JOURNAL OF GENETICS

JOURNAL OF GENETICS

Volume I. 1910–1911

CONTENTS.

No. 1 (November, 1910)

No. 2 (March, 1911)

No. 3 (August, 1911)

No. 4 (November, 1911)

Correction. On Plate XXXIV, *to face* p. 208, *for* "Monopodial" *read* "Sympodial," *and for* "Sympodial" *read* "Monopodial."

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WHITE FLOWERED VARIETIES OF *PRIMULA SINENSIS*.

By FREDERICK KEEBLE,

Professor of Botany, University College, Reading :

AND Miss C. PELLEW,

Research Student, Botanical Laboratory, University College, Reading.

[It was intended that this paper should be published simultaneously with an extensive memoir by Mr R. P. Gregory on inheritance in *Primula sinensis.* Mr Gregory's paper is already in type ; but owing to its length and to delay incidental to preparation of the coloured Plates illustrating it, we have been obliged to hold it over for the next number of the *Journal.*—EDD.]

White Flowered Varieties. White flowered varieties of *Primula sinensis* are of two kinds, one with red or reddish stems (coloured stems) and the other with green stems. Coloured stemmed whites, when crossed with a variety with coloured flowers, yield an F_1 with white or tinged white flowers. Green stemmed whites, when similarly crossed, yield an F_1 with coloured flowers. Since the white or tinged white F_1 plants give rise, on selfing, to white and coloured flowered plants in the proportion of three white to one coloured, it is inferred that the coloured stemmed whites carry the factors for colour, but that pigment formation is inhibited by the presence of a dominant white factor. Since, also, green stemmed whites give rise, when crossed with a colour variety, to a coloured F_1, it is inferred that they lack the dominant white factor as well as one or more of the colour-factors.

Thus, of white varieties of *Primula sinensis* hitherto investigated, those with coloured stems are "dominant whites," and those with green stems " recessive whites."

One exception to this rule is already known : the green stemmed, white variety Pearl having been shown to be a dominant white.

The purpose of this note is to record the existence of what appear to be exceptions to the rule of dominant white among coloured stemmed, white varieties.

The evidence is based on the gametic behaviour of Snow King, a variety which has white flowers and dark red stems.

Plants of Snow King, raised in 1908 from seed obtained from Messrs Barr, proved true to type, except for an occasional magenta flaking of the petals of a few plants. The variety again bred true to type in 1909.

In 1908, three plants of Snow King were used for crossing with the following coloured varieties :

Reading Pink (pale pink flowers, green stem).

Crimson King (dark red flowers, reddish stem).

Pink Stellata (pale magenta flowers, reddish stem).

A green stemmed variety with pink flowers a shade deeper than in Reading Pink, numbered 2 A.

It should be remarked that, in green stemmed, coloured flowered varieties of *P. sinensis*, the deeper flower colours of the self-coloured types are not fully developed. Such plants however carry the factors for the deep colours ; for, when they are crossed with coloured stemmed varieties with pale coloured flowers, the deeper shades are fully developed in the coloured stemmed offspring.

The F_1 generations, obtained from the crosses between Snow King and the several plants enumerated above, were as follows :—

Expt. No.	Cross	Description of F_1 plants
20·2	Snow King × Crimson King[1]	10 tinged white : 9 magenta
52	Reading Pink × Snow King[1]	5　,,　　,,　: 3　,,
200	Pink Stellata × Snow King	12　,,　　,,　(nearly pure white)
2 A	(Green stem × Snow King, flowers pink)	8 pale magenta

A uniform F_1 family of whites or tinged whites occurs in only one of these crosses. In No. 2 A, the F_1 consists of coloured flowered plants and, in Nos. 20·2 and 52, it is composed of tinged whites and coloured in about equal proportions.

[1] The same plant of Snow King was used in crosses 20·2 and 52.

In order to investigate the meaning of these results which are in disaccord with those obtained hitherto with coloured stemmed whites, coloured and white tinged plants of the F_1 generation were selfed, and the F_2 generation examined. The results were as follows:—

F_2 from coloured flowered F_1 plants.

Experiment No. 20·2, a magenta plant selfed.

F_2.   Observed   20 coloured : 8 white and flaked white.
       Calculated 21   ,,   7   ,,   ,,   ,,
          ,,   3   ,.   1   ,,   ,,   ,,

Experiment No. 52, two magenta plants selfed.

F_2.   Observed   54 coloured : 19 white and flaked white.
       Calculated 55   ,,   18   ,,   ,,   ,,
          ,,   3   ,,   1   ,,   ,,   ,,

Experiment No. 2 A1, two magenta plants selfed.

F_2.   Observed   77 coloured : 22 white and flaked white.
       Calculated 74   ,,   25   ,,   ,,   ,,
          ,,   3   ,,   1   ,,   ,,   ,,

F_2 from tinged white F_1 plants.

Experiment No. 20·2, a tinged white selfed.

F_2.   Observed   29 white and tinged white : 12 coloured.
       Calculated 33   ,,   ,,   ,,   8   ,,
          ,,   13   ,,   ,,   ,,   3   ,,

Experiment No. 52, two tinged whites selfed.

F_2.   Observed   63 white and tinged white : 15 coloured.
       Calculated 63   ,,   ,,   ,,   15   ,,
          ,,   13   ,,   ,,   ,,   3   ,,

Experiment No. 200·1, a white plant selfed.

F_2.   Observed   13 white : 9 coloured.
       Calculated 18   ,,   4   ,,
          ,,   13   ,,   3   ,,

In the F_2 from coloured plants we obtain approximately 3 coloured : 1 white, and in the F_2 from tinged white sister plants we have approxi-

mately 13 white (and tinged) : 3 coloured. A departure from the 13 : 3 ratio should be noted in Experiment 200·1. This must be attributed to the fewness of the F_2 plants grown, until more evidence can be obtained.

It was noticeable that some of the white plants of F_2 from white and coloured F_1, showed a considerable increase of flaking as compared with that observed in certain plants of Snow King. Among those flaked, white plants from coloured F_1 plants, there occurred one or two plants bearing flowers with a very faintly tinged ground.

Further investigations will, it is hoped, demonstrate the significance of these facts.

On the basis of the numbers obtained in F_2, we arrive at the following conclusions :—The plant of Snow King used in Experiment No. 200, which gives a tinged F_1, is homozygous (WW) for the dominant white factor.

That used in Experiment No. 2 A, which gives a magenta F_1, is homozygous (ww) for the absence of the dominant white factor. Since the flowers of this plant are white, it lacks a colour factor. That is, its gametic constitution is cw. Since the stem is red, the loss of colour factor has regard only to the flower and not the stem.

Writing Snow King cw and plant 2A, Cw,

$$F_1 = Ccw = \text{coloured.}$$

The plant of Snow King used in Experiments Nos. 20·2 and 52 which give both coloured and tinged white in F_1, is heterozygous (Ww) for the dominant white factor. Since the variety as a whole breeds true to whiteness, the heterozygous (Ww) plants must lack colour factors. Their gametic constitution is cWw.

Snow King (cWw) × Crimson King or Reading Pink (Cw).

$F_1 = CcWw$, white or tinged white and $Ccww$, coloured.

$F_2 = 9\ CW,\ 3\ cW,\ 3\ Cw,\ 1\ cw.$ $F_2 = 1\,Cw,\ 2\,Ccw,\ 1\ cw.$

   = 9 white + 3 white + 3 coloured + 1 white   3 coloured : 1 white.

   = 13 white : 3 coloured.

In order to investigate further the nature of the factors necessary for the production of colour in *Primula sinensis*, plants of recessive white Snow King were crossed with the recessive white, green stemmed varieties of Ivy leaf (for a plant of which we are indebted to Mr Bateson) and Snow-drift.

From Ivy leaf × Snow King an F_1 was obtained consisting of 4 flaked white on dark red stems, and 1 flaked white on reddish stem. Snow-drift by Snow King yielded an F_1 consisting of 24 magenta flowered plants with reddish stems. Thus a fully coloured F_1 is obtained as the result of a cross between two white flowered varieties. The F_2 generation from these crosses has not yet been obtained.

Table of Flower and Stem colour in F_2.

	Expt. No.	Stem			Flower colour				No. of plants not flowered	Cross
		Reddish	Dark red	Green	Magenta	Pink	White and tinged	Pale pink		
F_2 family from magenta F_1 plants	20·2·1	23	—	—	14	3	6	—	—	Snow King × Crimson King
		—	—	5	—	3	—	2	—	—	
F_2 family from tinged white F_1 plant	20·2·2	28	—	—	3	6	17	—	2	
		—	—	15	—	3	—	12	—	—	
F_2 families from magenta F_1 plants	52·3	23	—	—	10	7	6	—	—	Reading Pink × Snow King
		—	9	—	8	—	1	—	—	
		—	—	2	—	—	2	—	—	
	52·5	27	—	—	17	1	8	—	1	
		—	7	—	6	—	—	—	1	
		—	—	7	—	—	2	5	—	
F_2 families from magenta F_1 plants	52·4	32	—	—	7	2	23	—	—	
		—	9	—	—	—	8	—	1	
		—	—	14	—	—	12	2	—	
	52·6	15	—	—	—	1	14	—	—	
		—	5	—	3	—	2	—	—	
		—	—	5	—	—	4	—	1	
F_2 families from 2 magenta F_1 plants	2 A 1	21	—	—	16	—	4	—	—	2 A × Snow King
		—	5	—	5	—	—	—	—	
		—	—	6	—	—	1	4	—	
	2 A 5	39	—	—	30	—	9	—	—	
		—	8	—	5	—	3	—	—	
		—	—	21	—	—	6	16	—	
F_2 family from white F_1 plant	200·2	17	—	—	7	—	10	—	—	Pink Stellata × Snow King
		—	5	—	2	—	3	—	—	

THE INHERITANCE OF COLOUR AND OTHER CHARACTERS IN THE POTATO.

By REDCLIFFE N. SALAMAN, M.D.

INTRODUCTION.

THE experiments here described were begun in the spring of 1906 and are still being continued; the work has been carried on in my garden at Barley in Hertfordshire. Although the subject material of this research was my own choice, at the time it was determined on I was quite ignorant of the very special advantages as well as disadvantages which the Potato offers for the Mendelian student. To Professor Bateson and Professor Punnett I owe a debt of gratitude for the encouragement they have always given me and the time they have so kindly devoted to examining and criticising my work.

The potato plant as grown domestically in England is a perennial, that is to say, it is raised from tubers vegetatively year by year. Most of our varieties bear flowers, but only a very small proportion set seed; this peculiarity will be considered more fully later, and has already been dealt with in detail(9)[1].

The potato flower bears five anthers (sometimes six or seven) arranged in a cone through whose apex projects the stigma. The anthers dehisce at their distal extremities, the pollen, when there is any, falling on to the knob-shaped stigma which projects but a short distance beyond the cone's apex.

When cross fertilizations are made, the flower which is to act as the female parent is emasculated before the bud is open while both anthers and stigma are still unripe.

The flowers are borne as a cyme, on axial stalks, each bloom having a short stem about an inch long, and at a distance of half an inch

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[1] The numbers in brackets refer to the Bibliography.

below the base of the flower there occurs a ring of cork. In all potatoes the flowers have a great tendency to separate at this point from their stems: the tendency is more marked in those flowers where the anthers are sterile. If such a flower is used as the female parent the chances of a successful cross fertilization are somewhat less good than if the fertilization is made on one with fertile anthers owing to this habit of separation. In all potato plants, however, when grown out in the open, successful fertilization, be it "selfing" or "crossing," is a hazardous undertaking, and I personally do not succeed in getting more than about ·5 °/₀ of the individual flowers I handle to set seed.

Once the ovary begins to swell there is little fear of separation taking place at the cork ring, indeed the stem gradually thickens and carries the berry late into the autumn.

All my work has been carried on without placing the flowers in bags. The reasons for not adopting special precautions were that when bagged the flower invariably drops, that bees and the like never approach a potato flower though a small fly often lives in the bottom of the corolla, that the flower is constructed for self-fertilization, and that the quantity of pollen is so scanty as to render fertilization by the wind in the highest degree improbable. Each year I have sterilized a number of flowers and purposely left them unpollinated, in no instance has any fertilization taken place. In two instances out of some hundreds so treated the ovaries swelled till they attained a diameter of 3/16 in., but they contained no seed and dropped.

Although the potato, owing to its scanty pollen, its frequent sterility, and its delicate flower, is not an ideal subject for Mendelian research, it does still offer to the experimentalist one redeeming character. An individual plant can always be "carried on" by means of its tubers into the next season's work, and whether it be for the sake of comparison or for the purposes of further fertilization this property is of the utmost service.

The Scope of the Observations. Attention has been concentrated mainly on the heredity of characters of the tubers, for the haulm or foliage of the potato plant, though variable in habit of growth, size, shape, texture and colour, does not lend itself readily to this type of work. The foliage more especially is so variable in different parts of the same plant, whilst the differences between one type of foliage and another, however apparent, are so difficult to define that except in one instance, which will be considered later in detail, I have not made out anything sufficiently definite.

The colour of the stem is always correlated in some degree with that of the tuber, but whereas one meets with innumerable white-tubered plants, yet, as far as my experience goes, in all of these some colour may be found, if not in the stem, then in the shoot which emerges from the tuber in spring.

Very definite Mendelian segregation of colour in the stem occurs when the black or deep purple pigment, such as is seen in " Congo," is introduced, but in the case of the red- and white-tubered plants the quality of the pigment being constant, it is the quantity that varies and that is not readily to be measured. In one family of 100 seedlings I ascribed values to the colour as seen in the stem. The parent was a plant with a medium quantity of pigment in the stem. The degrees of pigmentation in the stems of the seedlings were divided into "strong," " medium," and " weak," and the numbers in each class bore to each other as nearly as possible the relation of 1 strong : 2 medium : 1 weak.

The absence of distinct and definable gradations between the various degrees of colour, as well as the possible personal bias in the classifica-tion, is my reason for not publishing the results of the observations on colour in stem and foliage which were made in every individual plant during the four years' work covered by this paper.

Observations on the colour of the flowers have been made, but only in the case of seedlings of the potato known as Lindsay's *etuberosum* has anything of interest been observed : a description of the phenomena in the flowers is given in the section dealing with this peculiar variety.

Observations on the pollen have disclosed some interesting facts in connection with heredity of sterility and have confirmed East's [4] observation of the relation between amount and viability of pollens.

The incidence of disease (*Phytopthora infestans*) has been closely watched, but only in the case of the Lindsay etuber, *q.v.*, has anything definite been observed.

The fact that there has been till now no really immune variety to work with has prevented any headway being made in this direction.

The Material used. All the observations, excepting those dealing with the peculiar variety already described by Sutton [8], and known as Lindsay's *etuberosum*, have been made with ordinary domestic varieties. The most useful of all the potatoes employed has been Sutton's " Flourball," which indeed gives the key to the understanding of them all. The black pigment was introduced by the potato known as the " Congo," a potato which is of a deep blue-black both within and without and which is used domestically for salads. One variety which

proved of value was a white kidney potato known as "Record." It was brought out by Messrs King, of Coggeshall, but it has entirely gone out of cultivation as far as could be ascertained, not only in England generally, but in my garden also, and my notes of its characters are unfortunately not very full.

I give here a list of the domestic varieties I have used.

In self and cross fertilization.	*For observations on pollen.*
A. Flourball (Sutton).	B. Varieties in list A.
Record (King).	Ringleader.
Congo.	Supreme.
Reading Russet.	Dutch Cornwall.
Red Fir Apple.	Peckover.
Queen of the Valley.	The Dean.
Bohemian Pearl.	Purple Eyes.
Sole's Kidney.	Up-to-Date.
Early Regent.	Duke of York.
Prof. Maerker.	
S. etuberosum.	S. commersonii
	S. tuberosum
	S. verrucosum ⎬ species.
	S. maglia

Several other varieties were used in class A without success.

STERILITY OF ANTHERS. CONTABESCENCE.

Darwin [3], in considering the origin of sterility, describes a condition not uncommonly found amongst plants of various families in which the anthers are more or less twisted up or aborted and contain no pollen. Darwin called this condition "contabescence," and described how it might be propagated by layers, cuttings, etc., and even by seed.

Gaertner first observed the condition and described a similar change affecting the female organ [6].

Bateson described in the Sweet Pea a similar phenomenon and found it recessive to fertile anthers [1].

The potato "Record," which possesses no pollen in its anthers, was crossed by Sutton's "Flourball," which possesses abundant pollen : 20[1] of the 32 F^1 plants which bore flowers not one of which contained any

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[1] In 1910 26 of the F^1 plants flowered and they were all sterile.

pollen. Two individuals of the F^1 family were fertilized by a derivative of "Flourball A," very rich in pollen, and gave rise to 39 plants, 19 of which bore pollen and 20 bore none: the expectation on the assumption that sterility is dominant being here equality.

In the "Congo" potato the anthers are entirely devoid of pollen, though they are not usually aborted or crippled. A plant of this variety was crossed by a "Flourball" seedling, and out of 18 F^1 plants which flowered, 8 had abundant pollen and 10 had none: here again the expectation was equality, "Congo" being heterozygous in sterility.

Two F^1 plants possessing abundant pollen were selfed, and of 44 plants examined, 41 possessed pollen and 3 possessed but a few grains of immature pollen. Why these plants should not have borne a fair quantity of pollen seeing that the F^2 parents must have been recessives and should have bred true, it is not possible to say. All three examples came out of one family.

A second cross with "Congo," viz. by "Reading Russet," gave only a small F^1 family, three plants bearing flowers, two containing pollen, and one none.

Similar results were obtained in the cross "Red Fir Apple" and "Reading Russet," F^1 being part pollen producers, part sterile, whilst F^2, from the pollen bearing F^1, gave 9[1] plants all pollen producers.

The flower of the "Red Fir Apple" is heliotrope in colour and the anthers are aborted.

"Queen of the Valley" has heliotrope flowers with sterile anthers. Crossed by "Flourball" one plant gave a series of F^1 plants of which some bore pollen and others none, although exact notes as to their characters in this family were not taken. One of the F^1 plants was crossed by a "Bohemian Pearl" seedling, and gave rise to a long line of pollen producers.

The heredity of male sterility in the potato is obviously the converse of that described by Bateson in the Sweet Pea, for the condition here is distinctly dominant. Bateson found it partially coupled with green axils in certain families. In the case of the potato, the only evidence of sterility being coupled with any other character was of a negative sort. Working with a large number of established varieties as well as with those plants which arose in the course of this work, I never found a plant possessing pale heliotrope flowers that had other than sterile and contabescent anthers, whilst those that were further tested proved

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[1] In 1910 22 more F^2 plants flowered and all possessed pollen in the anthers.

to be heterozygous as regards sterility of anthers.   No connection was observed between the condition of the male and female organs.

The presence of pollen in the anther being as we have seen a recessive character, it is of some interest to note how it behaves in selfed families.   Unfortunately these pollen observations were not begun till 1909, although the breeding experiments began in 1906. Still a good deal of information may be extracted from the early notes.

Thus, in 1906, a red-tubered seedling derived from a "Flourball" plant in 1904, was "selfed," and gave rise to a large number of seedlings.   One white-tubered plant (D) was reserved.   From this a further generation was bred, and from this again another, so that in this case the family has been handed through five generations, and in all the anthers have had abundant pollen though the quality of the pollen was bad.

Two other lines, A and G, derived from "Flourball," have been bred through three and four generations respectively, and the recessive character, viz. presence of pollen in the anther, has remained true.

The occurrence of spontaneous sterility, due to absence of pollen, has already been mentioned as having taken place in the F^2 generation of the family "Congo" × "Flourball"; it has also been observed in some other families where it was unexpected, but in all these cases it has occurred in normal and not deformed or strictly "contabescent" anthers.   It is possible that "contabescence" is not a simple character but that absence of pollen and deformity of anther are due to separate factors between which exists an intimate linking.

The relations between quality and quantity of pollen and the shape of pollen in varieties and species of *Solanum* are discussed elsewhere [9].

Heredity of Characters in the Haulm.

The difficulties in relation to haulm characters have already been adverted to; although to experts constantly reviewing crops of well-grown varieties it becomes comparatively easy to diagnose a variety by the general appearance of the foliage, and by inspection to designate at once such and such a potato as an "Up-to-Date" variety, or a "Ringleader" type, and so forth, yet if one closely compares any two foliages, taking corresponding specimens from various parts of the plant, it will be found very difficult to describe any constant differentiating character between any two varieties; there are differences no doubt,

but they do not admit of such definition as to fit them for Mendelian analysis.

The cross of "Red Fir Apple" and "Reading Russet" was made in 1906 for the purpose of tuber colour observations, and in 1909 a large family of some 120 individuals of F^2 plants were raised.

The "Red Fir Apple" has a somewhat distinctive foliage, the leaves are relatively small, ovate with sharp apices, peculiarly soft and silky to the touch, and, in addition, have a character which entirely distinguishes them from "Reading Russet" and most other varieties. The leaf has a peculiar twist in its axis, this twist being seen in all the upper leaves and often down to the lowest when the plant is 18 inches high or more.

The condition of leaf twist here in question must be clearly distinguished from that which occurs as a pathological condition in many varieties; in such cases the plants are dwarfed, the stems shrunken, the axes of the branches very shortened, and the leaves on them crowded together. The individual leaves also are much twisted, crenate and small.

In the "Red Fir Apple" the twist is less violent, it is not associated with crenation, and the plants are thoroughly healthy, vigorous and of good size.

"Reading Russet" possesses a much coarser foliage, the leaves are big, broad, blunt, flat, smooth, hard and coarse; the green colour is of a deeper shade than in "Red Fir Apple."

The four F^1 plants which were examined were intermediate as regards shape and texture of foliage, but resembled "Red Fir Apple" shape rather than "Reading Russet"; no twist in the leaf axis was observed.

In F^2 an analysis was made of the plant's foliage characters as seen in the table below.

The characters taken are all leaf ones.

"Reading Russet" shape.	Broad and blunt leaf.
„ „ texture.	Few stiff hairs, glazed surface to leaf.
"Red Fir Apple" shape.	Ovate, sharp apex to leaf.
„ „ texture.	Soft and silky.
Twist.	Twist in the axis of the leaf.
Intermediate shape.	Leaf shape neither "Reading Russet" nor "Fir Apple" in type, but resembling more closely the latter.
„ texture.	Softer than "Reading Russet" and harder than "Fir Apple."

FOLIAGE OF F^2 GENERATION.

"Reading Russet" texture.	"Reading Russet" shape	10
,, ,, ,,	Intermediate shape	1
Intermediate texture.	"Reading Russet" shape	4
,, ,,	Intermediate shape	40
,, ,,	"Fir Apple" shape	12
"Fir Apple" texture.	Intermediate shape	9
,, ,,	"Fir Apple" shape	42

The first two rows are braced together as **11**.

Total number of F^2 plants 118

Twist in leaf 27

In considering these figures it must be remembered that it is a matter not only of considerable difficulty to classify the living plants according to the shape and texture of their leaves, but that the personal element is paramount in such a classification. More particularly do such remarks apply to the consideration of texture and to the intermediate forms. Certain features, however, are readily and unmistakably recognized; these are the twist in the axis of the leaf and to a lesser degree "Reading Russet" shape.

The intermediate form of leaf is much more like the "Fir Apple" leaf than the "Reading Russet," and the former may therefore be considered dominant, whilst the twist in its leaf is recessive.

If the "Reading Russet" shape and texture are recessive, then it should occur combined in the F^2 family in the ratio of $1 : 15$ and here it is $1 : 12$.

The twist in the leaf occurred 27 times out of 118, that is practically in the ratio of $1 : 3$, and it was associated 23 times with the "Red Fir Apple" shape, the remaining four having intermediate shapes and none showing "Reading Russet" shape.

Allowing again for the difficulty in distinguishing the intermediate form from "Fir Apple" shape and texture, it would seem to be a fact that this peculiar twist in the leaf is definitely linked up with the "Fir Apple" characters of shape and texture. None of the eleven plants possessing "Reading Russet" shape showed the slightest sign of a twist. The same consideration leads one to believe that "Reading Russet" texture is coupled up with "Reading Russet" shape; ten out of eleven times it is recorded as being so linked whilst the eleventh

time "Reading Russet" texture was united to intermediate shape, which might possibly be an error of observation.

These observations demonstrate at least that such fleeting and difficult characters as leaf shape and texture in the potato segregate in the sexual generation.

This year[1] a fresh F^2 family of this cross is being raised, and close attention will be paid to their foliage character.

The Shape of the Tubers.

No character seemed at first sight more elusive and less likely of solution in respect to its heredity than that of shape. Whenever I spoke to experts I was told that from the best "kidney" types you could pick out "rounds," and that exhibitors had won prizes both for "rounds" and for "kidneys" from one and the same potato.

East (5) notes four cases where originally "long" tubered varieties produced as bud sports rounded tubers; in two cases these "round" tubers reproduced themselves vegetatively true to "roundness," while the other two relapsed in the following season.

The oval varieties he notes as producing on single plants entire crops of very elongated tubers, which however did not grow true in subsequent years.

My observations would lead me to think that these bud sports in "kidney" and oval potatoes are quite common and are to be explained by their heterozygous composition as regards "roundness."

A frequent cause of trouble in dealing with the shapes of tubers is the nomenclature. The terms used to describe the different shapes are sufficient for the purpose of the gardener, but they connote no scientific accuracy.

Where the cylindrical potato ends and the kidney begins, where the latter ceases and the "pebble" starts, and where both merge into the round is a problem which it would be hopeless to attempt to solve by the mere classification of tubers.

It is only by the isolation of a type and its fixation as pure when bred sexually that the problem can be solved.

In describing the shape of a potato, two points can be regarded as

[1] In 1910 out of 71 F^2 seedlings on Aug. 3rd 6 showed the "Fir Apple" twist, on Aug. 23rd 14 had developed it.

fixed, viz. the point from which the tubers grow out from the stolon, and the most distal point from that, which in 19 out of 20 cases coincides with the central of the crown of eyes at the distal end. It is from this eye that the earliest and strongest shoot grows out. The line between these two points is the long axis, the breadth and depth are respectively the greatest measurements in each direction measured at right angles to the long axis and to each other. Adopting the conventional terms for potato shapes, the names long, kidney, pebble, and round appear to have the following meanings:—

A long potato is one in which the long axis is between $1\frac{1}{2}$ and $2\frac{1}{2}$ times the greatest breadth, and the depth is equal to the breadth. The ends are either blunt, as in the "Congo," giving the tuber a cylindrical appearance, or they are pointed as in *B*, Plate XXIV.

A kidney potato is one in which the length is usually between $1\frac{1}{3}$ times and twice the breadth, and the depth is considerably less than the breadth, giving the tubers a flattened appearance which is characteristic. The measurements of three specimens, unselected, of well-known "kidneys" are :—

"Myatt's Ashleaf" :

	Length. Inches	Breadth. Inches	Depth. Inches	Ratio
(1)	2, 12/16	1, 9/16	1, 3/16	$= 44 : 25 : 19$
(2)	3	1, 7/16	1, 3/16	$= 48 : 23 : 19$
(3)	2, 4/16	1, 7/16	1, 2/16	$= 36 : 23 : 18$

"Sutton's Ideal" :

(1)	2, 7/16	1, 8/16	1, 4/16	$= 39 : 24 : 20$
(2)	2, 5/16	1, 10/16	1, 4/16	$= 37 : 26 : 20$
(3)	2, 4/16	1, 7/16	1, 4/16	$= 36 : 23 : 20$

"Table Talk" :

(1)	3, 1/16	1, 14/16	1, 6/16	$= 49 : 30 : 22$
(2)	3	2	1, 9/16	$= 48 : 32 : 25$
(3)	3, 1/16	1, 15/16	1, 8/16	$= 49 : 31 : 24$

"Sir John Llewellyn":

(1)	3	1, 10/16	1, 2/16	$= 48 : 26 : 18$
(2)	2, 13/16	1, 10/16	1, 4/16	$= 45 : 26 : 20$
(3)	2, 11/16	1, 13/16	1, 7/16	$= 43 : 29 : 23$

The Lapstone Potato is a bluntly elliptical or oval potato which is much broader than it is deep.

The Pebble Shape. This term includes a vast number of rather irregularly shaped tubers—tubers for the most part obtusely elliptical and almost as broad as they are long.

Below are some typical specimens:—

"Reading Russet," see Plate XXI.

	Length	Breadth	Depth	Ratio
(1)	2, 6/16	1, 15/16	I, 7/16	= 38 : 31 : 23
(2)	1, 15/16	1, 12/16	1, 3/16	= 31 : 28 : 19
(3)	1, 15/16	1, 13/16	1, 8/16	= 31 : 29 : 24

"Flourball," see Plate I.

	Length	Breadth	Depth	Ratio
(1)	1, 15/16	2, 1/16	1, 8/16	= 31 : 33 : 24
(2)	2, 3/16	2, 9/16	1, 13/16	= 35 : 41 : 29

Round Potatoes. The tubers are practically globular, as in "Windsor Castle."

An examination of these different descriptions is enough, almost in itself, to convince one of their artificiality, but when one comes to close quarters with them by breeding various pure lines and by crossing, one is soon convinced of the fact.

If Plate I, seedlings of "Flourball," be now examined, it will be seen that it is easy to pick out[1]

> Longs   Nos. 14, 48, 135.
> Kidneys   „   21, 87, 88, 123.
> Pebbles   „   74, 90, 91, 154, 179;

but a close inspection shows a number of tubers which might be described as round, but which are not globular. They are short, and as deep as they are wide, such as Nos. 40, 89, 92, 112, 132, 138, 155, 156, 162, 185—10 individuals out of a total of 43.

If now we turn to Plates II, III, IV, V we shall find a family of 100 individuals all bred from one of these peculiarly shaped tubers (*A*). The whole family present a striking uniformity of appearance and similarity to the parent. Exceptions, however, there are, and they are figured in full in Plates IV and V.

Turning to these plates we see photographed all the available tubers from each of these individual plants, and it will be at once seen that each individual plant in Plate IV contains striking examples of this "round" type amongst its tubers.

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[1] It should be said that the representatives of the individual plants here shown are when there are ovals and others more resembling "rounds" present on the same root, always the oval. The bias in favour of the "longs" as against the "rounds" has been purposely made in the composition of all the plates, in order that the recessive "round," when present, shall be free from the suggestion that it is only a variant form of the dominant "long." If therefore the effect to the eye be less convincing the deductions that are drawn rest on a firmer basis.

On Plate V, Nos. 67, 87, 91, 94, only further illustrate the fact that though certain tubers of a plant in this family may be more or less oval, yet other tubers on the same plant will be found to be of this peculiar "round" type.

One exception, however, stands out, and this is No. 100, which is definitely unlike the parent type and all its 100 other sister plants.

It is possible that it arose from a stray tuber and does not belong to this series at all—a view that has some plausibility, seeing that two years before "Flourball" seedlings were grown on this ground. Efforts are being made this year (1910) to obtain selfed seed from this plant.

On Plate VI a further illustration (G family) of this "round" type of potato is seen; it arose from a "Flourball" plant, but not the same one as the line A.

Seed from four of these plants has been saved and a batch of seedlings of G^4 were planted in October 1909 and hurried forward; on April 26, 1910, they were examined and all the seedlings bore tubers, varying from $\frac{1}{4}$ to $\frac{3}{4}$ in. diameter, true "rounds" in shape. Those of the G^3 seedlings which have formed tubers have also developed typically "round" ones[1].

It thus appears that there is a certain definite type of "round" potato that can be extracted from Sutton's "Flourball," and which can be bred sexually pure through at least two generations after having been isolated.

Before following further the evidence as regards the heredity of this type and its behaviour when crossed with other types, it will be best to discuss more fully its shape and variations.

The tuber shape, which is under consideration and which for the purposes of my work I have called "round," is to be found white, or coloured as red or black.

No relation has in the course of this research been shown to exist between shape of any kind and the pigmentation either of haulm or tubers.

The "round" tubers may be furnished either with "deep" or "fleet" eyes. It will be shown later that depth of the eye is itself a character inherited on Mendelian lines, and my experiments fail to show any relationship between depth of eye and shape of tuber. The size of the tuber is of course variable, but I have not found, however one may have

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[1] Aug. 29, 1910. Although the G family has not been completely harvested there is evidence that the G^3 family consists of three "longs" to one "round," and that the G^1 and G^4 families are pure to "roundness."

bred it, this type of "round" potato assuming large proportions; few examples with a diameter over 2 inches occur, although oval and kidney from the same original parent stocks may be of large size and weight.

A typical specimen of this "round" type is represented by the first tuber of G^6, Plate VI. The tuber is apple-shaped, its upper or proximal end as well as its distal or crown end is depressed, and the height is less than either its width or its depth. The actual dimensions are :—

Length	Breadth	Depth	Ratio
1, 5/16	2, 2/16	1, 1/16	=21 : 34 : 17

One of the tubers of the parent A has the following measurements:—

Length	Breadth	Depth	Ratio
1, 5/16	2, 2/16	1, 1/16	=21 : 34 : 17

The most characteristic feature is the stumpiness of the tuber in relation to its breadth.

Potatoes are raised commercially by the vegetative method, thus a crop of "Magnum Bonums" raised to-day should be regarded as merely an offshoot—a cutting so to speak—of a seedling raised some time before the year 1876. In other words the tens of thousands of tons which in the past 34 years have been grown of this stock are for scientific purposes merely replicas of a particular tuber of a particular individual, and hence the continuity through the intervening years of the variety's characters. Tubers that are grown by this vegetative means, within limits, reproduce themselves in their original shape more or less exactly, though I think, and hope to prove, that the degree to which a potato reproduces its shape vegetatively depends in large measure on its gametic constitution.

It may therefore be confidently expected that whilst a crop raised from a typical "round" such as A by vegetative means will remain perfectly true to type (and this indeed has been proved in the case of A itself, by growing it in 1908 and 1909), a crop raised say from the fifth tuber of No. 67, Plate V, might produce tubers more or less uniform and unlike the type A. A family raised by seed from any of the individuals, however aberrant in shape, will probably produce a set of seedlings at least as uniform as the family A itself.

The variation of this "round" type, if grown vegetatively, so far as my experience goes, is very slight or indeed none at all. The variations of the type as raised sexually by seed are slight but definite, being

towards greater length and approaching the pebble shape.   In diagram the type and extreme variation may be represented as below :—
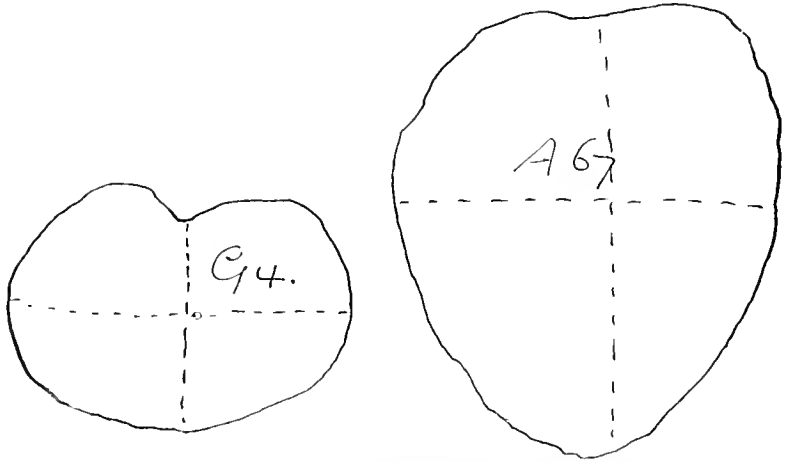
Fig. 1.   These drawings are tracings of sagittal sections of potatoes—the long and transverse axes are shown—the depth cannot be shown.

Height and breadth are here represented, the depth being relatively great.

The " round " type is not a potato that recommends itself for its beauty or its economic qualities as regards shape ; its merit is derived from the fact that there is very good reason to regard it as a gametically pure type, and that " roundness " in the sense in which it has been used here is a simple Mendelian character.   The further evidence in support of this thesis will appear as we proceed to discuss other shapes.

A seedling of " Flourball " was selfed in 1906, and in 1907 a large number of seedlings were raised from it, one only of which was again selfed in 1907.   The plant was carried forward by tubers to 1908, 1909 and 1910.   In both 1907 and 1908 it produced seed, but in these two years only four plants came to maturity, and they produced the tubers numbered in Plate VII, D^1, D^2, 1908, D^1 and D^2, 1909.   The seedlings from 1909 seed have not yet formed their tubers.

The tubers of plant D are quite unlike the " rounds " of the A family, they are oval and more or less kidney-shaped.   The offspring of these, only four in number (excluding the seedlings now growing), comprise distinct types.

D^2, 1908, a long pyriform tuber.

D^2, 1909, cylindrical tubers tending to kidney shape.

D^1, 1908, oval or blunt kidney with a sister tuber nearer circular.

D^1, 1909   „   „   „   „

The numbers in this case are all too small to draw precise deductions; all that can be said is that D does not represent a fixed type, that, on selfing, it gives both longs and ovals.

In 1908 this same D was crossed by A, and on Plate VIII the family is shown, or rather two families, because two D plants (D^1 and D^6) both grown from tubers of the original D of 1907 were fertilized by pollen of A.

A glance at the plate is enough to show that one has here two types of tubers, the "round" that we have already discussed on the one hand, and a series of ovals and kidneys on the other. The "rounds" are:

Nos. 3, 4, 5, 8, 13, 14, 15, 16, 18, 19.
3, 6, 7, 8, 10, 12, 14, 18, 19, 20, 21, 22, 28.

That is, 10 out of 19 in the first family, and 13 out of 30 in the second family. Total, 23 out of 49.

One has, in other words, "rounds" and not "rounds" in practically equal numbers; and it must be remembered that one counts here only those as "rounds" which come well up to the standard already given for a typical "round" such as either A, G^1 or G^6.

The result of this cross admits of a direct Mendelian interpretation, for inasmuch as A is pure to "roundness," D must be heterozygous in that character—a fact which was already strongly indicated before. And the "non-rounds" must be all heterozygous in shape. If now one examines more closely the "non-rounds," one sees that they are made up of good kidneys such as Nos. 1 ($D^1 \times A$), and 1, 4, 11 and 26 of ($D^6 \times A$); of cylindricals, such as 5 and 23 ($D^6 \times A$), while the remainder are ovals and pebbles difficult to place, but which include among themselves abundant examples of the same shape as the parent D.

The experiment therefore as portrayed in Plate VIII is capable of being interpreted as meaning, not only that an oval "pebble" such as shape D is heterozygous as to "roundness," but that a true kidney and a true cylindrical may also be heterozygous in the same degree. Further, if "roundness" (i.e. shortness of axis) is the one allelomorph here in action, then "non-roundness" or length is the other. Later evidence

will be given proving that there is a tuber shape true to length, but before bringing this evidence forward it will be necessary to discuss a little further the nature of the kidney and the shapes which are heterozygous.

Plate X shows a family derived from the cross of H^1, a kidney whose origin will be described later, and the typical "round" A. The "rounds" can be picked out most readily.

The typical "rounds" are :

Nos. 4, 6, 7, 16, 17, 19, 22, 25, 26, 27, 29, 30, 34, 35, 36, 38, 39, 40, 42, 45, 49,

i.e. 21 out of 44, practically half.

A kidney potato of so typical a shape as H^1 is therefore heterozygous in shape, and length, and must clearly be dominant to "roundness." Excellent specimens of kidneys occur in the family, and they must also be heterozygous.

It is interesting to note that No. 46 is more or less cylindrical, and that it is heterozygous and probably a merely variant form of kidney.

The hybrid nature, in regard to shape, of the kidney may be regarded as settled, that of the pebble follows as a necessity, but we have in support two sets of crosses.

A pebble-tubered plant H^{10} was crossed by the same "round" A as has been used before (see Plate XI). H^{10} is a typical pebble tuber and another of the same root-crop can be seen on Plate IX. The family, consisting of 47 individuals, is seen at once to break up into two types, the "round" and the ovals of different degrees.

The "rounds" :

Nos. 1, 2, 3, 4, 10, 11, 13, 13a, 15, 17, 18, 19, 26a, 29, 31, 32, 33, 34, 40, 46, 48, 49.

22 out of 47 are all typical.

Emerging from this union of pebble and "round" occur really good kidney tubers such as 26, 38 and 41, as good or better than those produced in the family $H^1 \times A$, where the parent was a typical kidney.

The next cross, and perhaps the most convincing, is represented in Plate IX. It was made between a kidney potato, "Record" on the one hand, and the pebble-shaped "Flourball" on the other. The offspring number 32, of which Nos. 12, 13, 18, 21, 24, 25, 26, 30 are all typical "rounds"; i.e. 8 out of 32, or 1 : 4, the expected proportion

if both the kidney and the pebble-shaped parent are heterozygous as regards shape, i.e. "length," and amongst the dominants some are excellent kidneys, others pebbles.   No. 3 is interesting because it shows on one and the same root a cylindrical potato and a pebble, a form which has just been shown to be heterozygous.

The arguments and the evidence in support of them, as to the heredity of the tuber shapes have, so far, all turned on the fact that there exists a variety of " round " potato which is recessive and breeds true; at the same time all examples that have been so far brought forward contain directly " Flourball " blood.   It might therefore be supposed that the whole structure of my contentions rest on this keystone—this " Flourball " derivative—and that if this latter be removed the argument and deductions would fall to the ground. It becomes necessary, therefore, at this stage to describe an experiment entirely free from such an objection, at least as far as I am aware.   A cross was made in 1906 between " Red Fir Apple " and " Reading Russet."   " Reading Russet " is a pebble-shaped potato and " Red Fir Apple " a long cylindrical. F^1 was not examined critically for shape; the note as to the 117 young seedlings raised in 1907 is that about one-quarter bore "round" tubers, of these only nine survived, and only five of them were reared in 1909.   Four individuals are shown in Plate XXI, and the fifth one, which was omitted, was a long-shaped tuber.   On the whole the evidence is rather in favour of F^1 being a mixture of "longs" and "rounds" in the proportion of $3 : 1$, but of the F^1 "rounds" we have no examples.   The F^2 generation, however, is represented by 120 individuals contained in the two families $L^{1(1)}$ and $L^{1(4)}$, both derived from the selfing of a kidney-shaped F^1 plant.

The first family, $L^{1(4)}$, consists of 60 individuals; of these 52 are represented in Plate XXII, and of the eight missing, five were long and three "round."   When the plate is examined, and still more the actual individuals, the "rounds," such as we have already become accustomed to, are to be found at once, and the following typical examples are seen, Nos. 1, 2, 22, 35, 37, 46, 47, 49, 61, 63 and 64, which in addition to the three not figured, makes the total of 14 out of 60 or nearly $1 : 3$.

The second family, $L^{1(1)}$, Plate XXIII, affords some very striking examples of typical "rounds" such as Nos. 6, 47, 52.   The family contains 59 tuber-bearing individuals, and of these Nos. 6, 10, 17, 19, 22, 24, 29, 30, 33, 40, 47, 52, 54, 61 are typical "rounds," i.e. 14 out of 59 or $1 : 3$.

In the two families containing 119 tuber-bearing individuals, 29 are "round," that is 1 in 3, as would be expected in an F_2 family from a heterozygous parent in which "roundness" was recessive.

It remains now to consider the evidence bearing on the existence and nature of the dominant shape in its pure form. So far, it has been shown that length of tuber is dominant and that the degree of dominance is variable, i.e. the hybrid form is not constant, the heterozygous tubers varying from a long kidney to an ovoid. On Plates XXII and XXIII, amongst the long tubers are undoubtedly pure dominants, but which exactly they are, and how to distinguish them from the impure dominants with certainty nothing but breeding experiments could determine.

It is, however, significant that by selecting those individuals whose tubers were the most uniformly long, it was found that out of the 119 members of the L family already described there were 34, or a little more than one-quarter, that could be picked out as being probably pure in respect to length.

Fortunately better evidence is to hand in respect to individuals homozygous in the character of length.

A potato, called "Sole's Kidney," yielded abundant seed in 1906, in 1907 several hundred seedlings were planted[1], and they all came true to type, viz. a long attenuated kidney, see Plate XXVI. One of these seeded and 50 seedlings were raised in 1909, and every one of these were long kidney form, see Plate XXVI. It would seem, therefore, that this potato C, "Sole's Kidney," is a pure dominant as regards length.

Another kidney, "Bohemian Pearl," was sown in 1907 and a very large number of seedlings (family B) raised; these were not examined very critically in respect to size and shape, but were noted as being uniformly long and pyriform: one selfed naturally, and of the five seedlings raised three bore long tubers, and two bore oval tubers, Plate XXV. These ovals are distinctly flattened and are not "rounds." They have been grown in 1909 and have retained their shape. Had there been any appreciable number of oval or "round" tubers in the first batch of 300 seedlings raised in 1907 it would undoubtedly have been noted; on the contrary, my own and my gardener's impression is that nothing but "longs" occurred. There is in my mind but very little doubt that the stock B is pure to length. Efforts are being made to self the oval tubered plants this season.

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[1] I was presented with several hundred of the seed of both these stocks by the Manager of the Cambridge University Farm.

In 1908 a cross was effected between a pebble-shaped tuber (M^5, Plate XXIV) and a seedling of the family B carried on by tuber from 1907[1]. The issue of this union forms a striking example of the effect of crossing a heterozygous by a dominant long. The whole family of 39 individuals is without exception long or oval, and includes the most elegant kidney and one or two cylindricals, see Plate XXIV.

In three experiments cylindrical potatoes were employed as the female parent. In the first "Red Fir Apple," a cylindrical, was crossed by "Reading Russet." There is good reason to believe that the F^1 family really consisted of three "longs" and one "round," though the small number of survivors, viz. 11 in the first season, does not assist one to any definite conclusion. Those of the F^1 family which survived 1909 are shown on Plate XXI. "Red Fir Apple," though long and cylindrical, is therefore in all probability heterozygous as regards length. It is of interest that, since it has been cultivated in my garden, it has become shorter and broader and less cylindrical; on the other hand "Congo," which was used in the second and third experiment, maintains its truly cylindrical shape. Plates XII and XXV.

In the second experiment "Congo" was crossed by a "Flourball" seedling of 1906. The "Congo" tubers are typically cylindrical, the seedling "Flourball" was not especially described[2], but the F^1 series, see Plate XXIX, consisting of 29 individuals, all of which bore kidney-shaped tubers, is evidence that the "Flourball" seedling's parent must have been "round" and that "Congo" must be a pure dominant; for if neither of these suppositions are true, then we should have expected pure "rounds," which are conspicuously absent, or if the "Flourball" seedlings were pebble or heterozygous in shape, then half of the K seedling family should be pure "longs," which they are not. F^2 families were raised from K^6 and K^9, both elongated and more or less kidney-shaped. The following proportion of "rounds" and "longs" occurred:

	Rounds	Longs
Family K^6	65	210
Family K^9	13	69
	78	279

[1] The B line planted in 1908 from the pollen of which this cross was made, was grown from long tubers arising both from the plant which gave the seed ball in 1908 and from its sister plants, sown indiscriminately.

[2] The absence of a description of shape implies that it was "round" or "pebble" shaped and not markedly distinct from the parent "Flourball."

i.e. $1 : 3\cdot6$. The families are illustrated in Plates XIII, XIV, XV, XVI, XVII, XVIII, XIX, XX.

In the third experiment "Congo" was crossed by " Reading Russet." Only four F^1 plants survived, and the tubers of these, Plate XII, are elongated, but here again the numbers are not large enough to draw conclusions from.

The dominant character of length in the tubers has been isolated or identified in the potato C, and is represented by a very elongated kidney; in B, where it is more pyriform; and in "Congo," where the ends of the tubers are blunted and the tuber has a cylindrical appearance.

It is not improbable, as was suggested earlier, that the allelomorphic pair to the character manifested in the "round" potato is length of axis, and that the kidney and cylindrical shapes, though inseparable with respect to length, are dependent on other factors governing shape besides that governing the length of the main axis.

The dominance of the long potato tuber over the short is analogous to the dominance of the giant over the dwarf plant, as Mendel showed in the Pea Family. This dominance probably rests on the same anatomical basis, viz. the respective length and number of internodes involved. Tubers are borne on underground stems, called stolons, and the eyes may be regarded as buds or nodes, so that the number of eyes present may represent the number of internodes condensed into the length of a tuber. A study of the tubers from this point of view is not yet complete, but it is quite clear that as a general rule the "round," i.e. short axis potatoes, have less eyes than the long axis ones, i.e. they represent fewer internodal lengths.

It has already been shown that the dominance of length is not equal in degree: sometimes the heterozygote is of the most attenuated form, but more often an intermediate shape is assumed varying from kidney to pebble and oval. The ordinary kidney of fair breadth is probably always an heterozygote.

The Variations in the Shape of Tubers. The amount of variation has already been indicated in the case of the "round" potato; in the "long" it is rather less. If "C" and "Congo" be taken as pure "longs," then, accepting the typical well-grown tuber of each sort, it is apparent that they are as to their proportion between length and breadth much the same, and the form is fairly uniform.

By far the greatest variation in shape, both amongst the individual members of the same family and the several tubers of the

same individual, is met with in the case of the heterozygous variety.

The examples of heterozygous potatoes which have been tested, viz. "Flourball" D^1, H^1, H^{10}, K^6, K^9 and L^1, varying as they do from kidney to pebble, testify to this.

The degree of variation in the shape of tubers of some given sort is in itself very variable, but I think it would be acknowledged that the kidney types vary most. A striking example of this is shown on Plate XXVIII, reproduced by permission of Messrs Sutton, where a kidney potato, "Superlative," is photographed in the clamp, and whilst the majority of the tubers are kidneys, a large percentage are best described as pebbles.

The variety H^1, Plate X, so clearly demonstrated to be heterozygous, is a remarkably uniform kidney shape, but out of less than half-a-bushel it is possible to pick out potatoes varying from a very long to an obtuse ellipse, Fig. 2.
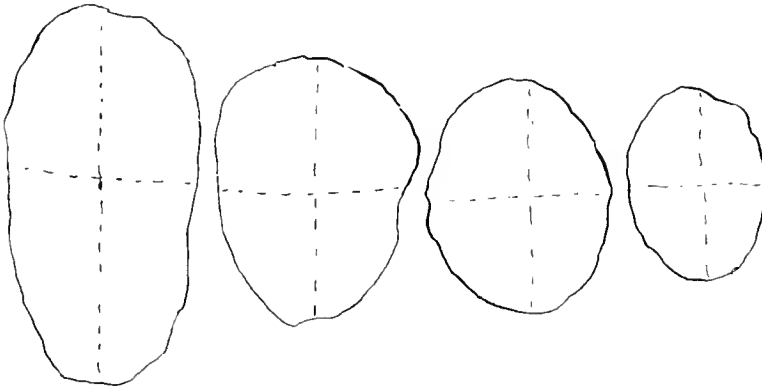
Fig. 2. These drawings are tracings of sagittal sections of potatoes of the individual H^1. The long and transverse axes are shown. The depth is less than the transverse diameter.

THE DEPTH OF THE EYE.

The potato tuber has scattered on its surface buds from which grow the shoots; the buds are known as "eyes."

The potato eye consists essentially of two parts, a central spot or shoot, and an overhanging ridge or brow which is curved, and whose concavity always points downwards or distally.

The eye is recognized to occur in two forms and is known as either

"shallow" or "deep." The "shallow" eye is a superficial eye, i.e. the central growing point is not depressed but is level with the general surface of the tuber and the brow is but very slightly marked.

Typically "deep" eyes are those of "Congo" and most of the family K ("Congo" × "Flourball" seedling) and A^{100}, whilst typically "shallow" eyes are seen in A^{27}; $H^1 × A$, Nos. 5, 37, 41. The "shallow" eye is a distinctive and an easily recognized feature. Briefly the "deep" eye is dominant to the "shallow," and the heterozygous "deep" eye is never quite so "deep" as the typically "deep" one. In "Flourball" the eye is "deep" but not remarkably so; of its seedlings 14 out of 43 were definitely "shallow." In the family A, of 98 seedlings 21 were "shallow," and A the parent may be regarded as having the standard impure "deep" eye.

The $D^1 × A$ families contain 16 "shallow"- and 33 "deep"-eyed individuals.

The $H^1 × A$ families contain 22 "shallow"- and 71 "deep"-eyed. K^9 is a further example of an impure dominant "deep"-eyed potato. Of the 73 seedlings of this family 23 are "shallow" and 51 "deep."

Two F^2 families were raised from the cross of "Red Fir Apple" × "Reading Russet." These two families differ a little in respect to the eyes. Both were raised respectively from sister tubers of the individual F^1 plant (L^1). Both parent plants grown from these tubers had "shallow" eyes, one family, $L^{1(4)}$, consists of 54 individuals, all of which carry "shallow"-eyed tubers. In the other family, $L^{1(1)}$, Plate XXIII, out of 55 individuals 5 (Nos. 4, 15, 51, 52, 59) must be described as medium, i.e. the eye is distinctly depressed and the brow is evident, though not heavily developed. The only other "shallow"-eyed potato that was selfed was "Bohemian Pearl," all the individual plants which have arisen from it that have come under my notice are "shallow"-eyed. Of the first generation there were some hundreds, of the second only five.

If all the families arising out of matings of impure dominant eyes be put together, we obtain the following:

	Shallow	Deep
"Flourball" seedling selfed	14	29
A	21	77
$D^1 × A$	16	33
$H^1 × A$	9	39
$H^{10} × A$	9	36
K^9	22	51
Total ...	91 to	265

This is almost exactly 1 : 3.

K^6 is an example of a pure "deep"-eyed potato; all the 284 seedlings of which are "deep"-eyed.

This family, K^6, further illustrates a curious phenomenon. Certain individuals, such as $K^{6(2)}$, Nos. 28, 84 and 95, appear at first sight to be "shallow"-eyed. When, however, they are examined with their sister tubers from the same plant, it will be seen that the "shallowness" is only present at those points where an outgrowth or protuberation is taking place : elsewhere in the same tuber or on its sisters, the eyes are "deep" $K^{6(5)}$. No. 28 is apparently "shallow," but here also outgrowths are just beginning. A true "shallow"-eyed potato is "shallow" in every tuber of the plant and a true "deep" is equally "deep" in every tuber. The heterozygote is more variable and, though "deepness" is dominant, the eye is often shallower than in the tubers of a pure dominant "deep" eye.

The potato "eye" is therefore, like shape, a distinct character inherited on Mendelian lines.

The Colour of Tubers.

The colour is due to the presence of pigmented cell sap in the cells of the superficial layers. The white skinned or, more correctly, yellow skinned tuber, owes its colour on the one hand to the presence of the cork in the upper layer of the corky tissue, and on the other to the absence of any red or purple pigment. The red potato contains a vermilion pigment in solution and the black potato, which is in reality an intense purple, derives its colour from a deep blue purple sap pigment which, seen under the microscope in contrast with the red, is quite distinct.

It was pointed out in the Introduction that potatoes of all colours, including the whitest—with white flowers—showed more or less purple pigment in the shoots, arising from the tubers in spring, if not in the haulm also. Vilmorin[10], in his catalogue of all the known varieties, makes three classes in which the tubers possess white shoots; it is probable that small deposits of pigment were overlooked. Out of the 1200 separate and distinct varieties he describes some 45 as having white shoots. Often the pigment occurs in punctate deposits which need a lens to distinguish them clearly, but the pigment is unmistakably present. From this fact it would seem clear that all tubers, coloured or not, possess the chromogen base, i.e. using the notation

employed in the Mendelian analysis by Bateson, Miss Saunders and others, all potatoes possess the factor *C*.   Miss Wheldale, who has very kindly examined many of my tubers from this point of view of pigment analysis, confirms this view.   If, then, colour can be present in the haulm and even in the shoot and still not be developed in the tuber, it would seem that there must be some factor which acts as a "developer" of pigment, and in its absence the tuber is white (yellow).   The supposition that this factor might be an inhibitor of colour is negatived by the fact that white are recessive to coloured tubers.

It is necessary now to observe how the potato plant behaves in actual breeding experiments.

The white potato breeds true.

Several hundred, about 600 in all, of seedlings of "Bohemian Pearl" and "Sole's Kidney," both white potatoes, were raised, and all the plants that bore tubers at all carried white ones only.

A "Bohemian Pearl" seedling was selfed and gave a half-dozen white-tubered seedlings.

A "Sole's Kidney" gave 300 white-tubered seedlings, and one of these selfed and produced fifty seedlings, all of which were white-tubered.

A white-tubered variety (*D*) extracted from "Flourball" has been bred now through three generations and gives rise to nothing but white-tubered plants.

The variety "Early Regent" sown this season has produced 125 white-tubered plants and none carrying coloured tubers.

The Colour Composition of the Red Potato.   If seedlings of "Flourball" be grown and these, after harvesting, divided up in respect to colour, it will be found that red-tubered plants are to white as 9 : 7.

The numbers in my experiments were :—

	1907	271 Red plants	217 White
June	1909	71 ,,	60 ,,
Oct.	1909	24 ,,	19 ,,
Aug. 13, 1910[1]	54 ,,	44 ,,
	Total	420 ,, :	340 ,,
	Ratio	9 ,, :	7·09 ,,

[1] There are still about 100 plants to be harvested.

The ratio 9 : 7 is one very well-known in Mendelian analysis and is evidence of the interaction of complementary factors belonging to separate pairs of allelomorphs.

Now if R be considered the factor which in presence of the developer D converts the chromogen into a red pigment, then the zygotic composition of "Flourball" should be written $RrDd$, which will on selfing give plants with the following composition :—

$$9\ RD = \text{Reds}$$
$$3\ Rd = \text{Whites}$$
$$3\ Dr = \text{Whites}$$
$$1\ dr = \text{White}$$

Further, it will be seen that there are five kinds of white and four of red plants, viz.—whites of the composition :—

$$Rrdd,\ ddrr,\ RRdd,\ rrDD,\ rrdD,$$

and reds of the composition,

$$RRDD,\ RrDd,\ RrDD,\ RRDd.$$

Of the red it is at present only possible to distinguish three kinds, viz.,

$RRDD$, $RrDD$, or $RRDd$ and $RrDd$. Of these $RrDd$ we know as the parent or type, the pigmentation of which is weak.

$RrDD$ or $RRDd$ has been raised twice out of "Flourball" seedlings, and each case has given red and white tubered seedlings in the proportion 3 : 1. Thus,

$$\text{Family } A \qquad 70 \text{ red} \qquad 27 \text{ white}$$
$$\text{\textquotedblright} \quad G^4 \quad 12 \text{ \textquotedblright} \qquad 5 \text{ \textquotedblright}$$

The colour of the tuber $RrDD$ is distinctly stronger than the colour of the ordinary "Flourball." There is good reason to hope that the type $RRDD$ will be isolated this season : such a potato will breed true to red. "Reading Russet," a pale red, selfed in 1909 and planted out this year, already gives evidence of a 9 : 7 ratio. Amongst the whites no certain distinction has yet been made between the possible kinds, nor have two whites been yet successfully mated ; an experiment which when the two whites contain, one the R factor and the other the D respectively, will probably give rise to a coloured potato[1].

[1] This year, 1910, a large number of crosses between various whites have been effected.

"Flourball" has therefore yielded three types of potato which have been identified by reason of their gametic qualities, namely, two reds, one giving reds to whites in the ratio 9 : 7, another red to white in the ratio 3 : 1, and a white variety.

In order to elucidate further the colour factors the white variety D was crossed by the 3 : 1 red variety A and the result was

<div align="center">27 Red to 22 White.</div>

This ratio is presumably to be taken as approaching equality, as 9 : 7 ratio would be here impossible.

If the formula of A be $RrDD$ then this particular white potato must be $rrDD$; similarly if A be $RRDd$ then the white variety must be $RRdd$. It is here assumed that $A = RrDD$, and the family D therefore will be represented by $rrDD$, it could of course be equally well $rrDd$.

A cross of peculiar interest was made between "Flourball" and a potato called "Record" which, although of attractive appearance, was of such frail constitution that it has entirely died out everywhere. The result of the cross was a family H. Of the 30 individuals which lived through the following years 19 were white and 11 red. The numbers are small, but enough at least to show that the whites are in a very distinct majority. If the notes of the H family be examined from its first origin, one finds that there were 28 whites to 12 reds and two with no tubers, and that the mortality has taken place amongst the white and tuberless.

The formula for "Flourball" was shown to be $RrDd$, and there are two possible formulas for a white potato which would, in union with "Flourball," give rise to a family having a majority of whites. They are $rrdd$ and $rrDd$ respectively;—the first would give a family of three whites to one red; the second would give a family of five whites to three reds. The numbers in the H family are not large enough to decide with certainty which formula for "Record" is the more correct. We have seen that the mortality affected those plants which were either white tuber bearers or tuberless, and that the approximation of the final result of two whites and one red is due to this mortality amongst the whites. Whether it is possible that plants pure to the absence of pigment factors are more weakly than others cannot, on the present evidence, be asserted, but the facts suggest such a possibility.

Two white-tubered members of the H family were crossed by the red potato A, whose gametic composition we may assume to be $RrDD$,

seeing that on selfing it gives three red and one white. The results were different in each case—

$H^1 \times A$ gave	29 red	19 white
$H^{10} \times A$,,	18 ,,	27 ,,
Total	47 ,,	46 ,,

In either case it is possible that larger numbers would have shown a nearer approach to equality.

It must however be noted that the family $H^{10} \times A$, had far less pigment in its stem than $H^1 \times A$, and that the possible results of mating whites with reds of A's composition are equality, if the white is *rrDD* or *rrdd*, or three red to one white if *Rrdd*.

One other cross was made between a pale red and a white-tubered plant.

"Queen of the Valley" was crossed by a red seedling of "Flourball" and the F^1 generation consisted of seven red to three white. One of these a pale red, M^5, was crossed by a white seedling of the white "Bohemian Pearl" B. Forty-one seedlings grew and 38 survived to form tubers. Of these

19 had red and 19 had white tubers.

This result of equality suggests that the composition of the two parents may have been—(M^5) $RrDd \times (B)$ $rrDD$. M^5 is probably $RrDd$ and not $RRDD$, $RrDD$, etc., because it is a particularly feeble red and might therefore be assumed to have the least possible factors that would give a red.

Two reds, one very deep red, viz. "Red Fir Apple," and the other a weak one, "Reading Russet," were crossed. "Reading Russet" has now been selfed, and this year we shall learn its composition, but its colour is weak like that of "Flourball," and it has probably the same gametic composition, viz. $RrDd$[1]. "Red Fir Apple" is of a very deep colour and might be $RRDd$. The F^1 raised were 117 seedlings, but only 11 of them came to maturity, viz. eight red, and three white, indicating, as would be expected from the union, a 3 : 1 ratio.

$$RRDd \times RrDd = 3 \text{ red} : 1 \text{ white}.$$

Two plants arising both from tubers of the same individual of the F^1 family, viz. L^1 and L^4, were selfed and produced in the F^2 generation large families in which the ratio of red and white was 3 : 1.

[1] The 1910 seedlings of "Reading Russet," so far as yet harvested, are divided into 14 red-tubered plants and 10 white-tubered.

The numbers in the latter are not conclusive in themselves, because only selections of these families were actually planted out; but amongst the young seedlings, before planting out, there were 23 red to 8 white and the appearance of the harvested selections fully bear out the suggestion of a 3 : 1 ratio.

Purple Coloured Tubers.—The "Congo" potato is a cylindrical potato of almost a black colour, the pigment extending within the tuber somewhat irregularly. The "Congo" flower, which is white with a purple tinge at the base of the petals, is completely sterile in the male organs, and it was therefore only used as a mother plant.

Two crosses were made—

1. *Congo × Reading Russet.* There were eight seedlings and only four survived until the late autumn of 1906, of these

> Two were black like " Congo,"
> Two bright red.

But on July 25, 1907, there was a fifth plant with white tubers which died out subsequently.

The numbers are too small to make any deduction as to ratios, but there is one factor of great importance which stands out, viz.—that out of a union of a deep purple and weak red, there have segregated out deep purple (black), bright red and white.

The next cross was—

Congo × Flourball Seedling. This cross was effected in 1906. The " Flourball" seedling was a stray plant growing in one of the experiment lines containing " Ringleader" and was used as pollen parent. " Ringleader" itself did not flower that year. Except that it was a red tubered variety nothing further can be told about it, as it was unfortunately not preserved. Its pollen was used in the cross with "Queen of the Valley" and, as has been mentioned before, it is probable, for the reasons already given, that it was a red of the formula $RrDD$ or $RRDd$.

The F^1 generation contained 29 plants and these were

> 13 Black tubers.
> 12 Red tubers.
> 4 White tubers.

Here again the important features are the complete segregation and the appearance of the white tubers.

Before discussing the possible constitution of " Congo," it will be best to consider the F^2 generation.

In 1908 two of the F^1 plants, viz. K^6 and K^9 both selfed and large families were planted; those of K^6 did well, the K^9 family fared badly in the wet summer of 1909.

K^6 *Family.* K^6, Plate XXIX, is a black (i.e. deep purple) potato. Several seedballs were collected from the plants, and one coming from a plant $K^{6(5)}$ was planted in its entirety. Originally 301, there were harvested but 160 seedlings. The tubers of the F^2 family separate at once into blacks, reds and whites in the proportion of 77 black, 29 red, 54 white; the reds are either quite pale and similar to "Flourball" or "Reading Russet," or they have more purple colour and resemble "Red Fir Apple."

Of the whites about one-sixth (9 in 54) are quite pure, i.e. no tinge of colour can be seen in the tubers or eye before sprouting, whilst the remainder may have a trace of colouring usually purple, in the eye or the skin and more especially in any scars following a wound by fungous disease or other lesion. Such pigment is minute in quantity and often needs a lens to demonstrate its presence. The reds are roughly of two kinds, a deep strong group, and a pale. The proportion between these is 23 deep red, and 6 pale red, and they can be classed fairly readily into these main groups. The blacks are all alike, viz. deep purple. In considering the factors which underlie the phenomena of colour in the red- and white-tubered potatoes we assumed the presence of the two factors R and D. The purple potato is obviously bringing a fresh factor besides these into the field and this new or "purpling" factor can be called P.

If K^6 has the gametic formula Pp, Rr, Dd, then on selfing we should get plants or biotypes with the following gametic constitutions:

27 plants of the composition PRD = purple.

9	,,	,,	PR	= white (tinged).
9	,,	,,	RD	= red.
9	,,	,,	PD	= white.
3	,,	,,	R	= white.
3	,,	,,	D	= white.
3	,,	,,	P	= white.
1	,,	,,	prd	= white.

The numbers for the K^6 family are :—

	Purple	Red	White
Calculated numbers ...	73	24	75
Actual Numbers ...	77	29	54

The results[1] are sufficiently close to give one some confidence that the phenomena are correctly represented by the assumption of the factors PR and D that have been supposed to be at work.

The sister family K^9 adds additional evidence of a strong nature. Several lots of seed of K^9 plants were sown and in all some 300 seedlings raised. The majority were however planted in selections and therefore are of no use for quantitative purposes. All the groups, however, coincided in one feature—none produced a single red tuber; and the evidence from the selected groups strongly favour the view that purples to whites were as $9:7$, whilst the groups that were planted in full give $26:14$. The parent plant of such a family must be homozygous in the purpling factor and heterozygous in its two other colour factors. To K^9, therefore, should be given the zygotic formula PP, Rr, Dd.

Having considered K^6 and K^9, we can now turn back to the original cross and the F^1 family. The F^1 family consisted of 13 purple, 12 red, 4 white. It is obvious that as regards P, "Congo" must be heterozygous, further we knew the "Flourball" seedling was red and therefore contained RD. If we represent the cross

"Congo" $PpRrDD \times$ "Flourball" seedling $RrDD$

we get   12 purple, 12 red, 8 white.

The result of these experiments on colour inheritance would seem to be (1) that whilst colour may be present in the stem to any degree, a special developer D is necessary to bring it out in the tuber, (2) that redness is dependent on a separate factor R, (3) that purple is dependent on a further one P, and (4) that the purple colour cannot be developed except in the presence of all three factors PRD.

In all the experiments there has been much to suggest that the degree of the "redness" is due to the homozygous condition or otherwise of the plant as regards both R and D, but the evidence has not been given in full because the classification into shades of "redness" would be too empirical and dependent on personal judgment. In one group the distinction was clearly made out, viz. in the family A where the formula was shown to be $RrDD$ (or $RRDd$) the deep reds were to the remaining reds as 24 to 48, whilst in the K^6 group the reds were 23 deep red to 6 pale red. Amongst the blacks (purple) no distinction could be made.

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[1] If the disproportionate mortality of the whites be remembered, the actual numbers will be seen to be not so far removed from the calculated ones. Thus the number of whites, had the mortality in all classes been equal, would be 66 instead of 54.

Solanum etuberosum.

The plant with which I have worked is identical with that used by Mr Sutton[8] and described and figured so fully by him. I obtained my tubers from Kew, whence it was sent to me with the name of "Maglia," though the misnomer was realized later. Mr Sutton has been good enough to see my plants growing, and has no hesitation in confirming that they are the same as his own obtained from Mr Lindsay of Edinburgh Botanical Gardens and which he has described under the name of "etuberosum." The Rev. Aikman Paton's supply of etuberosum was derived from mine, and his results, as far as they are published, confirm mine in many particulars.

It is not necessary to decide as to whether this plant is the one originally described by Lindley in 1834 as etuberosum; the general feeling is that it is not the same, but that it is a plant of the greatest interest is none the less true though its name be a borrowed one.

The contention of Sutton[8] that S. etuberosum is the parent plant of our domestic varieties has been considered by me in an earlier paper[9]. Wittmack[12] has also discussed this question, and though I do not share his opinion that etuberosum is an ordinary S. tuberosum variety I, nevertheless, agree with him that there is no reason to regard it as the parent type of our domestic varieties.

The etuberosum plant is a low growing one with very light green leaves which are of a different tone to any other I have had growing in my garden. It rather suggests the dusty appearance of the olive. The haulm spreads at its lower end, sending out lateral branches parallel to the ground.

The average size of the leaf is $2\frac{1}{4}$ inches by 1 inch; the surface is soft and rather woolly; the veins are marked, but the leaf not curled or rugose. Compared with most domestic varieties the nodes of the stem would be considered short, but they are, in proportion to the rather dwarf-like habits of the variety, about normal in length.

Pigment in the stem is red, patchy, extending feebly into the petioles, and visible in the axils. The flowers occur in close clusters, and are of an extremely beautiful lilac, which, viewed from above, has a peculiarly soft appearance. This is due to the fact that the pigment is on the under surface of the petal, that is outside when the flower is closed. This lilac colour differs considerably from the heliotrope seen commonly in domestic varieties. The anthers are delicate and form

a close cone similar to that seen in the various true wild species, and through the apex projects a short style ending in a simple knob. The anther contains abundant pollen.

The corolla is very definitely wheel-shaped, the tips of the petals recurve; they are rather sharp and hairy, and the calyx is hairy and its five processes are long.

The tubers are borne on rather long stolons. They are white and round, but the shape (Plate XXVII) is not typical of "round" as we have met it before in this paper. The tubers are irregular, neither oval nor long, but are often depressed at various points, so that although the general shape is round, the actual circumference is not necessarily circular.

The size is variable. When the tubers were first cultivated here they were not more than $1\frac{1}{4}$ inches in diameter; in 1909 I had some up to 3 inches in diameter.

The taste is bitter.

In 1906 Mr Sutton informed me that he had for over 20 years tried to self and cross this variety and had failed. In that year, however, a plant bore one berry. I, also, after repeated trials, in 1906 succeeded in making a cross. In 1907 Mr Sutton again obtained selfed berries, and some tubers I had sent to the North of Scotland set seed naturally and crosses were made. Hence, after over 20 years of observed sterility, this variety suddenly flowers out into fertility in Reading, Scotland and North Herts, which, as we shall see, has cost it dear. The tubers in both 1906 and 1907 showed no variation, except a slightly enlarged size. In 1908 when the plant first set seed naturally in Barley, it was noticed that the tubers of one plant had a slight violet tinge in the skin in places; this plant set seed in addition to one other, and 30 of the seedlings came from this plant. There is no evidence that the seedlings are, as a whole, different from those which did not show this vegetative variation.

The fertilization of the plants took place naturally, but at a date when all the other potato plants in my garden had ceased flowering and when some F^1 "Congo" crosses, which were close by, had already formed good-sized berries.

Immunity to Disease. (Phytophthora infestans.) During the culture of this variety in Reading it was noted for its immunity to disease. In my garden it was in

> 1906. Perfectly immune from disease in haulm and tubers.
> Three hybrid seeds only obtained.

1907. Very slight touch of disease on haulm, none in tuber. No seed.

1908. Slight disease in haulm, none in tuber. Set seed freely.

1909. No disease in haulm on September 3, but some later, considerable disease in tubers. No Seed.

1910. Some disease in haulm in August. Selfed and crossed seed.

The incidence of disease amongst the seedlings was remarkable, those attacked by disease were in some cases consumed away and all of them, excepting one which was but very slightly touched in the haulm and quite free in the tuber, were most seriously damaged. Out of 40 seedlings 34 were diseased and six were untouched, to these might be added the one only just touched by disease on a leaf or two, making seven. The ratio of $33 : 7$ is of course suggestive of a $3 : 1$ ratio. Resistance to disease being, as Biffen[2] found in the case of wheat, a recessive. Further careful observation will be needed before anything more definite can be asserted. It is a most striking fact that although the parent *etuberosum* plant was for 20 years and upwards noted for its immunity to disease, yet directly its sexual life begins that immunity goes. The chain of events, the fact that the F^1 family contains a number of immune plants, suggests that with the onset of sexual activity some disturbance in the mechanism by which the plant had hitherto security its immunity to *Phytophthora* had occurred—and that the dominantly susceptible state of the plant apparently heterozygous in this respect, has as it were been uncovered and its true nature laid bare.

The immune seedlings in 1910 demonstrated afresh their resistance to *Phytophthora*. The *etuberosum* seedlings were so planted that on either side of an immune plant was a susceptible one, whilst immediately behind was a row of ordinary domestic potatoes. The susceptible seedlings and the ordinary potatoes were devastated by disease. Before the end of July the haulms of both these latter were destroyed. Up till the beginning of September the immune plants were unscathed. Signs were not wanting that the immune plants had been attacked but had successfully withstood the enemy. Pale spots were seen on some of the green leaves during the height of the disease, whilst on these spots on a few fading leaves colonies of *Cladosporium epiphyllum* were found. The presence of the bright green healthy immune plants

standing out in the midst of the blackened and diseased débris which marked the site of their destroyed neighbours formed a very striking picture. Successful crosses have been made this year between the immune seedlings and domestic varieties.

The Flower. It has been already noted that the flower of this potato is of a very delicate lilac and that the pigment is on the under surface. The petal is entirely self-coloured; there is neither an intensification or a weakening of the general tone in the central region of the petal, as one so commonly finds in potato flowers.

The flowers of the seedlings offer considerable variations. Of the 40 plants 20 flowered, and of these—

Nine plants were exactly like the parent, i.e. uniform colouring on under surface;

Two plants were similar to parent but double the intensity of colour;

Three plants had the same general colouring as the parent, but with a deep-coloured tongue in the middle of the petal, and in one it was noted (probably true for all) that the colour in the tongue was both in the upper and in the lower coats of the petal;

Three plants had white flowers with purple tongues in the centre of the petal, the colour in the tongue being on the upper surface;

Three plants were pure white.

The sequence of the diverse flowers can be readily explained on the following hypothesis—that we have two pairs of characters at work—

A.	Colour.	*a.*	Colour absence.
B.	Uniform distribution of colour on under surface.	*b.*	Distribution of colour in a pattern on upper surface.

We then get—

6 : *Bb. Aa.* = Parent type.

2 : *Bb. AA.* = ,,   ,,   with deeper-coloured tongue.

1 : *AA. BB.* = ,,   ,,   but deeper colour.

3 : *A.* *b.* = White with coloured tongue.

3 : *a.* *B.* = White.

1 :   *ab.*   = White.

The numbers are too small to lay much stress on an explanation such as the one given, but the phenomena fall readily into line.

Shape of Tuber. The tubers of *etuberosum* are, as already mentioned, "round"—the seedlings comprise both "rounds" and "longs," and amongst the latter are kidneys. The numbers are 18 round, 14 long. It is evident that the "roundness" of *etuberosum* is of a quite different order and with a different hereditary value to that of the domestic varieties, and moreover, it is obvious that the "round" here is dominant to the "long," whereas in the domestic types it was recessive.

The Eyes. The eye of the parent tuber is "shallow" and very insignificant. The seedlings can, as regards the tuber eye, be at once divided into "deep" and "shallow."

These are 26 "shallow" to 8 "deep."

"Shallow" eye is therefore clearly dominant : in the domestic variety it is as clearly recessive.

The Colour of the Tuber. It will be remembered that, although the *etuberosum* tuber is white, yet in 1908 certain tubers were noted to have shown a slight purplish tinge. It is not therefore surprising to find that the seedlings are varied in colour and that the parental white is a dominant.

The colours of the seedling tubers are white and deep purple. The latter are identical in colour to those purple tubers dealt with in the earlier part of this paper.

The numbers of the different colourings are—

White	13	} 25.
White tinged	12	
Deep purple (black)	13.	

The numbers suggest that purple is a recessive character and that white is a simple dominant. In the domestic varieties the reverse is true. No reds were formed.

Crosses with Domestic Varieties. In 1906 I succeeded in effecting a cross with "Queen of the Valley." Three seedlings only grew, and they all died out. Mr Paton[7] crossed *etuberosum* by the white kidney "Duchess of Cornwall," and he obtained 13 seedlings, the colour of 12 of which he describes, viz.

9 white, 2 purple, 1 red,

showing the dominance of white. It is of further interest to note that he describes the shape of ten of them. Eight are "round" and two are "long" (kidney and oval), again showing the dominance of the *etuberosum* type of "roundness."

Crosses with S. etuberosum and maglia.

Sol. etuberosum × Sol. maglia (deep purple)

One seedling white tuber.

Sol. maglia × Sol. etuberosum.

One seedling white tuber.

Here again the "white" of *etuberosum* is dominant to the purple of the recognized species *maglia*.

The relation of S. etuberosum to other potatoes. Although the name "etuberosum" has been used in this paper, it has been done rather for convenience than with any idea of establishing its identity with the species described by Lindley.

Whether *S. etuberosum* is to be classed with the domestic varieties or as a native species is a question that may have an increasing import- ance. It has been shown in this paper that in respect to such important characters as shape, eye and colour of tuber it behaves in a diametrically opposite way to the domestic varieties, and it is, therefore, likely that it is distinct from them. On the other hand, its white is dominant to the *maglia* purple, and its own purple is also recessive; so that in respect to this character it certainly more closely resembles *maglia*.

The flower of *etuberosum* is much smaller and more compact than that of the domestic potato, and is much more like the wild *S. etuberosum* and *S. maglia*, and its scheme of colour as described here has no parallel amongst the domestic varieties.

There would seem, therefore, to be no adequate reason at all for classing *S. etuberosum* amongst domestic varieties; on the other hand, it has certain characters akin to those of recognized specific types, such as *S. maglia*.

It has been suggested that the diversity of the *S. etuberosum* seedlings shows it clearly to be a hybrid. That may be, but we can feel at least equally sure that its parents are not domestic varieties.

CONCLUSIONS.

Very briefly the following conclusions have been reached in this paper.

Domestic Varieties.

1. The twist of leaf, as seen in "Red Fir Apple," is a recessive character.

2.   Length of tuber is dominant to " roundness."

3.   Depth of " eye " is dominant to " shallowness."

4.   Purple is dominant to red in the tubers.

5.   Red is dominant to white, but is dependent on the presence of two factors in addition to a chromogen.

6.   *S. etuberosum* is not subject to the same laws of dominance as the domestic varieties of potatoes.

7.   That amongst the seedlings of *S. etuberosum* occur some which are at present immune to the attacks of *Phytophthora infestans.*

8.   That immunity to the attacks of *Phytophthora infestans* is in *S. etuberosum* a recessive character.

9.   *S. etuberosum* may be a hybrid and, if so, its parents are possibly native species.

I take this opportunity of tendering my thanks to my head gardener, Mr E. Jones, for the assistance he has rendered, and the great care he has shown in the raising of the seedlings.

DESCRIPTION OF PLATES.

PLATE I.

Tubers of seedlings of Sutton's "Flourball" selfed.   " Rounds " are—Nos. 40, 89, 92, 118, 132, 138, 155, 156, 162, 185.

PLATE II.

Family of seedlings of parent *A* selfed.   The majority of the tubers are normal "rounds"; the least typical "round " has been chosen to represent each individual root.   On Plates IV. and V. can be seen the sister tubers of the more abnormally shaped " round " tubers.

PLATE III.

A family continued.

PLATE IV.

All the available tubers of each root crop are shown of those individuals who vary from the typical " round."   In all cases one or more typical " rounds " occur in each root crop.

PLATE V.

Same as Plate IV.   No. 100 is probably a stray plant and not a member of this family.

PLATE VI.

The *G* family, consisting of six individuals with their root crops are shown. G^1, G^5 and G^6 are more or less typically "round."

PLATE VII.

The *D* family—Top row—Three tubers of parent plant. D^1 and D^2, 1908, are the seedlings raised in 1908 from *D* (1907) selfed. D^1 and D^2, 1909, are seedlings raised in 1909 from *D* (1907) selfed.

PLATE VIII.

Seedlings of the family raised from cross *D* × *A*. The family consists of half "rounds" and half "non-rounds." The "rounds" are Nos. 3, 4, 5, 8, 13, 14, 15, 16, 18, 19, and 3, 6, 7, 10, 12, 14, 18, 19, 20, 21, 22, 28.

PLATE IX.

Seedlings of the family raised from the cross "Record" × "Flourball." "Record" is a kidney, "Flourball" a pebble-shaped potato (neither parents shown). One quarter of the seedlings are "rounds," viz., Nos. 12, 13, 18, 21, 24, 25, 26, 30.

PLATE X.

Seedlings of the family raised from the cross H^1 (F^1 of family *H*, Plate IX) × *A*. Half the seedlings are "round," viz.: Nos. 4, 6, 7, 16, 17, 19, 22, 25, 26, 27, 29, 30, 34, 35, 36, 38, 39, 40, 42, 45, 49.

PLATE XI.

Seedlings of the family raised from the cross H^{10} (F^1 of family *H*, Plate IX) × *A*. Half the family are "rounds," viz.: Nos. 1, 2, 3, 4, 10, 11, 13, 13a, 15, 17, 18, 19, 26a, 29, 31, 32, 33, 34, 40, 46, 48, 49.

PLATE XII.

Family *J* raised from the cross "Congo" × "Reading Russet." The fifth seedling, a long white-tubered one, died out and is not shown here.

PLATES XIII—XVIII.

The family raised from the individual K^6 (F^1 of "Congo" × "Flourball" seedling, see Plate XXIX). This family for convenience has been divided into sub-families $K6^2$, $K6^3$, etc., according to the particular seedball from which the seedlings were grown. "Rounds" are to "longs" as 1 : 3 in this series, and the eyes are all deep with the exceptions noted in the text.

PLATES XIX, XX.

The family raised from selfing K^9 (F^1 of "Congo" × "Flourball" seedling, see Plate XXIX) the "rounds" are rather deficient, viz.: 13 to 60; the eyes are deep to shallow, 3 : 1.

PLATE XXI.

The family L, raised from the cross of "Red Fir Apple" × "Reading Russet." In the F^1, No. L^7, a kidney has been omitted.

PLATES XXII, XXIII.

F^2, family raised from L^1, selfed. The rounds are 1 in 4, viz.: Nos. 1, 2, 22, 35, 37, 46, 47, 49, 61, 63, 64 (Plate XXII). Five long- and three round-tubered individuals have been omitted. In Plate XXIII the "rounds" are Nos. 6, 10, 17, 19, 22, 24, 29, 30, 33, 40, 47, 52, 54, 61.

PLATE XXIV.

The family raised by crossing M^5 (F^1 of "Queen of the Valley" × "Flourball" seedling) × "Bohemian Pearl" long-tubered seedling. Nos. 2 and 20 which in the plate look "round" are in reality much flattened and are clearly not rounds. Two other typical long members of this family have been omitted.

PLATE XXV.

Examples of tubers, not from individual roots, of B.

"Bohemian Pearl" seedlings long and oval.

"Congo." The long tubers are much more common than the stunted.

"Red Fir Apple." The tubers in 1909 were all more or less stunted as shown in the Plate.

PLATE XXVI.

C, 1907, one of the seedlings of "Sole's Kidney."

C, 1909, representatives of 4 seedlings of C, 1907.

PLATE XXVII.

Family raised from selfing Lindsay's *etuberosum*. The long-tubered seedlings are here in the minority. The ravages of the disease are clearly seen.

PLATE XXVIII.

(Reproduced by kind permission of Messrs Sutton of Reading.) The kidney potato "Superlative" in clamp. The variability of shape amongst the kidney and pebble-shaped tubers is very marked.

PLATE XXIX.

The F^1 family raised by crossing "Congo" × "Flourball." The segregation of the colours Purple, Red and White are well shown. The shapes are all "long" and the eyes all "deep," demonstrating the dominance of these characters.

