo mpmp** has so far only been obtained in combination with **chch**.

zz plants, so far only obtained in combination with **chch**, have normal petals, but the calyx is abnormal, its base being more rounded than in any other variety of the species, and the calyx teeth everted.

ww plants have two types of flower (Fig. 3). In the original family the corolla was of about half the normal radius, the calyx being normal in size, in spite of dwarfing of the leaf and stem. This type breeds true. But when such plants are outcrossed to several types of normal, a majority of the **ww** plants in F_2 have a corolla reduced to little more than the tube. The genetical relationship of the two types is under investigation. Both types are fully fertile, if allowance is made for the fact that a number of plants die off between flowering and setting seed.

iviv plants had very much reduced flowers, and were rarely fertile in their first year. An account of these flowers is given by Gregory (p. 89).

nn plants invariably have greatly enlarged bracts and flowers. The flowers of **N n** plants are also abnormally large, and it is probably for this reason that commercial plants often prove to be **N n**. The flower structure of **nn chch** plants is normal, but **nn Ch** flowers of the short-stemmed types have large calyces. The enlargement may be moderate, or may give rise to leaf-like structures. These roughly resemble the leaves of the same plant, *i.e.* are controlled by the same factors.

Habit.

Apart from the semi-lethal dwarfing factors **c** and **w**, and other hitherto unanalysed dwarfs, the main factors affecting habit are **Ch**, **N**, **Q** and **U**.

ChCh has a compact habit, **chch** open, while **Ch ch** (var. *pyramidalis*) is intermediate.

nn plants fall into three main types (Fig. 10), all characterised by very large bracts. Type 1 is very compact with a short flower stem and large flowers, the first to open having unusually large calyces. In addition to this normal spike, which never sends up a second tier of flowers, type 1 has three flowers on long pedicels coming from the base of the plant, all with enormous leaf-like calyces. The first bracts are also very large and inserted at the base and could easily be taken for leaves. Type 1 **chch** has not been identified with certainty.

Type 2 has a stem of normal length. The flowers are large, though not as large as in type 1. The calyces are only leafy in presence of **Ch**. The bracts are very large, but could hardly be taken for leaves, if only because they are inserted well up the stem.

Type 3 is intermediate. Some flowers are borne on the main stem as in type 2. Others are borne on single stalks arising from the base.

The genetical relationship of these types is not yet quite clear. Type 1 breeds true, and in an F_2 from type 1 and **NN** most of the **nn** plants belong to types 2 and 3. Type 1 can be recovered again in F_3. It thus seems likely that type 1 differs from the normal by possessing **nn** and at least one other pair of recessive factors, which make little difference to **N** plants, and are to be regarded as specific modifiers of **nn**.

qq plants have a rosetted habit, with more and smaller leaves than **Q**. The central flower spike is normal, but there may be many smaller spikes clustering round. In **Q** plants there are seldom more than two or three spikes in flower at a time, all being normal in height.

Two fasciated plants first appeared in an F_2 from **qq** by normal. They had the general character of **qq** plants, except that the stem was large and flat, the flowers being more crowded together than in normal plants. On selfing one of these plants a wide range of variation was obtained, ranging from normal, apparently **Q** plants, to cushions of small leaves which never threw up a flowering spike (Fig. 9, class 3). On further selfing normal plants were obtained on the one hand, also a moderately stable line of fasciated plants. On selfing these give a range from rosetted plants like ordinary **qq** to cushions which do not flower. However, the majority are intermediate, with numerous small leaves, and a stem which is generally thickened and may show various kinds of fasciation, including occasional hollow stems (Fig. 8), such as are common in fasciated *Pisum*, *Campanula* and other plants (cf. Worsdell, 1929). This ring fasciation is, however, rare.

The tip of the scape in fasciated plants almost always ends in a patch of rudimentary stigmata, sometimes accompanied by small leaf-like structures. These take the place of a second tier of flowers.

The factorial basis of fasciation is not yet clear. However, on crossing to normal the F_1 is quite normal, and in F_2 about 18 per cent. of fasciated plants has been obtained, including extreme forms. We have provisionally ascribed fasciation to a single recessive factor **u**. If this is so it is certain that other factors are concerned. At present no simple hypothesis will cover all the facts. It is hoped that it may be possible to find linkages for one or more of the factors concerned, in which case analysis will be easier. Meanwhile we assume a main recessive factor **u**, though the assumption is quite provisional.

Bract form.

The systematic study of bract form was begun by Dr Edgar Anderson, to whom we are much indebted for allowing us to use his material. Bracts fall sharply into two classes, namely small bracts up to 0·6 cm. in length borne on **N** plants, and large bracts borne by **nn** plants.

Apart from **N**, bract form depends on **Ch**, **P**, **F**, **Y**, **O**, **Mp** and **T**. The standard (**chch**) bract varies in different lines. The bracts are always small, and have from one to four lobes. They tend to be narrow in **yy** plants, and to have more lobes in $\mathbf{f^1f^1}$ and **pp** plants. But it would be very difficult to classify a **chch** plant by its bracts.

On **Ch** plants the bracts are larger, and particularly broader, and have usually five to eleven lobes. **p** and **f** tend to make the lobes narrower and more pointed, **y** more narrow, **oo** to reduce the number of lobes. The most striking effect is the great reduction of lobes due to **tt**. They may be reduced to mere serrations. **T** is probably the only factor which can be detected with complete certainty on **N Ch** bracts.

The bracts of **nn** plants are large structures, often exceeding 15 cm. in length in type 1, where they may take on the full function of leaves. Indeed it is common to find type 1 plants a year old growing vigorously without any leaves, and assimilating with their bracts and calyces. The lowest bracts are most leaf-like, and in type 2 **nn Ch ch** or **nn chch** plants the bracts of the third tier of flowers may be quite normal.

The leaf-like bracts never resemble leaves completely, though they possess normal petioles. Those associated with normal "palm" leaves are generally asymmetrical, with extra lobes at the base, and rather more oblong than the normal leaf (Figs. 25 and 26). Crimp, fern, tongue, oak and maple leaves (Figs. 27–34, 36) are each associated with a corresponding type of leafy bract, easily recognisable, though generally distinguishable from the leaf. The most striking divergence is seen in the case of **tt oo pp** (Fig. 35), whose bracts commonly consist of a single strap-like lobe, while leaves have at least three lobes.

The gradation in bract types is well seen in type 3 plants. In the first tier the bracts are leaf-like, and their form is determined by the same factors as that of the leaves. **Ch** has no definite effect. In the third tier the bracts are only slightly larger than those of **N** plants, and their form is dominated by **Ch**, but seems also to be influenced by other factors in much the same way as in **N** plants. The bracts of the second tier are intermediate. We thus have the extremely interesting situation that a given organ is controlled by one or another set of factors according to its place on the plant. Putting the matter in another way, the assumption by the bracts of normal form and normal relation to other factors is delayed for some months in **nn** plants. This is, however, slightly misleading, as the bracts of the first tier on a second spike are distinctly more leafy than the second and third tiers on the first stem, which appeared earlier.

Single factor ratios.

Tables VIII–X show the single factor ratios so far recorded from 1905 to 1931 inclusive. They cover the offspring of all plants known from their parentage to be heterozygous, *i.e.* derived from a cross of dominant by recessive and conversely. A large number of matings of heterozygotes of less well-authenticated pedigree yield similar results.

TABLE VIII.

Single factor segregation from mating **X x** × **xx**.

Factors	No. of families	**X x**	**xx**	D	σ	P	k
S–s	123	3459	3552	+ 46·5	41·8	0·27	+0·027
B–b	236	5614	5475	– 69·5	52·7	0·19	–0·025
G–g	263	7281	6791	–245	59·1	0·00003	–0·065
L–l	96	3223	3093	– 65	42·5	0·13	–0·040
V–v	13	742	669	– 36·5	18·8	0·05	–0·098
F–f^{s}	1	26	18	– 4	3·32	0·23	–0·31
F–f^{l}	46	2117	1834	–141·5	31·4	0·000007	–0·134
Ch–ch	119	4962	4828	– 67	49·5	0·18	–0·027*
P–p	26	1427	1420	– 3·5	26·7	0·89	–0·005?
D–d	60	1498	1523	+ 12·5	27·5	0·65	+0·017*?
E–e	11	253	253	0	11·2	1·0	0
Y–y	3	44	43	– 0·5	4·67	0·86	–0·023?
M–m	22	492	458	– 17	15·4	0·36	–0·069
W–w	5	40	14	– 13	3·67	0·0004	–0·65
R–r	9	315	284	15·5	12·2	0·20	–0·098
K–k	21	389	407	+ 9	14·1	0·12	+0·046
J–j	2	69	74	+ 2·5	5·98	0·68	+0·072?
j–J	1	4	5	+ 0·5	1·50	0·74	+0·25?
Q–q	3	50	28	– 11	4·42	0·013	–0·44?
A′–A	95	3062	3255	+ 96·5	39·7	0·015	+0·063*
A–a	25	558	555	+ 1·5	16·6	0·93	–0·005?
O–o	6	111	112	+ 0·5	7·47	0·95	+0·009?

In these tables the fifth column gives the divergence D from expectation. A positive sign means that the number of recessives exceeded that expected. The sixth column gives σ, the standard error of the expectation. In a population of n expected to be segregating 1:1 this

TABLE IX.

Single factor segregation from mating **xx** × **X x**.

Factors	No. of families	X x	xx	*D*	σ	*P*	*k*
S–s	87	2898	2733	− 82·5	37·5	0·028	−0·057
B–b	111	3295	3167	− 64	40·2	0·11	−0·039
G–g	122	4012	3767	−122·5	44·1	0·006	−0·061
L–l	61	1965	1952	− 6·5	31·3	0·83	−0·007 ?
V–v	5	59	46	− 6·5	5·13	0·20	−0·220
F–f^{s}	1	32	47	+ 7·5	4·44	0·09	+0·47
F–f^{l}	28	816	608	−104	18·9	4×10^{-8}	−0·255
Ch–ch	64	2577	2290	−143·5	34·9	0·00004	−0·111*
P–p	26	1217	1243	+ 13	24·8	0·60	+0·021 ?
D–d	28	581	646	+ 23·5	17·5	0·18	+0·101*
E–e	6	202	237	+ 17·5	10·5	0·10	+0·173
M–m	24	264	255	− 4·5	11·4	0·69	−0·034 ?
R–r	6	181	163	− 9	9·28	0·33	−0·099
K–k	22	176	151	− 12·5	9·04	0·17	−0·142
J–j	3	198	217	+ 9·5	10·2	0·35	+0·088
j–J	30	472	521	+ 24·5	15·8	0·12	+0·138
Q–q	3	20	10	− 5	2·74	0·07	−0·50
A′–A	56	1513	1457	− 28	27·3	0·30	−0·38*
A–a	4	45	42	− 1·5	4·66	0·75	−0·067 ?
O–o	7	154	145	− 4·5	8·65	0·60	−0·059 ?

TABLE X.

Single factor segregation from **X x** *selfed or mating* **X x** × **X x**.