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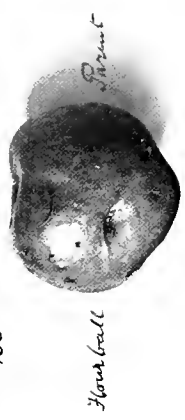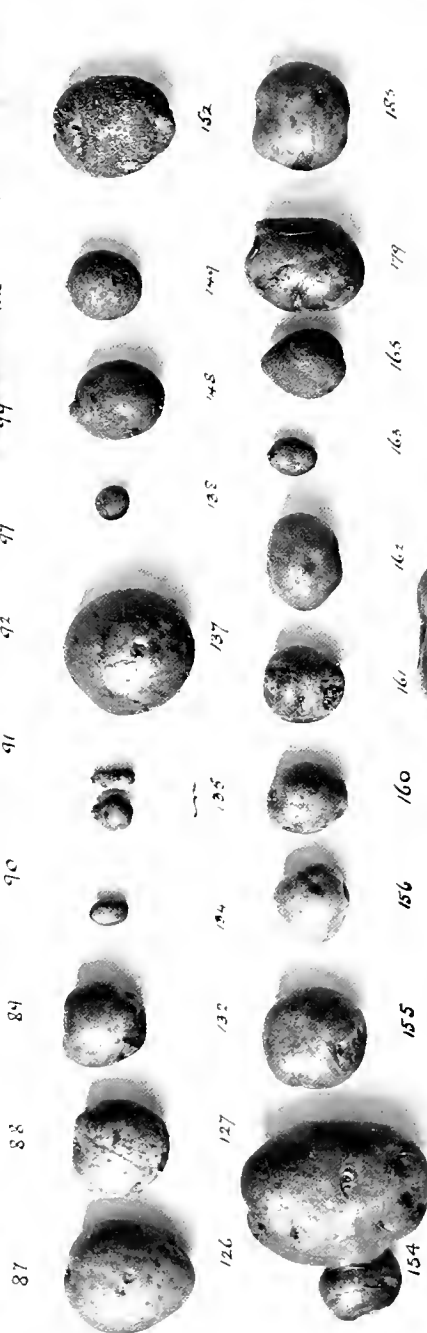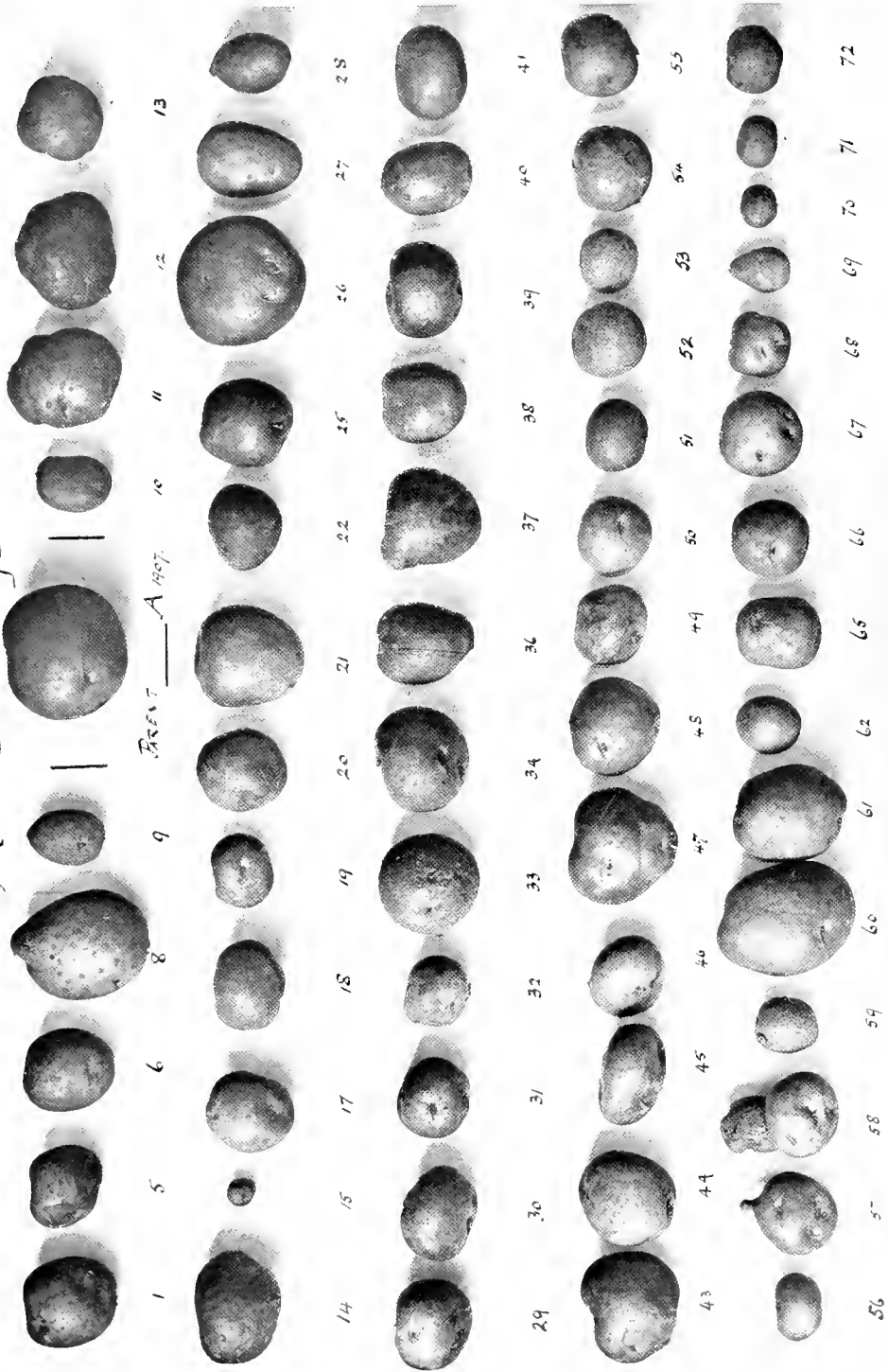
PLATE II

A Seedlings. Cont^d
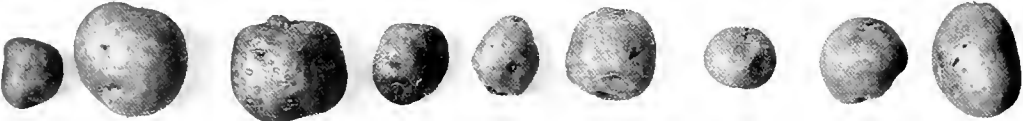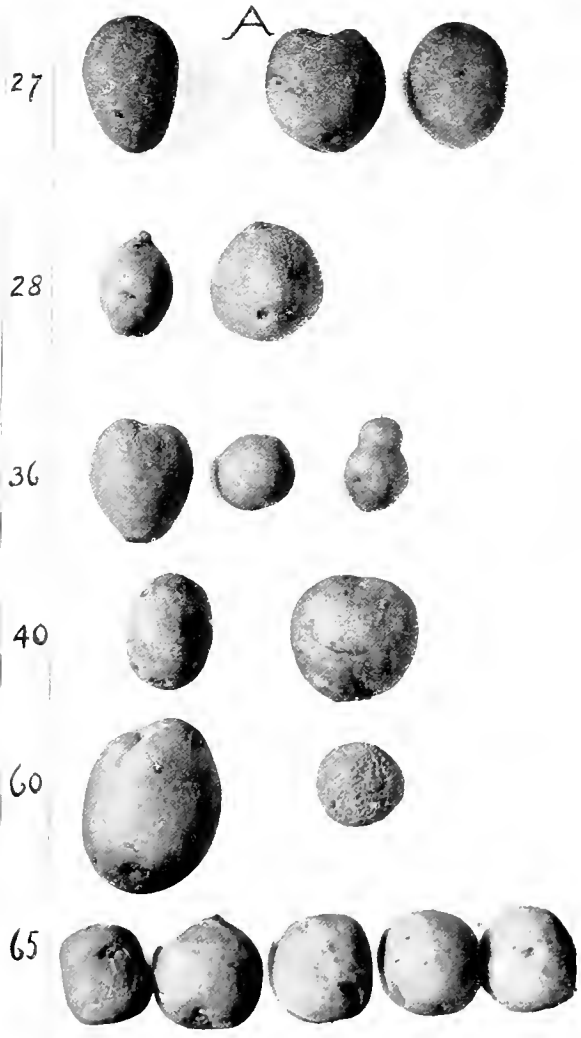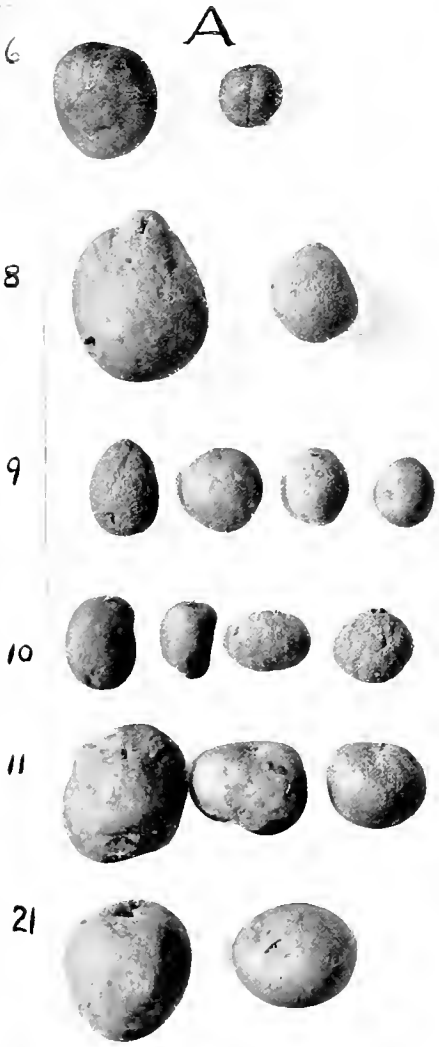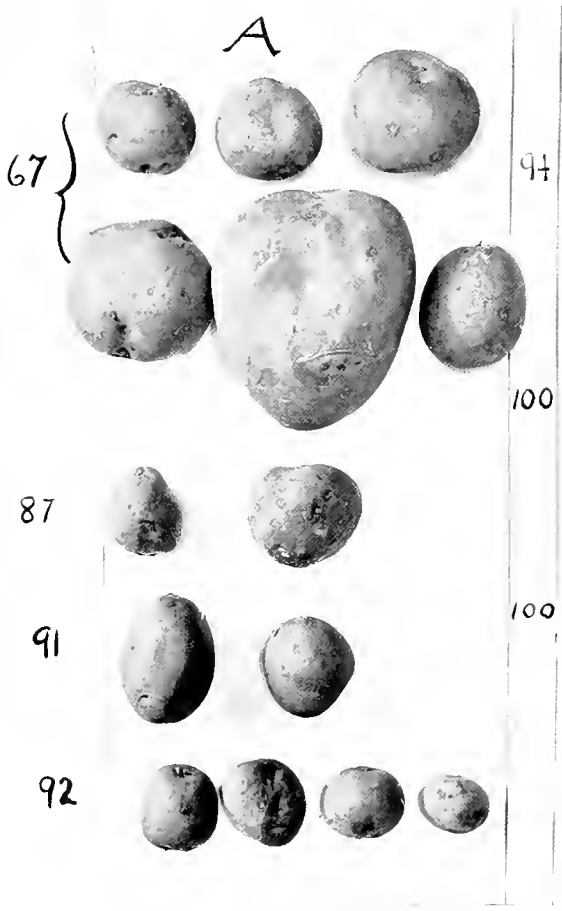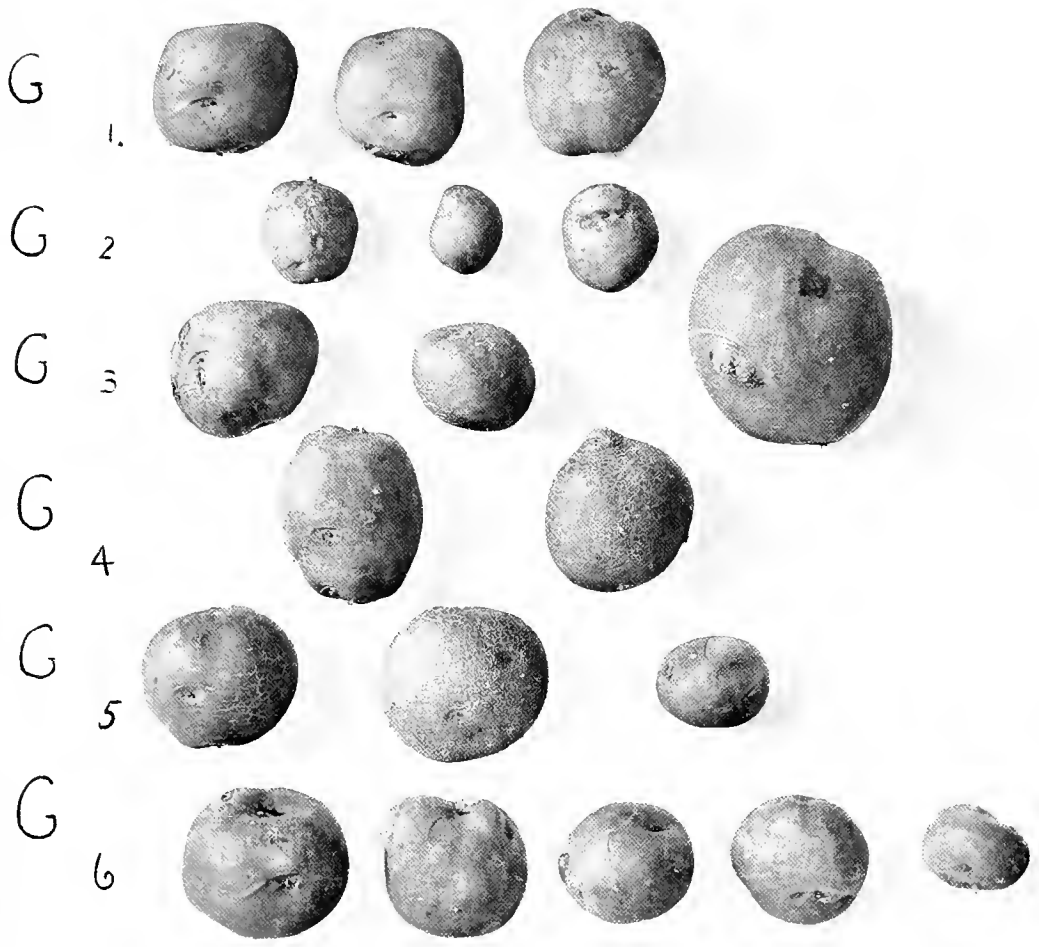
D

1907.
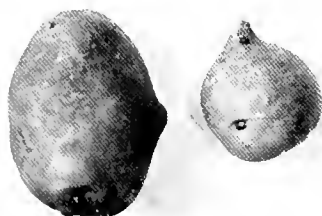
D¹ 1908

D² 1908

D¹ 1909

D² 1909
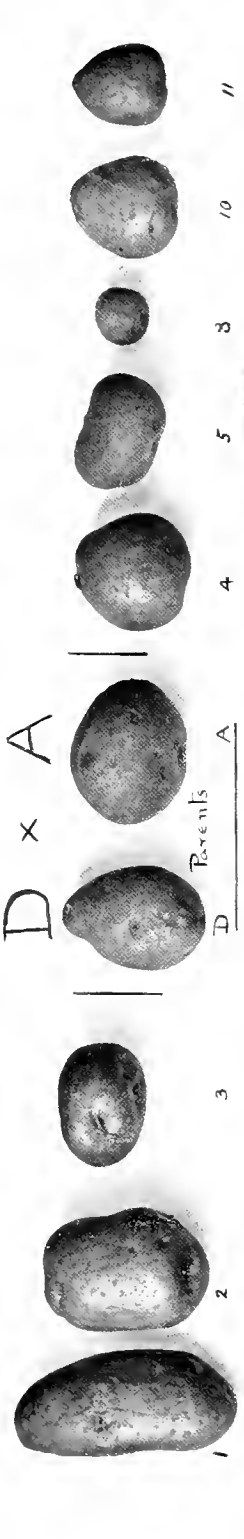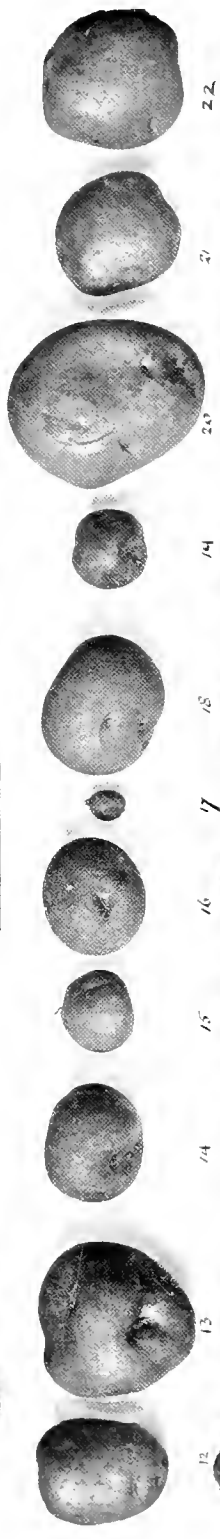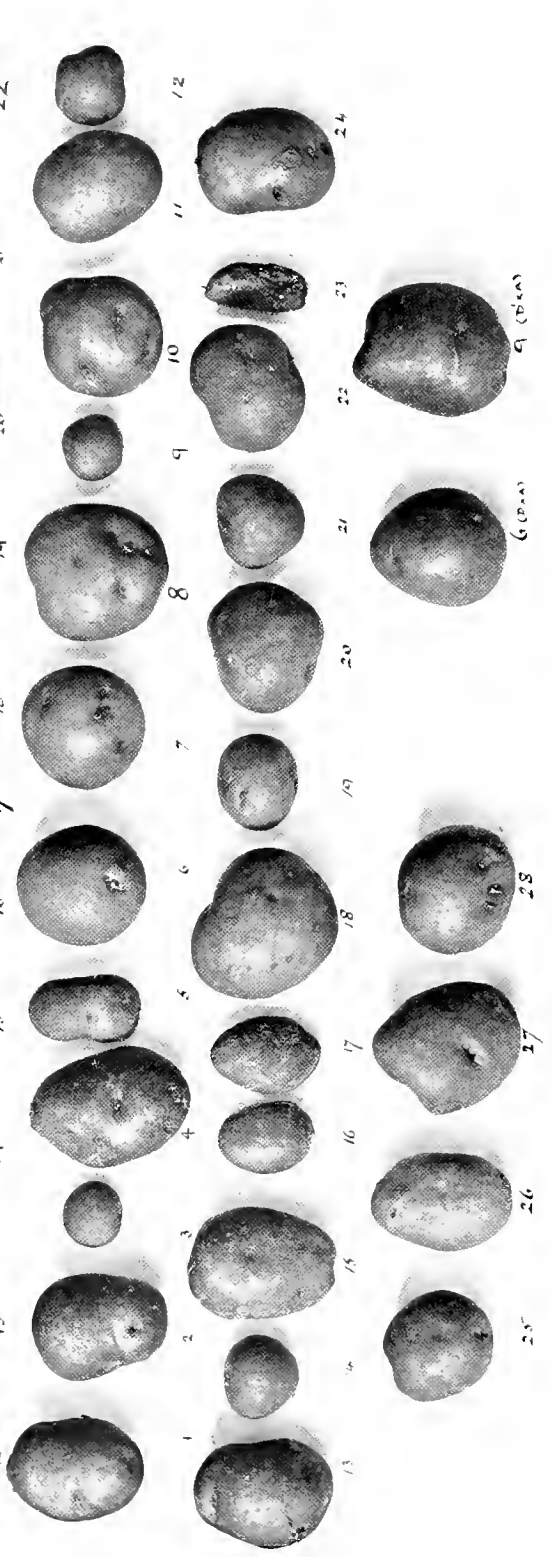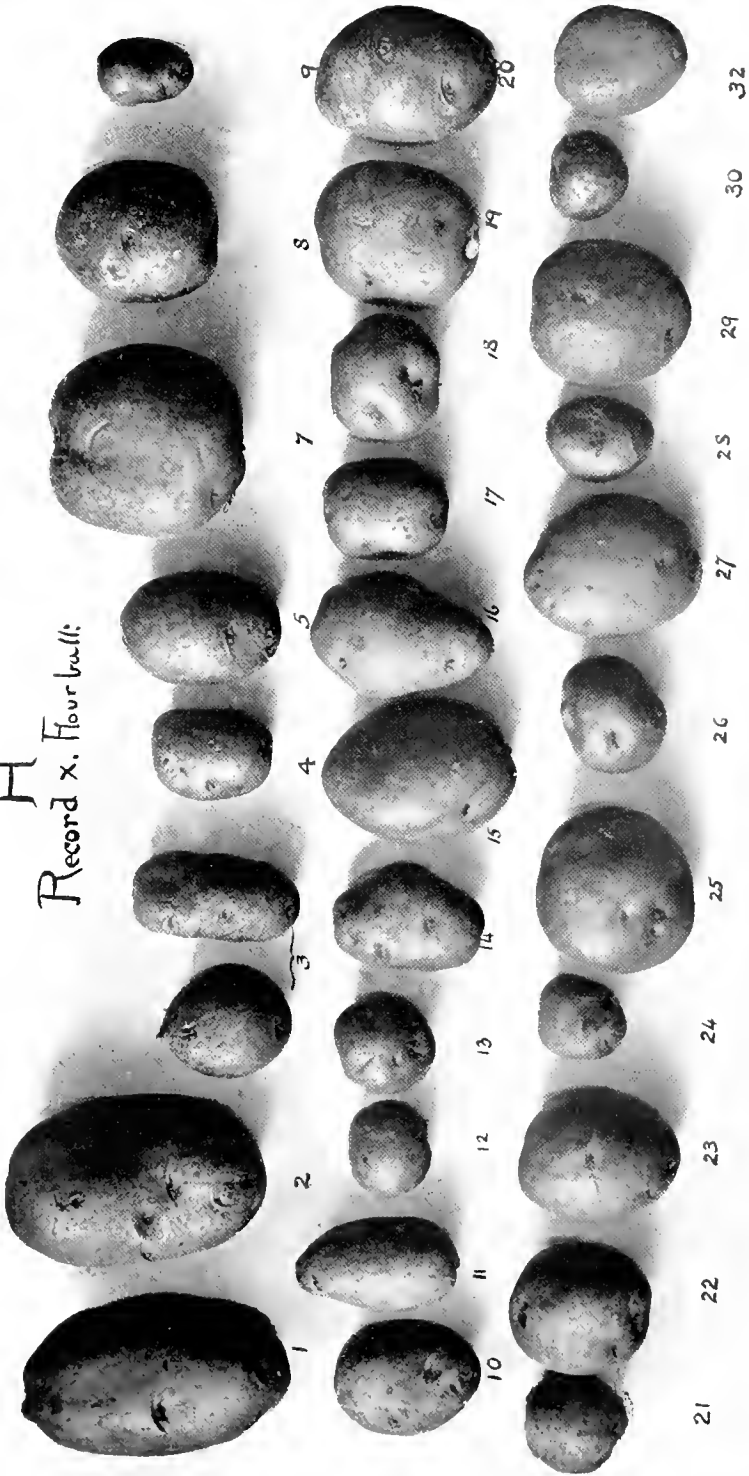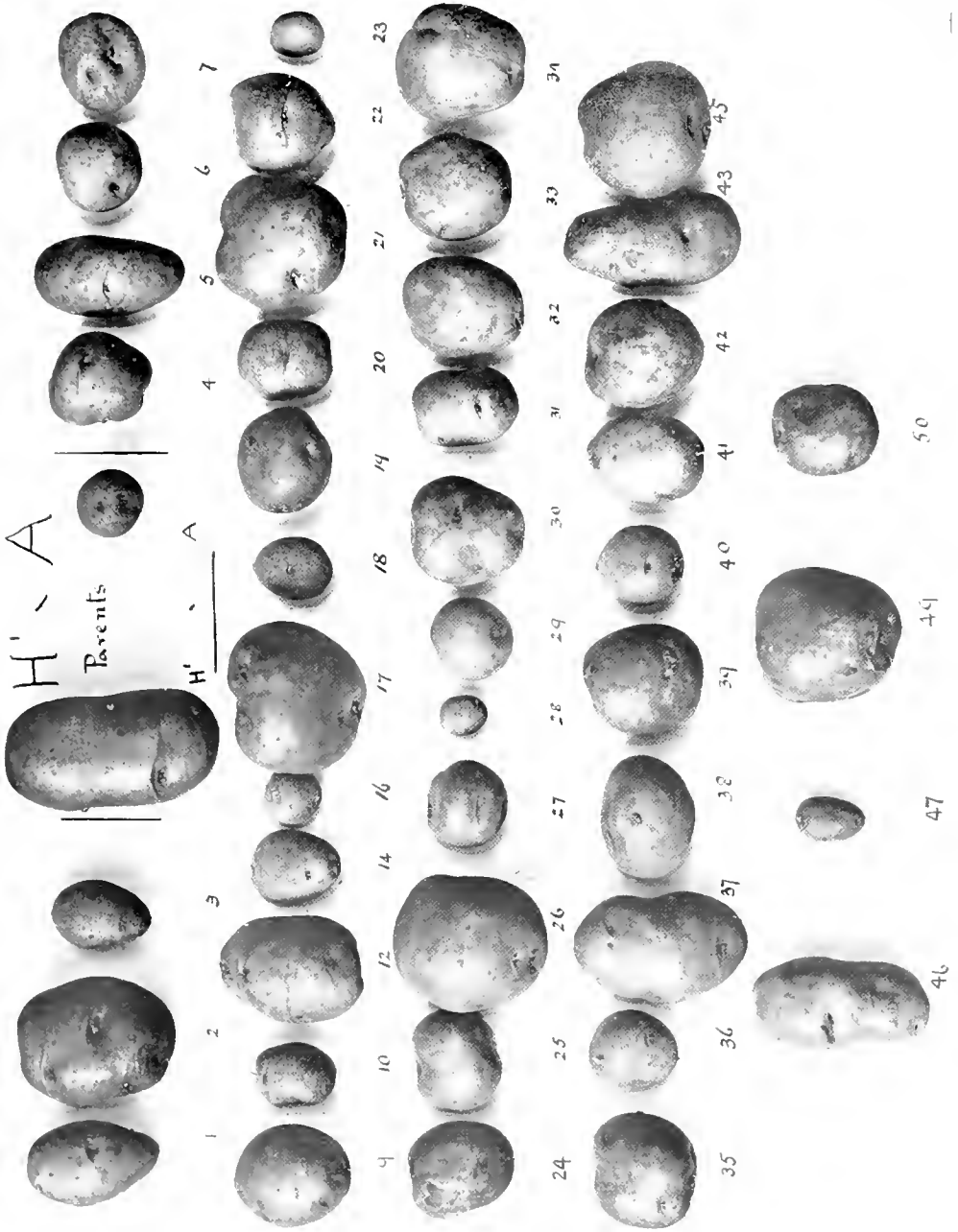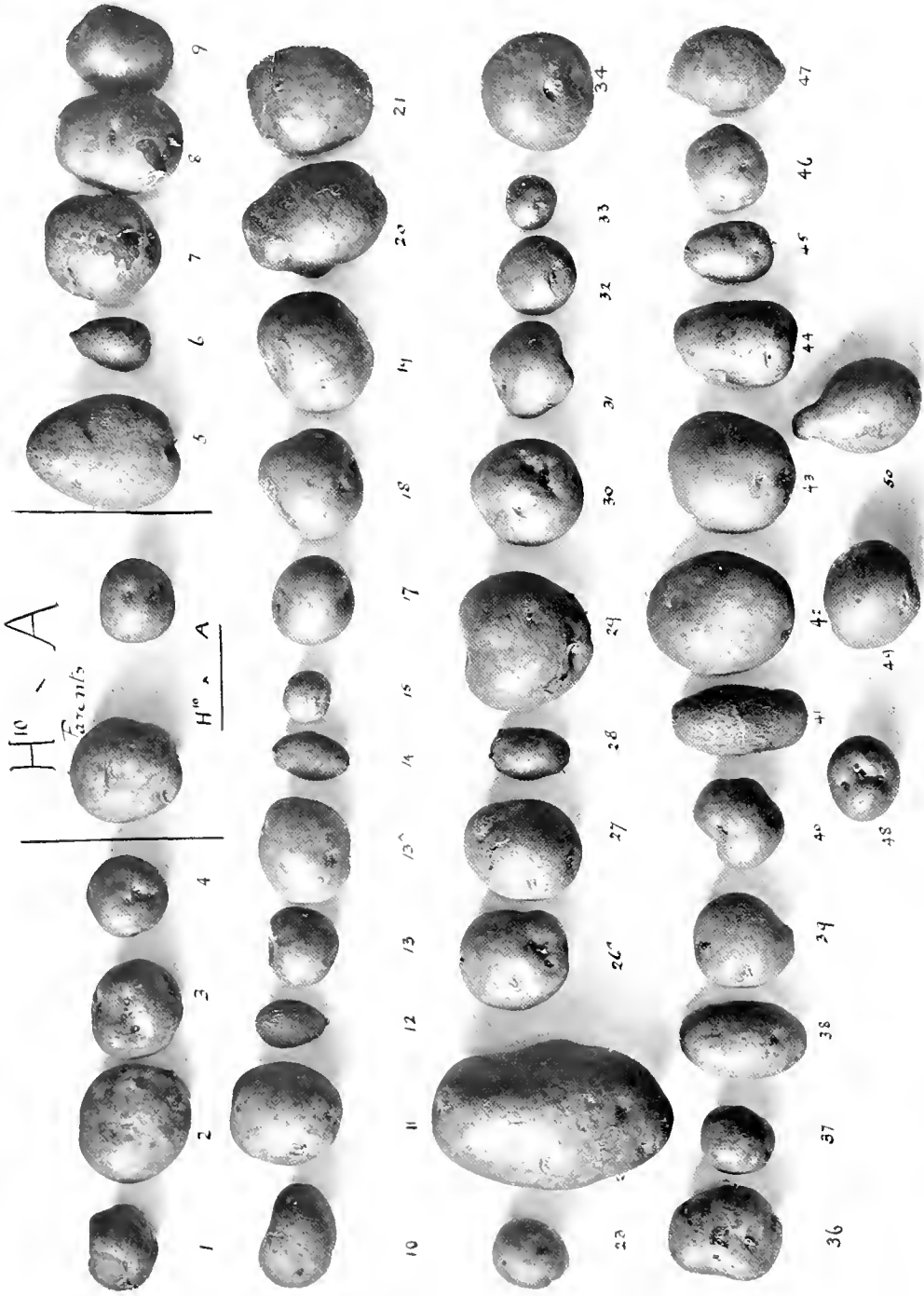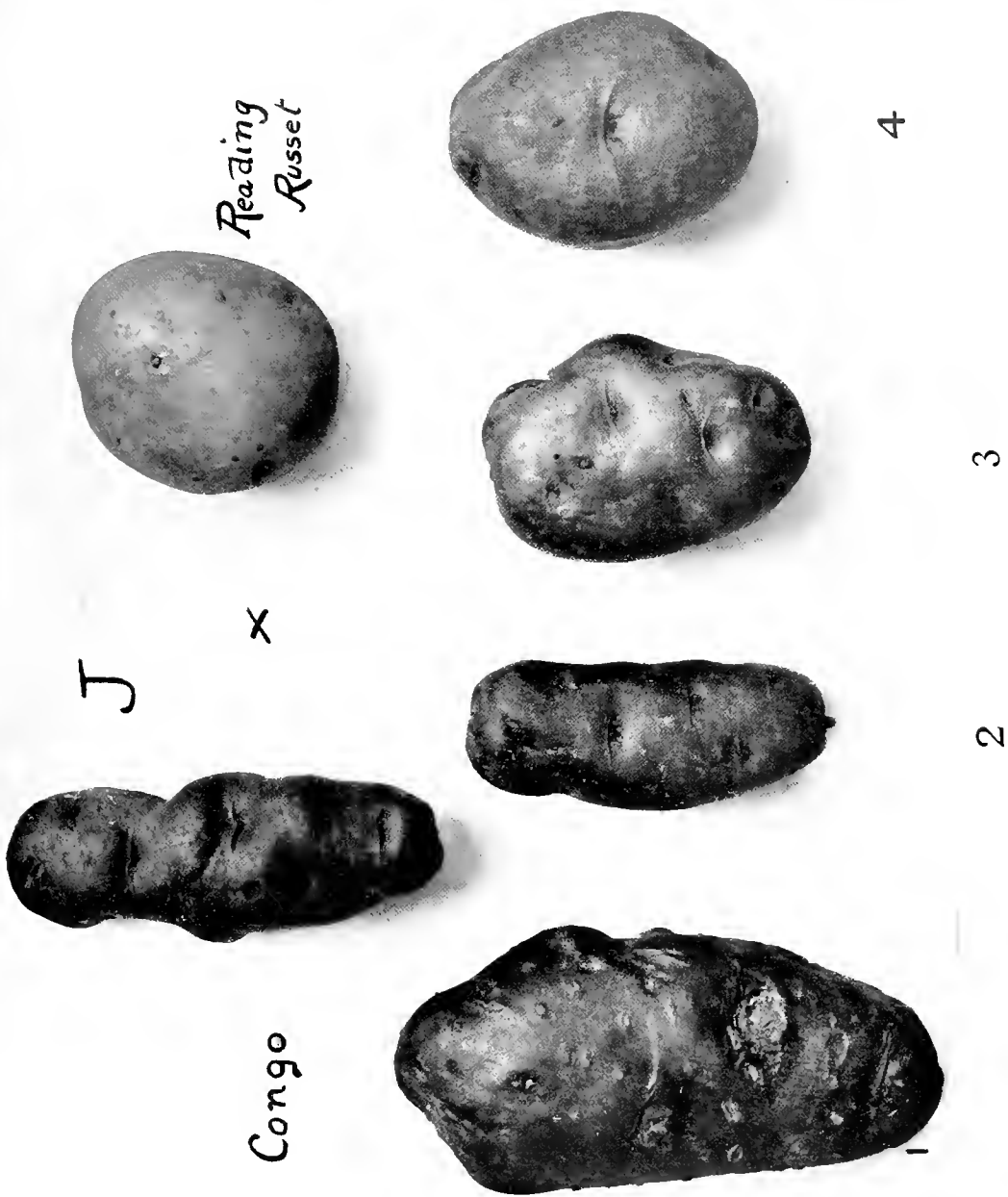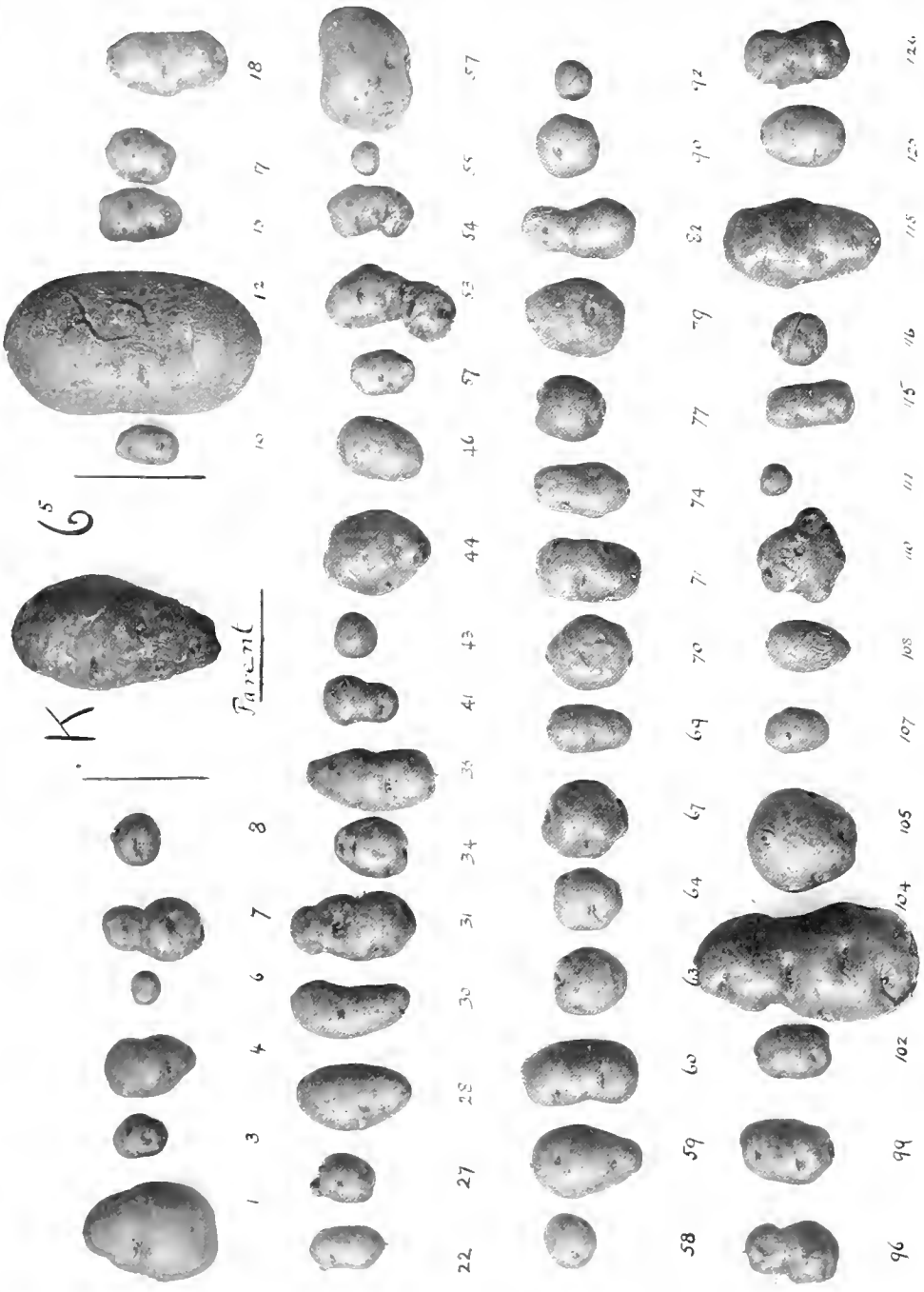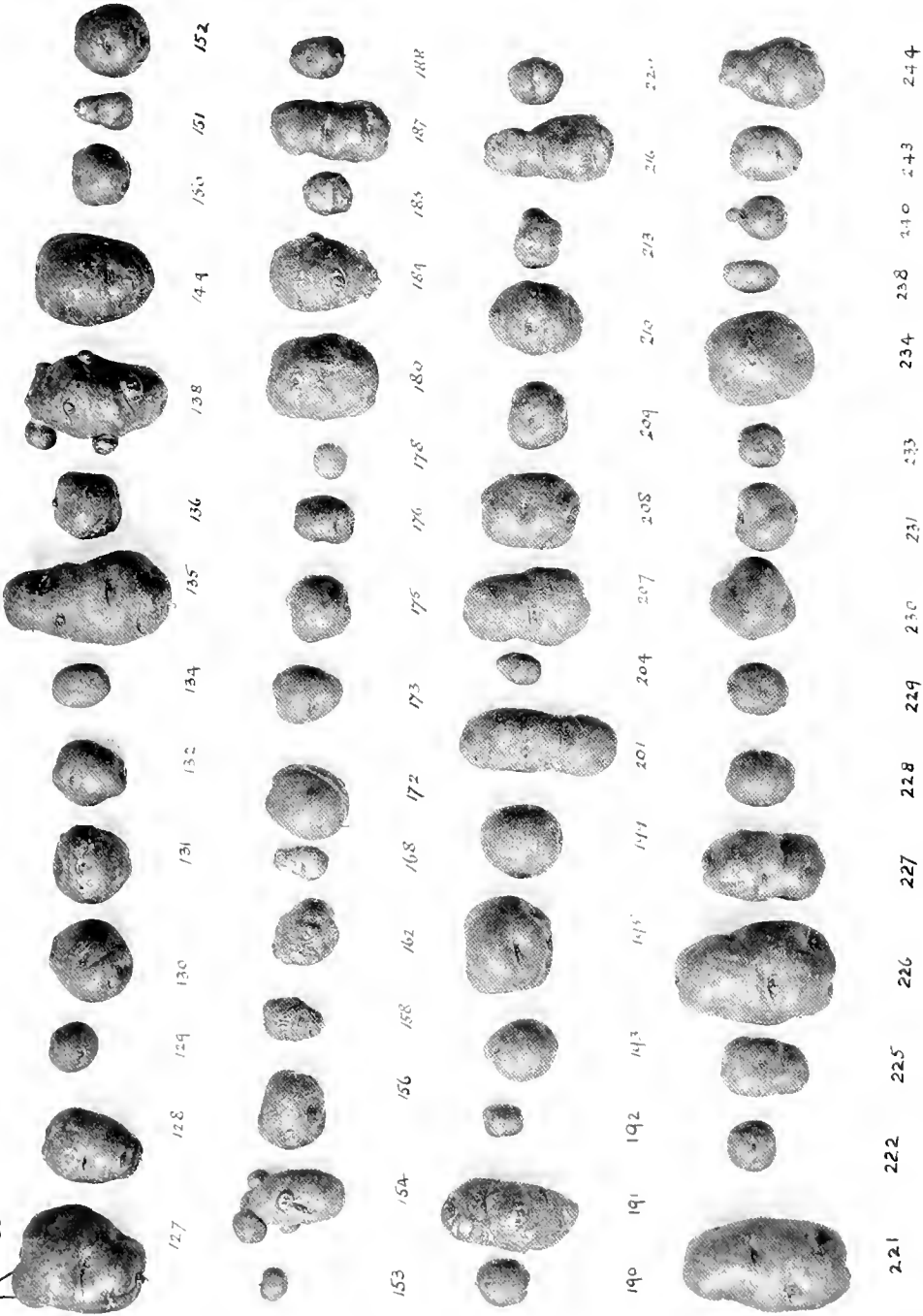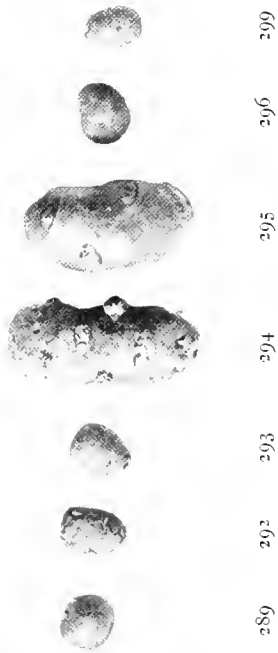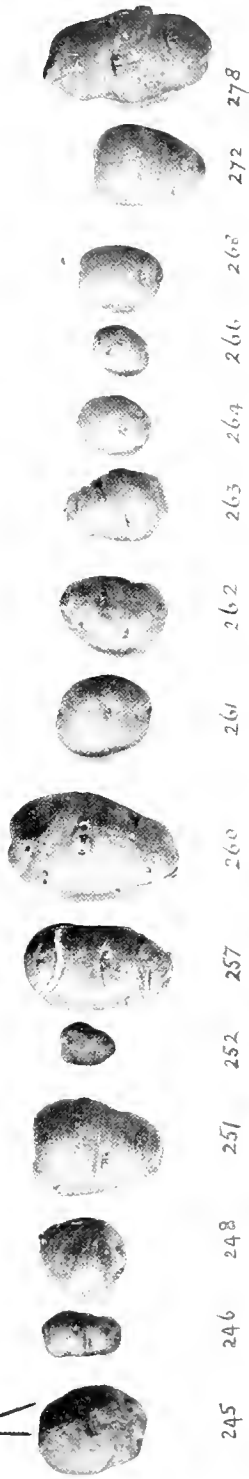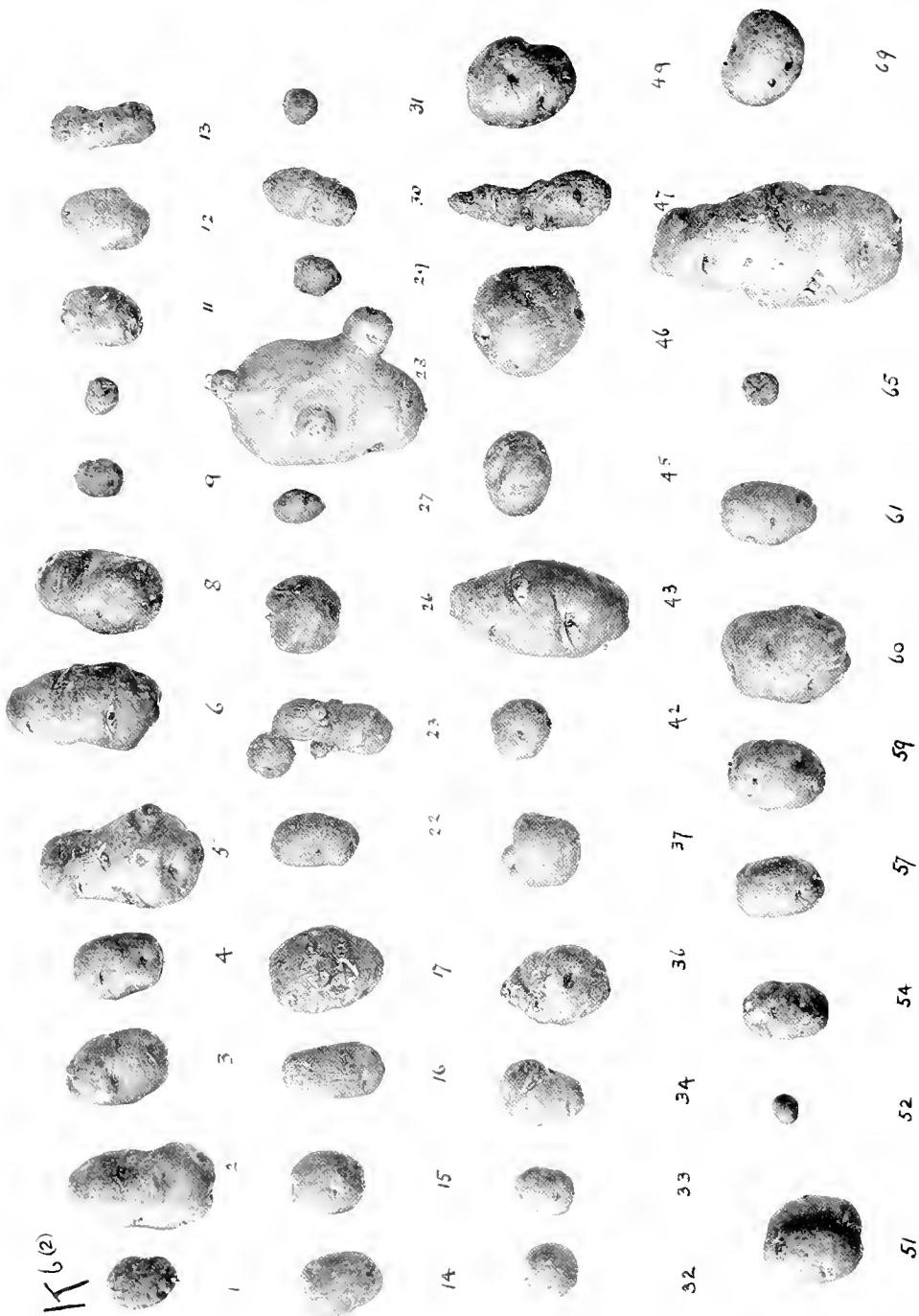
PLATE VIII

Record x. Flourball:

PLATE XIII

PLATE XVII

PLATE XVIII
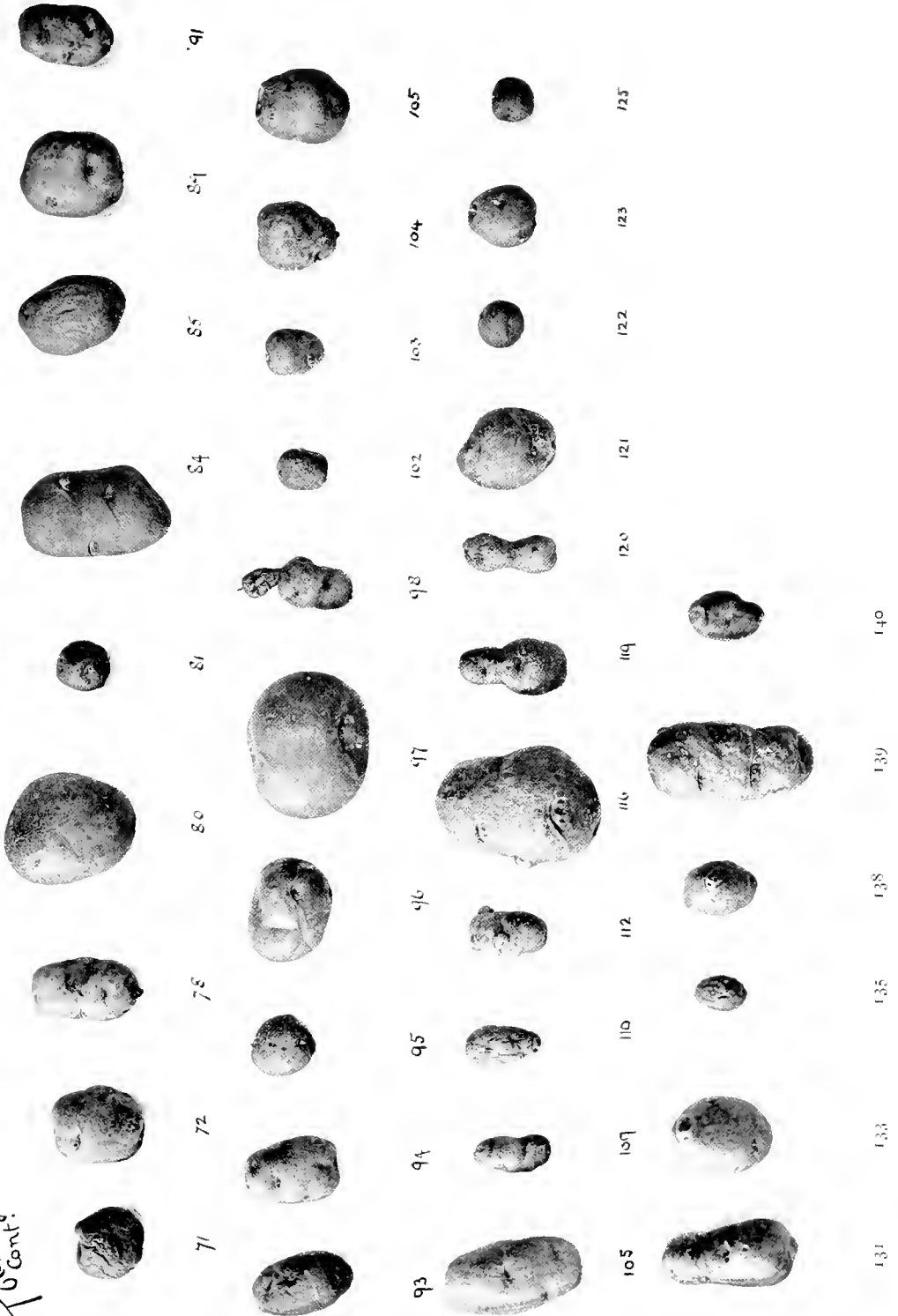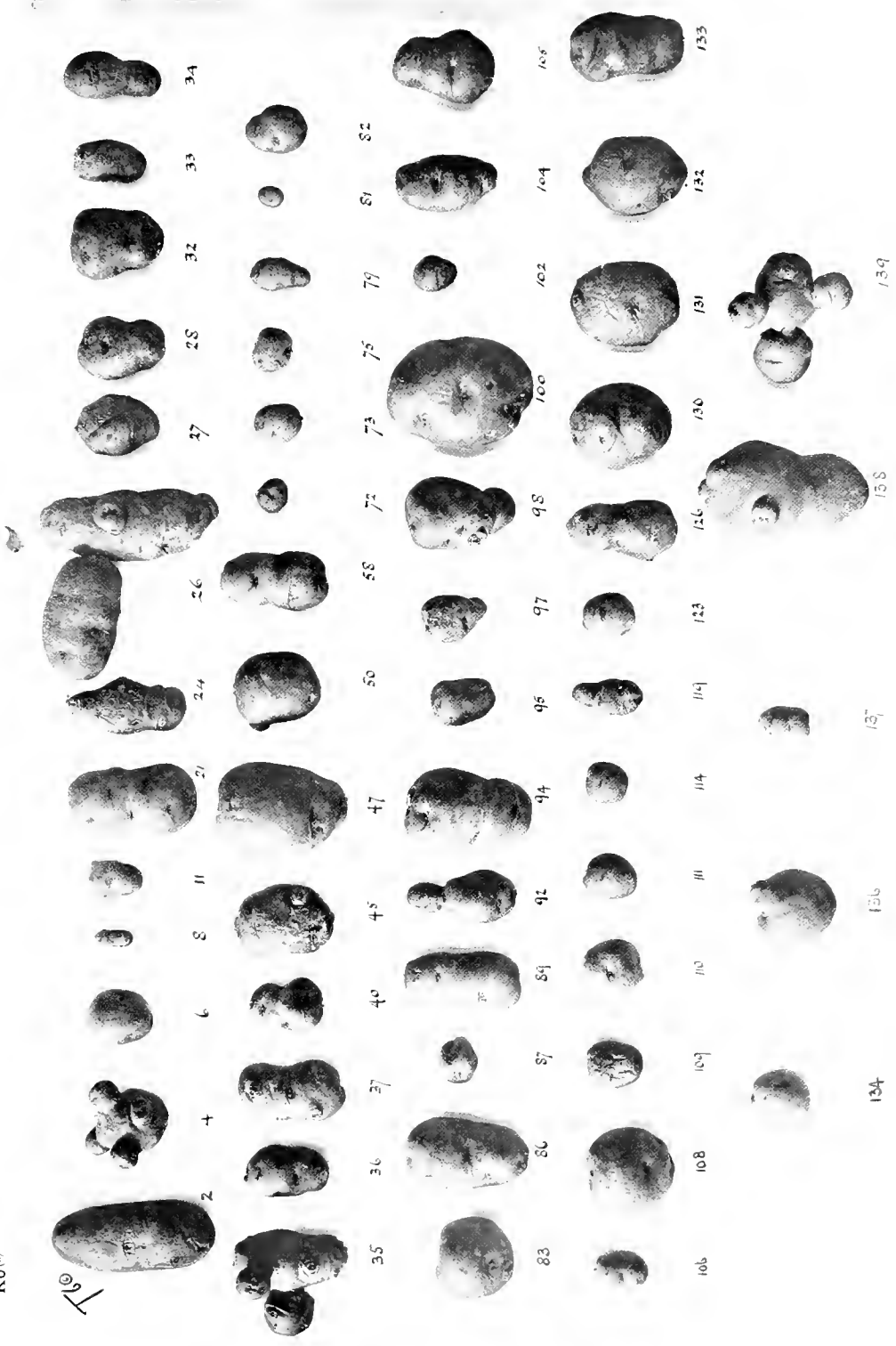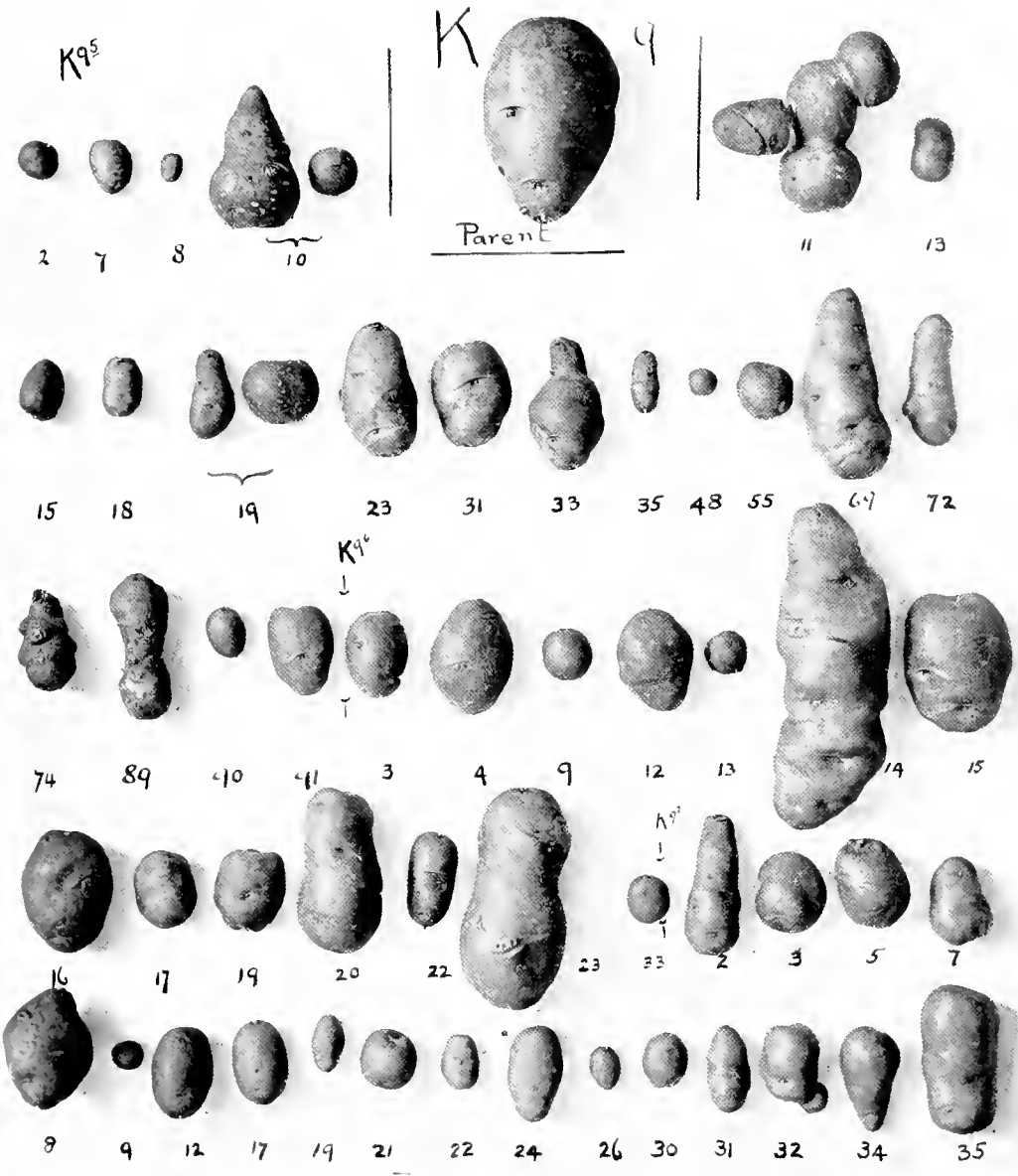
Line L

Firapple.   Reading Russet

Parents.

F 1.

1.   7.   9.   6.

PLATE XXIV
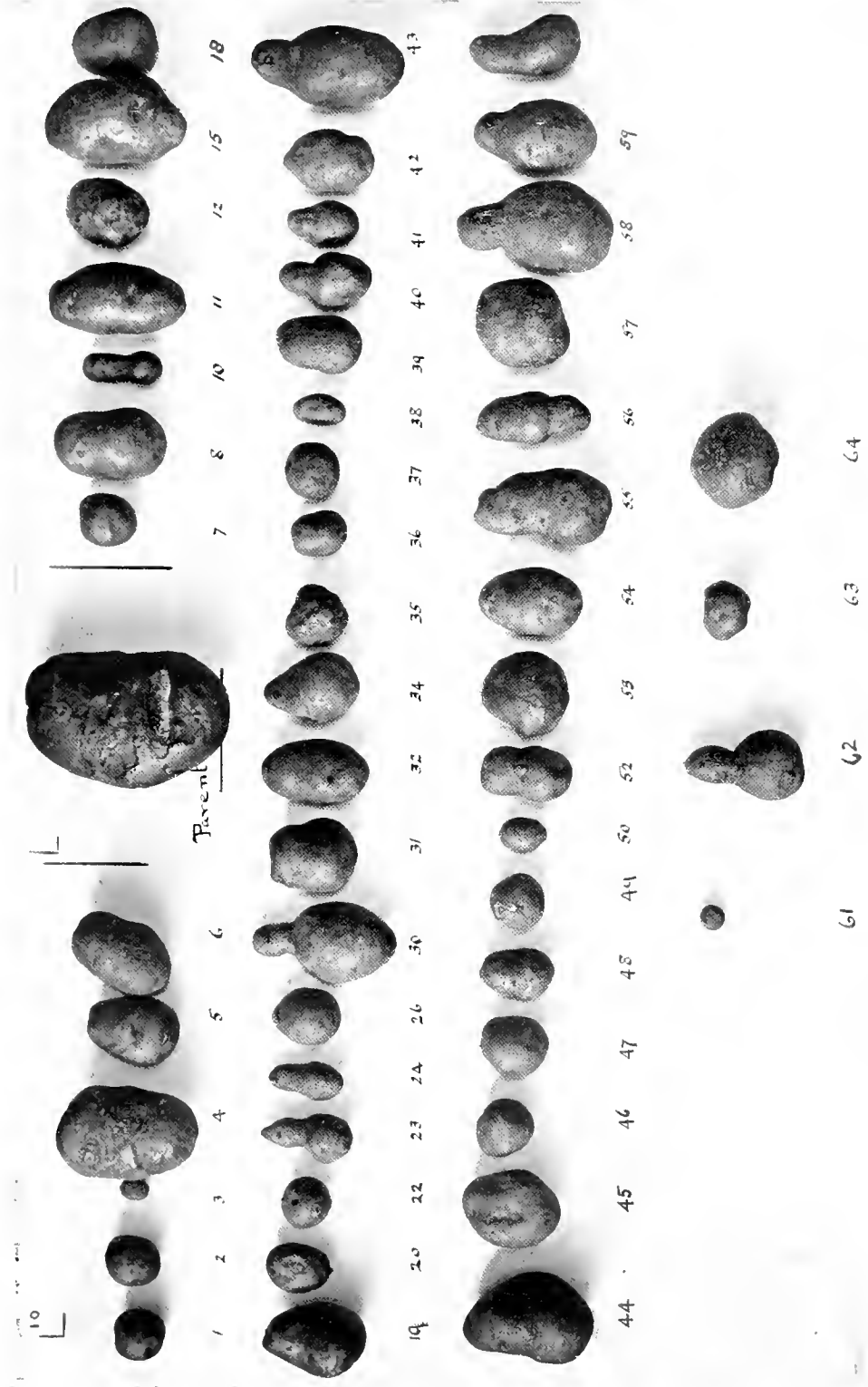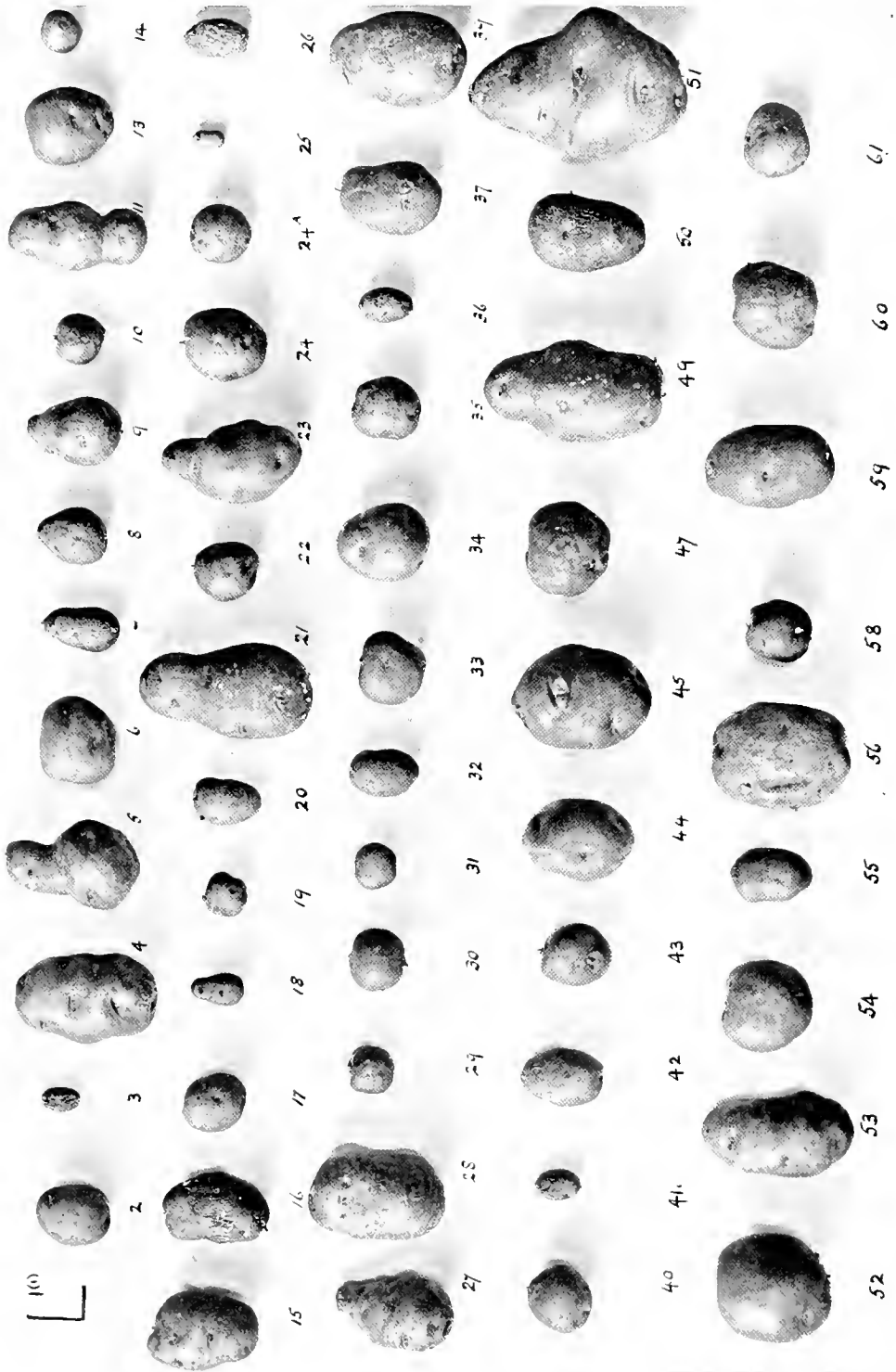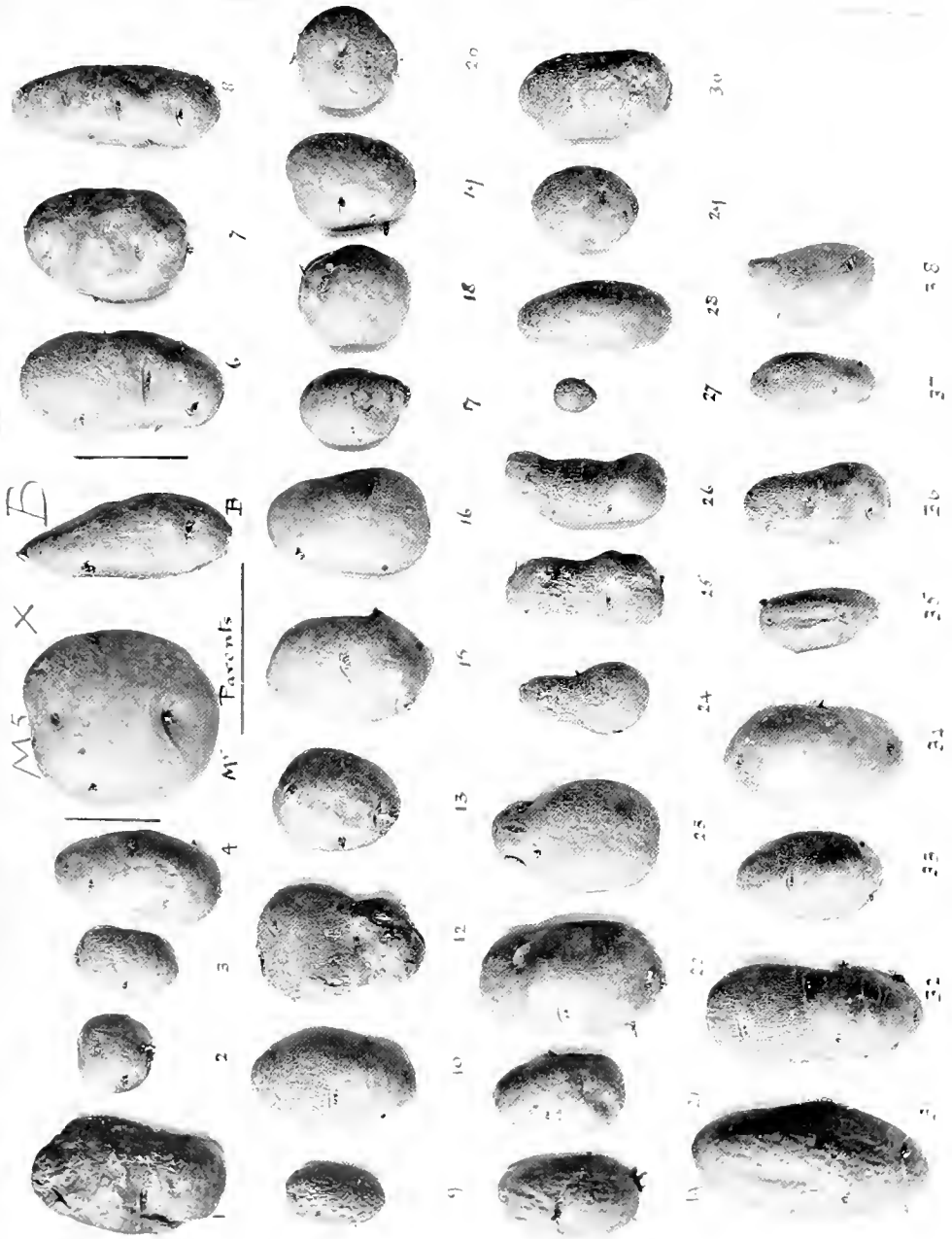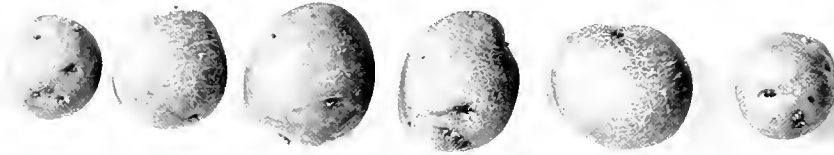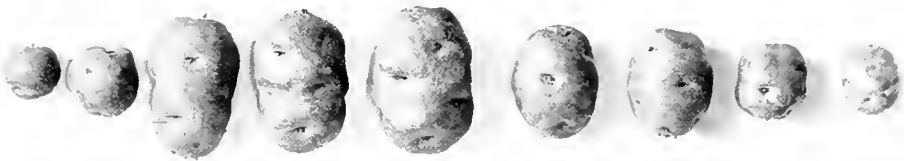
C

1907

C

seedlings   1909

PLATE XXIX

Flourball Seedling

Parents

CONGO

THE MODE OF INHERITANCE OF STATURE AND OF TIME OF FLOWERING IN PEAS (*PISUM SATIVUM*).

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THE experiments recorded in the present paper, though incomplete, throw some light on the nature of the Mendelian factors which determine stature in peas (*Pisum sativum*) and on the mode of inheritance of earliness and lateness of flowering in this species. The experiments were designed originally to investigate the latter problem—left undecided by Mendel's classical experiments on the inheritance of "time of flowering." As our work proceeded, it became evident that this function of the plant is not unconnected with certain, definite, morphological characters. Hence it becomes necessary to follow the course of inheritance of these characters, e.g. length of internode and thickness of stem. In doing this, we have been led to conclusions concerning, not only the relation of these morphological characters with flowering period, but, also, the part which these characters play in determining the stature of peas. We deal first with the latter point.

Stature. Certain garden races of *Pisum sativum* grow tall and give rise to tall-growing offspring; other races are dwarf and breed true to this character. Adopting Bateson's classification (1909, A) we call "tall," those varieties which grow 5—6 or more feet high, "dwarf," those which range from 9 inches to 3 feet. Between dwarf and tall are various "half-dwarf" races which reach a height of about 4 feet. The actual height attained by the various races is determined in any given

year, partly by gametic constitution and partly by the external conditions to which the plants are subjected during their growing period. Thus the two half-dwarf varieties Autocrat and Bountiful, used in our experiments, are so constant with respect to stature as to be described by Messrs Sutton and Sons, to whom we are indebted for seeds, as being, the former variety 3—4 feet, the latter $3\frac{1}{2}$—4 feet in height. Nevertheless, during the constantly wet summer of 1909 both Autocrat and Bountiful reached in the College Gardens at Reading an average height of 5—6 feet. We refer to these well-known seasonal fluctuations in height in order to point out that particular care is required in the interpretation of the results obtained in any one year and in the comparison of the statures of plants grown during different years.

The cross Autocrat and Bountiful and its reciprocal. This cross, made in 1907, and repeated in 1908, yielded an F_1 generation, the plants comprising which were considerably taller than either parent grown under like conditions. The average height of F_1 plants was 7—8 feet, that of the parent plants 5—6 feet.

F_1 selfed, yielded offspring (F_2) which ranged in height from 8 feet down to $1\frac{1}{2}$ feet. In all, 192 F_2 plants were recorded. Of this number, 61 plants were the progeny of a single F_1 plant of Autocrat × Bountiful grown in 1908. The remaining 131 plants of the F_2 generation were descended from four F_1 plants of the cross Bountiful × Autocrat. The seeds from these four plants were, owing to a mistake, harvested together. There is, however, no recognisable difference between the descendants of the single family from Autocrat × Bountiful and those derived from the four F_1 plants of Bountiful × Autocrat. We will therefore consider the 192 F_2 plants as a whole.

The F_2 plants, showing such marked differences among themselves with respect to height, fall into four groups which, for the moment, may be defined as follows:—F_1 type, Autocrat type, Bountiful type, and Dwarf type. Moreover, when classified in this way, the numbers of plants in the four groups show a close approximation to those expected in the F_2 generation derived from a dihybrid cross; that is one in which two pairs of characters are involved.

Thus: F_2 =

	F_1 type	Autocrat	Bountiful	Dwarf
Observed	114	33	32	13
Calculated	108	36	36	12
	9 :	3 :	3 :	1

Inspection of the parent plants, Autocrat and Bountiful, reveals the fact that, besides other, apparently minor, differentiating characters,

these two half-dwarf varieties are distinguished from one another by two well-marked characters, namely, length of internode and thickness of stem. Thus Autocrat, whose normal height is 3—4 feet, has *thick* stems (with large fleshy foliage of a bluish green colour) and *short* internodes of about 3 inches in length. Bountiful, whose normal height is $3\frac{1}{2}$—4 feet, has *thin* stems (with foliage smaller than that of Autocrat and of a yellowish green colour) and *long* internodes (5—7 inches). It may be noted incidentally that the rates of growth of these two varieties are very different; the growth in length of the axis of Autocrat being markedly slower than that of Bountiful. For example, when Autocrat and Bountiful are planted at the same time, Autocrat grows one foot whilst Bountiful grows two. The slowness of growth in length is associated with short internodes. The two varieties differ also with respect to mode of branching. Autocrat forms three to five branches at or near the ground-level. These branches develop at the same rate till they and the main axis are about 2 feet in height and then one axis takes the lead. Bountiful shows a less fixed mode of branching. Among the 1909 plants, some branched at the ground-level (2—4 branches), others formed their first branches a foot or so above the ground-level. Generally speaking, thick stem appears to be associated with branching, and thin stem with single stem, at the ground-level. We are engaged in endeavouring to work out the anatomical bases for thick as opposed to thin stem, and for long as opposed to short internodes, and the bearing of these factors on growth.

We will now consider the factors, thickness of stem and length of internode, in relation with stature. That these factors may be taken as valid representatives of those which determine height is evident from the following considerations:—

F_1 plants, 7—8 feet high, have all thick stems with long internodes (6—9 inches). If the factor for thick stems is represented by T, and its allelomorph (thin stem) by t, and if the factor for long internodes is represented by L, and its allelomorph (short internode) by l: then the gametic constitution of Autocrat is Tl, that of Bountiful is tL, and hence the gametic constitution of $F_1 = TtLl$. We ascribe the great height of F_1 plants to the presence of the factors T and L and to their dominance over t and l. The suggestion may be hazarded that the greater height and vigour which the F_1 generation of hybrids commonly exhibit may be due to the meeting in the zygote of dominant growth-factors of more than one allelomorphic pair, one (or more) provided by the gametes of one parent, the other (or others) by the gametes of the

other parents. This provisional interpretation of increased vigour of F_1 plants, has at all events the merit of being less obscure than the hypotheses which are current in the literature of plant physiology (Jost, 1907).

We return now to the F_1 of the crosses between Autocrat and Bountiful. Since the constitution of $F_1 = TtLl$, its gametes have constitutions :— $TL : Tl : tL : tl$, and hence, when F_1 plants are self-fertilized, we expect the usual $9 : 3 : 3 : 1$ ratio; i.e. in 16 plants, 9 with both dominants (T and L); 3 with one dominant; 3 with the other and 1 with the two recessives (t and l). That the expectation is realised is seen from the following table in which the results already given are recorded in terms of Tt and Ll.

$F_2 =$	F_1 type TL		Autocrat Tl		Bountiful tL		Dwarf tl
Observed	114		33		32		13
Calculated	108		36		36		12
	(9	:	3	:	3	:	1)

Of the 13 dwarf (tl) plants, all but one were below 3 feet in height, the three dwarfest being respectively $1\frac{1}{2}$, $1\frac{3}{4}$, and 2 feet. Table II gives the records of height, of thinness or thickness of stem, and of length of internode of the plants which we regard as true dwarfs. The classification is of course open to the objection that thick and thin are but qualitative terms, and that, in difficult cases, the criteria are purely subjective. An answer to this objection is that the records in Table II were made before we were aware that the characters "thin" or "thick" were of any considerable importance. We include in Table II the records of the characters of F_2 plants of a stature up to 4 feet. A comparison of the descriptions of the stems of the shorter plants (above the horizontal line in Table II) with those of the stems of the less short plants (below the line) confirms, as we think, the view which we have expressed above, that the dwarf plants have thin stems and also short internodes. With regard to the range of variation in height, both among the dwarfs, and among the plants of the constitution Tl, it is probable that the character of number of nodes, and also that of the position of the first flowers, are also of importance. It is hoped that further investigation of these characters among the F_3 families will determine this point.

We conclude from the above experiments that tallness in peas (*P. sativum*) depends on the presence of two factors, long internode, and

thick stem: that these factors are Mendelian in their inheritance; being dominant respectively to short internode and thin stem factors. Half-dwarf peas are of two kinds. One kind, represented by Autocrat, owes its semi-dwarfness to lack of the long internode factor. In the absence of this factor, the thick-stem factor cannot effect more than a sturdy, medium growth. The other kind of semi-dwarf lacks the thick-stem factor, and, in the absence of this factor, the long internode factor cannot build the stem-segments of a sufficient length to produce tallness in the plant. It may be urged that this, after all, is but a common-sense view of the way in which growth in length is effected: that only plants with long internodes among annuals are likely to be tall; and that only when stems are sturdy may internodes reach their full length. This may well be and it is certainly not a reproach to Mendelism that it may lead to the discovery of the obvious which, without the method, remains obscure.

The conclusions which we have reached as to the gametic constitution of tall, semi-dwarf and dwarf peas may be summarised thus:—

$$\text{Tall} = TL.$$
$$\text{Semi-dwarf} = tL \text{ or } Tl.$$
$$\text{Dwarf} = tl.$$

In a cross described by Lock (1905) we have what seems to us an interesting confirmation of this view of the chief factors involved in stature of *Pisum*. Lock's comment on the case is as follows (*op. cit.* p. 414):—"This cross seems to afford an example of remarkable intensification of both the allelomorphic characters of the same pair, viz. tallness and dwarfness—the former in F_1 and both in F_2 and later generations." The cross in question was one between Satisfaction—a variety which at Peradeniya grew to an average height of 4·6 feet—described as of robust growth (which we may take to mean thick stem), and with internodes of an average length of 1·74 inches, and a Native Pea of less than 3 feet in height, but varying much in different years, with thin stem, and internodes of an average length of $1\frac{1}{2}$ inches. In the four plants of the F_1 generation, the internodes were of an average length of 2·4 inches—longer than in either parent—the height of the F_1 plants was about 6 feet, and the number of internodes was the same as in Satisfaction. It would seem that in the increased length of internode of the F_1 plants (an average of 2·4 inches as compared with the 1·74 inches of Satisfaction) is seen the influence of thick stem on an internode which, when combined with thin stem, is of an average

length of $1\frac{1}{2}$ inches. In F_2, the preponderating type resembled the F_1 plants, and the appearance of dwarfs, shorter than either parent, with internodes of $1\cdot0$—$1\cdot2$ inches in length (the proportion of long to short being $19:6$), confirms our belief that the characters thick and thin stem, long and short internodes were the chief stature-factors involved in this cross. Probably the difference in the number of nodes introduces a complication, but the small numbers grown in F_2 and the lack of further records, prevent a full analysis. We should mention that this cross was made primarily by Mr Lock with the object of investigating the characters of the testa of the seeds of *Pisum*.

In conclusion, with respect to the question of tallness and dwarfness, it is evident that a closer investigation will reveal facts of great importance to an understanding of the physiology of growth.

Time of flowering: earliness and lateness. Certain varieties of peas are well known and prized for their stability with respect to time of flowering, and therefore it is to be supposed that the character is hereditary. Mendel many years ago commenced experiments with a view to determine the mode of inheritance, but few records of these experiments are left to us. In Mendel's memoir on the hybridizing of peas (1909B) we find the following:—"As regards the flowering time of the hybrids the experiments are not yet concluded. It can, however, already be stated that the time stands almost exactly between those of the seed and pollen parents, and that the constitution of the hybrids with respect to this character probably follows the rule ascertained in the case of the other characters."

By the use of the varieties Autocrat and Bountiful for such an experiment, the advantage is gained of a long space of time between the flowering periods of the two varieties: the former variety flowers, in normal seasons, about 30 days after the latter. Thus, in 1909, from sowings made in April, 23 out of 28 plants of Bountiful were in flower on June 2nd, whereas Autocrat, sown at the same time, was only just coming into flower on June 30th (see Table I). In spite, however, of the favourable nature of our material with respect to the character under consideration, we cannot claim to have arrived at a complete understanding of the mode of inheritance of earliness or lateness of flowering. Nevertheless, we publish our records, and our attempts to analyse them in Mendelian terms, since they appear to show definitely not only that the problem is capable of solution, but also the nature of the difficulties which have to be met before the solution is obtained. It will be seen from the records of the time of

flowering (Table I) that the F_1 generation is intermediate with respect to time of flowering between the parents Autocrat and Bountiful. In 1909, whereas 23 out of 28 plants of Bountiful blossomed by June 2nd, and whereas Autocrat was beginning to flower by June 30th, 10 of the plants of F_1 (of a total of 12) were in flower by June 21st; and the remaining plants were in flower by June 30th. The F_1 plants of Autocrat crossed Bountiful and those of the reciprocal cross, grown in 1908, confirm this result. From the appearance of such an intermediate form in F_1, it may be supposed, either that there is incomplete dominance of lateness over earliness, or that there are two (or more) factors connected with the time of flowering; the meeting of the two, or more, dominant and antagonistic factors, from either parent in the F_1 plant, giving an intermediate time of flowering. In the former case, the F_2 plants, obtained by selfing F_1, may be expected to give the $1:2:1$ ratio; but, though segregation of early and late occurs in F_2, it is not of this simple type. If we tabulate the observations on time of flowering, not of the F_2 generation as a whole, but of the several categories of that generation, viz. thick long (TL), thick short (Tl), thin long (tL), and thin short (tl), we obtain the results shown in the accompanying Table.

TABLE I.

The Accelerating Influence of Long Internodes on Time of Flowering of F_2 Plants.

(Times of Flowering of Bountiful, Autocrat and F_1 are given for purposes of comparison.)

Numbers of Plants in Flower

Thick Long	Thick Short	Thin Long	Thin Short	Date of Flowering	Bountiful	Autocrat	F_1
5	1	24	6	June 2	23	—	—
17	1	7	2	June 10	5	—	—
48	5	1	3	June 17	—	—	8
36	16	—	1	June 21	—	—	2
8	10	—	—	June 30	—	—	2
—	—	—	1	July 6	—	(a few beginning to flower)	—

These results show that plants with long internodes, of both thick- and thin-stemmed types, flower, on the whole, earlier than the short internode types. Since long internode is dominant to short internode, F_1 plants may be subject to the same accelerating influence with respect to time of flowering as those of the groups, long thick and long thin.

We suggest therefore that lateness is dominant to earliness, and that the reason why the plants of F_1 flower before those of the late parent Autocrat, is that they possess the factor for long internodes, their gametic constitution being *TtLl*. The fact that the position of the flowers on the stem, in F_1 plants, is about the same as in Autocrat, lends some support to the view that late is dominant to early. There was however a considerable range of variation in this character, both in Autocrat and in the F_1 plants. Moreover, owing to the branched habit of Autocrat and of the F_1 plants, and to the fact that this character was not considered until rather late in the season, it was impossible in some cases to recognise the main stem, i.e. the stem which flowered first, and this may have spoilt the records to some extent. This character of the position of the first flowers on the stem has been supposed to indicate time of flowering (1905b). Our records show that Autocrat bears its first flowers, on the average, at the thirteenth node, Bountiful at the seventh node, and the F_1 plants at the twelfth. Many records of this character were made among the F_2 plants. The average result of these records points to the conclusion that low-flowering indicates earliness, high-flowering lateness, but there were many exceptional cases among individuals. Further investigations among F_3 families, homozygous in respect of the many other characters involved, should provide a solution to this question.

Proceeding then on the basis that lateness is dominant to earliness, we observe, in the F_2 generation, that the flowering period spreads over more than a month, from June 2nd—July 6th, that whereas many (36) plants of F_2 flower as early as the early parent, few flower so late as Autocrat (Table I). That time of flowering is influenced by seasonal conditions is undoubted; but the marked differences in flowering-time between the various plants of F_2 show that the mode of influence of a given season is determined to a surprising degree by internal factors. A more detailed examination of the distribution of earliness and lateness of flowering among the F_2 plants, brings out several facts which lend support to the conclusions that time of flowering, though inherited, is modified in its expression in the zygote by morphological characters such as thickness of stem. As we have shown, the F_2 plants group themselves into four classes:—thick long (*TL*), thick short (*Tl*), thin long (*tL*), and thin short (*tl*). If we chose arbitrarily the date of flowering of Bountiful (June 2) as *early* and regard for our immediate purpose all plants flowering after this date as *late*, we find, on scrutinizing the distribution of lateness and earliness among these classes,

that most of the *thick-stemmed* plants with short or long internodes, are late (141 late, 6 early); that, of the thin, short-noded plants, 6 are early and 7 late, and that of the thin, long internoded plants, 24 are early and 8 are late. It is therefore apparent that there is a relation between morphological, vegetative characters and period of flowering. Thick-stemmed plants contain a very high proportion of late plants, thin-stemmed plants contain an almost equally large excess of earlies. As has been shown by Bateson, departures from normal, Mendelian expectation which manifest themselves by discriminate distribution of a character among the members of a generation, may be interpreted by the aid of the hypothesis of gametic coupling. Applying this hypothesis, and assuming that the coupling between thick stem and late factor is of the 7 : 1 : 1 : 7 order (Bateson, 1909, *op. cit.* p. 159), we arrive at the following results :—

	TLE	*TLe*	*TlE*	*Tle*	*tLE*	*tLe*	*tlE*	*tle*
Calculated on trihybrid scheme	81	27	27	9	27	9	9	3
Observed	109	5	32	1	8	24	7	6
Calculated on 7 : 1 coupling ...	99·6	8·4	33·2	2·8	9·2	27·6	2·8	8·4

T = thick stem, L = long internode, E = late flowering.

Though the numbers are not large enough to demonstrate the existence of 7 : 1 coupling between thick stem and late flowering factor, yet their general run and fairly close approximation to those expected on the basis of such coupling make it probable, in our opinion, that these two factors are connected with one another in this manner.

The nature of the influence exerted by the long-stem factor in inducing precocity of flowering we are not yet prepared to discuss, nor can we deal with the general physiological problems suggested by these observations; but will content ourselves with pointing out that, before a full analysis of physiological properties such as those of time of flowering can be made, a not inconsiderable amount of breeding work must be done with the preliminary object of obtaining suitable material, i.e. material which consists of groups alike in all respects save in the one which it is proposed to investigate. We learn from the foregoing preliminary experiments that it is not enough to cross any late with any early pea, for, as is indicated by these experiments, lateness and earliness are connected, in a manner not to be suspected on *a priori* grounds, with definite, morphological, vegetative characters.

TABLE II.

Autocrat × Bountiful and Reciprocal Cross.

Description of F_2 plants of Heights between 1½ and 4 feet.

Label	Date of Flowering	Height	Stem	Length of Internode	Foliage	D=Plants reckoned as Dwarf
5 × 3/5/10	June 2nd	1½ feet	Thin	3 inches	Very small	D
3 × 5/2/60	,, 9th	1¾ ,,	Thin	2¾ ,,	Bountiful type	D
3 × 5/2/13	,, 2nd	2 ,,	Thin	3 ,,	,, ,,	D
5 × 3/6/7	July 6th	2¼ ,,	Thin	1½ ,,	Very small	D
5 × 3/6/3	June 2nd	2½ ,,	Thin	2 ,,	Small (=Bount.)	D
5 × 3/4/34	,, 2nd	2½ ,,	Thin	2 ,,	? Intermed.	D
5 × 3/2/4	,, 2nd	2½ ,,	Thin	2 ,,	Bountiful	D
5 × 3/1/19	,, 16th	2⅔ ,,	Thin	3 ,,	Small	D
5 × 3/5/34	,, 30th	2½ ,,	*Thick*	5 ,,	? Intermed.	
5 × 3/6,6	,, 10th	2¾ ,,	? Thin	2 ,,	? ,,	D
3 × 5/2/20	,, 2nd	2½—3 feet	Thin	3 ,,	Bountiful	D
3 × 5/2/31	,, 21st	2½—3 ,,	? Thin	4 ,,	? Autocrat	D
5 × 3/2/14	,, 16th	2½—3 ,,	?	?	? Bountiful	D
5 × 3/5/12	,, 16th	3 ,,	? Thin	3 ,,	Intermed.	D
5 × 3/5/41	,, 21st	3 ,,	? Thin	4 ,,	Diseased	
5 × 3/1/5	,, 21st	3—3½ ,,	? Thick	3 ,,	?	
5 × 3/3/5	,, 30th	3—3½ ,,	? Thick	3—3½ inches	Small	
5 × 3/1/10	,, 16th	3½ ,,	Thick	3½ ,,	Small (=Bount.)	
3 × 5/2/8	,, 16th	3½—4 ,,	Thick	3 ,,	? Autocrat	
3 × 5/2/52	,, 2nd	3½—4 ,,	? Thick	4 ,,	Autocrat	
5 × 3/4/29	,, 21st	3½—4 ,,	? Thick	4 ,,	? Autocrat	

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STUDIES IN THE INHERITANCE OF DOUBLENESS IN FLOWERS.

I. PETUNIA.

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THE tradition that the production of double flowers is largely a matter of external conditions has already been shown in the case of *Matthiola* to be at variance with the results of breeding experiments carried on for several years[1]. The evidence, on the contrary, clearly shows that in this case doubleness, like the other characters investigated, is inherited according to definite laws, and in accordance with the Mendelian principle of segregation[2]. With a view to making a comparative study of the inheritance of doubleness in plants a series of experiments has now been undertaken in various other genera. In the case of Petunia the results have already reached a point at which a definite statement can be made, and it is with these results that the following account is concerned.

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[1] Of the many beliefs still held regarding the occurrence of doubles in Stocks, the only one which I have so far been able to confirm is that seed which has been kept produces a higher proportion of doubles than that more recently harvested. This appears to be true to the extent that the seeds destined to give rise to doubles retain their vitality rather longer than those which give rise to singles. The higher proportion observed is not therefore due to any effect of age on the constitution of the seed, but to an original difference in viability.

[2] A general statement of these results has already appeared, and a more detailed account is now in preparation. (See *Reports to the Evolution Committee, Royal Society*, II. p. 29, 1905; III. p. 44, 1906; IV. p. 36, 1908.)

The material used in these experiments included the following forms :—

(1) *P. violacea* (*phœnicia*). Flowers deep magenta with very dark throat. Pollen blue.

(2) *P. nyctaginiflora*. Flowers white with yellow flush in the throat. Pollen yellow. Of stouter habit than the preceding species and with larger flowers.

(3) *P. hybrida grandiflora*. Garden hybrids. (*a*) Flowers magenta or magenta and white, variously striped or blotched. Corolla plain edged. Pollen blue. (*b*) Var. *fimbriata*. Flowers nearly pure white. Corolla fringed. Sepals broad and slightly curled. (Lady of the Lake.)

(4) Countess of Ellesmere. A garden variety. Flowers rose-coloured with throat nearly white. Pollen white.

The plants were raised from seed. The two species *P. violacea* and *P. nyctaginiflora* and the garden form Countess of Ellesmere are all single-flowered. The seed from which the *grandiflora* plants were raised was stated to yield a proportion of doubles, and a mixture of singles and doubles was duly obtained. In growers' catalogues it is generally stated that the seed which is guaranteed to produce doubles has been obtained from flowers (i.e. singles) artificially fertilised with the pollen of doubles. This, as will appear presently, seems to be the only method of producing double-flowered plants from seed (see p. 60). The proportion of doubles obtainable is variously quoted as 20—40 per cent. The object of the present experiments was to discover under what circumstances doubles may be expected to occur, and also, if possible, to determine whether the proportion of doubles obtainable was constant.

A. DESCRIPTION OF THE DOUBLE FLOWER.

The plants which will bear double flowers may be recognised before the flower expands by the shape of the bud which is short, thick and blunt, whereas that of the single is long, slender and pointed. In the single flower we have a simple funnel-shaped corolla, five epipetalous stamens, and an ovary with a slender style terminating in the expanded disc of the stigma (see fig. 1). In many cases the connective is prolonged above the anthers in the form of a petaloid structure varying in size from a short process so small as to be easily overlooked after the

anthers have dehisced to flat expansions of considerable size (see fig. 7). But in these cases the stamens, always five in number, are otherwise normal. The gynœcium is also normal, and the corolla forms one petaloid funnel-shaped structure. The flower is obviously single. In the doubles the flower tube is filled with a number of additional petaloid structures and stamens (see figs. 2 and 3), or in rare cases mostly with additional stamens (see figs. 4 and 5). These extra petaloid structures are often variously folded, generally flat but occasionally funnel-shaped, more or less adherent below and free above. When folded the more deeply coloured, morphologically upper surfaces are generally opposed, the less deeply coloured, often hairy under surfaces being outside; but in the open flower the expanded upper portions of these structures come to lie for the most part with the upper surface exposed to view, thus giving a uniform colour effect. They vary considerably in size and number even in the different flowers on one individual. Many bear anther-like structures containing pollen, and some have occasionally been found with a structure resembling a stigma. The number of stamens proper is also variable, being usually more numerous in flowers with few petaloid structures and *vice versa*. The several members of the corolla and andrœcium may fuse to form an outer, single, conspicuous, and somewhat massive envelope, within which are concealed much smaller petal-like structures and stamens forming a central mass, which may arise at a distinctly higher level than the outer envelope owing to the development of an internode. Or they may form three or four well-developed envelopes composed of petal-like structures and adherent stamens which can be successively peeled off. A further important characteristic of the double flower is the malformation of the gynœcium. The whole structure is often completely deformed, but when this is not the case and the style and stigma appear to be normal, the ovary is seen to be larger than in the single, and when opened is found to contain perianth parts, stamens with well-formed pollen, and in some cases also ovules below or among these other structures. *All attempts to use the doubles as seed-parents however proved unsuccessful. Fertilisation produced no result. Hence the double character could only be introduced into the pedigree on the male side.*

The flowers on any individual are of one type, either all single or all double as the case may be. Among a large number of flowers from double-flowered plants only one was found in which both corolla and andrœcium appeared to be single, and in this case the flower was

malformed, the corolla being split and the segments curled; the ovary
was not opened.   The remaining flowers on the plant showed the usual
degree of doubleness.   Among the flowers of single plants only two were
observed in which there was any approach to doubling, and in each case
the remaining flowers on the individual were normal singles.   In one of
these flowers a single large petaloid structure had developed in the
corolla tube; in the other a similar structure arose near each of the five
stamens, the line of adhesion to the corolla coinciding with that of
a stamen and forming a common decurrent ridge.   It was noticed that
in single plants kept through the winter under unfavourable conditions
the first flowers produced in the following spring were often deformed,
the corolla being split and infolded but without showing any tendency
towards doubleness.

B.   Results of breeding experiments.

The general results of the experiments carried on during the last
five years may be briefly stated as follows:—

1.   When a single is crossed with a double, doubles as well as
singles occur in the first (F_1) generation.

2.   When such F_1 singles are self-fertilised[1] or fertilised *inter se* the
resulting offspring are all single.   *Doubles in fact are only obtained
when the pollen of doubles has been used to fertilise the seed-parent,
so that this operation must be repeated in each generation.*

3.   The proportion of singles in a mixed family is probably always
in excess of the doubles.

Details of the experiments are given in the accompanying Tables.
The results recorded in Tables I and II show that singles, whether
belonging to one of the type forms or derived from a previous cross,
when fertilised with pollen from a double yield a mixture of singles and
doubles in the first generation.   Out of a total of 41 families thus bred,
40 included some doubles.   As regards the remaining case in which no
doubles were recorded there is little doubt that their absence is due
solely to the small size of the family (4), and that a larger sowing
would have given the usual mixture.

[1] If protected under muslin or glass and left undisturbed *violacea* and *hybrida* rarely
set seed; even when artificially self-fertilised many pollinations give no result.   On the
other hand *nyctaginiflora*, under the same conditions will often set seed, and does so
readily when artificially fertilised with its own pollen.   Further experiments concerning
the sterility of these forms are now in progress.

It also seems clear that in such mixed families the singles preponderate. This was the case in 33 out of 38 families, and although in the remaining five the doubles were equal in number to the singles or slightly in excess, it is very improbable that the deficiency of singles in these cases is real. In families 9, 10, 31, and 33 the numbers recorded are too small to be conclusive, and in family 35 the result (9 single, 11 double) is within the range of deviation which might be expected to occur, if, as appears to be the case in several families, the true ratio represents but a slight excess the other way. At present the data available are hardly sufficient to determine with certainty the real proportion of singles and doubles occurring in these families. Until the general occurrence of doubles in unions of this kind had been established the number rather than the size of the families was of first consideration. If for the moment, however, we consider only those families with more than 10 members we find that they fall naturally into two principal groups, in one of which the numbers suggest the possible ratio 3 s. : 1 d., while in the other they approximate closely to the ratio 9 s. : 7 d. Grouping these families in this way we get the result shown below :—

Reference number of family	Number of offspring		Reference number of family	Number of offspring		Reference number of family	Number of offspring	
	Single	Double		Single	Double		Single	Double
3	19	4	1	82	67	25	22	11
7	14	4	2	54	35			
11	18	6	4	28	21	37	34	17
14	12	2	5	13	12			
19	15	2	6	10	9			
20	11	1	17	24	22			
24	18	2	22	9	6			
			26	17	13			
39	17	7	27	18	13			
			28	13	11			
			29	13	8			
41	12	3	32	24	21			
			35	9	11			
			36	53	35			
			38	16	14			
			40	14	9			
Total	136	31		397	307			
Where a ratio of 3 s. : 1 d. calculated to the nearest whole number would give	125	42	Where a ratio of 9 s. : 7 d. calculated to the nearest whole number would give	396	308			

9 families giving a total of 136 single, 31 double where a ratio of 3 s. : 1 d. would give 125 single, 42 double.

16 families giving a total of 397 single, 307 double where a ratio of 9 s. : 7 d. would give 396 single, 308 double.

2 families not included in either of the above groups giving a proportion of 2 single : 1 double.

As yet it is not clear whether the occurrence of these different ratios indicates that more than one factor is concerned in determining singleness and doubleness, or whether it results from the fact that the proportion of germ cells carrying singleness and doubleness varies in different individuals. In view of the results obtained with Stocks, the former explanation seems the more likely.

The results given in Tables III and IV show that singles belonging to the various type forms, whether self-fertilised or crossed with another type yield only singles (see Table III); and further, that cross-bred singles having one parent single and one double are equally unable to produce doubles when self-fertilised or fertilised *inter se* (see Table IV), although the same individuals yield both singles and doubles when crossed with pollen from a double.

It would therefore appear that the pollen of all the singles tested (23) was homogeneous as regards the presence of some factor x which is essential to the manifestation of singleness, and which is absent from some at least of the ovules. Whether the female germs are homogeneous in this respect, and are all thus deficient; or whether they are heterogeneous, some lacking the necessary factor and some not is at present uncertain. Precisely the same may be stated in regard to the pollen of the doubles. In some of the grains some necessary factor is evidently wanting, but whether this is the case in all the male germs is not yet clear. It may however be safely asserted that whichever alternative represents the true condition as regards the ovules in the single, the converse will be found to hold good for the pollen of the doubles. For the results obtained would equally follow whether it were the ovules of the single which were homogeneous and the pollen of the doubles that was heterogeneous, or whether the reverse were the case. Analogy with Stocks[1] would suggest that the first-mentioned

[1] In the account of the results obtained with Stocks (*Evolution Reports, loc. cit.*) it is stated that the homogeneous pollen of the heterozygous (ever-sporting) singles carries *doubleness* (i.e. absence of singleness), but that among the ovules some carry *doubleness* and some *singleness*. This mode of expressing the difference in constitution between the male and female germs is permissible if we suppose that the occurrence of singleness or

alternative may be likely to prove correct (viz. ovules of singles hetero-geneous, pollen of doubles homogeneous as regards absence of the factor x); but the fact that if this were so we should expect a certain pro-portion of Petunia singles to be homozygous as to singleness, and therefore incapable of yielding doubles when crossed with the pollen of a double, whereas, as a matter of fact, no such singles were met with, lends considerable support to the opposite view (viz. ovules of singles homogeneous, pollen of doubles heterogeneous in regard to absence of x).

Thus we find in Petunia the same peculiar type of gametogenesis which has already been shown to occur in *Matthiola*. In both cases segregation proceeds in such a way that certain factors are distributed differently among the ovules and the pollen grains. It may also be noted that in both instances doubleness behaves as the recessive character, singleness as the dominant, but in other respects the two cases present an interesting contrast. In the double Stock, as is well known, the flower is completely sterile, whereas in Petunia the male organs are functional in the double though the female are not. Further it appears that although both in the single Stock which constantly throws doubles, and in the single Petunia which yield doubles when fertilised by a double, the pollen is homogeneous in respect of some factor needed to produce singleness, the homogeneity is brought about by the absence of this factor in the Stock, by its presence in Petunia. Consequently doubles are obtained in the Stock when heterozygous individuals are self-fertilised, or fertilised *inter se*, but not in Petunia. Lastly, in the Stock a heterozygous single fertilised with double-carrying pollen yields an excess of doubles; in Petunia on the other hand singles crossed with pollen from a double yield a majority of singles.

Summary.

1. Single Petunias belonging to the following forms: *P. violacea, P. nyctaginiflora, P. hybrida grandiflora*, and Countess of Ellesmere, whether self-fertilised or crossed with each other, yield only singles.

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doubleness is determined by the presence or absence respectively of a single factor. Now however that the accumulated evidence points to the probability that more than one factor is involved this difference between the male and female germs is more correctly expressed in terms of *some factor the presence of which is essential to singleness* (as above in Petunia) than in terms of *the character singleness itself*.

2. Cross-bred singles derived from one single and one double parent also produce only singles when self-fertilised or fertilised *inter se.*

3. Singles crossed with pollen from a double yield doubles in the first generation.

4. In families containing a mixture of singles and doubles, the singles are in excess of the doubles. There is some evidence to show that in some cases the ratio approximates to 9 s. : 7 d. and in others to 3 s. : 1 d. The occurrence of the ratio 9 s. : 7 d. in many of the cross-bred families strongly suggests that more than one factor is concerned in determining the occurrence of singles and doubles, and this view is in harmony with the conclusions formed in the case of Stocks.

5. The male organs are functional in doubles, but the gynœcium is more or less deformed, and when fertilised yields no seed, hence the double character can only be introduced on the male side.

6. Doubleness behaves as the recessive, singleness as the dominant character.

7. Gametogenesis is of the peculiar type which has already been shown to occur in *Matthiola*, the factors for singleness and doubleness being distributed differently among the ovules and the pollen grains.

8. The pollen of the singles is homogeneous as regards the *presence* of some factor essential to the manifestation of singleness.

9. With regard to the constitution of the ovules of the singles and the pollen of the doubles it may be said that the results obtained on crossing are such as would occur, if either the ovules were homogeneous and the pollen heterogeneous as regards the *absence* of some factor needed to produce singleness ; or if conversely the ovules were heterogeneous and the pollen homogeneous in respect of this factor. The fact that all the singles appeared capable of yielding doubles when crossed with the pollen of a double points strongly to the first alternative, but the impossibility of making reciprocal crosses renders direct proof difficult.

TABLE I.

*Showing the mixture of singles and doubles obtained in F_1, in the case
of the type forms, from the cross single ♀ × double ♂.*

Form of union		Reference number of family	Number of Offspring	
Single seed-parent	**Double** pollen-parent		Single	Double
V	H	1	82	67
,,	,,	2	54	35
,,	,,	3	19	4
N	H	4	28	21
,,	,,	5	13	12
,,	,,	6	10	9
,,	,,	7	14	4
,,	,,	8	4	2
,,	,,	9	1	4
,,	,,	10	1	2
H	H	11	18	6
,,	,,	12	4	3
,,	,,	13	5	3
,,	,,	14	12	2
,,	,,	15	6	4
,,	,,	16	4	—
,,	,,	17	24	22
,,	,,	18	8	2
CE	H	19	15	2
,,	,,	20	11	1
,,	,,	21	3	1
,,	,,	22	9	6
,,	,,	23	7	1
,,	,,	24	18	2
,,	,,	25	22	11
CE	H (var. *fimbriata*)	26	17	13
,,	,, ,,	27	18	13
,,	,, ,,	28	13	11

$V = violacea.$ $N = nyctaginiflora.$ $CE =$ Countess of Ellesmere. $H = hybrida$ *gran-diflora.*

TABLE II.

Showing a similar mixture of singles and doubles resulting from the union single ♀ × double ♂, where one or both of the individuals employed was descended from a previous cross.

Form of union		Reference number of family	Number of Offspring	
Single seed-parent	**Double** pollen-parent		Single	Double
V	(single *H · N*) × double *H*	29	13	8
,,	,,	30	6	4
,,	,,	31	4	4
(single *H × N*) × double *H*	double *H*	32	24	21
,,	,,	33	4	4
,,	,,	34	6	3
,,	,,	35	9	11
(single *H × N*) × Self	double *H*	36	53	35
(*N* × double *H*)	(*N* × double *H*)	37	34	17
,,	,,	38	16	14
(single *H × N*)	double *H*	39	17	7
,,	,,	40	14	9
,,	,,	41	12	3

The total number of individuals belonging to the type forms used as seed-parents in experiments 1—41 was as follows :

6 plants of *Violacea*
7 ,,   ,, *Nyctaginiflora*
5 ,,   ,, Countess of Ellesmere
5 ,,   ,, *Hybrida grandiflora*
———
Total 23

TABLE III.

Showing that doubles do not occur when singles belonging to the various type forms are self-fertilised or intercrossed.

Form of union		Reference number of family	Number of Offspring	
Single seed-parent	**Single** pollen-parent		Single	Double
V	self	42	13	—
,,	,,	43	6	—
,,	,,	44	6	—
,,	,,	45	3	—
N	self	46	47	—
,,	,,	47	2	—
H	self	48	18	—
,,	,,	49	3	—
CE	self	50	9	—
,,	,,	51	4	—
,,	,,	52	4	—
V	N	53	14	—
,,	,,	54	6	—
N	V	55	60	—
,,	,,	56	49	—
,,	,,	57	36	—
,,	,,	58	35	—
,,	,,	59	23	—
H	P	60	many (total not recorded)	—
H	N	61	143	—
,,	,,	62	41	—
,,	,,	63	36	- -
,,	,,	64	22	—
,,	,,	65	many (total not recorded)	—
,,	,,	66	,, ,, ,,	—
$(N \times V)$	$(N \times V)$	67	10	—
$(N \times V)$	self	68	16	—
,,	,,	69	10	—
,,	,,	70	4	—
,,	,,	71	3	—
,,	,,	72	2	—
,,	,,	73	2	—
,,	,,	74	2	—
(single $H \times N$)	self	75	33	—
,,	,,	76	24	—

TABLE IV.

Showing that doubles do not occur when the singles derived from a cross with a double are either self-fertilised, or crossed with other singles similarly derived.

Form of union		Reference number of family	Number of Offspring	
Single seed-parent	**Single** pollen-parent		Single	Double
(single *H* × double *H*)	self	77	73	—
,,	,,	78	8*	—
,,	,,	79	8	- -
,,	,,	80	5	—
,,	,,	81	3	- -
,,	,,	82	3	—
,,	,,	83	2	—
(*N* × double *H*)	self	84	64	.
,,	,,	85	14	- -
,,	,,	86	13	.
,,	,,	87	3	—
,,	,,	88	1	
(single *H* × *N*) × double *H*	self	89	8	—
,,	,,	90	2	—
(single *H* × double *H*)	(single *H* × double *H*)	91	33	—
,,	,,	92	14	—
,,	,,	93	11	—
(single *H* × *N*) × double *H*	(single *H* × *N*) × double *H*	94	3	—
(single *H* × *N*) × double *H*	*N* × double (*N* × *H* = a double)	95	9	—
,,	,,	96	7	—

* A double which occurred in this batch was evidently a rogue as the flower had some of the characters of *nyctaginiflora*.

EXPLANATION OF FIGURES.

I am indebted for the accompanying figures to Miss D. F. M. Pertz, to whom I here tender my best thanks.

Fig. 1.　Single flower seen split longitudinally.

Fig. 2.　Usual type of double flower showing extreme petalody, seen from above. The functional stamens are concealed by petaloid structures. (See next figure.)

Fig. 3.　Similar flower seen in longitudinal section.

Fig. 4.　Less common type of double flower. Stamens numerous, but supernumerary petaloid structures few and small. The corolla tube is curiously folded so as to form a kind of cup round the stamens. (See next figure.)

Fig. 5.　Same flower in longitudinal section. Between the lower region of the corolla tube which rises vertically, and the upper part which lies horizontally is seen the curious double bend which forms the cup-like structure surrounding the stamens. The ovary is aborted.

Fig. 6.　Group of stamens and a small supernumerary petaloid structure belonging to the same flower showing fusion for some distance above the point at which they become free from the corolla tube.

Fig. 7.　Two stamens showing prolongation of the connective.
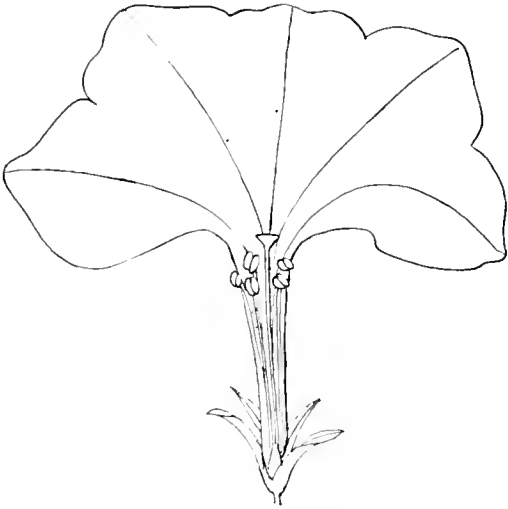
Fig. 1.
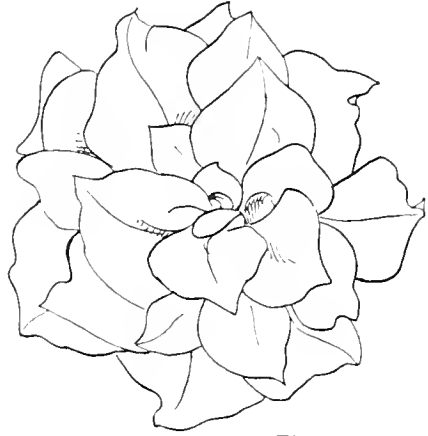
Fig. 2.
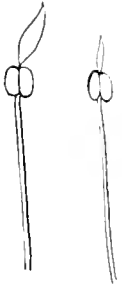
Fig. 7.
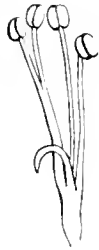
Fig. 6.
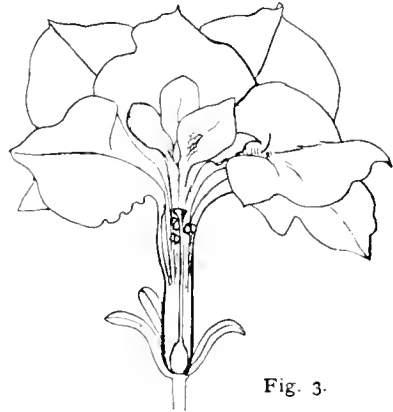
Fig. 3.
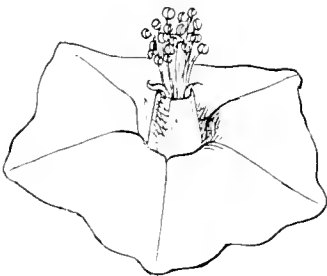
Fig. 4.
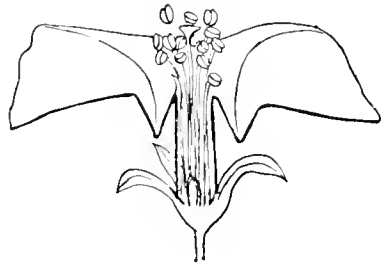
Fig. 5.

THE EFFECTS OF ONE-SIDED OVARIOTOMY ON THE SEX OF THE OFFSPRING.

By L. DONCASTER,

Fellow of King's College, Cambridge,

and F. H. A. MARSHALL,

Fellow of Christ's College, Cambridge.

(From the Physiology Laboratory, Cambridge.)

It is now widely believed that sex is determined not by conditions acting upon the organism after fertilisation, but by determinants or "factors" existing in the gametes themselves. Since this view came into prominence several hypotheses have been put forward, suggesting that gametes bearing the factor for one or the other sex are produced in separate gonads. Some have believed that in vertebrates one testis yields male-producing spermatozoa, the other female-producing, but this has been disproved in rats by Copeman[1]. It is also known to stock breeders that bulls from which one testicle has been removed, give calves of both sexes. Meanwhile evidence has been accumulated that in several groups of animals it is the egg rather than the spermatozoon which plays the more important part in sex-determination, and in accordance with this, the opinion has been held that one ovary produces female eggs, the other male eggs. That this is not a general rule is proved by the case of birds, which have only one ovary, and in Amphibia by the experiments of H. D. King[2], but in a recent book[3] Dr Rumley Dawson has maintained that this hypothesis is valid at least for man, and probably for other mammals. Direct evidence of a con-

[1] Experiments described at the Physiological Society, May 1908.

[2] *Biol. Bulletin,* xvi. p. 27, 1909.

[3] *The Causation of Sex,* London, 1909.

clusive kind is difficult to obtain in man, since even if children of both
sexes are born after single ovariotomy, it is rarely possible to prove that
the ovary has been completely removed. It therefore seemed worth
while to test the matter critically in some other mammal, and with that
object the experiments described below were made on rats.

Two female albino rats were taken, and in May 1910 the right ovary
with the greater part of the fallopian tube was removed from one of
them, and the same parts from the left side of the other. Both animals
rapidly recovered from the operation and on being put with a buck,
shortly became pregnant. The female from which the right ovary was
removed gave birth to seven young on July 8. The young all died soon
after birth, and one of them was almost entirely eaten by the mother.
The rest were preserved for examination, and it was found on dissection
that there were four females, one male, and one was too much decom-
posed before being preserved for its sex to be determined with certainty;
it appeared to be a female.

The rat from which the left ovary had been removed gave birth to
five young on July 28; one young died shortly after birth; it was dis-
sected when quite fresh and proved to be a male. The remainder lived
until August 22 when they were killed and dissected; there were three
females and one male, giving three females and two males in all. On
the same day the two rats which had been operated on were killed and
dissected. In neither could any trace of ovary or ovarian tissue be
found on the side from which the ovary had been removed. In that
from which the left ovary was taken out there was about $\frac{1}{4}$ inch of
fallopian tube, ending apparently blindly; in the other the right
fallopian tube had been cut off at its junction with the uterus. In each
case the uteri were normal. They were congested on both sides in the
rat lacking the right ovary, which was probably on heat at the time of
killing. In the female (left ovary removed) which had suckled its
young up to the time of killing all the mammae on both sides were
normal and functional. In both rats the remaining ovary was ex-
ceedingly large, and had doubtless undergone compensatory hypertrophy
in consequence of the removal of the ovary of the other side[1]. The
relatively large size of the litters (7 and 5) produced from one ovary
may be thus accounted for. That the litters were produced from one
ovary in each case is further shown by the fact that on microscopic
examination it was found that in the rat from which the right ovary was

---

[1] Cf. Carmichael and Marshall, *Journal of Physiology*, vol. xxxvi. p. 431.

removed the remaining (left) ovary contained at least seven corpora lutea, and the remaining (right) ovary of the second rat contained at least eight. These corpora lutea were all of similar age in each animal, and clearly distinguishable from the older luteal tissue present in the ovaries.

These facts seem to us to indicate without any doubt that in the rat it is not true that ova determining one sex are produced from one ovary, and those determining the opposite sex from the other, for each rat, with one ovary completely removed, produced young of both sexes. This does not of course prove that the " right and left ovary hypothesis" is not true for man, but its definite disproof for another mammal detracts from its probability. It should be pointed out however that the evidence for alternate male and female ovulations in man, collected by Dr Rumley Dawson and others, is not in any way affected. In our opinion the weakest part of his evidence is that dealing with the production of ova determining different sexes by the two ovaries, and it is not impossible that this hypothesis may be false, and yet that in general alternate ovulations may be of different sex, so making sex-prediction possible. It is very desirable that those who have extensive opportunities of testing this hypothesis—which involves knowing not only the date of birth and whether the child is " full time " in each case, but also whether the menstrual periods are normal and regular—should have the matter in mind and keep records whenever possible.

[*Note.* The operations described were performed by F. H. A. Marshall; the dissections by L. Doncaster.]

CONTENTS

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EXPERIMENTS WITH *PRIMULA SINENSIS*.

By R. P. GREGORY, M.A.,

Fellow of St John's College, Cambridge; University Lecturer in Botany.

CONTENTS.

INTRODUCTION.

THE experiments, of which the present paper is the outcome, were begun in 1903 by Mr Bateson and the present writer jointly, and in 1905 we published an account of our observations up to that time upon the inheritance of heterostylism[1]. Although I am alone responsible for the views put forward in the present paper, and for any errors which it may contain, the work with which it deals has been done in association with Mr Bateson, to whom much of such progress as has been made is due. Mr Bateson has given me the most generous help, not only in the elucidation of the results, but also in the practical business of carrying on the experiments. I am further indebted to him for giving house room to a large number of plants each year.

The plates illustrating the various coloured forms which have been met with in the course of the experiments are reproduced from the beautiful and accurate water-colour drawings of Miss M. Wheldale, of Newnham College, Cambridge.

I wish to take this opportunity of acknowledging again my indebtedness to Messrs Sutton and Sons, who have most kindly given assistance in many ways during the course of this enquiry.

My thanks are due also to the Botanic Garden Syndicate of Cambridge University, and to Mr R. I. Lynch, Curator of the Botanic Gardens, for the provision of housing, materials and labour.

The principal objects of our investigations in *Primula sinensis* have been the inheritance of heterostylism and of colour. At the same time records have been kept of certain other characters, the inheritance of which has been found to be, for the most part, of a simple type and does not require any special comment here[2].

Heterostylism[3]. The dearth of short-styled plants occurring in the families raised from the self-fertilized heterozygote, which was noticed in our earlier experiments, is still maintained even in the larger numbers now obtained. On the other hand the same plants, crossed by the long-styled, give an excess of short-styled offspring. Our results do not as yet give a decisive answer as to whether these divergences,

[1] Bateson and Gregory, *Roy. Soc. Proc.* B, Vol. 76, 1905, pp. 581—586.

[2] Some of these results have already been mentioned; see Bateson : "The progress of Genetics since the rediscovery of Mendel's papers," *Prog. Rei. Bot.*, Vol. I. 1907, pp. 373, 383; *Mendel's Principles of Heredity*, Camb. Univ. Press, 1909. Gregory: "The inheritance of certain characters in *Primula sinensis*," *Brit. Assoc. Rep.*, Leicester, 1907, pp. 691—693.

[3] Bateson and Gregory, *l.c.*

in opposite directions in the two cases, are to be regarded as merely accidental, or whether they may have some significance, either in connexion with observed differences in the fertility of the various unions between plants of different form, or in other ways (p. 83).

Colour. The colour of the stems and flowers in the coloured races is due to the presence of coloured sap. The colour may be absent from the flowers, which are then white, or from the stems, which are then green. Colour, both in flower and stem, is presumably produced, as in other cases, by the interaction of two or more complementary factors. I have had no decisive case of the production of an F_1 with coloured flowers from the mating of two albinos, but Keeble and Pellew[1] record a coloured F_1 from the mating of the red-stemmed "Snow King" with the green-stemmed "Snowdrift." Similarly as regards the stem-colours, I have no example of the production of a coloured F_1 from the mating of two green-stemmed plants, but in two cases (p. 97) heterozygous plants with coloured stems have given unmistakably the ratio 9 coloured : 7 green stem.

There exist several distinct types of coloration, both of the stem and of the flowers. Thus, the stem may be fully and evenly coloured (Plate XXX, figs. 1, 2), or it may possess only a faint colour, which is most easily recognized in the young leaves and leaf-stalks (Plate XXX, fig. 5). The faint colour is, in some cases, an elusive character, and the plants bearing it are only with difficulty to be distinguished from those devoid of colour in the stem. The inheritance of these two kinds of pigmentation of the stem may be explained most simply if we assume the existence of two separate and independent chromogen factors, each of which reacts with the common activator to produce, one the full colour, the other the faint colour (p. 96).

The colours of the flowers and stems are inter-related in such a way that the more deeply coloured flowers never occur in conjunction with stems wholly green. Flower-colours may then be divided into two classes, namely, *full* colours, which are found only on plants having fully coloured stems; and *pale* colours, which occur on plants having green or faintly coloured stems. *White* flowers may be associated with stems of any kind.

When the albino "Snowdrift" (Plate XXX, fig. 7) was crossed with types having fully coloured flowers and stems, the F_2 contained only one real albino to every fifteen pigmented forms. These coloured forms were of three kinds, (1) full colours on red stems, (2) a type known in

[1] *Journ. of Genetics*, Vol. I. 1910, p. 4.

horticulture as "Sirdar" (Plate XXX, fig. 4; Plate XXXI, figs. 44, 45), (3) pale colours on faintly coloured or green stems. The "Sirdars" have a peculiar distribution of the colour. The pigment of the petals is one of the full colours, but it occurs in separate minute dots and the edges of the petals are white. Associated with flowers of this kind, the stems have pigment at the bases of the petioles and pedicels, the rest of the stem and leaves being green. The inheritance of the "Sirdar" character may be described conveniently if the "Sirdars" be looked upon as belonging to the fully coloured series, while they lack a factor, the presence of which is required to bring about the even distribution of the colour which is found in the full colours. The full colours and "Sirdars" together constitute three-fourths of the total F_2 population. The remaining one-fourth consists of pale colours and whites in the ratio 3 : 1. The significance of the ratio 15 pigmented forms : 1 albino, and the relation of the pale colours to the full colours, is discussed in the text (pp. 103, 104).

The full colours are divisible into three classes, namely, (1) shades of magenta, (2) shades of red or crimson, (3) shades of blue.

The pale flower-colour is always a shade of pink, never magenta or red. This colour, in its deepest shade, is that of Sutton's "Reading Pink" (Plate XXX, fig. 13).

Full colours are dominant to pale colour; magentas are dominant to reds, and blue is recessive to all magentas and reds.

Whites may be dominant or recessive to colours.

Suppression of colour, partial or complete, by dominant factors is a common phenomenon in *Primula sinensis.* Some of these factors affect the colour of the flowers only, and one, at least, affects the colour of both flowers and stems.

When plants, which otherwise would have coloured flowers, are homozygous in the factors which suppress flower-colour, the flowers are quite white (dominant whites); when they are heterozygous in the inhibiting factors, the flowers are sometimes white, but are more often tinged with colour, the depth of the tinge varying with the races used and with the temperature of the house.

As regards the suppression of flower-colour, the evidence reveals a curious complication in that the operation of two inhibiting factors, affecting distinct areas, can be separately traced. Of these factors, one suppresses colour in the peripheral parts of the corolla, the other affects the gynoecium and central part of the corolla. In consequence it follows that in F_2 from fully coloured plants with *coloured* stigmas × dominant

whites, there appears the peculiar type known as "Duchess" (Plate XXXI, figs. 27, 28), in which the flower is white peripherally and has a coloured centre. The mating of "Duchess" with plants having coloured flowers and *green* stigmas, gives a tinged white F_1, exactly like that produced by the mating of coloured, red stigma × dominant white.

Various light shades of flower-colour behave as dominants to the deep shades; this dominance is due to the presence of factors which effect the partial suppression of the colour. These factors are quite distinct, as regards their inheritance, from those described in the preceding paragraph.

Similarly, the light shades of stem-colour are dominant to the deep shades. The suppression of stem-colour is only partial, even in plants homozygous for the suppressing factors, and no dominant green stems are known.

Flowers of a light shade may be borne by plants having deeply coloured stems, but the deep flower-colours never occur on stems not deeply coloured. It is clear, therefore, that the factor which effects the partial suppression of stem-colour exerts its action also upon the flower-colour.

Besides the varieties constituted by combinations of the factors already enumerated, there occur various types having flakes or patches of colour (Plate XXXI, figs. 56—59)[1]. As in other cases where such flaking has been encountered, the genetics of these varieties is not altogether clear, but in the case of *Primula sinensis*, as will be seen on reference to the text (p. 122), it is possible to frame a hypothesis which would give results consistent with those observed.

Gametic Coupling and Repulsion (p. 124). Complete repulsion between the factor for the structural character of short-style and the magenta colour-factor was observed in a series of experiments in which short-styled salmon-pinks were mated with various long-styled plants carrying the magenta factor.

The cases of partial gametic coupling which have been met with are interesting in that, in many of them, the two middle terms of the F_2 series are much larger, relatively to the end terms, than they are in the majority of cases previously recorded. In the case of the coupling between magenta colour and green stigma, the results of several experiments approximate closely to the expectation based on the hypothesis that a coupling of the form $7 : 1 : 1 : 7$ is present in the

---

[1] Flaked forms must be carefully distinguished from "Sirdars."

gametes of one sex only, those of the opposite sex consisting of equal numbers of the four kinds (p. 128). Other cases however are apparently not susceptible of complete explanation on these lines, and it seems possible that they may indicate the existence of lower forms of coupling than any given by the gametic series

$$n - 1 : 1 : 1 : n - 1.[1]$$

Further experiment however is needed before any definite opinion can be expressed upon this point.

The history of *P. sinensis*, since its introduction into England in 1820, has been given by Mr A. W. Sutton[2], and further notices by other writers have appeared from time to time[3]. It is interesting to notice that the earliest illustrations[4] of the species represent short-styled plants of the ordinary habit (not *stellata*) with palmate leaves, light red stems, and light magenta flowers—all dominant characters.

HETEROSTYLISM.

In an earlier report Mr Bateson and the writer showed that the inheritance of the characters of long and short style is of a simple Mendelian type, the short style being dominant[5].

All the short-styled plants originally obtained for the purpose of these experiments proved to be heterozygous, but from their progeny pure short-styled plants have now been obtained. Nine such plants

---

[1] Bateson, Saunders and Punnett, *Rep. Evol. Comm. Roy. Soc.* IV. 1908, p. 3. Lower series would be given by the general expression

$$n - x : x : x : n - x$$

where x is any odd number less than $\frac{n}{2}$. The expression may be made a general one, including all forms of partial repulsion as well as coupling, if x be taken as any number less than n. The F_2 series would then be given by the expression

$$3n^2 - x(2n - x) : x(2n - x) : x(2n - x) : (n - x)^2.$$

[2] *Journ. Roy. Hort. Soc.* Mar. 1891, XIII. p. 99.

[3] *Gard. Chron.* 1889, p. 115; *Ibid.* 1890, p. 564; *Ibid.* 1892, p. 12; *Ibid.* 1902, p. 269.

[4] *Bot. Reg.* 539, May 1, 1821, under the name *P. praenitens*, and Lindley's *Collectanea Botanica*, Tab. VII, 1821. The plants figured in the two works are clearly of very similar, if not identical, types. In Lindley's plate the drawings of the dissected flower apparently represent the short-styled form; the flowers shown on the plant have rather the appearance of long-styled flowers.

[5] Bateson and Gregory, *Roy. Soc. Proc.* B, Vol. 76, 1905, pp. 581—586.

have been used as parents: their offspring are shown in the following table:

Cross	Number of short-styled plants used	Short-styled	Long-styled
Pure short-styled × Self	8	252	0
Pure short-styled ♀ × Long-styled ♂ ...	5	290	0
Long-styled ♀ × Pure short-styled ♂ ...	4	247	0
Totals	—	789	0

Several thousand plants have been raised from crosses of (long-styled × long-styled), all the offspring being long-styled.

Heterozygous short-styled plants.

The results of crosses in which heterozygous short-styled plants were used are shown in the accompanying table (p. 80).

Although the results are in general harmony with simple expectation, yet the observed numbers diverge rather widely from the calculated ones[1]. The divergences are, moreover, in opposite directions according as the cross is of the type ($DR \times DR$) or of the type ($DR \times R$) and the reciprocal form. The heterozygous short-styled plants, self-fertilized, show a deficiency of short-styled offspring as compared with the expected ratio of 3 short : 1 long; the same plants, crossed either way with long-styled plants, give an excess of short-styled offspring. In the former case the divergence from the ratio 3 : 1 is more than twice as great as the probable error of a random sampling taken from a population mixed in that ratio; and an equally great divergence occurs in the results of the crosses ($DR \times R$) and ($R \times DR$) taken together[2].

---

[1] The results of two experiments, each of which would have the effect of slightly increasing the divergence, have been excluded from the totals given in the Table (p. 80). In each case a long-styled plant ♀ was crossed by a short-styled ♂; the ♂ parents were known to be heterozygous, but the offspring, 9 in the one case, 5 in the other, consisted of short-styled plants only. The cases are excluded owing to the possibility that the two short-styled plants were behaving in a manner similar to that of the abnormal case described on p. 84. One other very aberrant family has also been excluded, owing to the possibility of error. This family was produced from a mating (F_1 ♀ × long-styled ♂) and consisted of 27 short-styled and 9 long-styled plants (expected equality).

[2] The probable error for random sampling of N individuals of two kinds mixed in the proportion $p : q$ is given by the formula $p.e. = \cdot6745 \dfrac{\sqrt{Npq}}{(p+q)}$. The errors given in the table show the probable departures from the exact ratios 3 : 1 and 1 : 1 respectively for the numbers concerned. I am indebted to Mr A. B. Bruce, of the Cambridge University Department of Agriculture, for this formula.

Table showing the results of experiments with heterozygous short-styled plants.

	Short-styled × Self				Short-styled ♀ × Long-styled ♂				Long-styled ♀ × Short-styled ♂			
	Number of experiments	Short	Long	Expect.	Number of experiments	Short	Long	Expect.	Number of experiments	Short	Long	Expect.
Short-styled plants showing themselves to be heterozygous on crossing	7	158	59	3 : 1	8	92	79	1 : 1	11	114	98	1 : 1
F₁ short-styled plants from crosses of Short × Long	25	739	270	3 : 1	12	151	140	1 : 1	6	25	25	1 : 1
Totals … …	32	897	329	3 : 1	20	243	219	1 : 1	17	139	123	1 : 1
Calculated numbers	—	919·5±10·2	306·5±10·2	—	—	231·0±7·35	231·0±7·35	—	—	131·0±5·5	131·0±5·5	—

382 Short   382 Long

362·0±9·1   362·0±9·1

342 Short   342 Long

Table showing individual families raised from the cross $(DR \times DR)$.

Year	Number in family $= p$	Short	Long	Ratio $(x : 1)$	px	$d = (2 \cdot 91 - x$	d^2	pd^2
F_1-shorts × self								
1905	19	14	5	2·80 : 1	53·21	·11	·1210	2·299
	21	10	11	0·91 : 1	19·11	2·00	4·0000	82·000
	22	15	7	2·14 : 1	47·08	·77	·5929	13·044
	26	20	6	3·33 : 1	86·66	·42	·1764	4·586
	46	33	13	2·54 : 1	116·90	·37	·1369	6·298
	31	20	11	1·82 : 1	56·43	1·09	1·1881	36·831
	23	18	5	3·60 : 1	82·79	·69	·4761	10·950
	51	40	11	3·64 : 1	185·70	·73	·5329	27·178
	22	18	4	4·50 : 1	99·00	1·59	2·5281	55·618
	25	19	6	3·17 : 1	79·25	·26	·0676	1·690
	79	61	18	3·39 : 1	267·80	·48	·2304	18·202
	27	20	7	2·86 : 1	77·23	·05	·0025	·068
	106	76	30	2·53 : 1	268·18	·38	·1444	15·306
	11	6	5 ⎫					
	12	7	5 ⎬	1·25 : 1	33·75	1·66	2·7556	74·101
	4	2	2 ⎭					
1906	84	60	24	2·50 : 1	210·00	·41	·1661	13·952
	83	62	21	2·95 : 1	244·80	·04	·0016	·133
	17	14	3	4·67 : 1	79·38	1·76	3·0976	52·659
	22	15	7	2·14 : 1	47·08	·77	·5929	13·044
	114	81	33	2·45 : 1	279·40	·46	·2116	24·122
1908	61	47	14	3·36 : 1	204·90	·45	·2025	12·353
	24	18	6	3·00 : 1	72·00	·09	·0081	·194
	39	32	7	4·57 : 1	178·20	1·66	2·7556	107·468
	40	31	9	3·44 : 1	137·60	·53	·2809	11·236
Other heterozygous shorts × self								
1904	20	16	4	4·00 : 1	80·00	1·09	1·1881	23·762
	10	6	4 ⎫	3·00 : 1	105·00	·09	·0081	·162
	10	9	1 ⎭					
1905	17	12	5	2·40 : 1	40·80	·51	·2601	4·422
1906	48	32	16	2·00 : 1	96·00	·91	·8281	39·749
1907	68	51	17	3·00 : 1	204·00	·09	·0081	·551
1910	44	32	12	2·67 : 1	117·50	·24	·0576	2·534
Totals	1226	897	329	84·83 : 29	3569·75	—	—	654·816

Weighted mean ratio $= \dfrac{\Sigma px}{\Sigma p} : 1 = \dfrac{3569 \cdot 75}{1226} : 1 = 2 \cdot 91 : 1.$

Probable error of weighted mean ratio $= \cdot 6745 \sqrt{\dfrac{\Sigma pd^2}{\Sigma p \, (n-1)}}$

$$= \cdot 09.$$

Ratio $= 2 \cdot 91 \pm \cdot 09 : 1.$

Table showing individual families raised from the crosses
(DR × R) and (D × DR).

Year	Number in family $=p$	Short	Long	Ratio $(x:1)$	px	$d=(1{\cdot}23-x)$	d^2	pd^2
F_1 *Short × Long.*		*Short ♀*						
1905	8	3	5 ⎫					
	6	2	4 ⎬	·41 : 1	9·84	·82	·6724	16·1376
	10	2	8 ⎭					
	30	16	14	1·14 : 1	34·20	·09	·0081	·2430
	47	34	13	2·62 : 1	123·14	1·39	1·9321	90·9087
	18	10	8	1·25 : 1	22·50	·02	·0004	·0072
	33	15	18	·83 : 1	43·01	·40	·1600	5·2800
	20	8	12	·67 : 1	13·40	·56	·3136	6·2720
	21	13	8	1·62 : 1	34·02	·39	·1521	3·1941
	36	20	16	1·25 : 1	15·00	·02	·0004	·0144
	28	11	17	·65 : 1	18·20	·58	·3364	9·4192
	34	17	17	1·00 : 1	34·00	·23	·0529	1·7986
F_1 *Short × Long.*		*Short ♂*						
1905	11	4	7 ⎫					
	10	6	4 ⎬	·82 : 1	25·42	·41	·1681	5·2111
	10	4	6 ⎭					
	8	3	5 ⎫					
	7	5	2 ⎬	1·37 : 1	26·03	·14	·0196	·3724
	4	3	1 ⎭					
Other Heterozygous Shorts.		*Short ♂*						
1904	12	7	5 ⎫					
	5	2	3 ⎭	1·13 : 1	19·21	·10	·0100	·1700
	10	7	3 ⎫					
	14	7	7 ⎭	1·40 : 1	33·60	·17	·0289	·6936
1907	32	17	15	1·13 : 1	36·16	·10	·0100	·3200
	49	28	21	1·33 : 1	65·17	·10	·0100	·4900
1910	28	13	15	·87 : 1	24·36	·36	·1296	3·6288
	21	11	10	1·10 : 1	23·10	·13	·0169	·3549
Other Heterozygous Shorts.		*Short ♂*						
1904	32	17	15	1·13 : 1	36·16	·10	·0100	·3200
	1	1	0 ⎫					
	6	3	3 ⎬					
	9	5	4 ⎬	1·38 : 1	26·22	·15	·0225	·4275
	3	2	1 ⎭					
1905	20	9	11	·82 : 1	16·40	·41	·1681	3·3620
	24	12	12	1·00 : 1	24·00	·23	·0529	1·2696
	6	5	1 ⎫					
	15	6	9 ⎭	1·10 : 1	23·10	·13	·0169	·3549
1907	50	33	17	1·94 : 1	97·00	·71	·5041	25·2050
1910	46	21	25	·84 : 1	38·64	·39	·1521	6·9966
Totals	724	382	342	28·80 : 25	891·88	—	—	182·4512

$$\text{Weighted mean ratio} = \frac{\Sigma px}{\Sigma p} : 1 = \frac{891\cdot88}{724} : 1 = 1\cdot23 : 1.$$

$$\text{Probable error of weighted mean ratio} = \cdot6745 \sqrt{\frac{\Sigma pd^2}{\Sigma p\,(n-1)}}$$

$$= \cdot10.$$

$$\text{Ratio} = 1\cdot23 \pm \cdot10 : 1.$$

This would seem to imply the presence of some disturbing cause affecting the regular Mendelian distribution, but it is important to ascertain what reliance may be placed on the ratio determined from the sum of all the families taken together. If the total results be tested by the discordance of the results in the individual families which make up the total[1], it is found that, in the case of the $(DR \times DR)$ crosses the approach to the normal 3 : 1 ratio is close, the observed result being $2.91 \pm .09$: 1 (Table, p. 81). In the $(DR \times R)$ and $(R \times DR)$ crosses the observed result is $1.23 \pm .10$: 1 (Table, p. 82) the theoretical ratio for 724 plants being $1.0 \pm .01$: 1.

Examined in this way, the results obtained at present perhaps scarcely afford a clear indication as to whether the above noted divergences are to be regarded as merely accidental, or whether they may have some significance in regard to the observed differences in the relative fertilities of the various kinds of legitimate and illegitimate unions.

Any significance, which the foregoing results may have in this connexion, lies in the possibility that the observed differences in the fertility of the legitimate and illegitimate unions[2] may be, in part, due to differences in the fertility of the various kinds of *gametic* unions, or rather (since the results of the matings $(DR \times R)$ and $(R \times DR)$ are in substantial agreement) to differences in the mortality of the three kinds of zygotes arising from these unions.

All the experiments on relative fertility are in agreement in showing that the union (short-styled plant × short-styled plant) is distinctly the least fertile, while the legitimate unions are the most fertile. Assuming that all forms of gametic union are equally fertile, the cross $(DR \times DR)$ would give offspring in the proportion 1 DD : 2 DR : 1 RR while the cross $(DR \times R)$ would give 1 DR : 1 RR. But if there are differences in the fertility of the various kinds of gametic union, the observed deficiency of short-styled offspring in the cross $(DR \times DR)$ might be due to the small number of *pure* short-styled plants which are produced, while the excess of short-styled offspring in the cross $(DR \times R)$ might be due to greater fertility of the union $(D \times R)$ as compared with that of the union $(R \times R)$.

[1] I am greatly indebted to Mr F. J. M. Stratton, of Gonville and Caius College, Cambridge, for this method of examining the results.

[2] See Darwin, *Forms of Flowers*, pp. 38—43, 246. Darwin found that the ratio of the fertility of the two legitimate unions taken together to that of the two illegitimate unions was 100 : 53. With this ratio that given by my experiments agrees very closely, but the fertility of the long-styled form, whether fertilized by its own or by the other form of pollen, is greater in the case of my plants than that observed by Darwin. The figures are

	Long × Short	Short × Long	Long × Long	Short × Short
Average number of seeds per capsule	33	25	21	11

It is to be presumed that the short-styled plants used by Darwin and Hildebrand included, like mine, heterozygous as well as pure individuals.

If we assume for the moment that the observed divergences from the simple Mendelian ratios are due to differences of this kind, then, if θ_1, θ_2, θ_3 represent respectively the fertilities of the gametic unions Short × Long, Long × Long, and Short × Short, the results described above would give

$$\theta_1 : \theta_2 : \theta_3 = 100 : 89 : 44.$$

These figures are quantitatively in general agreement with the relative fertilities, as determined by the average number of seeds per capsule, of the various kinds of union between plants of different form, the corresponding figures being 132 or 100 : 84 : 44 (see p. 83, footnote). The comparison must not be pressed too far, since the actual fertilities of the various unions, observed in any set of experiments, would depend in part upon racial characters. The agreement is however rather suggestive and, taken in conjunction with the results of our examination of the observed numbers by other methods, is sufficient to justify further investigation.

The point can be tested experimentally by determining the constitution of all the short-styled plants in a number of large F_2 families; we should then find whether there is any significant divergence from the theoretical proportion of 1 pure : 2 heterozygous short-styled offspring.

Abnormal Cases.

A case was described in the previous report[1] in which the entire series of crosses made with a certain short-styled plant (No. 6/3) showed a definite and consistent departure from the normal expectation. The evidence already given showed that No. 6/3 behaved as an ordinary heterozygous short-styled plant when used as the female parent in crosses with long-styled plants, while its male gametes almost exclusively bore the dominant character[2]. The case promised to be of some interest, but unfortunately all the plants used as parents for succeeding generations proved to be normal pure short-styled plants, giving short-styled offspring only, when selfed and crossed either way with long-styled plants. No further elucidation of the case is therefore possible. The F_2's from crosses of this race with long-styled plants showed normal distribution of shorts and longs in the offspring, and are included in the F_2 table given on p. 80. The results of all the crosses in which this particular race was used are recorded in the tables given on pp. 85, 86.

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[1] Bateson and Gregory, *loc. cit.* p. 584.

[2] By an unfortunate error the statement made in the first paragraph on p. 585 of the previous report is inverted. The context makes it clear that the statement should have read: "the *ovules* of No. 6 gave a mixture of longs and shorts, and consequently were of two kinds, while all the plants raised from it as *male* were shorts."

Table showing the results of crosses made with No. 6/3 and its progeny in direct descent.

Short-styled parent	× Self			Short-styled ♀ · Long-styled ♂			Long-styled ♀ × Short-styled ♂		
	Number of family	Short-styled	Long-styled	Number of family	Short-styled	Long-styled	Number of family	Short-styled	Long-styled
6/3	37/4	4	0	39/4	4	2	24/4	3	0
				40/4	6	1	35/4	4	0
				43/4	3	0	72/4	7	0
				45/4	4	2	74/4	1	0
					17	5		15	0
37/4	126/5	22	0	127/5	3	3	80/5	14	0
				128/5	11	21	87/5	10	0
							104/5	17	0
							143/5	9	1
							149/5	8	0
							177/5	14	0
							183/5	14	1*
							205/5	46	2
							213/5	17	0
					14	24		149	4 (?3)
126/5	21/6	27	0	[126/5 was not used for crosses of this type			[126/5 was used as ♂ parent in one cross, which gave no seeds]		
21¹/6	24/7	25	0	27/7	27	0	2/7	12	0
				28/7	33	0			
					60	0			
21²/6	25/7	41	0	[21²/6 was not used for crosses of this type]			3/7	2	0
							58/7	18	0
								20	0
21³/6	26/7	54	0	29/7	23	0	4/7	54	0
				31/7	43	0	57/7	68	0
				32/7	33	0			
					99	0		122	0

* Recorded as "doubtful."

Table showing the constitution of the F₂'s raised from crosses in which 6/3 and its progeny were used.

'F₁ Short-styled plant	F_1 Short-styled × Self (DR × DR)			F_1 Short-styled ♀ × Long-styled ♂ (DR × R)			Long-styled ♀ × F_1 Short-styled ♂ (R × DR)		
	Number of F_2 family	Short-styled	Long-styled	Number of F_2 family	Short-styled	Long-styled	Number of F_2 family	Short-styled	Long-styled
24¹/4	98/5	15	7						
35¹/4	124/5	10	11	125/5	3	5			
40²/4	132/5	33	13						
43¹/4	133/5	20	6	{134/5	2	8	{ 96/5	4	7
				{135/5	2	4	{ 112/5	6	4
							{ 146/5	1	6
45¹/4	136/5	20	11	{137/5	16	14			
				{138/5	10	8			
45²/4	139/5	18	5						
65²/4*	174/5	11	5						
72¹/4	201/5	40	11	{202/5	15	18	182/5	3	5
				{203/5	34	13			
128¹/5	22/6	62	21						
143¹/5	24/6†	60	24						
4¹/7	7/8	32	7						
27¹/7	20/8	47	14						
28¹/7	21/8	18	6						
58¹/7	28/8	31	9						
	Totals	420	150		82	70		17	22

* The origin of the F_1 plants is shown in the preceding table. 65²/4 was a short-styled plant raised from the double pollination (see Bateson and Gregory, *l.c.* p. 585) of a long-styled ♀ × self and 6/3.

† Two plants from this family were bred from and gave respectively :

	× Self		24¹/6 ♀ · Long-styled ♂		Long-styled ♀ · 24¹/6 ♂	
	Short	Long	Short	Long	Short	Long
21¹/6	61	0	38	0	58	0
24²/6	76	21	—	—	—	—

LEAF-SHAPE.

There is a considerable range of variation in the form of the leaf in *Primula sinensis*. Besides the common palmate and fern-leaf varieties, Messrs Sutton have raised a strain in which the peculiar lobing of the leaf is repeated in the petals, which also somewhat resemble the leaf in form[1]. Of other types, the Ivy-leaf is described below; while I have

[1] *Roy. Hort. Soc. Journ.* Vol. xxxv. Pt. 1. 1909, p. xxxvi. The leaves of this variety are described as approaching those of Ivy ; it may be well, therefore, to point out that the character is a different one from that of the strain to which I have applied the name of " Ivy-leaf " in this paper.

this year obtained a plant which possesses very deeply palmatifid leaves. In addition to these variations, which affect the general aspect of the leaf, there also occur less noticeable ones; as an illustration the case may be cited of a plant, which occurred in an F_2 family this year, the leaves of which had serrate, instead of the usual crenate, margins.

Palmate and Fern-leaf[1].

The palmate character is dominant, though a slight difference can sometimes be recognized between the pure and heterozygous palmate types. The shape of the leaf has been recorded in 27 F_2 families raised from crosses between palm- and fern-leaf, the numbers obtained being 1370 palmate, 457 fern-leaf (*expectation: 1370·25 : 456·75*).

Ivy-leaf.

In 1907 Mr A. W. Hill kindly gave me a monstrous plant (Plate XXX, fig. 5) which occurred among a batch of seedlings raised by him from seed obtained from a nurseryman. The leaves are palmate, but the margins are not crenate, as they are in the ordinary form of leaf. This peculiarity of the leaves is always accompanied by abnormal development of the flowers, which are very much reduced. The abnormality is much more marked in the early flowers than in the later ones, and if the plants be grown as biennials or perennials it is generally possible to obtain good seed from such as survive. A seedling raised from the original plant is shown in Plate XXXII, fig. 60. It will be seen that the early leaves (the lower ones in the photograph) have more divided edges than the later ones, and bear a closer resemblance to the leaves of the ordinary palmate form.

The absence of crenation of the leaf margin behaves as a recessive character. The F_1 from the cross with the ordinary palmate form is a normal palmate plant. The F_2's raised from ($F_1 \times$ self) have given 703 palmate, 241 Ivy (*expectation: 708·0 : 236·0*). Crossed with the ordinary fern-leaf, the Ivy-leaf gives again a normal *palmate* plant (Plate XXXII, fig. 61). This F_1, selfed, gives an F_2 (Plate XXXII, fig. 61, the bottom row of plants) consisting of normal palmates, normal fern-leaves,

[1] Bateson: "The progress of Genetics since the rediscovery of Mendel's papers," *Prog. Rei. Bot.*, Bd. 1, 1907, p. 373; *Mendel's Principles of Heredity*, Camb. Univ. Press, 1909, p. 24.

palmate ivy-leaves and fern ivy-leaves, the numbers obtained at present being

	Palm.	Fern.	Palm-Ivy.	Fern-Ivy.
	173	50	46	21
Expectation :	163·1	54·4	54·4	18·1

It is clear therefore that we are dealing with two independent characters, namely, (1) the shape of the leaf and (2) the crenation of the margin; and it is the absence of the latter character which is accompanied by the abnormality of the flower structures which is characteristic of the Ivy-leaved variety.

Considering the character of crenation only, the crosses have given 922 crenate, 312 non-crenate (*expectation : 925·5 : 308·5*).

Habit.

The hybrid between the typical *P. sinensis* and the "*stellata*" variety is the well-known "*pyramidalis*" form[1].

The principal characters in which the parent types differ from one another are:

Sinensis.	*Stellata.*
(1) Inflorescence compact.	Early elongation of the main axis above the primary umbel, with production of secondary and tertiary umbels.
(2) Shorter pedicels.	Long pedicels.
(3) Calyx cylindrical, with numerous teeth; more or less enclosing the unfolded corolla.	Calyx tube narrowing at the top and shorter, so that the corolla protrudes before beginning to unfold; calyx teeth = the number of the petals (5).
(4) Corolla lobes imbricate, crenate.	Corolla lobes scarcely, if at all, overlapping; heart-shaped.

The hybrid is intermediate between the two parents; in respect of the characters of the inflorescence it approaches more nearly to the *stellata* form ; the calyx has 10—15 teeth ; the degree of crenation of the margins of the petals is somewhat variable, but generally well marked.

From the study of a plant (No. 54/9, see Plate XXXII, fig. 64) which Messrs Sutton kindly gave me last year, it is clear that a plant, although capable of producing offspring nearly resembling the *sinensis* type, may itself approach somewhat nearly to the *stellata* form.

A series of flowers taken from the plant in question is shown in Plate XXXII, fig. 64. There is some range of variation in the corollas of individual flowers, some of which are scarcely crenate at all ; the plant also resembled the *stellata* form in its elongated axis and long pedicels.

The plant, when selfed, gave 21 offspring, of which 2 were true *stellata*, 12 were clearly intermediate, 7 approached *sinensis*, but of these seven 3 showed a strong

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[1] Bateson, *Mendel's Principles of Heredity*, Camb. Univ. Press, 1909, pp. 26 and 68.

tendency to the development of high spires of flowers, and the corollas protruded from the calyx in the young bud.

A detailed study of the various characters of these offspring suggests that we are not yet justified in regarding the differences between the *sinensis* and *stellata* types as depending upon one factor. If it should prove that the characters of the axis, of the calyx and of the corolla may be inherited independently, the character designated here as *stellata* must be taken to refer to the form of the corolla.

The *stellata* form used in the great majority of my experiments was a strain known as "Primrose Queen" (Plate XXX, fig. 12, and Plate XXXII, figs. 62 and 63, No. 37/9). The F_2, resulting from the cross of this with a plant of the typical *sinensis* habit, consists of *sinensis, pyramidalis* and *stellata* forms. The original "Ivy-leaf" plant also proved to be a *stellata* form. When this plant is used, Ivy-leaves of course appear in the F_2, in addition to the forms already mentioned. The F_2 Ivy-leaves are presumably of different forms, corresponding with the forms met with in the normally developed plants, but, owing to the poor development of the flowers and inflorescence, it is impossible to say more than that, in some, the petals were more or less crenate.

It is not easy to draw a sharp line of distinction between the *pyramidalis* forms and the true *sinensis* type; in the following table they are therefore grouped together.

The numbers obtained are

		$F_1 \times$ Self				$F_1 \times$ Stellata.	
	Number of F_2 families	Sinensis and inter-mediate	Stellata	Ivy	Number of F_2 families	Sinensis and inter-mediate	Stellata
	19	1030	342	—	3	40	35
Expectation ...	—	*1029·0*	*343*	—	—	*37·5*	*37·5*
Crosses in which Ivy-leaf was used	2	151	67	71	—	—	—
Total ...	21	1181	409	—	—	—	—
Expectation ...	—	*1192·5*	*397·5*	—	—	—	—

DOUBLE FLOWERS.

Two types of doubling of the flowers in *Primula sinensis* are known to me, in both cases in long-styled plants, though experiments are in progress which, it is hoped, will give short-styled doubles[1].

[1] Short-styled doubles of the type shown in Text-fig. A, have now (Feb. 1911) been obtained, in the F_2 from short-style, single × long-style, double. So far as the morphology of the corolla is concerned, the short and long-styled doubles very closely resemble one another; they differ of course in the size of the pollen grains and in the length of the style.

In the more common double (Text-fig. A), the supernumerary segments are inserted at the throat of the tube, one segment occurring opposite each petal. The anthers are somewhat exsert, and are attached just at the base of the supernumerary segment; the position of the anthers might easily lead one to suppose that the flower was "thrum-eyed," were it not for the long style and the size of the pollen. The supernumerary segments are *reversed*; that is to say, the external side resembles the upper (internal) surface of the normal petal, while the internal side is like the back of the latter[1].

A   B
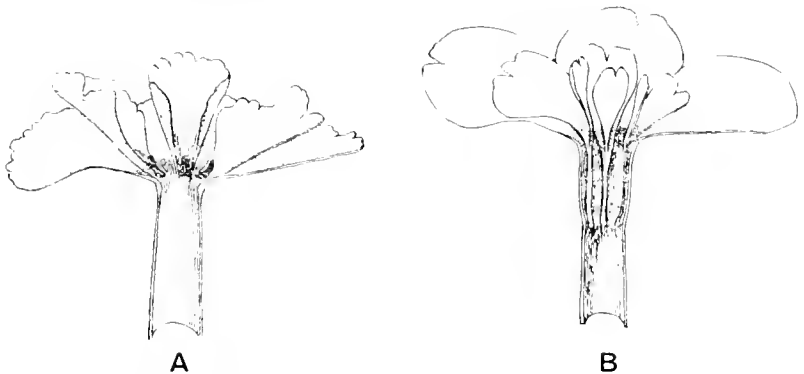
In the old-fashioned double (Text-fig. B) the doubling is more complete than in the more usual form, and a number of supernumerary segments occupy the centre of the flower[2]. The supernumerary segments are of different orders: the primary segments are inserted, one opposite each petal, on the corolla tube at the constriction which, in the normal type, would mark the position of the stamens. These primary segments are *not* reversed, but they bear secondary supernumerary segments which show the reversal[3]. The latter are attached to the primary segments at, or rather below, the region corresponding with the throat. Our plants of this type are of a pale pink so that the reversal of the colouring is not so conspicuous as in the full coloured races of the ordinary double, but it shows clearly in that the yellow "eye" at their base is on the external side, while the internal side resembles the outside of the primary segments and of the ordinary petal. The plants bear no stamens at all and the female organs are generally represented by

[1] Cf. Masters, *Vegetable Teratology*, 1869, p. 449.

[2] Cf. Masters, *loc. cit.* p. 315.

[3] In both kinds of doubles the morphology of the reversed segments is obscure, and it is not clear that these structures are of the same nature in the two cases.

a group of foliar carpels[1], surrounding an axis on which are borne naked ovules. Proliferation of the axis is frequent. Hitherto I have not been able to raise any seed from these plants, but some cuttings, taken late in the season and only coming into flower in May last, have developed what appear to be normal ovaries, and it is hoped that experiments will be possible in the future.

Inheritance of ordinary double.

The ordinary form of doubleness is a recessive character[2]. When crossed with singles, it gives a single F_1, which on self-fertilization gives singles and doubles in the proportion of 3 : 1. The actual numbers obtained in 15 families are 762 singles, 284 doubles (*expectation: 784·5 : 261·5*)[3].

The double race used in all the foregoing experiments had its origin in a white single obtained from a nurseryman in 1903. The plant proved to be heterozygous, throwing singles and doubles. Every degree of doubleness was exhibited among the various individuals of this race, and the phenomenon was repeated in some of our F_2's. On the other hand, certain plants, derived from the same strain, produced nothing but full doubles, and in the F_2's from their crosses with singles, the distinction between the singles and the doubles was quite sharp, all the latter being fully double.

CHARACTERS OF THE "EYE" OF THE FLOWER.

In the majority of horticultural strains the yellow or yellowish-green "eye" of the flower occupies a small and well-defined area round the mouth of the corolla tube. Besides this type of eye there exist two other kinds; in the first, the eye occupies a much larger area, the yellow colour extending well over the bases of the corolla lobes ("Primrose Queen," Plate XXX, fig. 12 and Plate XXXII, figs. 62 and 63, No. 37/9); the second type is represented by the white-flowered race "Queen Alexandra," in which the eye is not distinguished from the rest of the corolla, the whole flower being uniformly white (Plate XXX, fig. 11 and Plate XXXII, fig. 62, No. 34/9).

Eye-characters are inherited quite independently of any of the other characters which I have studied, but they affect certain other characters with which they may occur in combination in the same

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[1] Cf. Masters, *loc. cit.* pp. 262, 297.

[2] Bateson, *Mendel's Principles of Heredity*, Camb. Univ. Press, 1910, p. 199.

[3] The discrepancy is almost entirely due to one F_2 family which consisted of 66 singles and 45 doubles. Five other F_2's from the same parents however gave 188 singles, 61 doubles.

individual. The effect of the large yellow eye in giving rise, in the absence of the factor for short-style, to the "homostyled" form has been fully described on previous occasions[1]. Both the large yellow eye and the white eye have effects when combined with certain colour characters of the flower. Certain coloured forms possess a blotch of deep colour, which in flowers with the ordinary eye occupies a well-defined area at the base of the corolla lobes (Plate XXXI, figs. 50, 51). If this character be combined with the large yellow eye, the deep colour is, so to speak, pushed further outwards, and forms a rather ill-defined band round the periphery of the area occupied by the pigment of the eye[2]. But, so far as my observations go, when "Queen Alexandra" is crossed with the same coloured race, the blotch of deep colour is not developed in the F_2 plants which have the white eye, though the corresponding forms with the ordinary eye are blotched.

(1)   Large yellow eye × small eye.

The accompanying table (p. 93) shows the results, inclusive of those previously published[3], which have been obtained from crosses of the "homostyled" plants with both short- and long-styled plants having the ordinary eye. The crosses in which the F_2 plant was selfed show a considerable deficiency of large-eyed offspring, and in those cases in which the small-eyed parent was short-styled, the deficiency is almost confined to the short-styled offspring. The crosses of the form $(DR \times R)$ have given results which, in the aggregate, do not differ appreciably from expectation, though again, in those cases where we are also concerned with short and long style, the distribution of the offspring among the four types is not very smooth[4], and is particularly irregular in one aberrant family (given separately in the table) where the excess of short-styled offspring with the small eye is very marked.

It is only in the early years, however, that any great discrepancy manifests itself. Very few crosses have been made with short-styled parents since 1906; but experiments with long-styled plants have been

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[1]   Bateson and Gregory, *loc. cit.* pp. 582—584.

[2]   For illustration of flowers of this kind see Bateson, *Mendel's Principles of Heredity.* Camb. Univ. Press, 1910, Plate VI. figs. 19, 21.

[3]   Bateson and Gregory, *loc. cit.* p. 584.

[4]   In this connexion it must be borne in mind that in the crosses between short and long style there is throughout a deficiency of short-styled offspring when the F_1 is selfed, and an excess when the F_1 is crossed with the long-styled. This would, of course, have a disturbing effect in cases such as that under notice.

Table showing the constitution of the F₂ families raised from crosses between small eye and large eye.

Short-styled, small eye × Long-styled, large eye (homostyle)

Year	Number of F₂ families	Short, small eye	Long, small eye	Short, large eye	Long, large eye	Number of F₂ families	Short, small eye	Long, small eye	Short, large eye	Long, large eye
	F₁ × Self					*F₁ × Long large eye*				
1905	5	147	44	35	21	{4 / 1}	39 / 20	27 / 5	32 / 7	20 / 4
1906	1	62	26	14	4	—	—	—	—	—
1907	—	—	—	—	—	—	—	—	—	—
1908	1	26	9	5	0	—	—	—	—	—
1910	—	—	—	—	—	—	—	—	—	—
Totals	7	235	79	54	25	5	59	32	39	24
Expect	—	221·0	73·7	73·7	24·6	—	38·5	38·5	38·5	38·5

Long-styled, small eye × Long-styled, large eye (homostyle)

	Number of F₂ families	Small eye	Large eye	Number of F₂ families	Small eye	Large eye
	F₁ × Self			*F₁ × Long large eye*		
1905	6	183	51	9	93	107
1906	6	243	66	2	15	18
1907	4	525	168	—	—	—
1908	1	66	21	—	—	—
1910	6	381	137	—	—	—
Totals	23	1308	443	11	108	125
Expect	—	1380·75	460·25	—	116·5	116·5

The above figures combined give

F₁ × Self

	Number of F₂ families	Small eye	Large eye
	30	1712	522
Expectation ...	—	1675·5	558·5

F₁ × Long, large eye

	Number of F₂ families	Small eye	Large eye
	16	197	188
	—	192·5	192·5

continued, and the totals for the last three years are 972 small-eyed, 326 large-eyed (*expectation: 973·5 : 324·5*). It is therefore impossible to attach any great importance to the discrepancy in the early years, though at the same time it remains unexplained.

(2) White eye × small yellow eye.

The white-eyed race ("Queen Alexandra") is a recent addition to my collection and only a few F_2 families have been raised from crosses in which it takes part.

The heterozygote resulting from the cross with a small-eyed race can be distinguished, on close examination, from the pure "Queen Alexandra" by a faint appearance of yellow or yellowish-green, which is most pronounced on the rays corresponding with the median line of each petal (Plate XXXII, fig. 62, No. 35/9)[1]. Three F_2 families have been raised from the self-fertilized hybrid, and have given 182 white eye and heterozygous, 67 small yellow eye (*expectation: 186·75 : 62·25*).

(3) White eye × large yellow eye.

The heterozygote resulting from this cross is not distinguishable to the eye from that of the preceding case (Plate XXXII, fig. 62, No. 36/9). The one F_2 family raised from the hybrid by self-fertilization has given 52 white eye and heterozygous, 12 large yellow eye (*expectation: 48 : 16*). An attempt to separate the pure from the heterozygous white-eyed offspring gave 19 with no trace of colour in the eye, 33 with faint yellow rays.

COLOUR.

The various forms of red stem, and the colours of the flowers, are due to the presence of coloured sap. Both in the stem and in the flower the simple colour may be modified by the action of numerous factors which affect its distribution, intensity and tint. There is a close relation between the colour of the flower and that of the stem, in that fully coloured flowers are only produced by plants having fully coloured stems. The deepest colour in the flowers of a green-stemmed plant is that exhibited by the pale pink strain known as "Reading Pink" (Plate XXX, fig. 13), while the white-edged type exemplified in "Sirdar" is characteristic of plants in which the stem-colour is restricted to the

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[1] The contrast between the yellow rays and the white ground is somewhat intensified in photographic reproduction.

collar and bases of the petioles (Plate XXX, fig. 4; Plate XXXI, figs. 44, 45). The degree to which colour is developed in the stem may therefore be taken as an index of the limits within which the colour of the flowers will be confined. All the red-stemmed whites which I have examined were found to be white in virtue of factors which inhibit the development of colour in the flower, though their range of action does not extend to the stem[1].

A. Stem-Colours.

Various types of coloured stems are illustrated in Plate XXX. The plants shown in figs. 1, 2, 4 and 5 all possess, in varying degrees, the common purplish-red sap. Sap of this colour is present in the stems of all the races which have the usual magenta or red flowers, and though there are, no doubt, minor differences in the tint in different races, it is scarcely possible in practice to make any distinction between forms which differ in so slight a degree. There are, however, two kinds of flower-colour which are associated with distinctive stem-colours; in the races which have blue flowers the stem has a corresponding colour, as compared with that of the commoner purplish-red types; while the clean red stem, shown in fig. 3, is, so far as my observations go, limited, in the fully coloured form, to the strain known as "Orange King" (fig. 8).

In coloured stems the red sap may be distributed over the whole of the stems and petioles (Plate XXX, figs. 1 and 2), or it may be developed only in certain regions, the other parts being green. Fig. 4 shows a form in which the colour occurs only in the collar and bases of the leaf and flower stalks; in plants with coloured flowers this type of stem is always associated with a peculiar distribution of the flower-colour which is characteristic of the strain known as "Sirdar" (Plate XXXI, figs. 44, 45). In fig. 5 there is represented a lower type of stem-colour, in which the colour is most pronounced in the young petioles. It is often only faint, and is sometimes scarcely discernible in the older leaf stalks, so that the character is somewhat elusive. It is dominant to the complete absence of sap-colour exhibited by "Snowdrift" (fig. 7), but the discrimination between the various types in F_2 is difficult, the more so since "Snowdrift" brings in a factor which reduces the apparent colour to a minimum.

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[1] Keeble and Pellew record the existence of a recessive white on red stem (*Journ. Genetics*, Vol. i. 1910, p. 1).

In the foregoing types the colour extends into the root-stock and roots, and in the faintly coloured forms its presence is much more easily detected there than in the stem, where the colour of the sap is masked by the green colour of the chlorophyll.

The plant represented in fig. 6 is the "Ivy-leaf." In this form the colour can be recognized most readily in the young petioles, and it also appears, though more faintly, in the pedicels. In older leaves the colour may be noticed at the base and sometimes along the edges of the leaf-stalk. It does not appear to extend to the root-stock and roots.

Outline of the inheritance of stem-colour.

In its general outlines, the inheritance of stem-colour is simple. Thus, the red-stem crossed with a green-stem gives an F_2 in which the red-stemmed offspring are either approximately 9 in 16, or 3 in 4, according to the constitution of the green-stemmed parent. The full colour crossed with the faint colour (fig. 5) gives, in F_2, 3 of the former to 1 of the latter, and similarly the faint colour behaves as a simple dominant to the complete absence of colour.

Although the character of the stem in "Sirdar" is, in its lighter shades, not very different in appearance from that of other faintly coloured types, the inheritance of stem-colour can be most simply explained if the "Sirdars," which appear in certain F_2's, are regarded as forming a part of the fully coloured population, lacking, however, in the factor (F) which effects the even distribution of the colour in the stems and flowers. We have then a factor (R) for colour, and epistatic to R, and without effect in its absence, a distributing factor F^1. In order to provide for the existence of the forms with some faint colour in the petioles we require to assume the existence of another factor (Q) determining this character, which is independent of R and F and is unaffected by them, except in so far as the faint colour is not discernible when R and F are present.

In crosses between plants with the lower grade of stem-colour and those without colour, the last factor (Q) only comes into play, and the 3 : 1 ratio is obtained in F_2 (Table, p. 98, II.). Since "Sirdars" have only occurred in my experiments in cases in which "Snowdrift" was

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[1] The use of a so-called distributing factor is intended merely as providing a simple means of formulating the observed results. The relation which subsists between the "Sirdar" types and the self-colours is probably different from that which obtains between flakes and self-colours (p. 122).

used, we are justified in assuming that all the other races which have been used possess the factor F; consequently, crosses between the full-coloured stem and the faint colour merely exhibit the segregation of the factor R, the effect of Q, which is present in all the offspring, being masked when R is also present (Table, p. 98, III.). The same applies to the crosses between the full colour and the green stem, but in this case one-third of the offspring have clean green stems (Table, p. 99, IV.).

In the F_2's from crosses between "Snowdrift" and races with fully coloured stems "Sirdars" occur; and if the factors inhibiting flower-colour be absent, the F_2 is found to contain approximately, in every 16 plants, 9 with fully coloured stems and flowers, and 3 "Sirdars"; while of the remaining 4, 3 may have faint colour in the petioles, or they may all be devoid of colour in the stem, according to the presence or absence of the factor for faint colour in the coloured parent. The total numbers obtained in these crosses (Table, p. 99, V. C) show some divergence from the expectation set forth above, in giving an excess of "Sirdars." The divergence is however almost entirely due to the results obtained from the first two families raised, which gave 142 full, 75 "Sirdar" and 67 faint and green. In the later experiments a close approximation to the theoretical proportions has been maintained, the numbers obtained being 329 full, 110 "Sirdar," 134 faint and green. In crosses between "Snowdrift" and red-stemmed dominant whites, the "Sirdar" character cannot be determined with any accuracy in those offspring which have white flowers. In these F_2's the observed numbers of full-coloured stems and light stems (including "Sirdars") approximates very closely to the expected ratio of 9 : 7 (Table, p. 99, V. B).

There remain however cases in which the 9 : 7 ratio is clearly indicated in F_2's from which "Sirdars" are absent (Table, p. 98, I.). Only two such cases have been met with, but the result strongly suggests that, in *Primula*, as elsewhere, at least two complementary factors are necessary for the production of colour. In one of the cases, the character of faint stem-colour was not recorded separately, and we only know that the family consisted of 51 fully coloured and 33 light or green stems. In the other case, the coloured parent was a dominant white, and the offspring consisted of 49 fully coloured, 13 with colour in the petioles, and 25 devoid of colour, or 49 fully coloured, 38 light stems $(9 : 7 = 48 \cdot 94 : 38 \cdot 06)$. In so far as reliance can be placed upon the distinction between plants with faint colour in the petioles and those devoid of colour, this result further suggests that one comple-

mentary factor (C) is common both to the factor for full colour (R) and to that for faint colour (Q), so that the combination CR gives full colour[1], and the combination CQ gives faint colour in the collar. The constitution of the hybrid would then be $Cc\ Rr\ Qq$, and the F_2 would consist of the three types in the proportion of 36 full : 9 faint : 19 green, or, in a total of 87 plants, 48·94 : 12·23 : 25·83.

The only matings of the "Ivy-leaf" from which F_2's have as yet been obtained, are its crosses with "Snowdrift" and with full-coloured forms. The F_2 from the cross with "Snowdrift" is chiefly interesting in connexion with the partial suppression of stem-colours, and is considered more fully under that head (p. 101). Unlike the majority of the experiments on stem-colour, in which the observed results agree with the expectation very fairly closely, there is a great dearth of light-stemmed offspring in the F_2's from the crosses between "Ivy-leaf" and plants with fully coloured stems. The deficiency is most marked in the class in which the light colour is combined with the "Ivy-leaf" habit, but is also apparent, though in less degree, in the light-stemmed plants of the normal kind. There do not however appear to be sufficient grounds for supposing that any novel phenomenon occurs in these cases.

Table showing the results of experiments in regard to stem-colour.

I. *Red stem $(C\ RF\ Q) \times$ Green stem $(c\ rF\ q)$*

					Light 33	
				Colour in petioles 13		Green 25
F_1 selfed	1 family	Red	51			
,,	,,	Red	49		38	
Totals	...	100			71	
Expectation $(9:7)$	96·2				74·8	

II. *Faint colour in petioles $(C\ Q) \times$ Green stem $(C\ q)$*

| F_1 selfed | 9 families | Faint colour | 366 | No colour seen | 130 |
| Expectation $(3:1)$ | | 372·0 | | 124·0 |

III. *Red stem $(C\ RF\ Q) \times$ Faint colour $(C\ rF\ Q)$*

| F_1 selfed | 11 families | Red stem | 384 | Faint colour | 120 |
| Expectation $(3:1)$ | | 378·0 | | 126·0 |

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[1] Strictly speaking this combination gives the parti-coloured type "Sirdar," but as no "Sirdars" appear in this F_2 we are not here concerned with the *distribution* of the full colour.

IV. *Red stem (C RF) × Green stem, no colour seen (C rF)*

F_1 selfed	11 families	Red stem	395	No colour seen	128
Expectation (3 : 1)			392·25		130·75
F_1 × green stem	6 families	,,	99	,,	104
Expectation (1 : 1)			101·5		101·5

V. *Crosses giving "Sirdars."* Red stem (C RF Q) × "Snowdrift" (C rf q)

In 1905 many plants were discarded as seedlings; as there is no record of the flower-characters of these plants, the "Sirdars" cannot be distinguished from the other light-stemmed types. In the F_2's from ("Snow-drift"×dominant white) the flower-characters of a proportion of the family are masked by the presence of the dominant white character, and in such cases the "Sirdars" cannot be certainly distinguished from other light stems.

A. 1905 crosses.

F_1 selfed	4 families	Red stem	76	Light stem (including "Sirdar")	47
Expectation (9 : 7)			69·2		53·8

B. Dominant white × "Snowdrift."

F_1 selfed	8 families	Red stem	440	,,	337
Expectation (9 : 7)			437·1		339·9

C. Coloured, red stem × "Snowdrift."

F_1 selfed	11 families	Red stem	471	"Sirdar" 185	Faint colour and green	201
Expectation (9 : 3 : 4)		482·1		160·69		214·25

VI. *Red stem × "Ivy-leaf."*

		Red stem		Light stem	
		Palmate	Ivy	Palmate	Ivy
F_1 selfed	7 families	626	197	177	44
Expectation	...	587·25	195·75	195·75	65·25
		823		221	
		783·0		261·0	

The red stem of "Orange King" (Plate XXX, fig. 8).

"Orange King" originated in horticulture a few years ago, and was obtained by Messrs Sutton as a sport from "Crimson King." The "Orange King" character of flower and stem is recessive to that of "Crimson King," and in the F_2 the two forms reappear in numbers approximating to the 3 : 1 ratio. This result would indicate that a single factor suffices to restore those characters which differentiate "Orange King" from "Crimson King." The only other matings of "Orange King" of which I have experience are those with "Snowdrift." The hybrid resulting from this cross is indistinguishable to the eye from the hybrid between "Crimson King" and "Snowdrift." The

"Orange King" characters of stem and flower are however so intimately associated that the fuller consideration of this case may be deferred until the section dealing with flower-colour (p. 114).

Partial Suppression of Colour.

The light shades of the colour in the stem are dominant to the intense shades. This fact is well illustrated in the F_2's from ("Ivy-leaf" × deep red stem), where the red-stemmed plants fall into two sharply separated categories. The numbers obtained are:

		Light	Intense
3 families	...	157	49
Expectation	...	*154·5*	*51·5*

Similar sharply divided categories are found in families raised from the cross of a deep red stem with the F_1 of ("Snowdrift" × deep red stem). The numbers obtained in these crosses are:

		Light	Intense
9 families	...	198	202
		+3 doubtful (occurred in one family)	
Expectation	...	*equality.*	

It is clear from these cases that the light class, taken as a whole, may be explained as being due to the presence of a single factor, epistatic to the factors for colour, which diminishes the intensity of the pigmentation (pallifying factor). In the F_2's produced by the self-fertilization of the F_1 from the cross ("Snowdrift" × deep red stem) there are forms intermediate between the light and the very dark red stems, and the separation between the classes is by no means sharp. No doubt many of these intermediate forms are the result merely of heterozygosis in the factors for colour and for its partial suppression. In different pure races, however, and in the hybrids produced by their matings, colour is developed to very different degrees, and in order to account for the detailed phenomena it would probably be necessary further to elaborate the simple scheme put forward here, which is intended only to apply to the general outlines of the phenomena of the partial suppression of stem-colour.

The partial suppression of flower-colour follows, in general, very similar lines to that of stem-colour, but is independent of the latter, at least to the extent that light flowers may occur on deeply coloured stems.

In the lower grades of stem-colour the same relation subsists between the light and intense states as in the fully coloured types, but the separation of the categories is

of course a matter of much greater practical difficulty. The point has been studied with some care in the cross ("Snowdrift" × "Ivy-leaf" [1]). The F_1 has a faint trace of colour in the young petioles; the F_2 consists of (1) plants with full colour in the young petioles, which grade through rather lighter forms to (2) those in which faint colour in the petioles can be recognized with certainty; and these again grade, through doubtful forms, to (3) those in which no colour can be detected. Precise numerical results cannot be given, but so far as can be judged the constitution of the families can be fully explained without the assumption of any other factors than those for colour and for its partial suppression.

B.   FLOWER-COLOURS.

The various colours exhibited by *Primula sinensis* may be classified as (1) full colours, which may exist either in the self or in flaked patterns (Plate XXXI, figs. 56—59), and are always associated with fully coloured stems; (2) "Sirdars" (Plate XXXI, figs. 44, 45), in which the characteristic distribution of the full colour is associated with a definite type of stem-colouring; and (3) pale colours (Plate XXXI, fig. 46) which occur only on green or faintly coloured stems.

White flowers may occur in association with stems of any kind, and may be dominant or recessive to colours. The dominant whites owe their character to the possession of factors which inhibit the development of colour in the flower (see under "Inhibition," p. 105).

The full colours and "Sirdars" may be sub-divided into blues, magentas and reds; in the pale class, however, no distinction of this kind can be drawn, for the pale forms which correspond with the magenta full colours (and give magenta offspring when crossed with a red) are quite indistinguishable to the eye from those which correspond with the red class (and give only red offspring when crossed with reds).

Colours belonging to all these classes appear in the offspring of certain hybrids; the sharpness of the separation between the various classes of full colours varies, however, in different cases, and though in the majority the classes are fairly readily distinguished, in others intermediate forms occur. Whether these intermediate forms are always heterozygous cannot yet be said; in the few experiments in which they have been tested they have proved to be so [2].

[1] The "Ivy-leaf" used in the experiments on stem-colour was heterozygous for the pallifying factor. Hence the appearance of "Ivy-leaf" here as the parent lacking the pallifying factor, and previously as the parent bringing in that factor.

[2] A plant with red stigmas, which probably belonged to the red class but had flowers of a colour somewhat intermediate between the magenta and red classes, has since proved to be homozygous for its type of colour.

I have not yet undertaken any systematic experiments with the blue-flowered strains of *Primula sinensis*. Blues occurred among the offspring of a certain magenta plant obtained in 1903, in such proportions as to corroborate the more extended results obtained by Messrs Sutton, which show that the blue colour is an ultimate recessive[1].

For the purpose of these experiments it has been found convenient to work mainly with well-known horticultural strains, which provide a series of fixed standards of colour. The colours of the races of which principal use has been made are illustrated in Plate XXXI. For convenience of reference descriptions of the various types are given below.

Description of strains used in experiments on colour.

Recessive White.

"Snowdrift." (Plate XXX, figs. 7, 10.) Fern-leaf, green stem, white, green stigma.

Pale colours.

"Reading Pink." (Plate XXX, fig. 13.) Palmate, green stem, pale-pink, green stigma.

Full colours.

Salmon Pink. Palmate, purplish-red stem (light), salmon-pink, green stigma, short style.

Rosy Magenta. (Plate XXX, figs. 19, 20.) Palmate, purplish-red stem (light), magenta (rosier than F_1 type, light), green stigma.

"Crimson King." (Plate XXX, fig. 9.) Palmate, purplish-red stem (deep), deep crimson, red stigma.

"Orange King." (Plate XXX, figs. 3, 8.) Palmate, red (not purplish-red) stem, pink flowers, red stigma.

Dominant Whites.

Double White. Palmate, green stem with colour in leaf bases (Plate XXX, fig. 6), double white flowers, green stigma.

"Primrose Queen." (Plate XXX, fig. 12.) Palmate, purplish-red stem (light), white flowers, green stigma, large yellow eye.

"Queen Alexandra." (Plate XXX, fig. 11.) Palmate, purplish-red stem, white, green stigma, white eye.

Colour uncertain (see p. 122).

"Ivy-Leaf." (Plate XXX, fig. 5, Plate XXXII, fig. 60.) Palmate, non-crenate, stellata, green stems with colour in leaf bases[2], flowers? very pale colour flaked, green stigma. The "Ivy-leaf" is a very monstrous type, the non-crenate character of the leaves being always accompanied by partial abortion of the floral organs. Stamens are often absent and the corolla may be reduced to a tube surrounding the style, without petal-lobes. Petal-lobes, when developed, may be only small strap-shaped structures. Owing to the poor development of the corolla the colour of the plant used in the experiments cannot be determined with certainty. Such plants as survive usually become fertile in the second year, producing however

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[1] Bateson's *Mendel's Principles of Heredity*, Camb. Univ. Press, 1909, p. 135.

[2] The colour is insufficiently shown against the dark background in the plate.

only small quautities of pollen. A very common character of the " Ivy-leaf " is that the axis of the inflorescence forms a more or less conical elongation above the whorl of pedicels, at the apex of which carpellary structures may be developed, or ovules may be borne on an exposed disc, which is sometimes surrounded by small lobed expansions (probably carpels) each terminating in a knob resembling a stigma [1]. In extracted F_2-forms with green stigmas these expansions are green, in those with red stigmas they are coloured.

Outline of the inheritance of flower-colour.

When a plant with fully coloured stems and flowers is crossed with the albino "Snowdrift," the F_2 consists of

Full-colours, "Sirdars," Pale colours and Whites

in the ratio of 9 full : 3 "Sirdar" : 4 pale colour and white. Although the number of whites recorded in these F_2's is somewhat less than 1 in 16, there can be no doubt, I think, that this represents the proportion in which they really occur[2].

In a family of this kind, the plants having fully coloured stems *always* have fully coloured flowers; that is to say, the full colour, when present, is distributed throughout the whole plant. Consequently, it is not necessary in this case to draw a distinction between stem-colour and flower-colour, since the colour of both behaves as a single unit[3]. The inheritance of the full colour, then, follows the scheme outlined in the case of stem-colour (p. 96), in which the relation of the "Sirdars" to the full colours is also explained.

The place of the pale colours in the scheme must be left undecided until further data are available. It may prove that they constitute an independent series of colours, comparable with the faint stem-colours in their relation to the full colours; or they may perhaps result from the resolution of the combination of factors to which the full colour

[1] The structures described by Mr L. Crawshay in a malformed Primula (*Journ. Roy. Hort. Soc.* xxxvi. 1910, p. xxix) are apparently of the same nature.

[2] The discrepancy is almost certainly due to the difficulties attending the separation of the pale colours from the whites. The fact that we have sometimes detected a trace of colour in pure "Snowdrift," when the plants have been kept cool, points in the same direction.

[3] Keeble and Pellew's experiments (*Journ. Genetics*, Vol. I. 1910, p. 1) indicate that in certain pigmented forms one, at least, of the factors which determine the production of colour may be absent from the flowers, which are then white, though it is present in the stem, which is therefore coloured. This evidence that, in certain cases, the factors for colour are not distributed throughout the whole plant, is indirectly supported by the results of my experiments with the red-stemmed dominant white "Primrose Queen" (pp. 116, 123).

is due. If the former suggestion should prove to be correct, the fact that all our fully coloured races, when crossed with "Snowdrift," have given pale colours in F_2; and the further fact that two heterozygous "Sirdars" have thrown only "Sirdars" and whites, would be merely fortuitous results depending on the particular races which have been used. It may be noted that, if the pale colours are an independent series, certain matings between F_2 "Sirdars" and pale pinks should give full colours, while others should not do so; the alternative case would seem to imply that *all* these matings should give full colours.

The primary colour of the fully coloured flower is red[1]. The numerous shades of red are due to the presence or absence of factors which reduce the intensity of the pigmentation, and other factors which produce slight changes of tint. In the simplest cases the magenta class may be regarded as due to the action of a factor epistatic to the factors which give rise to the red colour; in other cases, however, the proportions of the magenta and the more rosy class indicate the 9 : 7 ratio (see under "Rosy Magenta," p. 110); and in yet another case an intermediate, mated with a clean red, gave typical magentas among its offspring. There exist corresponding shades of magenta for many, if not all, the numerous shades of red.

The flaked or splashed forms of coloured flowers show a considerable range of variation in the degree to which the flaking is developed, and in the size and form of the coloured areas. The distinction between the red and magenta colours in flakes is often attended with some difficulty. In self-coloured red flowers it will often be noticed that a bluer tint is developed at the edges of the petals, and in forms in which the colour is weakly developed just round the eye a similar bluish tint will be noticed in this region. In the same way, there seems to be a tendency for the red colour to pass into a bluer tint at the edges of the coloured stripes and splashes, and in flowers showing fine as well as coarse splashes, it is often to be noticed that the coarse splashes are red, while the minute dots of colour, viewed with the naked eye, would certainly be put down as magenta[2]. My experience of flaked flowers is limited to the F_2's of crosses in which the "Ivy-leaf" took

[1] The relations of blue to the other colours have not been worked out. The fact that blues appeared in small numbers in a cross in which the rest of the coloured offspring were red suggests that blue is either hypostatic to red, or, if it forms an independent series, is masked by red.

[2] A somewhat similar difficulty occurs in the "Sirdar" type, owing to the optical effect of the intermingled coloured and colourless dots. In this case, however, the distinction between magentas and reds can be made readily with the help of a microscope.

part; the results are such as to indicate that the flaked condition behaves as a recessive to the self-colour (see, however, p. 122).

The pale-coloured flowers on green stems are scarcely affected in appearance by the presence or absence of the numerous factors which produce such marked changes in the fully coloured types of flower. It is often by no means easy to recognize the pale colour when it occurs in the flaked condition; this is no doubt an optical difficulty, for the lower forms of this colour in any case need careful examination in order to distinguish them from white. Among the pale-pinks there occur forms in which the colour is more pronounced peripherally, others in which it is central, others again in which it forms peculiar bands. But the difficulty of observation is such that no attempt has yet been made to study the inheritance of these variations.

Partial Suppression of Colour.

As in the case of stem-colours, the intense colours of the flowers are produced only in the absence of a factor which diminishes the intensity of the pigmentation, and so gives rise to the dominant light shades. The partial suppression of flower-colour may be brought about by either of two factors, of which one affects the flower only, the other the whole plant. Hence light flowers may occur in association with dark stems, but deeply coloured flowers are limited to plants with deeply coloured stems.

In many F_2's there occur classes intermediate between the lightest and the very deep types, but, though the existence of such classes may be clear enough, it is difficult, if not impossible, to draw any sharp line between them, and, as in the case of stem-colours, it must remain undecided whether one pallifying factor, in its various pure and heterozygous combinations, is sufficient to account for all the shades, or whether a series of such factors is involved.

The factors which effect the partial suppression of colour seem to differ in degree rather than in kind from the factors which, in pure races, completely inhibit the development of colour in the flower.

Inhibition.