Factors	No. of families	XX + X x	xx	*D*	σ	*P*	*k*
S–s	83	5096	1879	+135·25	36·2	0·0002	+0·162
B–b	114	9072	3082	+ 43·5	49·7	0·38	+0·019
X–x	4	170	72	+ 10·5	6·74	0·12	+0·247
G–g	180	14386	4584	−158	59·6	0·01	−0·044
L–l	134	10188	3341	− 41·25	50·4	0·41	−0·016
V–v	78	4548	1481	− 26·25	33·6	0·43	−0·023
F–f^{s}	9	839	201	− 59	14·0	0·00003	−0·281
F–f^{l}	75	5184	1609	− 89·25	35·8	0·013	−0·067
f^{s}**–f**^{l}	5	536	200	+ 16	11·7	0·17	+0·119
Ch–ch	187	14861	4962	+ 6·25	35·2	0·86	+0·002* ?
P–p	22	2115	748	+ 32·25	23·2	0·161	+0·061
D–d	93	6177	2010	− 49	39·2	0·21	−0·024
d–D	9	374	139	+ 10·75	9·81	0·27	+0·115
E–e	31	2444	782	− 24·5	24·6	0·32	−0·040
Y–y	58	3786	1184	− 58·5	30·5	0·05	−0·062
M–m	86	5700	1699	−150·75	37·2	0·00005	−0·106
H–h	23	1573	418	− 79·75	19·3	0·00004	−0·203
W–w	8	601	62	−103·75	11·2	2×10^{-20}	−0·69
R–r	33	2242	666	− 61	23·4	0·009	−0·109
K–k	43	2164	683	− 28·75	23·1	0·21	−0·053
N–n	20	1740	562	− 13·5	20·8	0·51	−0·031 ?
J–j	32	2129	676	− 25·25	22·9	0·30	−0·047
j–J	32	2019	786	+ 59·75	22·9	0·009	+0·118
Q–q	14	1242	333	− 60·75	17·2	0·0004	−0·196 ?
A′–A	36	2611	864	− 4·75	25·5	0·85	−0·007* ?
A′–a	9	1668	560	+ 3	20·4	0·88	+0·007 ?
A–a	69	4069	1327	− 22	31·8	0·49	−0·022
O–o	37	2724	938	+ 22·5	26·2	0·39	+0·033
T–t	12	1095	378	+ 9·75	16·6	0·56	+0·036 ?
Mp–mp	6	724	202	− 29·5	13·2	0·026	−0·163
Iv–iv	17	1496	482	− 12·5	19·3	0·65	−0·033 ?
U–u	2	221	39	− 26	6·98	0·0002	−0·47 ?
I–i	2	240	61	− 14·25	7·51	0·06	−0·258

is $\frac{1}{2}\sqrt{n}$, in a population expected to be segregating 3:1 it is $\frac{1}{4}\sqrt{3n}$. From the value of $D \div \sigma$ we calculate from a table of the probability integral the chance P that so considerable a deviation could be due to sampling. In Tables VIII–X there are 75 ratios, so that we should expect, even if no causes were disturbing the Mendelian expectation, to find at least one value of P of 0·013, and three or four values where D exceeded 2σ, a criterion of significance commonly employed. On the other hand there is no serious doubt that divergences having a probability of 0·001 or less are not due to sampling errors.

But it does not follow that such divergences are due to the action of the factors segregating. A factor may give an abnormal ratio for three reasons. It may affect the viability of gametes or zygotes carrying it. The genotype may be variable in its expression, *e.g.* some genetically recessive plants may not show the character concerned. Or there may be linkage with other genes or chromosomal abnormalities which upset the ratios. Many examples of all three types of divergence are known in *Drosophila*. In most cases we can rule out the second possibility, at least as regards recent work. Thus **mm** plants do not always show a complete whorl of extra petals, but always have the anthers set high up in the tube of **ss** flowers. It is, however, possible that the low ratios found for **q** may at least in part be due to this cause. The other two both operate in the material presented.

The last column of Tables VIII–X gives an expression of the relative viability of the recessives. For each **n** recessives expected on the hypothesis that Mendel's laws are exactly followed $n\ (1 \times k)$ appear. The values of k are generally negative. An asterisk is used to denote the fact that the recessive factor is one present in the original type, and not a new mutant. In families where **D** and **J** are not fully dominant, **DD** and **JJ** can be scored as if they were recessives. Values of k which are doubtful because P is large, or scoring uncertain, are queried.

The factors giving grossly abnormal figures ($P < 0{\cdot}01$) are **s**, **g**, $\mathbf{f^s}$, $\mathbf{f^l}$, **Ch**, **m**, **h**, **w**, **r**, **q** and **u**. In the case of **s** and **ch** there was an excess of recessives, otherwise an excess of dominants, *i.e.* a greater viability of the normal type. These various cases must be examined individually.

In the case of **S** there is an insignificant excess of recessives from the mating **S s** × **ss**, a possibly significant defect from **ss** × **S s**, and a large and clearly significant excess from **S s** × **S s**. The obvious explanation is that **S** and **s** gametes and **S s** and **ss** zygotes have about equal viability, but that **SS** zygotes are at a disadvantage. It is certainly our experience that they are sterile. A line pure for **S** has never been kept in existence for many years on end. But if they were handicapped from the start we should expect to find evidence of it in the following case. **S** and **B** are linked, and from **S b . s B** selfed 81·4 per cent. of the **S bb** plants should be **SS**. To account for the shortage of **SS** + **S s** plants from **S s** selfed we should have to postulate that **SS** plants had only 71·2 per cent. of the viability of **S s** and **ss**, the latter being taken as equally viable. This would reduce the proportion of **bb** to 0·766 of the expectation. Actually the figures are 70 **S B**, 31 **S b**, 28 **s B**, 3 **s b**. We should thus expect 28 × 0·766 or 21·4 **S b**. There is no indication of a semi-lethal effect of **SS**. We propose to investigate the matter further.

gg zygotes are in serious defect in all three matings, and it seems probable that they are actually handicapped to the extent of about 4–6 per cent. There is no suggestion that **g** gametes of either gender are particularly handicapped.

The shortage of $\mathbf{f^s f^s}$ from $\mathbf{F\ f^s}$ selfed is probably an indication of low viability. Crimps are short in seven of the nine families, and the two exceptions are small families of 47 and 38 plants respectively. As, however, all the factors in the second chromosome give abnormal rates from time to time this may conceivably account for the phenomenon. There can be no reasonable doubt that Lee's crimp ($\mathbf{f^l f^l}$) is relatively inviable. The crimped plants in mixed families are slow growing and often look unhealthy. On the other hand the pure lines containing $\mathbf{f^l f^l}$ are quite vigorous and fertile when single (**MM**). It seems likely that they contain other factors which produce a satisfactory physiological balance. On out-crossing these factors are largely lost by segregation. Similar phenomena are common in *Drosophila*. Sutton's crimp does not appear unhealthy, but may well be so, though probably less than its more extreme allelomorph.

The figures for **Ch** are not, we think, significant of any difference of viability. Let us consider the cross **chch** × **Ch ch** which gave the most aberrant figures. From 1905 to 1920 this cross gave 1147 **Ch**, 1248 **ch**; from 1921 to 1931 it has given 1430 **Ch**, 1042 **ch**. An attempt was made, without much success, to analyse the cause of these fluctuations (see p. 33). The deficiency of **mm** is not clearly significant. The ratios fluctuate wildly. Among the families from **M m** selfed are one of 97 **M**, 11 **m**; another of 156 **M**, 87 **m**. It appears to be a matter of chance that on the whole the recessives are more often in defect. This is borne out by the fact that the figures from back-crosses are quite normal.

H is linked with **M**, and this may account for some of the shortage of **hh**. But it is more likely that the variegation of the cotyledons found in some **hh** plants causes infantile mortality among them. **hh** plants are always late in flowering.

ww plants are clearly abnormal, and there is nothing surprising in the fact that their viability is only about 30 per cent. of that of their normal sisters. Preliminary observations suggest that **cc** plants will be almost as weak. **rr** plants are also probably somewhat weak. The ratios are fairly consistent. The fact that **rr** plants are rather late in flowering may also have a certain influence here, but will certainly not account for the whole of the deficiency, as few plants die during the flowering period.

The deficiency of **qq** plants may be due to errors in scoring. In certain families the scoring was doubtful. These have been omitted. But **qq** may well be weaker than **Q**. The figures for **U** are only based on two families, and it is not unlikely that a factor causing so serious a disturbance of growth is semi-lethal.

A thorough statistical analysis of the data on which Tables VIII–X are based would include a test, in the case of each set of families grouped together, for homogeneity. That is to say it would be desirable to determine whether, for example, the 123 families derived from the mating **S s** × **ss** differed among themselves more than could be accounted for on the basis of random sampling. It is at once obvious that such families as those involving **Ch** do differ among themselves to a far greater extent than can be explained by the chances of sampling.

We therefore contented ourselves by applying the χ^2 test to two groups of families, both of which were fairly homogeneous. For the 35 families from mating **O o** selfed we took the expected values of recessives as in each case one-quarter of the total. Thus the value of χ^2 gives not merely a test of homogeneity, but a test of the possibility that the families had been derived by sampling from a strictly Mendelian population. $\chi^2 = 39{\cdot}97$, $n = 35$, $\therefore\ P = 0{\cdot}53$, *i.e.* there is an almost even chance of obtaining as good a fit by random sampling. The agreement is therefore quite satisfactory.

In the case of the families derived from **R r** selfed we rejected eight small families totalling 197 plants, in which the flower colour had not been scored in all the members, since other factors such as **V**, not believed to be linked with **R**, were segregating. This left 25 families containing 2080 **R**, 631 **rr**. These gave a divergence of 46·75 from expectation, the standard error being 22·5, *i.e.* the odds were over 25 to 1 against the divergence from Mendelian expectation being due to chance. The proportion of recessives is 0·2328. The question now is as follows. Can these 25 families be regarded as random samples from a population of which 23·28 per cent. consists of recessives, or must we suppose that in different families the recessives were eliminated to a significantly different extent? Here $\chi^2 = 20{\cdot}36$, $n = 24$, $\therefore P = 0{\cdot}72$, *i.e.* the odds are over 2 to 1 against obtaining as good a fit by random sampling. Whatever may have been the agency that was working to reduce the number of recessives, it was working in an extremely uniform manner. Indeed had it not been for one family of 75 **R** and 37 **rr** the fit would have been suspiciously good. We are therefore justified in concluding that a considerable proportion of our groups of families is homogeneous material which may legitimately be grouped. In the 60 families just considered there were probably no lethal factors segregating in the chromosomes carrying **O** and **R** respectively. This is quite probable in view of the highly inbred nature of the pure lines which have formed the starting-point for most of this work.

When, however, we consider even a group of families which apparently agrees fairly well with Mendelian expectation, such as those from **Ch ch** × **chch**, we find a very different state of affairs. Taking three of the most aberrant of the 119 families we find **Ch** and **chch** in the numbers 56:22, 185:135 and 21:48. The divergences from expectation, divided by the standard errors, are 3·85, 2·69 and 3·23. Thus it would be reasonable to expect three families as aberrant as this owing to sampling errors in a group of a hundred million. The chances are about a million to one against finding them in a group of 119. As there are other families about equally aberrant, the probability that the irregularity of the whole series is due to chance is vastly less. Nevertheless the majority of the families show no sign of disturbing factors, and we can only say that the causes of deviation from Mendelian expectation are about as likely to work in favour of **Ch** as **ch**, and that there is no evidence that either of these factors, in itself, is favourable to survival.

The values of k are of some interest from the point of view of natural selection. Let us first consider the mutant types which do not give gross deviations from Mendelian expectation. These are due to the factors **b**, **x**, **l**, **v**, **p**, **D**, **e**, **y**, **k**, **n**, **j**, **A′**, **a**, **o**, **t**, **mp**, **iv** and **i**. We reverse the values of k for **D** and **A′**, so that a negative value of k always means a favouring of the normal type. There are 14 positive and 26 negative values of k. The odds are 17 to 1 that this is not due to chance. The median value of k is $-0{\cdot}022$, *i.e.* on the whole these almost neutral mutants have a disadvantage of about 2 per cent. in the period of the life cycle covered by our work. This would be quite sufficient to make them into rarities in a few centuries if natural selection were allowed to act. No factor appears as advantageous in all three tables, but **p**, **j**, **o** and **A′** appear as advantageous in two out of three, while **e** is once advantageous, once neutral and once disadvantageous. The figures for **p** are certainly irregular, as are those for **Ch**, with which it is linked. Of the others, **j** and **o** can be scored in the seedling stage, and it would be possible to obtain very large numbers to test the ratios which they give. At present we can only say that they must be very nearly without effect on the ratios.

Of the other mutant types we may say that, roughly speaking, the proportion of **gg** falls 5 per cent. below the expected values, those of $\mathbf{f^1f^1}$, **mm** and **rr** 10 per cent. below, those of **hh** about 20 per cent. below and those of **ww** 67 per cent. below. The figures for the remainder do not yield a clear result. To sum up, of 24 mutant types 19 are neutral or slightly disadvantageous, four definitely disadvantageous, and one semi-lethal.

Unfortunately this study only extends to a part of the life cycle. It takes no account of fertility, and this differs considerably in different races. Thus to take two examples, doubles of the **xx** type are almost completely sterile; doubles of the **mm** type, although fertile enough if fertilised by hand, do not readily set natural seed. Moreover, some of the types which give approximately normal ratios under careful conditions of culture, would not do so in a rather less favourable environment. Thus **kk** plants are particularly sensitive to cold.

It is of some interest to sum the various figures of Tables VIII–X. Omitting the figures for **W**, **Q** and **U** we have:

X x × **xx**	35,647 **X x**	34,648 **xx**
xx × **X x**	20,706 **X x**	19,638 **xx**
X x × **X x**	109,577 **X**	35,651 **xx**

There is no serious evidence that any of the factors considered affect the viability of pollen more than of ovules. While the above figures suggest it, it may be noted that only seven of the eleven deviations for the nearly neutral factors in back-crosses with heterozygous pollen parent are against the mutant type, while eight are against it when the seed parent is heterozygous.

The fact of linkage greatly complicates the discussion of single factor ratios. Thus **B** is linked with **S** and **G** both of which give abnormal ratios. And a large proportion of the data concerning it are taken from linkage experiments in which **S**, **G** or both were also segregating. It would seem that the various influences acting on the ratio must about neutralise one another. However, it is probable that the ratios in different families where **B** is segregating show an abnormally large dispersion, as in some cases **S** and **G** would be so linked as to favour **B**, in others **b**. For this reason no very great significance can be attached to the ratios actually found in these cases. On the other hand the factors **D**, **E**, **M**, **Y**, **H**, **K**, **O** and **Mp** have only rarely been used in linkage experiments giving positive results, and hence the ratios given by them are little distorted in this way.

ABNORMAL RATIOS IN THE SECOND LINKAGE GROUP.

As pointed out by Gregory, de Winton and Bateson, the factors of the second linkage group are particularly prone to segregation in abnormal ratios. An attempt was made to elucidate the reason for this, but although several thousands of plants were bred, the attempt failed, though some information was gained.

In 1926 a **Ch P/ch p** plant was selfed, giving quite a good ratio for both factor pairs. It is generally possible to pick out plants heterozygous for **Ch** or **P**, and this was done. In 1927 five pairs of doubly heterozygous plants were crossed reciprocally to **chch pp**, so that their aberrations from normal ratios both as males and females could be tested. In 1928 eight **Ch ch pp** plants from their progenies were crossed reciprocally with **chch Pp** plants taken from the same group. In 1929, seven such pairs of reciprocal crosses were made. Thus five plants were tested as males and females as regards segregation of **Ch** and **P**, and 15 each as regards **Ch** alone and **P** alone. Only four crosses gave families of less than 50.

It was at once clear that **Ch** gave more aberrant ratios than **P**. The cross-over value of these two factors is 30·7 per cent. on the female side, 39 per cent. on the male side. Hence it would seem that the cause of disturbance is located in the chromosome nearer to the locus of **Ch** than to that of **P**. In the 1927 crosses all five plants gave aberrant ratios for **Ch** on the male side, the ratios for **P** being in all cases less aberrant. The results are summarised in Table XI.

It will be seen that in every case **Ch** gametes were produced in excess. The deviations in column 7 and the standard errors refer to the **Ch** figures. In four cases the deviation exceeds three times the standard error, in the fifth it is two to four times the standard error. The deviations are therefore clearly significant. In one family only is there a significant deviation on the female side, in the opposite direction.

Of the plants tested in 1928, five of the eight **Ch ch** plants gave a significant deviation (over twice the standard error), in all cases on the male side, four giving excess of **Ch** gametes, one an excess of **ch**. Two of the **P p** plants deviated significantly, giving an excess of **p** gametes on the male side. Of the plants tested in 1929 two of the **Ch ch** plants deviated significantly as females, while one **P p** plant deviated significantly as a male. We thus have in all thirteen cases of deviation on the male side, and three on the female. However, in addition a number of other females deviated by more than their standard error, and some of these deviations are doubtless significant.

TABLE XI.

ChP/chp. Parent		**Ch**	**ch**	**P**	**p**	*D*	σ
63^1	♀	21	49	43	27	14	4·2
	♂	38	7	14	31	15·5	3·4
63^3	♀	68	71	70	69	1·5	5·9
	♂	77	26	65	38	24·5	5·0
63^5	♀	41	49	46	44	4	4·7
	♂	46	18	31	33	14	4·0
63^7	♀	6	7	9	4	0·5	1·8
	♂	110	77	106	81	16·5	6·8
63^{10}	♀	28	26	29	25	1	3·7
	♂	65	19	34	50	23	4·6

The most hopeful explanation of these results is on the hypothesis that certain plants are heterozygous for a factor which handicaps pollen tubes containing it. Such plants will probably hand on this factor in half their ovules. Hence we should expect that where a plant gives an aberrant ratio as a male, its mother, when used as a male, would behave in the same way. In the three cases where this hypothesis can be tested, it is correct. However, two plants which deviated as females only had fathers which deviated significantly as males only, though one deviated by 1·4 times the standard error as a female. But the other gave very good equality, 28 **P**, 29 **p**. Hence the lethal factor hypothesis, though not disproved, does not rest on a very solid foundation. Another possible hypothesis is that we are dealing with something like self-sterility factors. In this case a given heterozygote should give significantly different ratios when tested as a male on different females. This experiment has not been tried. Moreover, it would not explain the abnormal behaviour of certain heterozygous females. The main experiment was broken off because it became clear that by the third year the causes of abnormal ratios had become largely eliminated. The plant $63^1/27$ is of interest owing to its almost *Oenothera*-like behaviour, the ovules mainly carrying **ch**, the pollen **Ch**. It is possible that the selfed progeny of such a plant might pass into a condition of forced heterozygosis, and thus render the establishment of a genetically pure line impossible.

MUTATION.

The following factors have appeared during the course of the experiments:

h, p, w, u, mp, c, sp, z.

No other certain examples of mutation have occurred. Occasional appearances of other factors in families where they were not expected can all be explained as errors, though some may have been due to mutation.

h[1] may or may not have originated by mutation at Merton. It appeared in one of the two F_2's raised from the cross of sterile double with diploid single. This family contained **H** 69:12.

Two interpretations are possible. Mutation may have occurred at Merton or the sterile double may have been **H h**. If so the mutation of **H** to **h** probably occurred at some time during the vegetative propagation of the double, since harlequins had not been described previously.

p (Figs. 4 and 5) appeared in nine out of 28 plants in a family 184/22 from a selfed plant. Since neither of the parents of this plant was derived from self-fertilisation the mutation had probably occurred in an earlier generation. In 1907 Mr Leonard Sutton sent Mr Bateson a sport which, to judge from a drawing, may have been **pp**. It was not used as a parent.

w (Fig. 3) occurred in a family 91/25 derived from the self-fertilisation of a plant both of whose parents were members of families derived from self-fertilisation. The mutation may thus have occurred in one of these parents. 91/25 consisted of 78 plants of which ten were "Feeble-minded." A sister plant of the parent gave 49 normal plants when selfed.

u (Figs. 8 and 9) appeared in 59/28, an F_2 from two pure lines, Elwes' white, and "Queen of the Pinks." 59/28 contained two fasciated plants out of 83. Further comment is deferred until the relationship between **U** and **Q** is determined.

mp (Figs. 21, 22, 36, 38) appeared in 70 out of 314 plants of 400/29, an F_2 from a pure line (Czar) and a plant of complicated ancestry. The mutation may have occurred at any time during three generations.

c (Fig. 11) and **sp** both appeared in the same family, 173/30, an F_2

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[1] See Plate XII, figs. 14 and 15, Gregory, de Winton and Bateson (1923).

from two approximately pure lines, "Primrose Queen" stellata, and "Feeble-minded." Of 64 plants, four were **cc**, and did not flower. Of the remaining 60, eight were "Feeble-minded." Of the other 52, 42 were **A**, and ten **aa**, of which one was **aa sp sp**. It is not yet known whether **sp** can be seen except on **aa** plants. If so the shortage of **spsp** is remarkable.

Ten plants of this family other than **cc** were tested by self-fertilisation or crossing *inter se*. Five, including the **spsp**, proved to be **C c**, but none gave **spsp**. The occurrence of two mutations in a family is remarkable.

zz (Fig. 12) occurred in the progeny of an X-rayed plant. Comment is deferred, as the effects of X-rays are under investigation.

In addition dwarf and deformed plants have occurred. These are generally sterile, and are not necessarily due to mutation. One dwarf type appears to be due to two recessive factors, and is still under investigation.

MULTIMUTATION OF THE FACTOR **e**.