In the red-stemmed "Dominant Whites[1]," the whiteness of the flower is due to the presence of a substance which inhibits the

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[1] Gregory, *Rep. Brit. Assoc.*, Leicester, 1907, p. 692.

development of colour in the flower[1]. It has recently become clear that this inhibition is due to the action of two separate components, each of which has its own localized effect. The one component is present in the majority of the races which have coloured flowers, in the form of a factor which prevents the development of coloured sap in the ovary, style and stigma, and gives the green stigma. The second factor, on the other hand, affects only the peripheral parts of the corolla, and in the absence of its fellow, gives rise, in fully coloured forms, to the characteristic "Duchess" type of flower (Plate XXXI, figs. 27, 28), in which coloured sap occurs only in the gynoecium and in the flushed eye of the corolla[2]. In the pale colours the stigma is only faintly coloured, and the presence of coloured sap can be most easily detected in the placenta and ovules. The recessive green stigma (which corresponds with the recessive white flower, and is green through the absence of colour and not from its inhibition) has been recognized experimentally in F_2 plants from the crosses of "Snowdrift" with "Crimson King." The factors for inhibition may of course be present in plants which are devoid of the factors for colour; thus the green stigma of "Snowdrift" is of the dominant kind, and other green-stemmed whites have been met with, which possess both the factors for inhibition.

Plants which contain the factors for colour and are heterozygous for the inhibiting factors have tinged white flowers with green stigmas, the depth of the tinge varying with the intensity of the underlying colour (Plate XXXI, figs. 21, 24—26, 32). A heterozygous form of "Duchess" is represented in "Sir Redvers Buller" (Plate XXXI, fig. 29), and various other forms, depending on the presence or absence of the magenta and other factors epistatic to colour, exist (figs. 30, 31). In all of them the peripheral part of the corolla is tinged to a greater or less degree, and the full colour is only developed immediately around the eye.

One other character of flower-colour should be mentioned here. In certain varieties there occur spots of deep colour on the petals just external to the eye (Plate XXXI, figs. 50, 51). The inheritance of this character is, in itself, simple; but the full development of the spots is limited by the operation of other factors[3]. Thus, the deep spots are

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[1] In certain races belonging to this class an occasional splash or stripe of colour may often be observed, sometimes in only one or two, sometimes in many of the flowers.

[2] The flush round the eye is often only faint, especially in flowers of the *stellata* variety. The flush is an independent character limited to plants with red stigmas (see p. 120).

[3] Bateson, *Mendel's Principles of Heredity*, Camb. Univ. Press, 1909, p. 138.

not fully developed unless the stigma is coloured; nor, even if the stigma be coloured, are they developed in plants which have the white eye of the "Queen Alexandra" type (Plate XXX, fig. 11)[1]. Again, the spots are deeply coloured only in deeply coloured flowers, their appearance in flowers of a light shade somewhat resembling that which they assume in plants with green stigmas. The limitation imposed in these cases results from the dominance of an inhibiting character. There are also limitations due rather to the lack of a coloured base; the spot is not visible in pale-coloured flowers, nor again in the flaked patterns of full colour, unless it should happen that the colour is distributed in any of the petals in a wide stripe covering the area occupied by the spot. Such petals exhibit the spot, which may not be visible in other petals of the same flower.

Plants in which the development of the spot of deep colour is inhibited by the factor for green stigma have flowers of a definite type, characterized by the presence of a well-defined brownish spot. The character is a different one from the diffuse brownish band which appears in some plants as the flowers fade (Plate XXXI, figs. 54, 55), and is very clearly marked in the young flowers (Plate XXXI, fig. 50), becoming less conspicuous as they grow older (fig. 51). This "ghost" of the spot is well seen in the F_1 from ("Crimson King" × "Rosy Magenta"), and in the F_2 all the plants with red stigmas have the spot of deep colour. The inheritance of the character is further illustrated in the subjoined experiments in which a series of F_2 pale pinks were crossed with "Orange King."

	Green stigma		Red stigma	
Reference Number	Ghost of spot	No spot	Spot	No spot
36/10	12	—	9	—
37/10	—	—	8	3
38/10	—	—	6	3*
39/10	—	2	—	—
40/10		No plants		
41/10	—	—	4	1
42/10	6	7	—	—
43/10⎱ 44/10⎰		No plants		
45/10	3	—	—	—
46/10	9	7	—	—
47/10	6	—	—	—

* These three had light stems, and a brownish marking in the region of the spot somewhat resembling the marking which represents the spot in plants with green stigmas.

[1] In plants with the large yellow eye the spot is pushed outwards, so that it occupies the same position relative to the eye pigment as it does in the usual type (see Bateson, *loc. cit.* Plate VI, figs. 19, 21).

Experimental results. (1) Pale colours.

Pale-pink (Plate XXX, fig. 13; Plate XXXI, fig. 46). Pale-pinks have occurred in the F_2's of all my crosses between full colours and "Snowdrift," as well as among the progeny of certain heterozygous full colours obtained from various sources. It is also the characteristic coloured form thrown by heterozygous dominant whites having green or only slightly coloured stems. If the pale-pink be crossed with "Snowdrift" the resulting F_1 shows some dilution of the colour.

Heterozygous pale-pinks can throw nothing but pale-pinks and whites, and this they do in the proportion of 3 pinks : 1 white, the numbers obtained being 51 pink, 16 white. One of these plants crossed with "Snowdrift" gave 23 pink, 17 white.

My experiments throw no definite light on the question of the dependence of the colour on two complementary factors, a chromogen and a ferment, but in this connexion the cross between "Ivy-leaf" and "Snowdrift" should be mentioned. Both parents appear white, while the hybrid has definite though faint colour in the flowers. In F_2 plants with definitely coloured flowers form approximately 9 in every 16 plants, the observed number being 144 coloured in a total of 273 plants. Subsequent experiments with the "Ivy-leaf," however, suggest the possibility that, instead of its being a white, as I had supposed, it may have the very pale pink colour in the flaked condition (see p. 122).

The pale-pinks may or may not carry the magenta factor. Of 10 pale-pinks tested by crossing with reds, 6 were pure for the magenta factor and gave 65 offspring, all magenta; 2 were heterozygous and gave 30 offspring, 14 magenta, 16 red; and 2 were without the magenta factor and gave 16 offspring, all red. One other, mated with a magenta throwing magentas and reds, gave 5 magenta, 5 red, and was therefore without the magenta factor.

The same set of experiments served to reveal other characters carried by the pale-pink. Nine F_2 pale-pinks from the cross ("Crimson King" × "Snowdrift") gave offspring when crossed with "Orange King." In the resulting families there occurred intense and light colours, in one case rosy-magentas as well as the usual kind, in another case deep crimson-magentas together with reds very like "Crimson King," while in some cases the spot of deep colour was present in all the offspring having coloured stigmas, in others in only a proportion of them[1]. One pale-pink without colour in the stem was found to have

[1] See Table, p. 107.

the recessive kind of green stigma, all the offspring resulting from its mating with "Orange King" having coloured stigmas[1]. As was to be expected from the origin of the pale-pinks, none of the offspring showed the colour characters of "Orange King," the stem-colour being always purplish-red, and the colours of the flowers those of types found in "Crimson King" F_2's (Plate XXXI, figs. 33, 36, 39, 41, 43). The pale-pink strain "Reading Pink," crossed with "Orange King," gives a red (Plate XXX, figs. 15, 16) rather towards the magenta side of the class and having purplish-red stems.

(2) Full colours.

Salmon-pink. The race of this colour which has been used for experiment was derived from a heterozygous crimson, or crimson-magenta, which threw forms like itself, together with salmon-pinks and blues. The crosses in which this race has been tested give very simple results, since the race was pure for the light colour, and was without factors producing the minor variations of tint. Heterozygous salmon-pinks may throw pale-pinks only, or whites may appear in addition; in either case the proportion of full colours in the offspring follows the stem character. Crosses between such heterozygous salmon-pinks and either "Snowdrift" or the pale-pink carrying magenta show the simple operation of the magenta factor; crosses of this kind have given 44 magenta, 52 pale colours.

Salmon-pink × "*Snowdrift.*" The F_1 from this cross is a magenta with light red stems. In the F_2 there were obtained, in 3 families:

Full colours		"Sirdars"		No colour in stems	
Magenta	Salmon	Magenta	Salmon	Pale-pink	White
57	16	16	6	19	10
52·3	*17·4*	*17·4*	*5·8*	*23·3*	*7·8*

The expectation, given in italics, is based on the scheme already set forth, namely, that the full colours represent the "Sirdars" + a factor which effects the even distribution of the colour.

The salmon-pink is one of the few short-styled races with which as yet detailed experiments upon the inheritance of colour have been made[2], and a most interesting relation between the structural character

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[1] See Experiment 41/10 in the Table, p. 107. The pale-pinks used in Experiments 37/10 and 38/10 had faintly coloured stigmas.

[2] The obvious advantages of working with pure horticultural strains entail the disadvantage of working exclusively with long-styled plants, since the short-styled form is eschewed by florists.

of short-style and the magenta colour has been revealed. In the F_2's bred from plants heterozygous for both characters, the salmon-pinks are invariably short-styled. The results clearly indicate complete repulsion in gametogenesis between the two dominant factors, short-style and magenta. The case is dealt with fully on p. 125.

Rosy-Magenta. For the strain of this colour with which experiments have been made I am indebted to Messrs Sutton. Very similar types appear, as part of the magenta class, in the F_2's of certain crosses between reds and either "Snowdrift" or pale-pinks carrying magenta. The colour of the root-stock in this race bears the same relation to the colour which appears in the ordinary magentas as does the flower-colour in the two cases. The cross with "Snowdrift" gives an F_1 of the ordinary magenta type. In the F_2 the rosy-magentas take the place of the reds, but the distinction between the two classes is of course less obvious than that between magentas and reds. Like the salmon-pink, the rosy-magenta does not carry the factor for faint colour in the stem, and in the light class the stems and roots are devoid of coloured sap, so far as can be seen. The F_2 obtained in one experiment of this kind suggests a ratio of 9 magentas : 7 rosy-magentas, the numbers obtained being :

Reference Number	Full colours		"Sirdars"		No colour in stem	
	Magenta	Rosy-magenta	Magenta	Rosy-magenta	Pale-pink	White
9/9	37	22	14	10	14	4

In the next two, however, the usual 3 : 1 ratio obtains :

Reference Number	Full colours		"Sirdars"		No colour in stems	
	Magenta	Rosy-magenta	Magenta	Rosy-magenta	Pale-pink	White
23/9	19	7	8	2	4	2
17/10	62	25	22	6	36	4
Totals	81	32	30	8	40	6

One can scarcely believe that the result shown in Experiment No. 9/9 is only a fortuitous departure from the 3 : 1 ratio, nor does it seem likely that it is due to experimental error in the separation of the classes, for both No. 9/9 and No. 23/9 were recorded within a day, or two of one another, and in each case the separation of the classes was confirmed by another observer. The same rosy-magenta parent was used in Experiments 9/9 and 23/9, and one of its offspring in Experiment 17/10. The different results are not necessarily contradictory, for if the difference between magenta and rosy-magenta

does, in reality, depend upon the combination of two factors (of which "Snowdrift" must be assumed to have both) the rosy-magenta used in the 1909 experiments may have been heterozygous for one of them, without giving us any clue other than that which is suggested by these experiments. The mating between a sister plant of the rosy-magenta used in experiment No. 17/10 and a dominant white gave magentas and rosy-magentas in F_2. The separation between the two classes was somewhat doubtful, but they apparently consisted of 20 and 19 plants respectively. So far as this observation carries weight, it tends to support the view that the difference between the two classes depends on the combination of two factors.

"*Crimson King.*" In all its crosses "Crimson King" gives a great variety of coloured forms in F_2, and it is clear, both from the number of these forms, and from the comparative rarity with which the "Crimson King" type itself reappears, that its visible characters result from the interaction of several factors which are partially or wholly independent of one another in segregation.

A series of F_2 forms from the cross with the dominant white "Queen Alexandra" is shown in Plate XXXI, figs. 22—43. The types possessing some form of inhibition will be dealt with under that head (p. 115). Among the coloured forms (figs. 33—43) various types of light and dark magentas and reds occur, with or without the coloured stigma. This last character is recessive to the factor inhibiting the development of colour in stigma, and the observed numbers of green (colourless) stigmas and red stigmas approximate very closely to the ratio $3:1$. But in the great majority of my experiments the two kinds of stigma are not evenly distributed among the magentas and reds, and there is clear indication of the existence of partial gametic coupling between the two factors magenta and green stigma (p. 127). "Crimson King" has the factor determining the spot of dark colour on the petals and accordingly this character appears in deeply-coloured flowers which have the coloured stigma and the ordinary or large yellow eye.

"*Crimson King*" × "*Snowdrift.*" The F_1 from this cross is an ordinary (light) magenta. The F_2 contains fully coloured forms corresponding with those just described[1], and in addition to these there occur magenta and red "Sirdars" (figs. 44, 45) in light and deep forms, pale-pinks (fig. 46) and whites, the last two classes having green

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[1] The white eye is a character derived from "Queen Alexandra" and does not appear in the experiments with "Snowdrift."

or only faintly coloured stems. The magenta and red classes form parallel series of light and intense shades; the two classes as a whole are readily distinguished, though there usually occurs a small number of individuals whose proper position may be a matter of some doubt. In this connexion it may be remarked that the presence of the red stigma seems to have the effect of giving the flower in general a redder appearance than that of the corresponding type with green stigma.

Two F_2 families raised from this cross in 1907 show some departure from the normal in the ratio of full colours and "Sirdars"; the numbers obtained were:

	Full colours				"Sirdars"				Pale class	
	Magenta		Red		Magenta		Red		Pale-pink *	White
	Stigma green	Stigma red	Stigma green	Stigma red	Stigma green	Stigma red	Stigma green	Stigma red		
	33	15	12	5	14	9	6	2	24	5
	19	16	8	4	24	8	10	2	29	9
Totals	82	31	20	9	38	17	16	4	53	14
	113		29		55		20		67	

* The distinction between these two classes is not sharp.

The case does not perhaps merit any great consideration in view of the return to the normal ratio when the experiment was repeated in the succeeding years, and the lack of any other indications of a departure from the normal distribution of self-colours and "Sirdars."

Three families raised subsequently gave:

	Full colours				"Sirdars"				Pale class	
	Magenta		Red		Magenta		Red		Pale-pink *	White *
	Stigma green	Stigma red	Stigma green	Stigma red	Stigma green	Stigma red	Stigma green	Stigma red		
	16	7	7	5	9	2	1	2	12	4
	14	3	6	1	5	3	2	0	11	1
	13	4	3	5	1	0	1	0	12	1
Totals	43	14	16	11	15	5	4	2	35†	6
	57		27		20		6		41	

* Distinction not sharply drawn.
† Of 6 of these which had some colour in the stem, 4 had coloured stigmas, 2 green.

The five families taken together give 245 magentas, 82 reds; 234 green stigma, 93 red stigma; the calculated numbers in each case being 245·25 of the larger class, 81·75 of the smaller. In the first two

experiments the distribution of the two kinds of stigma among the two classes of colours follows the normal 9 : 3 : 3 : 1 ratio, being :

		Magenta green stigma	Magenta red stigma	Red green stigma	Red red stigma
Full colours	...	82	31	20	9
Sirdars	...	38	17	16	4
Totals	...	120	48	36	13
Expectation	...	*122·0*	*40·7*	*40·7*	*13·6*

In the later experiments there is considerable departure from this distribution, the first class being small and the last large. But it is to be noticed that in these two cases there is considerable departure from the normal ratio of 3 : 1 in each of two pairs of characters under consideration, the numbers observed being 77 magenta, 33 red; and 78 green stigma, 32 red stigma. There seem to be no grounds for regarding this discrepancy as other than a chance departure from the normal, but it of course has a very material effect on the numbers observed in the four groups when the two pairs of characters are considered in conjunction with one another. If the theoretical ratio of 9 : 3 : 3 : 1 be weighted so as to allow for the two discrepancies a fairly close approximation to the observed numbers is obtained :

	Magenta green stigma	Magenta red stigma	Red green stigma	Red red stigma
Observed numbers	58	19	20	13
Expectation from weighted ratio	*54·6*	*22·4*	*23·4*	*9·6*

There is therefore no clear indication that partial gametic coupling between the factors for magenta and green stigma occurred during the gametogenesis in the F_1 plants used in these experiments; the point is of some interest because partial coupling of these two factors is clearly indicated in many of the experiments in which "Crimson King" was used.

"*Crimson King*" × *Rosy-Magenta*. The F_1 from this cross is a magenta of a rather deeper kind than that of the F_1 from ("Crimson King" × "Snowdrift"). In the F_2 there occurs, in addition to the ordinary magentas and reds, a curious parti-coloured type in which irregular masses of full colour are distributed over a lighter ground. These "Strawberries" (Plate XXXI, fig. 49) apparently belong to the red class and only occur in small numbers, probably as one in 64 of the total offspring.

The magentas and reds may be subdivided into classes differing from one another in a minor degree. Thus, in the red class there

are dark reds, of which a few approximate to "Crimson King," terra-cottas of two shades, one bluer (Plate XXXI, fig. 47), the other a clean red (fig. 48) and light reds corresponding with both the shades of terra-cotta; in the magenta class a similar series of forms occurs. The grading between the sub-classes is close and I am not able to give any precise numerical results as to the proportions of the various types. The distribution of the green and red stigma among the magentas and reds clearly indicates the existence of partial gametic coupling between the factors for magenta and green stigma (see p. 127).

F_3 families have been raised from certain of the F_2 forms in the hope of elucidating their relations to one another and to the "Straw-berries." The bluer terra-cotta appears to be differentiated from the red kind by the addition of a single factor, but for the most part the results are complex and further data are required for their detailed analysis. One result, however, is of interest in connexion with the relation between the magenta and red colour. An F_2 plant with peculiar deep rosy flowers and red stigma, when selfed, gave forms like itself and strawberries; a light red with green stigma, self-fertilized, gave light reds, terra-cottas of both shades, and strawberries, all with green stigma. The two plants were crossed together recipro-cally, and the two families thus obtained consisted of typical *magentas*, reds (including light reds and terra-cottas) and strawberries, all with green stigma.

"*Orange King.*" (Plate XXX, fig. 8.) "Orange King" originated with Messrs Sutton as a sport from a strain of "Crimson King": it bred true from its first appearance. The F_1 from the cross with "Crimson King" bears an exceedingly close resemblance to the latter; the mature flowers of the hybrid are probably not to be distinguished from those of the pure race, but in the young flowers there is a slightly more magenta tint than in the pure strain of "Crimson King" with which I have worked. In the F_2 from this cross there were obtained 55 plants like the F_1, and 14 "Orange King"; some very slight differences in the depth of the colour were noticeable among the latter. The ex-tracted "Orange King" had the true red stem-colour, as compared with the purplish-red colour of the forms resembling "Crimson King."

"*Orange King*" × "*Snowdrift.*" The F_1 of this cross is indistin-guishable to the eye from that of the crosses of either the Rosy-magenta or "Crimson King" with "Snowdrift." The constitution of the F_2 follows the general lines of the F_2 from ("Crimson King" × "Snowdrift") but is of course rather more complex, since the F_1 is

heterozygous for the factor determining the *purplish*-red stem and deep colour of "Crimson King," which is present both in that race and in "Snowdrift." In addition therefore to the types found in the "Crimson King" F_2, there appear extracted "Orange Kings," and a new class consisting of plants with pink or pale-pink flowers and stem-colours ranging from red collar to reddish stem. These plants are no doubt derivatives of "Orange King," whose appearance they rather recall; but further experiment is required upon this point, as well as upon the further point as to whether the "Sirdar" character is recognizable as such, if, and when, it occurs in the "Orange King" series of pigments. The numbers obtained in two F_2 families were :

Full colour	"Sirdar"	"Orange King"	Pink, red collar to reddish stem	Pale pink, faint tinge or no colour in stem	White, green stem
111	33	5	29	52	12

178   64

The numbers given in the last three classes can only be regarded as approximately representing their relative sizes, since one can hardly avoid some experimental error in a separation guided by external appearance only. It will be seen that, if the pink class prove to be derivatives of "Orange King," the numbers obtained agree with the expectation based on the hypothesis suggested by the result of the cross ("Crimson King" × "Orange King"), namely, that the subtraction of a single factor will suffice to explain the behaviour of the "Orange King" type of pigment.

The existence of some form of partial gametic coupling between the magenta and green stigma is clearly indicated (see p. 127).

(3) Inhibition of Colour in the Flower.

All the red-stemmed whites with which I have worked have been found to possess the factors which inhibit the development of colour in the flower; when crossed with the albino "Snowdrift," they have given colours in F_2. Since fully coloured flowers only occur in conjunction with fully coloured stems, the stem-colour of the dominant white is a guide to the flower-colours which may appear in the F_2; those with full red stems will give full colours, while those with no more than a tinge of colour in the stem can only give pale-pinks. The precise ratio in which the coloured forms appear in F_2 is still in doubt. In the F_2's consisting of whites and pale-pinks only the former are in excess of the expected ratio of 13 : 3. Owing to the difficulty of distinguishing these faint colours, no great weight could be attached

to this discrepancy, were it not that in some F_2's, which contain plants with fully coloured stems, there is again a considerable excess of whites in the red-stemmed class, where the distinction between white and coloured forms can be made with certainty. The numbers which have been obtained are[1]:

Dominant White Parent	Red stem			Stems not fully coloured (including those resembling "Sirdar"[*])	
	White	Magenta	"Sirdar"	Pale pink	White
"Giant White"	{18	5	0	2	4
	{33	8	3	6	33
"Primrose Queen"	66	13	5	7	36

[*] Without the character of the flower-colour as a guide it is scarcely possible accurately to distinguish the "Sirdar" type of coloured stem from other low grades of stem-coloration.

Before passing to a detailed consideration of these results, it is well to recall the fact that in the F_2 from crosses between plants having coloured flowers and stems × the albino "Snowdrift," *all* the red-stemmed offspring have coloured flowers, whites being found only in the green-stemmed class. These results, together with the fact that all my red-stemmed whites proved to be dominant whites, suggested that the factors for full colour are common to the whole plant, and that, in general, red-stemmed whites are white in virtue of the suppression of the colour in the flower by inhibiting factors[2].

Turning now to the results of the crosses between "Giant White" × "Snowdrift," it will be seen that the red-stemmed class consists of whites and colours, in proportions which do not diverge so greatly from the expected ratio (3 : 1) as to exclude the possibility of accounting for all the whites on red stems as resulting from the suppression of colour in the flower.

In the red-stemmed class of the F_2 from "Primrose Queen" × "Snowdrift," however, the whites are much more than three times as numerous as the plants with coloured flowers. The observed ratio of colours to whites agrees closely with the expectation based on the hypothesis that the production of colour in the flower, even in the red-stemmed offspring of this cross, depends upon two complementary factors, for both of which the F_1 was heterozygous. An F_1 heterozygous for these factors and for inhibition, would give an F_2 consisting of 9 coloured : 55 white; the numbers obtained are 13 coloured, 66 white (*expectation: 11·11 : 67·89*).

[1] The earlier experiments only give qualitative results, as many plants were discarded before the characters of the flower could be accurately determined.

[2] Gregory, *Rep. Brit. Assoc.*, Leicester, 1907, p. 692.

Other experiments made with " Primrose Queen " definitely support the view as to its constitution which is entailed by this hypothesis. The results of Keeble and Pellew's experiments with the red-stemmed "Snow King"[1] indicate that in certain cases the factors for colour may be absent from the flower, though present in the stem, and consequently that certain red-stemmed plants may have white flowers in the absence of inhibition. On the other hand, the mode of inheritance of the full colour in my crosses between coloured, red stem × " Snowdrift" suggests that in certain other cases the factors for colour are common to the whole plant, both stems and flowers.

Dominant white × *Coloured, green stigma.* The simplest cases illustrative of the operation of the factors which inhibit the development of colour in the flower are those in which a dominant white is crossed with a coloured form having green stigmas. The F_1 in these cases is white or tinged-white, the depth of the tinge depending, under uniform conditions[2], upon the intensity of the colour of the coloured parent, and to some extent upon the particular race of dominant white used. The F_2 from this cross consists of whites, tinged whites and colours, all with green stigmas. The numbers obtained are :

$F_1 \times$ Self			$F_1 \times$ coloured, green stigma		
Number of F_2 families	White and Tinged white	Coloured	Number of F_2 families	White and Tinged white	Coloured
17	782	271	3	59	58
Expectation	*789·75*	*263·25*		*Equality*	

The experiment has been repeated in a slightly different form by crossing coloured plants with the F_1 of (Dominant white × Recessive white). The numbers obtained from these crosses are :

Reference Number of F_1 plant	White	Coloured
28/4	12	13
4/6	92	86
26/6	58	74
30/6	43	55
51/9	42	46
Totals	247	274
Expectation	*260·5*	*260·5*

[1] *Journ. Genetics,* Vol. I. 1910, p. 1.

[2] The depth of the tinge is dependent upon the conditions under which the F_1 is grown, and its maximum development is only obtained by keeping the house as cold as is possible without injury to the plants. At higher temperatures very little tinge is developed, and the F_1 from the cross of such an intense colour as " Crimson King " with a dominant white is scarcely tinged.

The "dominant white" parent of Nos. 26/6 and 30/6 was one which gives a very fully tinged F_1 when crossed with "Crimson King" —the coloured race with which 26/6 and 30/6 were mated; the excess of coloured offspring shown in their crosses may therefore be in part due to experimental error, through the inclusion of some deeply tinged forms with the light colours, and in the absence of any other indications of departure from normal segregation one does not feel inclined to attach any great weight to the discrepancy shown here.

Dominant white × *Coloured, red stigma.* The F_1 from this cross is again a tinged white with green stigma (Plate XXX, fig. 18; Plate XXXI, fig. 21). The F_2 from one of these crosses—that between "Queen Alexandra" and "Crimson King"—is illustrated in Plate XXXI, figs. 22—43. As concerns the factors for inhibition, the F_2 consists of four classes, namely, (1) whites and tinged-whites, with green stigma (Plate XXXI figs. 22—26); (2) plants in which the peripheral part of the corolla is white or tinged, the central part flushed, with red stigma ("Duchess" and "Buller" types; figs. 27—31); (3) coloured, green stigma (figs. 33, 34, 38—41); (4) coloured, red stigma (figs. 35—37, 42, 43). The four classes are in the proportions of 9 : 3 : 3 : 1, the observed numbers being :

White and tinged-white, green stigma	"Duchess" and "Buller" forms; red stigma	Coloured, green stigma	Coloured, red stigma
193	61	65	21
Expectation 191·25	63·75	63·75	21·25

"*Duchess.*" The "Duchess" types which appear in these F_2's are shown by experiment to be homozygous for the peripheral inhibiting factor. Crossed with a coloured, red stigma, they give "Sir Redvers Buller," which in turn gives "Duchess," "Buller," and fully coloured, all with red stigma. The F_2 types resembling "Buller" are therefore those which are heterozygous for the peripheral inhibiting factor.

"*Duchess*" × *green stigma.* "Duchess," crossed with plants with green stigma, gives a *white* or *tinged-white* F_1. The result is the same whether the parent having the dominant green stigma be a coloured form or a recessive white ("Snowdrift"), except that in the former case the F_1 has a rather deeper tinge.

In certain cases the flowers of the F_1 have a distinct tinge of colour in the corolla-tube, just below the region of the insertion of the anthers, although no tinge at all may be discernible in the petals[1]. The charac-

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[1] A similar character has been observed in one other experiment where the F_1 from (Dominant white × Crimson, green stigma) was crossed with a dominant white. In this case the character was coupled with that of short-style.

ters of the F_2's from the various crosses which have been made are shown below :

Cross	Number of families	Description
" Duchess " × " Snowdrift "	2	21 plants. White, petals tinged, no tinge in tube.
" Duchess " × " Sirdar "	1	28 plants. White, no tinge seen.
" Duchess " × " Ivy-leaf "	1	42 plants. White, with faint tinge in petals ; no tinge in tube.
" Duchess " × Dominant White	1	8 plants. White, with distinct tinge in tube.
" Duchess " × F_1 (Dominant White × " Snowdrift ") 2		White, no tinge seen, 15 plants ; White, tinged in tube, 14 plants.
" Duchess " × Rosy-Magenta	1	12 plants. White, rather fully tinged in petals.

The F_2 from the cross between " Duchess " and " Snowdrift " contains a long series of types, for to the various inhibited and coloured forms corresponding with those obtained in the F_2 from (Dominant white × Coloured, red stigma) there are added the " Sirdars," pale-pinks and whites on green stems which are characteristic of the F_2's from crosses between " Snowdrift " and plants possessing the factors for colour. And since the " Duchess " used in these experiments was of the red class, red as well as magenta forms of each coloured type are present. The numbers obtained in three families were :

Red stems			Green stems, red collar ("Sirdar" types)				Pale-pinks	Whites
Green stigma		Red stigma	Green stigma		Red stigma		Red collar	No colour seen in stem	No colour seen in stem
White and Tinged white	Coloured	Tinged white and Coloured	White	Sirdar	Tinged White	Sirdar			
117	47	37	47	14	18	7	5	19	56

The tinged whites with green stigma are of two kinds, namely, (1) those which resemble the F_1 in having a more or less evenly distributed tinge, which becomes more pronounced as the flowers fade, and (2) those with a definite central tinge surrounding the eye and most conspicuous in the young flower. All the tinged whites with red stigma have the colour disposed in the centre after the " Duchess " style.

At the time when these families were recorded the distinctive character of the forms resembling " Buller " had not been recognized, and some of them were included with the class " Coloured, red stigma "; in the table the two classes of red-stemmed plants with red stigma are therefore taken together; it will be noticed that there is a deficiency

in these two classes as compared with the corresponding classes with green stigma; on the other hand in the "Sirdar" classes the proportions of green stigma and red stigma are slightly less than 3 : 1, but further experiment is required before any suggestions can be made as to any possible significance of these departures from normal distribution.

A further generation was raised by selfing one of the offspring of the cross ["Duchess" × F_1 (Dominant white × "Snowdrift")]. The most interesting point brought to light by this experiment is the fact that there occur whites (? with no tinge) having red stigmas, but *without* the central flush of deep colour which is characteristic of the "Duchess" strain[1]. The numbers obtained were :

Red stem			Green stem, red collar		No colour in stems
White, green stigma	White, red stigma	Duchess, red stigma	White, green stigma	White, red stigma	White, green stigma
34*	13†	4	16	5	19

* Two with definite central tinge.
† Three with definite central tinge.

Tinged-whites with red stigma and without the central flush occurred also among the offspring of a cross between "Duchess" and the F_1 of ("Ivy-leaf" × "Crimson King"). From this cross 31 plants were obtained, 16 with green stigma, 15 red stigma. Those with green stigmas were white or slightly tinged (like the F_1 of "Dominant white" × coloured, red stigma); those with the red stigma were deeply tinged, but whereas some were of typical "Duchess" or "Buller" types, others were without the deep central flush.

The deep central flush of "Duchess" and "Buller" is therefore not a necessary consequence of the absence of the factor inhibiting colour in the stigma; it would appear rather that the character is an independent one, but, like the deep spot of colour just external to the eye (p. 106), is dependent for its full development on the presence of colour in the stigma. We may surmise that the definite central tinge found in some whites with green stigmas represents this character in combination with the green stigma.

Green stigma in coloured flowers. The results showing the behaviour of the green and red stigma in crosses between colours are :

Number of families	Green stigma	Red stigma
4	315	116
Expectation	323·25	107·75

[1] In *Stellata* flowers the "Duchess" flush is often only poorly developed, but the phenomenon is of a different kind from that referred to here.

(4) Flakes.

The F_2's from crosses between the "Ivy-leaf" and coloured races contain flakes (Plate XXXI, figs. 56—59) in addition to the self-colours.

"*Ivy-leaf*" × "*Crimson King*." The F_1 of this cross, and of that between "Ivy-leaf" and "Orange King," is indistinguishable to the eye from the F_1 of the crosses between "Snowdrift" and the same coloured races.

In the F_2, the self-coloured flowers on red stems constitute a series of types similar to those of the F_2 from ("Crimson King" × "Snowdrift"); the same series is probably repeated in the flaked patterns, though the distinction between the shades of red and magenta is much less easily made in the flakes. The flaking may be coarse, the coloured areas taking the form of wider or narrower radial stripes (Plate XXXI, fig. 56), or very fine flakes may be present in addition to the coarser ones (fig. 58). The flaking appears generally to be strongly marked in plants with red stigmas (figs. 57, 59).

As in many other cases, the distribution of green and red stigmas among the magentas and reds clearly indicates the existence of partial gametic coupling (see pp. 127, 128).

All the offspring with light stems have some amount of colour in the bases of the leaves, as does the "Ivy-leaf" itself. The light-stemmed class consists of pale-pinks, and whites flaked with pale colour. The flaking in this class may be very sparse, and in that case is inconspicuous as the colour is so faint, but it was observed in all the plants except four. The F_2 contains no "Sirdars."

The numbers obtained were:

		Red stems		Light stems		
	Reference Number	Self colour	Flake	Pale pink	White, flaked pale pink	White, no flake seen
61/10 62/10	Palmate leaves	97 173	33 42	30 35	6 25	2 2
	Total, palmate	270	75	65	31	4
61/10 62/10	Ivy leaves	24 +3 undetermined* 40 +11 undetermined*	10 16	2 12	0 3 +5 undetermined*	0 0
	Total, Ivy leaves	64 +14 undetermined*	26	14	3 +5 undetermined*	0
	Grand total	334	101	79	34	4

* Owing to the poor development of the flowers.

Taking the red- and light-stemmed classes together, the self-colours are 413, the flakes 135, numbers which suggest that the flaked condition is a simple recessive, the expectation in such a case being 411 colours : 137 flakes. The distribution of the self-colours and flakes among the red and light stems is however irregular, especially in the palmate plants of 62/10.

"*Ivy-leaf*" × *Dominant white*. Up to the present time F_2's have been raised from only one cross of this kind, that of ("Ivy-leaf" × "Primrose Queen"). The F_2 is noteworthy for two reasons : (1) no self-colours are obtained, all the coloured offspring being flaked ; and (2) no pale-pinks occur. The numbers are :

	Red stems		Light stems	
	White	Magenta flakes	White	Flakes
Palmate leaves	93	26	36	—
Ivy leaves ...	43	4	8	—

The flakes grade from fully-flaked to small and sparse flakes of colour. It may be noticed that the young flower-buds of the flaked forms are quite strongly tinged, even though the flaking may prove to be sparse. The great excess of whites, as compared with flakes, among the Ivy-leaved offspring is probably of no great significance, as it may well be due to the reduced corollas of the Ivy-leaves. The plants with light stems were carefully examined in view of the results obtained from the cross of ("Ivy-leaf" × "Crimson King"), and no trace of flaking was observed in any. It may be remarked however that both "Primrose Queen" and "Ivy-leaf" carry the factor which partially suppresses flower-colour, and even the full colours are very light.

"*Ivy-leaf*" × "*Snowdrift*." The F_1 from this cross has definite, though faint, colour in the flowers. In the F_2, plants with definitely coloured flowers form approximately 9 in every 16 plants, the observed numbers being 144 definitely coloured in a total of 273 plants ($\frac{9}{16}$ of *273 = 153·5*). The plants recorded as definitely coloured were, so far as could be judged, self-colours; in one at least of the remainder the "ghost" of a coloured flake was recognized. In this cross, again, both parents bring in the factor which partially suppresses flower-colour.

Discussion of the "Ivy-leaf" crosses. The appearance of the "Ivy-leaf" plants and the characters of the F_1 obtained from their crosses with colours, led me to look upon "Ivy-leaf" as a recessive white ; but the result of the crosses with "Crimson King" suggests that this view will need revision, and that the plant may really possess the pale-pink

colour in the flaked condition. A re-examination of the parent "Ivy-leaf" in the light of this suggestion failed to reveal any definite coloration, but the pale colour is at best sometimes hard to discern and in the flaked condition might escape even close inspection, especially in such poorly developed flowers as are characteristic of the "Ivy-leaf." The suggestion is moreover supported by the fact that Keeble and Pellew[1] obtained a flaked F_1 from the cross of an "Ivy-leaf" of this strain with "Snow King." This view of the constitution of the "Ivy-leaf" would agree well enough with the results of the cross with "Snowdrift," for the latter possesses the factor for self, as against flaked, colour, and we should therefore expect a ratio of 9 self-coloured : 7 flaked and white.

In the same way the absence of pale-pinks in the F_2 of the cross with "Primrose Queen" may perhaps be put down to the difficulty of recognizing the colour in its most dilute and flaked condition[2]. The complete absence of self-colours from this F_2 is interesting in view of the results of the cross between "Primrose Queen" and "Snowdrift," and suggests some considerations as to the relation between flakes and self-colours. For if the self-colours result from the addition of a "distributing" factor epistatic to the factors for colour, it is clear that "Primrose Queen" must be without this factor; but in that case one-third of the coloured offspring obtained in the F_2 from ("Primrose Queen" × "Snowdrift") should be flaked, and no flakes have been obtained in this cross.

If, then, the conception of distributing factors is to be retained, it would be necessary to construct an elaborate scheme of factors, for the existence of which there is at present no evidence. In the absence of such evidence, it is more simple to suppose that one, at least, of colour factors may exist either in the flaked or in the distributed condition. The F_1 from (self-colour × flake) then appears self-coloured because the flaked character is masked when the flower as a whole is coloured[3]; and the segregation which takes place in the hybrid consists in the

[1] *Journ. Genetics*, Vol. I. 1910, p. 4.

[2] Flaked pale-pinks have now (Feb. 1911) been definitely recognized in F_3 from this cross. A red-stemmed magenta flake, self-fertilized, gave two kinds of offspring, namely (1) plants with red stems and flowers flaked magenta, (2) plants almost devoid of colour in the stem, in the flowers of which the flakes of pale pink were recognized with certainty. Temperature of the house, 55° F.

[3] Whether any *pale* self-colours, crossed with flakes, would give an F_1 of a visibly flaked character depends upon the relation between full and pale colours, which is not yet fully understood.

separation of the flaked and distributed forms of the same factor, and not in a segregation of the factors for flaked and for self-colour from their respective "absences."

On this hypothesis the results of the crosses with "Primrose Queen" may be explained as in the subjoined scheme, where

> X, Y, the colour factors in the distributed condition;
> X', Y', the colour factors in the flaked condition;
> R, inhibition.

Assuming the constitution of the parents to be "Snowdrift" $= xYr$; "Primrose Queen" $= XyR$; "Ivy-leaf" $= XY'r$; then

> "Snowdrift" × "Primrose Queen," $F_1 = XxYyRr$,
>> F_2 should give   9 *self*-coloured : 55 white
>> Observed   13   „   : 66[1] „
>> *Calculated*   *11·1*   „   : *67·9* „
>
> "Ivy-leaf" × "Primrose Queen," $F_1 = XXY'yRr$,
>> F_2 should give   3 *flakes* : 13 whites
>> Observed   26   „   : 93[1]   „
>> *Calculated*   *2·3*   „   : *96·7*   „
>
> "Ivy-leaf" × "Snowdrift," $F_1 = XxYY'rr$,
>> F_2 should give   9 self-coloured :   7 flaked and white
>> Observed   144   „   : 129   „
>> *Calculated*   *153·5*   „   : *119·4*   „

The conception of the relation between the flaked and self-colour characters set forth above does not pretend to do more than provide a means by which the results of the experiments may be described. It brings us no nearer the solution of the problem as to how the flaked distribution is brought about, nor is it intended as implying that the colour-factors themselves may not be the same in the flakes as in the self-colours, the mode of distribution of the colour being determined independently.

Gametic Coupling and Repulsion.

Evidence has been obtained of the existence of (1) a repulsion between the factor for the structural character of short-style and certain factors affecting the colour of the flower, and (2) of a partial coupling between two colour factors.

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[1] The numbers given are those obtained in the red-stemmed class only, since the distinction between coloured and white green-stemmed plants is not critical.

(1) *Repulsion between short-style and colour characters.*

Short-style and Magenta-colour. The results of my crosses in which a short-styled coloured race (Salmon-pink, p. 109) was mated with various long-styled plants carrying the magenta factor, show that in the gametogenesis of the hybrids so produced, a complete repulsion between the factor for short-style and the magenta factor takes place. The numbers obtained in these experiments are given below, together with the expectation based on the assumption of complete repulsion between the two factors under consideration.

Magenta short-styled F_1, giving magentas and salmon-pinks.

		Short-style		Long-style	
		Magenta	Salmon	Magenta	Salmon
Observed Numbers	...	54	18	24	0
Expected	,, ...	*48*	*24*	*24*	*0*

Tinged-white short-styled F_1, giving tinged-white, magenta, and salmon-pink.

	Short-style			Long-style		
	Tinged-white	Magenta	Salmon	Tinged-white	Magenta	Salmon
Observed numbers	157	46	19	66	20	0
Expected ,,	*173·25*	*38·5*	*19·25*	*57·75*	*19·25*	*0*

Tinged-white short-styled F_1, giving tinged-white, magenta, salmon-pink, and blue.

	Short-style				Long-style			
	Tinged-white	Magenta	Salmon	Blue	Tinged-white	Magenta	Salmon	Blue
Observed numbers	15	4	3	2	10	6	0	0
Expectation (omitting blues)	*21·4*	*4·7*	*2·4*	—	*7·1*	*2·4*	*0*	—

The deficiency in the tinged-white short-styles is referred to below.

Short-style and inhibition. Certain families raised from one heterozygous short-styled tinged-white (No. 51/9) have shown an interesting departure from the normal distribution of the four kinds of offspring. The results of the experiments made with this plant are:

		Offspring			
		Short-style		Long-style	
Reference Number	Cross	Tinged-white	Coloured	Tinged-white	Coloured
66/10	51/9 × Self	25	7	9	3
67/10	51/9 ♀ × Long-style, coloured ♂	4	9	11	4
68/10	51/9 ♀ × Long-style, coloured ♂	5	6	5	5
79/10	Long-style, coloured ♀ × 51/9 ♂	7	14	17	8

In Experiments 66/10 and 68/10 the distribution is normal, but in Nos. 67/10 and 79/10, where we expect equality of all four classes, the two middle classes are much larger than the end terms, and though the total numbers are small, the divergence is such that it can scarcely be dismissed as fortuitous.

The relative sizes of the four classes in the families Nos. 67/10 and 79/10, indicate that any repulsion which may take place must be of a low order. The family of 67/10 was raised from seeds obtained from two capsules; but in Experiment 79/10, pollen was taken from only one flower, so that the low type of repulsion indicated by the constitution of that family cannot be regarded as due to a mixture of families of more than one kind.

For the solution of the problems presented by the results of these experiments further data are required. The constitution of the F_2's obtained from our other plants heterozygous for short style and for inhibition, throws little light on the case. In these families the distribution of the four kinds of offspring does not depart very greatly from the normal. The numbers obtained are:

		Short-style		Long-style	
		White and Tinged-white	Coloured	White and Tinged-white	Coloured
Observed	...	327	126	128	39
Expected	...	*348·75*	*116·25*	*116·25*	*38·75*

There are small departures from the 3 : 1 ratio in the cases both of the short- and long-style and of inhibition and colour; the deficiency of dominants of both kinds has of course a marked effect upon the size of the first category.

The excess in the two middle classes and the deficiency in the first class appear to be more or less constant throughout the families, which, combined together, furnish the totals given above.

Short-style and tinge in corolla-tube. In one experiment clear indications were obtained of a coupling between the short-style and a tinge in the corolla-tube just below the level of the anthers. So far as the character of the petals was concerned, the family consisted of tinged-whites and whites; of the whites, however, some were tinged in the tube, others were colourless. Of the short-styled whites, 20 were tinged in the tube, 1 was colourless; of the long-styled whites 5 had the tinge and 11 were colourless. The ratio of short- to long-style in this family was very much less than the expected 3 : 1, the numbers being 33 short, 21 long. The asymmetry of the four classes is no doubt

partly a result of this, and the numbers obtained suggest that a coupling of a fairly high order was present.

(2) *Coupling between colour characters.*

With the exception of the mating between " Crimson King " and " Snowdrift," all the experiments in crossing either " Crimson King " or " Orange King " (red, red stigma) with plants carrying the factors for magenta colour and green stigma, have given results which point clearly to the existence of a partial coupling between these factors in gametogenesis. The results in general show some deficiency of the two dominant characters, magenta and green stigma, as compared with the expected ratio, in each case, of $3\,D : 1\,R$; the classes consisting of plants having one or both recessive characters are therefore unduly large, and it is necessary to make allowance for this in attempting to compare the observed numbers with the expectation calculated upon various systems of partial coupling. The distribution of the four characters in the offspring possessing fully-coloured flowers and red stems is set out below :

		Magenta		Red	
Cross	Reference Number	Green stigma	Red stigma	Green stigma	Red stigma
" Orange King " × "Snowdrift " ...	10/9	19	4	6	6
	11/9	28	9	6	8
	33/9	54	13	12	14
	Total	101	26	24	28
"Crimson King" × Rosy Magenta ...	17/9	85	24	24	21
	18/9	73	12	15	22
	24/9	81	18	19	17
"Crimson King" × "Queen Alexandra"	32/10	19	5	5	4
	33/10	20	2	7	3
	Total	39	7	12	7
"Crimson King" × " Ivy-leaf " ...	61/10	69	23	14	15
	62/10	137	30	28	18
	Total	206	53	42	33

Constitution of F_2

In these results, that obtained in No. 18/9 stands alone in that the fourth term of the series is distinctly larger than either of the middle

terms. On the basis of the $3:1:1:3$ system of partial coupling, the 122 plants of which the family consists should be distributed in the proportions of

78·1 magenta, green stigma :   13·3 magenta, red stigma :
13·3 red, green stigma :   17·2 red, red stigma.

The distribution thus calculated would, however, give magenta : red = green stigma : red stigma $= 3 : 1$, while the observed numbers are magenta 85, red 37 ; green stigma 88, red stigma 34. That is to say, there is a deficiency of plants bearing the dominant characters, and, consequently, the first term will be smaller and the fourth term will be larger than the calculated numbers. Apart from this divergence, there is a close approximation between the observed and calculated numbers, and there can be little doubt that the partial coupling was of the type $3:1:1:3$.

The crosses between "Orange King" and "Snowdrift" have given results which may perhaps allow of the same explanation, but in the remaining experiments the fourth term is definitely smaller than the middle ones. Each family was raised from seed obtained from several capsules borne on one plant ; and, until the completion of experiments which are now in progress, it is not possible fully to analyse the results. For the time being it may be pointed out that a very close approximation to the observed numbers is given by the assumption that a coupling of the form $7:1:1:7$ is present in gametes of one sex only, gametes of the opposite sex being produced in equal numbers of all four kinds. The numbers are

	Magenta, green stigma	Magenta, red stigma	Red, green stigma	Red, red stigma
Observed	411	98	97	78
Calculated for $7:1:1:7$ *coupling in gametes of one sex only*	416·8	96·2	96·2	74·8

As was stated above[1], the distribution of the four kinds of offspring in the F_2's from the cross ("Crimson King" × "Snowdrift") gives no clear indication of the existence of any form of partial coupling during gametogenesis of the F_1. In two F_2 families raised in 1907, the results differ very little from the simple $9:3:3:1$ ratio. In the later experiments there is some departure from this ratio, principally due to the dearth of plants carrying the positive characters, magenta and green stigma.

[1] p. 113.

In conclusion, it may be pointed out that here, as elsewhere, families raised from sister plants do not necessarily follow the same system of distribution. Thus the parent of the family 18/10, which apparently conforms to the $3:1:1:3$ system, was the sister plant to the parent of the family 17/10, in which the fourth term is smaller than the middle ones.

Note added February 17, 1911. Since the foregoing was written some interesting results have been obtained in connexion with the phenomena of coupling and repulsion. These results are briefly described below. The constitution of a certain type of coloured flower, which was previously uncertain, has also been ascertained.

Coupling and repulsion. (1) *Magenta and short-style.* On p. 125 a series of experiments is described in which a complete repulsion between the factors for short-style and magenta colour is shown. It will be noticed that in this series of experiments one of the dominant characters was possessed by the one parent race, the other by the other parent. In a new series of experiments a race possessing both dominant characters (i.e. magenta, short-style) was mated with races which had the recessive characters only. The results show that when the cross is made in this way, *partial coupling* takes place between the factors for the two dominant characters.

In the experiments in which the recessive parent was a long-styled red with double flowers, the coupling shown is almost certainly of the form $7:1:1:7$; in these experiments there is no indication that coupling occurs between either the factor for short-style or that for magenta and any third factor.

In a second set of experiments, in which the recessive parent was the long-styled "Crimson King," the form of the coupling between magenta and short-style is as yet uncertain, the numbers obtained being almost exactly intermediate between the expectation based on the series $7:1:1:7$ and that based on the series $15:1:1:15$. In these experiments there is clear evidence that the factor for magenta is coupled, not only with the factor for short-style, but also with the factor for green stigma. The coupling between magenta and green stigma is of a much lower order than that between magenta and short-style.

(2) *Light red stem and green stigma.* A new instance of complete repulsion between two factors has been obtained. The factors are (1) the pallifying factor for stem colour (p. 100), and (2) the factor for green stigma. This repulsion was observed in the progeny of a cross between "Crimson King" and "Ivy Leaf." Certain individuals of the F_2 from this cross were tested by self-fertilization. Three of these plants, all having light red stems and green stigma, were found to be heterozygous in these characters, giving offspring having either light or dark red stems, and either green or red stigmas, but *none* of the dark-stemmed offspring had red stigmas.

Flower-colour. The deeply tinged type of flower shown in Plate XXXI, fig. 32, the constitution of which was formerly in doubt, has proved itself to be heterozygous for the factors which inhibit flower-colour. Self-fertilized, it has thrown tinged whites with green stigma, "Duchess" and "Buller" types with red stigma, coloured with green stigma and coloured with red stigma. The flush shown in the "Duchess" and "Buller" types is of a very deep kind, and the coloured types have flowers of a very deep crimson, at least as deep as that of "Crimson King."

DESCRIPTION OF PLATES.

The figures illustrating the colours of the flowers are from water-colour drawings by Miss M. Wheldale.

PLATE XXX.

Figs. 1—7 illustrate various types of coloration of the stem.

Fig. 1.   Dominant white with deep purplish-red stem.

Fig. 2.   Dominant white with light purplish-red stem.

Fig. 3.   "Orange King," red stem (cf. the more usual purplish-red colour of the stem).

Fig. 4.   "Sirdar." The characteristic distribution of the flower-colour, which is associated with this type of stem, is shown in Plate XXXI, figs. 44, 45.

Fig. 5.   Green stem, with slight purplish-red colour in young petioles.

Fig. 6.   "Ivy-leaf." Non-crenate leaves, and monstrous flowers. Stems green, with some purplish-red colour in young petioles.

Fig. 7.   "Snowdrift," stem devoid of sap-colour.

Figs. 8—20 illustrate the colour of the flower of various pure races and F_1's.

Fig. 8.   "Orange King" (cf. fig. 3).

Fig. 9.   "Crimson King."

Fig. 10.   "Snowdrift" (cf. fig. 7).

Fig. 11.   "Queen Alexandra" (dominant white, white eye).

Fig. 12.   "Primrose Queen" (dominant white, large yellow eye).

Fig. 13.   "Reading Pink." The deepest colour found in association with green stems devoid of sap-colour.

Fig. 14. F_1 ("Reading Pink" × "Snowdrift").

Figs. 15 and 16.   Young and mature flowers of the F_1 from ("Reading Pink" × "Orange King").

Fig. 17. F_1 ("Crimson King" × "Snowdrift").

Fig. 18. F_1 ("Crimson King" × Dominant white, ordinary eye).

Figs. 19 and 20.   Rosy-magenta, young and old flowers.

PLATE XXXI.

Figs. 21—43 illustrate the cross between "Crimson King" and "Queen Alexandra."

Fig. 21 is the F_1; figs. 22—43 illustrate the series of F_2 forms.

Figs. 22—26.   Inhibited whites, green stigma.

Fig. 22.   White, white eye.

Fig. 23.   White, ordinary eye.

Fig. 24.   Tinged-white, white eye (F_1 type).

Fig. 25.   Tinged-white, ordinary eye.

Fig. 26.   Fuller tinged-white, tinge central

Figs. 27—31.   Plants with the factor for inhibition of colour in periphery of petals, but with red stigma.

Fig. 27.   Red "Duchess," F_1 type of eye.

Fig. 28.   Magenta "Duchess," F_1 type of eye.

Fig. 29.   "Sir Redvers Buller" (red), ordinary eye.

Fig. 30.   Red "Buller" of rather bluer type, white eye.

Fig. 31.   Magenta "Buller," ordinary eye.

Fig. 32.   Light red, ? inhibited form, green stigma [1].

Figs. 33—37 represent types belonging to the Red class.   Figs. 33, 34, green stigma; figs. 35—37, red stigma.

Fig. 33.   Red, ordinary eye.

Fig. 34.   Red (bluer type), white eye.

Fig. 35.   Red, white eye.

Fig. 36.   Red, ordinary eye, band of deep colour round the eye.

Fig. 37.   Deep red, white eye.

Figs. 38—43 represent types belonging to the Magenta class.   Figs. 38—41, green stigma; figs. 42, 43, red stigma.   Figs. 41 and 43 are corresponding forms with green and red stigma respectively.

Fig. 38.   Magenta, F_1 type of eye.

Fig. 39.   Magenta, ordinary eye.

Fig. 40.   Fuller magenta, white eye.

Fig. 41.   Rosy-magenta, ordinary eye.

Fig. 42.   Magenta, F_1 type of eye.

Fig. 43.   Rosy-magenta, ordinary eye, spots of deep colour round the eye.

Figs. 44—45 represent additional coloured types which occur in the F_2 from ("Suow-drift" × "Crimson King").

Fig. 44.   Red "Sirdar."

Fig. 45.   Magenta "Sirdar."

Fig. 46.   Pale-pink on green stem (cf. figs. 13, 14).

Figs. 47—49.   Other types belonging to the red class from the F_2 from ("Crimson King" × Rosy-magenta).

Fig. 47.   Terra-cotta (bluer type), green stigma.

Fig. 48.   Terra-cotta, green stigma.

Fig. 49.   Strawberry.

Figs. 50—55 represent various types of special coloration just external to the eye.

Figs. 50, 51.   Magenta, red stigma, with the spots of deep colour which are only fully developed in flowers possessing the red stigma.   Young and mature flowers.

Figs. 52, 53.   Magenta, green stigma, corresponding with the foregoing types.   Young and mature flowers.

Figs. 54, 55.   Young and mature flowers of a magenta with green stigma, showing the rather diffuse band of brownish colour, which only becomes conspicuous in the older flower (fig. 55).

Figs. 56—59 represent Flaked types.

Fig. 56.   Flakes medium to coarse; no fine flakes, green stigma.   *Stellata.*

Fig. 57.   Some coarse flakes; finer flakes rather peripheral in distribution; red stigma. *Stellata.*

Fig. 58.   Fully flaked, coarse and fine flakes, green stigma.

Fig. 59.   Fully flaked, coarse and fine flakes, red stigma.

[1] See note added February 17, 1911, p. 129.

PLATE XXXII.

Fig. 60.   Seedling plant of "Ivy-leaf," showing the non-crenate leaves.

Fig. 61.   Illustrating the cross between "Ivy-leaf" and "Snowdrift" (Fern-leaf, crenate).

Top row: "Ivy-leaf" (left), "Snowdrift" (right).

Middle: F_1 (palmate, crenate).

Bottom row: the four F_2 types (1) palmate, crenate, (2) palmate, non-crenate, (3) fern leaf, crenate, (4) fern-leaf, non-crenate.   The four types occur in the proportions $9:3:3:1$.

Fig. 62.   Showing the F_1's from crosses of the white-eyed race "Queen Alexandra" with the large-eyed "Primrose Queen," and with "Snowdrift" (ordinary eye).

Top row: "Primrose Queen," No. 37/9; "Queen Alexandra," No. 34/9; "Snowdrift," No. 1/9.

Second row: 36/9 F_1 from ("Primrose Queen" × "Queen Alexandra").

35/9 F_1 from ("Queen Alexandra" × "Snowdrift").

Fig. 63.   Showing the F_1's from crosses of the large yellow eye, *stellata*, with the ordinary eye in the *stellata* and typical *sinensis* forms.

Top row: *Stellata*, white, ordinary eye, No. 55/9; "Primrose Queen," No. 37/9; "Snowdrift" 1/9.

Second row: 48/9 F_1 from (*Stellata*, ordinary eye × "Primrose Queen").

38/9 F_1 from ("Primrose Queen" × *sinensis*, ordinary eye).

Fig. 64.   Showing the variation in the form of the corolla in a plant No. 54/9 and its offspring.

Top row: flowers from the same plant, No. 54/9.

Second and third rows: Flowers from four plants illustrating the various types produced by the self-fertilization of 54/9.   The flowers from each plant are arranged in pairs, one above the other.   The first three represent the nearest approach to *sinensis*, the intermediate and the *stellata* types in the Giant form.   The last pair of flowers are those of a *stellata* plant which did not possess the Giant character of its parent.

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PLATE XXX

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PLATE XXXI
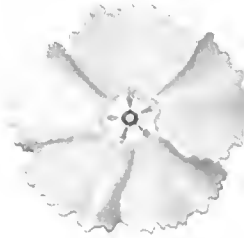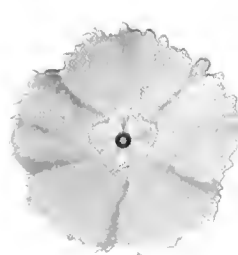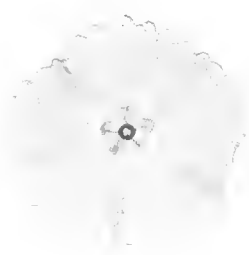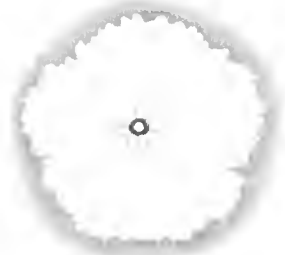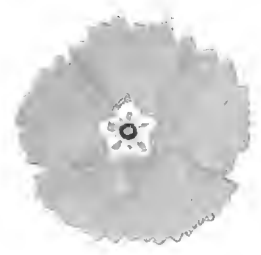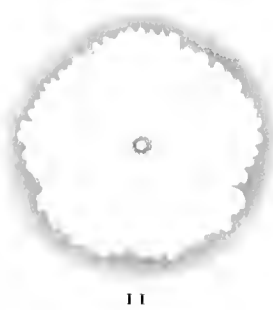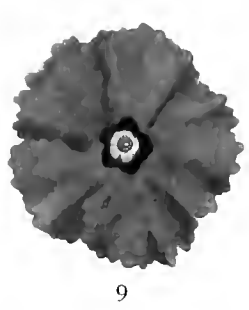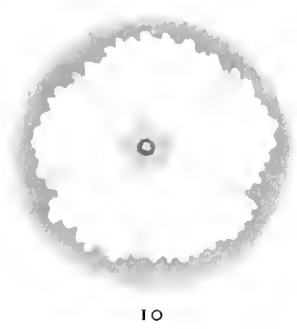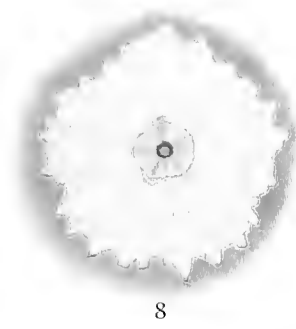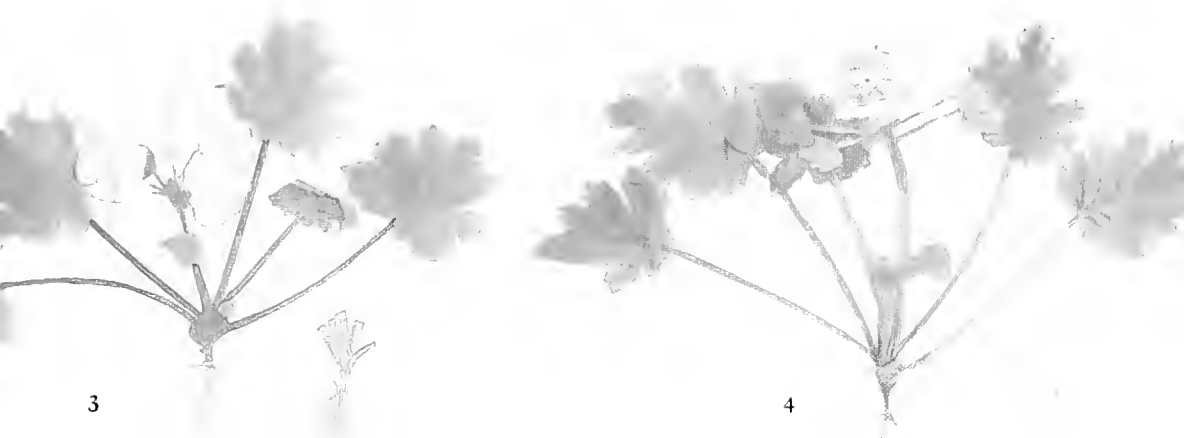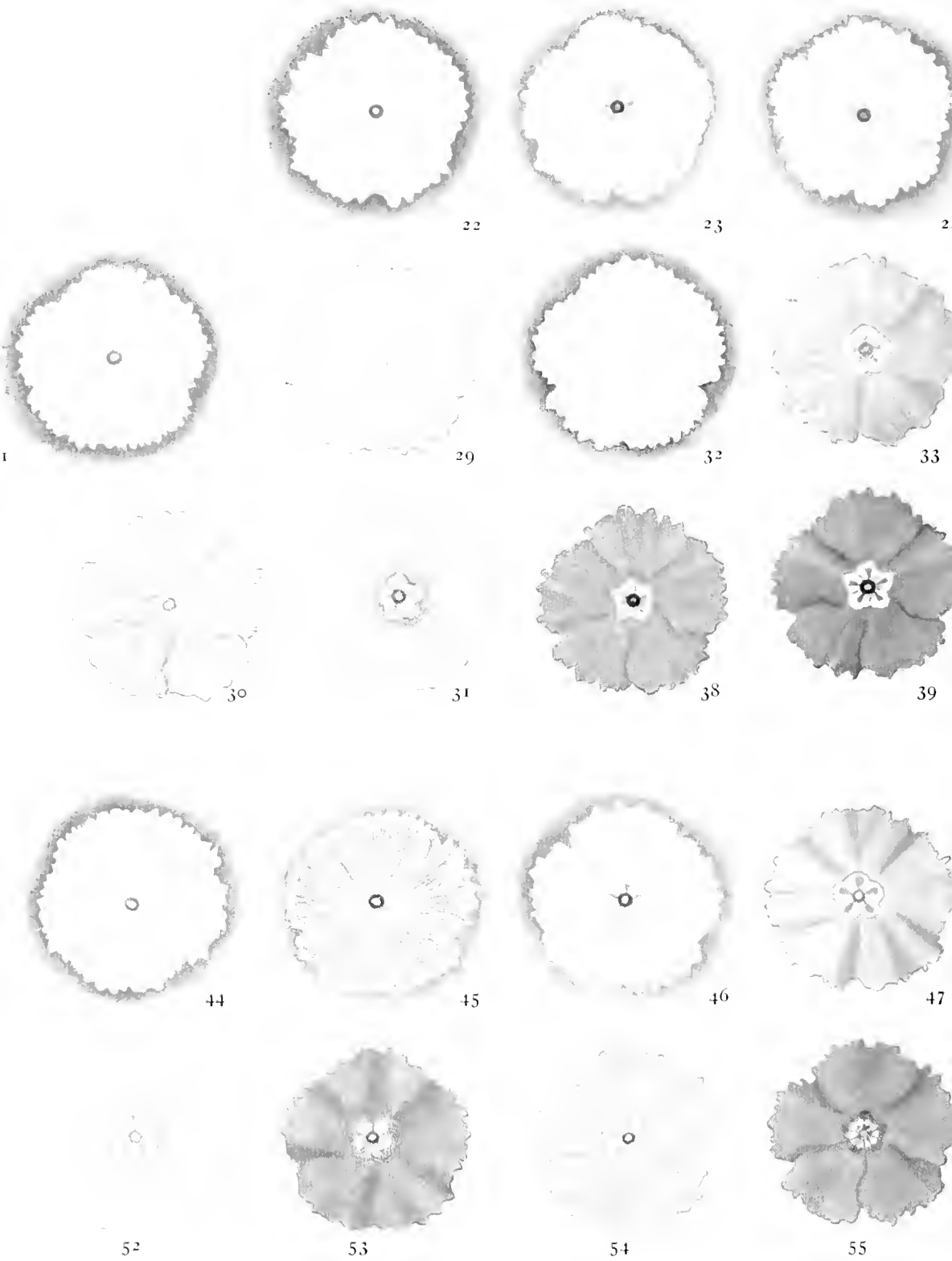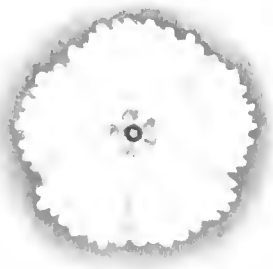
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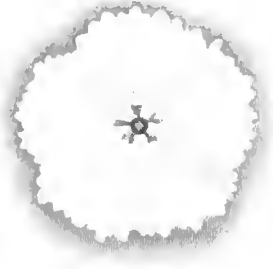
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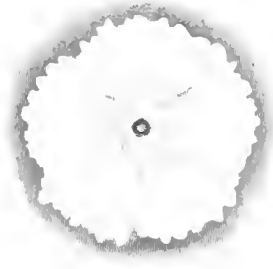
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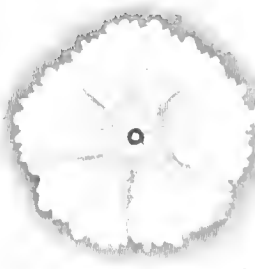
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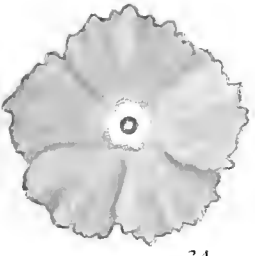
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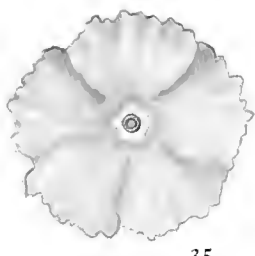
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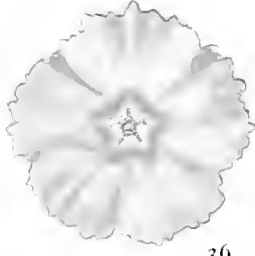
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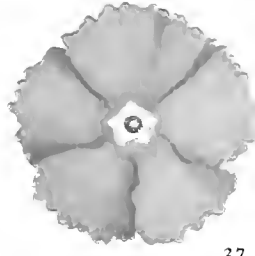
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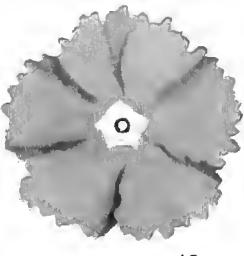
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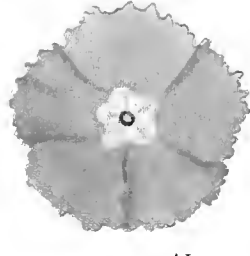
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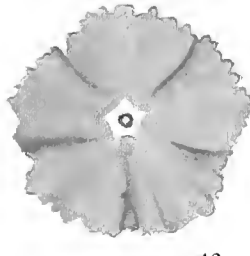
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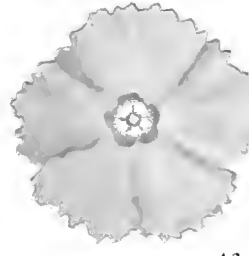
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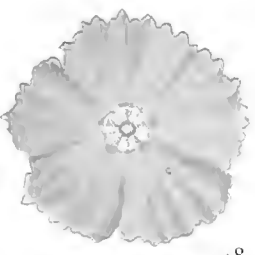
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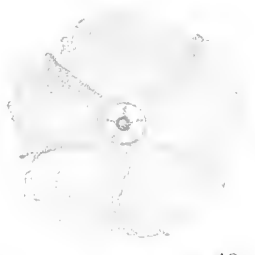
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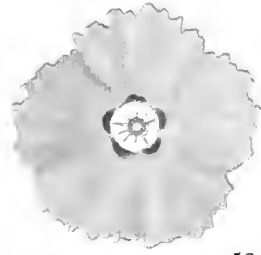
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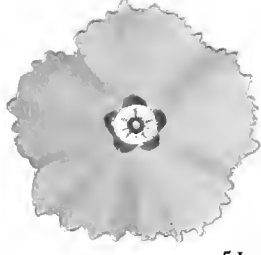
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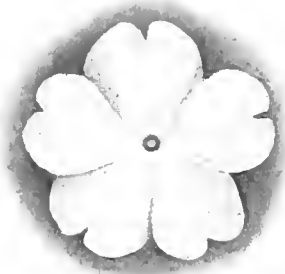
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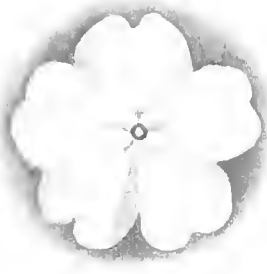
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Fig. 60

Fig. 61

PLATE XXXII
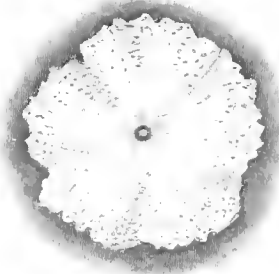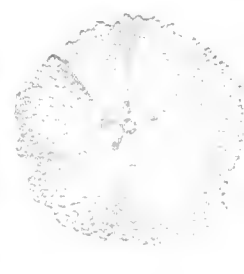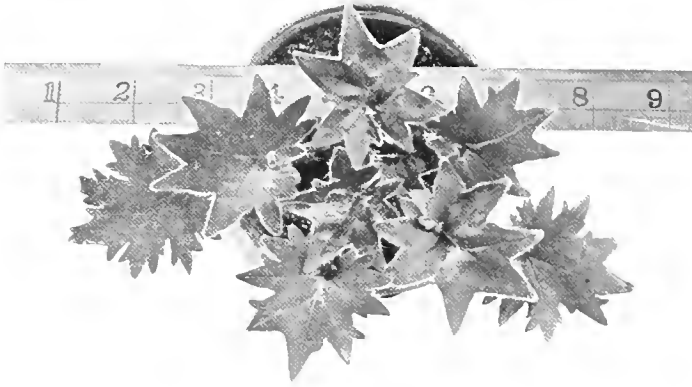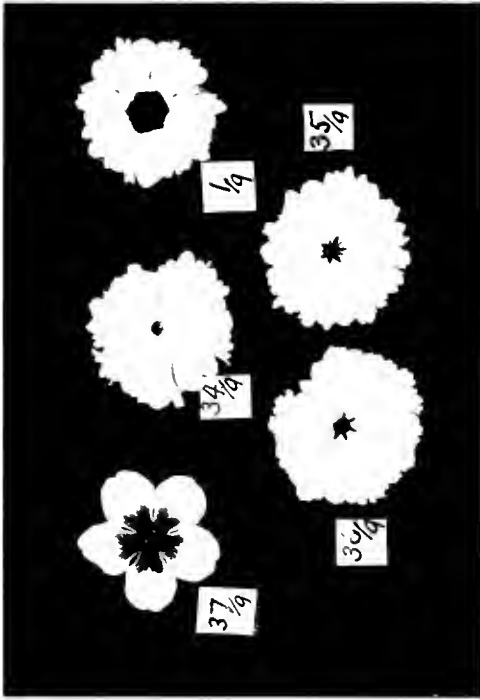
Fig. 62
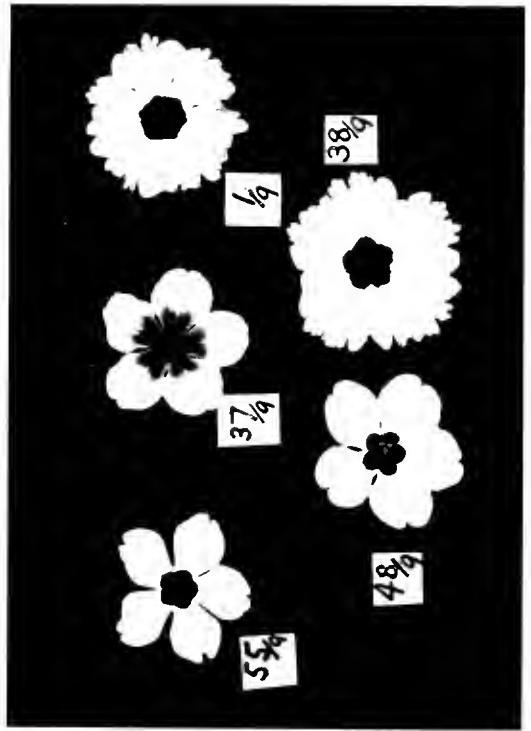
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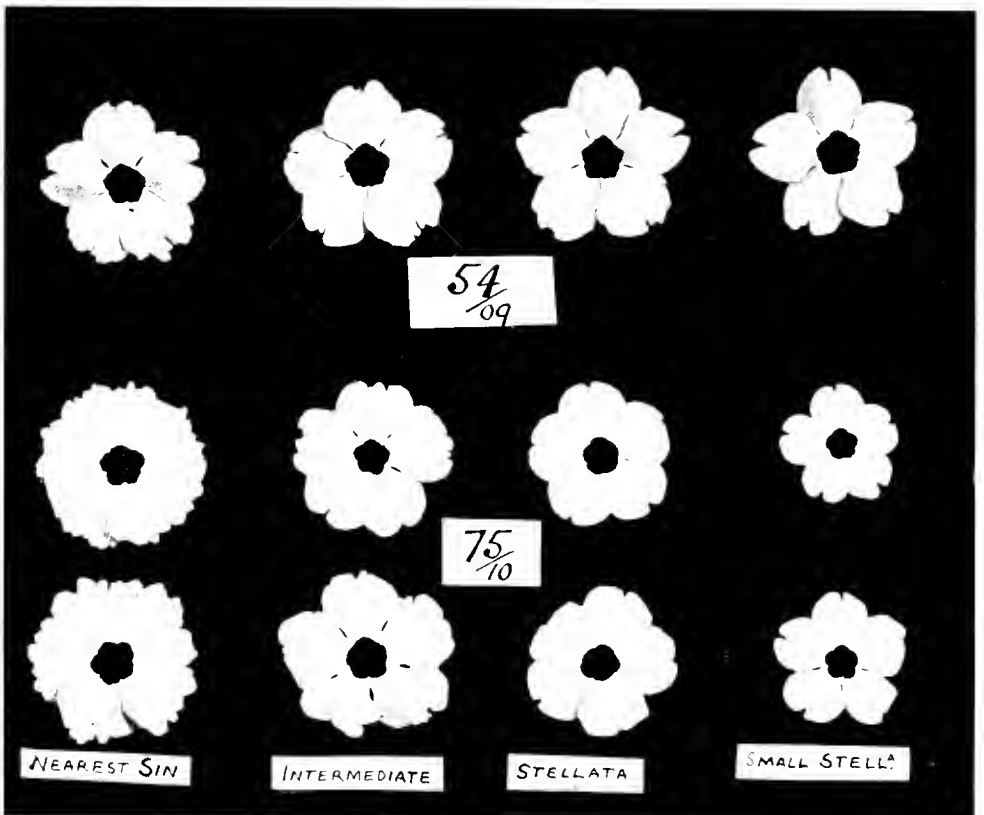
Fig. 64

ON THE FORMATION OF ANTHOCYANIN.

By M. WHELDALE,

Fellow of Newnham College, Cambridge.

NATURE OF PROBLEM AND PRELIMINARY STATEMENT OF CONCLUSIONS.

THE problem to which I have attempted to give a solution in the following pages may be briefly stated as follows:—what are the chemical processes which underlie the formation of anthocyanin?

In my attempt to arrive at some solution I have used as data the results of observations upon the general distribution of pigment, its formation in relation to other metabolic processes and to the chemical constituents of the tissue: also the conditions, both natural and artificial, which lead to its appearance, and lastly, the detection of enzymes which may be involved in its production.

As an outcome of this general investigation, I venture to bring forward an hypothesis which may afford in many respects an explanation, in terms of chemical reactions, of the mechanism underlying the phenomenon of soluble pigment formation. At the same time I may say that I look upon my suggestions as tentative and as having value possibly only in so far as they combine together into a general scheme a number of more or less isolated facts. I fully realise that the underlying causes of such a phenomenon are of a complex nature and may in reality demand a very different explanation from that which I am able to offer.

The ultimate object of the enquiry is the identification of the Mendelian factors for colour. There is little doubt that the formation of anthocyanin does involve a series of progressive reactions each of which is controlled by a certain enzyme. In variation, whatever that may be, the loss of these enzymes gives rise to different colour varieties. Hence the greater the complexity of the pigment-forming process

in any species, the greater the number of derivative varieties we may expect to appear under cultivation. Only an exact knowledge of the chemical reactions involved in the formation of pigment will enable us to explain the mechanism of colour inheritance and the cause of differences between varieties.

The main conclusions arrived at in the present paper may be summarised as follows :—

(1)   The soluble pigments of flowering plants, collectively termed anthocyanin, are oxidation products of colourless chromogens of an aromatic nature which are present in the living tissues in combination with sugar as glucosides.

(2)   The process of formation of the glucoside from chromogen and sugar is of the nature of a reversible enzyme action :

$$\text{Chromogen} + \text{sugar} \rightleftarrows \text{glucoside} + \text{water.}$$
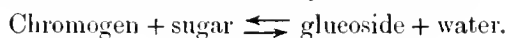
(3)   The chromogen can only be oxidised to anthocyanin after liberation from the glucoside and the process of oxidation is carried out by one or more oxidising enzymes :

$$\text{Chromogen} + \text{oxygen} = \text{anthocyanin.}$$
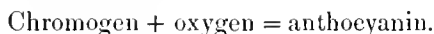
(4)   From (2) and (3) we may deduce that the amount of free chromogen, and hence the quantity of pigment formed at any time in a tissue, is inversely proportional to the concentration of sugar and directly proportional to the concentration of glucoside in that tissue.

(5)   The local formation of anthocyanin which is characteristic of the normal plant is due to local variation in concentration of either the free sugars or the glucosides in the tissues in which the pigment appears. The abnormal formation of pigment under altered conditions is due to differences in the concentration of these same substances due to changes in metabolism brought about by these conditions.

(6)   On the above hypothesis the formation of anthocyanin is brought into line with that of other pigments produced after the death of the plant, as, for example, indigo, the respiration pigments of Palladin, etc.

Results obtained by Previous Investigators.

Although the soluble pigments of plants have afforded material for a considerable amount of investigation, the sum total of results gives us very little knowledge either of the composition of these substances or of the processes which underlie their formation.

With regard to their chemical nature, I have previously(19) given reasons for the statement that the red, purple and blue pigments, collectively termed anthocyanin, are oxidation products of chromogens of an aromatic nature[1]. That, moreover, these chromogens, in the form of glucosides, are present in solution in the cell-sap throughout the living tissues and in the unoxidised state cause no colouration, but under certain conditions through the agency of an oxidase the chromogens may be oxidised to pigments, i.e. anthocyanin. This point of view is in agreement with that held by other investigators: Wigand(21), Pick(16), Mirande(9), Laborde(7), Overton(13) and Palladin(14), who have considered the soluble pigments either to be themselves aromatic compounds or to be intimately connected with tannins and allied substances.

That oxygen is necessary for pigment formation and that the oxidation is probably brought about through the agency of an oxidase has been suggested by Mirande(9), Palladin(14), and by Buscalioni and Pollacci(1).

Katić(5) and Molliard(11) have also shown experimentally that oxygen plays an important part in the appearance of pigment in certain organs.

So far, however, no hypothesis has been formulated as to the more exact mechanism of pigment formation, the reasons for its appearance only under certain conditions and for its localisation in definite organs and parts of the plant.

Wigand(21), it is true, has pointed out that the occurrence of anthocyanin in autumnal leaves, evergreen leaves in winter, injured or dying leaves, flowers and ripening fruits, indicates a connection between lessened assimilative activity and the production of pigment, though the nature of the connection remains unexplained.

Overton(13), on the other hand, basing his conclusions on results obtained from feeding leaves and plants with sugar solution, maintains that increase of sugar in the cell gives rise to formation of anthocyanin. He considers the pigment itself to be a glucoside of which the non-sugar part is a tannin-like compound.

Again no indication is given as to the exact nature of the connection between the excess of sugar and the appearance of pigment.

Katić(5), Molliard(11), Mirande(9) and Palladin(14) also support the statement that an accumulation of sugar increases the formation of

[1] In many cases, probably, members of the flavone and xanthone classes of compounds.

pigment. In addition Katić has shown experimentally that the production of pigment, though dependent upon the presence of oxygen, is independent of the presence of carbon dioxide.

Some important additions to our knowledge concerning the formation of anthocyanin have recently been published by Combes(3). This author has shown that the reddening of leaves is accompanied by an accumulation of oxygen in the tissues and that the disappearance of pigment on the other hand is accompanied by a loss of oxygen. In addition he has shown that red leaves contain proportionally greater amounts of glucosides and sugars than green leaves of the same plant. Combes considers the cause of oxidation to be this accumulation of glucosides and sugars which may arise from various external causes. These substances accelerate the processes of oxidation and hence the gaseous exchange may be fundamentally modified.

STATEMENT OF HYPOTHESIS.

From evidence which will be given in detail later I have been led to conclude that the formation of anthocyanin from a chromogen depends upon two processes, in which two different enzymes at least are involved.

The first reaction is reversible and may be expressed as follows:—

Glucoside + water $\rightleftarrows$ chromogen + sugar.
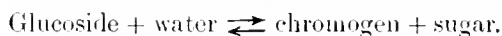
The same enzyme may be supposed to accelerate both the synthetic and hydrolytic reactions.

The second reaction is one of oxidation and is carried out by an oxidising enzyme or oxidase:—

Chromogen + oxygen = anthocyanin.
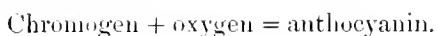
It must be further assumed that the chromogen can only be oxidised after liberation from the glucoside.

On the basis of this hypothesis, it follows that the amount of anthocyanin in any tissue depends upon the amount of free chromogen, and the latter, in accordance with the reversibility of the first reaction, is directly proportional to the concentration of glucoside and inversely proportional to the concentration of sugar in the tissue.

The frequent appearance of pigment, under abnormal conditions, in tissues which are normally unpigmented, justifies the supposition that every part of an anthocyanic plant is provided with this mechanism for the formation of pigment.

The local appearance of pigment in various plant tissues thus resolves itself into a matter of local variations in the concentration of sugars and glucosides in the tissues.

In order to test the validity of the hypothesis as stated above, it must be ascertained whether the conditions which give rise to formation of pigment are such as would influence the amount of glucosides and sugars present, and in this way it should be possible to demonstrate a connection, if it exists, between the two phenomena.

I have classified my evidence from various sources under the following headings :—

(1) Analogous reactions.

(2) Distribution of anthocyanin.

(3) Concentration of sugars and glucosides in various tissues.

(4) Existence of enzymes.

(5) Sugar-feeding.

EVIDENCE FROM ANALOGOUS REACTIONS[1].

Many of the reactions involved in plant metabolism are known to be of a reversible or balanced nature. Excess of sugar, for instance, may be converted into starch and thereby stored up in an insoluble form which is again hydrolysed into sugar when required. Similarly oils may be hydrolysed into fatty acids and glycerine, and these products again synthesised into oils. Synthesis and hydrolysis are also continually taking place between the disaccharides and the monosaccharides. Cane-sugar is synthesised from glucose and fructose and hydrolysed into the same products: dextrose is synthesised into maltose which is hydrolysed into dextrose and so forth.

As a typical reversible reaction we may quote the hydrolysis of ethyl acetate. When ethyl acetate is treated with water, hydrolysis into acetic acid and ethyl alcohol commences at once, but as soon as any products of hydrolysis are formed, the reverse action is also set up, namely the synthesis of ethyl acetate from acetic acid and ethyl alcohol. Hence in any mixture of the four substances, ethyl acetate, acetic acid, ethyl alcohol and water, two opposite reactions will proceed at different rates :—

Ethyl acetate + water $\rightleftarrows$ ethyl alcohol + acetic acid.

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[1] In connection with enzyme action I have freely quoted from Bayliss, *The Nature of Enzyme Action*, 1908.

After a time a certain relative concentration of the four constituents results and at this stage the velocities of the two reactions are equal and equilibrium is established.

If to a system of this kind, a catalyst, such as hydrochloric acid, is added, the equilibrium position has been shown to remain unaltered. From this it may be inferred that both the hydrolytic and synthetic reactions are equally accelerated by the catalyst.

In plants the greater number of reversible reactions are of a hydrolytic nature and are controlled by special catalysts, known as enzymes, produced by the living organism.

It is now known that a considerable number of these enzymes, as, for example, invertase, maltase, lipase, diastase and emulsin, can be extracted from the living tissues and their activities can be demonstrated under artificial conditions outside the plant. It is then found that in many cases the velocity of the hydrolytic reaction is so much greater than that of the synthetic that the equilibrium position is very near complete hydrolysis. When such is the case, we may infer that there is some, though very little, reversibility of the reaction. Hence if enzymes behave in the same way as inorganic catalysts, it should be possible to show that they are able to again synthesise the products they produce in hydrolysis if the right conditions can be found.

Croft Hill was the first observer to give experimental proof that enzymes accelerate synthetic processes, though in the special case investigated by him the synthesised product was an isomeric form of the compound hydrolysed. From a concentrated solution of glucose he obtained, through the action of maltase, small quantities of isomaltose which was again hydrolysed in dilute solution.

Since then many other cases have been discovered, such as the synthesis of the ester, ethyl butyrate, by lipase from a mixture of ethyl alcohol and butyric acid, of the glucoside, salicin, from saligenin and glucose, and of cane-sugar by invertase from glucose and fructose.

The value to the plant of even a slight reversible action has been pointed out by Bayliss(1A), for if the synthesised product is removed from the sphere of action as rapidly as it is formed, either owing to its insolubility or by translocation, a considerable amount of synthesis may eventually take place.

There is also in many enzyme actions a special retarding influence exerted by the respective products of action in addition to that due to reversibility of the reaction. Usually the retarding effect exerted by one of the products of action is greater than that exerted by the other;

or again one may have a retarding influence and the other none, as for instance in the case of invertase, which is retarded by fructose, whereas glucose has no effect.

There is little doubt that the retarding influence is due to the fact that the enzyme enters into some form of compound with the sugar and is thereby removed from the sphere of activity, with the resultant slowing down of the hydrolytic process.

There is a similar retardation in many cases in the synthetic process due to the combination of enzyme with the substrate. A full account of these retardation processes is given by Bayliss in *The Nature of Enzyme Action.*

The enzymes with which we are chiefly concerned in the present paper comprise the glucoside-splitting class. The term glucoside is applied to a large number of substances occurring in plants, all of which have the property of being hydrolysed by enzymes or by acids into glucose and one or more other products such as alcohols, aldehydes, phenols, etc.[1]

In some cases a glucoside, as, for example, xanthorhamnin, is only hydrolysed, as far as we know, by one particular enzyme, rhamnase, though sometimes one enzyme, such as emulsin, will hydrolyse a considerable number of different glucosides, i.e. arbutin, salicin, coniferin, syringin, helicin, amygdalin, aesculin, daphnin, and others.

An interesting point in connection with the glucoside-splitting class of enzymes is the rapidity with which the hydrolytic reactions take place when the plant is submitted to the action of chloroform vapour or other anaesthetics. Injury to the tissues will also bring about the same result. This reaction is readily detected if the products of hydrolysis have a characteristic odour, as for instance in the case of cyanogenetic glucosides, of which amygdalin is the best known example. Amygdalin occurs in bitter almonds and in the kernels of peaches, apricots, plums and other fruits of the Rosaceae. By emulsin it is hydrolysed according to the equation :—

$$C_{20}H_{27}O_{11}N + 2H_2O = C_7H_6O + HCN + 2C_6H_{12}O_6$$

amygdalin   benzaldehyde   hydrogen cyanide   glucose
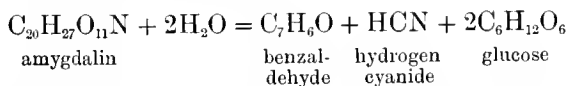
and the progress of the reaction can be detected by means of the characteristic odour of the products.

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[1] An account of these substances is given by E. F. Armstrong in *The Simple Carbchydrates and Glucosides.*

The mustard oil glucosides, sinigrin and sinalbin, occurring in mustard and other Cruciferae, also give products with a characteristic odour of mustard oil on hydrolysis :—

$$C_{10}H_{16}O_9NS_2K + H_2O = C_3H_5CNS + C_6H_{12}O_6 + KHSO_4$$

sinigrin   allyl sulpho-cyanide
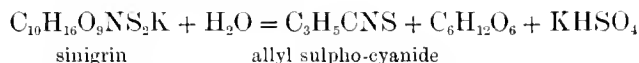
The hydrolysis of glucosides on autolysis in chloroform or through injury, can also be detected when the non-sugar component of the glucoside molecule is an aromatic substance, which when free from glucose is subsequently oxidised to a coloured compound through the agency of an oxidising enzyme (oxidase); in this case the development of colour indicates the progress of the reaction.

In some genera the pigments produced in this way after death or injury to the plant are red, purple or blue, and hence attention has been drawn to the phenomenon, and the products so formed have been used commercially for dyeing purposes. The best known examples are the "indigo plants," *Indigofera spp., Isatis tinctoria, Polygonum, tinctorium*, etc.

The processes taking place in the formation of indigo have been very fully investigated and can be expressed as follows :—

$$C_{14}H_{17}O_6N + H_2O = C_6H_{12}O_6 + C_8H_7ON$$

indican   glucose   indoxyl

$$2C_8H_7ON + O_2 = 2H_2O + C_{16}H_{10}O_2N_2$$
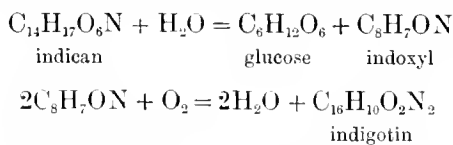
indigotin

The first reaction is brought about by a glucoside-splitting enzyme, indimulsin, which hydrolyses the glucoside, indican ; the second by an oxidase which oxidises the colourless indoxyl to the pigment indigotin or indigo.

Another striking example is the rapid formation of a bright red pigment in the flowers and leaves of *Schenkia blumenaviana* on autolysis in chloroform as described by Molisch(10).

Though the formation of a brightly coloured pigment after death is a comparatively rare phenomenon, yet many plants rapidly turn brown or reddish-brown when placed in chloroform vapour. The same effect is produced by mechanical injury and sometimes by immersion in absolute alcohol (*Mirabilis Jalapa*). Extracts from such plants give a blue colour with guaiacum tincture and there is little doubt that the production of pigment is due to the oxidation of an aromatic substance through the activity of the oxidase.