Like many other flaked forms, **ee** does not breed quite true. Altogether **ee** selfed and crossed *inter se* have given 3225 flaked and 25 whole coloured, or 0·77 per cent. of back mutations. However, these figures require further analysis. The main experiment took place with a strain of flaked plants obtained from Messrs Sutton. They were **gg**, and hence the flakes were clearly marked. From 1924 to 1930 they were self-fertilised, and after 1925 selected for large number and size of flakes. The original plant was giving a mixture of plants with large and small pigmented areas, but after the first year a plant with large areas bred true, while a sister with small areas segregated. It is not yet certain whether this was due to modifying factors or to several **e** allelomorphs. Selection had no obvious result after the first year. On selfing a fully coloured flower on a flaked plant, only flaked offspring were obtained. From 1924 to 1931 we obtained four whole coloured and 355 flaked. The whole-coloured plants were self-fertilised. Three behaved as normal **Ee**, giving whole coloured to flaked in the ratios 31:8, 22:5 and 14:5. On selfing two of the whole-coloured plants in these three families, families of 8 **E**: 2 **ee** and 16 **E**:4 **ee** were obtained. But two out of six whole-coloured plants back-crossed to **ee** gave 9 red:0 flake, and 11 red:0 flake. The other four proved to be **Ee** and gave 14 whole coloured and 30 flaked in all. In 1929 two plants of this line were X-rayed while flowering, and seed taken from the flowers which were believed to be undergoing meiosis at the time of X-raying. In 1930 they gave families of 35 and 17, all flaked. On selfing the 35 we obtained 32 families, of which 24 contained 419 flaked and no red. The remaining eight families contained flaked and red in the numbers 11:1, 17:1, 24:2, 19:3, 17:1, 24:1, 26:3, 14:2. The other 17 plants gave 16 families containing 321 flaked and no red, and one containing 21 flaked and two red.

Other lines of flaked plants were derived from whites. Their self-fertilised offspring consisted of 1363 flaked, and no reds. A cross between two of these lines, however, gave one whole-coloured plant and 21 flaked. This whole-coloured plant behaved as **Ee**. Selfed it gave 52 **E**:22 **ee**, and crossed, with a flake as male 24 **E**, 35 **ee**, the reciprocal cross giving 15 **E**:16 **ee**. Of the 52 whole-coloured derivatives from selfing, five were crossed with flaked, and all five behaved as **Ee**, giving 99 whole coloured and 103 flaked in all.

The whole question is still under investigation, but the following provisional conclusions may be drawn. X-raying had no significant effect. The proportion of whole-coloured plants was raised from four coloured among 355 flaked, or 1·1 per cent., to 16 coloured among 1095 flaked, or 1·4 per cent. Treating these figures as a fourfold table we find $\chi = 0{\cdot}44$. As χ has a normal distribution with unit standard deviation, this is not significant. But comparing Sutton's flaked line which gave 355 flaked and four whole coloured, with the other lines which gave 1383 flaked and one coloured, we find $\chi = 3{\cdot}37$. The method is not very exact with such small figures, but the difference is probably significant, *i.e.* different flaked lines differ in their capacity for producing whole-coloured plants. The investigations of Demereč (1928, 1929) show that such differences may be due either to allelomorphs of different stability, or to other factors. We hope to be able to decide which of these causes is operating in our case.

It is also clear that two different types of whole-coloured plants are produced by flaked. The first type, of which we found four examples, behaves as **E e**, the second, of which we found only one, behaves as **ee**, but has an unusual tendency to produce whole-coloured plants. Such a plant may perhaps be regarded as a chimaera in which the somatic tissue is mainly **E e**, the gametic, however, being **e**.

SUGGESTED HOMOLOGIES.

The genetics of colour in the Vernales group of *Primula* has been investigated by Chittenden (1928) and Buxton (1932), Chittenden concerning himself with species crosses, Buxton with the varieties of

P. acaulis. Chittenden found a factor **R** for anthocyanin production, and more doubtfully an intensifier **D** of anthocyanin in *P. Juliae,* while *P. acaulis* and *P. elatior* carried a factor **Y** for yellow flavone, and *P. elatior* carried a factor **I** inhibiting anthocyanin production, some plants being heterozygous for it.

Buxton reports a factor **Y** for yellow flavone, **B** for anthocyanin, and a factor **S** which changes blue anthocyanin to red. A factor **W** suppresses the white flavone, so that the flowers do not turn yellow in ammonia, and converts carmine flowers into magenta.

Of these factors Chittenden's **R** may be identical or allelomorphic with Buxton's **B**. Otherwise the blue primrose and *P. Juliae* should give 1/16 yellows and whites in F_2. They may be provisionally homologised with our **V**. **Y** is probably absent in *P. sinensis* as it is in *P. Juliae.* Chittenden's **I** may be homologous with our **D**. Buxton's **W** appears to be homologous with our **B**. His **S**, according to Scott-Moncrieff (1932), leads to the production of primulin in place of a diglucosidal anthocyanin present in the blue (**ss**) primrose. If **R** carries out a transformation of this kind in *P. sinensis* it is certainly less thoroughgoing than that carried out by **S** in *P. acaulis.* The homology is thus not very clear, though possible, so that we can make the very tentative homologies suggested in Table XII. The factor **S** for heterostylism is presumably the same throughout the genus *Primula.* None of the other structural factors can be homologised.

TABLE XII.

Chittenden	R	Y	—	I	—
Buxton	B	Y	W	—	S
de Winton and Haldane	V	Absent	B	D	?R

V and **J** perhaps correspond to the general factors for anthocyanin production found elsewhere, *e.g.* **C** in *Pisum,* **C** and **R** in *Lathyrus* and *Matthiola.* **K** finds a parallel in the oxidising factor which converts pelargonin into cyanin in *Pelargonium* (Scott-Moncrieff, 1931). Multimutating recessives resembling **E** are found in *Antirrhinum* (Baur, 1926), *Delphinium* (Demereč, 1931) and elsewhere. The sterile doubles (**xx**) resemble doubles found in other plants much more than do the fertile (**mm**) doubles. **X** may be tentatively homologised with **S** of *Matthiola* (Philp and Huskins, 1931) etc. No other factors seem to have obvious homologues.

FACTORIAL COMPOSITIONS OF SOME COMMERCIAL STRAINS.

All British commercial plants are **ss**. Continental seed is often mixed, containing some **S** plants. The following are the factorial compositions of some well-known strains, referred to dilute magenta green-stigma stellata as standard.

Diploids.

Sutton's Coral Pink	**kk gg bb ii ChCh**
,, Crimson King	**KK gg bb ii ChCh**
,, Royal White	**DD ChCh**
,, Etna	**bb gg ll ii ChCh**
,, Reading Blue	**rr ii ChCh**
,, Duchess	**bb gg DD ChCh**
,, Queen of the Pinks	**bb vv ii mm ChCh**
,, Double White Purity	**BB vv ii mm ChCh**
,, Coral Pink Star	**kk gg bb ii**
,, Vesuvius Star	**bb gg ii Ch ch**
,, Czar	**gg rr ii ChCh**
,, White Star	**DD A′A′ ll**

yy, $\mathbf{f^s f^s}$ and other recessive plants occur in mixed strains.

Tetraploids.

Sutton's Giant Royal White	$\mathbf{D_4\ Ch_4}$
,, ,, White	$\mathbf{D_4\ v_4\ Ch_4}$
,, ,, Pink	$\mathbf{b_4\ Ch_4}$
,, ,, Crimson	$\mathbf{b_4\ g_4\ Ch_4}$
,, Symmetry Star	$\mathbf{b_4}$
,, Giant White Star	$\mathbf{D_4}$

The above represent our analyses, but are subject to uncertainty for several reasons. Thus in a white **DD GG** any recessive other than **g** may occur without altering the flower colour. And tetraploid strains may breed true, or very nearly so, for a long time, and yet contain a few triplex (*e.g.* **DDD d**) plants.

Small amounts of seed carrying other factors may be obtained from the John Innes Horticultural Institution on application.

SUMMARY.

1. This paper describes the action and interaction of 25 pairs of allelomorphic factors, two sets of three multiple allelomorphic factors,

and three doubtful pairs of allelomorphic factors in the diploid *Primula sinensis*. Of these factors two or three are dominant to the original type, one was probably a cause of polymorphism in it, the remainder are recessive. Twelve of the factors affect anthocyanin, four affect the plastids of the flower, three of them also having structural effects. The remainder have purely structural effects, four acting mainly on flower structure, six mainly on leaf structure, and one mainly on bract structure. In addition one extra-nuclear factor governs the colour of leaf chloroplasts.

2. The stem and leaf anthocyanin depends mainly on four factor pairs. If all four are segregating, apparently almost continuous variation is obtained, but analysis is possible when only one or two segregate at a time. One particular genotype recessive for two of these factors is female sterile.

3. Petal colour depends mainly on 11 factor pairs. An attempt is made to explain their interaction on biochemical lines. Whites may be due to the joint action of two dominant inhibitors **D** and **G**, or to various combinations of four recessives.

4. Heterostylism is controlled by three factor pairs. One affects style length and anther insertion, and pollen grain size, the second anther insertion and doubleness, the third style length and flower plastids.

5. The flower plastids are controlled by two factor pairs and two sets of three allelomorphs. These generally also affect the flower or leaf, at least in suitable combinations. Large eye size tends to be associated with crimping of the leaves and serration of the petal margin.

6. The other four factors governing leaf shape which have so far been studied interact much as might be expected, except that the most abnormal type is a double recessive, and the loss of a third factor gives a much more normal triple recessive.

7. The flower structure in **chch** plants (probably the original type) is not much affected by the factors governing leaf shape. But the dominant factor **Ch** not only alters the flower structure, but renders it sensitive to the action of factors which otherwise affect the leaves only.

8. The recessive factor **n** converts the bracts into leaf-like organs, and they then become sensitive to the factors governing leaf-structure. The calyx is similarly, but less, affected.

9. Data are given for single factor ratios. Eighteen factors are nearly neutral in their effect, the numbers of the mutant types not deviating significantly from Mendelian expectation. Six factors appear to have

definitely harmful effects, the numbers of the mutant types found ranging from 95 to 33 per cent. of the expected values.

10. Six to eight new factors have appeared during these experiments. In four cases the evidence for mutation is clear.

11. The factor e for flaking mutates back to normal about once in 600 life cycles.

In conclusion we must thank the Department of Scientific and Industrial Research for a grant made to one of us enabling him to obtain the assistance of Miss Scott-Moncrieff.

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EXPLANATION OF PLATES I—XIII.

The photographs were all taken by Mr H. C. Osterstock, who also copied the coloured plate from the original.

PLATE I.

Fig. 1. Styles of (*a*) normal pin (**s A**), (*b*) normal thrum (**S A**), (*c*) large eye pin (homostyled, **s a**), (*d*) large eye thrum (**S a**), enlarged.

Fig. 2. (*a*) Normal calyx round ripening capsule of an oak-leaved plant, (*b*) everted calyx.

Fig. 3. (*a*) Normal "feeble" plant with petals somewhat reduced, (*b*) "Feeblest" plant with corolla reduced to a tube.

PLATE II.

Fig. 4. Sinensis peculiar eye (**Ch p**).
Fig. 5. Stellata peculiar eye (**ch p**).
Fig. 6. Sinensis tongue peculiar eye (**Ch t p**).
Fig. 7. Sinensis tongue oak peculiar eye (**Ch t o p**).
Fig. 8. Fasciated plant with hollow stem.

PLATE III.

Fig. 9. Three fasciated plants from same family, all the same age.

Class I. Near normal, flowers nearly over. Note rudimentary stigmata and small leaf near tip of scape.

Class II. Several flower spikes of same age. More leaves and much later flowering than Class I. At least one stem fasciated.

Class III. Cushion of small leaves with no sign of a flower spike. These plants may flower when over a year old but are apt to damp off beforehand.

Fig. 10. Three plants of leafy bract (**nn**). Class I, Class II, Class III.

PLATE IV.

Fig. 11. "Cup" plant (**cc**).
Fig. 12. "Claw" plant (**zz**).

PLATES V, VI AND VII.

Front and back view of a petal, corolla tube, calyx and bract enlarged.

PLATE V.

Fig. 13. Sinensis type (**Ch**).
Fig. 14. Stellata type (**ch**).
Fig. 15. Sinensis peculiar eye (**Ch p**).
Fig. 16. Stellata peculiar eye (**ch p**).

PLATE VI.

Fig. 17. Tongue sinensis (**t Ch**).
Fig. 18. Tongue sinensis peculiar eye (**t Ch p**).
Fig. 19. Tongue oak sinensis (**t o Ch**).
Fig. 20. Tongue oak sinensis peculiar eye (**t o Ch p**).

PLATE VII.

Fig. 21. Maple sinensis peculiar eye (**mp Ch p**).
Fig. 22. Maple crimp stellata (**mp f ch**).
Fig. 23. Oak sinensis (**o Ch**).
Fig. 24. Oak fern sinensis peculiar eye (**o y Ch p**).

PLATES VIII, IX AND X.

ront and back view of a petal, corolla tube, calyx and bract.

PLATE VIII.

Fig. 25. Sinensis leafy bract (**Ch n**).
Fig. 26. Stellata leafy bract (**ch n**).
Fig. 27. Crimp sinensis leafy bract ($\mathbf{f^1}$ **Ch n**).
Fig. 28. Crimp stellata leafy bract ($\mathbf{f^1}$ **ch n**).

PLATE IX.

Fig. 29. Fern sinensis leafy bract (**y Ch n**).
Fig. 30. Fern stellata leafy bract (**y ch n**).
Fig. 31. Oak sinensis leafy bract (**o Ch n**).
Fig. 32. Oak stellata leafy bract (**o ch n**).

PLATE X.

Fig. 33. Tongue sinensis leafy bract (**t Ch n**).
Fig. 34. Tongue stellata leafy bract (**t ch n**).
Fig. 35. Tongue oak sinensis peculiar eye leafy bract (**t o Ch p n**).
Fig. 36. Maple sinensis leafy bract (**mp Ch n**).

PLATES XI AND XII.

From photographs of leaves.

PLATE XI.

Fig. 37. Type, **F O Y T Mp**.
Fig. 38. Maple, **F O Y T mp**.
Fig. 39. Tongue, **F O Y t Mp**.
Fig. 40. Crimp (Lee's) sinensis, $\mathbf{f^1}$ **O Y T Mp Ch**.
Fig. 41. Oak, **F o Y T Mp**.
Fig. 42. Crimp oak, **f o Y T Mp**.
Fig. 43. Crimp (Sutton's), $\mathbf{f^s}$ **O Y T Mp Ch**.
Fig. 44. Fern, **F O y T Mp**.
Fig. 45. Crimp (Lee's) fern sinensis, $\mathbf{f^1}$ **O y T Mp Ch**.

Plate XII.

Fig. 46. Oak fern tongue, **F o y t Mp.**
Fig. 47. Oak maple, **F o Y T mp.**
Fig. 48. Oak fern, **F o y T Mp.**
Fig. 49. Fern tongue, **F O y t Mp.**
Fig. 50. Crimp maple, **f O Y T mp.**
Fig. 51. Fern maple, **F O y T mp.**
Fig. 52. Tongue maple, **F O Y t mp.**
Fig. 53. Oak tongue, **F o Y t Mp.**
Fig. 54. Fern tongue maple, **F O y t mp.**

Plate XIII.

Primula sinensis (stellata), "wild" type. Copied from W. J. Hooker's *Exotic Flora*, Vol. II, Pl. 105.

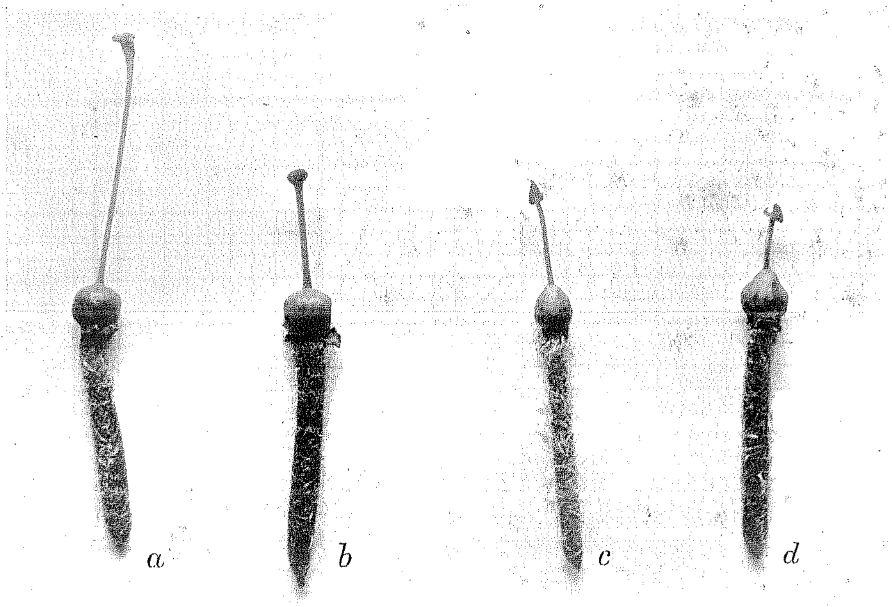
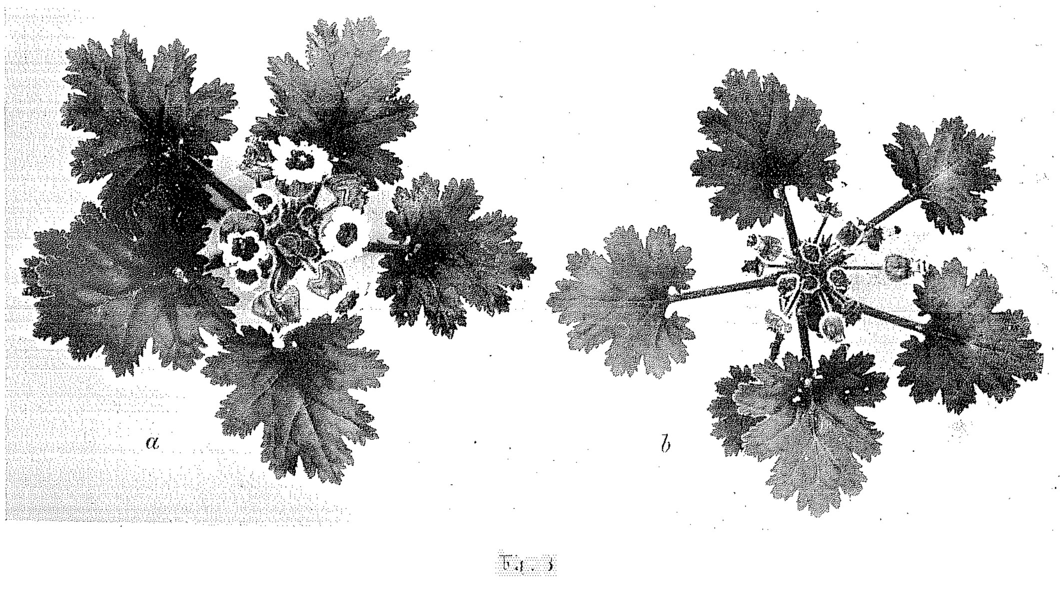


Fig. 1.

Fig. 2.



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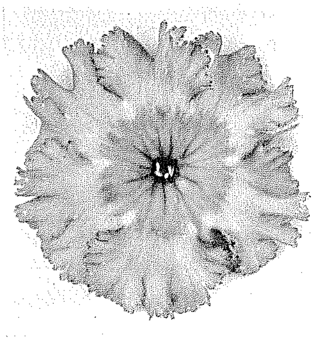

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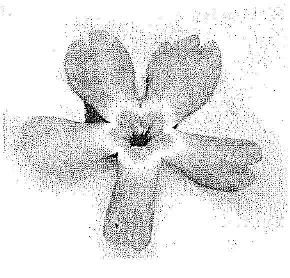

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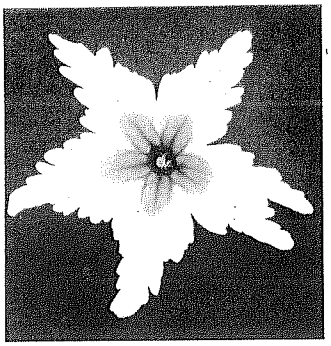

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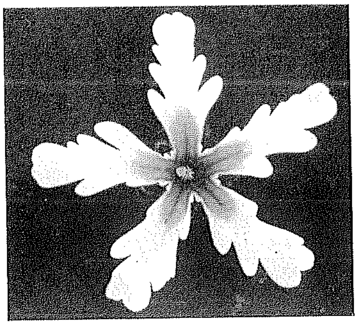


Fig. 7.

Fig. 8.


Class I
Class II
131
30
11-4-30
Class III

Fig. 9.

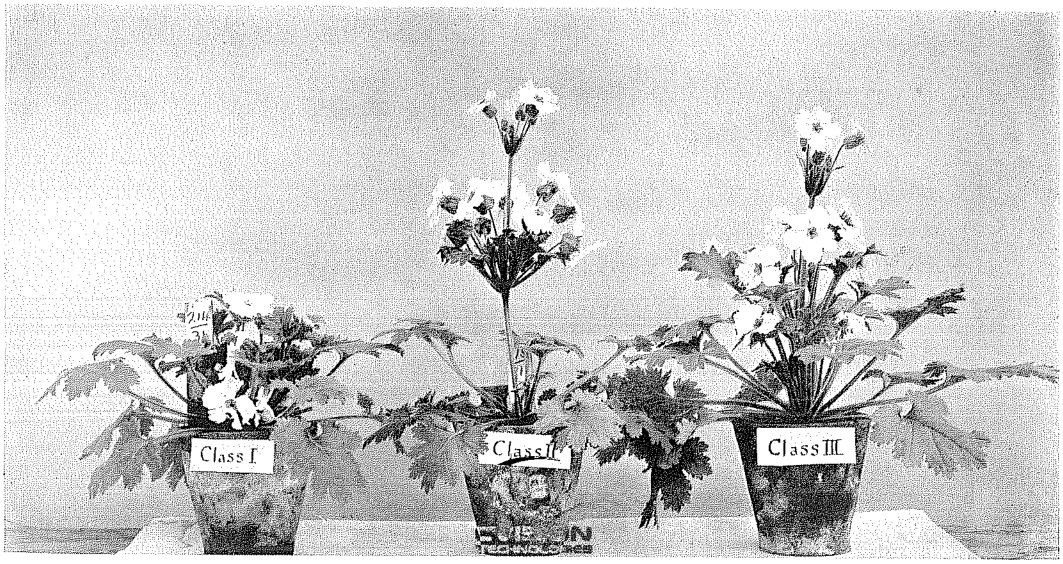

211
31
Class I
Class II
Class III

Fig. 10.