This appearance of pigment on autolysis is especially frequent among genera of the Labiatae, Boraginaceae, Scrophulariaceae and Umbelliferae, though it is also generally characteristic of some of the genera in most Natural Orders. Often, as in the Ranunculaceae, this phenomenon is peculiar to all species of certain genera (*Anemone, Helleborus, Clematis, Trollius, Caltha* and *Aconitum*), which rapidly yield brown pigment on autolysis in chloroform, whereas all species of other genera (*Ranunculus, Paeonia, Aquilegia* and *Thalictrum*) give no colour in the same time of exposure.

It is probable that the processes involved in the formation of post-mortem pigments are in all cases analogous to those known to take place in the production of indigo. The aromatic chromogen, from which the pigment is produced, is combined with sugar in the form of a glucoside in the living cell. In such a form the chromogen cannot be attacked by the oxidase. When the cell is subjected to chloroform vapour, the velocity of the hydrolytic reaction is accelerated and the whole of the glucoside is split into chromogen and sugar. The free chromogen is then fully oxidised by the oxidase.

According to the view held by Palladin(14), these aromatic glucosides, together with the glucoside-splitting and oxidising enzymes, form an important system in the plant for the purpose of oxidising respirable materials, and the post-mortem pigments have been termed by him "respiration pigments." In the living unpigmented cell, the processes of oxidation, reduction and the glucoside-splitting reaction are so balanced that no free pigment appears. To quote Palladin(15):— "Einer sparsamen Hausfrau vergleichbar, hält die Zelle die Chromogene verschlossen und verausgiebt sie in geringen Mengen für Oxydationsprozesse. Die Ausgabe wird durch ein die Prochromogene spaltendes Enzyme besorgt."

To the chromogen in combination with sugar as a glucoside, Palladin has applied the term "prochromogen." He also includes anthocyanin among the respiration pigments, but does not offer any very definite explanation of the appearance of anthocyanin in various plant organs.

I am inclined to believe that anthocyanin itself has no direct respiratory function in that it is absent from albino varieties, which do not appear to suffer from the loss of pigment, since they grow and reproduce quite as vigorously as the pigmented types.

From the description of enzyme actions given above it will be seen that a series of reactions such as I have supposed to take place in the

formation of anthocyanin is known to occur in connection with the oxidation of aromatic compounds in the plant. The essential difference between such reactions as lead to the formation of indigo, and those which have been suggested for anthocyanin, lies in the nature of the oxidase. In the former case the oxidase continues its function after the death of the cell, but so far there is no evidence of anthocyanin being formed in extracts from the plant[1], and it seems highly probable that it is a process which is difficult or perhaps impossible to induce under artificial conditions. The nature of the oxidases concerned will be discussed later.

DISTRIBUTION OF PIGMENT.

The various organs of the plant in which anthocyanin may appear can be enumerated as follows:

Under normal conditions.

(1)   Veins, midribs and petioles of many leaves. Herbaceous stems and the young stems of shrubs and trees.

(2)   Leaves of red-leaved species (*Amaranthus*, *Coleus*, etc.).

(3)   Leaves of red-leaved varieties of green-leaved types (*Fagus*, *Corylus*, *Beta*, *Atriplex*, etc.).

(4)   Young developing leaves (*Quercus*, *Rosa*, *Crataegus*, etc.).

(5)   The older leaves of many plants (*Fragaria*, *Aquilegia*, etc.), and sometimes the whole plant (many Umbelliferae, *Galium aparine*, etc.) towards the end of the vegetative season.

(6)   Variegated leaves in which the chlorophyll is absent from certain areas.

(7)   Flowers and ripe fruits.

Under abnormal conditions.

(1)   Leaves which have been injured either mechanically or through the attacks of insects and fungi.

(2)   Autumnal leaves.

(3)   Leaves exposed to low temperatures, such as evergreen leaves in winter (*Hedera Helix*, *Ligustrum vulgare*, *Mahonia sp.*, etc.).

(4)   Leaves exposed to drought.

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[1] Except in so far as I have been able to induce a formation of colour in an extract from *Primula* flowers by means of Horseradish peroxidase in presence of hydrogen peroxide. *Proc. Camb. Phil. Soc.* Vol. xv. 1909.

Leaves. The majority of leaves during the active vegetative period are entirely without soluble pigment so far as the eye can detect. Nevertheless it is possible that the leaves of anthocyanic plants may contain a small amount of pigment though it is not apparent as such. The leaves of albinos, for instance, are frequently of a brighter and lighter shade of green than leaves of the pigmented type even when the latter are without obvious pigment, and this difference can often be detected before the plant flowers. The deeper colour may, however, be due to some other cause.

When pigment is present in the veins and midrib, as is normally the case in many leaves, it is usually confined to the epidermal (generally upper) and sub-epidermal layers.

In leaves which are more or less permanently red (*Amaranthus spp.*), the pigment is commonly present in the epidermis only, both upper and lower, all over the leaf, but in the midrib and veins it may appear in the sub-epidermal layers also.

In red-leaved varieties (*Atriplex hortensis* v. *rubra*, *Beta vulgaris* v. *rubra*, etc.) arising from a green-leaved type, the pigment is again usually only present in the epidermis, both upper and under, of which the cells are intensely coloured.

It is an interesting fact that the guard-cells of the stomata in the epidermis of permanently red-leaved plants and red-leaved varieties are colourless when all the surrounding epidermal cells are intensely coloured.

The cases of abnormal formation of pigment in leaves may now be considered. If a leaf is subjected to any kind of injury, this is accompanied in many plants by a more or less intense colouration of the tissues. The injury may be a mechanical one, such as tearing of the lamina, partial breaking of the midrib, petiole or stem, or the removal of a portion of the midrib. In each case the leaf becomes pigmented in the part distal to the point of injury. Sometimes the whole leaf when severed from the plant and lying in a fairly moist situation will turn red or purple. Injury may also be brought about by attacks of insects, leaf-boring larvae, aphides and fungi. In all such cases pigmentation results.

Sections of leaves which have been injured show a different distribution of pigment from those which are normally coloured. Anthocyanin is most frequently present in the palisade parenchyma, often in the spongy parenchyma, and more rarely in the epidermis and veins, unless these were originally coloured in the normal leaf.

Hence we may state that in injured leaves the formation of pigment commences in tissues which in the healthy plant are usually unpigmented.

The same internal distribution of pigment is found in leaves reddened by low temperature, i.e. autumnal leaves and evergreen leaves in winter, and also in the older dying leaves of plants at the end of their vegetative season or after exposure to drought.

It is an interesting coincidence that the phenomenon of increased pigmentation accompanying age is also characteristic of young developing leaves. In these again the pigment is formed in the assimilating tissue, chiefly palisade parenchyma, though it may also appear in the epidermis.

Anthocyanin is very frequent in variegated leaves and it is then often limited to the stripes or patches free from chlorophyll (variegated *Zea Mais*). In other cases (*Codiaeum sp.*, *Acalypha sp.*, *Tradescantia sp.*), the whole leaf may be pigmented.

Stems and Petioles. The distribution of pigment in petioles, herbaceous stems and the young stems of trees and shrubs is very much the same as in the midribs of leaves. Anthocyanin is usually confined either to the epidermis alone or to one or more sub-epidermal layers in addition, of which the cells are frequently collenchymatous in structure.

Flowers and Fruit. In the corolla, anthocyanin is located in the epidermis, usually both upper and under, sometimes only upper. The upper pigmented epidermal cells are almost always more or less prolonged into papillae but this prolongation is less characteristic of the under epidermal cells.

In fruits the colouring matter may be limited to the epidermis and sub-epidermal layers or may extend into the inner tissues.

Concentration of Sugars and Glucosides in various Tissues.

To ascertain the relative concentrations of sugars and glucosides in the different tissues of a leaf is a difficult problem.

The presence or absence of glucose can be detected micro-chemically by means of Fehling's solution (22), and to some extent glucose, fructose, maltose and cane-sugar can be differentiated micro-chemically by a modification, employed by Grafe (4), of Senft's (17) phenyl hydrazine method. For detection of differences in amount I have not found these methods reliable.

Since no absolute reliance can be placed on the above tests, it is only possible to draw deductions indirectly from such evidence as we possess from other sources.

Broadly speaking the concentration of sugars in a leaf depends upon :

(1)   The assimilative activity.

(2)   The starch-forming activity.

(3)   The rate of translocation of sugars.

Since these three factors are more or less interdependent and form in co-operation a self-regulating mechanism, the concentration of sugar as the outcome of their combined activities may under normal conditions remain fairly constant.   But if a tissue has assimilative without starch-forming power or *vice versa*, we have perhaps some basis for conjecture as to the concentration of its sugar-contents compared to that of other tissues possessing both activities.   There is a like possibility if the different activities are affected in varying degrees by changed conditions, and this question will be considered again in connection with abnormal reddening in leaves.

The question of the concentration of aromatic glucosides in a leaf is even more problematic.   Kraus(6) has given experimental evidence for regarding the assimilating leaf as the seat of metabolism of aromatic substances.   This author found, as a result of analysis, that aromatic compounds[1] accumulate in a cut leaf exposed to illumination but decrease in a leaf kept in darkness.   He moreover states the amount of aromatic substances formed to be proportional to the assimilative activity of the leaf.

Palladin(14) also holds the view that the aromatic materials of a plant are manufactured from the carbohydrate series.   In corroboration of his view, he quotes the results of Waage(18), who obtained an increased amount of phloroglucin in leaves fed on glucose solution ; also those of Büsgen(2), who found that the tannin contents of plants increase in glucose cultures.

On such evidence as we have, we may say that the concentration of aromatic substances in a leaf depends upon :—

(1)   The amount of sugars present in the leaf.

(2)   The rate of translocation of aromatic substances.

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[1] In this case, tannins, but the precise nature of the products is immaterial provided they belong to the aromatic series.

In the formation of anthocyanin the following reactions must be taken into consideration :—

Aromatic glucoside + water $\rightleftharpoons$ aromatic chromogen + sugar.

Sugar $\longrightarrow$ aromatic chromogen.

Aromatic chromogen + oxygen = anthocyanin.
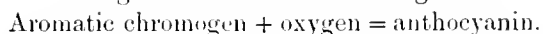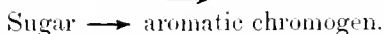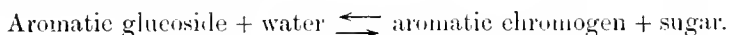
The following possibilities may therefore arise. The amount of pigment is directly proportional to the amount of free chromogen. Increase of sugar would naturally lead to decrease of free chromogen, but if at the same time additional chromogen is formed from the sugar, the ultimate concentration of the glucoside, if it is not removed by translocation, will be increased to such a degree that the final result is an increase of free chromogen accompanied by formation of pigment.

A decrease of sugar, on the other hand, will increase the free chromogen, but at the same time it will lead to a decrease in the concentration of the glucoside, so that the final result is a decreased amount of free chromogen and less possibility of pigment formation.

Or to state the case rather differently : so long as the concentration of glucoside remains low either as a result of translocation or of decreased formation, the amount of free chromogen is negligible, but if the concentration of glucoside is raised beyond a certain point as a result of diminished translocation or continual formation, the synthesis of free chromogen and sugar can no longer take place and the former becomes oxidised to anthocyanin.

In the normal green leaf the absence of pigment from the mesophyll is in all probability due to the rapid translocation of aromatic glucosides away from the leaf. It is difficult to ascertain the precise reason for the presence of pigment when it appears in the epidermis of the lamina and in the epidermis and sub-epidermal layers of the veins and petiole. It may be caused either by low concentration of sugar or by increased concentration of glucosides due indirectly to excess of sugar. These tissues are without chlorophyll and the power to assimilate, but at the same time they are also apparently devoid of starch-forming capacity, since starch does not as a rule appear in them, so that the sugar concentration may or may not be greater than in the mesophyll of the leaf.

In general the chlorophyll-containing tissues are most free from pigment, the non-chlorophyllous more frequently pigmented. Hence the appearance of pigment is undoubtedly connected with the concentration of sugar, but I am at present unable to give the exact sequence of events which affects the reversibility of the reaction.

That a relationship exists between pigmentation and assimilation is further borne out by the appearance of anthocyanin in old leaves, variegated leaves (with parts free from chlorophyll), autumnal leaves, leaves exposed to drought or low temperature and in flowers and ripening fruits. In all these cases the same difficulty arises as to the real cause, since the starch-forming power may be diminished as well as the assimilative. Starch does not as a rule appear in petals; and in fruits the colouring matter is often limited to the epidermis and sub-epidermal layers which are free from starch though the flesh of the fruit may be full of starch. In variegated leaves the chlorotic portions, in which pigment often appears, are unable to form starch. I have made a number of observations upon the starch contents of green leaves and of leaves, from the same plant, reddened as a result of cold, drought, etc., and I have found the red leaves almost invariably to contain less starch than the green.

It must also be borne in mind that the translocation of both sugar and glucosides may be hindered by low temperature, drought, age, etc. I am inclined to believe, in the absence of more direct evidence, that the reddening under these conditions is due to diminished translocation of glucosides combined with increased formation of these substances due to the presence simultaneously of excess of sugar.

Results lately published by Combes(3) corroborate this view to some extent. Combes has made comparative estimations of the glucosides and sugars in both red and green leaves of *Ampelopsis hederacea* in which reddening was due to light intensity, and in *Rosa canina*, *Mahonia aquifolium* and *Sorbus latifolia* showing autumnal colouration.

His results may be expressed as follows:—

			Sugars	Dextrins	Glucosides	Insoluble Carbohydrates
Ampelopsis hederacea	...	green	·74	2·78	2·43	2·42
		red	·98	1·88	2·79	5·02
Rosa canina	... ...	green	2·42	1·30	8·22	9·72
		red	2·64	1·23	8·24	5·33
Sorbus latifolia	... ...	green	·71	1·15	2·20	11·99
		red	·80	1·07	2·52	1·20
Mahonia aquifolium	...	green	·57	·80	3·41	2·38
		red	1·30	·60	4·30	8·78

From these numbers we see that the concentration of glucosides and sugars in red leaves is greater than in green, that of dextrins greater in green than red, whereas the amount of insoluble carbo-

hydrates varies, being sometimes greater in one, sometimes in the other.

Since the concentration of *both* glucosides and sugars is greater in the red leaves, it is reasonable to interpret the pigment formation as being due to accumulation of glucosides, in which case the reaction

$$\text{Glucoside + water} \longrightarrow \text{sugar + chromogen}$$
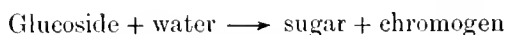
would give rise to more free sugar (apart from other causes) in the red than in the green leaf from which the glucosides are continually removed, so that the concentration of glucoside is lowered

$$\text{Sugar + chromogen} \longrightarrow \text{glucoside + water.}$$

Kraus(6) has also shown that red autumnal leaves contain more aromatic substances than normal red leaves.

Results, however, which are more convincing than these just stated, are those connected with the phenomenon of reddening produced by injury. Instances have already been quoted of pigment formation due to injury to the cortical tissues of the midrib and petiole or to the removal of a portion of the midrib or main veins of a leaf. According to Kraus(6) the path taken by aromatic substances in translocation is the vascular system of the leaf, but whether by the phloem or the surrounding parenchyma is not stated. In any case injury to the vascular system of the leaf or the living tissues of the petiole or stem would involve an accumulation of glucosides in the parts distal to the point of injury. It has been recently suggested by Mangham(8) that the sugars travel from the leaf by the phloem. If such is the case, the injury may also lead to accumulation of sugars and hence indirectly to more glucoside.

Combes(3) has shown that decortication in spp. of *Spiraea* induces reddening of the leaves above the point of operation. A similar observation has been made by Kraus for *Cornus alba*, and I have myself observed a similar result following upon decortication in *Ribes Grossularia* and a species of *Salix*.

Combes(3) has shown by analysis that there is a large increase of both glucosides and sugars in the leaves of *Spiraea* which had reddened as a result of decortication.

The following are the numbers given :—

		Sugars	Dextrins	Glucosides	Insoluble Carbohydrates
Spiraea paniculata	green	2·21	1·01	1·64	10·75
	red	4·26	·92	6·15	26·58

Kraus(6) also found that some cut leaves redden when placed in water in bright sunshine, and on analysis gave greater quantities of aromatic substances than control leaves kept in the dark.

EVIDENCE FOR THE PRESENCE OF ENZYMES.

If the formation of anthocyanin is dependent upon enzyme action, it should be possible to obtain evidence of the existence of both glucoside-splitting enzymes and oxidases in the tissues of anthocyanin plants.

Glucoside-splitting enzymes. For the detection of glucoside-splitting enzymes I have employed the following method. The tissue to be examined is well ground and thoroughly washed with $75°/_{0}$ alcohol: it is then dried in air and extracted with distilled water. These processes are carried out as far as possible under sterilised conditions. The water extract is then added to a definite quantity of salicin solution and kept, together with a control flask, at a temperature of from $36°$—$40°$ C. for 24 hours. The following reaction then takes place :—

Salicin + water = saligenin + glucose.
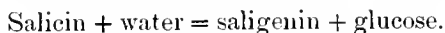
The saligenin is extracted from the liquid by shaking with ether and after evaporation of the ether its presence can be detected in the residue by means of ferric chloride with which it gives a violet colouration.

By this method I have demonstrated the presence of a glucoside-splitting enzyme in the following :—leaves of *Corylus Avellana, Rumex crispus, Taraxacum officinale* and *Primula sinensis,* flowers of *Cytisus scoparius, Aquilegia vulgaris, Viola tricolor, Antirrhinum majus, Primula sinensis, Narcissus pseudonarcissus, Cheiranthus cheiri, Fritillaria imperialis, Polyanthus sp., Helleborus orientalis, Pyrus japonica, Prunus avium, Galanthus nivalis, Narcissus Tazetta, Pelargonium zonale,* and tubers of *Solanum tuberosum.*

These results show that glucoside-splitting enzymes are widely distributed. In other species a negative result was obtained but this is to be expected, since all such enzymes may not be able to hydrolyse salicin.

If glucose solution is added to the salicin solution plus the enzyme the hydrolysis of the salicin is greatly retarded.

Also if the preliminary treatment with alcohol as described above is omitted and a water extract is made from the fresh plant tissues and added to salicin, very little or no hydrolysis of the latter takes place.

This retardation is doubtless due to the fact that the water extract contains, in addition to the enzyme, the glucosides and sugars present in the plant. Thus the products of hydrolysis of the glucosides derived from the plant would retard or entirely prevent hydrolysis of the salicin added. By treatment with alcohol, all glucosides and some part of the sugars are removed previous to extraction with water.

Oxidases. It has been previously mentioned that Palladin(14) considers anthocyanin to be a respiration pigment. That oxygen is necessary for its production has been shown experimentally both by Molliard(11) and Katić(5).

The dependence of pigment formation on the presence of oxygen can be readily demonstrated in a very simple way. If cut leaves of *Taraxacum officinale* are placed in sugar solution so that the lamina is partially immersed, reddening only takes place in the portion exposed to air and not in the submerged part. The oxygen may also be excluded by greasing part of the leaf with vaseline. The greased portion remains green while the ungreased portion develops a considerable quantity of pigment. Similar results have been obtained with leaves of *Heracleum sphondylium, Sambucus nigra* and *Hieracium sp.*

Apparently no reverse process of deoxidation takes place when a coloured leaf is greased so as to prevent all gaseous exchange. If anthocyanin constitutes a medium for the transference of oxygen, we should expect the colour to disappear as a result of reduction when coloured leaves are deprived of oxygen, especially since respiration is one of the last " vital processes " to disappear. The strongest argument against Palladin's hypothesis is the existence of well-developed albino varieties of an almost innumerable number of species.

The question of the oxidising enzyme presents some difficulty. In all plants forming post-mortem pigments, oxidases can be detected by means of guaiacum tincture, with which the extracts give a strong and rapid direct action. Yet blueing of guaiacum is not limited to these cases, for a less rapid direct action is also given by other plants (*Lathyrus, Matthiola*), which do not form pigments on autolysis. All the guaiacum-blueing species I have examined have been anthocyanic, and the possibility suggests itself that the oxidases may form anthocyanin in the living plant but a post-mortem pigment after death. There is some evidence in favour of this supposition: first, when a plant forms anthocyanin and also a post-mortem pigment, the former is converted into the latter on autolysis and the organs which contain

most anthocyanin produce the greatest quantity of brown pigment. Secondly, when fully pigmented flowers of the type in any species (cultivated spp. of *Chrysanthemum, Petunia* and *Pyrethrum*) give a strong oxidase reaction, tinged or less intensely coloured varieties frequently give a less strong reaction, which may indicate that some part of the oxidising mechanism has been lost from the varieties, as I have previously suggested(19) for *Lathyrus* and *Matthiola*.

On the other hand, very many anthocyanic plants give no direct action with guaiacum, although nearly all living tissues give an indirect action (i.e. after addition of hydrogen peroxide). It is possible that the direct action is inhibited in these cases by some strong reducing substance in the plant. It is also more than probable that anthocyanin oxidases are of a nature totally different from those connected with respiration pigments and may, many of them, not react with guaiacum. For the present no other explanation appears available.

Some work on oxidising enzymes has been recently published by Moore and Whitley (12). These authors do not support the hypothesis of Bach and Chodat, i.e. that an oxidase consists of a mixture of two enzymes, an oxygenase which acts upon certain substances in the plant forming peroxides and a peroxidase which transfers the additional oxygen atom from the peroxide to other bodies.

When both enzymes are present, the plant extracts have a direct blueing action on guaiacum, but when the peroxidase exists alone, hydrogen peroxide must be added before blueing results (indirect action).

Moore and Whitley suggest that only one enzyme—peroxidase—is involved in the process and that the blueing, to a greater or less degree, of guaiacum by plant extracts, is due to the existence of more or less organic peroxide in the tissues and that no special enzyme involved in the formation of peroxide can be detected.

This point of view greatly simplifies the conception of oxidation processes. I am nevertheless of the opinion that peroxide formation in the plant may be controlled by an enzyme, though it may not be possible to extract this substance and to obtain an expression of its activities under artificial conditions.

Since, moreover, the presence of organic peroxides in plants is directly connected with the appearance of post-mortem pigments, it must follow that the metabolism of this class of plants differs in some fundamental respect from that of others; and in my opinion such a constitutional difference may quite well involve the existence of at least one special enzyme.

SUGAR-FEEDING.

It is obvious that in the consideration of such an hypothesis as that which I have formulated, any evidence of a connection between increased pigmentation and increased concentration of sugars brought about by artificial feeding of plants or parts of plants with various sugars would be of considerable value.

Such a method of research has been adopted by Overton(13). This author maintains that the conversion of sugar into starch is lessened by a lowering of the temperature. Hence the pigment of autumnal leaves and evergreen leaves in winter is due to excess of sugar induced by low temperature.

In order to test his hypothesis, Overton made a number of sugar-feeding experiments with both water and land plants. The water plants were grown either submerged or floating in solutions of cane-sugar, glucose, fructose, etc. In the case of land plants, the cut ends of leafy stems or the petioles of leaves were placed in the solutions.

Many of the species used (*Hydrocharis morsus-ranae, Utricularia spp., Lilium Martagon, Ilex aquifolium, Hedera Helix, Ligustrum vulgare, Saxifraga spp., Crassula spp., Aquilegia vulgaris, Taraxacum vulgare, Eupatorium cannabinum* and *Epilobium parviflorum*), showed increased formation of pigment, but in other cases (*Potamogeton spp., Lemna spp., Fritillaria imperialis, Mahonia aquifolium, Anthriscus sylvestris, Rubus spp.*, white flowers of *Pelargonium zonale*, and *Anemone japonica*) there was a negative result.

Increased colour sometimes appeared in control plants kept in distilled water under good illumination.

Corroborative results have also been obtained by Katić(5) with plants of *Hydrilla, Elodea canadensis, Hydrocharis morsus-ranae*, leaves of *Sagittaria natans, Canna indica, Veronica chamaedrys, Rosa sp., Saxifraga cordifolia, Pittosporum undulatum* and *Bellis perennis*.

Overton has proved his results to be due to the chemical nature of the dissolved substance and not to any osmotic action by the use of control solutions of neutral salts, i.e. sodium chloride, sodium sulphate, potassium sulphate of osmotic strengths equivalent to those of the sugar solutions employed. In no case where a neutral salt was used, was there any increase in pigmentation. In *Lilium Martagon*, an increase of pigment resulted from the use of ethyl and methyl alcohol solutions.

In view of Overton's suggestion that increased sugar concentration may under some conditions be brought about by a decreased starch-forming capacity, I thought it possible that some connection might exist between the reddening of leaves and starch formation in sugar-

cultures. I therefore made a number of sugar-feeding experiments with various species and at the same time I examined the starch contents of the leaves after this treatment.

The leaves employed were first kept in the dark until starch-free, and a piece of each leaf was placed, after this treatment, in methylated spirit as a control. Portions of the same leaf were then floated, upper surface downwards, in two dishes, one containing $3°/_\circ$ cane-sugar solution, the other distilled water. Both dishes were placed under a bell-jar together with a dish containing strong caustic potash solution, air being allowed to enter the bell-jar only by means of a tube containing soda-lime. Control dishes of sugar solution and distilled water containing further portions of the same leaf were placed under a bell-jar without potash solution. After an interval of from 7–10 days, any development of pigment was noted, and the leaf portions were then placed in methylated spirit until colourless and sections, after treatment with strong chloral hydrate solution and iodine, were examined for starch contents.

The results are tabulated as follows :—

Species	3 per cent. cane sugar −carbon dioxide	Distilled water − carbon dioxide	3 per cent. cane sugar +carbon dioxide	Distilled water +carbon dioxide	Development of Pigment either with or without carbon dioxide
Viola tricolor	no starch	no starch	no starch	no starch	+
Capsella bursa pastoris	abundant starch	no starch	abundant starch	abundant starch	−
Lactuca sativa	no starch	no starch	no starch	no starch	+
Reseda lutea	abundant starch	no starch	abundant starch	abundant starch	+
Matricaria sp.	abundant starch	no starch	abundant starch	abundant starch	−
Cheiranthus cheiri	abundant starch	no starch	abundant starch	considerable amount of starch	−
Nicotiana tabacum	abundant starch	no starch	abundant starch	abundant starch	−
Aquilegia vulgaris	some starch in places	no starch	no starch	no starch	+
Epilobium sp.	abundant starch	no starch	abundant starch	some starch	−
Ilex aquifolium	very little starch	no starch	very little starch	no starch	+
Ligustrum vulgare	no starch	no starch	very little starch	no starch	+
Mahonia aquifolium	very little starch	no starch	crammed starch	crammed starch	+
Rumex crispus	very little starch	no starch	very little starch	no starch	+
Rubus fruticosus	crammed starch	no starch	crammed starch	no starch	−

These results show that there is some connection between production of pigment and the capacity for forming starch from the sugar provided. As a rule, the leaves which turn red are those which form least starch from the sugar solution and several, in fact, form very little or no starch even under normal conditions.

Hence experiments on sugar-feeding further strengthen the view that reddening is due to an increase in the concentration of sugar which ultimately leads to an increase in concentration of glucosides; the latter, being formed from sugar, naturally accumulate in excess since there can be no translocation from the severed leaf.

Palladin(14) also maintains that the amount of aromatic chromogen is increased by sugar-feeding. In his experiments equal portions of leaves of *Rumex patentia* were placed in water and 20°/₀ cane-sugar respectively. After four days the pieces in cane-sugar had developed anthocyanin, those in water none. The sugar-fed and the control portions were then heated with water and equal amounts of the extracts treated with horse-radish peroxidase and hydrogen peroxide. The extract from the sugar-fed portions produced considerably more pigment than that from the control portions. This view is quite in accordance with my suggestion that sugar-feeding leads to increase of free aromatic chromogen.

With *Vicia Faba* leaves in sugar-cultures Palladin obtained a different result. In this case the extracts gave less not more pigment with peroxidase and hydrogen peroxide, whereas cultivation in water only increased the amount of free chromogen. As an explanation Palladin suggests that the free chromogen combines with sugar to form a glucoside—prochromogen—and as such cannot be oxidised by the oxidase.

I should suppose the explanation to be as follows :—The chromogen in *Vicia Faba* is of a different nature from that in most plants in that it is oxidised by tyrosinase, and we may therefore suppose it to be a tyrosin-like compound and not capable of being synthesised from sugar alone. The increased concentration of sugar would only form a glucoside from the existing chromogen and thereby decrease the amount of free chromogen and would not increase the total amount of glucoside. Cultivation in water would tend if anything to decrease the amount of sugar and hence the amount of free chromogen would increase. It may be also added that sugar-culture does not produce colour in *Vicia Faba* leaves.

The question as to whether sugar-feeding does or does not directly

increase the concentration of aromatic glucosides is one which can only be solved by *quantitative* estimation. I am at present engaged in experiments in connection with this point.

Application to Mendelian Factors.

A question which now arises is how this hypothesis I have formulated fits in with our knowledge of the relationship between colour-varieties and the type from which they are derived.

In the first place I shall deal with a variation which, though comparatively rare, may be most closely connected with the reactions controlled by the glucoside-splitting enzymes.

There are anthocyanic species which have given rise to varieties having some organ or part fully pigmented with anthocyanin, whereas, in the type, the same organ or part is unpigmented or only slightly so. The following are examples :—

> Flower.   The type in *Bellis perennis, Cyclamen persicum, Primula acaulis, P. elatior, Cheiranthus cheiri, Crataegus oxyacantha, Achillea millefolium*, is either without, or is only slightly tinged with, anthocyanin, but fully coloured varieties are known.

> Leaf.   *Fagus sylvatica, Coryllus Avellana, Beta vulgaris, Atriplex hortensis, Perilla nankinensis, Canna indica, Plantago major, Brassica sp., Lactuca sativa*, produce red-leaved varieties.

> Fruit.   The orange and banana have varieties in which the flesh and pericarp respectively are pigmented with anthocyanin.

We may assume that the coloured varieties arise through the loss of some factor from the type, and in some cases it has been shown that the coloured variety is recessive to the type. If the petals and leaves of the coloured varieties are examined microscopically, it is found that the pigment is invariably limited to the epidermal cells, and it is reasonable to suppose that the loss of the factor is also limited to the epidermis. Previously (19) I have termed this unknown factor a reductase or inhibitor, but if the views I have expounded in the present paper are correct, the appearance of pigment in the epidermis might be explained on the supposition that the enzyme controlling hydrolysis and synthesis of the glucoside is absent from this tissue. Hence the chromogen is free from sugar and can be oxidised. In the type the

11—2

equilibrium position is such that very little or no free chromogen is present in the tissues subject to the variation : in the variety the equilibrium position is possibly one of complete hydrolysis and the tissue as a result becomes considerably pigmented.

In the second place, there are anthocyanic species in which the type has coloured flowers, and has given rise to a large number of derivative varieties. Many of these have been fully described in Mendelian literature, and several classes of varieties can be recognized which are applicable to a number of different species.

The main classes can be distinguished as :—

   I.   The blue or purple anthocyanic class.

   II.   The red anthocyanic class.

   III. The albino or non-anthocyanic class.

Both I. and II. may in many cases exist in sub-classes common to both ; i.e.

   (*a*)   The tinged class.

   (*b*)   The pale class.

   (*c*)   The deep class.

There is no further evidence in the present paper beyond that which I have previously given(20) as to the nature of the factors, the absence of which causes loss of blueing power and albinism respectively. They are in all probability oxidising enzymes, though I am by no means unwilling to admit that blueing may in some cases, considering the great number of possibilities in plant-metabolism, be due to alkalinity of the cell-sap brought about by some definite enzyme action. I am uncertain as to the nature of the factor, the absence of which causes the tingeing.

I. (*b*) constitutes the type in many species and deeper varieties of both red and blue classes, i.e. I. (*c*) and II. (*c*) are known. They are recessive to the type and are due to the loss of some factor. It now seems probable that this factor is not a partial inhibitor or limiting factor of a reductase nature such as I have suggested, but a controlling enzyme, i.e. one which synthesises and hydrolyses the glucoside. Whereas loss of this enzyme may give rise to coloured varieties when the type is merely tinged and quite unpigmented, when the type is already coloured the loss deepens the colour by increasing the amount of pigment formed.

Sometimes the loss is limited to the flower only—*Lathyrus, Matthiola, Althaea, Cheiranthus*; in other cases, the intense pigmentation of the

flower is accompanied by increased pigmentation of the epidermis of the leaves which in the type are unpigmented : example—deep-flowered varieties of *Antirrhinum majus, Dianthus barbatus*.

It is difficult to devise a method for demonstrating the absence of an enzyme when the latter may be confined to the epidermis alone. It is possible that some micro-chemical method may be found.

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FURTHER EXPERIMENTS ON THE INHERITANCE OF COAT COLOUR IN MICE.

By FLORENCE M. DURHAM.

In Report IV of the Evolution Committee of the Royal Society, I published a preliminary account of the results of my breeding experiments to determine the inheritance of coat colour in mice. I now propose to complete that account by giving the results of my investigations into the genetic behaviour of pink-eyed mice with coloured coats and also of yellow mice.

I propose to begin with an account of the pink-eyed mice with coloured coats, but at the same time to leave the question of the behaviour of pink-eyed mice with yellow coats until I deal with dark-eyed yellow mice, and to confine myself at first to pink-eyed mice of any coat colour except yellow.

The albinos have been dealt with in Report IV. The pink-eyed mice with coloured coats as stated in Report IV have only apparently unpigmented eyes. Examination of sections of the eyes microscopically reveals the presence of pigment both in the retina and iris. The amount of pigment present is however so little, that it is extremely difficult to say of what colour it is.

There is a correlated absence of pigment in the hairs of these mice, so that they are much paler in colour than any of the corresponding varieties of dark-eyed mice. But this absence of pigment in the eyes and hair of the pink-eyed mice has a genetic significance different from that of the dilution of coat colour in the dark-eyed mice. For in the case of the dark-eyed mice, the absence of a factor which effects the dense deposition of pigment in the hairs gives rise to what are known as the dilute forms, and for each coloured type there is a dilute variety. The pale colours of the pink-eyed mice are not due to the same cause, and cannot be explained in the same way. For pink-eyed mice behave genetically like the concentrated and diluted varieties

of dark-eyed mice and carry the conditions of concentration and dilution just as they do, and in their colourings the effects of these are shown. The paleness of colour therefore which accompanies the pink eye must be due to some other cause. This statement however applies only to those mice in which yellow pigment is absent. For it is possible to produce pink-eyed yellow mice with hair as deeply pigmented as that of dark-eyed yellow mice. These will be dealt with later on. Also in the case of the pink-eyed agouti mice, while the black and chocolate pigments are there in very much diminished quantities the yellow banding may be as deeply coloured as in the hair of the ordinary agouti. It is possible to arrange the pink-eyed mice in classes corresponding to those which have been distinguished among the dark-eyed mice.

Pink-eyed mice which behave genetically like black mice are of a pale greyish colour and were named lilacs by Mr Darbishire(6) who was the first to breed them and kindly gave me two living specimens.

In order to distinguish them from other lilac mice, on account of their colour, I have called them "blue lilacs." They breed perfectly true mated *inter se*. Mated with chocolate mice, they never throw any other colour but black in F_1.

In the F_2 generation from this mating two new varieties appear which I have named "chocolate-lilac" and "champagne" ("*café au lait*" of Cuénot) respectively.

The chocolate-lilacs vary very much in appearance in depth of colouring, but the colour is always browner than that of the blue lilac more resembling that of the silver fawn. For this reason I called them chocolate-lilacs, and I thought at first they were a chocolate variety of the pink-eyed mouse. But when mated with chocolate mice they throw a mixture of blacks and chocolates.

Chocolate-lilacs mated together throw blue lilacs, chocolate-lilacs and champagnes.

The champagne mice, mated with chocolates, throw only chocolates and are I believe the pink-eyed variety of chocolate. Mated *inter se*, they breed perfectly true, I therefore regard the blue lilacs as the homozygous pink-eyed variety of the dark-eyed black mouse, the chocolate-lilac mouse as the heterozygous variety of dark-eyed black (throwing chocolate) and the champagne as the homozygous chocolate pink-eyed form.

When the various forms are mated with the dilute forms of dark-eyed mice, blues or silver fawns, then in the F_2 generation pink-eyed

mice without the factor for concentration are produced. These when mated with blues or silver fawns throw only the dilute varieties, whereas pink-eyed mice descended from unions between pink-eyed mice and dark-eyed mice of the concentrated form only throw concentrated forms when mated with the dilute varieties. There is a great deal of variation in the depth of colour of the pink-eyed mice and I think that the presence or absence of the factor for concentration accounts for this. Unfortunately I did not recognize this fact early enough in my experiments to be able to give numbers in support of this view. In the case of the champagne mice, however, a different variety which I called "silver champagne," arose and always appeared in the F_2 generation from a mating between champagne and silver fawn. These silver champagnes mated with dilute forms always gave dilute forms.

When the chocolate lilac mouse is mated with the ordinary wild colour or golden agouti mouse, the F_1 is always golden agouti. All possible forms should appear in F_2. Black, chocolate, golden agouti, cinnamon agouti, blue lilac, chocolate lilac, champagne, pink-eyed golden agouti, pink-eyed cinnamon agouti.

The pink-eyed agoutis, golden and cinnamon, are very much alike in appearance. In fact at first and for some time I took the pink-eyed cinnamon agouti to be a pale or dilute form of the pink-eyed golden agouti, and owing to the small amount of pigment present, I thought that the pink-eyed golden agouti must be the cinnamon variety. However, the genetic behaviour of the two forms when mated with chocolate showed their differences.

The pink-eyed golden agouti gives only golden agouti when mated with chocolate and the pink-eyed cinnamon agouti gives only cinnamon agoutis as a result of mating with chocolate.

The small amount of pigment present makes the microscopical determination very difficult.

Pink-eyed coloured mice are recessive to dark-eyed mice and when mated *inter se* never throw the dark-eyed form.

Taking all the results irrespective of colour and classifying only according to eye-colour, then as a result of mating pink-eyed mice with dark-eyed mice in F_2 I obtained

875 dark eye, DE, 303 pink eye, PE, observed
883·5 ,, 294·5 ,, calculated.

From matings between heterozygous DE with PE

105 DE, 113 PE, observed
109 109 calculated.

In the case of the first mating I made between blue mice and blue lilac the numbers yielded in the F_2 generation are peculiar.

Instead of a ratio of 9 : 3 : 4 as I expected, I got 27 blacks, 17 blues and 18 blue lilacs.

The F_1 mice were black and therefore the blue lilacs were carrying the determiner for concentration.

The formula for the blue lilacs may be represented as eDB, where e is the absence of dark eye, D the factor for concentration, B the factor for blackness.

The blue mouse can be represented as EdB, where E is the presence of dark eye, d is the absence of concentration.

The figures given above may possibly be an indication of spurious allelomorphism between the factor for dark eye and the concentration factor.

The F_2 mating would then be $EdeD \times EdeD$. The results would then be a ratio of 2 black to 1 blue to 1 blue lilac, giving calculated results of 31 black to 15·5 blue to 15·5 blue lilac.

I was unable to repeat the combination owing to either the blues used being heterozygous in chocolate or the blue lilacs heterozygous in concentration.

If this interpretation be correct, then all the blacks should be heterozygous and all the blues homozygous. Unfortunately I only mated a few of the offspring. 6 blues only were mated and 3 of these died without young, the remaining 3 were homozygous; 5 blacks were mated, 3 died without young, one had only 4 young and these were all black, and the fifth was heterozygous.

The results of mating chocolate-lilac mice with dark-eyed varieties may give rise to various heterozygous forms.

Thus the F_2 generation of a mating between chocolate-lilac and blue (giving black F_1) was

19 black, 2 blue, 5 blue lilac, 6 chocolate-lilac.

If the mating was $EeDdBb \times EeDdBB$, the calculated numbers would be 18 black, 6 blue, 4 blue lilac and 4 chocolate-lilac.

From a mating of chocolate-lilac and black heterozygous in blue giving black F_1, I got

10 black, 4 blue, 6 blue lilac and 2 chocolate-lilac.

If the mating were as above between $EeDdBb \times EeDdBB$, there should be 12·3 black, 4·3 blue, 2·7 blue lilac and 2·7 chocolate-lilac.

Blue lilac × chocolate, eeDDBB × EEDDbb gives black F_1.

			Black	Chocolate	Blue lilac	Chocolate-lilac	Champagne
F_2.	Observed	...	21	6	0	4	6
	Calculated	...	20·7	6·9	2·3	4·6	2·3

Here no blue lilacs were obtained but an excess of champagnes.

Blue lilac × chocolate, eeDdBB × EEDdbb gives blues and blacks.

		Black	Blue	Chocolate	Silver fawn	Blue lilac	Chocolate-lilac	Champagne
F_2.	Observed	4	3	0	0	1	1	0

Chocolate-lilac × chocolate, eBeb × EbEb gives blacks and chocolates F_1.

F_2 from blacks

		Black	Chocolate	Blue lilac	Chocolate-lilac	Champagne
Observed	...	16	7	0	3	0
Calculated	...	14·4	4·8	1·6	3·2	1·6

From black and chocolate

		Black	Chocolate	Blue lilac	Chocolate-lilac	Champagne
Observed	...	8	16	0	0	5
Calculated	...	10·8	10·8	0	3·6	3·6

From chocolate × chocolate

		Black	Chocolate	Blue lilac	Chocolate-lilac	Champagne
Observed	...	—	38	—	—	16
Calculated	...	—	40·5	—	—	13·5

Blue lilac × silver fawn, eeddBB × EEddbb giving blue F_1.

		Blue	Silver fawn	Blue lilac	Chocolate-lilac	Champagne
F_2.	Observed	43	19	3	10	3
	Calculated	43·9	14·6	4·9	9·7	4·9

Chocolate-lilac × silver fawn, eeddBb × EEddbb giving blue F_1.

		Blue	Silver fawn	Blue lilac	Chocolate-lilac	Champagne
F_2.	Observed	...	16	13	6	0	2
	Calculated	...	20·7	6·9	2·3	4·6	2·3

The champagnes in these last two cases were silver champagnes.

Silver fawn × champagne giving chocolate F_1,

$$EeDdbb × EeDdbb.$$

		Chocolate	Silver fawn	Champagne
F_2.	Observed	5	2	5
	Calculated	6·75	2·25	3

These champagnes should have been of two sorts, champagne and silver champagne.

Silver fawn × *champagne* giving silver fawn F_1,

<div align="center">

Eeddbb × *Eeddbb*.

</div>

		Silver fawn	Silver champagne
F_2. Observed	...	11	2
Calculated	...	9·75	3·25

Chocolate heterozygous in pink-eye × *chocolate-lilac*,

<div align="center">

Eebb × *eeBb*.

</div>

		Black	Chocolate	Chocolate-lilac	Champagne
Observed	...	2	3	2	3
Calculated	...	2·5	2·5	2·5	2·5

Blue × *champagne* giving black F_1,

<div align="center">

EeDdBb × *EeDdBb*.

</div>

		Black	Blue	Chocolate	Silver fawn	Blue lilac	Chocolate-lilac	Champagne
F_2. Observed	4	0	2	1	0	1	1
Calculated	3·5	1·17	1·17	·4	·5	1	·5

Blue × *champagne* giving blue and black F_1,

<div align="center">

EeddBb × *EeDdBb*.

</div>

		Black	Blue	Chocolate	Silver fawn	Blue lilac	Chocolate-lilac	Champagne
F_2. Observed	8	10	3	4	4	2	2
Calculated	9	9	3	3	2	4	2

Blue carrying chocolate × *champagne* giving blue and chocolate,

<div align="center">

EeddBb × *EeDdbb*.

</div>

		Black	Blue	Chocolate	Silver fawn	Chocolate-lilac	Champagne
Observed	...	2	3	4	1	1	0
Calculated	...	2·1	2·1	2·1	2·1	1·3	1·3

Blue heterozygous in pink-eye and chocolate × *champagne*,

<div align="center">

EeddBb × *eeDdbb*.

</div>

		Black	Blue	Chocolate	Silver fawn	Chocolate-lilac	Champagne
Observed	...	3	0	5	3	1	1
Calculated	...	1·6	1·6	1·6	1·6	3·2	3·2

Blues carrying pink-eye mated together,

<div align="center">

EeddBB × *EeddBB*.

</div>

		Blue	Blue lilac
Observed	...	19	6
Calculated	...	18·75	6·25

Golden agouti × *chocolate-lilac* gives golden agouti F_1,

$$GgBbEe \times GgBbEe.$$

	Golden agouti	Cinnamon agouti	Black	Chocolate	Pink-eyed agouti	Pink-eyed cinnamon agouti	Blue lilac	Chocolate-lilac	Champagne
F_2. Observed	83	8	31	2	26	7	0	11	4
Calculated	72·9	24·3	24·3	8·1	24·3	8·1	2·7	5·4	2·7

Golden agouti × *pink-eyed agouti* gives golden agouti F_1.

	Golden agouti	Pink-eyed agouti
F_2. Observed ...	32	17
Calculated ...	36·75	12·25

Cinnamon agouti mated with chocolate-lilac giving cinnamon agouti F_1.

	Cinnamon agouti	Chocolate	Pink-eyed Cinnamon agouti	Champagne
F_2. Observed ...	14	4	3	1
Calculated ...	12·3	4·1	4·1	1·4

Agouti heterozygous in pink-eyed agouti × *pink-eyed agouti.*

	Agouti	Pink-eyed agouti
Observed ...	11	8
Calculated ...	9·5	9·5

Agouti heterozygous in pink-eye and chocolate × *pink-eyed agouti heterozygous in chocolate.*

	Agouti	Cinnamon agouti	Black	Chocolate	Pink-eyed agouti	Pink-eyed cinnamon agouti	Blue lilac	Chocolate-lilac	Champagne
Observed	7	0	2	1	10	0	0	1	0
Calculated	5·85	1·95	1·95	·65	5·85	1·95	·65	1·3	·65

Agouti heterozygous in pink-eye and chocolate × *black ditto.*

	Agouti	Cinnamon agouti	Black	Chocolate	Pink-eyed agouti	Pink-eyed cinnamon agouti	Blue lilac	Chocolate-lilac	Champagne
Observed	6	1	10	3	0	6	0	2	4
Calculated	9	3	9	3	3	1	1	2	1

Pink-eyed agouti × *pink-eyed agouti.*   From this mating I obtained

Pink-eyed agouti	Pink-eyed cinnamon agouti	Chocolate-lilac
37	4	8

There were no blue lilacs and no champagnes. The explanation of this may be that the pink-eyed agoutis were not all carrying the same characters.

Another case I cannot explain is the following :

An albino heterozygous in E was mated with a yellow carrying agouti. From the agoutis F_1 of this union I obtained

17 agouti, 5 black, 1 chocolate-lilac, 1 champagne and 8 albinos.

There were no chocolates, no cinnamon agoutis, no pink-eyed agoutis of either sort, and no blue lilacs.

I have tried other matings of various sorts but the numbers yielded are too small to be worth quoting.

Yellow Mice.

The genetic behaviour of yellow mice differs in various particulars from that of other mice; and there is at present no very satisfactory explanation possible to account for this.

Hagedoorn (1) is the only one among many breeders of yellow mice whose experiences are not in accordance with my own. But from his account of his experiments, it is clear that he was using a different type of yellow mouse from that employed by the rest of us.

The type, which I and other breeders have used, must be regarded as a heterozygous dominant. For it never breeds true, no homozygous form has yet been obtained; and when mated with mice of other colours than yellow, some of the offspring are always yellow. Hagedoorn's mouse was a recessive and did breed true. His experiments are of interest as showing that another type of yellow mouse exists, but his results need not be considered further here.

I made 185 matings in all between yellows bred in every kind of way, but every one of these yellows proved to be heterozygous.

As a result of 127 matings between yellows I obtained 448 yellows and 232 other colours. I purposely excluded from the list all matings from which sables and albinos were obtained, so as to count only the pure yellow forms. Albinos can carry the yellow determiner, and the sable mouse, which is perhaps only a variant of the yellow, presents so many peculiarities as I shall show later on that for the present purpose I preferred to exclude it.

As a result of 104 matings between yellows and other colours I have obtained 297 yellows and 336 other colours.

The problem created by the absence of pure yellows has been discussed by Cuénot (2), Castle (5), Wilson, Morgan and others. There are two possibilities: (1) that in fertilization the zygotes, yellow × yellow, are never formed; (2) that these zygotes are formed but perish. If they are not formed we should expect the ratio of yellow to non-yellow to approximate in F_2 to $3 : 1$, because the number of spermatozoa is indefinitely large; if on the other hand such zygotes are formed and perish, the F_2 ratio should be $2 : 1$.

The F_2 numbers obtained are as follows :

		Yellow	Non-yellow
Cuénot (2) ...	...	263	100
Castle (5) ...	...	800	435
My own ...	...	448	232
		1511	767
Expectation at 2 : 1		*1518·6*	*759·3*
Expectation at 3 : 1		*1708·5*	*569·5*

From these figures there can I think be no longer any serious doubt that the pure yellow zygotes are actually formed in fertilization, but that for some unknown cause they are unable to develop. The case becomes therefore exactly comparable with that observed by Baur(7) for the *varietates aureae*, which form albino embryos incapable of existence.

It has been argued that if this representation is correct the average numbers per litter should be less for the mating yellow × yellow than for yellow mated with some other colour, and Cuénot and Castle record a difference of this kind, giving the following averages:

			Yellow × Yellow	Yellow × Non-yellow
Cuénot	...	...	3·38	3·74
Castle	...	...	4·71	5·57

From my experience I incline to doubt whether much importance can be attached to differences of this order.

The following averages have been compiled from an ample series, 75 litters being the lowest included.

yellow × yellow	3·90 young
yellow × other colour	3·97 ,,
black × black	4·60 ,,
black × other colour (not yellow)	3·99 ,,
chocolate × chocolate	3·96 ,,
chocolate × other colour (not yellow)	3·93 ,,
agouti × agouti	3·47 ,,
agouti × other colour (not yellow)	3·32 ,,
albinos × other colour (not yellow)	4·27 ,,

I have not mated albinos together often enough to make it worth while to compare the results of mating albino × albino with the other figures.

Only mice which lived long enough to have their colours determined are included in these averages, but Castle's figures evidently are based on the numbers actually born. It is clear nevertheless that large differences exist where no special disturbance, analogous to that we are

considering, is to be suspected, and I doubt whether the observations can be used either for or against the conclusion that the ratio of yellow to non-yellow in F_2 is $2 : 1$.

The non-viability of pure yellows raises an important physiological question, but we have no indication as to what may be its cause. It should be remembered that the mortality may, for aught we yet know, occur at any age between fertilization and maturity.

In the report to the Evolution Committee(3), I have already stated, that the pigments of the eye of the yellow mouse may be black or chocolate but never yellow. If the yellow mouse throws chocolate young but never black the eye will be found to be pigmented with chocolate, often chocolate pigment will also be found in the hairs of this animal.

A yellow mouse which throws black young will have black pigment in the eyes and some black pigment will always be found in the hair. I have never found black pigment in the hair of a mouse with chocolate only in the eyes.

I have examined several hundred yellow mice and never found an exception to this statement.

The hair and the eyes are a key to the genetic behaviour, or one may equally well say the genetic behaviour is the key to the pigments of the hair and eyes of the yellow mouse. Both black and chocolate pigments will be found in the eyes of the yellow mouse with agouti determiner.

Yellow mice are subject to an abnormal development of fat in their tissues. All the fat depôts become loaded to an extraordinary degree. This development of fat renders them unable to breed. It is a well-known fact to the breeders of Fancy mice.

The question of dilution is also a difficulty in yellow mice. Yellow mice vary very much in their colouring. Some are very deep yellow, some much paler, some are deeply coloured dorsally and very light underneath, pale almost to whiteness. I do not mean piebald, but the colour fades off gradually to a very pale cream. The result is that it is very difficult and often impossible to decide whether a mouse belongs to the dilute variety or not. Of course many mice are so pale all over, one would not hesitate to class them as dilute yellows, that is creams. But there is a very large section whose classification can only be determined by their genetic behaviour. To illustrate the difficulty I will mention the case of two mice which I bred together and classed

as creams and they threw chocolates. If they had been real creams they should have thrown silver fawns. Another cream mouse which I had grew a chocolate streak, late in life, down its back, a reversal of the ordinary procedure.

When yellows are bred with pink-eyed mice, pink-eyed yellows will appear in F_2 as deeply coloured as the original yellow mouse which was grand-parent. As stated before the yellow bar of the pink-eyed agouti mouse is so deeply coloured and so bright that the inexperienced observer would put them in the yellow class. I believe that the so-called pink-eyed yellow mice of Plate's (4) classification must be really pink-eyed agoutis, either golden or cinnamon.

The pink-eyed yellow mice when produced behave exactly like the dark-eyed yellows. I have never succeeded in obtaining a homozygous pink-eyed yellow and when mated together they do not throw 3 yellows to 1 other colour; mated with any other colour they always throw some yellows. The dark eye is dominant to the pink eye, but the yellow colour behaves independently of the eye colour when pink-eyed yellow is mated with dark-eyed any other colour.

Pink-eyed yellows mated together throw pink-eyed yellows, blue lilacs, chocolate-lilacs and champagnes according to their genetic constitution.

From the matings of pink-eyed yellows I have obtained the following results,

17 matings $PEY \times PEY$ gave 57 PEY, 45 PE other colour.

19 matings $PEY \times PE$ other colour gave 32 PEY, 33 PE other colour.

Before proceeding to give the tables of the results of the various matings I have carried out, I must now refer to two cases in which I obtained yellow mice by breeding together other varieties than yellow. In each case the mice had pink-eyed ancestry.

Case I. This mouse was not strictly speaking a yellow mouse. I could not class it as an agouti simply or as a sable. It was very yellow in colour, with the agouti barring on the dorsal surface and a yellow belly. It resembled a very yellow agouti with a yellow belly.

Its ancestry is shown by the following scheme:

```
    Pink-eyed chocolate-lilac        Yellow throwing agoutis
            1188            ×              1450
         ┌─────────────────┴──────────────────┐
            1667 ♂          ×              1555 ♀
      ┌─────────┬─────────┬────────┬────────────────┬──────────┐
   3 black   3 agoutis   1 blue   1 pink-eyed    1 yellow
                                    champagne     agouti
                                                   1825
```
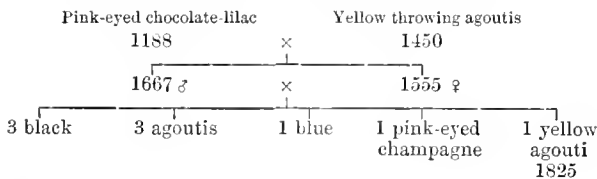
Both 1667 ♂ and 1555 ♀ were agoutis and not to be distinguished in any way externally from any ordinary agouti.

I mated the yellow agouti mouse (1825 ♂) with 6 does, but unfortunately the matings were not all successful. With a chocolate ♀ there were 20 young (not one of which was agouti), 1 yellow, 4 blacks, 7 sables, 1 chocolate yellow belly, 3 chocolates, 3 albinos, 1 chocolate-lilac.

Mated with a yellow mouse carrying chocolate he gave 2 yellows, 2 sables, 3 blacks and 1 chocolate.

I tried him four times with agouti mice but in each case there was no result. I had hoped by such matings to obtain agoutis which would throw yellows or sables.

None of the offspring mated together produced any agoutis.

Case II. A champagne ♀ was mated with an agouti ♂. In the first generation there were

> 1 agouti, 4 cinnamon agouti, 1 chocolate.

The agouti which was a ♂ was mated with the only ♀ a cinnamon agouti, and there resulted

> 1 sooty yellow, 2 silver cinnamon agouti and 1 black.

Unfortunately death carried off the yellow before she could be mated. Subsequent litters of the parents did not contain any yellows.

In the subjoined tables the calculations are made on a 2 to 1 basis instead of the ordinary 3 to 1, adopting the conclusion indicated above.

TABLE OF RESULTS.

Dark-eyed Yellows.

Yellows carrying chocolate mated together :

Yellow	Chocolate	
136	68	observed
136	68	calculated

Yellows carrying chocolate × chocolate :

Yellow	Chocolate	
66	46	observed
56	56	calculated

Yellows carrying black and chocolate mated together :

Yellow	Black	Chocolate	
65	35	9	observed
72	27	9	calculated

Yellows carrying black and chocolate × chocolate :

Yellow	Black	Chocolate	
23	11	9	observed
21·4	10·7	10·7	calculated

Yellows carrying black × chocolate :

Yellow	Black	
6	18	observed
12	12	calculated

Yellows carrying black and chocolate × black heterozygous in chocolate :

Yellow	Black	Chocolate	
25	17	18	observed
30	15	15	calculated

Yellows carrying black × black :

Yellow	Black	
29	24	observed
26·5	26·5	calculated

Yellows heterozygous in black, chocolate and albino mated together :

Yellow	Black	Chocolate	Albino	
59	27	5	30	observed
45·3	34	11·3	30·4	calculated

Albinos heterozygous in yellow and chocolate × chocolate heterozygous in albino :

Yellow	Chocolate	Albino	
12	5	7	observed
8	4	12	calculated

In the following tables the yellows are not separated into yellows and creams on account of the difficulty stated above of distinguishing between them.

Yellows heterozygous in chocolate and silver fawn mated together :

Yellow and Cream	Chocolate	Silver fawn	
5	7	5	observed
11·2	4·2	1·4	calculated

Yellows heterozygous in chocolate and silver fawn × silver fawn :

Yellow and Cream	Chocolate	Silver fawn	
33	11	13	observed
29·0	14·5	14·5	calculated

Yellows heterozygous in chocolate and silver fawn × chocolate heterozygous in silver fawn:

Yellow	Chocolate	Silver fawn	
13	10	9	observed
16	12	4	calculated

Yellow heterozygous in black and albino × albino heterozygous in yellow and black :

Yellow	Black	Albino	
5	2	7	observed
4·6	2·3	6·9	calculated

Yellow × Agouti gives Yellow and Agouti.

F_1 yellow × F_1 yellow :

	Yellow	Agouti	
	60	32	observed
	61·2	30·6	calculated

F_1 yellow × F_1 agouti :

	Yellow	Agouti	
	38	32	observed
	35	35	calculated

Yellow heterozygous in agouti × chocolate :

	Yellow	Agouti	
	19	19	observed
	19	19	calculated

Yellow heterozygous in agouti × black :

	Yellow	Agouti	
	11	18	observed
	14·5	14·5	calculated

Yellow × Chocolate-Lilac gives Yellow and Black.

F_1 yellow × F_1 yellow:

Dark-eyed yellow	Black	Chocolate	Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
46	12	3	24	0	1	9	observed
48	18	6	16	2	4	2	calculated

Here there was an excess of champagnes, no blue lilacs and only one chocolate-lilac.

F_1 yellow × F_1 black :

Dark-eyed yellow	Black	Chocolate	Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
26	20	2	11	0	15	3	observed
28·8	21·6	7·2	9·6	2·4	4·8	2·4	calculated

Here there was an excess of chocolate-lilacs, no blue lilacs.

Dark-eyed yellow heterozygous in pink-eye × pink-eyed yellow :

Dark-eyed yellow	Black	Chocolate	Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
34	5	5	27	0	2	7	observed
26·4	9·9	3·3	26·4	3·3	6·6	3·3	calculated

Yellow × Pink-eyed Agouti gives Yellows.

$F_1 × F_1$:

	Dark-eyed yellow	Agouti	Pink-eyed yellow	Pink-eyed agouti	
	25	17	11	5	observed
	28·8	14·4	9·6	4·8	calculated

Dark-eyed yellow heterozygous in chocolate and pink-eye :

Dark-eyed yellow	Chocolate	Pink-eyed yellow	Champagne	
11	9	1	1	observed
9·6	4·8	4·8	2·4	calculated

Dark-eyed yellow heterozygous in chocolate and pink-eye × chocolate heterozygous in pink-eye :

Dark-eyed yellow	Chocolate	Pink-eyed yellow	Champagne	
8	7	1	6	observed
8·4	8·4	2·8	2·8	calculated

Yellow heterozygous in pink-eye × blue lilac :

Dark-eyed yellow	Black	Chocolate	Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
2	0	2	2	1	2	0	observed

Yellow heterozygous in pink-eye × chocolate-lilac :

Dark-eyed yellow	Black	Chocolate	Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
4	2	4	2	0	0	2	observed

Yellow heterozygous in pink-eye and chocolate × champagne :

Dark-eyed yellow	Chocolate	Pink-eyed yellow	Champagne	
1	4	3	9	observed

Here there is an excess of pink-eye.

Pink-eyed yellow × pink-eyed yellow heterozygous in black and chocolate :

Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
25	3	15	1	observed
28 8	3·6	7·2	3·6	calculated

Here there is an excess of chocolate-lilac possibly due to the fact that some of the yellows were heterozygous in blue lilac only and others in chocolate only, and those mated together would give chocolate lilacs only, no blues and no champagnes.

Pink-eyed yellow × pink-eyed yellow heterozygous in chocolate only :

Pink-eyed yellow	Champagne	
18	12	observed
20	10	calculated

Pink-eyed yellow × pink-eyed agouti :

Pink-eyed yellow	Pink-eyed agouti	
15	7	observed
11	11	calculated

Pink-eyed yellow heterozygous in pink-eyed agouti :

Pink-eyed yellow	Pink-eyed agouti	
12	8	observed
13·2	6·6	calculated

Pink-eyed yellow × chocolate-lilac :

Pink-eyed yellow	Blue lilac	Chocolate-lilac	Champagne	
8	2	8	3	observed
10·4	2·6	5·2	2·6	calculated

Pink-eyed yellow · champagne :

Pink-eyed yellow	Chocolate-lilac	Champagne	
7	4	7	observed
9·0	4·5	4·5	calculated

Sable Mice.

Among the yellow mice I used for my experiments were some individuals, which produced sables when mated with blacks or chocolates. As these appeared very early in my experiments, I at first concluded that sables would always result from such matings. Subsequent investigation however showed that the power to produce sables was limited only to certain mice and that it was a hereditary quality. At present I am unable to offer a scheme which correctly represents the relation of sables to the other colours.

Sable mice are well known to the Fancy. They differ from yellow mice in having a dark black or brown streak down the middle dorsal region while the rest of the mouse is yellow. The streak may be very narrow, when the mouse is said to be a light sable, or very broad when the mouse is a dark sable. As a general rule, the hairs in this dark streak show an agouti pattern, being black or chocolate barred with yellow. But this does not mean that the mouse is carrying agouti determiner. But it is possible to produce sables in which the barring of the dorsal hairs is absent, and at various times I have had black, blue, chocolate and silver fawn mice which differ only from the ordinary forms by having yellow bellies, and which from their genetic behaviour must be classed with the sables. They always moulted subsequently into ordinary sables.

The appearance of the sable mouse varies very much according to age. During the first few months the marking is very definite, but as age comes on the sable appearance is lost, so that a mouse, which was a very good specimen at three months may be hardly distinguishable from an ordinary yellow mouse at 18 months old. The amount of yellow in its colouring increases with the successive moults.

Sables are not to be confused with *sooty* yellow mice, which result from mating ordinary yellows with blacks or chocolates. The sooty yellow is a dirty colour all over and never shows a definite pattern.

I have never bred a homozygous sable mouse. Bred together, sables may throw sables, yellows, blacks, chocolates, and also agouti, if they are carrying the agouti determiner.

Yellows carrying the sable determiner mated together will throw sables, and sables mated together may throw yellows. By mating together yellows carrying sable I have obtained

111 yellows, 38 sables, and 69 other coloured mice.

By mating yellows carrying sable with other coloured mice, not yellows, I have obtained

78 yellows, 55 sables, and 80 other coloured mice.

Mating together sables, I have obtained

161 sables, 43 yellows, and 142 other coloured mice.

Mating sables with other colours, not yellow, I have obtained

93 sables, 90 yellows, and 174 other coloured mice.

Examination of the records suggests, that there is more than one sort of sable mouse, and that it is possible to produce sables which never throw yellows at all.

Thus I had as a result of 5 matings between blue sables, 29 blue sables, and 23 blue mice, and no yellows at all.

4 matings between blue sables and dark sables gave

16 sables and 8 other colours (no yellows).

7 matings between blue sables and blue gave

20 blue sables and 19 blues.

On examination of the results produced by mating sables together, I find that the matings in which yellows were produced, the offspring consist of 62 sables, 43 yellows and 64 other colours, while the offspring of the matings in which no yellows were produced, consist of 99 sables and 78 other colours, suggesting a 9 to 7 ratio.

The matings of sable × other colour show that the families in which yellow appeared consisted of

48 sables, 90 yellows, and 107 other colours,

in the remaining families there were 45 sables and 67 other colours.

Matings between sables and yellows without the sable determiner give

23 yellows and 18 other coloured mice, no sables.

Matings between yellows carrying sables with sables give

14 yellows, 28 sables and 17 other coloured mice.

These results suggest that sable is recessive to yellow. But at the same time it seems extraordinary that some of the sables should be able in their turn to throw yellows, and at present no adequate explanation is forthcoming. The fact that there is probably more than one kind of sable may supply the basis for explanation, but the question ought to be more fully worked out.

Sables, like yellow mice, show a tendency to become abnormally fat.

Besides obtaining ordinary sable mice, another form appeared unexpectedly in my experiments. These I called reversed sables, because in them the agouti pattern was reversed. The base of the hairs was yellow and the barring was black or chocolate.

This marking was only apparent in the young mouse; after about 6 months these mice moulted completely yellow, but it was a very conspicuous feature in early life.

I twice obtained mice which were agouti all over with the pattern reversed. They behaved exactly like sables and never threw any agouti young.

Matings between sables in which the reversed sables appeared gave

49 sables, 21 reversed sables, 19 yellows, 41 other colours.

Matings between sables and other colours, not yellow, in which reversed sables appeared,

12 sables, 12 reversed sables, 9 yellows, and 29 other colours.

The reversed sables are recessive to the other sable, mated together they produced reversed sables and other colours but never ordinary sables, and mated with ordinary sables did not produce reversed sables.

Sables which could throw reversed sables when mated with reversed sables, gave

10 sables, 8 reversed sables, 5 yellows, and 18 other coloured mice.

Owing to the great variation which obtains amongst sables, it has not been possible to classify them very satisfactorily.

Matings between dark sables (broad dorsal streak) × light sables (narrow dorsal streak) gave

8 dark sables, 3 light sables, 10 other colour.

Dark sable by yellow gave

10 dark sable, 5 light sable, 8 yellow, 8 other colour.

Sable × agouti gave

7 sable, 7 yellow, 17 agouti.

Sable × heterozygous agouti gave

29 sable, 26 yellow, 15 agouti, 23 black, 4 chocolate.

F_1 sables from sable × agouti gave

17 sable, 8 yellow, 5 agouti, 4 black, 2 chocolate.

Yellow carrying sable × yellow carrying agouti

6 sable, 14 yellow, 7 agouti.

Agouti Mice.

I have made some further matings between agoutis on account of the suggestion made by Cuénot (2) that a chocolate mouse was to be regarded as the dilute form of black. He made this suggestion in order to account for the results of breeding agouti by chocolate.

I therefore mated agouti with blue (dilute black).

F_1 was all agouti.

F_2 gave 30 ag., 13 dil. ag., 10 black, 4 blue,

32   10·7   10·7   3·6 calculated.

These dilute agoutis are well known to the Fancy as Silver Brown, though a better name would be silver agouti. According to Cuénot the cinnamon agouti would be the dilute form, and not the silver browns.

If cinnamon agouti is mated with silver fawn (dilute chocolate) the F_1 is cinnamon agouti.

F_2 39 c. ag., 10 dil. c. ag., 9 choco., 4 silver fawn,

34·8,   11·6,   11·6,   3·9 calculated,

so that in both cases of golden agouti and cinnamon agouti it is possible to produce a diluted form.

Other matings are : agouti × silver brown gives agouti F_1:

	Agouti	Silver brown	
F_2	45	16	observed
	45·75	15·25	calculated

Silver cinnamon × silver fawn gives silver cinnamon :

	Silver cinnamon agouti	Silver fawn	
F_2	25	10	observed
	26·25	8·75	calculated

Agouti × cinnamon agouti gives agouti F_1:

	Agouti	Cinnamon agouti	
F_2	9	4	observed
	9·75	3·25	calculated

This evidence is perfectly consistent with the scheme which I previously published(3) expressing the relations of black, chocolate, blue, silver fawn, to each other, and shows conclusively that Cuénot's representation of chocolate as a dilution form of black is incorrect.

Finally I wish to record the result of mating agoutis together heterozygous in black. The results should yield a ratio of 3 to 1, but my numbers are not in accordance with this ratio.

I obtained 76 agouti, 37 blacks.

The agoutis which result from mating agouti with black are much darker than the ordinary agouti and very often there is a markedly dark streak down the middle of the back.

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By L. DONCASTER, M.A.,

Fellow of King's College, Cambridge.

IT has been shown by various cytologists, especially in the United States, that in certain insects and other animals, the sex of the individual is related to the presence or absence of a particular chromosome in the nucleus of one of the gametes from which that individual was produced. It has also been frequently pointed out that the behaviour of the chromosomes in the maturation of the gametes is exactly adapted to bring about Mendelian segregation, if the members of an allelomorphic pair of characters are determined by a pair of chromosomes which separate in gametogenesis. In the Currant Moth (*Abraxas grossulariata*) I have shown[1] that a pair of very definite Mendelian characters is intimately associated with sex, in such a way that one of them is never borne (before fertilisation) by eggs which will produce females. The two forms have the typical *grossulariata* character, and the *lacticolor* character respectively, and breeding experiments show that the *grossulariata* determinant is never borne by female-determining eggs. It therefore seemed that a study of the gametogenesis of this species offered exceptional hope of showing the relation between a Mendelian character and a chromosome, if such relation exists. The investigation cannot be regarded as completed, but in the account which follows of the results obtained, it will be seen that the hope of identifying a chromosome as the bearer of a hereditary character has not been fulfilled, although other phenomena of considerable interest have been observed.

[1] *Evolution Committee Roy. Soc. Report*, IV. 1908, p. 53.

Since it is in the egg that the incompatibility between the sex determinant and a body character is found, logically it is in the maturation of the egg that the chromosome which determines this character, if it exists, should be sought. But the practical difficulties in studying the maturation of an egg provided with a thick shell are so great that the spermatogenesis was investigated first, in order to find out whether any differences exist between the chromosome groups in the pure forms of the two varieties, and in the heterozygote produced by crossing them.

The spermatogenesis lasts for a considerable period in the late larval and early pupal stages; during the first week or so of pupal life all stages may be found from spermatogonia with division-figures, through growth stages to spermatocytes with first and second divisions, and the conversion of the spermatids into spermatozoa. The testes are divided into several compartments, each containing numerous follicles, and within these compartments at one end or side spermatogonia are found, and from these the later stages may be traced in fairly regular order, all the cells in one follicle being at nearly the same stage. The male and female pupae can be distinguished by the pits representing the genital openings of the moth, and the material was prepared by opening male pupae in Ringer's fluid (NaCl 0·7 gr., $CaCl_2$ 0·23 gr., KCl 0·3 gr., Water 1000 c.c.), removing the orange-coloured testes which are united in the middle dorsal line, and fixing them for about half to one hour in Flemming's strong fluid. After being well washed in water, and taken gradually through successive alcohols into cedar oil, they were embedded in paraffin and cut into sections 6μ in thickness. They were stained on the slide with Heidenhain's Iron Haematoxylin. Testes of larvae were also examined in the same way.

The spermatogonia are rather small, and not so clearly divided into follicles as in the later stages. Some follicles or groups of cells show mitoses, in which the chromosomes form a flat equatorial plate and very regular anaphase figures, but the chromosomes are so small and numerous that I have not been able to count them with complete accuracy. The number however is clearly at least 50 (Fig. 1), and a study of the later divisions makes it probable that it is in reality 56.

After the last spermatogonial division the nuclei undergo a growth stage, during part of which the chromatin takes the form of a great number of fine granules almost filling the nucleus. Some groups of cells among the spermatogonia occasionally degenerate, and produce masses of deeply staining material. As growth proceeds, the normal

cells become very definitely arranged in follicles, in which a space begins to appear in the centre. From this stage onwards threads may be seen running out from the cells into the cavity of the follicle, ending in small vesicles or transparent masses of cytoplasm. Frequently it can be made out that these threads are attached to the centrosome of the cell, as described by Meves (*Anat. Anz.* XIV. p. 1), and in some cases it appears that there are accessory threads like those figured by Meves in the Bee (*Arch. Mikr. Anat.* Bd. LXX. p. 414).

From this stage onwards the fate of the different follicles varies, for as Meves[1] has described in *Pygaera* and Voinov[2] in other Lepidoptera, there are two distinct types of spermatogenesis. The first and more normal type is found chiefly in larvae before pupation and in very young pupae (1—3 days), but both types are found concurrently except in advanced pupae, in which only the second is usually found. In the first type the primary spermatocytes enlarge considerably, and before the maturation divisions the nucleus contains about 28 chromosomes scattered round the nuclear membrane (Fig. 2). These then form a flat equatorial plate, in which 28 chromosomes may easily be counted[3]; they are not all equal in size, but none can be identified as differing conspicuously from its fellows (Figs. 3—5). Seen in side view, the chromosomes are elongated or dumbbell-shaped, and after division they travel to the poles with great regularity and form a vesicular nucleus (Figs. 7, 8, 9). From the rarity of its occurrence this stage probably persists but a short time, and it breaks down to give a second division spindle. Here again the chromosomes are regularly arranged, and 28 may usually be counted without difficulty, about half the size of those of the first division (Fig. 10). The cells divide (Figs. 11, 12), and give rise to spermatids which develop into spermatozoa in a manner closely similar to that described by Meves in the "eupyrene" spermatozoa of *Pygaera*.

In the second type of spermatogenesis the growth-phase of the primary spermatocytes appears to be shorter, and they prepare for division when their diameter is conspicuously smaller. The nuclei contain a number of chromatin granules, which in the prophase of

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[1] *Arch. Mikr. Anat.* Bd. LVI. (1900), p. 565, and Bd. LXI. (1903), p. 62.

[2] *Arch. Zool. Exp. et Gén.* 1903, Notes et Revues, p. xlix.

[3] In one testis of a heterozygote between the *grossulariata* and *lacticolor* varieties some equatorial plates appear to contain 29 chromosomes. In some figures this appears to be due to the fact that a few of the chromosomes have already divided, for some are markedly smaller than the rest, but in one case 29 can be counted in which there is no direct evidence for division (Fig. 6).

the first division are mostly arranged round the membrane, and approach 50 in number (Fig. 13). As the division approaches there are indications that these small chromatin masses become associated in pairs, and before the spindle is formed between 20 and 30 of these pairs may be counted (Fig. 14). This doubleness is much less pronounced in spermatocytes of the first type, and in them the preliminary diploid condition is not found. The first division of these smaller cells differs greatly from that described above, for the equatorial plate is so irregular that an exact count has never been possible; the number of chromosomes, however, approaches 28 (Figs. 15, 16). The anaphase figures are very remarkable; at the beginning the chromosomes usually show a dumbbell-like shape, but they do not all divide simultaneously, with the result that while those in the centre of the equatorial plate still retain their position, those near the edge have divided and the halves may have nearly reached their respective poles. The spindle thus may appear almost covered with scattered chromosomes, which finally all reach the poles; a vesicular nucleus is then formed and the cell divides (Fig. 17).

The second spermatocytes appear to begin their division almost immediately; it is essentially like the first except that the cells, spindles and chromosomes are distinctly smaller and the arrangement of the latter even more irregular (Figs. 18, 19). At the close of the division the cells become spermatids, with a vesicular nucleus and conspicuous "Mitochondrien Körper," differing from those produced by the large regular spermatocytes only in their smaller size (Fig. 20, *a, b*).

It will be seen that the process described is closely similar to that found by Meves in *Pygaera*, except that a single spermatid nucleus is formed instead of each chromosome forming a small separate vesicle. *Abraxas* also differs from his description in the fact that the "normal" spermatogenesis occurs chiefly in the late larval and early pupal stages, and the small irregular spermatocytes are most conspicuous in the rather later pupae. In my first sections of pupae several days old I found no large regular spermatocyte divisions, and even in pupae 3—5 days old they are often quite scarce; while in larvae not yet spun up some search may be required before the small irregular type is found[1]. According to Meves both types occur in about equal numbers in the pupae of *Pygaera*.

[1] I owe the suggestion that the regular type might occur more frequently in larvae, and that the irregular type may be abnormal, to Prof. E. B. Wilson, who has kindly examined some of my preparations.

The later development of the small spermatids appears to be identical, as far as I have been able to follow it, with that of the "apyrene" type in *Pygaera* as described by Meves. When the developing spermatozoa become aggregated in bundles, it may generally be seen that these are of two sizes; in the larger the nuclei are at one end, being transformed into the heads of the spermatozoa, but in the smaller the nuclei are scattered along the tails of the spermatozoa and appear to be degenerating. A few such degenerating nuclei may sometimes be seen in the large bundles (Fig. 21, *a, b*). In teased preparations of the testes of the imago, the small spermatozoa in which the nuclei have degenerated appear to remain in bundles, which suggests that only the large nucleate ones are functional in fertilisation. This is confirmed by sections of testes of the imago in which nearly all the spermatozoa are of the small degenerate type, while in the vas deferens nearly if not quite all are of the normal kind. Probably therefore the degenerating spermatozoa do not leave the testis. In the imago the degenerate spermatozoa are in the same stage as in the pupa; I have not seen the final stages leading to complete loss of the nuclei described by Meves in *Pygaera*.

In conclusion, it should be said that the observations here described apply equally to pure (wild) *grossulariata*, to the variety *lacticolor*, and to the heterozygote between the two varieties. The formation of "apyrene" spermatozoa is thus not connected with the *lacticolor* variety, and my observations do not give any indication of the cause of the phenomenon. The suggestion of Meves that "apyrene" spermatozoa are capable of fertilising an egg but not of transmitting the paternal hereditary characters is not borne out by breeding experiments, nor do these confirm the suggestion that the two types of spermatozoa determine different sexes in the fertilised egg.

I have only made a cursory examination of the mitoses in the germ-cells of the female, but those in the egg-tubes (oogonia) of a full-fed larva do not differ recognisably from the spermatogonial mitoses described above.

PLATE XXXIII.

EXPLANATION OF FIGURES.

All the figures except Fig. 21 were drawn with a Zeiss immersion apochromat. 3 mm. N. A. 1·40, and Compens. Oc. 12.

Fig. 21, *a, b* was drawn with a 12 mm. objective.

Fig. 1.   Spermatogonial mitoses.
    a.   Equatorial plate in face; about 54 chromosomes visible.
    b.   Metaphase in side view.
Figs. 2—9.   First spermatocyte divisions, large "normal" type.
Fig. 2.   Early prophase: chromosomes on nuclear membrane. The nucleus extends through more than one section: only those in one section are represented.
Figs. 3—6.   Equatorial plates in face. Fig. 3, wild *grossulariata*; Fig. 4, *lacticolor*; Fig. 5, heterozygote. These three show 28 chromosomes. Fig. 6, heterozygote, showing 29 chromosomes, probably owing to premature division of one.
Fig. 7.   Equatorial plate, side view.
Figs. 8, 9.   Early and late anaphases.
Figs. 10—12.   Second spermatocyte division, large "normal" type.
Fig. 10.   Equatorial plate. *a.* heterozygote. *b. lacticolor.*
Fig. 11.   Equatorial plate, side view.
Fig. 12.   Telophase.
Figs. 13—19.   Spermatocyte divisions, small irregular type.
Fig. 13.   Early prophase of first division ; the nucleus extends through about three sections, one of which is represented. There were altogether over 50 chromosomes.
Fig. 14.   Later prophase, one section of nucleus. Altogether 18 double and 10 or more single chromosomes were counted.
Fig. 15.   Equatorial plate of first division. 31 chromosomes appear to be present, probably owing to premature division.
Fig. 16.   Same stage, side view.
Fig. 17.   Anaphase of first division, showing scattering of chromosomes.
Figs. 18, 19.   Second spermatocyte division, early and late anaphases.
Fig. 20.   Spermatids in process of conversion into spermatozoa. Reconstructions combined from more than one section.
    a.   (Above) large "normal" type ("Eupyrene," Meves).
    b.   (Below) small abnormal type ("Apyrene," Meves).
Fig. 21.   (Drawn with ½ in. objective.) Bundles of nearly mature spermatozoa.
    a.   (Above) normal "Eupyrene."
    b.   (Below) abnormal "Apyrene."

PLATE XXXIII
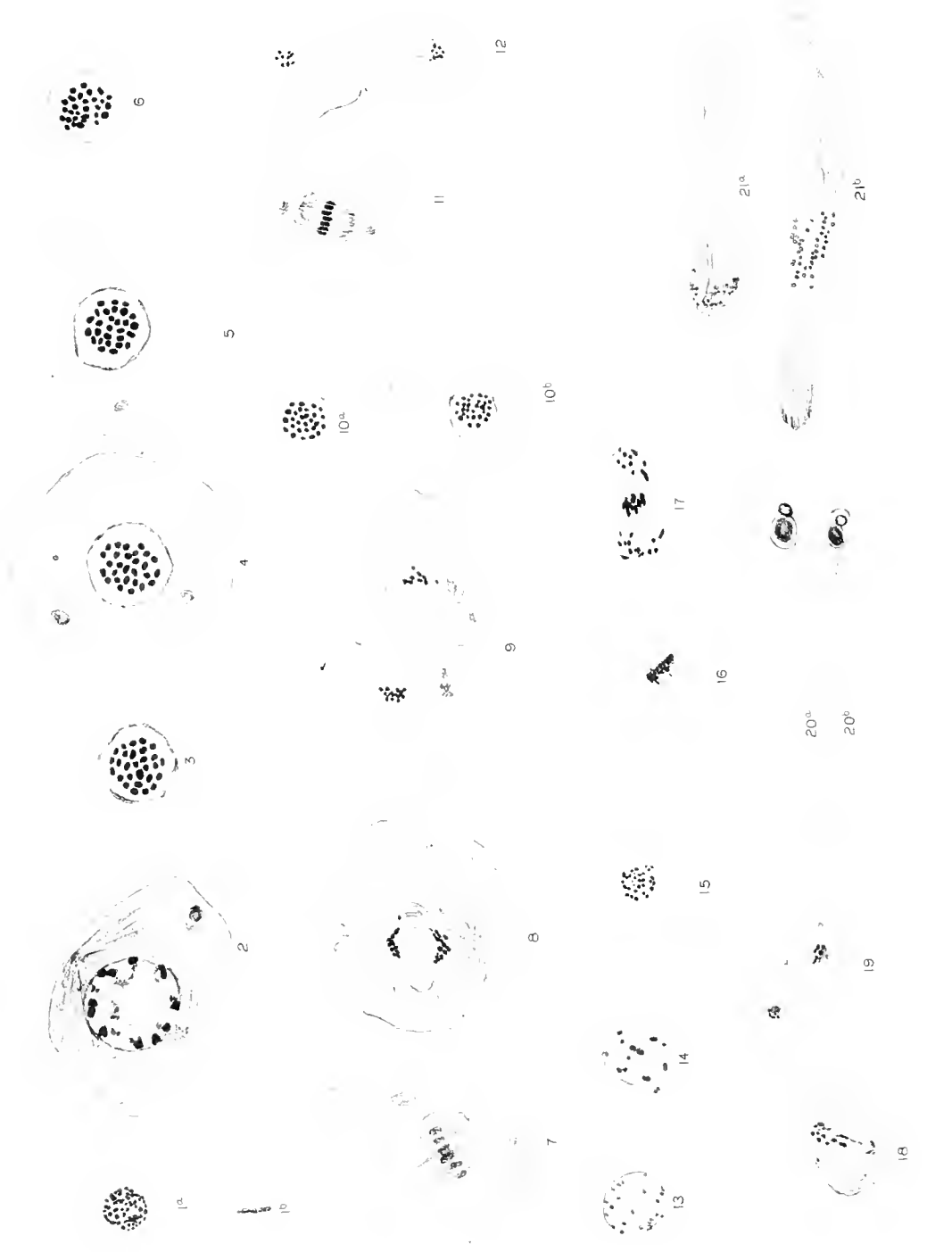
THE INHERITANCE OF THE PECULIAR PIGMENTATION OF THE SILKY FOWL.

By W. BATESON, M.A., F.R.S.
AND R. C. PUNNETT, M.A.

CONTENTS.

INTRODUCTION.

DURING the past six years we have been engaged upon a series of experiments connected with the inheritance of the peculiar pigmentation of the Silky Fowl. A brief account of the general features of this interesting case has already been published by one of us[1], but as our experiments are now concluded we are able to give in greater detail the evidence upon which our views are based. As a description of the Silky Fowl may be found in any of the standard works on poultry it is unnecessary for us to dwell upon the characters of the breed except in so far as they enter into this particular series of experiments. One of its most remarkable features is the extraordinary abundance of black pigment which is generally distributed among most of the mesodermal

[1] W. Bateson, *Mendel's Principles of Heredity*, 1909, p. 181.

tissues of the body. Seen through the thin epidermis this pigment gives the bird the appearance of a fowl with a black skin, deep purple comb and wattles, and dark slaty shanks. The iris is heavily pigmented, and the usually white earlobe takes on a more or less intense turquoise tint which is especially noticeable in the hens. The somatic peritoneum, the periosteum and pia mater are inky black from the pigment with which they are crowded. The splanchnopleure is much less pigmented, and the liver seen through this looks its normal colour. The muscles also have a blackish appearance, but we have not made any histological examination to determine the exact distribution of the pigment here. It is apparently confined to membranes of mesodermal origin, and is absent from the lungs, liver and other viscera, while at the same time the plumage is white. There is never any trace of it in the allantois, or other foetal membranes.

Our experiments with this breed were begun with the idea of investigating the nature of the form of comb by which it is characterised, but we had not proceeded far before it became evident that the inheritance of the peculiar pigmentation promised more interesting and novel results. As the case presents features unlike any hitherto met with elsewhere it will be convenient if we give a brief outline of the main results and of the interpretation before passing to a detailed examination of the experimental data.

General statement of results.

The breed with which the Silky was originally crossed was a strain of Brown Leghorns which had been in our possession since 1899. The first indication of something unusual was the definite difference found in the reciprocal crosses between these two breeds. While the mating of Silky ♀ × Brown Leghorn ♂ resulted in chicks of both sexes with little pigmentation, the mating of Brown Leghorn ♀ × Silky ♂ gave a markedly different result. From this mating the ♂ chicks had only a little pigment and were indistinguishable from those resulting from the previous cross, but the ♀ chicks were all deeply pigmented, differing but little in this respect from a pure Silky[1]. On breeding the F_1 birds together there resulted in either case an F_2 generation consisting of

[1] The F_1 chicks all had coloured plumage and subsequent breeding showed that the white of the Silky behaved as a simple recessive (cf. *Rep. Evol. Comm. Roy. Soc.* iv. 1908). Our experiments have led us to infer that the pigmentation is quite independent of the colour of the plumage.

chicks of various grades of pigmentation ranging from the deepest pigment to none at all. The F_2 generation however presented certain distinctions according as a pigmented, or a non-pigmented F_1 hen was used (see p. 193).
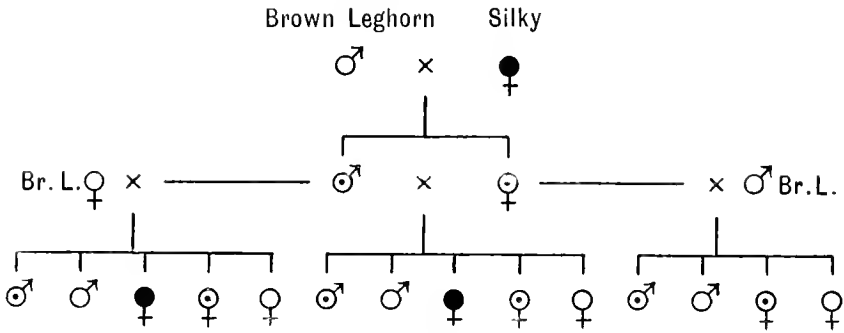
Fig. 1.
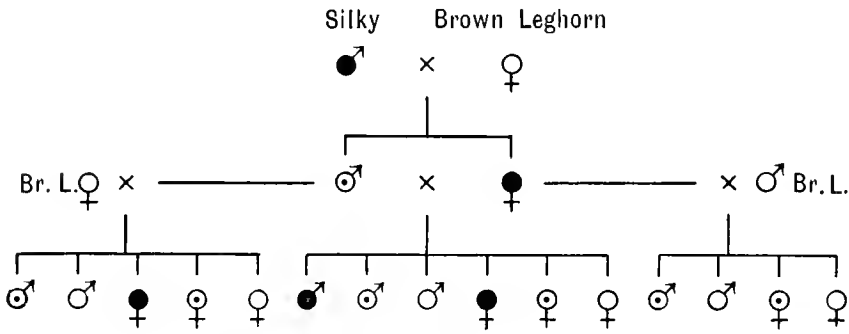
Fig. 2.

In these figures

♂ ♀   represent unpigmented birds.

♂ ♀   „   deeply pigmented birds.

♂ ♀   „   birds with some grade of pigmentation other than the deeply pigmented type.

The F_1 birds were also crossed with the pure Brown Leghorn and the results were strikingly different according as the sex of the F_1 was male or female. When the F_1 ♀ was crossed with the Brown Leghorn ♂ none of the offspring were deeply pigmented, and this was true for the

pigmented F_1 ♀ as well as for the unpigmented. But when the F_1 ♂ was crossed with a Brown Leghorn ♀ about one in eight of the offspring were deeply pigmented *and these were always females*. To assist the reader in following this somewhat complicated case we append a rough scheme. It will be understood of course that the scheme gives no indication of the proportions in which the various classes are produced, neither for the moment do we attempt to differentiate between the various grades of pigmentation other than the fully pigmented state.

We may now state briefly the interpretation to which our various experiments have led us. We consider that three factors are involved of which two are directly concerned with the degree of pigmentation. These are (α) a *pigmentation* factor (P), and (β) an *inhibition* factor (I) which can prevent the full development of the pigmentation[1]. The various grades of pigmentation met with depend upon the various compositions of the zygotes in regard to these two factors; e.g. a bird of the constitution $PPii$ will be fully pigmented, a bird of the constitution $PpIi$ will be slightly pigmented, while birds of the constitution $ppII$, $ppIi$, or $ppii$ will be unpigmented (see also p. 200).

The third element with which we are concerned in these experiments is *sex*. Here we have made certain assumptions. We regard the female as differing from the male in possessing a special element, F, of which the hereditary behaviour is like that of any other Mendelian factor. Moreover we consider that the female is always heterozygous for this factor so that the zygotic constitution of a female is Ff while that of a male is ff. Further we suppose that in such zygotes as are heterozygous for both F and I there occurs a repulsion between these two in gametogenesis so that F and I do not pass into the same gamete. We may allude to the cases of the inheritance of the *lacticolor* variety of *Abraxas grossulariata*[2] and of the red eye of cinnamon canaries[3] in which similar phenomena can be shown to follow the same system of descent.