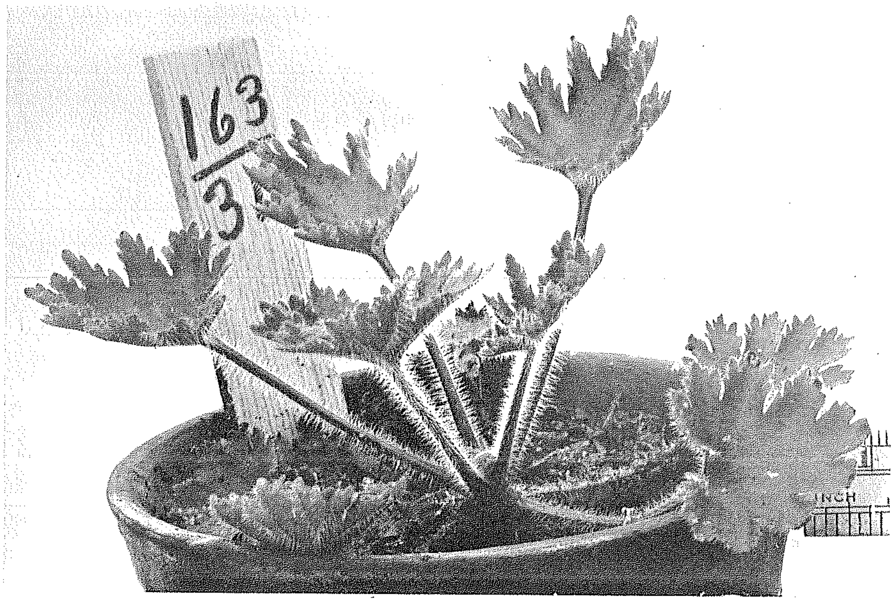


Fig. 11.

Fig. 12.

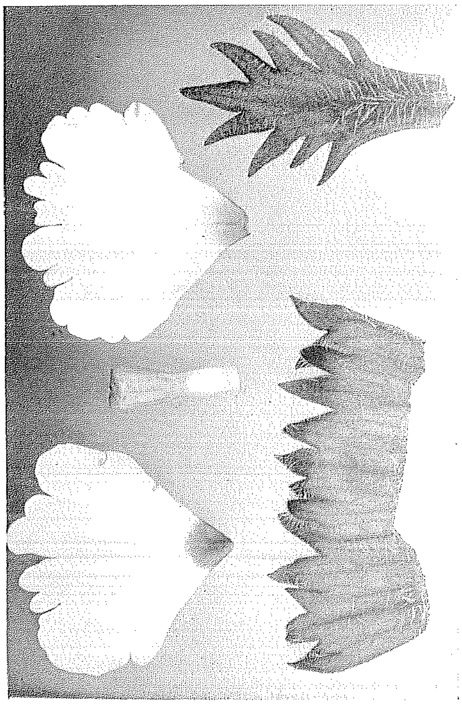


Fig. 13.

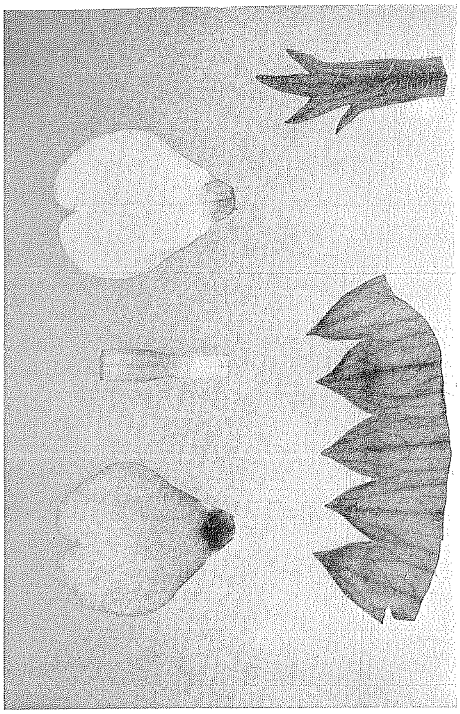
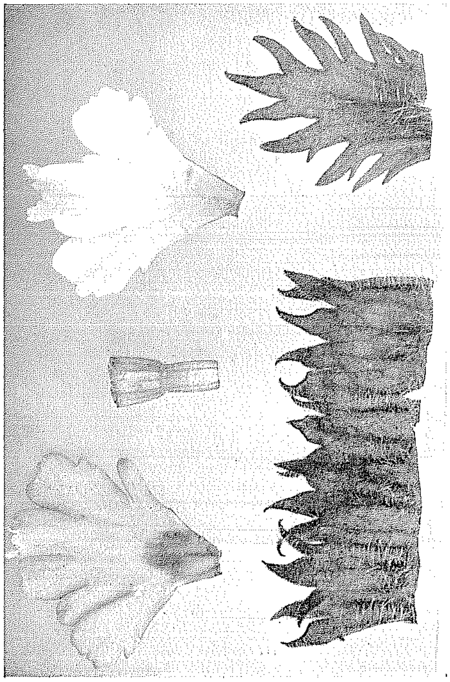


Fig. 14.



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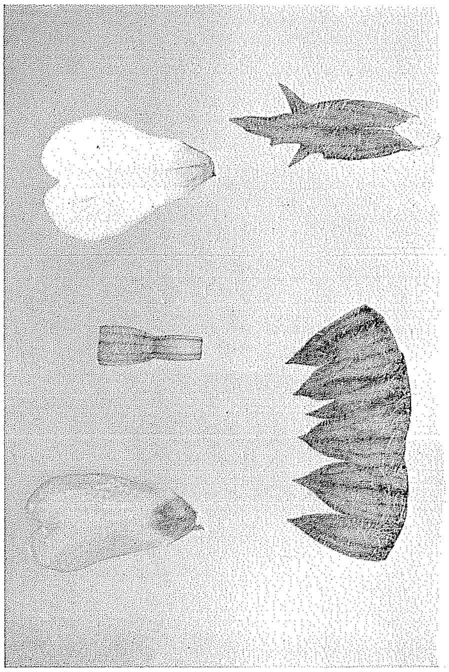

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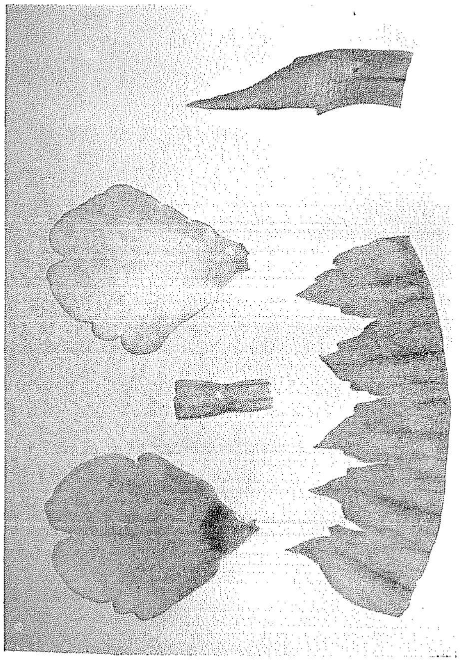

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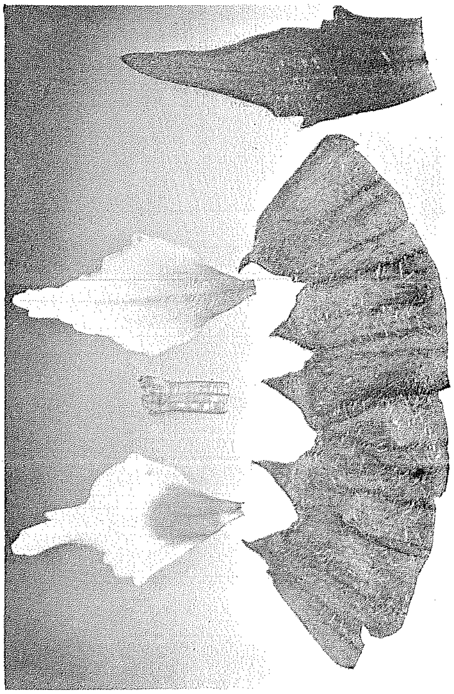

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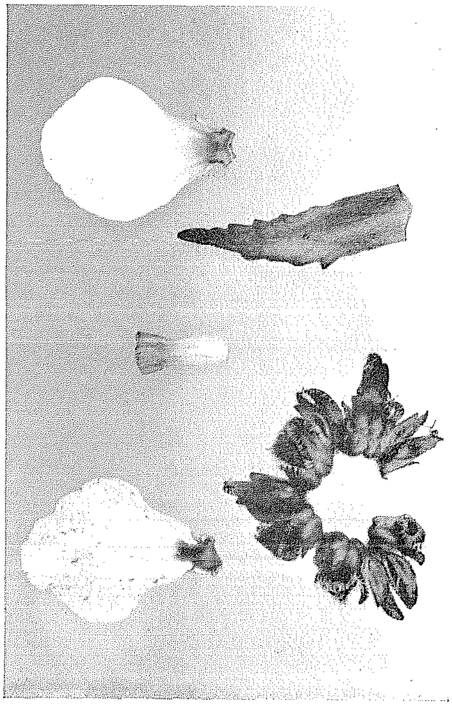

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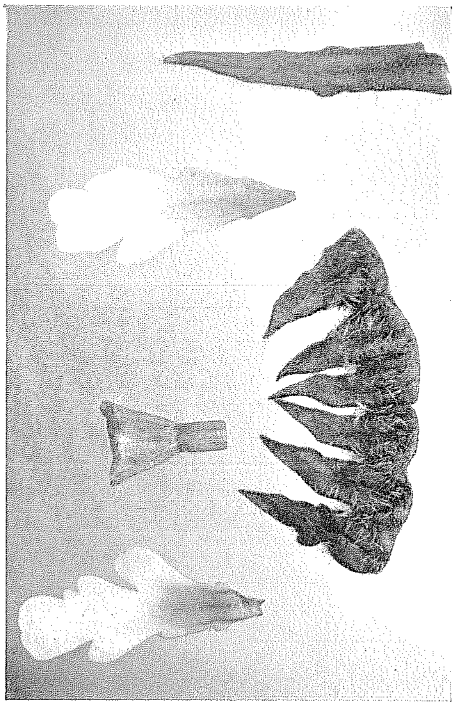

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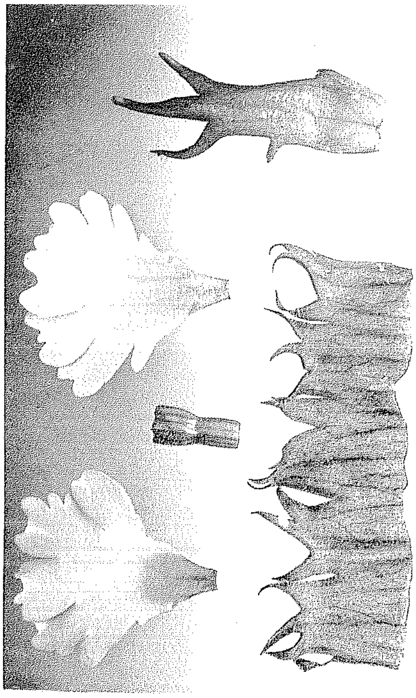

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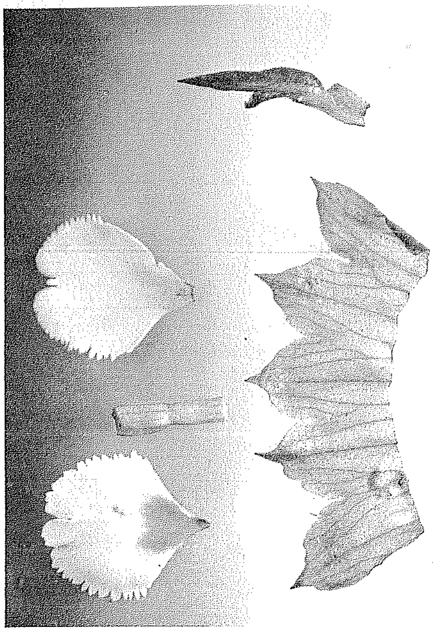

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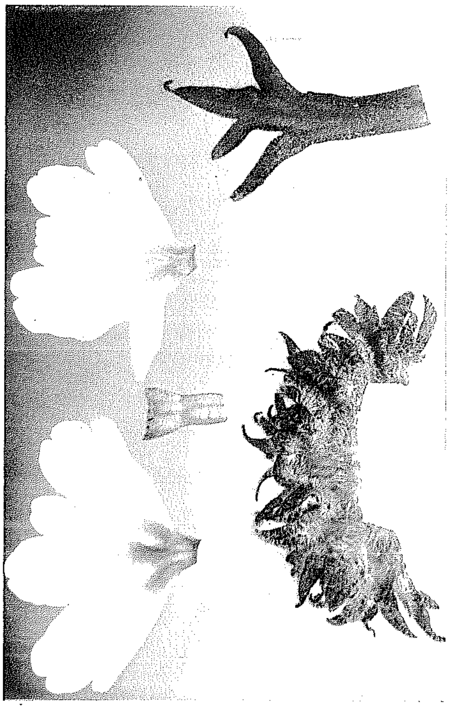

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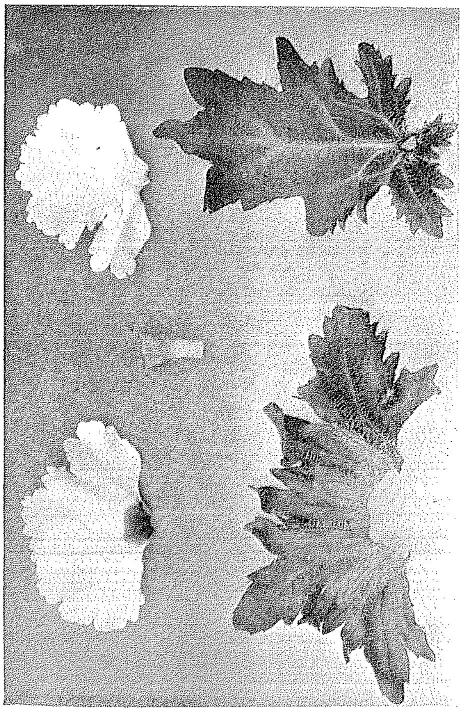

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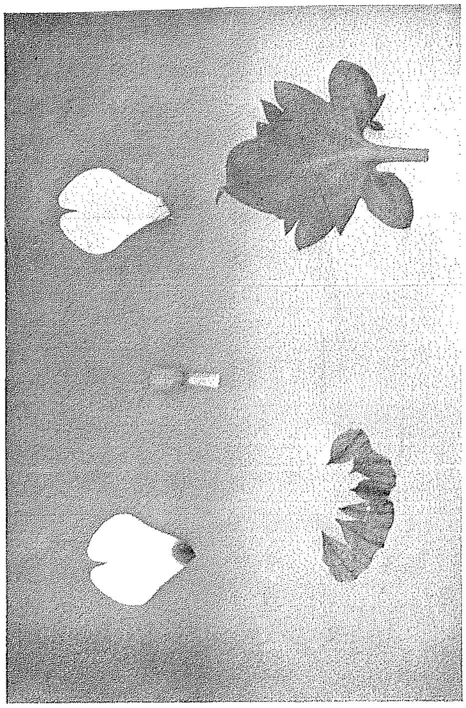

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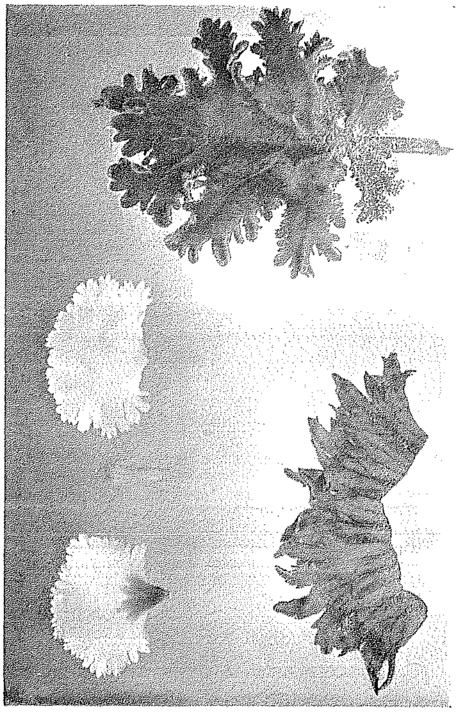

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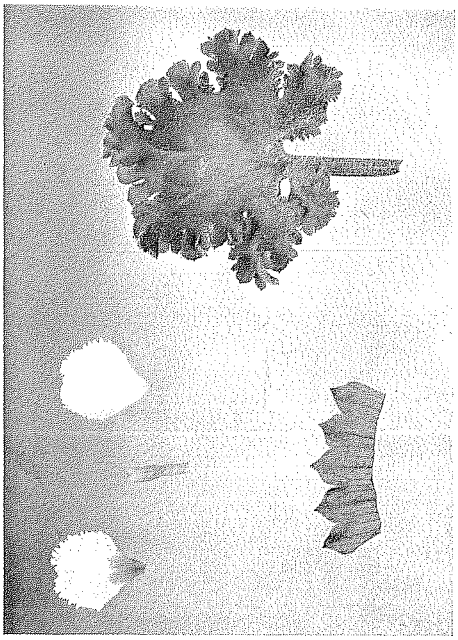

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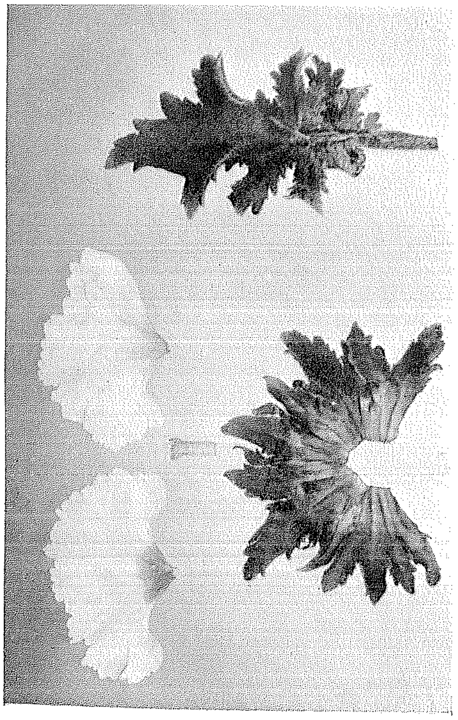

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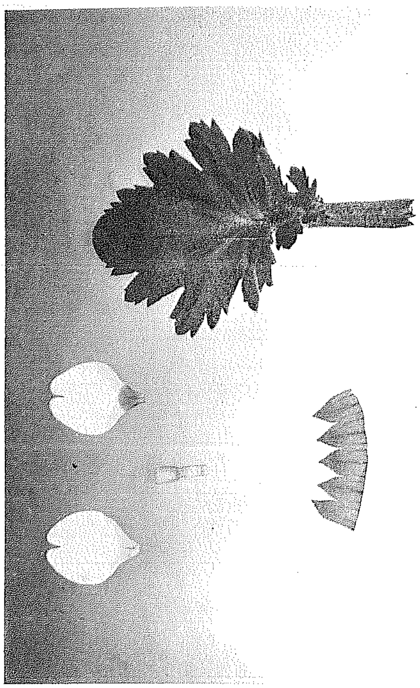

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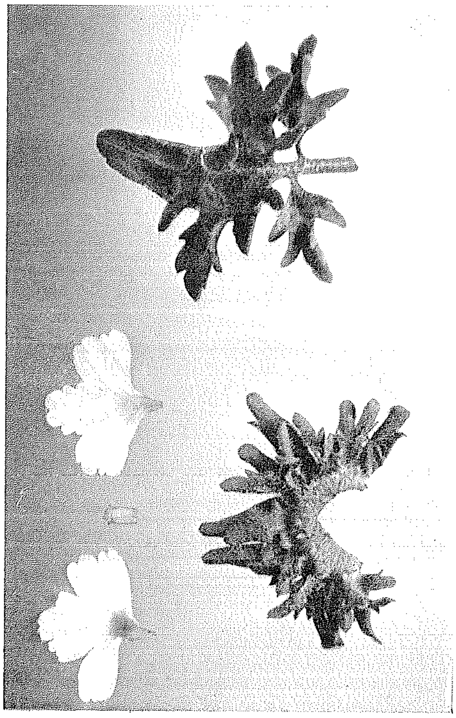

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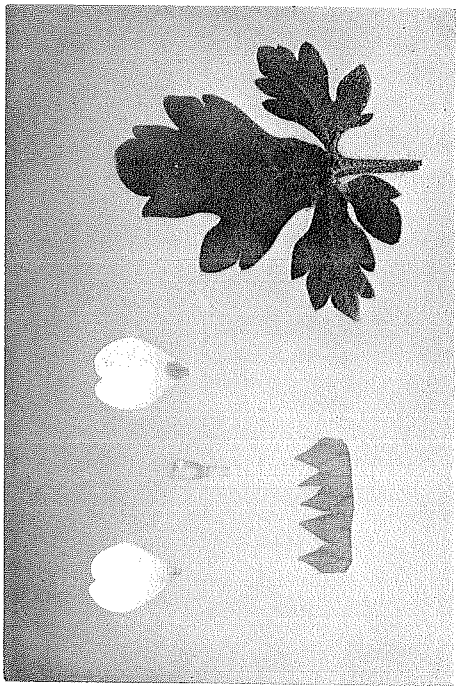

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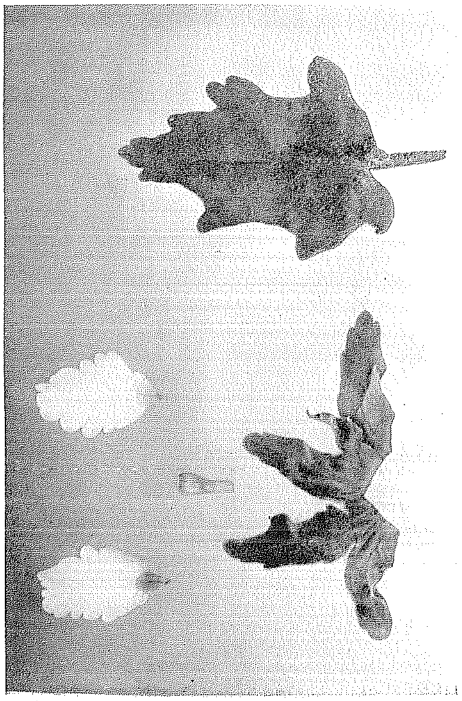