It must be expressly stated that the suggestion that females are heterozygous for *femaleness* is offered without prejudice as to the possibility that males may also be heterozygous in *maleness*. The systems followed by the descent of colour-blindness[4] in Man and by

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[1] The condition of the gamete from which either or both of these factors are absent we shall denote in the conventional way by the use of the corresponding small letters p and i.

[2] Doncaster, L., *Reports to the Evolution Committee of the Royal Society*, IV. 1908.

[3] Durham, F. M., *Reports to the Evolution Committee of the Royal Society*, IV. 1908.

[4] *Mendel's Principles*, 2nd imp., 1909, p. 195, note.

that of the white eye recorded by Morgan in *Drosophila*[1] clearly point to the existence in those cases of a repulsion between a factor for maleness (M), and factors respectively for colour-blindness and for the red eye. The operation of the system of sex-limitation is similar in all these examples, the only difference being that in the one group the repulsion is from the factor F, in the other from the factor M.

$$[\male]$$
$$iiPPff$$
gives
gametes
$$iPf \brace iPf$$

$$[\female]$$
$$IippFf$$
gives
gametes
$$\begin{Bmatrix} Ipf \\ ipF \end{Bmatrix}$$

×

$$[\female]\ IippFf$$
gives
gametes
$$\begin{Bmatrix} Ipf \\ ipF \end{Bmatrix}$$

×

$$[\male]\ IiPpff$$
gives
gametes
$$\begin{Bmatrix} IPf \\ Ipf \\ iPf \\ ipf \end{Bmatrix}$$

×

$$iiPpFf\ [\sex]$$
gives
gametes
$$\begin{Bmatrix} iPF \\ iPf \\ ipF \\ ipf \end{Bmatrix}$$

×

$$IIppff\ [\male]$$
gives
gametes
$$\begin{Bmatrix} Ipf \\ Ipf \end{Bmatrix}$$

Ipf iPf $\male$	ipF iPf $\female$	IPf iPF $\female$	IPf iPf $\male$	IPf ipF $\female$	IPf ipf $\male$	Ipf iPF $\female$
Ipf Ipf $\male$	ipF Ipf $\female$	Ipf iPF $\female$	Ipf iPf $\male$	Ipf ipF $\female$	Ipf ipf $\male$	Ipf iPf $\male$
Ipf iPf $\male$	ipF iPf $\sex$	iPf iPF $\sex$	iPf iPf $\male$	iPf ipF $\sex$	iPf ipf $\male$	Ipf ipF $\female$
Ipf ipf $\male$	ipF ipf $\female$	ipf iPF $\sex$	ipf iPf $\male$	ipf ipF $\female$	ipf ipf $\male$	Ipf ipf $\male$

Fig. 3.

Recognition of the existence of factors both for femaleness and for maleness of course involves the assumption that ova bearing F can only be effectively fertilised by sperms not bearing M, and *vice versa*. For that supposition no independent evidence yet exists, and we note that

[1] Morgan, *Science*, 1910, N. S. xxxii. p. 120.

Morgan[1] has made observations on *Cumingia* (Mollusca) distinctly unfavourable to it.   At present however we think it is the most acceptable account of the facts ascertained both as to the heredity and the variability of sexual characters.

$$[\male]$$
$$IIppff$$
gives
gametes
$$\left.\begin{array}{l} Ipf \\ Ipf \end{array}\right\}$$

$$[\female]$$
$$iiPPFf$$
gives
gametes
$$\left\{\begin{array}{l} iPF \\ iPf \end{array}\right.$$

×

Br. Legh.
$$[\female]\; IippFf$$
gives
gametes

$$\left.\begin{array}{l} Ipf \\ ipF \end{array}\right\}$$

$$[\male]\; IiPpff$$
gives
gametes

$$\left\{\begin{array}{l} IPf \\ Ipf \\ iPf \\ ipf \end{array}\right\}$$

$$IiPpFf\;[\female]$$
gives
gametes

$$\left\{\begin{array}{l} IPf \\ Ipf \\ iPF \\ ipF \end{array}\right\}$$

Br. Legh.
$$IIppff\;[\male]$$
gives
gametes

$$\left\{\begin{array}{l} Ipf \\ Ipf \end{array}\right.$$

×   ×   ×

Ipf IPf $\male$	ipF IPf $\female$
Ipf Ipf $\male$	ipF Ipf $\female$
Ipf iPf $\male$	ipF iPf $\female$
Ipf ipf $\male$	ipF ipf $\female$

IPf Ipf $\male$	IPf Ipf $\male$	IPf iPF $\female$	IPf ipF $\female$
Ipf IPf $\male$	Ipf Ipf $\male$	Ipf iPF $\female$	Ipf ipF $\female$
iPf IPf $\male$	iPf Ipf $\male$	iPf iPF $\female$	iPf ipF $\female$
ipf IPf $\male$	ipf Ipf $\male$	ipf iPF $\female$	ipf ipF $\female$

Ipf IPf $\male$
Ipf Ipf $\male$
Ipf iPF $\female$
Ipf ipF $\female$

Fig. 4.

The Silky Fowl normally breeds true to the fully pigmented condition and we consequently represent the cocks and hens of this breed as *ffPPii* and *FfPPii* respectively.   The Brown Leghorn on the other hand never produces pigmented birds and we therefore regard it as being entirely without the factor *P*.   But it possesses the inhibitor factor *I*; and for reasons which will appear later the cock must be

[1] Morgan, Payne, and Browne, *Biol. Bull.* 1910, xviii. p. 76.

normally homozygous and the hen heterozygous for this factor. Con-
stitutionally therefore we look upon the cocks and hens of this breed
as being respectively $ffIIpp$ and $FfIIpp$. To illustrate what we
imagine to happen in the several generations produced by mating
a Silky $\male$ with a Brown Leghorn $\female$ as well as in the reciprocal cross
we have drawn up the appended schemes (Figs. 3 and 4) for comparison
with Figs. 1 and 2. These schemes also indicate the composition on
our hypothesis of the generations shown and we may now proceed to
test their validity by the facts witnessed in these and other forms of
mating.

Detailed results of the various crosses.

1. The F_1 generation.

(α) *From the Silky* $\female$.

[Nature of mating $FfPPii \times ffppII$.]

We have bred from Silky $\female$ × Brown Leghorn $\male$ on two occasions
and in neither case had any of the chicks more than a slight amount
of pigment (cf. Fig. 1). Many of these were reared and in the adult
state were almost indistinguishable in general appearance from pure
unpigmented birds. Careful examination however revealed traces of
pigment as patches either on the wattle, skin, or shanks. In most
cases the presence of some pigment was most readily detected beneath
the skin in the periosteum of the femoro-tibial or of the tarso-metatarsal
joints. Dissection showed that some pigment was nearly always present
in the ribs and in the occipital region of the skull. There was frequently
a little peritoneal pigment more especially in the region of the ribs
and some in the occipital pia mater. The amount of pigment varies
somewhat and may be very slight. In some cases the chicks are
recorded in our notes as being without pigment, but most of these

TABLE I.

			Males			Females		
Reference		Nature of mating	Full	Some	None	Full	Some	None
1905	Pen 16, 349	Silky $\female$ × Br. L. $\male$	—	5		—	2	
1907	,, 7, 495	,, ,,	—	8		—	8	
1909	,, 7, 150	F_2 $\female$ × ,,	—	7		—	13	

records refer to birds which were not killed and critically examined. The extent to which the pigment development is inhibited exhibits individual variation, and it is likely that in some birds the inhibition is so complete that they are indistinguishable from birds which lack the pigmentation factor. Here we may mention also that we bred from a fully pigmented F_2 hen (♀ 150, see p. 197) with results similar to those which we obtained from the Silky hens.

(β)   *From the Silky* ♂.

[Nature of mating $Ffpp\,Ii \times ff PP ii.$]

Our original Silky ♂ was mated at different times with two pure Brown Leghorn hens. The F_1 males from this mating were precisely similar to those produced from the reciprocal cross. The F_1 hens however were nearly as deeply pigmented as the Silky (cf. Figs. 2 and 4). To the one exception, a slightly pigmented ♀, we shall return later (p. 200).

TABLE II.

Reference			Nature of mating	Males			Females		
				Full	Some	None	Full	Some	None
1905	Pen 51,	404 }	Br. L. ♀ × Silky ♂	—	8		8	—	—
1906	,, 18,	404 }							
1908	,, 18,	281 }	,, ,,	—	29		31	1	—
1909	,, 18,	281 }							

2.   The F_2 generation.

(α)   *From the Silky* ♂.

[Nature of mating $FfPpii \times ffPpIi.$]

In Figure 3 we have already indicated the results which are to be expected from this form of mating. One quarter of the total offspring should be completely unpigmented while the remainder should be equally divided between the fully pigmented and the partially pigmented classes, the expected ratio being three fully pigmented, three partially pigmented, and two unpigmented out of every eight birds. Moreover the ratio should be the same for each sex. In Table III the results of six such matings between F_1 birds are given. There is a slight excess of fully pigmented ♀♀ due to the unusually high proportion of such birds in one of the matings (1909, Pen 4, 329), but on the whole the facts are in close accord with expectation.

TABLE III.

	Reference		Nature of mating	Males			Females		
				Full	Some	None	Full	Some	None
1907	Pen 15,	283	$F_1 ♀$ (full pig.) $\times F_1 ♂$	11	6	4	9	11	9
	,, 23,	114	,,	2	6	1	6	3	3
1907) 1908)	,, 22,	121	,,	6	7	6	6	6	4
1908	,, 5,	467	,,	7	—	4	11	8	4
1909	,, 4,	329	,,	11	13	9	22	8	6
	,, 22,	148	,,	3	3	3	5	2	1
1909) 1910)	,, 20,	374	,,	11	20	7	15	17	11
			Total	51	55	34	74	55	38
			Expectation	52·5	52·5	35	62·5	62·5	42

(β) *From the Silky ♀.*

[Nature of mating, $FfPpIi \times ffPpIi.$]

As indicated in Figure 4 expectation is here different from that in the preceding case where the F_1 ♀ was from the cross Brown Leghorn ♀ × Silky ♂. The slightly pigmented F_1 ♀ is here heterozygous for the inhibitor factor, I, and there comes into play the repulsion between I and F so that all the male gametes produced by such birds contain I, while this factor is carried by none of the female gametes. From this mating therefore we should not expect any fully pigmented males since every bird of this sex must contain I. Nevertheless, as the data in Table IV show, many of the males resulting from this mating were recorded as being heavily pigmented. By far the greater number of chicks in this generation were killed and recorded on hatching, and a peculiarity of the ♂♂ booked as fully pigmented lay in the fact that the toes of these birds were always light in colour. We regard these birds as of

TABLE IV.

	Reference		Nature of mating	Males			Females		
				Full	Some	None	Full	Some	None
1906	Pen 9,	467	$F_1 ♀$ (unpig.) $\times F_1 ♂$	1	3	1	2	—	2
1907	,, 11,	459	,,	6	8	1	5	11	1
	,, 20,	461	,,	2	14	8	10	7	4
1908	,, 19,	459	,,	—	2	3	2	3	—
	,, 19,	393	,,	3	14	8	5	7	6
	,, 22,	467	,,	—	1	—	4	—	—
			Total	12	42	21	28	28	13
			Expectation	18·75	37·5	18·75	26	26	17

the constitution $ffPPII$ or $ffPPIi$ and suppose that in the presence of a double dose of the pigmentation factor the effects of the inhibitor are in considerable measure overcome in the younger stages. In corroboration of this view we may state that we reared several of these deeply pigmented $\male\male$ and that they all became far less heavily pigmented in appearance as they approached maturity. In external appearance indeed they showed little more pigmentation than the F_1 cocks. This explanation is the natural one if we regard the constitution of the slightly pigmented F_1 $\female$ as $FfPpIi$, and further evidence (p. 198) in favour of this view will be adduced from an entirely different set of experiments.

3. $F_1 \times$ Brown Leghorn.

(a)   *Brown Leghorn* $\female \times F_1 \male$.

[Nature of mating, $Ffpp Ii \times ffPpIi$.]

On our hypothesis this form of mating should give a specific result, for while the $\male\male$ should all be either without, or with comparatively little, pigment, one quarter of the $\female\female$ should be fully pigmented (cf. Figs. 3 and 4). We have bred a considerable number of birds (nearly 700) in this way, and the figures given in Table V show that this expectation is closely realised. None of the 336 $\male\male$ produced

TABLE V.

	Reference		Nature of mating	Males			Females		
				Full	Some	None	Full	Some	None
1906	Pen 9,	207	Brown $\female \times F_1 \male$	—	28	8		29	
	,, 33,	248	,,	—	8	1		1	
	,, 33,	159	,,	—	13	5		13	
1907	,, 11,	203	,,	—	34	8		24	
	,, 12,	264	,,	—	13	3		8	
	,, 12,	159	,,	—	19	3		18	
	,, 15,	347	Br. L. $\female \times F_1 \male$	—	34	11		37	
	,, 16 $\female \female$ Br.L.		Brown $\female \times F_1 \male$	—	18	2		14	
	,, 20,	129	,,	—	22	7		19	
	,, 22,	101	,,	—	42	8		28	
	,, 23,	98	,,	—	24	7		18	
1908	,, 5,	101	,,	—	17	3		20	
	,, 16,	345	Br. L. $\female \times F_1 \male$	—	20	7		16	
	,, 22,	129	Brown $\female \times F_1 \male$	—	40	8		31	
1909	,, 20,	347	Br. L. $\female \times F_1 \male$	—	4	1		4	
			Total	—	336	82		280	
			Expectation	—	*336*	*90·5*		*271·5*	

were deeply pigmented, while of the 362 ♀♀ 82 were deeply pigmented, a proportion approximating fairly closely to the expected quarter. We should add that owing to a deficiency of pure Brown Leghorns some of the hens used were light-shanked brown birds of Brown Leghorn extraction. With regard to the transmission of pigmentation these behaved similarly to the pure race.

(β) F_1 ♀ (unpigmented) × Brown Leghorn ♂.

[Nature of mating, $FfPpIi \times ffppII$.]

Two F_1 ♀♀ of this nature were crossed with a Brown Leghorn ♂ and gave 26 ♂♂ and 18 ♀♀ of which none were deeply pigmented. This again fits in with our hypothesis (cf. Fig. 4), for no deeply pigmented birds are to be looked for from this mating.

4. F_1 × Fully pigmented ($PPii$) birds.

(α) F_1 ♂ × $PPii$ ♀.

[Nature of mating, $FfPPii \times ffPpIi$.]

The expected result from this form of mating is equal numbers, in both sexes, of chicks with deep pigmentation and of chicks with some pigmentation. We have made this mating twice with the following results:

TABLE VI.

		Males		Females	
Reference	Nature of mating	Full pigmentation	Some pigmentation	Full pigmentation	Some pigmentation
1906 Pen 33, 349	Silky ♀ × F_1 ♂	5	2	3	5
1909 ,, 17, 114	F_2 full pig. ♀ × F_1 ♂	20	18	19	22
	Total	25	20	22	27
	Expectation	23·5	23·5	23·5	23·5

These results are obviously in close accord with expectation, but it must be mentioned that ♀ 114 also gave one ♀ chick recorded as *without pigmentation*.

(β) F_1 ♀ (slightly pigmented) × Silky ♂.

[Nature of mating, ♀♂$PpIi$ × ♂♂$PPii$.]

Since on the hypothesis the gametes produced by the F_1♀ are ♀Pi, ♀pi, ♂PI, and ♂pI it follows that all the female chicks will contain P without I, while of the male chicks all will be heterozygous for I while half will be homozygous for P. In discussing the nature of the

F_2 generation from this type of F_1 ♀ we have already seen reason for supposing that the male chicks of the constitution $PPIi$ are practically fully pigmented on hatching, but that the pigment becomes much reduced with advancing age. Hence the expectation for the present type of mating is that all the ♀ ♀ will be deeply pigmented, and that the ♂ ♂ will hatch either as deeply pigmented chicks, or as chicks with some pigment only—these two classes being produced in equal numbers. Table VII gives the results of the two cases in which we have made this mating. While the general result is in accordance with expectation the Table shows that there are two ♀ ♀ from each mating which are not fully pigmented. To these exceptions we shall recur later (p. 200).

TABLE VII.

Reference		Nature of mating	Males			Females		
			Full	Some	None	Full	Some	None
1907 1908	Pen 18, 459	F_1 ♀ (slight pig.) × Silky ♂	12	13	—	28	2	—
1907 1908 1909	„ 9, 467 „ 16, 467	„ „	12	18	—	28	2	—
		Total	24	31	—	56	4	—
		Expectation	*27·5*	*27·5*	—	*60*	—	—

(γ) F_1 ♀ (*fully pigmented*) × *Silky* ♂.

[Nature of mating, ♀ ♂ $Ppii$ × ♂ ♂ $PPii$.]

Since the gametes of neither parent carry the inhibitor factor and since those of one parent all contain the pigmentation factor, the expected result of this mating is fully pigmented chicks only, of both sexes. The mating has been made on three occasions and as Table VIII shows the results are in accordance with expectation.

TABLE VIII.

Reference		Nature of mating	Males Full pigmentation	Females Full pigmentation
1907	Pen 18, 121	F_1 ♀ full pigmentation × Silky ♂	17	3
1907 1908	„ 18, 114	„ „	10	15
1907 1908	„ 9, 283	„ „	15	19

We have already alluded to the deeply pigmented hens which resulted from crossing the F_1 ♂ with the Brown Leghorn ♀. On our

hypothesis these birds are in constitution $FfPpii$ and consequently should give the same result as the deeply pigmented F_1 ♀ when crossed with a pure Silky ♂. We have made this cross on two occasions and in accordance with expectation all the chicks were deeply pigmented (cf. Table IX).

TABLE IX.

Reference			Nature of mating	Males Full pigmentation	Females Full pigmentation
1907	Pen 18,	344	♀ $Ppii$ × Silky ♂	11	12
1907	,, 9,	376	,, ,,	10	12

5.   Crosses with deeply pigmented F_2 birds.

In the course of our experiments we have made crosses with two deeply pigmented F_2 birds, viz. ♂ 40 (from Pen 15, 283 of 1907) and ♀ 150 (from Pen 23, 114 of 1907). Each of these birds was as deeply pigmented in the adult stage as the pure Silky, and when bred together they gave only fully pigmented offspring (12 ♂♂ and 21 ♀♀). ♂ 40 was also mated with a pure Brown Leghorn ♀ and gave 21 ♂♂ with some pigment together with 33 deeply pigmented ♀♀. But he is recorded as giving also one deeply pigmented ♂ and 2 ♀♀ which were not deeply pigmented. To these exceptions we shall return and will merely state here that we regard them as due to a peculiarity in the behaviour of the Brown Leghorn hen. ♀ 150 behaved like a pure Silky when crossed with a Br. L. ♂ (p. 192), and we look upon both these F_2 birds as of the constitution $PPii$.

6.   The $ppii$ strain.

In this account we have so far been concerned with the results of various crosses between the Silky and the Brown Leghorn breeds. By a happy accident we are able to adduce independent and cogent evidence in favour of the interpretation which we have put forward. In 1907 we bought a Silky ♂ which proved to be heterozygous for P (i.e. $Ppii$). Mated with an Egyptian hen, a brown bird with light coloured shanks, he gave *unpigmented as well as deeply pigmented hens.* Two of these unpigmented birds were mated back to the heterozygous Silky ♂ in 1908 and as was expected gave deeply pigmented and unpigmented birds of both sexes, viz. 18 ♂♂ deeply pigmented, 15 ♂♂ unpigmented, 21 ♀♀ deeply pigmented, 17 ♀♀ unpigmented. In this way we were able to establish a strain of birds *containing neither*

the pigmentation nor the inhibiting factor in either sex. These birds, on our system of notation, must be represented as *ppii*, and the possession of such a strain provided us with the means of testing the constitution of the F_1 (Silky × Brown Leghorn) birds in the simplest and most direct way.

The F_1 ♂ on the hypothesis produces four kinds of gametes in equal numbers, viz. *fPI*, *fPi*, *fpI* and *fpi*. Crossed with *Ffppii* such a bird should give in both sexes equal numbers of birds with and without pigment. Again among the pigmented birds there should be equal numbers of deeply pigmented birds, and of birds with a small amount of pigment only. Table X shows that these expectations were closely realised in fact.

TABLE X.

	Reference		Nature of mating	Males			Females		
				Full	Some	None	Full	Some	None
1909	Pen 4,	408	♀ *pp ii* × F_1 ♂	1	3	1	—	3	4
	,, 17,	274	,,	8	8	16	6	6	20
	,, 22,	261	,,	5	4	5	3	3	8
			Total	14	15	22	9	12	32
			Expectation	*13*	*13*	*25*	*13*	*13*	*27*

We have also made a similar set of experiments to test the gametic output of the slightly pigmented F_1 ♀ (ex Silky ♀ × Br. L. ♂). The constitution of such birds on the hypothesis is *FfPpIi* and owing to repulsion between *F* and *I* the gametes produced are of four kinds only, viz. *FPi*, *Fpi*, *fPI*, *fpI* (cf. p. 188). Mated with ♂♂ of the constitution *ppii* such birds should give equal numbers of pigmented and unpigmented chicks in both sexes. And since the female gametes which contain *P* all lack the inhibiting factor, all the ♀♀ pigmented

TABLE XI.

	Reference		Nature of mating		Males			Females		
					Full	Some	None	Full	Some	None
1909	Pen 3,	467	F_1 (slight pig.) ♀ × ♂ *ppii*		—	1	2	—	1	1
1909 } 1910 }	,, 13,	459	,,	,,	—	11	9	16	2	12
1909 } 1910 }	,, 25,	393	,,	,,	—	23	17	24	—	21
1910	,, 22,	4 ♀ ♀	♀ *Pp Ii*	× ♂ *ppii*	1	67	67	61	1	56
			Total		1	102	95	101	4	93
			Expectation		—	*99*	*99*	*99*	—	*99*

at all should be deeply pigmented. On the other hand all the male gametes of the F_1 ♀ which contain P contain also I, and consequently none of the pigmented ♂♂ produced should be deeply pigmented. Table XI which gives the details of four such experiments shows how closely this expectation is realised, and offers strong corroborative evidence of the view here taken of the nature of the gametes produced by this type of F_1 ♀. The five exceptions recorded we shall refer to again (p. 200).

The Constitution of the Brown Leghorn Hen.

While the Brown Leghorn ♂ is homozygous for the inhibiting factor, the ♀ is on our hypothesis always heterozygous for this factor. And since we assume repulsion to take place during gametogenesis between the factors F and I it follows that she produces two kinds of gamete, viz. Fpi and fpI. The possession of the $ppii$ strain enabled us to devise a pretty experiment to test this view. By mating a Brown Leghorn ♀ with a cock of the constitution $ffppii$ we obtained a number of unpigmented chickens of both sexes. On our hypothesis only the ♂♂ should receive the inhibiting factor, being in constitution $ffppIi$, while the ♀♀ should be $Ffppii$, and consequently lacking the inhibiting factor. This difference between the sexes with regard to the inhibiting factor should be brought out by a cross with fully pigmented homozygous birds ($PPii$), for while the females should give only fully pigmented chicks, the males may be expected to produce fully pigmented and partially pigmented chicks of both sexes in equal numbers. During the present year a cockerel (ex Br. Leg. ♀ × $ppii$ ♂) was mated with a pure Silky hen, and four sister pullets were put with an F_2 fully pigmented ♂ (No. 40, ex Pen 15, 283 of 1907) already shown to be $PPii$ in constitution. The results are shown in Table XII and are in accordance with expectation.

TABLE XII.

	Reference		Nature of mating	Males			Females		
				Full	Some	None	Full	Some	None
1910	Pen 8,	150	Silky ♀ × ♂ (ex Br. L. ♀ × $ppii$ ♂)	1	4	—	3	3	—
	,, 24,	4 ♀ ♀	♀ ♀ (ex Br. L. ♀ × $ppii$ ♂) × ♂ $PPii$	18	—	—	26	—	—

EXCEPTIONS.

In our account we have mentioned certain exceptions which occurred in several of the various matings.   These are :

Table II, p. 192 .	ex Br. L. ♀ × Silky ♂	1 ♀ partially pigmented
p. 197 .	ex Br. L. ♀ × $PPii$ ♂, F_2	{ 2 ♀ ♀ partially pigmented { 1 ♂ fully pigmented
Table VII, p. 196 .	ex F_1 ($PpIi$) ♀ × Silky ♂	4 ♀ ♀ partially pigmented
Table XI, p. 198 .	ex F_1 ($PpIi$) ♀ × $ppii$ ♂	{ 4 ♀ ♀ partially pigmented { 1 ♂ fully pigmented

In all these cases the ♀ ♀ should have been fully pigmented and the ♂ ♂ should have been partially pigmented on our hypothesis.   It will be noticed that wherever these exceptions occurred the mother was a bird heterozygous for both F and I.   These cases raise the question whether the normal repulsion between F and I in such birds may not occasionally break down, and whether in addition to Fi and fI gametes they may not produce FI and the complementary fi gametes. This appears the more likely as in two out of the four cases a fully pigmented ♂ also appeared as an exception; and in Table VII even if such birds appeared they would not be noticed, since fully pigmented ♂ ♂ are one of the classes normally produced from the mating of slightly pigmented F_1 ♀ and the Silky ♂.   We incline therefore to think that upon occasion the repulsion between factors may be imperfect, though whether this imperfection is sporadic, or whether it can be conceived as part of some orderly scheme we do not yet know enough to say.

THE GRADES OF PIGMENTATION.

The dependence of pigmentation upon the presence or absence of two factors (P and I), as well as upon the heterozygous or homozygous condition of the individual with regard to either or both of them, would naturally lead the observer to look for a considerable range of variation in the pigmented condition.   For in the full zygotic series are the nine possible combinations, $PPii$, $Ppii$, $PPII$, $PPIi$, $PpII$, $PpIi$, $ppII$, $ppIi$, $ppii$.   The great majority of the chicks with which we dealt in these experiments were killed and recorded on hatching, and our practice was to refer them in so far as pigmentation was concerned to one of the following grades, viz. none, faint, slight, some, moderate, much, full, very full.   Though not corresponding accurately to the various zygotic constitutions, these empirical grades nevertheless

afford some indication of them. Where P is not present the bird is always unpigmented, though with regard to I it may be either II, Ii, or ii. Where I is absent the bird is nearly always fully pigmented whether homozygous or heterozygous for P, though it is probable that chicks recorded as with much pigment may sometimes have been in constitution $Ppii$. The birds classed as "very fully" pigmented were probably in most cases $PPii$ though sometimes they may have been exceptionally deeply pigmented birds of the constitution $Ppii$. Where both P and I are present some pigment would appear to be always present though the amount is subject to fluctuation. Thus F_1 birds of both sexes (ex Silky ♀ × Brown Leghorn ♂), and the ♂ birds (ex Brown Leghorn ♀ × Silky ♂) are of the constitution $PpIi$, but in respect of the intensity of their pigmentation they might belong to either of our three classes "slight," "some," or "moderate," and our experience has been that these classes grade very much into one another. Birds with "much" pigmentation are in general either $PPII$ or $PPIi$, though an occasional bird of the $PpIi$ class might be referred to this group. The class $PpII$ is doubtless to be found among the birds with "faint" or "slight" pigmentation.

The grade of pigmentation would also appear to differ somewhat in the two sexes, for among birds similarly constituted for these two factors P and I the females are generally a little more pigmented than the males[1].

This case of the Silky pigmentation is interesting in connection with the production of intermediate forms. In an F_2 family bred from Silky ♀ × Brown Leghorn ♂ all the nine possible zygotic combinations of P and I occur in one or other sex. It would be possible to choose birds of such breeding and to arrange them in a series exhibiting continuous gradation from full pigmentation to none at all. Yet we now know that such a series is due to the interaction of three definite factors (inclusive of the sex factor), and that the continuity in variation manifested is in reality founded upon a discontinuous basis. Moreover we may point out that the mating of partially pigmented males of the constitution $PPIIff$ with partially pigmented females of the constitution $PPIiFf$ would result in the establishing of a race breeding true to an intermediate condition of pigmentation in spite of the underlying discontinuity involved.

[1] This fact is interesting in connection with the common experience of fanciers that in black-feathered breeds which have yellow skins, it is easy to obtain males with clear yellow shanks, but the females almost always have some black pigment in the shanks.

SILKY CROSSES OTHER THAN WITH THE BROWN LEGHORN.

During the course of our experiments we have crossed the Silky with other fowls beside the Brown Leghorn, but as the crosses with the last named promised the most definite results our attention and resources were mainly devoted to these. We may however mention a few points of interest which have arisen in connection with some of the other crosses.

Our original Silky ♂ was mated in 1906 to a white Rosecomb bantam. All the chicks (5 ♂♂ and 7 ♀♀) were deeply pigmented on hatching though as they reached maturity the pigment became less marked in the cockerels. A few cases are already on record in which a Silky was crossed with another breed and all the resulting offspring of both sexes were deeply pigmented[1]. It is worthy of note that in such cases the breed with which the Silky was crossed possessed dark shanks. This was certainly so for the Spanish used by Tegetmeier and Darwin as well as for the Rosecombs used by ourselves; and we infer, though this is not explicitly stated, that it was also true for the frizzled fowls used by Davenport.

We may mention two cases from our experiments which are consistent with this view. When a Silky ♂ was mated with a dark-shanked mongrel ♀ (F_2 ex White × Brown Leghorn) 2 out of the 13 male chicks produced were fully pigmented. The remaining 11 male chicks exhibited a varying amount of pigment, while all the 11 female chicks showed the full pigmentation (1906, Pen 18, 150). In the other case an F_1 ♂, ex Silky ♀ × Brown Leghorn ♂, was also crossed with a dark-shanked mongrel Leghorn hen bred similarly to the last (1906, Pen 9, 604). Out of the 19 male chicks from this mating two were deeply pigmented, while with light-shanked hens the cock gave the usual result (cf. p. 194). We must suppose therefore that the factor or factors upon which shank pigmentation depends can influence the factors concerned with the development of the pigment found in the Silky fowl, but at present we do not know sufficient about the nature of these factors to make any more definite statement.

Though our experiments have led us to infer that the strain of Brown Leghorns with which we worked was homogeneous in respect of the factor modifying pigmentation we nevertheless have evidence

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[1] Cf. Tegetmeier, *The Poultry Book*, 1873, p. 268; Darwin, *Animals and Plants*, 2nd edit., 1899, p. 253; Davenport, *Inheritance in Poultry*, 1906, p. 60.

suggesting that this is not necessarily the case for all light-shanked
birds. An example may serve to illustrate our meaning. During
1908 and 1909 the fully pigmented F_2 ♂ mentioned on p. 197 was
crossed with a Brown Leghorn ♀ and gave a typical result, viz. slightly
pigmented ♂♂ and fully pigmented ♀♀. During both of these seasons
he was also run with a light-shanked ♀ belonging to our recessive
white strain[1]. With her he gave 19 male chicks varying from slight
to moderate pigmentation, but of the 18 female chicks 8 were fully
pigmented and 10 showed only a slight to moderate amount of pigment
(1908–9, Pen 24, 53). From this and other similar experiments it
seems natural to infer that some light-shanked hens may carry other
factors capable of modifying the Silky pigmentation besides that which
we have been able to demonstrate in the Brown Leghorn.

Lastly we may refer to a cross which we made between our original
Silky cock and a hen which was homozygous for the dominant white
factor (1907, Pen 18, 397). All the offspring (18 ♂♂ and 22 ♀♀)
showed some pigment, sometimes a good deal, and this as a rule was
distributed in small irregular patches, but we were unable to notice
any difference between the two sexes. We think it not unlikely that
the hen used was potentially a dark-shanked bird, and that the
offspring of both sexes would have exhibited full pigmentation had not
its development been in some way checked by the dominant white
factor. The results however were complex and lack of opportunity
prevented us from following up the cross, but we have thought it worth
placing these cases on record since they indicate that radical differences
in constitution may exist among light-shanked birds, and that the
behaviour of our strain of Brown Leghorns with regard to the Silky
pigmentation is not necessarily typical of birds with unpigmented
shanks.

[1] An account of the origin of this strain will be found in *Reports to the Evolution
Committee of the Royal Society*, III. p. 19, IV. p. 28.

STUDIES IN INDIAN COTTON.

By H. M. LEAKE.

CONTENTS.

INTRODUCTION.

COTTON forms one of the main crops of large tracts throughout India and is consequently of considerable agricultural importance. The fibre of the majority of the forms found under cultivation is, however, very poor and in a few cases only of sufficient quality to find a market in England. The consumption is chiefly local and an important industry has arisen with numerous mills the bulk of whose out-turn is coarse yarn and cloth for which a considerable demand exists. The problem of improvement in the quality of the raw product is one which has exercised the minds of numerous investigators throughout India for nearly a century and was referred to the author as the problem of most pressing importance when he entered Government service in 1904. The experiments were commenced at Saharanpore in 1905 when a series of the Indian forms were first grown and observed and they have been pursued without interruption first at that place and later as part of the work carried on by the Research Section of the United Provinces' Agricultural Department at the

Cawnpore Station. Though the practical conclusions have of necessity throughout received detailed attention the wider aspect has not been neglected. The broadest interpretation, in fact, has been placed upon the subject in the belief that by such means only can the breadth of view be obtained which is essential to that comprehensive understanding of the group of types under experiment which alone will lead to success in practice. With this aim in view the range of the indigenous forms has, as far as possible, been determined, the various types isolated and grown in pure culture, and crosses made between them.

The fact that the ultimate goal of the experiments is the improvement of the forms generally cultivated has nevertheless imposed certain restrictions which it is necessary to review here. The object is exclusively an improvement of the forms grown in the United Provinces. These Provinces are characterised by a comparatively severe winter, of a severity sufficient not only to check all growth in the cotton plant but to render all previously-formed branches incapable of flower production. Before this can occur, a considerable amount of fresh growth must take place and, by the time flowers commence to form, the brief temperate period has given place to a summer so intensely hot and dry that little or no fruit is set. Forms, therefore, such as are commonly cultivated in the milder districts of Southern India have been grown only with considerable difficulty. It has been found practically impossible to isolate pure types of these and in many cases the only record is one of complete failure to pass from one generation to the next. A full investigation of such forms can only be accomplished in a climate more suited for their cultivation.

During the past few years there has been frequent reference in India to "plant-to-plant" selection as a means of improving the quality of the staple. This term "plant-to-plant selection" is one which has received extended application in India and is there used to denote that selective process by which the crop is grown from the seed of definite selected plants. Fertilisation is allowed to take place naturally and the effects of possible cross-fertilisation are disregarded. It is a method which has been advocated on the assumption that cross-fertilisation does not occur in nature—a view that has been maintained by Gammie (8 and 9). On the other hand observations to the contrary have been made by Balls (1) working in Egypt on a different series of types and in India by Burkill (4), Fyson (7) and the author (11). Also throughout their work both Middleton (13) and Watt (19 and 20) constantly indicate their belief, not only that natural crossing takes place, but that

certain of the races recognised by them have directly arisen by the intercrossing of other extant races. It is not proposed to enter into this question here, and it will suffice to say that abundant proof that crossing is of frequent occurrence has been forthcoming since the author's first note (11) on this subject[1]. Under the circumstances, however, a word as to the procedure adopted in the present experiments is necessary.

The seed received from all sources has invariably given a crop containing numerous, and frequently most diverse, forms. The seed of those appearing recognisably distinct is collected and sown separately[2]. From the similarity or dissimilarity of the offspring the purity or the reverse of the parent can be determined. If the parent appears to be pure the most typical individuals among the offspring are selected and the flowers of these are protected. The form is, in future generations, raised from the seed of flowers thus self-fertilised only. The unit of the parental series on which these experiments are based is, therefore, a series of individuals derived by repeated self-fertilisation through a greater or less number of generations, from a single individual. Such a unit may form the sole representative of a type but, in the majority of cases, the type, as defined, includes several such units usually distinguishable by some small difference in one of the characters. The unit is, therefore, comparable to the "pure line" of Johannsen.

In all cases when it is proposed to make a cross, the flower of the seed parent is emasculated in bud after removal of the petals and, after emasculation, both before[3] and after fertilisation, protected by a paper bag for two days by which time the stigma has usually dropped. The flower from which the pollen is to be obtained is also protected in like manner before the bud opens. The manipulation is simple and among several hundreds of plants in the F_1 generation not a single case of accidental selfing has occurred. The parental types have been grown in each successive season from the seed of protected flowers. In the majority of instances the bud is simply covered with a bag which is removed after two days. This method has been found, however, to lead to a considerable degree of sterility and in some cases it has been necessary to adopt the method of intercrossing different plants of the

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[1] *Vide* also Balls (2) which has appeared since the above was written.

[2] Since several characters are not recognisable until ripe fruit is developed, it is usually impossible to select these plants until it is too late in the season to obtain seed from them by self-fertilisation.

[3] The flower is never fertilised at the time of emasculation. Compare Hartley (23).

same generation. Such crossing is confined to individual plants of the same pure line and its success is of some interest in view of the facts noted by Darwin (5)[1]. Where the produce by self-fertilisation is required, as in the F_1 and subsequent generations, the flower is invariably protected in spite of the considerable labour of handling some 9000 flowers in the course of four to six weeks. In no case has the produce of an unprotected flower been included in the results given below.

THE GENUS GOSSYPIUM AND THE TYPES USED IN THE INVESTIGATIONS.

For reasons which will appear in the course of this paper the author does not consider it advisable at the present time to put forward any scheme of classification to which reference can be made for identification of the types handled by him. Nor is he able to accept in full any of the classifications hitherto advanced. Only those types to which reference is made are therefore briefly described and referred to their place in the schemes in current use. The oldest of these are the classical studies of the genus *Gossypium* by Todaro and Parlatore (15 and 14) where comprehensive schemes for the classification of the genus are to be found. At a more recent date *The Indian Cottons* have been dealt with by Gammie (9) and lastly Watt has reviewed the whole genus in full detail in his *Wild and Cultivated Cottons of the World* (20).

The Indian cottons fall into two marked groups distinguished from each other by the type of secondary branching. Arising from the main axis, which is invariably a monopodium, the secondary branches may either be monopodia or sympodia. The type in which *all* the secondary branches are sympodia has not been observed though it frequently happens that individual plants of certain types exhibit sympodial secondary branching only (cf. Pl. XXXIV, facing p. 208).

Nevertheless, in pure races, the number of monopodia produced at the base of a sympodial type is invariably limited and the two groups stand in obvious contrast on this point.

Monopodial branches are in most cases, though not invariably, ascending while the sympodial branches are usually spreading and the two groups lie in marked contrast to the eye. This difference appears to be fundamental and not limited to the appearance. The flowers are invariably borne on sympodia which take the form of leafy cymes or, more strictly, monochasia. In the sympodial group, therefore, the

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[1] See also Goebel, K. in *Darwinism and Modern Science*, p. 401.

Monopodial type.   Sympodial type.

flowering period commences with the development of the secondary branching, while in the monopodial group this period is delayed until the tertiary branches arise. In India the cultivated monopodial types are in the minority and occupy distinct tracts. Cross-fertilisation between the different types is consequently of rare occurrence, arising under exceptional conditions only, and intermediate types are few. The sympodial types on the other hand are widely cultivated throughout continuous areas and consequently, in the absence of any control over the seed supply, have become inextricably mixed through natural cross-fertilisation. The occurrence of crossing between the monopodial and sympodial types is, as in the case of the monopodial types, sufficiently infrequent even where these types are grown in close proximity. The monopodial commence flowering about five months after the sowing period while the sympodial are in full flower in three months and are producing only stray flowers when the monopodial types are in flower. While, therefore, natural crosses are fairly frequently observable among the offspring of monopodial types, such crosses have not occurred within the author's experience among the offspring of sympodial types grown in like proximity.

The types which have been employed in the experiments detailed below are characterised in the subjoined list. In this list no attempt has been made to arrive at a full and accurate botanical description of each type. The references to the current schemes of classification will sufficiently indicate the broad outlines of the type in question while below are given only such characters as it is desirable to emphasise owing to the position they occupy in the course of the experiments about to be detailed.

Monopodial types.

Type 1. Perennial; secondary branches ascending sharply at an acute angle. Leaf factor[1] is less than entire 2; plant almost glabrous. Bracteoles small, triangular, margin entire or dentate. Corolla yellow.

This plant is the *G. obtusifolium* Roxburgh Flora Indica of Gammie (9) and Watt (20). The various forms to which the specific name *obtusifolium* has been given at different times have been dealt with by Burkill (21).

Type 2. Perennial; with secondary branches spreading. Leaf with a factor less than 2. Stem and leaves densely covered with short hairs.

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[1] A detailed account of the leaf factor is given below (p. 221). It is the value obtained for the ratio $a - b : e$, *vide* Fig. 1, p. 220.

Bracteoles deeply auriculate or reniform, deeply serrate, spreading in fruit. Corolla yellow, petals small. Stigma heavily glandular. Capsule inflated and nearly spherical with a sharp mucronate apex.

This plant is the *G. herbaceum* Linn. of Todaro (16) and Gammie and the *G. obtusifolium* var. *Wightiana* of Watt (20).

Type 3. Perennial "tree cotton"; secondary branches ascending sharply at an acute angle. The entire plant of a deep red, or purple colour. Leaf with a factor greater than 3; frequently with an extra tooth on one or both sides of the central lobe. Bracteoles small, triangular; margins entire or with the tip dentate. Corolla deep-red. Stigma eglandular. Capsule usually 3 celled, ovate.

This plant is the *Gossypium arboreum* of Linn. Sp. Pl.; Parlatore (14); Todaro (16); and the *G. arboreum* type of Gammie (9) and Watt (20).

Sympodial types.

Annuals with a few only, or none, of the lowest secondary branches monopodia, the remainder sympodia; the monopodial branches ascending and the sympodial spreading.

Type 4. A tall plant, in later stages drooping under the weight of fruit. Leaf large, with factor less than 2; lobes commonly 3 or with two small accessory basal lobes. Young stem and leaves sparsely hairy. Bracteoles small, entire or with few small apical teeth, closely enveloping bud and fruit. Corolla yellow with deep-red "eye." Petals large, semi-transparent. Stigma eglandular or with few glands only. Capsule commonly 3 celled, ovate.

This plant is the *Gossypium indicum* Lamk. of Gammie (9) and *G. Nankin* var. *bani* of Watt (20).

Type 5. An erect plant, in later stages drooping under the weight of fruit. Leaf factor less than 2; lobes 5—7. Young stem and leaves hairy. Bracteoles large, entire or with few small apical teeth loosely enveloping bud and in fruit sometimes reflexed. Corolla yellow with deep-red "eye"; petals opaque. Stigma eglandular or with few glands only. Capsule commonly 3—4 celled, ovate.

Type 6. An erect plant differing from type 4 in the greater rigidity the main stem and the angle at which the secondary monopodia arise, in this case about 45°, and in the corolla which is white. The petals are small, scarcely projecting beyond the bracteoles.

Type 7. Plant erect with secondary monopodial branching, when developed, sharply ascending. Leaf factor less than 2; flower white.

This type differs from the last in two respects. The secondary monopodial branches, if developed, are sharply ascending. Frequently, however, they are absent, and even when present reduced in number in plants where the growth of the main axis has not received a check, to one, or at most, two with vigorous growth. The plant is consequently strongly asymmetrical. For the same reason the length of the vegetative period is very brief and the first flowers develope while the plant is still quite small. Growth continues throughout the season, the plant maintaining a marvellous fertility.

Type 8. A tall plant, in later stages drooping under the weight of fruit. Leaf factor greater than 3; lobes 5—7 with an extra tooth, on one, or both sides of the central lobe, frequently developed. Young stem and leaves hairy. Bracteoles entire or with few apical teeth. Corolla yellow with deep-red "eye." Stigma eglandular or with few glands only. Capsule 3—4 celled, ovate.

Type 9. A plant differing from (6) in the colour of corolla only which is white and scarcely protrudes beyond the bracteoles.

Types (4)—(9) fall into the *G. neglectum* and *G. roseum* of Todaro (16), the *G. neglectum* Tod. of Gammie (9) and the *G. arboreum* vars. *neglecta* and *rosea* of Watt (20).

Type 10. A tall plant with the main stem weak and early drooping. Leaf factor greater than 3; lobes 5—7. Bracteoles entire or with few apical teeth, large and continuing to grow with the developing boll. Corolla pale-yellow with deep-red "eye." Stigma eglandular. Capsule ovate very large with numerous seeds.

This plant is the *G. cernuum* of Todaro and Gammie and the *G. arboreum* var. *assamica* of Watt (20).

Type 11. A tall plant with leaf factor greater than 3; leaf lobes 5—7; stem and leaves of a deep-red or purple colour; bracteoles entire or with few apical teeth. Corolla with deep-red "eye," petals white, tinged with pink along margin and the portions exposed in the bud.

This plant is the *G. sanguineum* Hassk. var. *minor* of Gammie (9).

In the above description no reference has been made to the glands which occur on the under-surface of the main ribs of the leaf. The presence, absence and number of these glands was at one time considered a point of some systematic importance. For the present it may be noted that most of the types above described can be divided into three groups; that in which the leaf has no glands, that in which the leaf commonly has 3 glands, and an intermediate group, in which the majority of the leaves possess only one gland situated on the

under-surface of the mid-rib. A detailed discussion of the leaf glands is reserved for subsequent treatment.

THE EXPERIMENTS.

In the crosses that have been made between pairs of the above types the characters that have been observed in greatest detail include the following :

    (*a*)   The colour of the corolla.

    (*b*)   The red colouring matter of the sap.

    (*c*)   The leaf factor.

    (*d*)   The type of branching and length of vegetative period.

    (*e*)   The leaf glands.

3 (*a*).   *The colour of the corolla.*

In all the types of Indian cottons now under consideration, there occurs at the base of each petal a deep-red or purple spot or "eye." The remainder of the petal is uniform, either yellow in colour or white, while in the two types, 3 and 11, the colour is red (cf. Plate XXXV). The red colouration of the petals in these two types is simply a manifestation of the red sap colour which is present throughout the plant. It is not characteristic of the petals alone and cannot be dealt with exclusively as such.

According as the factor producing the yellow colour is present or absent, there arises a simple pair of allelomorphic characters peculiar to the corolla, of which the presence of the colour producing factor is dominant. This is shown in the cross between a type with yellow petals and one with white petals.

The results of such a cross between type 4, with a yellow, and type 6, with a white, flower are set out in Table I.

In the F_1 generation of this cross the plants are all yellow, the colour being indistinguishable from the yellow of the parent type 4. The yellow is completely dominant.

In the F_2 there occurs a separation into two groups, yellow-flowered and white-flowered. The numbers handled are not large and small weight can be attached to the ratio of 2·1 yellow to 1 white obtained, in which the proportion of yellow is considerably below expectation. It is noteworthy, however, in this connection that throughout the provinces where these types are cultivated, although the crop presents

a remarkable range of intermediate types, the white-flowered types are recognisably the hardier. On the correlation that apparently exists between hardiness and white flower there is, at present, no definite information available but such correlation would tend to produce a preponderance of whites.

The figures for the F_3 generation are unfortunately meagre owing to the large loss (some $90°/_\circ$) of young seedlings caused by the early continuous nature of the rains in 1909. The figures are too few to afford any numerical guide as to the proportion of pure dominants among the yellow F_2 plants. They indicate, however, that in the F_2 generation there occur plants of the type DD giving only yellow offspring and others of the type DR which give both yellow and white offspring. The F_2 plants with a white corolla on the other hand give whites only. These results are in entire agreement with those recorded by Fyson (7) and a comparison of the two series of results gives strong evidence as to the part played by vicinism in the field.

Type 10 is characterised by a flower in which the full yellow of the petals of the type previously considered is replaced by a pale but distinct yellow. This pale yellow behaves as a simple recessive to the full yellow. From a cross between this type and type 8 which is characterised by a full yellow petal the F_1 generation is obtained in which the petal is indistinguishable from that of the parent type 8, the full yellow thus being completely dominant. In the F_2 out of 140 plants, 41 possessed the pale yellow corolla giving a ratio of 2·4 plants with full, to 1 with pale, yellow petals. Similarly the full yellow in type 2 appears to be completely dominant over the pale yellow of type 10 giving, in the F_1, plants of which the petal colour is indistinguishable from that of the parent type 2, and, in the F_2, 91 plants with full yellow, and 66 plants with pale yellow, petals. In both these cases and in the latter especially there occurs a large excess in the actual, over the expected, number of recessives which it is necessary to indicate though without further comment since, through inability to cope with the entire series of experiments as at first planned, a number of crosses, including those involving type 10, had to be abandoned after the F_2 generation had been recorded and the presence of this excess has not formed the subject of further experiment. In no case has the pale yellow flowered been crossed with a white flowered type.

It may be here noted that these are the only two cases in which complete dominance has been observed in the cottons under consideration.

In all other cases, as will subsequently appear, dominance is incomplete. The fact may be contrasted with the observation of Balls (1) in another group of cottons in which the impure form is recognisable as of a pale lemon yellow distinct from the full yellow of the parent.

3 (b).   *The red colouring matter of the sap.*

In types 3 and 11 a red anthocyanic colouring matter is present in the sap and communicates an intense red to the entire plant—stem, leaves and flowers. This colour is especially marked in the young chlorophyll bearing tissues, but it is also distinct in such organs as the stigma, anther and fruit. The young leaves are of an intense purple which fades, however, as the leaf developes until in the mature leaf, only the ribs and veins show the colouration distinctly, the lamina retaining merely a slight, and, in cases, barely distinguishable, colour. From the remaining types this colouring matter is absent and their foliage is green, and the petals either white or yellow.

The F_1 generation of a cross between either of the types 3 and 11, and, in fact, any type in which the red colour occurs, and the types in which the colour is absent, bears the red colour which may be said to be dominant. The intensity of the red colour is, however, sufficiently diminished to render the cross readily distinguishable from the parent.

The F_2 generation is readily separable into two sections according to the presence or absence of the red colour. The proportion of coloured individuals to colourless which has been obtained in the experiments under review are given in Table II.

Among the coloured individuals, however, there is a considerable range of intensity in the red sap. In the foliage this is apparent in the extent to which the colour suffuses the leaves. In the least intense form the mid-rib and two main lateral ribs of a young, but fully expanded, leaf are suffused, and the minor veins and lamina green. Further intensification occurs when the larger veins appear as red lines set in the green lamina, and finally the whole lamina may be suffused as in the red parental type 3. The records of this character in its relation to foliage character show the colours as limited to (*a*) the ribs, (*b*) the veins, or (*c*) the lamina diffused throughout. While the limits between these three are not very distinct, the division offers a fair guide to the purity or reverse of the plant under consideration in regard to this character.

Table III (*a*) shows that in 5 cases out of 66 an error was made in

over-estimating the intensity of the colour, while in 2 cases only out of 138 the error was made in the direction of under-estimation giving a combined error of approximately 1 in 25. In Table III (b) a larger error occurs, the intensity of the colour having been over-estimated in 4 cases out of 63 and under-estimated in 22 cases out of 212, making a combined error of 1 in 10. As a generalisation it may be said that in the intensity of the colour in the leaf there exists a character by means of which it is possible to separate with a fair degree of certainty the pure dominants of the form DD from the impure dominants of the form DR.

The presence of the red factor does not, however, merely find its expression in the leaf. As has been stated it is universally present and is readily identified in organs devoid of chlorophyll such as the petals. Under these circumstances it would seem probable that the intensity of the colour would be most readily determined in an organ like the petal where the colour is not masked. A reference to Table IV will show, however, that this is not so. Gradation in the case of the petals does not occur as one of intensity but one of area. The petal is either entirely red or red with areas, greater or less in extent, situated round the eye in which the red colour is absent. Such plants, in the case of a cross between a red, and a yellow, flowered type have been recorded as having the petals *red on yellow*. As Table IV (a) indicates, among 201 plants, 30 were recorded as having the petals *red* and the remaining 171 plants as having the petals *red on yellow*. Actual experiment has, however, shown that in reality 63 of the plants used as parents were of the form DD. The petal colour, therefore, failed to distinguish between the pure, and impure, forms in 33 cases out of 201. This error of approximately 1 in 6 compares very unfavourably with the error of 1 in 25, which was obtained when the colour of the leaf was considered.

Table IV (b) is derived from the cross between a type with red, and one with white petals, and in it only that section of the F_2 generation in which the dominant yellow occurs has been considered. In this example an error occurs in 49 out of 196 instances making an error of 1 in 4. In both cases the error is considerably enhanced when the determination is made on the flower instead of the leaf. In spite of the masking effect of the chlorophyll, therefore, the intensity of the sap colour is most readily identified in the young leaf and, determined in this manner, affords the most accurate guide to the purity, or impurity, of the plant with respect to this character.

The results detailed in Table II may now be expanded to include greater detail and the group possessing sap colour divided according to the intensity of that colour. This expansion is effected in Table V. Correcting the totals in this table as far as subsequent experiment renders possible the numbers become, DD 373, DR 810, RR 384, giving a ratio of $1\cdot00 : 2\cdot17 : 1\cdot03$. The widest variation from the expected result occurs in the cross between type 2 and type 3. This is a cross between two monopodial types, and, for reasons already explained, it has been found almost impossible to handle this cross, which has not, in consequence, been carried beyond the F_2 generation. It is impossible, therefore, to say how far the lack of the pure dominant form is real. It is noticeable that this lack is associated with a large proportion of the impure *vein* form and that, consequently, the determination from the leaf may not be as accurate as in the cases more fully investigated.

In the above considerations on the behaviour of the red colouring matter in the sap no distinction has been drawn between the various types used in which this colouring matter is absent. It is necessary briefly to consider these types under two groups, namely those in which the petals are yellow and those in which the petals are white. It is the identical cross made by Major Trevor Clarke and, as described by Watt (20) (page 336), one on which he founded great hopes. These experiments of Trevor Clarke are the subject of frequent note in the Journal of the Agri-Horticultural Society of India of that date (1867–1870), but no full details have been traceable. A similar cross is referred to by Fletcher (22). Here again full details are not given but, in as far as both red and yellow flowered plants appeared in the F_1 generation, it would appear that the red parent plant was a heterozygous form.

(i) *Type* 3 × *type* 4. Type 3 possesses a full red colour both in the foliage and flower which in type 4 is absent, the foliage of this type being consequently green and the petals yellow. The cross, which has been carried as far as the F_3 generation, may be taken as an example of the case in which the first of these groups is employed. The results obtained from this cross are set out in Table VI. The numbers obtained in this series bear a ratio in close accordance with Mendelian expectation and it is evident that in this cross an example of the simplest case occurs, namely that in which a single pair of allelomorphic characters is concerned. This pair is composed of the two factors—presence or absence of the red colouring matter—the present condition possessing partial dominance over the absent. This being so, it follows

that the red parent must possess the yellow factor in addition to the red. That this is so will be seen from an examination both of the base of the petal, which usually exhibits a slight yellow colouration on the external surface, and of diseased flowers, in which the petal almost approximates to the *red on yellow* condition of the impure cross.

(ii) *Type* 3 × *type* 9. As far as the present discussion is concerned this cross differs from the last only in the fact that one of the parents, type 9, has a white, instead of a yellow, petal. The cross is of considerable interest because on it have been based the greatest hopes of obtaining an improved cotton suitable to the needs of the United Provinces and the results have consequently been investigated in some detail. The present interest, however, does not arise from this aspect but concerns the flower colour. In the F_1 generation the corolla is indistinguishable from that of the F_1 of the cross previously described and is of the class which has been above denoted as *red on yellow*, the red petal having round the eye a border of greater or less extent of yellow. (Pl. XXXV.)

From the self-fertilisation of the F_1 generation plants are obtained which can by corolla character be divided into four groups:

(1) Corolla red or red on yellow.
(2)   „   red on white.
(3)   „   yellow.
(4)   „   white.

In addition to the two original, two additional types of corolla have made their appearance. If now, as in the previous cross, the colour of the foliage is taken into consideration six groups become recognisable. These are:

	Flower		Foliage				
(1)	corolla red		colour extending to lamina.				Pl. XXXV. 4
(2)	„	„ on yellow	„	„	„	veins.	„ XXXV. 5
(3)	„	„ on white	„	„	„	lamina.	„ XXXV. 6
(4)	„	„ „	„	„	„	veins.	„ XXXV. 7
(5)	„	yellow	colourless.				„ XXXV. 8
(6)	„	white	„				„ XXXV. 9

This behaviour is readily explained on the assumption that two pairs of allelomorphic characters are here being dealt with:

(*a*) Presence of the red factor which has been shown to be dominant to absence of the same.

(*b*) Presence of the yellow factor which has been shown (p. 213) to be dominant to absence of the same.

The red type 3 possesses the two dominant, and the white type 9 the two recessive, factors. Denoting these two pairs by the letters Rr and Yy, the two parental types will bear the constitution RY and ry, and the six groups which have been recognised the constitution given below with the numerical proportion between the individuals which is assigned to each group:

$$
\begin{array}{lll}
(1) & RRYY \ldots & 1 \\
& RRYy \ldots & 2 \end{array} \Big\} 3 \\
\left. \begin{array}{lll}
(2) & RrYY \ldots \ldots & 2 \\
& RrYy \ldots \ldots & 4 \end{array} \right\} 6 \Big\} 9
$$

$$
\left. \begin{array}{lll}
(3) & RRyy \ldots & 1 \\
(4) & Rryy \ldots & 2 \end{array} \right\} 3
$$

$$
\left. \begin{array}{lll}
(5) & rrYY \ldots & 1 \\
& rrYy \ldots & 2 \end{array} \right\} 3 \Big\} 3
$$

$$
(6) \quad rryy \ldots \ldots \ldots \quad 1 \qquad 1
$$

The plants of the first group can be separated into two subsidiary groups, the members forming the one being pure with regard to both characters, while those forming the other will be pure with regard to the red, and impure with regard to the yellow, character. Groups (2) and (5) can be similarly divided and in all cases this division will be recognisable in the offspring. How far these assumptions are borne out in experiment will be seen from Table VII where the results of this cross are set out in detail. In all cases the expected groups have been formed and the actual numbers are in close accordance with those expected on the above scheme.

The facts concerning the petal colour and the red anthocyanic colouring matter of the sap are, therefore, fully explained on the assumption that two pairs of allelomorphic characters enter into consideration, these two pairs being composed of the two factors producing the red colour and the yellow colour respectively, the presence of the colour producing factor being in both cases the dominant, and its absence, the recessive, condition.

Starting with the red and the white flowered type, it has been found possible not only to produce, but to produce in a state of purity, two other types, one having a *yellow* (Pl. XXXV), and the other a *red on white* (Pl. XXXV), flower. Apart from complications introduced by the consideration that one of the parents is a monopodial, late flowering type, which may be put aside for the moment, the *yellow* flowered form is recognisable as type 8, and similarly the *red on white* flowered

form is comparable to type 11, a type which is found cultivated in the Punjab.

The conclusions drawn from the results obtained from the series derived from the direct crosses as described above, receive confirmation from a second series obtained from crosses between the F_1 generation and the parental type. Owing to illness and consequent limitation of the working period, it became impossible to complete the records of this season and a part of this series had to be abandoned. The somewhat meagre records which were obtained are tabulated in Table VIII. The number is too small to admit of any numerical comparison, the character of the offspring can alone be considered. In all cases involving one pair of characters only, the cross with the dominant parent has given only dominant and intermediate forms and that with the recessive parent only recessive and intermediate forms. In the single instance in which two pairs are concerned the cross between the intermediate form ($RrYy$) and the parent possessing both dominant characters ($RRYY$) has given offspring similar to the pure dominant ($RRYY$ and $RRYy$) or to the F_1 intermediate ($RrYY$ and $RrYy$), while that with the parent possessing both recessive characters has given, in addition to the form with both recessive characters, three of the four recognisable intermediate forms, that with a red (or red on yellow) flower and colour extending to the veins ($RrYy$), that with red on white flower and colour extending to the veins ($Rryy$) and that with a yellow flower ($rrYy$). These forms are, in all cases, such as would be expected. In the one case where the recessive only has been obtained, the number of individuals (2) is too small to make the absence of the intermediate form a matter of any moment.

Before concluding this section the cross between type 3 and type 10 may be briefly referred to. It has been already shown (p. 213) that the pale yellow of type 10 is recessive to the full yellow of types 2 and 4, and from the experiments last quoted it is apparent not only that a yellow underlies the red in the petal of type 3, but that this yellow is identical with the full yellow of type 4. It would, from this, appear probable that the cross between type 3 and type 10 would be comparable with the cross between the two types 3 and 9 just discussed. This expectation is borne out in experiment. The plants of the F_1 generation of this cross are in all their petal characters similar to those of the cross between type 3 and type 9, that is of the form which has been denoted by the term *red on yellow*. In the F_2 generation four types of plants as distinguished by their petal colour appear:

(*a*)   Corolla red or red on yellow.

(*b*)   „   red on pale yellow.

(*c*)   „   yellow.

(*d*)   „   pale yellow.

The number of individuals occurring in each group has been found as follows :

(*a*) 263, (*b*) 88, (*c*) 83, (*d*) 17.   Except for the paucity of the individuals in group (*d*) these numbers agree fairly with the Mendelian ratio of 9 : 3 :: 3 : 1.

Further the two groups (*a*) and (*b*) are capable of subdivision in accordance with the degree to which the red colouring matter suffuses the leaf.   Owing, however, to the crosses from type 10 being discarded, no full records of this appearance are available and it can only be noted that, to the extent of these incomplete records, the two crosses between types 3 and 9 and between types 3 and 10 are strictly comparable.

3 (*c*).   *The leaf factor.*

The term *leaf factor* has been described by the author in his first introductory note to the cotton work undertaken by him (11).
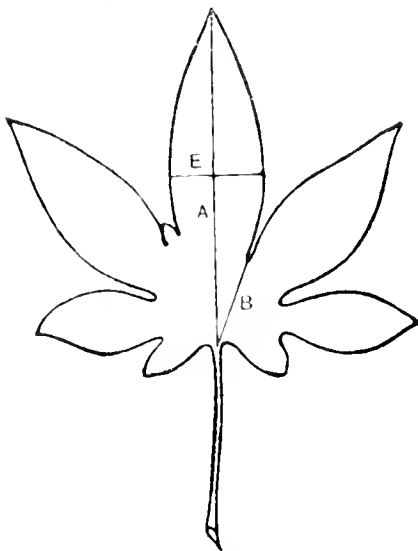
Fig. 1.

It is the numerical value obtained by dividing the difference between the two measurements *a* and *b* in the accompanying diagram

(Fig. 1) by the measurement e. It is not proposed to enter into a detailed discussion as to the significance of the constancy of this factor for the various types of Gossypia. It may be noted, however, that its identification was purely empirical and it is not to be taken as an absolute figure for each leaf of a plant; there is a fair range of fluctuation as would be expected in the measurements of any series of multiple organs. In spite of these fluctuations it is a matter of little difficulty to recognise what may be termed a "typical" leaf and there is a very marked agreement between the leaf factor, as determined on such "typical" leaves, of individuals of the same type.

The degree to which the leaf is incised forms a striking feature of the plant and has been adopted freely as a means of classification. Todaro (16) divides the Indian group (subsectio Indica) of Gossypia into two sections:

A. Lobi breves, ratione longitudinis latiusculi.

B. Folia palmato-partita, lobis angustis, oblongis, vel elongato-lanceolatis.

Gammie (9), though he does not accord this character of the leaf a primary position in his scheme of classification, throughout refers to two groups with the leaf lobes either broad or narrow.

Watt (20) uses the leaf character to subdivide the section of "Fuzzy seeded cotton with united bracteoles." He distinguishes three groups:

Leaves two-thirds palmately (sometimes almost pedately) 3—7 lobed.

Leaves half-cut into 3—5 (mostly 3) lobes.

Leaves less than half-cut into 5 (more rarely 3 or 7) lobes.

It will be noticed that while these three schemes deal generally with the same character there is some difference in detail in the exact points involved. Watt simply deals with the degree of incision which is, perhaps, most closely given by the ratio $\frac{a}{b}$.

Todaro's group B, as fully defined, is distinguished by not only the factor $\frac{a}{b}$ but by the breadth of the lobe, thus including the measurement e; while for his group A he makes use of an expression which is, perhaps, the best form of definition that could be found for the author's "leaf factor." Gammie refers simply to the ratio $\frac{\text{length}}{\text{breadth}}$ of the lobe, which is identical with the leaf factor.

In a preliminary series, among other measurement determinations,
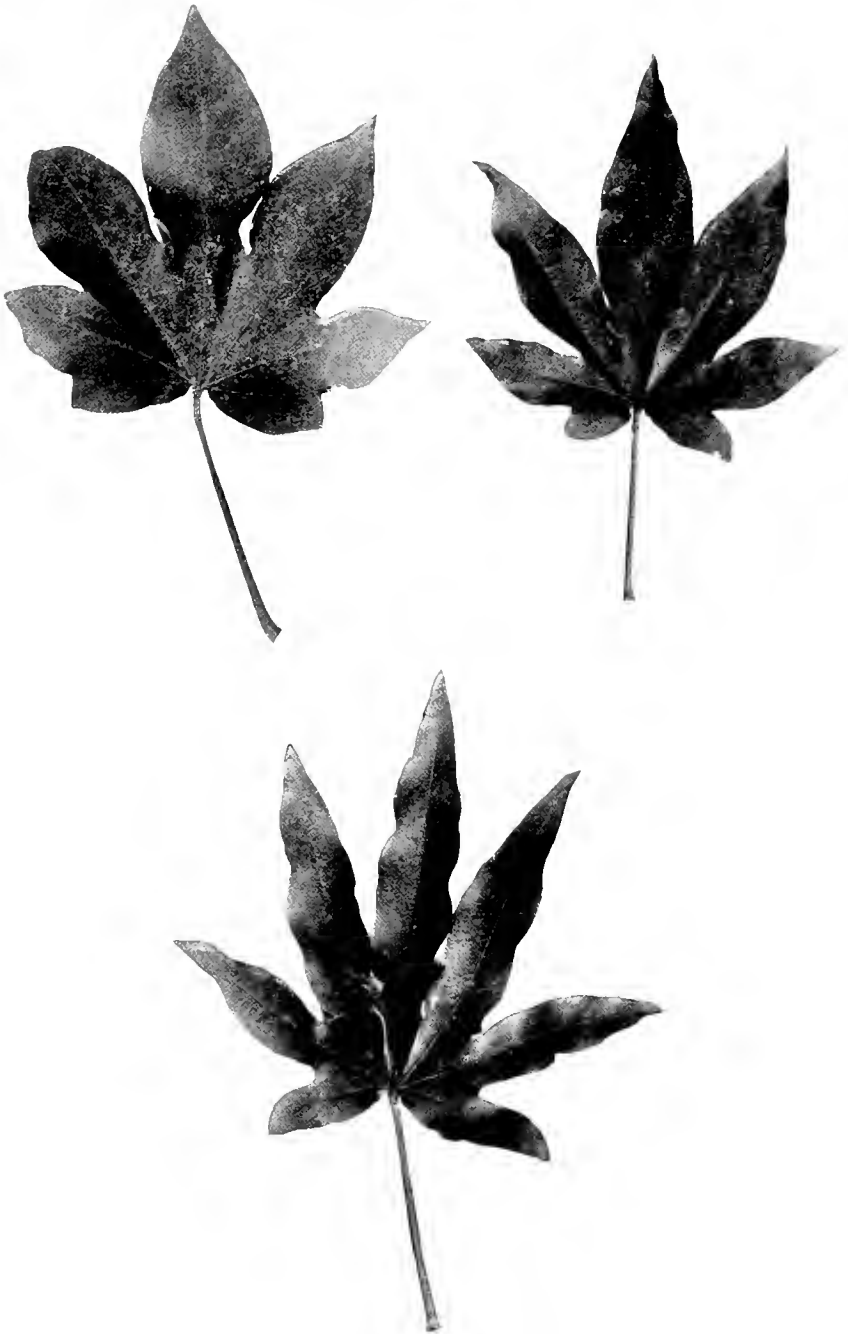
Fig. 2.

The top left figure is that of a broad lobed leaf, with leaf factor less than 2; the bottom figure is that of a narrow lobed leaf with leaf factor greater than 3; the top right figure shows an intermediate leaf with leaf factor 2·5.

the ratio $\frac{a}{b}$ was determined for a large series of plants but was found to be quite inconstant and useless as a means of identifying types which were readily distinguishable by eye. On the other hand in the leaf factor an expression was found not only for such differences as are of sufficient magnitude to be recognised by the eye but also for such as, though definite and constant, are elusive to the eye and incapable of adequate verbal definition. While there is thus found in the leaf factor a means of defining and expressing to a degree of minuteness hitherto impossible, what appears to be a unit character of the cotton leaf, it is necessary to beware of pressing it too far. It is physically impossible to measure every fully developed leaf and obtain from such measurements an average. "Typical" leaves must be selected and in such selection the door is opened for the introduction of a considerable personal element. In the experiments recorded determinations have been made on at least two such "typical" leaves from each plant and the average between the two values so obtained is taken as the leaf factor of the individual.

Before dealing with this character in detail therefore both the magnitude of the error met with in these determinations and the exact meaning to be ascribed to the term "typical" require brief consideration.

It is clear that a larger experimental error is to be expected in the leaf factor of types with narrow lobed, than those with broad lobed, leaves. In the latter case the three measurements employed in the calculation are all large and errors of measurement proportionately small. In the former case, on the other hand, the divisor e is small and the errors proportionately large. The experimental error, consequently, increases as the value of the leaf factor rises. When this value falls below 2 the error, which is accepted, is normally less than 0·15 from the mean (giving a total range of 0·3) and, when this value lies above 3, this error may reach 0·3 (with a total range of 0·6). These figures indicate the extreme variation met with. Where the error exceeds this amount duplicate determinations have been made.

The recognition of this leaf factor was, as has been stated, in the first place purely empirical and resulted from an attempt to find some method of denoting by symbols the differences between the various characteristic shapes of the cotton leaf. In the selection of leaves used in the determinations certain precautions were found to be necessary and were consequently adopted. That such precautions were

necessary receives recognition in the use of the word "typical." These precautions require examination since, in a purely arbitrary determination of this nature, some control is required to ensure that the restrictions imposed by their use are not of a nature to render valueless the figures so obtained. Such a check has been found in the measurement of the leaves of one individual of each of the several pure types isolated, only the earliest leaves of the main stem and the diminutive leaves at the base of each branch being excluded. These measurements were made at intervals of about a week throughout the season, each leaf being thus measured as it became fully expanded. The results of one such determination in the case of a plant of type 5 are set out in Table IX. For the purpose of their understanding the leaves may be grouped into four sets:

(1)   Leaves borne on the main stem.
(2)   „   „   monopodial secondary branches.
(3)   „   „   tertiary branches.
(4)   „   „   sympodial secondary branches.

It will be noticed that the monopodial secondary branches alone bear tertiary branches which are almost invariably sympodial. The values obtained for the average leaf factor of these four groups are respectively:

(1) 1·82,   (2) 1·84,   (3) 1·73,   (4) 1·72.

It will be noticed that the leaf factor of the leaves borne on the monopodia is definitely larger than that of the leaves borne on the sympodia whether these be secondary or tertiary branches. The value of the leaf factor as determined for the leaves arising from the monopodia, differs by between 0·06 and 0·04 from the value obtained by the empirical method of selection of "typical" leaves. This error lies well within the limits of the experimental error as defined above. The "typical" leaf, therefore, may be defined as that leaf which possesses a factor having a value equal to the average of the factors of all leaves arising from the monopodial branches. It is not, as was anticipated when the author's earliest note (11) was published, the average of the factors of all the fully developed leaves. This result is in perfect accord with the main precaution which on empirical grounds it has been found advisable to take, namely, to select leaves from the monopodia. It is these leaves that the eye naturally selects as being typical of the plant. It is perhaps unnecessary to detail more than one further precaution which it has been found advisable to adopt. This is to avoid the

determination of the value e where an accessory notch (*vide* Fig. 1, p. 220) occurs in the re-entrant angle at the base of the main lobe. Such precautions are obviously necessary and cannot affect the value of the leaf factor as a definite character.

The determination of the leaf factor for many thousands of plants has brought one remarkable feature into prominence. While every value has been obtained for the leaf factor from 1 ("broad" lobed) to 5 ("narrow" lobed) no case has been observed in which a plant with intermediate value (between 2 and 3) for the leaf factor breeds true to this character. All pure plants, and consequently all types, are divisible into two distinct groups:

    (1)   With a leaf factor less than 2.
    (2)   ,,   ,,   greater than 3.

Within the limits 1 to 2 occur all the "broad" lobed types, while within the limits 3 to 5 occur all the "narrow" lobed types[1].

The accuracy of the expression—that is, the measure of agreement between different individuals of one type—is such that it is possible to recognise within, and isolate from, a type, otherwise pure, races separable only by the leaf factor. It seems probable that the existence of such "pure lines," to use Johannsen's term (10), is a phenomenon of general occurrence throughout this series of Gossypia and in some of the types such forms have been isolated. Thus within type 4 occur three "pure lines" with leaf factors of 1·37, 1·46 and 1·64 which have been isolated, and from type 9 "pure lines" with leaf factors of 3·34 and 3·59 which have similarly been isolated. Opportunity has not been forthcoming for treating this question in the detail it deserves and it seems probable that with a more detailed examination the number might be considerably increased. Indications of the existence of such "pure lines" are apparent in Table X.

The behaviour of the leaf factor when crossing occurs.

When a plant with leaf factor less than 2 is crossed with a plant with the leaf factor greater than 3 the leaf factor of the plants of the F_1 generation is found to approximate to the mean of the two parental leaf factors. Table XI illustrates this point. At the time the crosses were made the character had not been identified and the figures given

[1] In the fields plants are frequently found with a leaf factor less than 3 and greater than 2, and on this fact among others the author has based his views on the occurrence of cross-fertilisation under natural conditions (11).

for the parental leaf factors are not those of the actual plant but the average of the type as given by the offspring (produced by self-fertilisation) in the two subsequent generations. In two cases only is the variation from the parental mean at all marked and in both these this difference is not shown by the reciprocal.

In the F_2 generation a continuous series of forms is produced in which every value of leaf factor between the parental limits is obtained. Diagram 1 illustrates one such case and is derived from the series given in Table XIII (*b*). It is here noticeable that, while the series appears continuous, in that every value of leaf factor (within the limits imposed by the experimental error) occur, the number of individuals is by no means regularly distributed throughout the series—in other words, the frequency of each class exhibits marked variation. The curve is, in fact, multimodal (Davenport (6)) and possesses three modes. The position and value of these modes are instructive. While the values of the outer modes differ but slightly from the values of the two parental leaf factors, the value of the intermediate mode shows a fair degree of approximation to the value of the mean between the leaf factors of the two parental types. The proportion between the number of individuals grouping themselves about these three points is $1 : 22 : 1$. The curve retains its trimodal nature, if for the actual values obtained by direct measurement of the leaves of individual plants—the values here given—the mean value of the leaf factor of the F_3 offspring be substituted.

A similar curve has with one exception been obtained in every case submitted to a critical examination. In this instance, the cross between type 2 and type 3, there is no trace of a multimodal curve and the ratio between the number of individuals in each group (Table XIII (*a*)) diverges markedly from that obtained in the instance given above. Lack of opportunity and the difficulty of handling a cross between two monopodial types have rendered it impossible to continue investigation into the behaviour of this cross and for the present it must remain undecided whether, on further examination, this too will fall into line with the example more fully investigated or whether a different series of phenomena is here instanced.

So far the results have been described in outline only, and as a close examination of the tables will show, are only approximate. Complete agreement is, perhaps, hardly to be expected in dealing with a character which, as has been already shown, cannot be measured with absolute accuracy. It will be observed that the modal values of

the leaf factor in all cases exceed the corresponding parental or mean parental value, the excess being practically identical (0·31, 0·35 and 0·38) in the three cases. This excess, though small, appears definite but has so far received no explanation.

Type 4 × Type 8
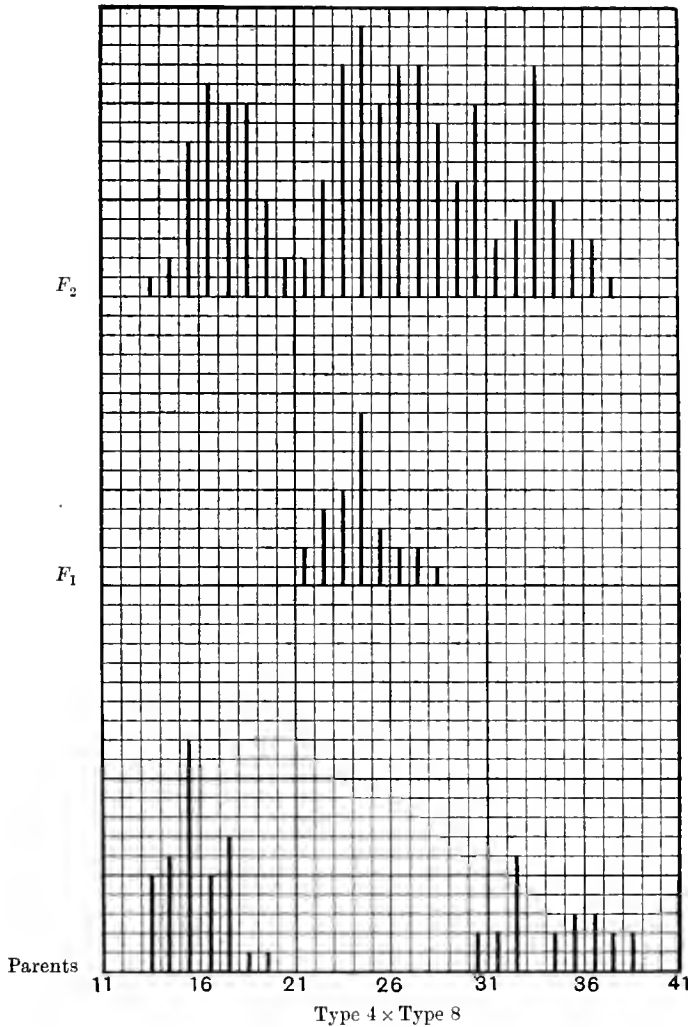
Diagram 1.

In one case only has each plant of the F_2 generation been self-fertilised and the F_3 generation raised from the seed so obtained. The results are set out in Table XIV. In this table the extreme and

intermediate groups are given in a condensed form so that the offspring of all plants, the average leaf factor of whose offspring differs by 0·10 or less, are grouped together. Full details of individual plants are only given at the two points where the change from the pure to the impure form takes place. It will be seen from this table that a marked difference exists in the behaviour of the individuals belonging to the three groups into which the F_2 parents fell. The offspring of those F_2 individuals of which the leaf factor was less than 2 have, with few individual exceptions, a leaf factor which is less than 2. In the same manner the offspring of plants with the leaf factor greater than 3·2 have a leaf factor which is greater than 3. As will be seen from the table the exceptions are relatively few and it may be said in general terms that the individuals of the two groups, having the leaf factor less than 2 and greater than 3·2 respectively, are pure with regard to this character. The dotted vertical lines in the Table drawn between the columns representing the values 2·1 and 2·2, and between those representing the values 2·8 and 2·9, indicate the limits of experimental error recognised in the two groups. It will be noticed that in 5 only out of 1283 cases the limiting value of 2·1 is exceeded and in 7 out of 1274 cases the limiting value of 2·9 is not reached. These exceptions will form the subject of further investigation. It is, of course, possible that these plants have been introduced by accident. Nothing, however, in the further examination of these individuals lends support to this view.

The third group, which is characterised by the intermediate value of the leaf factor, is not, like the previous groups, pure in this respect. Such plants have invariably given offspring which, as a group, exhibit the entire range of values obtained for the leaf factor. It will be noted that, though this variability exists, the average value of the leaf factor of the F_3 generation from this intermediate group differs but slightly from the mean of the two parental values and further that the number of individuals comprising the three groups are in almost complete accordance with Mendelian expectation (1 : 2·04 : 1), while the mean values of leaf factors for the three groups taken severally show but slight variation from the values obtained for the corresponding groups of the F_2 generation.

It is impossible to avoid being impressed by the similarity which exists between these results and the more typical examples of Mendelian phenomena.

It has frequently been pointed out (*vide* Bateson (3), p. 53) that

dominance, which formed so striking a characteristic of the earlier experiments on these lines, holds no position of fundamental importance in Mendel's own statement of his law. In the present instance there is a complete absence of dominance and the direct offspring of a cross are as markedly distinct from one, as they are from the other, parent. It is possible, however, to discern more than this. The two factors appear capable of blending in any proportion, and there thus appear a continuous series of forms showing all stages from the typical broad lobed individual, with a leaf factor less than 2, to the typical narrow lobed individual with the leaf factor greater than 3. Owing, however, to some influence, of which, as yet, nothing is understood, these various degrees of blending do not occur with equal frequency. This is greatest at the point represented by a blending of equal proportions of the two factors and becomes less and less as this proportion becomes unequal, but increases again when the proportion of one or other of the factors is reduced to a negligible quantity or is entirely absent.

This capacity of blending in unequal proportions is further shown by a comparison between the value of the leaf factor of the F_2 parent with the mean value of that of the F_3 offspring. This comparison is given in the three last columns of Table XIV. The difference between these two values for the whole series is 0·07, a figure well within the limit of experimental error, which is, however, in a few individual cases exceeded. It may be generally stated, therefore, that the value of the parental leaf factor is the mean of the values for the offspring. Consequently, when unequal blending occurs in any plant, the number of offspring falling within the group whose leaf factor enters in greatest proportion into the blending will exceed the number of offspring which fall within the other group. In other words the ratio of the offspring having a leaf factor less than 2 to offspring having a leaf factor greater than 3 will increase as the parental leaf factor diminishes from the mean value of 2·6 and will conversely diminish as the parental leaf factor increases from this mean. That this is the case the detail columns of Table XIV clearly show.

It is now necessary to glance for a moment at the lower limit of the "narrow" lobed group. It has been stated that this limit is 3·0, a figure which has, with one exception, been adopted in Table XI. Reference to Table XIV, however, will show that the lower limit for the pure forms with narrow lobed leaves is 3·2—a figure which exceeds the value of the corresponding parental leaf factor. In this connection it is noteworthy that a value of 3·5 is throughout obtained for the

16—2

mean leaf factor of this group. It is possible that this figure, 3·52, more accurately represents the true value of the narrow lobed parent than that actually obtained by experiments (3·13). This latter figure is based on six determinations only and it is a matter for regret that more determinations were not possible. Not only, as has already been remarked, is type 3 difficult to handle, owing to its monopodial habit, but it has been found to be in a marked degree self-sterile. In the first generation only six plants were obtained by self-fertilisation, while in the second, numerous attempts were all unsuccessful. While, therefore, the value 3·13 has been adopted in these calculations it must be noted that this value is extremely low for the type 3 as determined on a set of pure, but unrelated, plants of this type. Acceptation of the figure 3·52 as more nearly representing the true parental value, while accounting in full for the difference of ·38 found between the value of the narrow lobed parent and that of the corresponding F_1 group, accounts only partially for the difference of 0·35 between that of the parental mean and of the intermediate group, and fails entirely in the case of the difference of 0·31 between the broad lobed parent and its corresponding F_1 group. These differences must for the present remain without explanation.

The few cases in which the F_1 generation has been crossed with the parent types are given in Diagrams 1 and 2. In all cases the F_1 intermediate, when crossed by the broad lobed parent, has given only intermediate and broad lobed offspring and, when crossed by the narrow lobed parent, only intermediate and narrow lobed offspring. The number of intermediates is far too small for any value to be attached to comparison of their relative numbers and of the mean value of leaf factor. It is impossible, therefore, to draw any further conclusion than that, within the limits imposed by their paucity, these figures are in complete accord with the expectation based on the conclusions derived from the direct series.

3 (d). *The type of branching and the length of the vegetative period.*

The differences which exist in the form of the secondary branches and in the length of the vegetative period between the various types under consideration have been briefly noted above (p. 209). The intimate connection which has been found to exist between these two characters in the Indian cottons has already been pointed out by the author in Part 2 of his introductory note (12). In a still earlier

publication Balls (1) foreshadows a similar interrelation between the type of secondary branching and the length of the vegetative period in the Egyptian and American upland[1].

Since the publication of the note referred to, a most interesting communication from J. V. Thompson to the Agri-Horticultural Society of India has been met with in the Journal of that Society for the year 1841, in which the intimate relation between the type of branching and date of flowering is clearly indicated. In this communication he states:

"The cultivated varieties of cotton I find may be divided into two classes, viz. early and late kinds; this precocity or tardiness being inherent in the particular variety, and derived from a peculiarity hitherto unnoticed, and which it will not be difficult to explain. It may be observed that all the varieties have a natural tendency to produce a central main stem furnished with a leaf at intervals of a few inches; in the axillae of each leaf-stalk resides a *pair* of germs or buds, placed in the same plane or side by side; one of these germs is destined to produce flowers only, the other only branches. In the *early* kinds the former or flowering branches alone are developed, while the *late* kinds expend their force exclusively in the production of multiplying branches. This peculiarity must for ever unfit these late kinds for a cold climate, such as Northern India." For the full communication, which is of some length, the reader is referred to the original source (18). Sufficient has been quoted, however, to show how fully the importance of the connection between the branching habit and the length of the vegetative period had thus early been recognised. The importance of two axillary buds, which is also indicated, has previously been dealt with by the author (12) in a preliminary note but has no concern with the experiments now under treatment.

It has already been noted, when defining the types which have been employed in these experiments, that the Indian cottons fall into two well-defined groups, those in which the secondary branches are always, or nearly always, monopodia, and those in which the secondary branches are always, or nearly always, sympodia. As long as observation

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[1] Since the above was written Bulls. 147 and 155 Bureau of Plant Industry, U.S. Department of Agriculture have been received. In these the authors draw attention to this same point. According to them, however, this character is induced to vary in the types investigated by them as a consequence of change in environment. This and other differences in the method of branching between the observations of these investigators and those of the author are not concerned with the subject matter of this paper and must be left for consideration at a subsequent period.

is limited to pure types these two groups are readily distinguished. When, however, the progeny of crosses between types belonging to these two groups come to be considered, every gradation between the two extreme forms is found and it becomes a matter of extreme difficulty in individual cases to define the degree of approximation to one or the other extreme type. In such intermediate plants the passage from one type of secondary branching to the other is usually abrupt, the earlier branches being monopodia and the later sympodia. It is, therefore, possible to divide the main stem into two portions, a lower portion in which the branches are monopodia and an upper portion in which the branches are sympodia. The character can then be conveniently expressed as the percentage of the entire stem bearing monopodial branches. Expressed in these terms a pure monopodial type is indicated by the number 100 and a pure sympodial type by the number 0. It has already been stated that no pure type has been isolated which invariably produces sympodial secondary branches only. A few monopodial branches may in all cases occur at the base of the primary stem. It is convenient, therefore, to denote these also by the symbol 0 which indicates all such sympodial types as have been found to breed true. In like manner the symbol 100 may be used to denote cases in which a few of the most apical branches are sympodial. In the earlier experimental stages it was considered sufficient to recognise four divisions only:

(1)   The full monopodial type indicated by 100.

(2)   Approximately three-quarters of the secondary branches monopodial, indicated by the symbol 75.

(3)   Approximately one-half of the secondary branches monopodial, indicated by the symbol 50.

(4)   The sympodial type indicated by the symbol 0. Recently the separate forms have been recorded in greater detail by which the fraction, recorded in tenths, of the main stem bearing monopodial secondary branches is used as a basis for division. By this method 10 groups are formed, the relation of which to the four groups given above is shown below.

100		75		50			0		
100	90	80	70	60	50	40	30	20	10	0
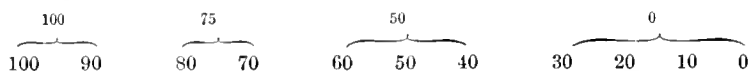
In this notation the figures 100 and 0 apply respectively only to individuals in which sympodial and monopodial secondary branches are entirely absent.

It is clear that this system of record, though the best that has been devised, is subject to considerable disadvantage. It is, at the best, approximate and moreover the determination is only possible when the main stem has received no check to growth. In practice this continued growth of the main stem is rendered a fact of comparatively infrequent occurrence from the climatic conditions prevalent at the early stages of growth. These conditions favour insect life of all kinds and the larval stage of *Earias* sp. is commonly met with on the cotton plants. This pest penetrates the young stem at the leaf axil and from this point bores its way downwards. The stem so attacked withers and growth is continued by an enhanced development of the secondary branches. In such cases it becomes difficult and frequently impossible to determine this character even approximately.

The length of the vegetative period is most readily expressed in the number of days from the date of sowing to the appearance of the first flower. Unlike the previous character this lends itself to accurate record. The fields are visited daily and the plants in flower for the first time noted. Yet numerous subsidiary influences are here found to affect the date of production of the first flower and render the figure, though accurate in itself, only approximately accurate as an indication of a definite individual character. The more important of these influences may be here referred to.

In the first place, there has been found a considerable seasonal variation; that is, a considerable difference in the length of the vegetative period of a pure type from one year to another. Hence the figures obtained for one year only are strictly comparable and it is possible to compare the results of two or more years by introducing a seasonal factor by the addition (or subtraction) of which the results of any two years are rendered comparable. This is illustrated in the column of Table XV for the years 1907 and 1908.

In the second place the length of the vegetative period is materially influenced by the method of cultivation. Two methods have been employed in the course of these experiments. In the first the seed is sown in pots and the young plants, when a month to six weeks old, planted out. In the second the seed is sown in the ground about a month after the sowings in pots have been effected. Here only indirect comparison is possible and the effect of such variation in the method of cultivation is shown by a comparison between the third and the first two columns of Table XV.

Unfortunately no records are available by which the direct influence

of the method of cultivation may be calculated, for in no case has the same type been grown by both methods in a single season. In 1907 and 1908 all the pure types were grown in pots, while in 1909 they were sown in the field. To obtain a comparison between the two methods of cultivation it is necessary to resort to an indirect method based on the crosses. In 1908 the entire F_2 generation obtained from the crosses was raised in pots while of the seed of these plants only that of which a small amount was available was, in 1909, sown in pots, the remainder being sown in the field. In Table XVI is given the result of the comparison between the length of the vegetative period of the offspring of plants having a similar period when these offspring are grown under the two conditions. The difference due to the method of cultivation varies from a minimum of 21 days to a maximum of 31 days and, generally speaking, the greater the length of the vegetative period the greater will be this difference.

A similar result is reached from a comparison of Tables XVIII—XXI. Tables XVIII and XX are based on the pot series and involve only the seasonal difference between the two years 1908 and 1909, which is found to be five and three days respectively. In Tables XIX and XXI, based on the field series, in addition to this seasonal difference there also occurs the difference due to the method of cultivation, and the combined differences are in the two cases 31 and 28. By subtraction the average difference due to method of cultivation alone is found to be in the one case 26, and in the other 25 days.