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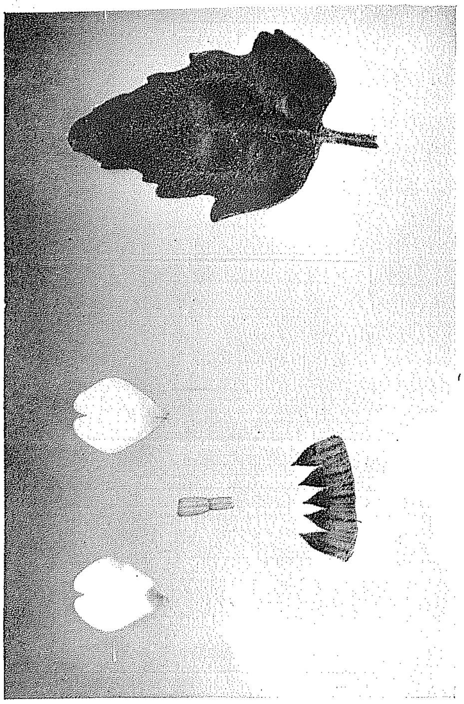

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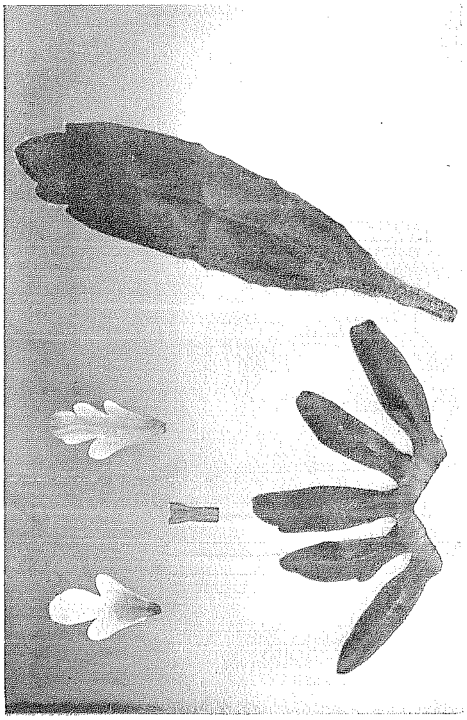

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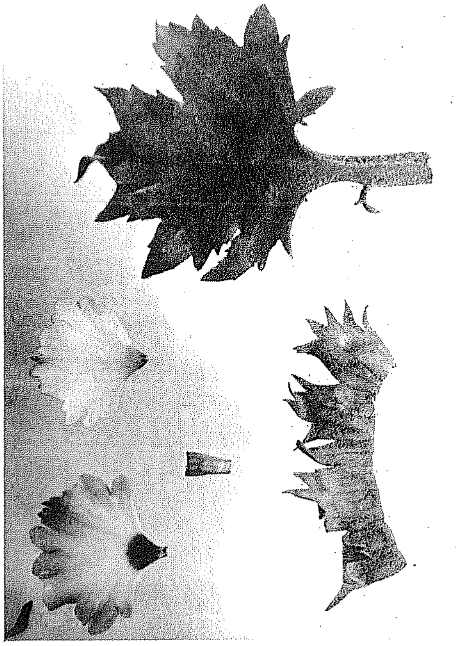

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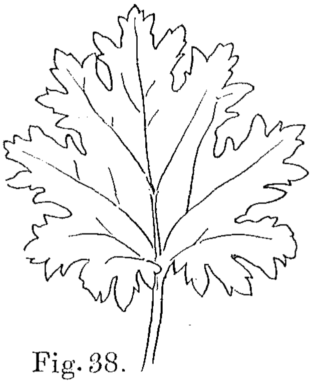
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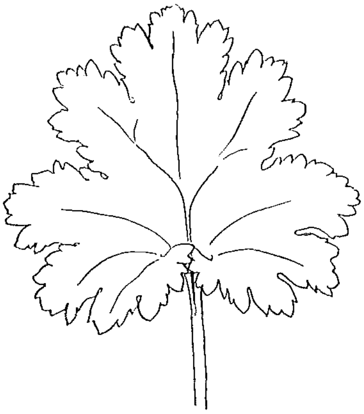
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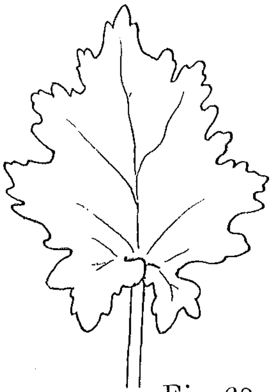
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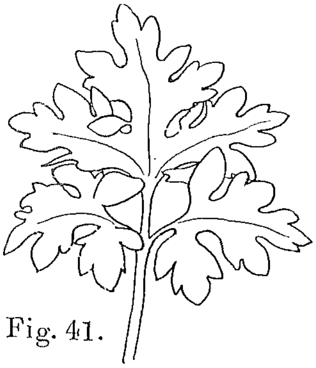
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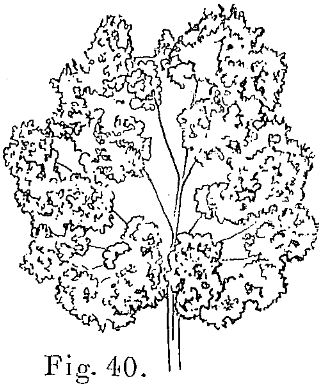
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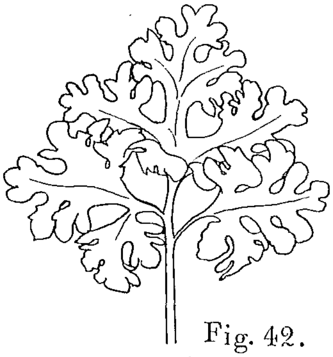
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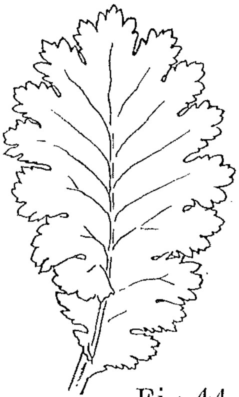
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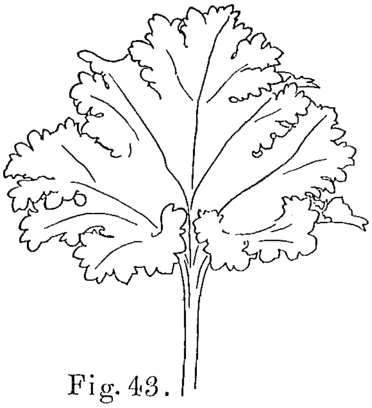
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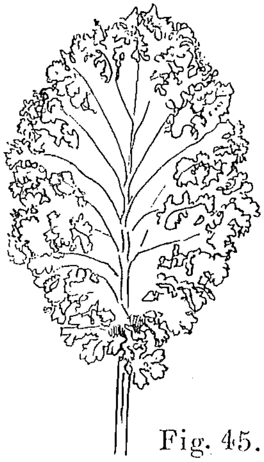
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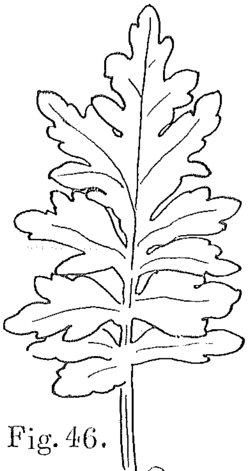

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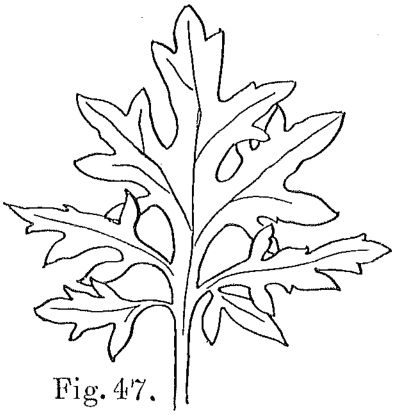

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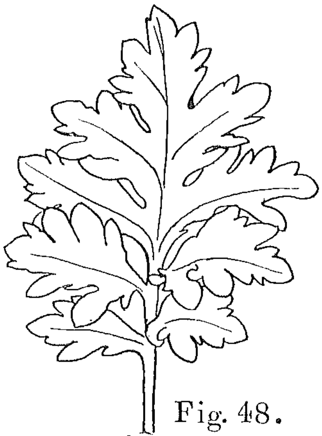

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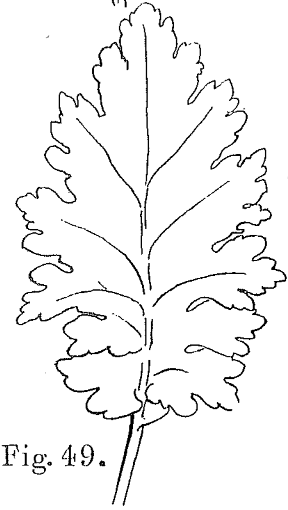

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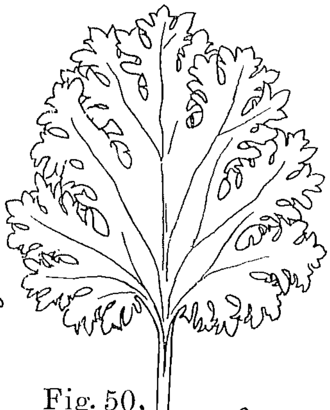

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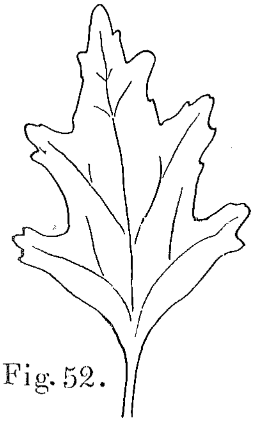

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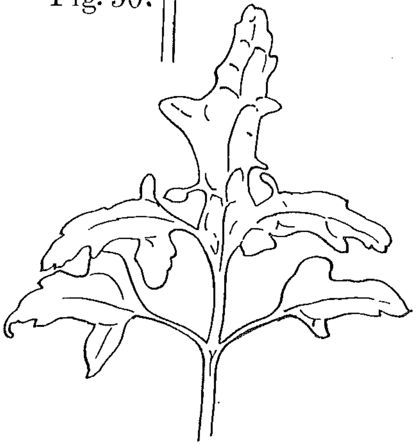

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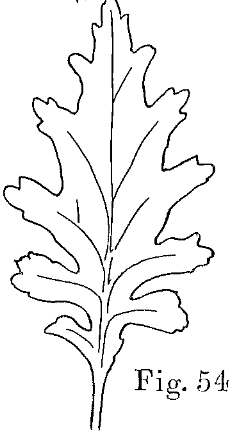

Fig. 54.


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