From the above it is noticeable that the difference in length of the vegetative period due to the method of cultivation is fairly constant for all types, increasing only slightly with the increase of what may be termed the standard vegetative period of the plant. The seasonal difference, on the other hand, depends in considerable measure on the type, being less for early flowering than for late flowering types. While, therefore, it is possible to reduce two series, differing only in the method of cultivation, to one standard, this is not possible when a seasonal difference enters into consideration.

In addition to these two main causes, which, it will be noticed, affect the entire series, the length of the vegetative period of individual plants may be influenced through several minor causes and the actual figures, though accurate in themselves, are thus rendered only approximate as a record of the standard length. Thus in a few cases the young flower buds have been observed to fall without opening (*vide* note to Table XVII) and an abnormally long vegetative period has been

the consequence. Again, dwarfing arises through numerous causes and leads to delay in the production of the first flowers. In one case plants of a monopodial type, with a normal vegetative period of over 200 days, commenced flowering within 100 days from the date of sowing and before they had been planted out. All cases where any such abnormality is apparent have been omitted from the following records.

The interrelation between the type of branching and the length of the vegetative period.

The two characters just dealt with are mutually dependent. A plant of the sympodial type will commence flowering shortly after the secondary branches have developed, while a plant of the monopodial type will not flower until the tertiary branches develope. This lengthening of the vegetative period is shown in Table XV, in which the length of the vegetative period of some of the more important types are recorded. The interdependence becomes still more marked when a continuous series, such as is obtained in the F_2 and subsequent generations of a cross, is considered. For this purpose the plants may be associated into groups in which the length of their vegetative periods is similar, each group being formed by the plants which flower during a ten-day interval. This method has been adopted for the series derived from the F_2 generation of the crosses between types 3 and 4 and between types 3 and 9, and the results are recorded in Table XVII (cf. author's note). The figure given opposite each ten-day interval indicates the average type of branching occurring in plants falling within that interval and is obtained by adding the numbers indicative of the type of branching of each plant (100, 75, 50 or 0) and dividing by the total number of plants.

Tables XXII—XXV show the same interrelation in the F_3 series only in a slightly different and more detailed manner, the ten stages latterly recognised in the type of branching as above described, and two- and five-day intervals being respectively substituted for the four stages and the ten-day intervals. The closeness of the interrelation is given by the coefficient of correlation (Davenport (6)). This has been worked out for the series given in Table XXIV and found to be ·6819.

This interrelation, or correlation, is, therefore, a definite fact dependent on the limitation of the flower-producing habit to the sympodial branches. What appear to be two characters are merely two outward expressions of the same structural peculiarity. In other words a

definite reason exists for the correlation between these two measurable and apparently distinct characters, and it is permissible to select the one that appears to be more reliable for the purpose of recording the habit of the plants under consideration.

While in neither case has an accurate method of record been obtainable, the date of appearance of the first flower is at once more readily determined and obtainable in a larger number of instances. The measure of the length of the vegetative period, therefore, probably affords a means of indicating the habit of the plant which is more accurate than the direct record of the percentage of monopodial second-ary branches, and has been adopted to record the behaviour of this character when plants of the two groups are intercrossed.

The habit of the offspring from a cross between monopodial and sympodial types.

In the F_1 generation derived from a cross between a plant belonging to a monopodial and one belonging to a sympodial type, the length of the vegetative period is intermediate between those of the two parental types. This is shown by Table XXVI in which the relative lengths of the vegetative periods of the F_1 generation and of the two parental types are detailed. This table further shows that while the F_1 genera-tion is intermediate in this respect, it does not hold a position corresponding to the mean of the two parental values but in all cases approaches the sympodial type. In this table the seasonal variation is eliminated by comparison of the F_1 generation with the offspring of the parent plants.

In the F_2 generation the plants form a continuous series in which every stage from early flowering to late flowering forms occurs. It is noticeable, however, that while those individuals of the F_2 series which have the shortest vegetative period are in flower as soon as, or even before, the plants of the parental type, in no case does the vegetative period equal in length that of the monopodial parental type. In other words, while the full sympodial type appears comparatively frequently the full monopodial type only rarely does so. The divergence from the mean length of the parental vegetative periods noticed in the F_1 gene-ration is here even more marked.

Diagram 2 illustrates these results for a single instance of a cross between a monopodial and a sympodial type. Owing to the seasonal variation above noted it is impossible to compare the periods for

successive generations directly, and each must be compared with the
values for the parental series grown in the corresponding season.   It is
impossible here to distinguish more than one mode; there is no trace

Type 3 × Type 10
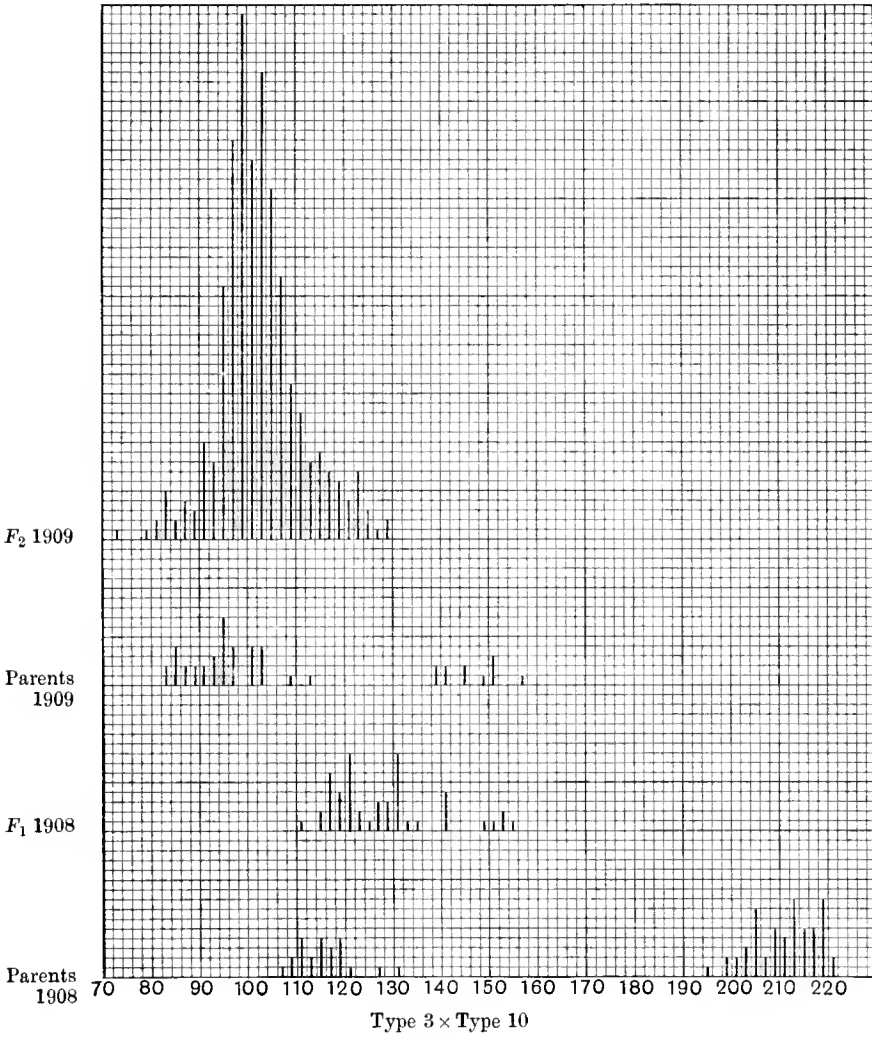
Diagram 2.

of a curve of frequency with three modes such as was found in the
case of the leaf factor, nor has any instance of such a curve been
obtained for the character under consideration.

In the present instance there appears to exist an example of partial dominance combined with incomplete resolution of the component factors in the subsequent generations. It must, however, be admitted that the experimental error is undetermined and, from a consideration of Tables XVIII—XXI[1], this would appear to be considerable in comparison with the magnitudes under measurement, and sufficiently large to render the character ill adapted to such analysis as has been attempted. The impossibility of determining this error was in itself sufficient to render the advisability of attacking this question as a purely theoretical problem exceedingly doubtful. The behaviour of this character is, however, a matter of vital practical importance. As has been stated, it is essential that a plant should be of the sympodial type if its cultivation in the United Provinces is to be a commercial success. At the same time the majority of Indian cottons with a really valuable staple belong to the group of monopodial types. The chief hope of improvement of the cotton crop in the United Provinces, therefore, has been based on the isolation of pure sympodial forms with the staple of the monopodial type.

3 (e). *The leaf glands.*

There frequently occur on the under surface of the leaf one to three (and rarely four) glands. When there is a single gland it is situated on the midrib a short distance from the point where this leaves the petiole. In addition to this gland, two more glands may occur similarly situated but on the two main lateral veins—giving three glands in all. The stage in which only one of these laterally situated glands developes is commonly met with. In one or two cases only have four glands been observed and in all such cases the additional gland is situated on the midrib. It is not a condition which enters into the course of these experiments.

The number of glands is definite and as a leaf character lends itself to ready determination. But the leaf is a multiple organ of the plant and it becomes possible for a plant to possess leaves differing in the number of their glands. Difficulty arises in this case similar to that met with in the leaf factor, and such as of necessity arises when the

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[1] Of these tables No. XVIII only is given in extenso. The subsequent Tables XIX—XXI are abbreviated and give the combined details for those plants the average dates of flowering of whose offspring fall into successive five-day periods. These three tables, in their expanded form, agree in all particulars with Table XVIII.

character of a multiple organ is employed as a plant character, owing to the character, definite for the organ, being indefinite for the plant.

It is possible, however, to recognise two distinct forms in which the leaves are either all eglandular or all glandular. It is true that an intermediate condition has rarely been observed in which a few of the leaves may bear a minute and rudimentary gland. The condition is, however, extremely rare and though the plant would on direct observation usually be entered as eglandular its true character will be identified through the occurrence of glandular offspring on selfing.

If plants belonging to a single type and bearing glandular leaves be arranged in series according to the proportion of leaves bearing 1, 2 or 3 glands, the series will be practically continuous. Nevertheless it has been found possible to recognise three fairly distinct stages which have received the following notation :

(1) Glands 1 ; in which all or nearly all the leaves bear a single gland.

(2) Glands 1—3 ; in which the majority of the leaves bear one gland but those of the main stem and possibly one or two of those of the monopodial branches bear three glands.

(3) Glands 3—1 ; in which the majority of the leaves, including all those of the main stem and monopodial branches, bear three glands. A few leaves of the sympodial branches may also bear three glands.

It has been found possible to isolate and grow in a state of purity forms in which the leaves are eglandular and forms which fall within the third stage as given above. Plants with the leaf glands 1—3 on the other hand have invariably given mixed offspring[1].

There remains for consideration the second stage in which the leaves have a single gland only. This too may occur as an intermediate condition between the eglandular form and that with glands 3—1, and in such cases does not breed true. It appears probable, however, that it may also occur as a pure form. Within the author's experience plants of type 2 have invariably leaves with one gland, but, for reasons already given, this type has not been very fully investigated and, perhaps, to an extent hardly sufficient to justify the statement that one leaf gland is characteristic of the type though there can be little doubt that a pure form of type 2 so characterised does exist. This pure form with a single leaf gland does not enter further into the present

[1] The two cases noted in Table XVIII form apparent exceptions to this statement but must, in the absence of further evidence, be considered as extreme instances of divergence from the expected ratio.

experiments in which the 1-gland stage will be grouped with the 1—3 stage to form one intermediate group.

Excluding types 1—3 and 11, in all the remaining types two forms have been isolated which are characterised respectively by the absence of leaf glands and by the presence of these glands in the 3—1 stage, and both these forms have been pure bred. In type 1 the three forms have all been observed but their purity or the reverse has not been tested by experiment; type 2 has already been dealt with; in type 3 the 3—1 gland form has alone been met with, while of type 11, though the 3—1 form has similarly been the sole one observed, it is impossible to speak with much certainty since the plants on which the observations have been made are all derived from a single source.

In the cross between type 3 and type 4 to which reference has already been made an eglandular form of type 4 was used as parent. This cross, therefore, illustrates the behaviour of this gland character under the influence of cross-fertilisation and the results are set out in Tables XXVII and XXVIII. In the F_1 generation the plants are uniformly of the intermediate form (glands 1—3) while in the F_2 generation the two parental forms reappear. It will be observed from Table XXVII that while the ratio between the eglandular and glandular forms agrees closely with the expectation there occurs among the glandular forms a large excess of that with the glands 3—1 and the same is found to hold among the F_3 offspring of the impure F_2 parents (Table XXVIII, last two columns).

That this excess is due to the classification of certain intermediate forms as pure 3—1 forms is proved by the fact that 52 individuals which had been so characterised were found to be in reality impure. The F_2 plants must in fact be considered as forming continuous series from the pure eglandular form to the pure glandular 3—1 form though, from the very nature of the case, the former is more readily identified than the latter. It has been seen that plants with a single leaf gland occur; and, if the 1—3 stage be considered as the full intermediate, this stage must be considered as an approach to the eglandular condition. In the same manner there appears to occur a stage which approaches the fully glandular condition sufficiently closely to be with difficulty separated from it. By examining the plants at the end of the season it is possible to distinguish two conditions which may be termed the 3—(1) stage, in which even the latest leaves of the monopodia bear three glands, and the 3—1 stage, in which these bear only one or at most two glands. It is not yet certain, however, that this distinction

will afford a means of separating the impure forms, nor is it a method which becomes available till after the work of fertilisation is long over. At present no method of discriminating with certainty between the pure and impure forms during the major portion of the life of the plant has been discovered.

<div align="center">CORRELATION.</div>

One instance of correlation has already been dealt with in section 3 (d) on the type of branching and the length of the vegetative period. In this instance the correlation was seen to depend on a recognisable feature—the flowers are only formed as a development of the apical buds of the sympodia the growth of which is carried on by the main lateral bud. In the present section reference will be made to two other instances of correlation, but in them the feature on which the interrelation between the two characters depends is thus not recognisable.
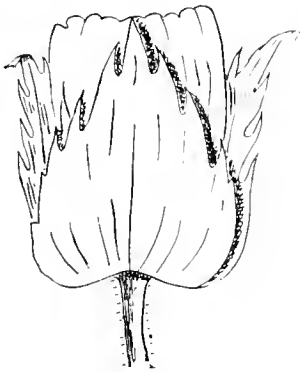
Fig. 3.   Fig. 4.

There appears to be complete correlation between the size of the petal and the colour of the flower. If the petals be white in colour they will be small and hardly project beyond the bracteoles; on the other hand, if the colour be yellow, they will be large in length, about twice that of the bracteoles (*vide* Figs. 3 and 4)[1].

[1] The difference is well shown by a comparison between Plates 14 A and 16 Watt (20).

The petals may be of one of two sizes, either small, when they lie
within the bracteoles whose length they do not exceed, or large, when
they project beyond and are about double the length of the bracteoles
(*vide* Figs. 3 and 4). The exact size of the larger petal varies somewhat
with the particular type but in no case approaches that of the smaller,
and the two stand in marked contrast without intermediate form.
There appears to be complete correlation between the size of the petal
and the colour. The smaller petal is invariably white and the larger
petal invariably yellow. Among the plants under experiment, which
now amount to over a hundred thousand, and among cottons under
cultivation in the field no single exception has been observed. The
correlation holds with the simple yellow and white types and also with
those types in which a red colour is superimposed. It follows from
this that all plants with a *red on yellow* flower, such as type 3, have
large petals, while plants with a *red on white* flower, such as type 11,
have small petals. The cross between types 3 and 9 illustrates this
point well; in all cases both plants with red on yellow, and those with
yellow flowers, whether pure or impure, have large petals, while in the
plants with red on white flowers, whether pure or impure, and in those
with white flowers, the petals are small.

A further instance of correlation, and one which is of considerable
importance both practically and on account of its bearing on the argu-
ment of section 3 (*d*), has been found to exist between the presence of
the red colouring matter and an increase in the length of the vegetative
period. There is a distinct retardation of the commencement of the
flowering period when the red sap colour is present. This is shown in
Table XXIX. In this table the unit is a plant of the F_2 generation
and the figure is, for the pure forms, taken as the average of the F_3
offspring and, for the impure forms, as the average calculated from
only those F_3 offspring which are, judging by the depth (to lamina), or
absence, of the red colour, pure in this character.

In the light of this correlation it is necessary to reconsider the
results detailed in section 3 (*d*). In that section attention was drawn
to the monomodal curve as indicating incomplete resolution. No
distinction was, however, made between plants with, and plants without,
the red colouring matter. It would appear possible that a separation
of the plants into two groups dependent on the presence or absence of
the red colouring matter might disclose two trimodal curves, whose
presence is rendered obscure through superposition. Table XXIX,
however, in which such a separation is effected, shows no such trimodal

curves and it has not been possible to obtain from the records available any clear indication of their existence. For the present, therefore, it is impossible to do more than recognise that in this correlation between the flower colour and the length of the vegetative period may lie the explanation for the failure of the early and late flowering characters to fall into line with other Mendelian phenomena.

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TABLE I[1].

Flower Colour.   Type 4 (yellow coloured) × Type 6 (white flowered).

F_1		68 plants all yellow flowered			
F_2	ratio	109 plants yellow flowered 2·1			52 plants white flowered 1
F_2 plants used as parents		21			13
		5	10^2	6	13
F_3	yellow	65	35	34	0
	white	0	0	11	100

[1] No difference has been observed between the direct cross and its reciprocal.   The two have, therefore, been grouped together in this and subsequent tables.

[2] Number of offspring too small to be a reliable guide to purity of parent.

TABLE II.

The occurrence of the red colouring matter in vegetative organs.

Types	Coloured RR and Rr	Colourless rr	Total
3×2	106	29	135
3×4	224	69	293
3×5	299	102	401
3×8	180	64	244
3×9	374	120	494
3×10^{1}	351	100	451
Total	1534	484	2018
Ratio	3·17	1	4·17

[1] Determined on flower colour only.

TABLE III.

The intensity of the red colouring matter in the leaf as an indication of purity.

Leaf of F_3 parent recorded as	Constitution, as determined by F_3 offspring, of the form		Total
	RR	Rr	
(a) Type 3 × Type 4			
Lamina	61	5	66
Veins	2	20	22
Ribs	0	116	116
Total	63	141	204
Ratio	1	2·2	
(b) Type 3 × Type 9			
Lamina	59	4	63
Veins	13	2	15
Ribs	9	188	197
Total	81	194	275
Ratio	1	2·4	

TABLE IV.

The intensity of the red colouring matter in the petal as an indication of purity.

Flower of F_2 parent recorded as	Constitution, as determined by F_3 offspring, of the form		Total
	RR	Rr	
(a) Type 3 × Type 4			
Red	28	2	30
Red on yellow	35	136	171
Total	63	138	201
Ratio	1	2·2	
(b) Type 3 × Type 9			
Red	11	3	14
Red on yellow	46	136	182
Total	57	139	196
Ratio	1	2·4	

TABLE V.

The F_2 generation of crosses between type 3, in which the red colouring matter is present, and types in which it is absent.

		Coloured — RR (Lamina)	Coloured — Rr (Veins)	Coloured — Rr (Ribs)	Coloured — Rr (Total)	Colourless (rr)	Total
(1)	3 × 2	10	23	73	96	29	135
	Ratio	1			9·6	2·9	
(2)	3 × 4	59	24	90	114	55	228
	4 × 3	18	—	33	33	14	65
	Total	77[1]	24[2]	123	147	69	293
	Ratio	1·1			2 1	1	
(3)	3 × 5	44	5	62	67	35	146
	5 × 3	71	3	114	117	67	255
	Total	115	8	176	174	102	401
	Ratio	1·1			1·7	1	
(4)	3 × 8	33	5	58	63	38	134
	8 × 3	26	6	52	58	26	110
	Total	59	11	110	121	64	244
	Ratio	1			2·0	1·1	
(5)	3 × 9	46	5	132	137	69	252
	9 × 3	51	15	124	139	52	242
	Total	97[3]	20	256	276[4]	121	494
	Ratio	1			2·8	1·2	
	Grand total	358	86	739	825	384	1567
	Ratio	1			2·3	1·1	

[1] 5 of these shown by experiment to be impure.
[2] 2 ,, ,, ,, ,, pure.
[3] 4 ,, ,, ,, ,, impure.
[4] 22 ,, ,, ,, ,, pure.

TABLE VI.

Flower colour. Type 3 (red flowered) × Type 4 (yellow flowered).

F_1.........38 plants with flowers red on yellow and the red colouring matter extending to veins.

F_2	RR (Foliage lamina)	Rr (Ribs or Veins)	RR+Rr (Total coloured)	rr (Colourless)
	77	147	224	69
Ratio	1·1	2·1		1
Used as parents	61 lamina / 2 veins	5 lamina / 136 veins	204	68

F_3	RR (Lamina)	Rr (Ribs or veins)	RR+Rr (Total coloured)	rr (Colourless)
	1328 832	1692	2524 773	1245[1]
Ratio	1·07	2·18		1·90

[1] And 4 red plants. A consideration of other characters indicates that 2 of these are without doubt either volunteer plants or have arisen through an accidental mixing of seed.

TABLE VII.

Flower colour. Type 3 (red flowered) × Type 9 (white flowered).

F_1 Type 3 × Type 9........48
Type 9 × Type 3........19
‾‾
67 plants with red colouring matter as far as veins and the flower with petals red on yellow.

F_2	RRYY, RRYy (lamina) (red)	RrYY, RrYy (veins) (red on yellow)	RRyy (lamina) (red on white)	Rryy (veins) (red on white)	rrYY, rrYy (green) (yellow)	rryy (green) (white)
Ratio	89 2·8	193 6·0	30 1·0	78 2·4	96 3·0	25 0·8
Expectation	3	6	1	2	3	1
Used as parents 18	27	39 16¹	17 5¹	52	17 6¹	22

F_3	RRYY, RRYy (lamina)	RRyy (lamina)	RrYY, RrYy (lamina)	RrYY (veins)	rrYY (green)	RrYY, RrYy (lamina) (red)	RrYY, RrYy (veins)	Rryy (lamina) (red on white)	Rryy (veins) (red on white)	rrYY, rrYy (green) (yellow)	rryy (green) (white)	RRyy (lamina) (red on white)	RRyy (lamina) (red on white)	Rryy (veins)	rryy (veins) (red on white)	rrYY (green) (yellow)	rrYy (green) (white)	rryy (green) (white)
Foliage (lamina)	(lamina)	(red on white)	(lamina)	(veins)	(green) (yellow)	(lamina)	(veins)	(red on white)	(veins)	(green) (yellow)	(green) (white)	(lamina)	(lamina)	(veins)	(veins)	(green) (yellow)	(green) (white)	(green)
Flower (red)	(red on white)	(red)	(red on yellow)	(green) (yellow)	(red)	(red on yellow)	(veins)	(red on white)	(red on white)	(yellow)	(white)	(red on white)	(red on white)	(red on white)	(white)	(yellow)	(white)	(white)
201	381	118	125 16¹	250 51¹	141 30¹	265	622	95	232	308	90	215 12¹	204	445	189	249 25¹	682	243	313
Ratio in each group	2·6	1	1	2	1·1	2·9	6·9	1·0	2·6	3·5	1	1·1	1·1	2·3	1	2·8	1
Expectation in each group	3	1	1	2	1	3	6	1	2	3	1	1	1	2	1	3	1

¹ Number of offspring too small for reliable identification of the group.

TABLE VIII.

Flower colour. F_1 plants × parents.

	Red (lamina)	Red (veins)	Red on white (lamina)	Red on white (veins)	yellow	white
(Type 2 × Type 3) × Type 3						
¦red (lamina) × yellow¦ × red (lamina)	13	31	—	—	—	—
(Type 2 × Type 3) × Type 2						
¦red (lamina) · yellow¦ × yellow	—	2	—	—	8	—
(Type 3 × Type 4) × Type 3						
¦red (lamina) × yellow¦ × red (lamina)	21	6	—	—	—	—
(Type 3 × Type 4) × Type 4						
¦red (lamina) × yellow¦ × yellow	—	6	—	—	1	—
(Type 3 × Type 9) × Type 3						
¦red (lamina) × white¦ × red (lamina)	18	15	—	—	—	—
(Type 3 × Type 9) × Type 9						
¦red (lamina) × white¦ × white	—	2	—	6	3	3
(Type 4 × Type 6) × Type 4						
¦yellow · white¦ × yellow	—	—	—	—	8	—
(Type 4 × Type 6) × Type 6						
¦yellow × white¦ × white	—	—	—	—	—	2

TABLE IX.

Detail of individual of type having leaf factor 1·88.

	Number of leaves	Leaf factor	Tertiary branches		Number of leaves	Leaf factor
Main stem	31	1·82				
Secondary branches						
(*a*) Monopodial						
arising from leaf 7	9	1·81				
			Sympodial			
			arising from leaf	8	2	1·64
			,,	,, 10	3	1·66
arising from leaf 8	21	1·86				
			arising from leaf 10		2	1·72
			,,	,, 12	3	1·74
			,,	,, 13	2	1·70
			,,	,, 15	1	1·79
arising from leaf 9	17	1·90				
			Monopodial			
			arising from leaf	5	3	1·74
			,,	,, 6	3	1·86

TABLE IX (*continued*).

Number of leaves	Leaf factor	Tertiary branches	Number of leaves	Leaf factor
		Sympodial		
		arising from leaf 8	4	1·78
		,, ,, 10	3	1·72
		,, ,, 11	3	1·81
		,, ,, 12	3	1·66
		,, ,, 13	3	1·74
		,, ,, 14	1	1·83
		,, ,, 15	3	1·76
		,, ,, 17	3	1·64
		,, ,, 18	4	1·64
arising from leaf 10	12	1·86		
		arising from leaf 8	2	1·75
		,, ,, 10	1	1·68
		,, ,, 11	1	1·74
		,, ,, 13	2	1·87
		,, ,, 14	3	1·75
arising from leaf 11	23	1·91		
		arising from leaf 5	2	1 80
		,, ,, 7	2	1·84
		,, ,, 8	3	1·74
		,, ,, 10	2	1·73
		,, ,, 11	3	1·69
		,, ,, 13	3	1·76
		,, ,, 14	3	1·68
		,, ,, 15	1	1·71
		,, ,, 16	1	1·78
		,, ,, 18	2	1·72
		,, ,, 19	1	1·71
arising from leaf 12	19	1·84		
		arising from leaf 5	1	1·61
		,, ,, 6	2	1·65
		,, ,, 8	2	1·78
		,, ,, 11	2	1·73
arising from leaf 13	21	1·88		
		arising from leaf 5	1	1·71
		,, ,, 9	3	1·73
		,, ,, 10	3	1·76
		,, ,, 12	1	1·72
		,, ,, 13	4	1·78
		,, ,, 15	1	1·76
		,, ,, 16	2	1·69
		,, ,, 17	1	1·74
		,, ,, 18	2	1·77
arising from leaf 14	19	1·77		
		arising from leaf 6	1	1·52
		,, ,, 8	1	1·57
		,, ,, 10	2	1·75
		,, ,, 11	3	1·79

TABLE IX (*continued*).

	Number of leaves	Leaf factor	Tertiary branches		Number of leaves	Leaf factor
arising from leaf 15	15	1·76				
			arising from leaf 5	3		1·73
			,, ,, 6	2		1·85
			,, ,, 8	1		1·76
			,, ,, 10	1		1·68
arising from leaf 16	8	1·83				
			arising from leaf 5	2		1·73
arising from leaf 17	16	1·71				
,. ,, 18	13	1·97				
			arising from leaf 1	1		1·72
			,, ,, 5	2		1·55
			,, ,, 7	2		1·79
			,, ,, 11	2		1·73
arising from leaf 19	16	1·81				
			arising from leaf 1	6		1·87
			,, ,, 10	1		1·73
arising from leaf 21	14	1·78				
			arising from leaf 1	5		1·71
			,, ,, 2	1		1·79
			,, ,, 6	2		1·57
			,, ,, 7	1		1·59
Average of leaves on Monopodia	—	1·84	Average of leaves on tertiary branches	—		1·73

(b) Symodial

		Number of leaves	Leaf factor
arising from leaf 20		4	1·76
,, ,, 21		6	1·75
,, ,, 22		3	1·66
,, ,, 23		1	2·07
,, ,, 25		6	1·81
,, ,, 26		2	1·73
,, ,, 27		6	1·78
,, ,, 28		5	1·80
,, ,, 29		4	1·79
,, ,, 30		4	1·63
,, ,, 31		3	1·69
,, ,, 32		5	1·66
,, ,, 33		1	1·65
,, ,, 34		3	1·67
,, ,, 35		3	1·71
,, ,, 36		3	1·70
,, ,, 37		2	1·70
,, ,, 38		2	1·68
,, ,, 39		3	1·60
,, ,, 40		3	1·69
,, ,, 41		1	1·85
Average of leaves on Sympodia		—	1·72

TABLE X.

Variation of the leaf factor within the type.

	Extremes of leaf factor		Leaf factor (average of offspring)		Number of offspring used in determination	
	Max.	Min.	1907	1908	1907	1908
Type 4	1·57	1·17	1·37	—	32	—
	1·71	1·27	1·46	1·49	20	2
	1·92	1·42	1·65	1·73	17	5
Type 5	1·80	1·56	1·68	1·73	20	9
	1·94	1·73	1·78	1·80	20	14
	1·98	1·69	1·88	1·84	20	16
Type 6	1·98	1·69	1·81	1·88	20	20
Type 8	3·83	2·96	3·35	3·26	18	20
	3·64	3·55	3·59	3·71	2	10
Type 9	4·18	3·18	3·64	4·07	20	20
	4·34	3·80	4·16	—	20	—

TABLE XI.

The relation between the leaf factor of the F_1 generation of a cross and those of the parents.

Parents		Leaf factor of parents		Mean of parental leaf factor	Leaf factor of offspring	Difference	Number of F_1 individuals
Seed	Pollen	Seed	Pollen				
Type 3	Type 2	3·13	1·45	2·29	2·26	− 0·03	25
,, 3	,, 4	3·13	1·45	2·24	2·21	− 0·03	12
,, 3	,, 4	3·13	1·64	2·38	2·49	+ 0·11	13
,, 4	,, 3	1·46	3·13	2·29	2·42	+ 0·13	3
,, 4	,, 3	1·64	3·13	2·38	2·45	+ 0·07	9
,, 3	,, 5	3·13	1·78	2·45	2·70	+ 0·25	31
,, 5	,, 3	1·78	3·13	2·45	2·45	—	6
,, 2	,, 8	1·46	3·59	2·52	2·18	− 0·34	12
,, 2	,, 8	1·46	3·34	2·40	2·37	− 0·03	3
,, 8	,, 2	3·59	1·46	2·52	2·49	− 0·03	3
,, 8	,, 4	3·59	1·64	2·61	2·53	− 0·08	6
,, 8	,, 4	3·34	1·64	2·49	2·54	+ 0·05	9
,, 4	,, 8	1·46	3·59	2·52	2·36	− 0 16	13
,, 4	,, 8	1·64	3·34	2·49	2·42	− 0·07	18

TABLE XII.

The leaf factor.   *Type* 3 (l. f. > 3) × *Type* 4 (l. f. < 2).

Leaf factor 3·13.........1·40[1].

Mean 2·27.

F_1 15 plants.........mean leaf factor 2·21.

	<2	>2 and <3	>3
Leaf factor	<2	>2 and <3	>3
F_2 Number of individuals	64	143	83
Ratio	1	2·3	1·3
Mean leaf factor	1·71	2·57	3·54

	<2	>2 and <3·2	>3·2
Leaf factor	<2	>2 and <3·2	>3·2
Individuals used as parents	65	143	64
Ratio	1	2·3	1
Mean leaf factor[2]	1·72	2·62	3·51

	<2	>2	<2	>2 and <3	>3	<3	>3
Leaf factor	<2	>2	<2	>2 and <3	>3	<3	>3
F_3 Number of individuals	1222	5	784	1602	791	6	1273
Ratio	—	—	1	2·04	1	—	—
Mean leaf factor	1·71	1·62	2·62	3·42	3·51		

[1] The mean value between 1·35 and 1·46, the values of the *pure lines* used in this experiment. At the time when the original cross was made these two forms had not been isolated.

[2] The value of each individual is here taken as the mean of the values obtained from its offspring.

TABLE XIII.

The leaf factor.   Re-appearance of parental values in the F_2 offspring.

(a)   Type $2 \times$ Type 3.

Leaf factor 1·40.........3·13.

Mean 2·26.

F_1	21 plants .... mean leaf factor 2·33			
	Leaf factor	< 2	> 2 and < 3	> 3
F_2	Number of individuals	40	82	11
	Ratio	3·6	7·4	1
	Mean of leaf factor ...	1·63	2·43	3·41

(b)   Type $4 \times$ Type 8.

Leaf factor 1·52.........3·47.

Mean 2·49.

F_1	28 plants.........mean leaf factor 2·39			
	Leaf factor	< 2	> 2 and < 3	> 3
F_2	Number of individuals	47	102	46
	Ratio	1	2·2	1
	Mean of leaf factor ...	1·66	2·59	3·42

TABLE XIV. *The leaf factor.* F_3 *generation*

	1·2 and under	1·3	1·4	1·5	1·6	1·7	1·8	1·9	2·0	2·1	2·2	2·3	2·4	2·5	2·6	2·7	2·8	2·9	3·0	3·1	3·2
< 1·49	—	—	12	13	8	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
1·50—1·59	—	11	23	36	33	25	10	—	1	—	—	—	—	—	—	—	—	—	—	—	—
1·60—1·69	—	6	20	44	70	79	43	13	9	—	—	—	—	—	—	—	—	—	—	—	—
1·70—1·79	1	3	13	27	88	148	131	67	35	8	—	1	—	—	—	—	—	—	—	—	—
1·80—1·89	—	—	1	5	19	44	54	62	35	14	1	1	—	—	—	—	1	—	—	—	—
1·91	—	—	—	—	—	1	3	4	1	1	—	—	—	1	—	—	—	—	—	—	—
1·98	—	—	—	2	4	4	8	10	13	5	—	—	—	—	—	—	—	—	—	—	—
2·05	—	1	1	1	1	2	1	3	2	3	—	1	—	1	—	2	1	1	—	—	—
2·06	—	—	1	1	1	—	1	—	—	—	1	—	1	1	1	1	—	—	—	—	—
2·10—2·19	2	1	9	14	11	10	5	7	—	5	9	7	15	6	5	7	3	2	1	2	5
2·20—2·29	—	4	13	10	14	7	7	7	5	3	14	21	14	11	10	10	7	5	3	2	7
2·30—2·39	—	1	4	11	13	16	8	6	4	6	8	16	14	17	12	4	2	4	6	3	4
2·40—2·49	1	1	5	13	25	27	32	16	13	10	11	24	29	39	39	31	23	19	16	16	13
2·50—2·59	—	4	3	14	26	36	33	34	22	12	19	30	45	47	50	42	36	28	37	16	18
2·60—2·69	—	—	2	3	7	18	16	13	4	8	6	14	23	23	24	21	20	19	23	4	10
2·70—2·79	—	1	3	8	11	33	27	15	9	2	5	7	24	28	34	35	32	29	28	16	11
2·80—2·89	—	—	1	3	5	6	14	12	3	3	2	8	5	17	28	24	33	24	16	17	18
2·90—2·99	—	—	—	2	2	7	8	8	4	2	1	2	4	10	21	15	15	16	13	14	11
3·00—3·09	—	—	—	—	2	1	3	7	2	3	—	—	—	3	7	5	11	8	14	11	8
3·10—3·15	—	—	—	—	1	2	3	4	1	1	—	1	1	—	5	8	2	10	8	12	17
3·17	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	3	2	5
3·18	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	1	—	—
3·19	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—
3·20—3·29	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	2	10	10	9
3·30—3·39	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	7	10	9	15
3·40—3·49	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	14	17	31
3·50—3·59	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	5	6	8	12
3·60—3·69	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	8	12
3·70—3·79	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	2	5
3·80—3·89	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	—
3·90—3·99	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
4·24	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

from the cross. Type 3 × Type 4.

3·3	3·4	3·5	3·6	3·7	3·8	3·9	4·0	4·1	4·2	4·3	4·4	4·5	4·6	4·7	4·8 and over	Number of parents	Average of parents	Number of offspring	Average of offspring	Difference
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1·68	34	1·48	+0·20
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	1·66	149	1·54	+0·12
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	1·77	281	1·64	+0·13
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	1·75	522	1·74	+0·01
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	1·81	237	1·84	−0·03
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1·91	11	1·93	−0·02
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1·79	46	1·98	−0·19
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2·26	21	2·05	+0·21
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2·67	9	2·06	+0·61
5	3	—	—	1	1	1	—	1	—	—	—	—	—	—	—	5	2·31	141	2·18	+0·13
2	3	—	1	—	3	1	—	—	—	—	—	—	—	—	—	10	2·47	187	2·25	+0·22
8	5	1	1	3	—	1	—	—	1	—	—	—	—	—	—	8	2·38	179	2·35	+0·03
15	11	7	4	3	2	2	1	1	1	—	—	—	—	—	—	20	2·56	150	2·46	+0·10
16	19	13	10	6	8	2	5	2	1	—	—	—	—	—	—	24	2·68	634	2·51	+0·14
7	11	8	12	6	4	4	1	2	1	—	—	—	—	—	—	15	2·74	314	2·64	+0·10
20	11	17	8	10	10	6	7	6	8	5	1	—	1	—	—	20	2·73	468	2·71	−0·01
10	14	12	7	7	5	9	3	2	2	3	—	—	1	1	—	16	2·96	315	2 84	+0·12
6	7	6	6	10	6	4	8	4	3	1	2	—	—	—	1	11	2·92	219	2·95	−0·03
2	5	2	5	3	1	4	4	3	2	—	1	1	2	—	—	4	3·22	126	3·06	+0·16
14	6	4	10	5	5	2	4	3	1	—	—	—	—	—	1	7	3·02	131	3·12	−0·10
2	1	2	1	1	—	—	—	—	—	—	—	—	—	—	—	1	3·51	19	3·17	+0·34
1	1	1	2	—	—	—	—	—	—	—	—	—	—	—	—	1	2 91	8	3·18	−0·27
—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3·22	4	3·19	+0·03
9	5	4	5	2	3	—	—	—	—	—	—	—	—	—	—	3	3·47	61	3·23	+0·24
30	23	23	12	9	3	2	—	—	—	—	—	—	—	—	—	7	3 44	145	3·33	+0·11
36	47	27	29	18	17	12	6	2	3	1	—	—	—	—	—	14	3·51	274	3·44	+0 11
7	23	33	25	21	18	10	8	9	2	1	2	1	—	—	—	10	3 62	192	3·55	+0·07
23	24	44	40	33	25	18	18	8	10	5	—	1	—	1	—	13	3·72	274	3·65	+0·07
5	10	12	12	14	11	15	7	9	9	4	2	—	—	—	—	6	3·87	119	3·75	+0·12
1	4	9	4	6	9	3	6	6	8	6	1	1	2	—	—	4	3·95	70	3·85	+0·02
1	6	6	6	5	6	17	8	9	11	7	4	—	2	—	2	3	3·99	91	3·93	+0·06
—	—	—	—	1	1	2	2	1	1	2	1	2	3	—	1	1	3·92	17	4·24	−0·32

TABLE XV.

The length of the vegetative period as affected by the season.

Sown in		Pots			Field
Season		1907	1908	Difference = seasonal variation	1909
Type	3	116	210	+ 64	146
,,	4	83	111	+ 28	83
,,	5	80	110	+ 30	73
,,	6	90	114	+ 24	84
,,	7	—	96	—	62
,,	8	78	106	+ 28	72
,,	9	93	117	+ 24	92
,,	10	96	115	+ 19	94

Seasonal variation for monopodial types......64.
,,   ,,   ,, sympodial types.........25.

TABLE XVI.

The length of the vegetative period as affected by the method of cultivation.

	Type 3 < Type 4					Type 3 < Type 9				
	Pots		Field			Pots		Field		
Period in Days	Number of plants	Days	Number of plants	Days	Differ-ence	Number of plants	Days	Number of plants	Days	Differ-ence
Below 101	3	105	—	—	—	2	127	—	—	—
101—110	11	108	30	85	23	13	109	8	88	21
111—120	29	115	52	89	26	47	118	30	93	25
121—130	22	122	36	96	26	92	122	11	98	24
131—140	15	126	31	95	31	40	130	20	102	28
141—150	11	127	19	98	29	21	132	9	105	27
151—160	8	132	3	104	28	16	132	--	—	—
161 and over	2	123	--	—	—	3	135	—	—	—

TABLE XVII.

The length of the vegetative period.   The F_2 generation from the cross,
Type 3 × Type 4 and Type 3 × Type 9.

Intervals Number of days from sowing to flowering	Type 3 × Type 4		Type 3 × Type 9	
	Number of plants	Number indicative of type of branching	Number of plants	Number indicative of type of branching
Above 170	2	75	—	—
166—170	3	91	2	87
161—165	4	87	3	75
156—160	13	79	5 [1]	40
151—155	16	62	8	69
146—150	13	57	9	50
141—145	14	54	9	44
136—140	19	64	22	30
131—135	25	42	33	21
126—130	89	29	21	15
121—125	37	26	31	2
116—120	43	11	36	1
111—115	46	5	26	—
106—110	14	4	10	—
101—105	3	—	3	—
below 101	1	—	—	—

In this table, which is based on the F_2 generation, only the four degrees, indicated by the numbers 100, 75, 50, 0, of secondary branching have been recognised.

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[1] Of these five plants two are of the sympodial type.   One of these was dwarfed, and the date of appearance of first flower consequently very late.   The second produced flowers at the extremities of the sympodial branches only.   On account of these two plants, which appear somewhat normal, the figure for this interval is abnormally low.

TABLE XVIII. *The length of the vegetative period. The F₃ generation*

Field Number	78 and below	80	82	84	86	88	90	92	94	96	98	100	102	104	106	108	110	112	114	116	118	120	122
106	—	—	—	1	—	1	1	1	—	1	—	2	—	2	1	—	—	—	—	—	—	—	—
128	—	—	1	1	—	—	—	—	—	1	1	—	1	—	—	1	—	1	—	—	—	—	—
115	—	—	—	—	—	—	2	—	3	1	—	—	—	—	1	—	—	—	—	1	1	—	—
281	—	—	—	—	—	—	1	1	1	1	2	1	2	3	—	3	—	2	1	—	—	—	—
282	—	—	—	—	—	—	1	1	6	—	4	—	1	—	1	—	—	3	—	1	3	1	—
110	—	—	—	—	—	1	—	1	—	—	—	—	1	3	1	—	—	1	—	—	—	1	—
300	—	—	—	—	—	—	1	—	2	—	1	—	3	2	—	—	—	2	1	—	—	1	—
329	—	—	—	—	—	—	—	1	3	1	2	3	—	1	2	2	1	2	2	1	2	1	—
101	—	—	—	—	—	—	—	1	—	1	—	2	—	2	1	—	—	—	—	1	1	—	—
118	—	—	—	—	—	1	—	—	—	—	3	—	1	3	1	1	4	5	1	—	—	—	—
280	—	—	—	—	—	—	—	1	4	1	1	1	4	2	1	1	1	1	1	1	1	—	—
150	—	—	—	—	—	—	—	1	—	—	—	—	—	3	—	—	—	—	—	—	—	—	—
241	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	1	1	1	1	—	—	—	—
320	—	—	—	—	—	1	—	—	—	—	1	1	1	1	1	1	1	2	4	1	1	—	2
151	—	—	—	—	—	—	1	—	2	—	—	1	1	2	—	6	2	1	—	—	—	2	1
131	—	—	1	—	—	—	—	2	1	2	—	—	1	—	2	1	—	1	2	1	1	1	3
327	—	—	—	—	—	—	1	1	—	—	1	—	—	1	—	1	—	2	—	1	1	1	1
142	—	—	—	—	—	—	—	—	1	—	—	—	—	2	—	1	1	—	1	—	—	1	—
284	—	—	—	—	—	—	—	1	—	—	—	1	—	1	—	1	1	3	2	3	1	—	—
114	—	—	—	—	—	—	—	1	—	1	—	1	2	1	—	1	2	1	4	2	1	—	—
65	—	—	—	—	—	—	—	—	—	—	1	—	1	4	—	1	4	1	—	1	2	—	1
219	—	—	—	—	—	—	—	—	1	—	1	1	—	—	1	1	1	—	—	2	1	1	—
170	—	—	—	—	—	1	2	—	2	1	—	—	1	—	1	1	—	1	—	3	2	1	2
119	—	—	—	—	—	—	—	—	2	1	—	—	—	—	1	1	—	1	1	1	1	—	1
139	1	—	—	—	—	1	3	1	—	1	—	—	1	1	—	2	1	1	—	—	1	2	1
163	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	3	1	1	—	—	—	1
127	—	—	—	—	—	—	—	1	—	1	—	2	—	1	1	1	2	2	1	1	1	2	3
138	—	—	—	—	—	—	—	—	—	—	—	1	1	1	—	—	—	—	—	—	—	—	—
87	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	2	2	—	2	—	2	1
166	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	2	—	1	1	—	—	—	1
162	—	—	—	—	—	—	—	1	2	—	1	2	1	—	2	1	1	1	2	2	2	1	3
324	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	1	—	—	3	2	—	1	1
156	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	4	2	2	—	2	1	2
314	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	1	1	3	—
112	—	—	—	—	—	—	—	—	—	—	—	2	—	1	1	2	2	—	—	—	—	—	—
242	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	2	—	—	2	1	1	—	—
195	—	—	—	—	—	—	—	—	—	—	1	1	3	2	—	1	—	1	2	—	—	—	2
153	—	—	—	—	—	—	—	—	—	—	1	1	1	—	—	2	—	2	2	1	1	—	—
158	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	1	1	—	1	1	1	1	1
274	—	—	—	—	1	—	—	—	—	1	—	—	—	1	—	—	1	1	1	—	1	—	1
181	—	—	—	—	—	—	1	1	1	—	—	—	—	1	1	—	1	—	3	—	1	—	3
140	—	—	—	—	—	—	—	—	—	—	1	1	—	1	—	3	1	4	—	3	5	3	3
210	—	—	—	—	—	—	—	—	—	—	—	2	1	—	3	—	—	—	—	—	1	1	—
225	—	—	—	—	—	—	—	—	—	—	1	1	—	1	—	—	3	1	1	3	2	5	—
134	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1	1	—	2	—	—	—	—	—
264	—	—	—	—	—	—	—	—	—	—	1	1	1	—	1	—	—	1	—	—	—	—	2
254	—	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—	—	2	—	3	2	1	3
214	—	—	—	—	—	—	—	1	—	—	1	—	1	1	1	1	3	6	1	2	2	—	—
221	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	2	2	—	—

from the cross. Type 3 × Type 4. Pot Series.

124	126	128	130	132	134	136	138	140	142	144	146	148	150	152	154	156	158	160	161 and over	Number of plants	Parents	Difference	Offspring
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	107	− 10	97
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	112	− 14	98
—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	101	+ 2	103
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	18	100	+ 3	103
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	99	+ 5	104
—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	110	− 5	105
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	107	− 2	105
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	24	113	− 7	106
—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	109	− 2	107
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	102	+ 5	107
—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	98	+ 9	107
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	113	− 5	108
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	132	− 22	110
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	19	118	− 8	110
1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	115	− 5	110
1	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	22	115	− 5	110
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	114	− 4	110
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	111	− 1	110
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14	109	+ 1	110
1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	109	+ 1	110
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	108	+ 2	110
—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	124	− 13	111
1	1	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	21	114	− 3	111
—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	119	− 7	112
2	1	1	2	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	25	117	− 5	112
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	8	113	− 1	112
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	112	—	112
—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	117	− 4	113
2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	131	− 16	115
1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	115	—	115
3	2	1	1	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	31	113	+ 2	115
1	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	119	− 3	116
—	1	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	19	119	− 3	116
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	116	—	116
—	1	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	11	108	+ 8	116
1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	132	− 15	117
1	1	2	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	19	124	− 7	117
1	2	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	16	118	− 1	117
1	2	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	115	+ 2	117
3	2	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	155	− 37	118
1	1	—	1	1	1	—	1	—	1	—	—	—	—	—	—	—	—	—	—	20	127	− 9	118
4	4	3	2	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	13	120	− 2	118
3	2	—	—	1	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	16	130	− 11	119
3	—	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	128	− 9	119
1	1	—	—	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	11	119	—	119
1	2	—	1	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	13	148	− 28	120
—	1	—	2	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	18	141	− 21	120
2	4	6	2	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	36	130	− 10	120
—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9	126	− 6	120

TABLE XVIII

Field Number	78 and below	80	82	84	86	88	90	92	94	96	98	100	102	104	106	108	110	112	114	116	118	120	122
168	—	—	—	—	—	—	—	1	2	—	1	—	—	—	1	1	—	—	—	—	1	—	4
100	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	1	1	1	1	1
273	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	3	1	—
335	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1	1	1
71	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	1	—
187	—	—	—	—	—	—	—	—	—	—	—	1	2	3	—	—	1	—	1	—	1	3	2
182	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	1	—	—	—	—	—	1	1
132	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	2	2	—	—	3	2
147	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	—	—	—	1	2	—	1	1
90	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	2	—	3	—	1
179	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	4	—	—	1
310	—	—	—	—	—	—	—	—	—	—	—	—	2	2	—	—	—	1	—	—	1	6	4
97	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	3
263	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	2	2	1	—	—	—
224	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	2	—
223	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	3	—	—	—	1	1	3
328	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	1	—
155	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	2	—	—	2	1	1
275	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	2	2	2
259	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	1	1	1	1	—	3
246	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	2	—	2	3	1
75	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	—	1	1
193	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	4	—	—	1
194	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	2	2
266	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	3	2
249	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—
185	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	1	1	—	—	1	—	1
271	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	4
235	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
227	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	1	—
77	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	2	1	1
245	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
176	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
215	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
212	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	1	—	1	—	1	2	1	1
175	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
272	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
256	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
345	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1
229	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1
251	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	1	3
89	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
255	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
269	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
93	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
220	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1
245	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
211	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
240	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

(*continued*).

124	126	128	130	132	134	136	138	140	142	144	146	148	150	152	154	156	158	160	161 and over	Number of plants	Parents	Difference	Offspring
4	2	1	—	1	1	—	—	2	—	—	—	—	—	—	—	—	—	—	—	22	117	+ 3	120
1	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	11	117	+ 3	120
2	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	12	156	− 35	121
—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	124	− 3	121
3	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	123	− 2	121
3	—	1	2	—	3	1	—	—	—	1	—	—	—	—	—	—	—	—	—	25	122	− 1	121
2	1	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	12	121	—	121
—	2	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	15	120	+ 1	121
2	3	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	119	+ 2	121
—	—	2	1	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	12	141	− 19	122
—	1	2	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	11	129	− 7	122
7	4	—	2	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	31	112	+ 10	122
1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	166	− 43	123
—	3	2	1	2	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	17	141	− 18	123
—	2	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	128	− 5	123
3	1	1	1	—	4	—	—	—	1	—	—	—	—	—	—	—	—	—	—	22	128	− 5	123
1	1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	6	118	+ 5	123
1	3	—	1	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	15	118	+ 5	123
1	1	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	11	163	− 39	124
1	2	2	—	2	—	1	1	—	—	1	—	1	—	—	—	—	—	—	—	20	143	− 19	124
—	5	5	—	—	2	—	—	—	—	1	—	—	—	—	—	—	—	—	—	22	133	− 8	125
—	3	3	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	13	133	− 8	125
1	—	2	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	11	130	− 5	125
2	1	—	—	—	1	—	—	—	2	—	—	—	—	—	—	—	—	—	—	12	129	− 4	125
—	1	—	—	3	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	14	141	− 15	126
1	5	2	—	—	1	—	—	—	1	—	1	—	—	—	—	—	—	—	—	13	132	− 6	126
2	4	6	3	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—	—	25	126	—	126
1	5	—	—	—	—	—	2	—	1	—	—	—	—	—	—	—	—	—	—	16	153	− 26	127
1	1	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	133	− 6	127
—	1	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	6	131	− 4	127
1	—	4	1	2	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—	17	134	− 6	128
2	—	—	1	1	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	7	133	− 5	128
1	1	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	6	129	− 1	128
4	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	6	126	+ 2	128
4	2	4	5	4	4	1	1	1	—	1	—	—	—	1	—	—	—	—	—	36	124	+ 4	128
—	—	1	1	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	6	129	—	129
1	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	3	155	− 25	130
1	1	—	1	—	—	1	—	1	—	1	—	—	—	—	—	—	—	—	—	8	148	− 18	130
—	2	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	6	135	− 5	130
4	5	4	1	1	1	—	4	—	—	1	—	—	1	—	—	—	—	—	—	24	134	− 3	131
1	1	2	3	2	—	1	—	—	—	—	3	1	3	—	—	—	—	—	—	23	150	− 17	133
2	2	—	4	1	2	1	1	—	1	—	—	1	—	1	—	—	—	—	1	16	143	− 9	134
2	2	1	—	1	1	—	—	1	1	—	1	—	1	—	—	—	—	—	—	12	140	− 6	134
1	—	—	—	1	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	4	155	− 20	135
—	1	2	1	2	1	1	1	—	1	4	—	—	—	—	—	—	—	—	—	15	153	− 18	135
—	2	1	3	—	2	—	—	1	1	2	—	—	1	1	—	—	—	—	—	16	129	+ 6	135
—	2	—	2	1	1	—	1	—	—	1	—	2	—	—	—	—	—	—	—	10	138	—	138
—	2	1	1	1	1	—	1	1	2	—	1	—	1	—	1	—	—	—	—	13	139	—	139
—	—	—	—	—	1	1	1	—	—	—	—	—	1	—	—	—	—	—	—	4	133	+ 7	140

TABLE XIX.   *The length of the vegetative period.   The F_3 generation*

	Below 60	60	62	64	66	68	70	72	74	76	78	80	82	84	86	88	90	92	94	96	98	100
Below 80	—	—	—	—	—	—	—	2	3	4	3	4	1	1	—	—	1	1	—	—	—	—
80— 84	—	—	—	1	2	2	13	8	32	45	74	72	66	50	45	18	19	14	13	12	10	6
85— 89	—	—	—	1	—	1	6	8	15	44	68	83	78	59	57	40	31	33	45	30	33	28
90— 94	1	—	—	—	—	1	—	2	12	19	30	61	68	65	62	52	66	58	63	80	76	70
95— 99	2	1	—	—	—	—	—	3	4	5	13	18	26	31	39	44	32	35	68	75	94	97
100—104	—	—	—	—	—	—	—	—	1	—	1	2	3	3	1	6	5	7	16	20	30	27
105—109	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	4	1	1	2	3	10	12
110—114	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	1

TABLE XX.   *The length of the vegetative period.   The F_3 generation*

	84 and below	86	88	90	92	94	96	98	100	102	104	106	108	110	112	114	116	118	120	122	124	126
Below 104	—	—	—	—	3	2	1	1	—	1	—	1	1	—	1	1	—	—	—	—	—	—
105—109	—	1	2	3	5	7	7	5	5	7	13	7	6	17	12	16	13	6	5	1	—	2
110—114	—	—	1	6	3	10	7	8	16	17	21	20	21	31	31	34	46	35	23	26	30	9
115—119	—	—	—	2	7	8	5	9	8	21	20	22	18	34	46	58	79	76	57	64	60	36
120—124	—	—	—	1	4	1	2	5	7	7	9	10	11	11	16	40	36	53	44	63	70	46
125—129	—	—	—	—	1	1	2	2	4	2	3	3	4	5	10	26	32	42	41	63	86	66
130—134	—	—	—	—	—	—	—	—	—	—	2	1	2	1	2	9	14	16	17	30	44	42
135—139	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	3	3	9	11
140—144	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	2	—	1	4	8	5	
145—149	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
150—154	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE XXI.   *The length of the vegetative period.   The F_3 generation*

	64	66	68	70	72	74	76	78	80	82	84	86	88	90	92	94	96	98	100	102	104	106
Below 80	—	—	—	1	—	1	1	2	3	1	—	—	—	—	—	—	—	—	—	—	—	—
80— 84	—	—	1	3	1	7	8	5	2	4	3	4	5	1	7	1	1	3	—	1	—	—
85— 89	—	1	1	1	2	6	11	17	24	18	19	16	18	15	13	22	13	14	8	8	3	2
90— 94	1	—	—	1	3	8	14	20	27	18	24	24	16	29	40	42	35	48	27	22	21	11
95— 99	—	—	—	—	1	—	7	6	13	4	6	14	9	17	19	35	24	33	26	26	18	14
100—104	—	—	1	—	1	1	3	2	5	4	9	5	6	3	11	14	25	30	17	22	19	21
105—109	1	—	—	—	—	—	—	—	2	1	4	1	6	5	4	14	11	15	17	13	11	
110—111	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	2	2	3	4	6
115—119	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	4	3

from the cross. Type 3 × Type 9. *Pot Series.*

102	104	106	108	110	112	114	116	118	120	122	124	126	128	130	132	134	136	Number of Parents	Average of Parents	Number of Offspring	Average of Offspring	Difference
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	106	20	79	− 27
6	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	33	112	512	83	− 29
12	13	3	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	37	116	691	87	− 29
56	26	30	16	12	5	5	2	3	1	—	—	—	—	—	—	—	—	40	123	942	92	− 31
63	37	46	33	16	12	5	3	4	4	2	1	—	—	2	—	—	—	43	125	815	97	− 28
13	9	20	12	11	8	6	3	1	3	—	2	1	1	—	—	—	—	14	136	212	102	− 31
4	17	21	7	14	5	3	1	—	2	—	2	—	1	—	1	—	—	6	137	109	106	− 31
—	1	1	—	—	1	1	—	2	1	1	—	—	—	—	1	—	—	2	127	11	111	− 16

from the cross. Type 3 × Type 9. *Pot Series.*

128	130	132	134	136	138	140	142	144	146	148	150	152	154	156	158	160	161 and over	Number of Parents	Average of Parents	Number of Offspring	Average of Offspring	Difference
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	117	12	101	− 16
—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	119	142	108	− 11
10	5	2	1	2	—	—	—	3	—	—	—	—	—	—	—	—	—	28	120	418	113	− 7
25	24	13	10	5	3	4	2	—	4	4	—	—	—	—	—	—	—	47	122	724	117	− 5
42	39	24	15	9	15	5	6	8	6	2	1	—	—	1	—	—	1	41	126	610	122	− 4
78	47	37	31	20	25	19	16	19	18	20	2	1	2	1	—	—	—	47	130	729	127	− 3
40	48	24	28	21	18	19	32	25	9	11	12	8	4	2	—	—	2	37	132	483	133	+ 1
10	11	8	5	5	9	7	9	8	7	7	3	—	5	2	1	1	2	9	139	127	136	− 3
5	9	12	14	6	7	9	10	10	12	11	10	6	11	4	2	5	7	12	142	171	141	− 1
—	2	1	1	—	—	2	7	4	1	2	3	2	2	—	—	2	—	4	137	31	147	+ 10
—	—	—	—	—	—	—	—	1	2	—	—	1	—	1	1	—	—	1	154	6	154	—

from the cross. Type 3 × Type 9. *Field Series.*

108	110	112	114	116	118	120	122	124	126	128	130	132	134	136	138	140	140 and over	Number of Parents	Average of Parents	Number of Offspring	Average of Offspring	Difference
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	111	9	77	− 34
—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	116	57	83	− 33
1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	115	234	87	− 28
8	7	1	3	—	—	1	—	—	—	—	—	—	—	—	—	—	—	33	124	451	92	− 32
4	10	1	6	3	2	3	2	1	—	—	1	1	—	—	—	—	—	20	124	306	97	− 27
12	13	9	7	3	1	8	3	1	1	5	1	—	—	—	—	—	1	20	129	264	102	− 27
11	7	8	6	7	4	5	6	2	5	3	2	3	—	—	—	—	4	14	130	178	107	− 23
2	3	2	7	4	4	2	4	—	2	2	3	1	1	—	—	—	—	5	138	57	112	− 26
1	1	1	—	3	1	3	—	2	1	—	3	—	1	—	—	—	—	2	140	25	115	− 26

TABLE XXII.

The interrelation between the length of the vegetative period and the type of branching. Type 3 · Type 4. Pot Series.

Number of days	10	20	30	40	50	60	70	80	90	Branching 2 day period	5 day period
Below 90	3	6	2	—	—	—	—	—	—	19	19
92	2	4	4	1	—	1	—	—	—	27	
94	—	8	4	1	—	—	—	—	—	24	26
95	2	1	10	2	—	—	—	—	—	32	——
96	—	—	3	1	—	—	—	—	—	—	
98	—	3	4	3	—	—	—	—	—	30	31
100	2	4	4	4	3	1	—	—	—	33	——
102	—	4	2	1	2	1	—	—	—	34	
104	2	3	4	5	2	—	—	—	—	31	34
105	1	3	5	2	4	2	—	—	—	36	
106	—	3	4	2	1	2	—	—	—	—	
108	2	5	12	5	4	—	—	—	—	31	33
110	—	3	4	3	1	1	—	—	—	34	——
112	1	4	7	11	3	—	1	—	—	36	
114	1	1	5	3	4	3	1	—	—	42	35
115	—	4	5	1	1	1	—	—	—	35	——
116	—	—	5	—	—	1	1	—	—	—	
118	—	1	8	11	5	3	4	1	—	45	41
120	—	—	6	12	3	2	2	—	—	43	——
122	—	4	4	7	7	4	4	1	—	46	
124	—	2	4	4	3	5	1	1	—	46	47
125	—	—	4	2	7	6	1	—	—	50	
126	—	1	5	6	4	2	7	2	—	—	
128	—	—	2	2	3	6	7	4	—	61	56
130	1	—	2	4	4	4	6	2	1	58	——
132	—	—	—	2	9	4	5	1	1	59	
134	—	—	—	—	2	2	7	2	—	67	62
135	—	—	—	1	2	1	2	—	1	64	
136	—	—	—	—	—	2	2	1	—	—	
138	—	—	1	1	—	1	1	1	—	56	64
140	—	—	—	—	—	2	1	—	1	70	
142	—	—	—	—	1	1	1	3	1	73	
144	—	—	—	—	1	3	—	—	1	64	65
145	—	1	—	—	—	1	1	4	—	65	
146	—	—	—	—	—	4	1	—	—	—	
148	—	—	—	—	—	1	1	3	—	71	68
150	—	—	—	—	—	2	1	1	—	67	
152	—	—	—	—	—	1	2	—	—	67	
154	—	—	—	—	1	—	2	1	—	67	66
155	—	—	—	—	—	1	—	—	—	75	
156	—	—	—	—	—	—	—	—	1	—	80
158	—	—	—	—	—	—	1	—	—	70	
Average period	102	106	111	116	121	126	130	135	147		

TABLE XXIII.

The interrelation between the length of the vegetative period and the type of branching. Type 3 × Type 4. Field Series.

Number of days	10	20	30	40	50	60	70	80	90	Branching 2 day period	Branching 5 day period
Below 65	—	1	—	—	—	—	—	—	—	15	20
66	1	—	—	—	—	—	—	—	—	—	
68	—	1	1	—	—	—	—	—	—	25	18
70	3	2	1	—	—	—	—	—	—	16	——
72	4	6	3	—	—	—	—	—	—	19	
74	7	11	2	—	1	—	—	—	—	19	19
75	7	15	1	2	—	—	—	—	—	20	——
76	10	17	8	2	—	—	—	—	—	—	
78	27	40	29	7	1	—	—	—	—	21	21
80	46	65	32	12	1	1	1	—	—	21	——
82	30	76	58	16	7	6	—	—	—	25	
84	24	59	44	16	9	6	2	—	—	27	26
85	6	25	25	13	2	1	—	—	—	32	——
86	3	19	18	15	4	6	5	2	—	—	
88	17	33	35	26	13	11	4	2	1	33	36
90	7	17	19	22	12	11	5	2	1	39	——
92	5	20	15	16	13	7	13	1	—	40	
94	5	16	20	15	10	10	6	1	—	38	39
95	3	6	11	8	4	7	4	—	—	41	——
96	3	7	16	12	13	8	3	2	1	—	
98	6	12	24	31	18	18	10	5	—	43	44
100	4	14	21	30	23	31	16	4	2	47	——
102	8	8	18	28	32	20	20	3	2	47	
104	5	9	10	34	25	25	9	1	3	46	49
105	—	2	5	5	8	10	4	1	2	50	——
106	4	2	3	7	9	11	5	1	—	—	
108	—	4	9	12	10	19	12	3	—	52	52
110	—	—	2	12	9	18	9	3	1	56	——
112	—	—	1	8	13	10	8	1	1	55	
114	1	1	—	4	5	12	7	2	—	56	55
115	—	—	—	4	1	3	1	—	—	52	——
116	—	—	—	—	2	—	1	—	—	—	
118	—	—	1	1	2	6	5	1	—	60	58
120	—	—	—	2	4	2	3	—	—	55	——
122	—	—	1	—	2	—	4	1	—	61	
124	—	—	—	1	1	4	2	1	—	61	61
125	—	—	—	1	—	—	2	—	—	55	——
126	—	—	—	—	—	—	—	1	—	—	
128	—	—	1	—	—	1	—	—	—	45	59
130	—	—	—	—	—	—	—	—	—	—	——
132	—	—	—	—	1	1	—	—	1	66	66
134	—	—	—	—	1	—	—	1	—	65	
Average period	83	84	88	94	98	100	101	104	104		

TABLE XXIV.

The interrelation between the length of the vegetative period and the type of branching. Type 3 × Type 9. Pot Series.

Number of days	10	20	30	40	50	60	70	80	90	Branching 2 day period	Branching 5 day period
Below 85	—	—	—	—	—	—	—	—	—	—	—
86	—	—	1	—	—	—	—	—	—	30	
88	—	—	—	—	—	—	—	—	—	—	26
90	—	5	4	1	—	—	—	—	—	26	
92	—	5	5	1	1	1	—	—	—	31	
94	—	8	10	3	—	1	—	—	—	29	29
95	—	2	4	—	—	—	—	—	—	25	
96	1	6	4	1	—	—	—	—	—	—	
98	—	7	9	8	—	1	—	—	—	32	31
100	—	12	6	8	3	2	—	—	—	33	
102	—	5	16	6	—	2	—	—	—	33	
104	—	9	15	8	5	1	—	—	—	33	33
105	—	3	6	3	1	—	—	—	—	31	
106	—	7	8	3	2	—	—	—	—	—	
108	1	8	16	3	5	—	—	—	—	31	32
110	—	12	24	21	2	2	—	—	—	33	
112	—	21	24	15	6	2	—	—	—	32	
114	—	15	28	15	18	4	—	—	—	36	35
115	1	6	22	21	13	1	—	—	—	37	
116	1	7	17	26	4	5	—	—	—	—	
118	2	18	38	41	22	15	2	—	—	39	39
120	1	10	27	29	23	6	3	1	—	40	
122	—	13	17	36	27	13	4	2	—	45	
124	1	10	27	31	36	20	1	1	—	42	45
125	1	1	7	18	27	18	7	1	—	50	
126	—	1	5	7	14	16	5	—	—	—	
128	—	5	10	11	21	22	10	3	—	51	52
130	—	2	7	10	18	34	12	5	—	55	
132	—	1	5	15	11	19	13	2	—	53	
134	—	—	3	4	13	21	7	3	—	57	55
135	—	—	3	2	4	5	6	—	—	57	
136	—	—	1	2	3	6	7	1	—	—	
138	—	—	2	6	2	11	8	3	—	59	60
140	—	—	1	3	4	11	10	3	—	61	
142	—	—	1	4	5	10	9	1	—	58	
144	—	1	1	3	11	11	20	5	—	61	60
145	—	—	2	—	—	3	6	1	—	64	
146	—	—	—	1	3	6	5	5	—	—	
148	—	—	2	4	2	8	9	8	—	63	64
150	—	—	1	—	4	7	7	7	—	65	
152	—	—	—	—	1	4	8	7	—	70	
154	—	—	—	—	1	4	4	4	—	68	70
155	—	—	—	—	—	1	1	1	—	64	
156	—	—	—	—	1	3	1	—	—	—	
158	—	—	—	—	—	—	2	2	—	75	67
160	—	—	—	—	—	1	—	1	—	70	
162	—	—	—	—	—	—	—	2	—	80	
164	—	—	—	—	—	—	—	—	—	—	75
165	—	—	—	—	—	—	4	3	—	74	
Average period	116	110	113	118	123	129	137	144	—		

TABLE XXV.

The interrelation between the length of the vegetative period and the type of branching. Type 3 · Type 9. Field Series.

Number of days	10	20	30	40	50	60	70	80	90	Branching 2 day period	5 day period
Below 65	—	—	—	—	—	1	—	—	—	—	—
66	—	—	—	—	—	—	—	—	—	—	
68	1	1	—	—	—	—	—	—	—	15	24
70	—	3	1	—	1	—	—	—	—	29	—
72	1	2	3	—	—	—	—	—	—	20	
74	1	6	3	2	—	—	—	—	—	25	26
75	2	7	2	7	—	—	—	—	—	27	—
76	—	9	6	9	—	—	—	—	—	—	
78	6	11	14	16	1	—	—	—	—	29	27
80	9	17	21	7	2	1	—	—	—	27	—
82	7	18	15	7	2	3	—	—	—	28	
84	1	16	14	5	3	1	—	—	—	29	29
85	—	7	12	7	3	—	—	—	—	32	—
86	1	9	12	7	3	1	—	—	—	—	
88	1	6	12	16	5	1	1	—	—	36	33
90	2	15	15	9	3	3	—	—	—	31	—
92	1	10	19	14	13	3	—	—	—	36	
94	1	12	22	20	11	9	—	—	—	37	38
95	—	3	12	17	10	5	2	—	—	39	—
96	4	4	8	8	4	3	—	—	—	—	
98	2	12	12	30	26	12	1	—	—	41	41
100	1	6	10	17	15	7	5	—	—	43	—
102	1	5	9	20	15	13	2	—	—	44	
104	1	5	12	11	13	12	3	—	—	44	44
105	—	1	2	5	3	3	1	—	—	44	—
106	—	1	2	3	3	7	—	—	—	—	
108	—	—	1	11	9	10	3	—	—	51	48
110	—	1	—	8	5	10	1	—	—	50	—
112	—	—	—	4	5	4	2	1	—	54	
114	—	—	—	5	6	5	3	1	—	54	54
115	—	—	—	1	1	1	1	—	—	58	—
116	—	—	—	1	1	1	3	—	—	—	
118	—	—	1	2	3	3	2	—	—	53	53
120	—	1	1	3	—	1	1	1	—	47	—
122	—	—	—	3	1	3	4	—	—	57	
124	—	—	—	2	—	2	—	—	—	50	53
125	—	—	—	—	—	—	—	—	—	65	—
126	—	—	—	—	—	1	1	—	—	—	
128	—	—	—	—	1	1	2	1	—	66	67
130	—	—	—	—	—	2	3	—	—	66	—
132	—	—	1	—	—	1	4	1	—	64	67
134	—	—	—	—	—	—	1	—	—	70	
Over 135	—	—	—	—	1	2	—	—	—	—	
136	—	—	—	—	—	—	—	—	—	—	
138	—	—	—	—	—	—	—	—	—	—	
140	—	—	—	—	—	—	—	—	—	—	
Average period	85	86	89	95	98	104	113	121	—		

TABLE XXVI.

The relation between the length of the vegetative period of the F_1 generation of a cross and those of the parents.

Monopodial Parent		Sympodial Parent		Mean of Parents	F_1 generation			
Type	Days	Type	Days		Maximum	Minimum	Mean	Difference
Type 3	116	Type 4	83	114	108	80	94	20
,, 3	116	,, 5	80	113	111	77	98	15
,, 3	146	,, 8	78	112	118	82	96	16
,, 3	146	,, 9	94	120	123	88	105	15
,, 3	146	,, 7	62	104	78	93	86	18

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TABLE XXVII.

The leaf glands. F_1 and F_2 generations of the cross.   Type 3 (leaf glands 3—1) × Type 4 (leaf glands 0).

Leaf glands 3—1......Leaf gland 0
F_1 15 plants .... Leaf gland 1—3

F_2	Leaf glands ...		0	1—3	3—1	Total glandular
	Number of individual	.	68	113	100	213
	Ratio	. .	1	1·7	1·5	3·1
	Used as parents	...	64	107	90	197

		Pure	Impure	Pure	Impure	Pure	Impure
		60	4	2	105	38	52

	Corrected distribution	...	62	161	38	201
	Expectation ...	...	65	130	65	195

TABLE XXVIII.

The leaf glands. The F_3 generation of the cross. Type 3 × Type 4.

| Character of F_2 parent | No of plants | Leaf glands | | | Total glan-dular | Total F_3 indivi-duals | Expecta-tion | Character of F_3 offspring |
		0	1—3	3—1				
	60	1381	—	—	—	1381	—	Leaf glands 0
Leaf glands 0	1	8	4	0	—	—	—	
	1	4	2	1	—	—	—	
	1	32	0	1	—	818	872	Leaf glands 0
	1	18	1	0	—	—	—	
	4	62	7	2				
Leaf glands 1—3	1	—	23	—	—	—	—	
	1	—	6	—	—	1080	1744	Leaf glands 1—3
	2	—	29	—	—	—	—	
	105	557	822	899	1712	—	—	
Expectation ...	—	567	1131	567	1701	—	—	
Leaf glands 3—1	52	199	222	690	912	1591	872	Leaf glands 3—1
Expectation ...	—	278	556	278	834	—	—	
	38	—	—	679	—	679	—	Leaf glands 3—1

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TABLE XXIX.   *Correlation between the presence of the red*

Flower colour	Leaf colour	92	94	96	98	100	102	104	106	108	110	112	114	116	118	120
Type 3 × Type 4																
Pure forms																
Red on Yellow	lamina	—	—	—	—	—	—	—	—	—	1	—	3	4	6	4
Yellow	green	—	—	—	—	—	—	4	4	12	20	6	5	5	—	1
Impure forms																
{Red on yellow	lamina	—	—	—	—	—	—	1	—	—	3	1	2	3	10	12
{Yellow	green	1	1	1	—	4	3	—	5	11	9	15	11	18	11	4
Type 3 × Type 9																
Pure forms																
Red on yellow	lamina	—	—	—	—	—	—	—	—	—	—	—	—	—	2	1
Red on white	lamina	—	—	—	—	—	—	—	—	—	—	—	1	1	1	—
Yellow	green	—	—	—	—	—	—	—	—	—	1	2	1	3	3	1
White	green	—	—	—	—	—	1	—	1	—	2	2	—	4	3	1
(a) In one character only.																
Impure forms																
{Red on yellow	lamina	—	—	—	—	—	—	—	—	—	—	—	—	1	5	—
{Red on white	lamina	—	—	—	—	—	—	—	—	1	—	—	1	—	2	—
{Red on yellow	lamina	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—
{Yellow	green	—	—	—	—	—	1	—	—	1	2	—	1	3	1	—
{Red on white	lamina	—	—	—	—	—	—	—	—	1	—	1	1	2	—	2
{White	green	—	—	—	—	—	1	—	1	1	—	3	2	2	—	—
(b) In both characters.																
Red on yellow	lamina	—	—	—	—	—	—	—	—	—	—	1	3	2	2	2
Red on white	lamina	—	—	—	—	—	—	—	—	—	2	2	1	1	3	3
Yellow	green	—	—	—	—	—	2	2	1	8	2	6	5	2	5	1
White	green	—	—	—	—	3	2	—	2	5	1	3	4	1	—	1

colouring matter of the sap and a lengthened vegetative period.

122	124	126	128	130	132	134	136	138	140	142	144	146	148	150	152	154	156	158	160	Average
6	7	7	5	4	3	4	4	1	1	—	—	—	—	—	—	—	—	—	—	124
3	2	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	111
11	11	7	8	15	8	7	4	2	1	1	—	—	—	—	—	—	—	—	—	125
4	3	—	2	2	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	113
1	1	2	—	—	1	3	1	—	—	1	1	—	—	—	—	—	—	—	—	131
—	—	1	2	1	4	1	—	1	—	—	—	1	—	—	—	1	—	—	—	129
—	1	3	—	2	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	119
2	2	1	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	117
1	—	3	1	4	4	2	3	—	—	5	1	—	1	—	—	—	—	—	—	131
—	1	4	4	2	2	4	1	3	—	3	2	1	—	—	—	—	—	—	—	132
1	1	—	2	2	2	2	—	—	1	1	1	1	1	—	—	—	—	—	—	133
1	3	1	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	120
3	1	2	1	1	2	1	1	—	—	—	—	—	—	—	—	—	1	—	—	124
4	2	2	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	119
6	4	4	5	2	2	6	—	—	1	2	—	—	—	—	—	—	—	—	—	125
1	3	1	2	3	2	—	—	1	—	1	1	—	1	—	—	—	—	—	—	125
1	3	2	2	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	114
3	—	3	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	113

PLATE XXXV.

EXPLANATION OF FIGURES.

Petal Colours—Cross Type 3 × Type 9.

1.   Parent-Type 3.
2.   Parent-Type 9.
3. F_1 generation of cross.
4—9. F_2 generation of cross.
4.   Full red form—pure or giving 4 and 6.
5.   Impure red form—giving 4, 5 and 8 or 4, 5, 6, 7, 8 and 9.
6.   Pure red on white form—giving 6 only.
7.   Impure red on white form—giving 6, 7 and 9.
8.   Yellow form—pure or giving 8 and 9.
9.   Pure white form—giving 9 only.

HEREDITY AND THE JEW.

By REDCLIFFE N. SALAMAN, M.D.

THE object of this paper is to lay before Anthropologists some results in the domain of Ethnology which, though arrived at by methods as yet foreign to anthropological research, promise a rich harvest in every direction. Mendelian methods, by which is meant the analytical observation of specific characters in the individuals and their occurrence in the immediate offspring, have for the last decade been the all-powerful weapons of the modern student of heredity. To the Botanist and Zoologist who can plan his experiments as he will, the results have been immediate and surpassingly important. To the student of mankind, whether he be the anthropologist or the medical man, the application of the method is of necessity limited. It is impossible to frame his experiments according to design and it remains with the enquirer to search out from the confused mass of facts those which conform most nearly to the requirements of an experiment.

Painstaking collections of family histories and pedigrees have already shown that in man several abnormal conditions behave as unit characters. A classic example is that of Brachydactylism(5) in which the deformed hand condition is dominant to the normal. The principles which underlie Mendelian research are well known and need no repetition here. So far this type of research has hardly been applied to man except with respect to diseased or abnormal conditions of one sort or another. Some opponents of Mendelism have directed their criticism to the fact that when black mates with white in man, the offspring is a blend, and in future generations complete segregation does not occur. From this observation some have gone further and implied that to so complex and withal hybrid an animal as man, such crude principles as those of Mendelism could not be expected to hold good. The work of G. C. Davenport and C. B. Davenport(4) on the mating of negroes and whites shows that the problem is by no means

hopeless, and that the apparent absence of segregation on Mendelian lines is due to the fact that the difference between black and white is a matter not of one factor but probably of a series of distinct colour factors. Thus if it be assumed that the colour of the negro differed by four such positive characters from that of the white and that each of these in an ascending order were dominant to the one below, then the children belonging to the F_2 generation, that is, the grandchildren of the original cross, would only show one white-skinned individual in every 256; whilst if the number of intervening factors instead of being four were six, then a purely white individual would be expected to occur once only out of 4096 grandchildren. One feature examined by Hurst(7) gave consistent and valuable results, viz. eye colour. He clearly showed that eye colour might be of two kinds, that in which both surfaces of the iris were pigmented, the other in which only one surface was. The latter condition is recessive and gives rise to the true blue eye of the anthropologist. Where the dominant character is present the eyes are of various shades of brown or of green. The independence of this character in segregation is of the greatest importance when one considers how some anthropologists have talked of a blue-eyed, fair-haired, long-headed race as if it were an impregnable complex and not a synthetic accident. The further such researches as Hurst's can be carried into the heredity of individual features, the clearer will become our notions of racial types. The facts I am about to describe in relation to the Jews will, I think, bring this point out in a clearer light.

The racial position of the Jew has engaged the attention of all modern ethnologists. The problem is extremely difficult because, on the one hand, we have the oft asserted and by no means easily disproved statement of the Jews themselves that they are pure Semites, whilst observers such as Ripley, von Luschan and others, point out that the Jew of to-day has no uniform cranial characters, that on the whole he is decidedly brachycephalic, whilst the typical Semite such as the Bedawyn is essentially dolichocephalic.

Judt(10), whilst regarding the Jews as belonging to one type although with variations, is assured that they cannot be designated Semites on account of the prevalent brachycephaly.

Renan concluded that religion was the one bond of the Jews, and that there was no single but several Jewish types. Most authorities are at least agreed that the Jews up to the time of the destruction had freely intermarried with the surrounding people, and the Biblical

evidence supports this view. The words of Ezekiel—"Thy father was an Amorite and thy mother a Hittite"—were not said merely in scorn. There seems no reason to doubt that the original band of Abrahamites, themselves of the same Semitic stock as the Assyrians, had mixed during all the Biblical period with at least three different racial groups, with the native Semitic Canaanitish tribes similar to themselves, with the Hittites, and with the Amorites. The Hittites, of whom several conventionalised representations in Assyrian and Egyptian sculpture exist, are now considered to be practically identical with the present-day Armenians, the highly brachycephalic people who possess the so-called Jewish nose. Of the Amorites very little is known, but it is generally stated that they were a long-headed blonde race. It is quite possible that they were blonde and it is not at all improbable that the Amorites, like the Philistines, were non-Semitic and related to the Central European people. It is to the Amorites that the constant occurrence of blondeness amongst Jews is by most authors ascribed and the Pan-Germanic school go so far as to identify the Amorites with the Nordic race. This latter theory, fanciful at the best, is, as I hope to show, entirely repudiated by the observations I shall soon detail.

After the destruction of Jerusalem the Jews gradually spread throughout Europe and the north coast of Africa. In Egypt, Jewish colonies had existed for hundreds of years prior to this, and small outlying groups were doubtless settled elsewhere, but the penetration of Europe by Jews in any quantity began from the second century. It is not necessary here to follow in any detail the paths of their migrations. It should however be noted that from a very early date the division amongst the Jews into those of the African and Mediterranean Littoral, including the Iberian Peninsula on the one hand, and those of Central Europe on the other, was established. The former group are known as Sephardim, the latter as Ashkenazim.

The general type of face amongst the Sephardim is somewhat different to that commonly met amongst the Ashkenazim. The colouring is more uniformly dark, the nose less frequently characteristic. They resemble more closely the Southern European peoples. Notwithstanding this, the great majority may be always recognised as Jews by their appearance, whilst one frequently meets amongst purely Sephardic families individuals who are in no way different from their Ashkenazic brethren.

The Sephardim are often described as being the aristocrats of the race and of a finer and more delicate type and purer blood. Whether

the Sephardic community represents the aristocracy or not, depends upon what one means by the term. If by aristocracy is meant a dominating class of the same stock, or a conquering invading people, then the Sephardim hold, in respect to the Ashkenazim, no position as aristocrats. If, by aristocrats, a class is meant which has, so to speak, precipitated itself from out of the body of the general people by reason of superior mental or physical attainment, then again the Sephardim fail to establish their claim as aristocrats because, since the dispersion, the two sects have never lived in that close communion in which such precipitation could occur. On the contrary, the two classes have held themselves rigidly apart up to the last fifty years or so. The original distinction between the two groups would seem to have been essentially geographical. During the Middle Ages the Sephardic Jews lived under far better conditions than their Ashkenazic brethren in Europe, and in that way they were brought into much more intimate contact with general culture than the Ashkenazim who were thrown on their own resources. In this sense, therefore, the Sephardim may be considered aristocrats.

In point of view of the purity, that is to say the absence of mixture with outside blood, during the last 1800 years, there is no doubt that the Ashkenazim can show a far cleaner bill than the Sephardim who are known to have absorbed in no small quantity both Moorish and Iberian blood, so that the boast of blue-bloodedness comes to have a meaning other than that generally assumed.

The composite nature of the Jew as he left Palestine has already been stated and the question at once arises, was this complexity increased by intermarriage with European races during his wanderings? Many authorities, and recently more especially Fischberg(6), have argued that the Jew has absorbed, during the last two thousand years, blood from all the European stocks. Ripley is assured of it. Whilst it is obviously impossible to prove that there has been no intermixture during the last eighteen hundred years, yet it is, I think, more than probable that that intermixture has been absolutely minimal. The historic evidence is naturally incomplete on either side. Those who think the intermixture was important in quantity point out the well-known fact of the conversion to Judaism of considerable numbers in Rome, but they forget that it was these very Judaised Romans who were the early Christians. Then one is reminded that in the eighth century the kingdom of the Kozars in South Russia was converted to Judaism. This is true, but as Zollschan points out, all we know is,

that the King and his immediate court were converted; and according to Joseph Jacobs after the destruction of the Kozar Empire it was the Jews of that district who formed the Karaite sect, and this sect has remained absolutely distinct from the rest of the European Jews. A further wholesale conversion is that of the Falashas, an Abyssinian negroid people, of whom we shall have a little to say later. They do not, however, in any way affect the question of the purity of the present-day European Jews as there is no communion whatever between them.

When one considers the melancholy condition of the Jews in Central Europe throughout the entire Middle Ages, how they were despised and despoiled in every land, is it likely that any Gentile, much less any number, would willingly seek admission into their flock, especially when one remembers that the entry of the male Gentile necessitates the Abrahamic covenant? It might be thought that with the Renaissance and the spread of culture, the opportunity had arisen for a greater intimacy between the Jews and their Gentile brethren, but so far was this from being the case that it was now that the greatest paradox in history took place. To the Gentile, the period of the Renaissance brought culture and freedom of thought, to the Jew it brought the Ghetto and the bondage of the Rabbi. The Ghetto walls acted as an impenetrable barrier between Jew and Gentile up to the time of Napoleon, who was the first in Western Europe to break them down. In Galicia and Russia, where still the majority of Jews live, the Ghetto life—none the less real though the walls are gone—still exists. During the last two or three generations intermarriage has taken place and become increasingly common in Western Europe, but it has little bearing on our problem. The offspring of the intermarried in the great majority of cases, passes over to the Gentile population, whilst those that retain their connection with the Jewish community are cognisant of their origin. It would be possible to follow this question in far greater detail but I do not think that it would serve any useful end. All the historic evidence would seem to bear out the contention that from the second century till at least the beginning of the nineteenth, the Jewish people (Ashkenazim) in Europe absorbed into their own midst practically no blood from the races with whom they came in contact. At the same time it is known that a leakage, varying in degree, of Jewish blood to the outside was always taking place, and this loss occurred then as now, at such points on the periphery where the community came into the most intimate contact with the outside world.

Ethnologists may be said to agree that the Jew is not racially pure, but on the other hand they have to admit that the Jews constitute a definite people in something more than a political sense, and that they possess though not a uniform, still a distinguishing type.

Nothing is more confusing than the varied accounts of the shapes of head, nose, eyes, and colour of the hair of Jews in different countries, and if one's only acquaintance with Jews were through the literature of anthropology one would be inclined to think that the "chosen people" had no existence apart from books, and the imagination of the anti-Semites. It is with no small degree of comfort therefore, that one finds Ripley(12)[1] making the following statement. "Who has not, on the other hand, acquired a distinct concept of a Jewish face and of a distinctly Jewish type? Could such a patent fact escape observation for a minute?" Again Weissenberg(14) says "The Jew in an anthropological sense forms no specific type, but the facial expression is absolutely characteristic." Fischberg is not so whole hearted as to the general occurrence of this characteristic facial expression but he does recognise it and considers it not strictly a physical trait but rather an expression of the soul. Others will tell us that this Jewish expression, so impossible to define, is merely an emblem of the ceaseless wanderings and the countless agonies of the Jew—of the *tausend-jährigen Schmerz*, as Heine calls it. Others again tell us it exists because the Jew is landless, and if only he were once more back in his native land the facial type would vanish. All, however, practically agree that whether blonde or dark, tall or short, long headed or round headed, the Jew is a Jew because he looks like one. The peculiar facial expression is at least not the outcome of recent times. We have evidence of the greatest antiquity. In the Assyrian sculptures, 800 B.C., are depicted Jewish prisoners who are thoroughly Jewish (Pl. XXXVI. and Pl. XXXVII. fig. 1) and Petrie(11) has brought home from Memphis terra-cotta heads dating 500 B.C. of Jews at once recognisable by their Jewishness. On a forest roll of the pre-expulsion times in England, is a pen and ink sketch, or one might rather say a caricature of a certain Aaron, "Son of the Devil," dated 1277 which, crude though it is, hits off a distinctly Jewish type (Pl. XXXVII. fig. 2). The great master Rembrandt has given us numerous drawings of Jews. He was mainly attracted by the Sephardic Jews, but whatever the shape of their face may be, the curious expression that we recognise as Jewish, never escaped the artist. More interesting than the examples given of the persistence of this facial expression

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[1] *Loc. cit.* p. 399.

is the fact that the Samaritans of to-day who live in the land of their fore-fathers, have an unmistakable Jewish expression, and this though their heads are dolichocephalic and those of the majority of Jews brachycephalic.

At this point one might with advantage consider the relation which the existence of the *Kohanim* has to the question of Jewish type. The *Kohanim* are the traditional descendants of the tribe of Aaron. There is, of course, no written record of such descent, but the hall-mark, as a rule, is shown by the name of Cohen or some modification of it. It is not at all unusual, however, to find people not possessed of the name of Cohen, who are still *Kohanim*. It is most improbable that anyone could, and much less would, assume the title of *Kohen* without having a right by birth because it conveys neither social distinction nor advantage, whilst on the other hand, it brings in its train some un-doubted disabilities, the chief of which directly concerns us and is, that no Kohen, according to Jewish law, can marry a stranger, a proselyte or the daughter of a proselyte, or a divorcée: so that we have a sect whose descent may be regarded as strictly Jewish. If now we review the physiognomies of the various *Kohanim*, it will be found that they exhibit no type in any way distinct from that of other Jews. Every phase of Jewish bodily form will find its representative amongst the *Kohanim*, so that one is inclined very much to the view that whatever value may be ascribed, and I personally think a very high one may be, to the purity of descent of the *Kohanim* during the last 2000 years, practically the same value may be ascribed to their brethren amongst whom they live.

What the elements are which go to make up the expression of a face that is at once so elusive of description and yet so characteristic, it is difficult to say. The nose is often peculiar, not because of its length or even its convexity which may be often outdone in non-Jews, but by the heavy development of the nostrils. Jacobs has described this "nostrility" and has most aptly compared the Jewish nose to the figure six with a long tail. Remove the tail, he says, and the Jewishness will disappear. The eyes are generally elongated, and a fairly character-istic feature is the length of the upper eyelid. The face which exhibits the expression of Jewishness is never of the angular type with square jaw, a type which is indeed extremely rare amongst Jews. Far more usual is it to find rounded features, long sloping jaw, fairly developed chin which is round and not square, a good-sized forehead devoid of that angularity in the region of the temples which is not

uncommon amongst Teutonic people. However it may be brought about, there is no doubt that the character of Jewishness is a real one. Weissenberg(15) relates that he put several hundred photographs of Russians and Russian-Jews without peculiar dress or other distinguishing feature before two scientific friends, one a Jew, the other a native Russian. His Jewish friend picked out 70 $\%$ of the Jewish subjects correctly and the Russian 50 $\%$. If so high a percentage of Jews could be identified by their looks alone in a photograph it is not surprising that the opinion is current that the Jew may be recognised wherever he goes. Notwithstanding the fact that the great majority of Jews look Jewish, it cannot be denied that one meets, not rarely, individuals, perhaps more often men than women, who do not exhibit this type and who are either indistinguishable or at least practically indistinguishable from North Europeans. It is relying on these apparently non-Jewish faces, that Fischberg and others have rashly assumed that they are the direct results of mixture with the surrounding people. I think I shall be able to offer some evidence which will show that this view is untenable.

Impressed with the great frequency and the distinctiveness of the Jewish type of face, it occurred to me that this character might form excellent material for research on Mendelian lines. Intermarriage to-day with the English is very common in Anglo-Jewry, and one had only to follow out such cases of mixed marriage to obtain results comparable to those the genetic student has been obtaining in plants and animals. My method has been to collect personally, as far as possible, all cases of mixed marriage and to obtain the assistance of those on whom I could rely, and whose duty it was merely to state whether they considered the children of the mixed marriages of their acquaintance as Jewish or Gentile in appearance. Most of my observers were quite ignorant of the purpose of my examination and of the results I expected, whilst none were conversant with Mendelian or other theories of heredity. All who have assisted me have been themselves Jews and I have noted a distinct tendency on their part to claim, wherever possible, a Jewish type of face for the children they have examined, and although, as I shall show, the results are entirely in the opposite direction, yet what error there is, is distinctly towards increasing the number of supposed Jewish faces in the offspring of mixed marriage. Wherever possible, I have seen the children myself or have obtained photographs, but in at least half of them, I have had to rely on others. In doing so I have been rather encouraged than

otherwise by finding that the bias of my assistants has been always against the results which they, to their own surprise, have found. In all cases the Jew is of the Ashkenazic section and the Gentile is either a native of England or Northern Europe.

Briefly, the results of the intermarriage of Jew and Gentile may be stated thus (Table I).

TABLE I.

First Generation.

Number of Families	Father	Mother	Children		
			Gentile	Jew	Intermediate
50	Gentile	Jewess	88	15	4
86	Jew	Gentile	240	11	4
Total 136	—	—	328	26	8

In 50 families where the father was Gentile and the mother a Jewess, there were 88 Gentile-looking children, 15 Jewish, and 4 intermediate in type. In 86 families where the father was Jewish and the mother Gentile, there were 240 Gentile-looking children, 11 Jewish, and 4 intermediate. In both cases the intermediates are practically Gentile-looking. Adding the two classes together we find that there are 336 Gentile children to 26 Jewish, *i.e.* 13 Gentile to 1 Jewish. The result is a surprise to both the anthropologist and to the Mendelian. To the former who looks for blending, we have the fact that so far from blending, we have no less than 93 $\%$ of the mixed bred offspring resembling one parent only. To the Mendelian some surprise must occur, that the dominance is not absolute, but this is, to a slight extent, due to the Jewish bias in the observations, and to a much greater extent, to a Jewish permeation of the English people in certain localised districts which is much more prevalent than is generally suspected. I have, whilst making these observations, come across certain cases where I was assured that in a certain family the father was a Jew, the mother a Gentile. In one such I examined the children carefully and found that two were without doubt Gentile in appearance whilst one was equally without doubt Jewish. I then discussed the family history with the parents and I was able to obtain the pedigree shown in fig. 1 which at once explains the occurrence of the Jewish child. In another case I found a very similar state of affairs but I was unable to trace it further as the non-Jewish parent objected to elucidate the Jewish blood in her grandparent which she, however, admitted. In a third and fourth case where complete dominance was expected but not obtained, I have reason to believe that it will be discovered that the Gentile parent has Jewish ancestors.

In determining the nature of so complex a character as the facial
expression, the personal equation of the observer must play an important
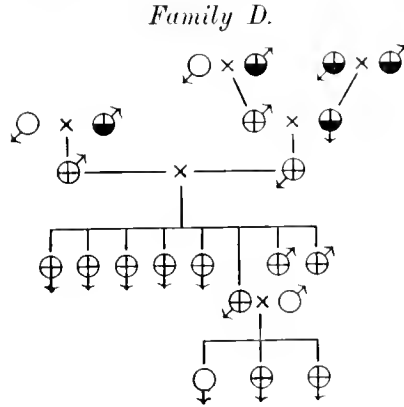part.   I have in some cases found that observers not specially acquainted

Family D.

Fig. 1.

○ = Jewish appearance.
⊕ = Gentile appearance.
⬤ = Gentile appearance and birth.

with the subject, although agreeing that a given individual of the first
generation is of Gentile appearance have yet felt that there was
somewhere lurking in the face an expression which suggested " Jewish-
ness " and there is very little doubt that such opinion may often be
well founded.   I have myself come across a few cases where without
doubt the recessive Jewish facial expression has come to the surface as
the individual grew older.   One case was particularly apparent.   The
parents were characteristically Jewish and non-Jewish respectively,
there was a large family of which I saw one personally and the
remainder in photographs.   Most of them were, to my mind, not Jewish
at all, but the one whom I was interviewing, though not in any way
strikingly Jewish, would probably have been recognised by many people
as such.   His age was about 45 and he assured me, and his assurance
was confirmed by his wife, that when he was a young man he was never
by any chance recognised as a Jew in public.   This same individual
has married a Gentile and has three children who are, I think, without
doubt totally non-Jewish in appearance.   It is not without surprise
that one finds that very many of the leading families of this country as
given in Burke, contain Jewish blood and I know of at least one case
where two parents, neither Jewish in appearance, have a daughter who

is typically Jewish. A reference to Burke showed that in the family
tree of both parents was Jewish blood.

To obtain portraits of families for the purpose of exhibition has
been a most difficult matter, but I am able to show in Plates XXXVIII.
and XXXIX. a few examples.

To the student of heredity, the phenomenon of dominance is, after
all, a matter of secondary importance. The vital question that he has
to deal with is, whether the character in question is one which
segregates or not, *i.e.* when in an individual the character and its
opposite are both present, are these two opposite characters represented
together in the sex cells or gametes, or does one go to one gamete and
the other to another? Two methods are open to us in testing this
question, one to observe the matings of the hybrid individual with
those possessing recessive character only, the other to observe the
matings of such hybrid individuals with each other. Of the matings
of hybrid with hybrid I have not found a single example. This is
hardly surprising when one considers the vastly greater choice the
hybrid has of finding his mate either in the Jewish community or
in the outside world. Of matings between hybrid and Jew I have
9 families where the Jew is the father and the hybrid the mother,
giving rise to 25 children, 13 of whom are undoubtedly Gentile and 12
are unequivocally Jewish.   4 families where the father is hybrid and
the mother Jewish, contain 7 children of which 2 are Gentile and
5 are Jewish. Taking the families together their offspring consist of
15 Gentile and 17 Jewish children, the Mendelian expectation being
equality.   Besides these matings, I have been able to collect a certain

TABLE II.

Hybrid and Jew.

Number of Families	Father	Mother	Children	
			Gentile	Jew
9	Jew	Hybrid	13	12
	,,	,,		
4	Hybrid	Jew	2	5
Total 13	—	—	15	17

number of families where a hybrid has married a Gentile. In 4 the
father is hybrid, the mother Gentile, with 8 offspring all Gentile in
appearance. In one the mother is hybrid and father Gentile with 3
Gentile offspring (cf. Table III). I have indirect knowledge of several
other families comprising a large number of children all of whom are

said to be Gentile in appearance, but I have not included them as the observations were not sufficiently reliable.

TABLE III.

Second Generation.

Number of Families	Father	Mother	Children	
			Gentile	Jew
	Gentile	Hybrid		
1	,,	,,	3	—
4	Hybrid	Gentile	8	—
Total 5	—	—	11	—

In figs. 2, 3, 4, and 5 are given further pedigrees showing the results of the matings of hybrid individuals with Jews and Gentiles respectively.
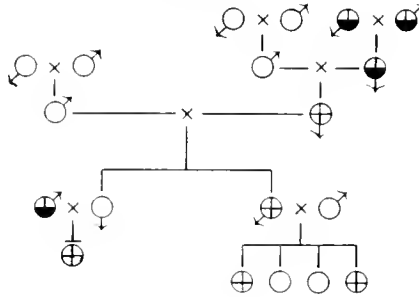
*Family **A**.*

Fig. 2.

Family B.

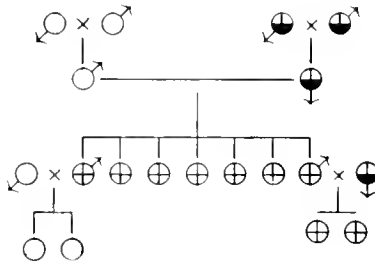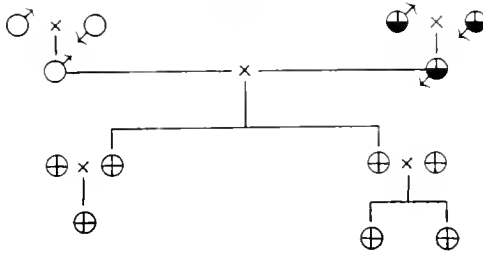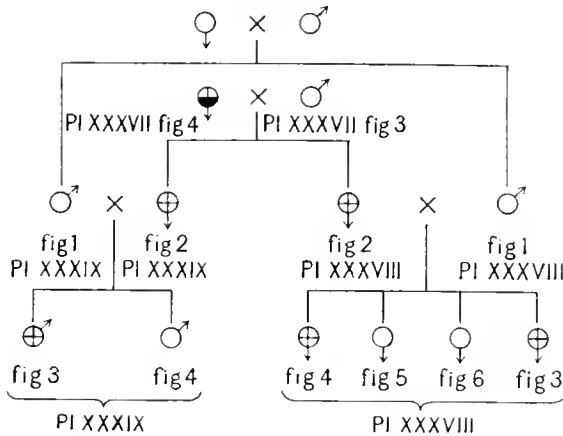Fig. 3.

Family C.

Fig. 4.

Family E.

Fig. 5.

○ = Jewish appearance.
⊕ = Gentile appearance.
◕ = Gentile appearance and birth.

The conclusion to which these results inevitably lead is that the Jewish facial type, whether it be considered to rest on a gross anatomical basis, or whether it be regarded as the reflection in the facial musculature of a peculiar psychical state, is a character which is subject to the Mendelian law of Heredity.

With the knowledge gained from these observations one can now understand the somewhat conflicting reports that travellers and others have given of those outlying Jewish communities which are found on the Malabar coast where they are known as the Beni-Israel; in China where they are known to the Chinese as the " people who remove

the sinew of the leg"; in Abyssinia where they are known as the Falashas, and in Jamaica and the West Indies. The Beni-Israel of India have been settled in India at any rate since 1400 of the present era, but traditionally from pre-exilic times. They are essentially a black people quite unlike the European Jew. They have always been looked down on by their white brethren in India and they have lived as the natives amongst whom they dwell, and with whom there is little doubt they have freely mixed. In the description of them given by Fischberg, he agrees that they are non-Jewish looking and dark skinned; he remarks, however, that every now and again a practically ordinary white skinned individual with Jewish features occurs amongst them. If, as is probable, the Jewish facial features are recessive to the native, then it is only what one should expect to find that the great majority of this isolated community are native-looking and that an occasional recessive should crop out from the mating of two hybrids.

The Chinese Jews are an even more isolated group who probably reached China through India, possibly a thousand years ago, but traditionally at a far earlier date. I have only seen photographs of these so-called Jews, in which they are typically Chinese in appearance, even as regards the eye shape[1]. The Chinese Jews have lost practically all knowledge of the tenets of Judaism and there is but little doubt that the Jewish facial type has been swamped by the Chinese.

The Falashas of Abyssinia are simply negroid. Some doubt whether they had at any time any Jewish blood or whether they were not merely converts by Jewish missionaries. Faitlovitch, who has spent many years amongst the Falashas, whilst admitting that they are not Jewish in appearance but on the other hand closely resemble the neighbouring black peoples, assures me that it is his belief that originally and at a very early period a considerable body of Palestinian Jews did settle in Abyssinia. The Jewish settlers freely intermarried with the natives at first, but during the last two hundred years they have become isolated. If the origin of the Falashas is such, then the swamping of the Jewish type of facial expression is only what would be expected when a recessive character is introduced into a community of dominants.

In Jamaica and the West Indies Jews, from the 17th century and onward, have played a very important part as traders and settlers.

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[1] Dr C. G. Seligmann informs me that in a number of crosses occurring in Australasia and the east, whether between Chinese and White, Malay and Melanesian, or Malay and White, the peculiar Mongolian eye with its epicanthus is always dominant. This fact is amply borne out in the photographs of the hybrids which he has shown me.

These Jewish settlers employed negro slaves, with a result that a number of their illegitimate children have founded families bearing Biblical names but negroid features.

It has already been noted that amongst the Ashkenazic Jews in England and elsewhere, one does meet with individuals who have not
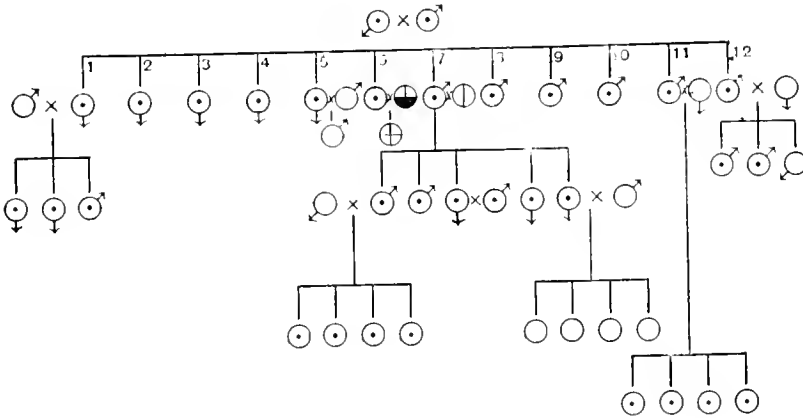

Fig. 6.

⊙ = Exaggerated Jewish type with long nose.
◯ = Jewish type—readily recognisable but not exaggerated.
◕ = Gentile appearance and birth.
⊕ = Gentile appearance, mixed Jewish-Gentile birth.
◑ = Gentile appearance, pure Jewish origin.

The original Parents were first cousins.

The Daughter (No. 6) whose features were of an extreme Jewish type married a Gentile and their child is totally un-Jewish in appearance. The Son (No. 7) married a woman of pure Jewish descent but with features entirely un-Jewish. All their children are of the exaggeratedly Jewish type.

a peculiarly Jewish facial type and in some cases the keenest eyed Jew would not recognise these men as his brethren. At other times it is only the superficial observer who fails to recognise the type. I have attempted to follow out the results of the mating of such non-Jewish-looking Jews who may be said to have a "pseudo-Gentile" appearance with Jews who have a pronouncedly Jewish cast of feature. The case whose pedigree is shown in fig. 6 is an interesting example, the Jewish features being of the most pronounced, whilst the pseudo-Gentile-looking mate is equally pronouncedly un-Jewish. All the children are as typically Jewish as the Jewish father. A sister of this same father, whose features are indeed almost a caricature, married an English

Gentile husband, and she has a child who is without a trace of Jewishness.

I have met with an abundance of cases which illustrate the same phenomenon, but I have not classified them statistically nor do I show the pedigrees, because it is rarely that one can describe individuals without the smallest possible hesitation, as " characteristically Jewish," " Jewish," or " non-Jewish " in expression, as one is able to do in this family.   Nevertheless, I have not met an exception to the rule that the pseudo-Gentile appearance is recessive to the fully Jewish, where the Jewishness of the features are strongly pronounced.   In those cases where the Jewishness of the features is weak and more or less conjectural, then in matings of such with the pseudo-Gentile type, both Jewish and non-Jewish types may be found amongst the children.

The results, therefore, seem to show with very little doubt, that this pseudo-Gentile face is an essentially different thing from its Teutonic counterpart.   Whereas the latter is dominant to the Jewish, the former is as decidedly recessive.   Such an apparent paradox as the dominance of one type and the recessiveness of an apparently exactly similar one is not unknown to the student of heredity.   It has been met with by Bateson and Punnett(1) in their research on the plumage of fowls, and by Bateson in the colour of flowers(3).   I have myself, working on heredity in potatoes(13), come across one case where the white potato is recessive to the purple and another where an apparently similar white is dominant to the purple.

The facts that have been described above may, I think, throw some light on the question of the purity or otherwise of the Jews.   The Jewish features have been shown to be recessive to the Northern European (and I have cases indicating that they are recessive to the native Italian), to the native Indian, to the Chinaman, and to the negro. If then the Jew had freely intermixed with the European races as some authors think is the case, it is obvious that, the characteristic facial type being recessive, it would have been rapidly swamped.   But the very reverse is the case: it is the one thing which practically all observers are agreed is common to the Jewish people.   It has been suggested by the Pan-Germanic school of Chamberlain and others, that whatever good qualities the Jews possess are due to the admixture in them of a fair-haired race, probably Amorites who were, according to these writers, of Germanic origin.   It is indeed more than probable that the fair features found amongst Jews are derived from Amorites or other people of non-Semitic blood in their early home, but it has

already been shown that this non-Jewish type found amongst Jews is recessive to the typically Jewish, whereas the German or Teutonic type is undoubtedly dominant; hence, if the non-Jewish type is Amoritic, then it is quite certain that the Amorites were not Germanic. Conversely if it is not derived from the Amorites, it is at least quite certain that it cannot be Teutonic in origin.

In marriages between Sephardic Jews of a markedly southern European or Spanish type and Ashkenazic Jews, the former's facial characteristics seem always to be dominant. This fact, when one remembers the infusion of Iberian blood in the Sephardim already referred to, is not indeed surprising.

In a previous paragraph, it was stated that many people regarded the Jewish expression as the result of age-long homelessness and persecution. Whether it is meant that this expression is acquired in the life of the individual or whether it is an example of the heredity of an acquired character, is not decisively stated. My results would seem to throw some light on this point. In the first instance, I have frequently seen new-born babies with an unmistakably Jewish cast of feature, and secondly, in those families arising from the mating of hybrid and Jew where the children are brought up in a Jewish home with Jewish surroundings, half the children are Jewish-looking, and half are non-Jewish, a fact which the inheritance of an acquired character fails to explain. Again, if the expression is the result of landlessness and the *tausend-jährigen Schmerz*, is it not peculiar that of two children born of the same parents and reared in the same home, one should have it and the other not? I think it is clear, therefore, that this Jewish facial expression is a fundamental character, and it is necessary to trace, if we can, its origin. All observers are agreed that it cannot be described as Semitic. It is seen in, but is not the peculiar property of the Armenians who certainly resemble the Jews and who probably have in some degree a common ancestry. Is it perhaps possible that this peculiar facial type has arisen from the fusion of characters derived from two or more of the original races from which the Jews sprang?

The experiments of Bateson and others(2) with the sweet pea, paralleled as they have been in the animal world, are not unsuggestive in this respect. On mating together two apparently similar but really distinct white sweet peas, they obtained the common purple pea. When this latter was bred *inter se*, it gave rise to a series of purples, reds and whites. Of each of these classes, some, when self-fertilised, bred

perfectly true, so that from the union of two apparently similar whites, arose such distinct and dissimilar individuals as the red and the purple pea. Could not this Jewish facial expression be due to the union of characters in a manner similar to that which gave rise to the purple in the pea? In this way one would be able to explain on the one hand the practically constant presence of the Jewish facial character, and on the other, the wide divergence of head characters and the rest, which is found throughout the Jewish communities of Europe.

It is necessary before leaving our subject, to enquire whether there are no other characters common to the Jew which are as frequently present as the facial expression, or which are in any way peculiar to Jews. There would seem to be two instances of such peculiarity which fulfil these conditions. The disease known as Amaurotic Family Idiocy, the victims of which die in early childhood, is probably unknown outside the Jewish people. Fischberg states that cases are met with outside, but all the authorities I have been able to consult agree that it is peculiarly Jewish. Another character which would seem to be peculiar to the Jewish people as a whole, is the absence of alcoholism in their midst. This is acknowledged by every authority. Indeed the Jewish Board of Guardians finds it unnecessary to make any special provision for alcoholic cases as distress arising from this cause does not occur more often than once in a thousand cases, and my own experience of over nine years at the London Hospital fully bears out the statement that drunkards are practically unknown. This absence of the desire for drink cannot be ascribed to the result of religious training. There seems to be a real lack of that desire for drink which is so common amongst the North European races.

The deductions which might be drawn from these two sets of facts can naturally have no very great weight, but they do, in conjunction with what has gone before, strengthen the view that complex as the origin of the Jew may be, close inbreeding for at least two thousand years, has resulted in certain stable or homozygous combinations of factors which react in accordance with the laws of Mendel and which may explain the occurrence of the peculiar facial expression recognised as Jewish.

DESCRIPTION OF PLATES.

PLATE XXXVI.

Jewish Prisoners bearing tribute from King Jehu to Shalmaneser II. 9th century, B.C., Brit. Mus.

PLATE XXXVII.

Fig. 1.   Jewish Prisoners at Iachish. 9th century, B.C., Brit. Mus.
Fig. 2.   Pen and ink sketch in margin of Essex Forest Roll, 1277 A.D.
Fig. 3.   Jewish parent of Family E.
Fig. 4.   Gentile parent of Family E. (see text, p. 285).

PLATE XXXVIII.

Fig. 1.   Man of pure Jewish birth, brother to the man represented in Plate XXXIX. Fig. 1, and husband to the woman shown in Plate XXXVIII. Fig. 2.
Fig. 2.   Daughter of Jewish and Gentile parents represented in Plate XXXVII. Figs. 3 and 4, and sister to woman shown in Plate XXXIX. Fig. 2, is non-Jewish in appearance.
Figs. 3 and 4 are the non-Jewish looking children of parents shown in Plate XXXVIII. Figs. 1 and 2.
Figs. 5 and 6 are the Jewish looking children of the same parents.

PLATE XXXIX.

Fig. I.   Man of pure Jewish birth brother to the man represented in Plate XXXVIII. Fig. I, and husband to woman shown in Plate XXXIX. Fig. 2.
Fig. 2.   Daughter of Jewish and Gentile parents represented in Plate XXXVII. Figs. 3 and 4.   Herself non-Jewish in appearance.
Figs. 3 and 4.   Non-Jewish and Jewish sons respectively of parents shown in Plate XXXIX. Figs. I and 2.
Figs. 5 and 6.   Two brothers thoroughly non-Jewish in appearance, the children of a father of Jewish birth and appearance, and of a Welsh Gentile mother.

Note.   I am greatly indebted to the ladies and gentlemen who have so kindly allowed me to use their photographs to illustrate this paper. Far more striking examples could have been shown, but permission to publish was in no case obtainable.

The description "Jewish" and "Non-Jewish" ascribed to the portraits is arrived at by personal knowledge and by the emphatic assurances of nearest relatives. It may be noted that photographs are not a really satisfactory means of demonstrating so peculiar a character as that of Jewishness.

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Fig. 3.

Fig. 4.

Fig. 1.

Fig. 2.

Fig. 4.

Fig. 6.

Fig. 3.

Fig. 5.

Fig. 1.

Fig. 2.

Fig. 5.

Fig. 6.

Fig. 3.

Fig. 4.

Fig. 1.

Fig. 2.

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ON GAMETIC SERIES INVOLVING REDUPLICATION
OF CERTAIN TERMS[1].

By W. BATESON, M.A., F.R.S.
and R. C. PUNNETT, M.A.

In a paper recently published[2] we gave a brief account of some peculiar phenomena relating to the coupling and repulsion of factors in the gametogenesis of the sweet pea and of several other plants. The view there stated was that if A and B represent two factors between which coupling or repulsion can exist then the nature of the F_2 generation depends upon whether A and B were carried into the F_1 heterozygote by the same gamete or by different gametes. If the heterozygote $AaBb$ is formed by the gametes AB and ab partial coupling between A and B occurs in F_2 according to a definite system, and it must be supposed that the gametes formed by the heterozygote belong to one or other of the series

$$3AB : Ab : aB : 3ab,$$
$$7AB : Ab : aB : 7ab,$$
$$15AB : Ab : aB : 15ab, \&c.$$

If on the other hand the heterozygote, $AaBb$, is formed by the gametes Ab and aB repulsion occurs between A and B, so that only the two classes of gametes Ab and aB are formed. In the account to which we have alluded we supposed that such repulsion was complete, and that the two classes of gamete AB and ab were not formed. Our work on sweet peas during the present summer has led us to modify our conception of the nature of the gametes produced in cases where repulsion occurs, and this modification will perhaps be made clearer if we begin by giving an account of the experiments upon which it is based.

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[1] This paper is also appearing in the 49th volume of the Brünn *Verhandlungen* which is to be published as a Mendel *Festschrift*.

[2] *Proc. Roy. Soc.* B, Vol. 84, 1911, p. 1.

During the years 1906 and 1907 we were engaged upon an investigation of the inheritance of the hooded character in the sweet pea, of which an account appeared in Report IV to the Evolution Committee of the Royal Society, 1908, pp. 7—15. Among several thousand plants bred and recorded in this set of experiments there occurred a single individual (in Exp. 35, R.E.C. IV, p. 15) exhibiting striking peculiarities in the form of its flowers. These were small and much deformed (cf. Pl. XL, fig. 1). The standard failed to become elevated, the keel was cleft distally so that the anthers were partially protruded, while the stigma projected far beyond the petals, and was carried on in the line of the carpels instead of being abruptly bent at right angles to them as in the normal flower. At the time of its discovery, in reference to the open "mouth," and the protruding "tongue" represented by the projecting style, the plant was dubbed "the cretin," by which term we shall subsequently refer to this peculiar malformation. The fact that the style protrudes is due to the malformation of the keel which is unable to curve the growing style and cause it to assume its natural position. Fuller experience of these cretins has shewn us that the petals may sometimes be nearly as large as in normal flowers (cf. Pl. XL, fig. 2), and that the standard may sometimes become elevated in the normal way (cf. Pl. XL, fig. 3). The size of the flowers may vary considerably on the same plant, and hitherto where the larger form of flower has occurred the plant has also borne others more nearly resembling the original type. The degree to which the keel is cleft also shews some variation, but in all cases these cretins have the peculiar and characteristic straight stigma.

Our original cretin was found in 1907 and was used as the pollen parent to fertilise various sterile[1] sweet peas. The F_1 plants, which flowered in 1908, were all indistinguishable from normal sweet peas. The normal form of flower (N) was completely dominant to the cretin (n), and fertility (F) of the anthers was of course dominant to sterility (f). We may draw attention to the fact that the crosses were in all cases of the nature $Nf \times nF$, one of the two factors entering with each gamete. In the following year a single F_2 family was raised and consisted of 51 normal fertile, 30 normal sterile, 33 cretin fertile, and 1 cretin sterile[1]. The cretin character behaved as recessive to the normal flower, but the

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[1] In this family and in one of those grown later both light and dark axilled plants occurred. In each case the dark axil went in from the fertile cretin parent, and in F_2 there is some coupling between the dark axil and fertility. The numerical results however are complex and must be left over for discussion until more material is available.

relative distribution of the different characters evidently pointed to some form of repulsion between the normal flower and fertility. Had it not been for the appearance of the single sterile cretin we could have regarded this case as one of complete repulsion between the factors N and F. The problem was to account for the sterile cretin, and at the time we were inclined to regard it as due to an unaccountable failure of repulsion between N and F. Lack of opportunity prevented us from following up this case in 1910, but in the present year we sowed the seed of the rest of the F_1 plants harvested in 1908 and obtained details of eight more families which are set out in the accompanying table (Table I).

TABLE I.

Reference Number		Normal fertile	Normal sterile	Cretin fertile	Cretin sterile
Number	5, 1909	51	30	33	1
,,	72, 1911	26	14	10	1
,,	73, ,,	21	12	12	1
,,	74, ,,	24	9	8	—
,,	75, ,,	22	4	4	2
,,	76, ,,	30	12	5	1
,,	77, ,,	78	43	32	3
,,	78, ,,	59	15	24	—
,,	79, ,,	25	12	15	2
Total	...	336	150	143	11
Expectation	...	*330*	*150*	*150*	*10*

These records shew that the appearance of a small proportion of sterile cretins is a constant feature in these families and we suggest that their presence may be accounted for as follows. The repulsion between N and F is to be regarded as partial, and of such a nature that the series of gametes produced by the F_1 plant is NF, $3Nf$, $3nF$, nf. Such a series of ovules fertilised by a similar series of pollen grains would give rise to a generation consisting of 33 normal fertiles, 15 normal steriles, 15 cretin fertiles, and 1 cretin sterile. As the figures given in Table I shew, this expectation is closely realised by the facts of experiment, and we have little hesitation in regarding this explanation as the correct one. Moreover we are inclined to go further and to extend the principle to all cases of repulsion in plants. We consider then that where A and B are two factors between which repulsion occurs in the gametogenesis of the heterozygote formed by union of

the gametes Ab and aB, the gametes produced by the heterozygote so derived form one or other term of the series

$$AB : \ 3Ab : \ 3aB : ab,$$
$$AB : \ 7Ab : \ 7aB : ab,$$
$$AB : 15Ab : 15aB : ab, \&c.$$

And if we take $2n$ as the number of gametes in the series we may generalise it under the expression $AB : (n-1)\,Ab : (n-1)\,aB : ab$. As the repulsion increases in intensity it is obvious that the zygotes of the form $AABB$ and $aabb$ will become relatively scarcer, for there will be only one of each of these two homozygous forms in the complete series of zygotes. At the same time the ratio of the three zygotic forms $AB : Ab : aB$ approaches more and more nearly to the ratio $2 : 1 : 1$ such as would occur if the repulsion were complete. This is brought out in the upper part of Table II where we have set out some of the gametic series in which partial repulsion is involved together with the series of resulting zygotes. The latter, as the Table shews, are covered by the general formula

$$(2n^2 + 1)\,AB : (n^2 - 1)\,Ab : (n^2 - 1)\,aB : ab^*.$$

TABLE II.

	Gametic series				Number of gametes in series	Number of zygotes formed	Nature of zygotic series			
	AB	Ab	aB	ab			AB	Ab	aB	ab
Partial repulsion from zygote of form $Ab \times aB$	1	$(n-1)$	$(n-1)$	1	$2n$	$4n^2$	$2n^2+1$	n^2-1	n^2-1	1
	1	31	31	1	64	4096	2049	1023	1023	1
	1	15	15	1	32	1024	513	255	255	1
	1	7	7	1	16	256	129	63	63	1
	1	3	3	1	8	64	33	15	15	1
	1	1	1	1	4	16	9	3	3	1
Partial coupling from zygote of form $AB \times ab$	3	1	1	3	8	64	41	7	7	9
	7	1	1	7	16	258	177	15	15	49
	15	1	1	15	32	1024	737	31	31	225
	31	1	1	31	64	4096	3009	63	63	961
	63	1	1	63	128	16384	12161	127	127	3969
	$(n-1)$	1	1	$(n-1)$	$2n$	$4n^2$	$3n^2-(2n-1)$	$2n-1$	$2n-1$	$n^2-(2n-1)$

Hitherto the only repulsion series which we have been able to identify with certainty is the one with which we have just dealt, i.e. $1 : 3 : 3 : 1$ series for the factors N and F.

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* The general formulae made use of here and in Table II are purely empirical, and offer a convenient way of calculating the nature of the zygotic series from any series of gametes.

It is probable, however, that the case of blue and long pollen[1] is one in which the repulsion is of the 1 : 7 order. Up to the present time we have had four families of the mating $Bl \times bL$ and the 419 plants recorded in F_2 were distributed in the four possible zygotic classes as follows :

Reference Number	Blue long	Blue round	Red long	Red round
Number 61, 1910	85	33	41	1
,, $F\,28$, ,,	60	20	23	—
,, $F\,31$, ,,	9	7	5	—
,, $F\,32$, ,,	72	35	28	—
Total	226	95	97	1

Though the evidence for partial repulsion rests here upon the single red round plant which occurred in family 61, it is in reality very much stronger than it appears at first sight, for the following reason. All the plants in the above four families were hooded, i.e. lacking in the factor for erect standard (E). As we have already pointed out[2], the three factors E, B, and L constitute a series such that if any two are brought into a zygote by different gametes repulsion occurs between them. Until the present round hooded red plant appeared we had never encountered this combination in any of our experiments. It cannot therefore be regarded as due to a stray seed from another family. And it is evident that if the repulsion between any pair of these three factors were complete such a plant could never arise. For in the normal course the *ebl* gamete could never be formed. Only two possibilities therefore are open. Either we must look upon it as an unaccountable mutation, or we must consider that the repulsion between B and L is partial. In the light of the evidence afforded by the cretin sweet pea we prefer the latter hypothesis, and we are inclined to regard the partial repulsion between B and L as of the 1 : 7 : 7 : 1 type. On this hypothesis we should expect one red round in every 256 plants (cf. Table II) whereas experiment gave 1 in 419. At the same time we recognise that the data are not yet sufficient to preclude the 1 : 15 : 15 : 1 system. It is worthy of note that the coupling between B and L is usually on the 7 : 1 : 1 : 7 system, and it would be interesting if in such cases as these the repulsion and coupling systems for a given pair of factors were shewn to be of the same intensity. In most cases this could not be tested in practice owing to the very large

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[1] Blue in the flower colour (B) is dominant to red (b), and long pollen (L) is dominant to round pollen (l).

[2] *Proc. Roy. Soc.* 1911, p. 7.

number of plants required. Thus the coupling between erect standard and blue is on the 127 : 1 : 1 : 127 system, and if the repulsion were of similar intensity we should expect only one hooded red in every 65,536 plants. We may, however, state that in this particular case we have grown over 4000 plants without meeting with a hooded red, so that the facts, so far as they go, point to a high intensity of repulsion for factors exhibiting a high intensity of coupling. It is obvious that the relation can only be worked out where the intensity of repulsion is low, and it is hoped that the case of the cretin may eventually throw light upon this point when the system in which N and F are coupled shall have been determined.

The question now arises how these gametic systems are formed. In each the characteristic phenomenon is that the heterozygote produces a comparatively large number of gametes representing the parental combinations of factors and comparatively few representing the other combinations. In describing the original case of coupling, namely that between the blue colour and long pollen in the sweet pea, we pointed out that no simple system of dichotomies could bring about these numbers, and also that it was scarcely possible that such a series could be constituted in the process of gametogenesis of a plant, in whatever manner the divisions took place. In saying this, regard was of course had especially to the female side, and this deduction has become even more clear in view of the fact that we now know a series consisting of 256 terms. It is practically certain that the ovules derived from one flower of the sweet pea, even if all collateral cells be included, cannot possibly be arranged in groups of this magnitude. A pod rarely contains more than nine or ten good seeds at the most, so that if we even reckon twelve potential seeds to the pod and eight potential gametic cells to the ovule, the total is still only 96, which is much too few[1]. Nevertheless our series of numbers is plainly a consequence of some geometrically ordered series of divisions.

There is evidence also from other sources that segregation may occur earlier than gametogenesis. Miss Saunders' observations on *Matthiola*[2] and on *Petunia*[3] proved that in those plants the factors for singleness are not similarly distributed to the male and female cells.

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[1] From the fact that in maize the endosperm characters are the same as those of the seed itself we know moreover that segregation must have been completed before the divisions at which the male and female cells which constitute the endosperm are set apart.

[2] Rep. Evol. Committee R. S. IV, 1908, p. 36.

[3] *Jour. Gen.* I. 1911.

The recent work of de Vries[1] on *Oenothera biennis* and *muricata* has provided other instances of dissimilarity between the factors borne by the male and female organs of the same flower. In all these examples it is almost certain that segregation cannot take place later than the formation of the rudiments of the carpels and of the stamens respectively. The only visible alternative is that in each sex the missing allelomorphs are represented by somatic parts of the sexual apparatus, which for various reasons seems improbable. There is therefore much reason for thinking that segregation can occur before gametogenesis begins, but there is no indication as to which are the critical divisions.

Now that we may regard the formation of four cells of composition AB, Ab, aB, ab, as the foundation both of the coupling- and of the repulsion-series the problem is manifestly somewhat simplified. The time, excluding gametogenesis, at which we can most readily imagine four such definite quadrants to be formed is during the delimitation of the embryonic tissues. It is then that the plant is most clearly a single geometrical system. Moreover the excess of gametes of parental composition characterising the coupling- and repulsion-series must certainly mean that the position of the planes of division by which the four quadrants are constituted is determined with regard to the gametes taking part in fertilisation. Though the relative positions of the constituents of the cells may perhaps be maintained throughout the history of the tissues, it is easier to suppose that the original planes of embryonic division are determined according to those positions than that their influence can operate after complex somatic differentiation has been brought about.

At some early stage in the embryonic development or perhaps in later apical divisions we can suppose that the $n-1$ cells of the parental constitution are formed by successive periclinal and anticlinal divisions of the original quadrants which occupy corresponding positions. The accompanying diagram gives a schematic representation of the process as we imagine it. Obviously it does not pretend to give more than a logical or symbolic presentation of the phenomena. If such a system of segregation is actually formed at the apex, it must be supposed that the axes of the system revolve with the generating spiral. Whatever hypothesis be assumed the following points remain for consideration.

1. We are as yet unable to imagine any simple system by which the four original quadrants can be formed by two *similar* divisions. Evidently there must be two cell-divisions, and if in one of them we

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[1] *Biol. Centralbl.* xxxi. 1911, p. 97.

suppose AB to separate from ab, we cannot then represent the formation of Ab and aB. Therefore we are almost compelled to suppose that the original zygotic cell forms two similar halves, each $Aa\,Bb$, and that the next division passes differently through each of these two halves, in the one half separating AB from ab, and in the other half separating Ab from aB. The formation of these four quadrants must take place
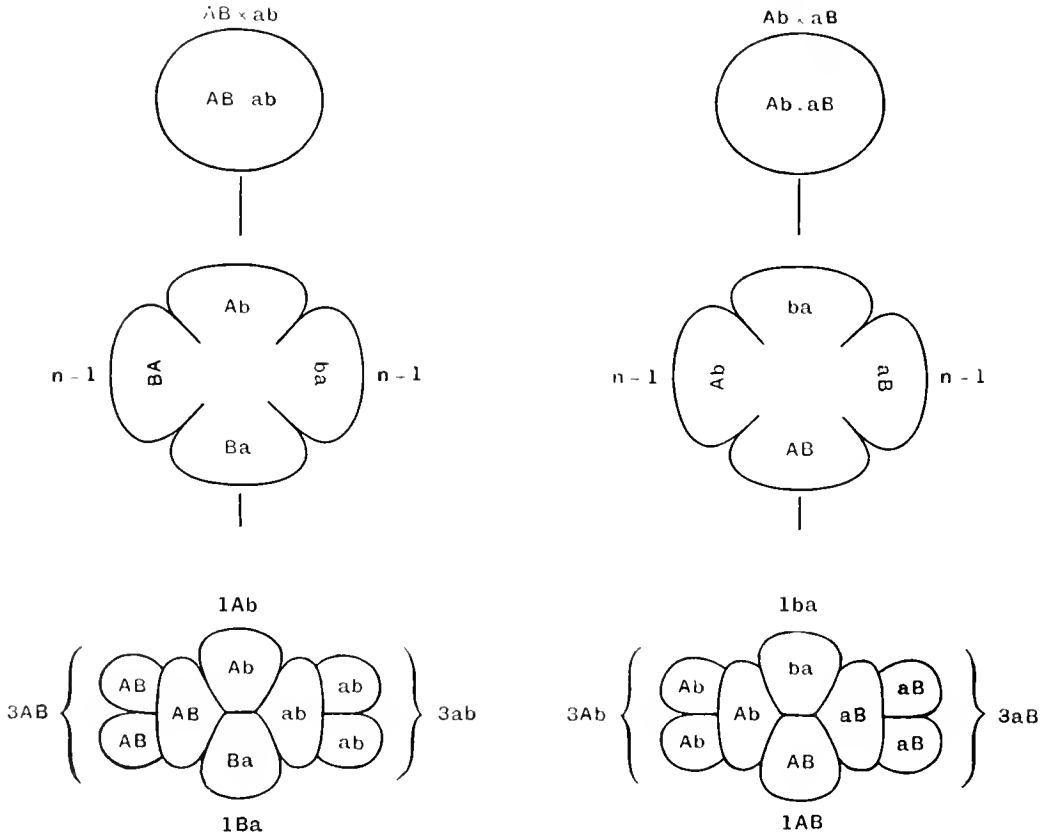
Fig. 4.

in every case in which there is segregation in respect of two pairs of factors. (For three pairs there must similarly be eight segments, and so on.) The *axes* of this system may well be determined by the position of the constituent parental gametes. Reduplication or proliferation resulting in $n-1$ gametes may then take place in either of the opposite pairs of quadrants according to the parental composition.

2. If in the gametes of any plant some factors are distributed according to one of the reduplicated series and other factors according to the normal Mendelian system—as we know they may be—the segregations by which such a system is brought about *cannot* have happened simultaneously. Moreover if various reduplications can take place very early in some individuals and not in others, we cannot imagine how the normal form of the plant remains unchanged, unless these reduplications affect tissues originally set apart as germinal.

As possibly significant we note here the fact that in the embryonic development of plants the order of the various divisions is known to be subject to great variation and it is not inconceivable that such disturbances of the order in which the planes of division occur may indicate variations in the process of segregation[1].

3. We do not yet know whether independent reduplicated systems can be formed in the same individual. In the sweet pea for instance we have not yet seen the consequences of combining blue, erect standard, and long pollen with the fertile-sterile, dark-light axil series, and much may be discovered when such families come to be examined.

Animals.

The phenomena seen in animals may well be produced by the segmentations in which the parts of the ovary or testis are determined. Hitherto no case of *coupling* has been found in animals. Among the phenomena of repulsion, however, of which many examples exist, certain suspicious cases have been observed which may mean that in animals reduplicated systems exist like those of the plants. Nevertheless at present it seems not impossible that the two forms of life are really distinguished from each other in these respects.

Terminology.

Lastly, in view of what we now know, it is obvious that the terms "coupling" and "repulsion" are misnomers. "Coupling" was first introduced to denote the association of special factors, while "repulsion" was used to describe dissociation of special factors. Now that both phenomena are seen to be caused not by any association or dissociation, but by the development of certain cells in excess, those expressions

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[1] See Coulter and Chamberlain, *Morphology of Angiosperms*, 1903, p. 187.

must lapse. It is likely that terms indicative of differential multiplication or proliferation will be most appropriate. At the present stage of the inquiry we hesitate to suggest such terms, but the various systems may conveniently be referred to as examples of *reduplication*, by whatever means the numerical composition of the gametic series may be produced.

EXPLANATION OF PLATE XL.

Fig. 1.   Photograph of the flowering stalks of two cretins. The flowers are here as fully opened as they usually become in this variety, and they are represented slightly smaller than natural size.

Fig. 2.   Flower of cretin which has larger petals than usual. The standard however is not elevated and the straight stigma protrudes beyond the rest of the flower.

Fig. 3.   In the centre two flowers from a cretin in which the standards are fully elevated. On the right are two other mature flowers from the same plant shewing petals of the usual cretin form. On the left are two old buds.

Fig. 1.

Fig. 2.

Fig. 3.

FURTHER EXPERIMENTS ON THE INHERITANCE OF "DOUBLENESS" AND OTHER CHARACTERS IN STOCKS.

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TABLE OF CONTENTS.

STATEMENT OF CONCLUSIONS ARRIVED AT IN THE EARLIER EXPERIMENTS.

THE experiments recorded in the present paper form a continuation of those of which I have already given some account elsewhere[1], and it may be well, before considering these later records, to recall the main conclusions given in the earlier accounts.

[1] Reports I—IV to the Evolution Committee of the Royal Society. In regard to "doubling" see II, 1905, p. 29; III, 1906, p. 44; IV, 1908, pp. 4, 36.

Double stocks are completely sterile, forming neither pollen nor ovules, and consequently they are always obtained from seed set by singles.

Among the singles certain strains breed true to singleness, producing only singles in successive generations, whether self-fertilised or inter-bred: these are referred to as *no-d-strains*. Other strains of singles, indistinguishable to the eye from those of the previous class, yield a mixed offspring of singles and doubles when self-fertilised or inter-bred, the doubles being mostly (? invariably) in excess of the singles—referred to as *d-strains*[1].

The behaviour of these two types of singles may be graphically contrasted thus:

no-d-single		*d*-single	
singles		singles	doubles (sterile)
singles		singles	doubles (sterile)
singles		singles	doubles (sterile)
and so on indefinitely.		and so on indefinitely.	
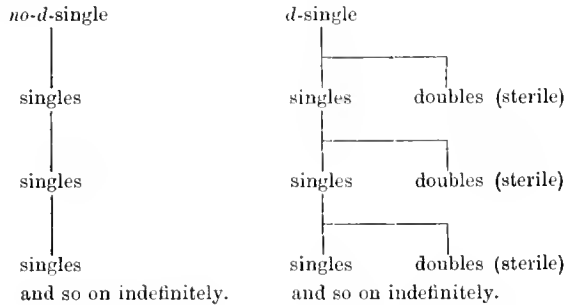
A strain composed entirely of *d*-singles would thus be "ever-sporting."

Further progress in the elucidation of this peculiar type of inheritance was made when it was shown that the eversporting character results from a difference in distribution of the factors concerned, among the ovules and the pollen grains respectively. In a single belonging to an eversporting strain the pollen grains all appear to behave alike and all carry doubleness, whereas the ovules are evidently heterogeneous, rather more than half carrying the double, and the remainder the single character. These conclusions were arrived at through the different results obtained in reciprocal unions between pure-breeding and ever-sporting individuals. For while *no-d*-single ♀ × *d*-single ♂ gives F_1 plants *all* throwing doubles on self-fertilisation, the reciprocal cross *d*-single ♀ × *no-d*-single ♂ gives F_1 individuals of two kinds, viz. those which, when self-fertilised, throw doubles, and those which breed true to singleness. The composition of the resulting generations in the two cases is compared below.

[1] *Crossbreds* are not here in question.

no-d-single   d-single   no-d-single

pollen × ovules   pollen × ovules

F_1 singles   singles   singles

F_2 singles   singles   singles   doubles   singles   singles   doubles

F_3 singles   singles   singles   singles   doubles   singles   singles   singles   doubles
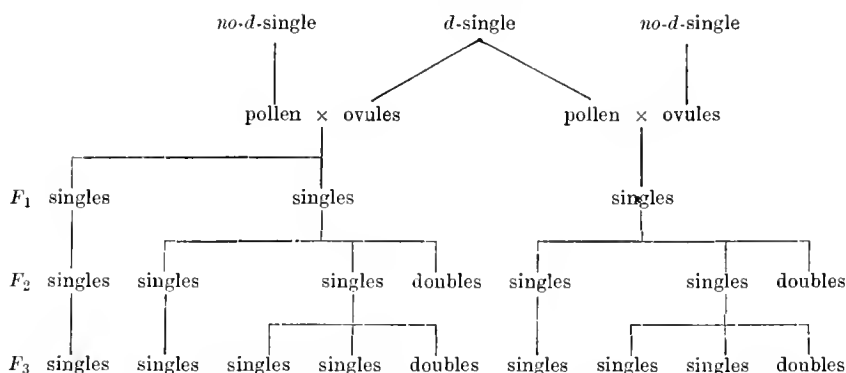
As there is no reason to suppose that the ovules and pollen of the *no-d-singles* are unlike in constitution, this difference in behaviour of the F_1 crossbreds resulting from reciprocal unions must be due to a difference in the composition of the ovules and pollen produced by the *d-singles*; and the experimental data are in accordance with the explanation already given, viz. that the *d*-singles produce two kinds of ovules, but only one kind of pollen grain[1].

Moreover this interpretation is confirmed by the fact that doubles are always produced in F_1 from a cross between two *d*-singles, whereas doubles are never obtained in F_1 when the mating is between a *d*- and a *no-d*-single. Doubleness in this respect behaves as a recessive.

So far the case is clear, and the explanation just given has been amply borne out by subsequent experiments. But certain points in the relations existing between singles and doubles still remained obscure. Though it was now clearly established that the appearance of doubles in Stocks is exhibited in an orderly and definite manner, and is entirely independent of external conditions, it still remained to determine the proportion of doubles thrown by the eversporting singles, and to ascertain, if possible, whether this proportion is constant. Doubleness behaves as a recessive to singleness; how then are we to account for the production of doubles in excess? Nor is doubleness the only character which behaves in this remarkable way. In a certain race of double-throwing singles, viz. sulphur-white, the plants are also eversporting in regard to plastid colour; every individual yields both whites

[1] The conception of a difference in constitution between the ovules and pollen grains of a plant was first put forward in 1908 in connection with the Stocks. It is interesting to find that a difference in reciprocal crosses among certain forms of *Oenothera* has led de Vries to the conclusion that differences between the ovule and pollen series of the same plant may also occur in this genus. (Cf. de Vries, *Biol. Centr.* 1911.)

and creams. From independent experiments[1] we know that white
plastid colour is dominant to cream, nevertheless among the offspring
of the sulphur-whites the dominant whites are not more numerous than
the recessive creams. Moreover the inheritance of plastid colour is
curiously bound up with the inheritance of singleness and doubleness;
for whereas in the sulphur-white race the singles, so far as experiment
has yet gone, are all white, the doubles are for the most part cream,
though a few are white like the singles. It was with the aim of
elucidating these phenomena that the present experiments were under-
taken, and in the following account I have attempted to show that by a
conception of coupling and repulsion[2] among the factors, and a peculiar
but definite distribution of the factors among the reproductive cells de-
pending upon their sex, these hitherto unexplained facts can be related
to our previous knowledge, and brought together into a general scheme.

LATER EXPERIMENTS ON THE INHERITANCE OF "DOUBLENESS" AND PLASTID COLOUR.

I. *Races which were obtained only in the double-throwing form.*

Two of the Ten-week wallflower-leaved varieties, viz. red (crimson)
and sulphur-white, appear to be obtainable only in the double-throwing
form. Direct proof of the eversporting character is obtained if doubles
are always found to occur when individuals of the race in question are
self-fertilised, while corroborative evidence is afforded by the indirect
method of crossing. For if the conclusion in regard to the character of
the pollen grains in eversporting races given above (p. 304) be correct,
it follows (1) that when an eversporting race is used as the pollen
parent in a cross with a true-breeding (*no-d*) race, doubles, though
absent in F_1, may be expected to occur in *every* family in F_2; (2) that

[1] Rep. Evol. Committee, IV, 1908, p. 35.

[2] The terms coupling and repulsion have been employed by Bateson and Punnett in
explanation of certain results obtained by them in the Sweet Pea, which seemed to
suggest that the inter-relation between certain factors was of the nature of attraction or
repulsion according as these factors were received separately from the parents or
associated together (see *Proc. Roy. Soc.* B, Vol. 84, 1911). In a later communication
which appeared after the present paper had been sent to press (see *Verhandlungen des
naturforschenden Vereines in Brünn*, Bd. XLIX. and also the present number of this *Journal
of Genetics*), these authors suggest the substitution of the general expression "reduplica-
tion of terms" to cover both cases. Pending the acceptance of other terms which will
serve to distinguish results which would have been classed under the head of coupling
from those coming under the head of repulsion the original terms are here retained, as
conveniently descriptive of the two types of results, not as connoting necessarily the real
cause of the phenomena.

when two eversporting races are bred together, doubles will, on the other hand, occur in each F_1 family as well as in each family in all later generations, just as when either race is repeatedly self-fertilised.

The evidence at present available in each case may be summed up as follows:

Red Race.

87 individuals were tested directly by self-fertilisation. The pedigree of these plants is shown below.

1	Parent plant (A)							
11	F_1 Plants derived by self-fertilisation from the parent plant A							
64	F_2	,,	,,	,,	,,	11 of the F_1 individuals		
3	F_3	,,	,,	,,	,,	3	,,	F_2	,,
7	F_4	,,	,,	,,	,,	1	,,	F_3	,,
1	F_5	,,	,,	,,	,,	1	,,	F_4	,,

Total   87

Doubles occurred in each of the 87 families (see Table III). Thus every attempt to breed out the doubles proved unsuccessful, and the evidence shows that this form, at least so far as the material used in these experiments is concerned, is eversporting. Efforts to obtain from other seed on the market a true-breeding (*no-d*) strain of this race proved equally unsuccessful. Two or three large firms to whom application was made were unable to supply such a strain[1].

[1] In the catalogues of the large Stock Growers the various stock races are catalogued in different colours, but not as a rule according as they do, or do not, produce doubles. It has however been found that commercial seed, stated to give only singles, does in fact breed true; and that from seed stated to yield doubles, doubles are obtained in such abundance that for testing purposes small sample savings are sufficient. It might perhaps be supposed that, since the aim of the grower is to produce seed which will yield as high a percentage of doubles as possible, a true-breeding strain, should it by chance appear, would be at once discarded; and hence the fact that it had not been found possible to obtain such a strain in the red race, might not necessarily indicate that no true-breeding individuals occurred when the race was cultivated without selection. But this assumption does not explain the fact, that in the case of the other sap-coloured forms employed, true-breeding seed is on the market and easily obtainable. There is no reason to suppose that modern taste demands a pure-breeding single in various other shades but rejects it if coloured red. Nevertheless there is no doubt that a pure-breeding red strain could at once be made by crossing an eversporting red with a *no-d* type. If the resulting crossbreds are self-fertilised, F_2 will contain a proportion of glabrous red singles some of which will be found to breed true. We may therefore safely class the red race with the other sap-coloured types as one which *can* exist both as a pure-breeding and a double-throwing form. Whether a non-double-throwing sulphur-white race, i.e. to say a white race composed entirely of individuals throwing a proportion of creams but breeding true to singleness, can exist, or not, we cannot tell. At present no such race is known, and we are unable to make it.

Sulphur-white Race.

62 individuals were self-fertilised, but in this case they were not all descended in one line. Their relationship is shown below.

1	Parent plant (A)[1]				
7	F_1 Plants derived by self-fertilisation from the parent plant A				
19	F_2	,,	,,	,,	,, 3 of the F_1 individuals
3	F_3	,,	,,	,,	,, 1 ,, F_2 ,,
1	Parent plant (B)[1]				
20	F_1 Plants derived by self-fertilisation from the parent plant B				
5	F_2	,,	,,	,,	,, 2 of the F_1 individuals
5	F_3	,,	,,	,,	,, 3 ,, F_2 ,,
1	Parent plant (C)				

Total 62

Families were obtained from each of these 62 individuals and *here again doubles occurred in every case* (see Table III). It is therefore evident that this race also is wholly composed of eversporting individuals. So much seems clear from the results of self-fertilisation, but it is only on crossing that the real explanation of these results becomes apparent.

Reciprocal crosses between *d*-strains and *no-d*-strains afford a convenient means of separately testing the ovules and the pollen of the *d*-strain, and it is through the different behaviour of such reciprocals that we are enabled to understand the true cause of the eversporting habit. At this point it will be convenient to consider transmission of the double character by the *pollen* in these two strains[2].

When the red or sulphur-white was used as the pollen parent in a cross with a pure-breeding (*no-d*) strain all self-fertilised F_1 plants, with three exceptions, produced a mixture of singles and doubles in F_2 (see Table IV). In view of all the evidence it is unlikely that any of these three cases really indicates a genuine exception; each will be fully discussed later (see pp. 309, 310).

The experiments with the red race were as follows:—

Pollen from 6 individuals of this race was used to fertilise 10 plants belonging to 4 different pure-breeding strains. The number of seed-parents in each case was as follows:

No-d-glabrous cream	4
,, ,, white	4
,, ,, flesh	1
,, hoary white (Brompton)	1
Total ...	10

[1] A and B were obtained from different growers.

[2] Transmission by the ovules will be dealt with in a later section (see p. 323).

91 of the resulting F_1 crossbreds were self-fertilised to produce F_2. The number of these F_1 plants derived from the 6 d-parents used as $\male$, representing in each case an equivalent number of pollen grains, were respectively

$$
\begin{array}{c}
57 \\
19 \\
7 \\
3 \\
3 \\
2 \\
\hline
\end{array}
$$

Total   91

Doubles occurred in every F_2 family. Each of the 91 pollen grains tested must therefore have been carrying the double character.

In the sulphur-white race 7 individuals were employed as the d-pollen-parent in matings with 9 individuals belonging to 3 different pure-breeding strains. The number of seed-parents used in each case was as follows :

No-d-glabrous cream			5
,, ,,	flesh		3
,,	hoary white (Brompton)		1
	Total	...	9

93 of the crossbreds were tested as in the red race. The number of these F_1 plants derived from the 7 d-parents were respectively

$$
\begin{array}{c}
22 \\
22 \\
16 \\
15 \\
8 \\
7 \\
3 \\
\hline
\end{array}
$$

Total   93

Doubles were obtained in 90 out of the 93 families. It remains to consider whether in the 3 families in which no doubles were recorded their absence is probably real or not. It would seem that in two of the three cases, at least, we may fairly regard the totals, viz. 8 and 17, as too small to be conclusive, for we find among the mixed families a case where the proportion of singles to doubles was as high as 20 : 1 (the actual numbers were 40 s. 2 d.). This being so, it is clear that the two cases in question fall within the range of what may be expected from

an F_1 crossbred, bred as above, but from which nevertheless doubles would be obtained if a further sowing was made. The remaining exception was a family of 33 singles, but even this total constitutes no very strong case for the genuineness of the exception, seeing that in another case a result of 40 s. 2 d. (see above) was actually observed. It represents, it is true, a greater excess of singles than was recorded in any other family of the same parentage, but much stress cannot be laid upon this point, since among the mixed F_2 families obtained when one of the sap-coloured forms was used as the double-throwing parent in similar matings, we find a case where the proportion of singles was as high as 30 : 1 (the actual numbers were 60 s. 2 d.). An equally high proportion *might* presumably be obtained with the sulphur-white; so that even in this last case it is quite possible that doubles would have occurred in a larger sowing. Another possibility is worth noting in this connection. The plant from which the F_2 family of 33 singles was derived was one of 46 obtained from pure-breeding creams which had been fertilised with the pollen of sulphur-whites. The other 45 all yielded a mixed offspring of singles and doubles. Now the strain of sulphur-white used in this experiment evidently did not contain the colour factor C found in the ordinary pure white glabrous race[1], for the mating with the cream produced offspring which were all cream, and, as we should expect under these circumstances, all glabrous. Thus the F_1 plants obtained from *crossing* the cream with the sulphur-white are indistinguishable in appearance from F_1 plants derived from the same cream parent by *self*-fertilisation. Where F_1 shows reversion in colour and surface character we know that we are dealing with a genuine crossbred, but in this case we have no such proof. It is in fact within the bounds of possibility that the F_1 plant which produced the 33 singles, although supposed to be a crossbred, may in reality have been a pure-bred resulting from accidental self-fertilisation.

To sum up the evidence in regard to these two double-throwing forms, red and sulphur-white :

Experiments carried through 6 generations showed that the 149 individuals tested were all throwing doubles. It therefore seems beyond doubt that both forms are genuinely eversporting—that in

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[1] As stated in the Evolution Reports one of the two factors C and R which are essential to the production of sap-colour is found in the pure white race, the other in the cream. As white is there represented as containing C and cream as containing R, it will be convenient to retain the same formulae here (see Report IV, p. 36). For a fuller account of the constitution of the sulphur-white, see p. 370 of the present account.

both cases *every* pollen grain is carrying the double character. This view receives strong confirmation from the results of cross-breeding. 184 pollen grains were tested by crossing with a pure-breeding form. From the mixed character of the F_2 families it was definitely ascertained that 181 of these grains must have been carrying doubleness. The absence of doubles in the 3 remaining families can scarcely be regarded as other than accidental, since if genuine it would presumably imply the production by the double-throwing forms of a certain number of single-carrying pollen grains, a condition which is not borne out by the results of self-fertilisation.

II. *Races which occur both in the form of double-throwing and non-double-throwing strains.*

The question now arises as to the behaviour of those races which can be obtained both in a pure-breeding and in a sporting form. Are these *d*-strains also strictly eversporting? In these cases is it also impossible to breed out the doubles? From the results which have now been obtained it would seem that to these questions we may safely return an affirmative answer. It will however be convenient to consider the evidence from the sap-coloured and the non-sap-coloured forms separately.

Commercial seed of both double-throwing and non-double-throwing strains was obtained in the case of the two glabrous non-sap-coloured forms white and cream, and of several sap-coloured forms, viz. very light purple or azure (both hoary and glabrous), light purple, dark purple, marine blue, flesh and copper (all glabrous)[1]. The seed supplied as giving only singles was found, as previously stated, to answer to description; in no case were doubles obtained from such seed either when the strains were self-fertilised, or bred together. The strains stated to give doubles were tested both (1) by self-fertilisation which affords the readiest means of detecting the sporting individual, though it leaves undetermined the share in the results to be attributed to pollen and ovules respectively; (2) by crossing with pure-breeding strains, a method which enables us to sample ovules and pollen independently of each other. In the latter case the experiment has to be carried to F_2 before a result is obtained.

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[1] Unless otherwise stated all races employed in these experiments were of the Ten-week class.

(*a*) *Sap-coloured races.*

i. Evidence from self-fertilisation.

The number of individuals tested in each case is shown below :

Number of Individuals Tested.

	Azure hoary	Azure glabrous	Light purple glabrous	Dark purple glabrous	Marine blue glabrous	Flesh glabrous	Copper glabrous	Totals
Parent plants	1	2	2	1	3	2	1	12
F_1 individuals derived from self-fertilisation of parent plants	5 (all of one family)	3 (all of one family)	21 (all of one family)	4 (all of one family)	19 (belonging to three families)	0	0	52
F_2 individuals derived from self-fertilisation of F_1 plants	0	2 (belonging to two families)	9 (belonging to six families)	2 (both from one family)	0	0	0	13
F_3 individuals derived from self-fertilisation of F_2 plants	0	9 (all of one family)	22 (belonging to five families)	0	0	0	0	31
Totals ...	6	16	54	7	22	2	1	108

Twelve individuals belonging to different sap-coloured forms were taken at random, and they and 96 of their descendants were self-fertilised. *Doubles were obtained from each of these* 108 *plants.* (For details see Table III.) Thus the evidence, so far as experiment has yet gone, indicates that the double-throwing strains of these forms now on the market are similar to the red and sulphur-white races in that they are genuinely eversporting, and that it is in fact impossible to breed out the doubles.

ii. Evidence from cross-breeding.

To obtain the further proof that the double character is being carried by *all* the pollen in each of these sap-coloured strains necessitates the raising of a large number of F_2 plants which have been bred by self-fertilisation from the mating *no-d* ♀ × *d* ♂ where the ♂ parent belongs to the sap-coloured form which is to be tested.

Up to the present 36 F_1 plants representing as many pollen grains contributed by 6 *d*-parents have been tested in this way. The parentage of these F_1 plants and the number of pollen grains tested in the case of each parent are shown below; the composition of the F_2 families will be discussed later (see p. 336 and Table IV); those marked thus * have already been recorded (see Report II, p. 37).

Number of F_1 plants tested	Matings from which the F_1 plants were derived	Number of pollen grains tested in the case of each ♂ parent
6	no-d-cream ♀ × d-light purple ♂ (plant A)	6
14	,, ,, × ,, ,, (plant B)	14
7	no-d-flesh ♀ × ,, ,, (plant B)	7
1	*no-d-dark purple ♀ × d ,, (plant C)	1
6	no-d-cream ♀ × d-azure ♂	6
1	*no-d-flesh ♀ × d-dark purple ♂	1
1	*no-d-white ♀ × d-copper ♂	1
Total 36		Total 36

All the 36 F_1 cross-breds yielded doubles in F_2; hence all the pollen tested must have been carrying the double character.

(b) *Non-sap-coloured races.*

The results recorded in the case of the glabrous white and cream races are less consistent than those obtained with the sap-coloured forms, but, if the conclusion which a review of all the evidence seems to render most probable should prove correct, viz., that in the case of the non-sap-coloured forms the seed obtained commercially was not homogeneous but of mixed origin, some of it being pure-bred and some cross-bred, such admixture would account for the discrepancies observed. On this view the facts may be taken to indicate that, where pure-bred material is used, the same results may be expected to follow whether a sap-coloured or a non-sap-coloured form is employed; and that these races, when pure-bred, are all in fact like the sulphur-white and the red, strictly eversporting.   The facts in full are given below.

i. Glabrous white race.

Seeds stated to yield doubles were procured from two different firms.   Sample sowings gave the expected mixture.   Certain singles occurring in this first and in later generations were tested as shown in Table I.

Both lots of seed gave a different result from that obtained with the sap-coloured forms, for here the singles appeared to be mixed, some giving doubles according to expectation, others not.   Thus in the one lot, plant A, and in the next generation plant K were presumably breeding true while plant B was not; in the other lot plants H and I and 21 of I's descendants evidently belonged to the sporting class, while plants C, D, E, F, G and J were in all probability breeding true.   We should not be surprised at a result of this kind if, either there had been some mischance or want of care in the handling of the seed before it was supplied, in which case we might regard the mixture of singles as

accidental and unimportant: or, if we had grounds for supposing that we were dealing with a race in which *some*, but not *all*, of the pollen grains were carrying doubleness. But neither supposition agrees well with the facts. The evidence from cross-breeding, so far as it goes, indicates that here, as in the sap-coloured forms, *all* the pollen grains carry the double character; for, as shown in Table I, 20 F_1 plants derived from the mating *no-d*-cream ♀ × *d*-white ♂ were tested, the pollen grains from which they were derived having been furnished half by plant *B* and half by plant *I*; *all yielded doubles when self-fertilised.* On the other hand the fact that results precisely similar to those described above were obtained with the cream race renders explanation on the accident theory very improbable.

ii. Glabrous cream race.

Seeds of the cream race were obtained from the same sources as those of the white, and here too, in accordance with expectation, doubles occurred in both sample sowings (see Table II).

In the case of lot 1 only three of the singles were tested, one (*A*) by self-fertilisation, the other two (*B* and *X*) by cross-breeding. All three yielded doubles, either in F_1 (as a result of self-fertilisation or of crossing with a *d*-strain) or in F_2 (when the mating was with a *no-d*-strain), as did also the two descendants of the self-fertilised plant *A* which were tested (viz. plants *N* and *O*). In addition to these 5 plants, 12 singles derived by cross-breeding from *B* were also tested; each yielded doubles in the next generation, a result which further confirms the eversporting character of plant *B*.

In the case of lot 2, where more individuals were bred from, the results indicate on the other hand that, as was found with the white race, the singles were mixed, some yielding doubles and some not. Out of 11 singles taken at random from this batch 10 were tested by self-, 1 by cross-fertilisation; of these, 4 (plants *C*, *D*, *E*, *F*) appeared to be breeding true[1], the remaining 7 (plants *G*, *H*, *I*, *J*, *K*, *L*, *M*) produced doubles either in the next generation, or in F_2 if the mating was with a *no-d*-strain as was the case with plant *M*. In the case of plants *G* and *H* the offspring were too few to give indication of the true

[1] The number of offspring obtained from plant *F* by self-fertilisation was only 3—far too small a total to be taken as proof that the absence of doubles is real, but the evidence from cross-breeding leaves no doubt that *F* was a pure-breeding single. Used as the ♂ parent in a mating with *no-d*-white it produced 10 plants in F_1, 9 of which were self-fertilised, yielding altogether a total of 70 plants in F_2 which were all single. Further, when used as ♀ with two *d*-strains the 23 individuals obtained in F_1 were all single.

Table I showin, by self-fertilisation, or by crossing

ı single individual. ● =a double individual.

Seeds from Source 1   + 2 ×   + 4 ●
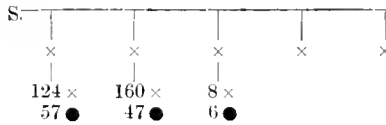
S.

124 ×   160 ×   8 ×
57 ●   47 ●   6 ●

Seeds from Source 2

Sample sowing of   Plant C × abrous cream) ✗   Plant I ×   Plant J × +11 × +7 ●
commercial seed
200 ×   240 ×

15 ×   — ×   5 ×   7 ×   8 ×   6 ×   2 ×   6 ×   5 ×   1 ×   4 ×   6 ×   62 ×   107 ●
5 ●   1 ●   6 ●   3 ●   12 ●   10 ●   4 ●   6 ●   6 ●   1 ●   4 ●   2 ●
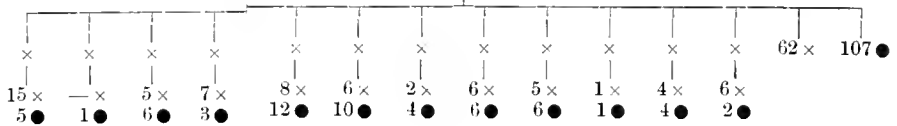
Table II ịing, and the results obtained.

Seeds from Source 1

Sample sowing of   Plant A ×   (no-d-glabrous flesh ♀) ✗ Plant X ×   + 8 ×   + 17 ●
commercial seed

Plant N ×   Plant O ×   ×   11 ●   ×   21 ×
33 ×   52 ×   44 ×
62 ●   70 ●   16 ●

Seeds from Source 2

Samp ß and   d-glabrous red ♂ ✗ Plant G ×
con te ♂

3 ×
14 ●   ×   ×   ×

23 ×

Seeds from Source 1

Sample sowing of
commercial seed

Plant A ×

× • (Plant K)

134 •

(no-d-glabrous cream) X Plant B •

+2 • +4 ●

66 •	98 •	121 •	56 •	116 •	49 •	107 •	124 •	160 •	8 •
28 ●	25 ●	32 ●	20 ●	37 ●	25 ●	39 ●	57 ●	47 ●	6 ●

Seeds from Source 2

Sample sowing of
commercial seed

Plant C •   Plant D ×   Plant E ×   Plant F •   Plant G ×   Plant H   (no-d-glabrous cream) X Plant I •   Plant J • +11 • +7 ●

200 •   245 ×   37 •   many •   many •   2 •   240 •
total not recorded   total not recorded

17 •

62 × 107 ●

15 •	5 •	7 ×	6 •	9 •	6 ×	7 •	8 •	56 •	— •	— •	— ×	—	3 •	1 •	5 •	5 •	10 ×	6 •	5 •	1 •	5 •	8 •	6 •	2 •	6 ×	5 •	1 •	1 •	6 •
5 ●	1 ●	6 ●	3 ●	2 ●	1 ●	1 ●	4 ●	21 ●	1 ●	1 ●	6 ●	1 ●	8 ●	4 ●	3 ●	10 ●	18 ●	5 ●	4 ●	1 ●	12 ●	12 ●	10 ●	1 ●	6 ●	6 ●	1 ●	1 ●	2 ●

Seeds from Source 1

Sample sowing of
commercial seed

Plant A •

(d-glabrous red ♀) X Plant B •

(no-d-glabrous flesh ♀) X Plant M •   +8 • +17 ●

Plant N •   Plant O •   2 ×   11 ●

33 •   52 •
62 ●   70 ●

2 •   11 ●

21 •

11 •
16 ●

24 ×	29 •	5 •	36 •	9 •	19 ×	13 •	22 •	40 •	10 •	20 •	14 •
24 ●	18 ●	12 ●	41 ●	17 ●	25 ●	19 ●	13 ●	26 ●	23 ●	16 ●	21 ●

Seeds from Source 2

Sample sowing of
commercial seed

Plant C •   Plant D ×   Plant E •

Plant P •   41 •

19 ×

14 •   19 •

(no-d-glabrous white ♀) X Plant F •   X d-glabrous red ♀ and   d-glabrous red ♀ X Plant G •
                                          d-glabrous white ♀

3 •
11 ●

3 •   23 •

9 •	10 ×	21 ×	2 •	10 •	5 •	1 •	1 •	8 •

Plant *J* ×

Plant *M* × **X**   ÷ 11 ×   + 8 ●
no-d-glabrous white ♂

S ×   Plant *R* ×   9 ×   9 ●

70 ×
108 ●

48 ×   19 ×
18 ●

44 ×   36 ×   37 ×   40 ×   30 ×
6 ●   10 ●   11 ●   10 ●   13 ●

Plant *K* ×

26 ×   2 ×   1 ×   4 ×   — ×   7 ×   3 ×   5 ×   — ×
9 ●   5 ●   5 ●   3 ●   2 ●   6 ●   7 ●   3 ●   1 ●

66 ×   93 ×   1 ×
27 ●   23 ●   1 ●

27 ×   81 ●

22 ×   2 ×   6 ×   1   25 ×   17 ×   8 ×   68 ×   40 ×   9 ×   44 ×
6 ●   1 ●   5 ●   2(

13 ×   13 ●

9 ×   3 ×   3 ×   18 ×   25 ×   21 ×   27 ×   19 ×   14 ×   29 ×   7 ×
4 ●   1 ●   1 ●   5 ●

Table II (continued)

Seeds from Source 2 (continued)

(no-d-glabrous white ♀) X Plant *H* ·

Plant *I* ·

Plant *J* ·

Plant *M* · X   +11 · +8●
no-d-glabrous white ♀

Plant *Q* ·   16 ·   34●   d-sulphur white ♀ X Plant *S* ·   Plant *R* ·   9 ·   9●

1 ·   4●   58 ×   6 ·   70 ·   48 ·   19 ·
            99●   12●   108●   18●

| 41 · | 36 · | 37 × | 40 · | 30 × | 55 × | 41 × | 50 × | 51 × | 33 × | 55 × | 56 · | 51 × | 39 × | 54 · |
| 6● | 10● | 11● | 10● | 13● | 8● | 6● | 17● | 9● | 15● | 7● | 14● | 12● | 14● | 15● |

Plant *K* ×

Plant *U* X no-d-glabrous white ♀   d-sulphur white ♀ X Plant *T* ·

| 4 · | 2 · | 9 · | 38 · | | 3 · | 2 × | · · | 26 × | 2 · | 1 · | 4 · | | 7 × | 3 · | 5 · | |
| 1● | 4● | 8● | 7● | | 1● | 2● | 2● | 1● | 9● | 5● | 5● | 3● | 2● | 6● | 7● | 3● | 1● |

6 ·

d-glabrous flesh ♀ X   X d-glabrous flesh ♂

| 66 · | 93 · | 1 · | 1 · | 10 × | 8 × | 99 · | 7 · | 16 × | 138 × | 20 · | 36 · | 79 · | 55 · |
| 27● | 23● | 1● | 1● | 3● | 4● | 32● | 1● | 3● | 39● |

10 ·   12 ·
4●   10●

27 ·   81●

| 22 · | 2 · | 6 · | 1 · | 12 × | 2 × | 3 × | 4 × | 3 · | 3 · | 1 · | 1 · | 6 · | 6 · | 5 · | | 3 · | | 7 · | 1 · | 7 · | · · | 7 · | | 25 · | 17 · | 8 · | 68 · | 10 · | 9 · | 11 · |
| 6● | 1● | 5● | 2● | 5● | 3● | 5● | 5● | 7● | 2● | 6● | 4● | 1● | 2● | 2● | | 2● | 2● | 1● | 4● | 1● | 1● | 2● | 5● |

d-hoary azure ♀ X ·   d-hoary azure ♀ X   29 ·
                                               7●

3 ·   8 ·   7   18 ·
6●   3●   7●

Plant *L* ·

| 9 × | 3 · | 3 · | 18 × | 1 · | 3 · | 25 × | 2 × | 2 · | 25 × | 15 · | 15 · | 3 · | 2 · | 7 · | 9 · | 9 · | 29 · | 31 · | 21 · | 28 · | 28 · | 13 · | 25 · | 21 · | 27 · | 19 · | 14 · | 29 · | 7 · | | 13 × | 13● |
| 4● | 1● | 1● | 5● | 1● | 1● | 8● | 3● | 4● | 5● | 7● | 5● | 1● | 2● | 2● | 1● | 2● | 1● |

X d-glabrous   d-sulphur X ·   X d-sulphur white ♀
  red ♂   white ♀
31 ·   92 ·   147 ·
                                     54●

proportion of single to double, but both plants were presumably producing an excess of doubles as was also apparently K, probably J, and certainly I; L on the other hand yielded a proportion of about 3 s. : 1 d., i.e., the proportion we should expect from a cross-bred rather than a pure-bred. In the next generation a single descendant from each of the two plants I and J was selfed, and both like their parents gave doubles in excess; both in short behaved like eversporting individuals as we should naturally expect. In the case of K and L however the results obtained in F_2 are not so easily comprehended, for in neither case did all the F_1 singles yield doubles in F_2. In fact the same diversity of behaviour exhibited by the *haphazard* collection of singles (plants C—M) is here found among the *sister* plants of a self-bred family derived from one of these singles (K). 48 F_1 descendants of K were tested, 1 (plant U) by cross-fertilisation only, 47 by self-fertilisation either alone or in addition to cross-fertilisation. [Where self-fertilisation shows that an individual was throwing doubles it is unnecessary for the present purpose to complicate the pedigree further by introducing into it the results of cross-fertilisation, and these results have therefore been omitted where the evidence from self-fertilisation was sufficient.] The former plant (U) and 40 of the latter again produced doubles in the next generation, but the remaining 7 yielded only singles, the numbers in these 7 families ranging from 8 to 68. How many among the 40 mixed families can be regarded as showing the true proportion of singles and doubles is uncertain, since in many the totals are very small; moreover the seed was not sown until two years after it was harvested, and in some cases germinated badly. (See later, p. 361, where the probability that seeds giving rise to singles and doubles respectively differ in viability is discussed.)

To sum up the foregoing results :

Plant K as a matter of fact gave a very slight excess of doubles, but among the F_1 singles derived from K some were evidently giving doubles in the proportion of only 1 d. : 3 s. while others were apparently breeding true to singleness. Some of the F_2 singles similarly yielded the proportion 1 d. : 3 s. in F_3. (See Table II.)

In the case of plant L, 31 F_1 descendants were tested by self-fertilisation; 18 of the resulting F_2 families included some doubles, 13 were composed entirely of singles, the numbers in the latter class of families ranging from 7 to 34. If we review these 18 families we find that in 13 the numbers agree well with the ratio 3 s. : 1 d., and that in the remaining 5, none of which included more than 6 individuals, there

is either equality or a slight excess of doubles. In the next generation this diversity of behaviour was again apparent; 3 F_2 plants belonging to 2 F_1 families, both of which included some doubles, were tested by cross-breeding. One was used as ♂ in a mating with the d-red strain and gave a total of 36 *all single*. Another was employed as the ♂ parent with two individuals of the eversporting sulphur-white race and gave a total of 92 (58 + 34) offspring again *all single*. The third individual, which was sister to the last-mentioned plant, and was similarly used as the ♂ parent in a mating with the same two sulphur-white individuals and also with another sulphur-white plant gave, on the other hand, a mixture of singles and doubles, the singles in each case being largely in excess. These results may be summarised thus: L itself yielded singles and doubles in the proportion of 3 s. : 1 d.; when self-fertilised the resulting F_1 singles proved to be mixed, some yielding again 3 s. : 1 d., others apparently breeding true to singleness; whether also some of the F_1 singles were yielding a higher proportion of doubles than 1 in 4 is not certain. In the F_3 generation a similar result was obtained, some of the F_2 singles were evidently breeding true to singleness, while others gave an excess of singles when mated with an eversporting form.

There remain the plants M and X about which all that can be said is that both were evidently able to throw doubles, but whether in excess, or not, there is not sufficient evidence to determine.

Among the various matings of the cream race with other forms, only two happened to be carried out in such a way as to enable the double-throwing character of the pollen to be tested independently of the ovules as is the case when a *no-d*-strain is used as the ♀ parent in the cross. 16 of the F_1 plants resulting from these two unions were self-fertilised, viz., 1 F_1 from the mating *no-d*-flesh ♀ × d-cream (plant X) ♂ and 15 from *no-d*-white ♀ × d-cream (plant H) ♂, and each yielded doubles in the next generation. The total number of pollen grains belonging to the two non-sap-coloured forms, which were tested in this way, is then 20 from the white race (see p. 314) and 16 from the cream, *and all proved to be carrying the double character.*

We find then that seed of the double-throwing strains of white and cream, as supplied commercially, appears to differ from similar seed of the sap-coloured races in that it is not homogeneous. Though the plants raised are uniform and true to type in respect of other characters such as flower colour and character of leaf surface, they differ in behaviour as regards the double-throwing characters. They behave in fact as we

should expect a population to behave if it was composed of double-throwing and non-double-throwing individuals of the same race breeding indiscriminately together. Under these conditions we should expect that some individuals would yield an excess of doubles, and that others would breed true to singleness, and that in the latter case the succeeding generations would be homogeneous and would behave like their parents. Further, that other individuals though yielding a mixture of singles and doubles would give an excess of singles. The plants yielding an excess of singles would be cross-breds due to cross-breeding between the eversporting and the true-breeding single, and each succeeding generation of their descendants, if self-bred, would prove heterogeneous, and give again true-breeding singles and singles giving a minority of doubles.

From the facts detailed in the preceding pages it therefore seems reasonable to suppose that in the case of the sulphur-white and the various sap-coloured strains employed the samples of commercial seed investigated were harvested from homogeneous populations composed of eversporting individuals only. That in the case of the white and cream races the populations from which the seed was collected included pure-breds and cross-breds, some of the pure-breds being eversporting, some true-breeding. A sample sowing in the case of these two strains might therefore very well produce all three types of single, as indeed appeared to be the case with the cream, where A, B, H, I and J appeared to be eversporting, C, D, E and F true-breeding, L and probably K either cross-breds or the offspring of cross-breds. The remaining plants, viz. G, M and X, were also producing doubles, but the evidence is insufficient to determine whether they were pure-breds or cross-breds. This explanation indeed appears to be the only one tenable, for the facts which have been given may be taken to put out of account any question of accident in the handling of the seed before it was supplied, or of the frequent occurrence among eversporting forms of pollen grains carrying the single character.

III. *Proportion of doubles obtained from the eversporting strains when self-fertilised or inter-crossed.*

i. *When self-fertilised.* (For details see Tables III, VI, VII, and VIII.)

As previously stated (Report III, p. 45) eversporting individuals, when self-fertilised, usually give an excess of doubles. It may be noted

in passing that the proportion of single and double plants among self-bred offspring of eversporting forms presumably indicates the proportion of single and double-carrying ovules in the parents, since the ♀ gametes are being tested, so far as appears, against a uniform standard—the double-carrying pollen grain. A survey of the numbers recorded (see Table III), especially where the totals are fairly large, whether obtained as the result of a considerable sowing from one individual or by summing the results of small sowings from many individuals, leads to the conclusion that the real ratio of single to double is either exactly 7 : 9, or that it lies somewhere between this and equality. The proportion is in fact such as we might expect from imperfect gametic coupling where two pairs of allelomorphs are concerned. Coupling on a 7 : 1 basis for example gives the precise ratio 7 : 9; a 15 : 1 series gives 7·5 : 8·5 and the next higher term in the series a still nearer approach to equality. On the whole the balance of evidence seems to point to a 15 : 1 series, but very large numbers would be required to enable us to decide this point with certainty, and until these are available we may conveniently represent the ratio of the two forms by the general expression

$$7 + x \text{ single} : 9 - x \text{ double},$$

where x has some value less than 1. We may suppose that the value for x is probably the same in all the strains investigated and that the considerable divergences occurring in many cases where the numbers are small are not real but the outcome of a topographical scheme of distribution of the different ♀ gametes, in consequence of which the flower unit may not afford an average sample. It is as though the arrangement of the ♀ gametes were regulated by some coarse mechanism, so that in regard to such small regions as a single fruit or part of a fruit, there may be great irregularity of grouping. With a view to avoiding any effect of unconscious selection in the samples sown, the practice was adopted of sowing all the seeds belonging to some definite unit or area, as *e.g.* all from one fruit, or from one side of the fruit, or if fewer still were required the necessary number were taken in order from one end of the pod, and not selected at random from the mixed seed of many pods. Several cases selected for further sowings on account of the aberrant result obtained in the first instance from small samples, later gave totals in accordance with expectation. It is this irregularity of distribution which renders it difficult to determine whether the higher or the lower of the ratios given above should be accepted as correct.

ii.   *When inter-crossed.*

Table showing the totals *obtained in* F_1 *from various matings between two eversporting forms.   (For details of the families, see Table VI.)*

Type of Union		Number of matings	Number of singles	Number of doubles
d-glabrous cream ♀	× *d*-glabrous white ♂ ...	2	2	6
,, ,, ♀	× *d*-glabrous red ♂	2	5	16
d-glabrous red ♀	× *d*-glabrous cream ♂ ...	3	14	29
,, ,, ♀	× *d*-glabrous sulphur-white ♂	4	147	163
d-glabrous sulphur-white ♀	× *d*-hoary white ♂	7	87	108
,, ,, ,, ♀	× *d*-glabrous red ♂	21	231	311
,, ,, ,, ♀	× *d*-glabrous white ♂	1	7	8
,, ,, ,, ♀	× *d*-glabrous azure ♂	3	35	44
,, ,, ,, ♀	× *d*-gabrous light purple ♂ ...	2	2	23
d-hoary azure ♀	× *d*-glabrous sulphur-white ♂	1	9	8
d-glabrous flesh ♀	× *d*-glabrous azure ♂ ...	1	2	3
d-glabrous light purple ♀	× *d*-glabrous red ♂	1	14	7
d-glabrous red ♀	× *d*-glabrous light purple ♂ ...	1	8	7
d-glabrous azure ♀	× *d*-glabrous red ♂	1	23	24
Totals exclusive of cases where suspected[1] creams were used		50	586	757
d-glabrous cream ♀	× *d*-hoary white ♂	1	13	13
,, ,, ♀	× *d*-glabrous sulphur white ♂	3	22	35
d-glabrous sulphur-white ♀	× *d*-glabrous cream ♂ ...	3	139	63
d-glabrous cream ♀	× *d*-glabrous flesh ♂ ...	1	12	10
d-glabrous flesh ♀	× *d*-glabrous cream ♂ ...	1	10	4
d-hoary azure ♀	× *d*-glabrous cream ♂ ...	1	3	6
Totals including cases where suspected[1] creams were used		60	785	888

Table showing the totals *obtained when the* F_1 *cross-breds from the above matings between eversporting forms were crossed back with one of the eversporting parent types.   (For details of the families, see Table VIII.)*

Type of Union		Number of matings	Number of singles	Number of doubles
Glabrous red ♀	× (glabrous red × glabrous sulphur-white) ♂ ...	2	48	50
Glabrous red ♀	× (glabrous sulphur-white × glabrous red) ♂ ...	3	31	26
(Glabrous sulphur-white × glabrous red) ♀	× glabrous red ♂	1	3	3
(Glabrous sulphur-white × glabrous red) ♀	× glabrous sulphur-white ♂	25	305	377
(Glabrous red × glabrous sulphur-white) ♀	× glabrous sulphur-white ♂	2	21	30
Glabrous cream × glabrous sulphur-white) ♀	× glabrous red ♂	2	13	19
	Totals	35	421	505

[1] Suspected, that is, of being of cross-bred origin and not truly eversporting.

As shown in an earlier account[1] and in the accompanying Tables, matings between two double-throwing parents invariably gave doubles in the next generation. We should expect, unless other complexities are indicated, that the results in such matings will be the same as when either d-parent is self-fertilised, and that the proportion of doubles obtained from a cross will, as in the case of self-fertilisation, furnish an index of the proportion of double-carrying ovules produced by the d-seed-parent.

Altogether 1673 plants were raised in the present experiments in F_1, from 60 matings between various d-strains, representing an equivalent number of ovules from 45 d-seed-parents; or, if we exclude all matings in which the cream plants K and L were employed on the ground of suspicion as to their purity, we have 1343 F_1 individuals from 50 matings in which 37 d-seed-parents were used. If all these 50 families are summed together, we get a total of 586 singles and 757 doubles, or almost exactly 7 s. : 9 d.[2] A certain number of these d-seed-parents were also self-fertilised, and we are therefore able to compare the effects of own pollen *versus* foreign pollen on identical individuals.

The results were as follows:

From crossing 15 individuals with pollen from		
d-individuals of other strains	248 singles	298 doubles
where a ratio of 7 s. : 9 d. would give ...	239 ,,	307 ,,
or 7·5 s. : 8·5 d. would give ...	256 ,,	290 ,,
From self-fertilisation of these same individuals	437 ,,	539 ,,
where a ratio of 7 s. : 9 d. would give ...	427 ,,	549 ,,
or 7·5 s. : 8·5 d. would give	457½ ,,	518½ ,,

Again, 35 matings were made, in which F_1 from two eversporting forms was crossed back with one of the eversporting parent types. If the 35 F_2 families are summed together, we get a total of

421 singles and 505 doubles,

where a ratio of 7 : 9 would give

405 singles and 521 doubles,

and a ratio of 7·5 : 8·5 would give

434 singles and 492 doubles.

[1] Rep. Evol. Committee, IV, 1908, Table II. p. 40.

[2] In certain cases the results obtained from one fruit were unexpectedly divergent from those of another, and a considerable sowing had to be made before an indication of the probable ratio was obtained. But where large numbers were recorded the results appeared sufficiently uniform to justify the inclusion of the whole series in one total as above.

Numbers approximating either to the one ratio or the other were similarly obtained when these F_1 cross-breds were *self*-fertilised. These results will be discussed later. (See Section V, and Table VII.)

From these facts it seems clear that among these eversporting forms self-breeding and inter-breeding give similar results.

IV. *Constitution of the zygote and segregation in the eversporting forms.*

In any attempt to construct a formula which shall represent the behaviour of the eversporting forms, so far as it is at present known, the following points must be taken into account:

(1) All the self-bred single descendants of an eversporting individual appear to be also eversporting.

(2) It also seems certain that all individuals of the eversporting types employed yield an excess of doubles. The evidence points to a proportion of $7 + x$ single to $9 - x$ double, the value of x being less than 1. We may take it that the occurrence of such a ratio precludes the possibility of the appearance of singles and doubles being determined by the presence or absence of *one* factor only.

(3) All the pollen grains of an eversporting individual apparently carry doubleness, whereas the ovules are mixed, some carrying doubleness and some singleness.

(4) The inheritance of singleness and doubleness appears to be quite independent of surface character (whether hoary or smooth) and of the character of the sap (whether coloured or colourless), but in certain cases, if not in all, it seems to be in some way bound up with the inheritance of plastid character (whether white or cream). In the present account therefore we may disregard surface character and sap colour, but it will be convenient to consider plastid character simultaneously with that of singleness and doubleness.

With regard to the conclusion given under (2) it may be noted that where more than one factor is concerned in the manifestation of any character it becomes *theoretically* possible for this character to appear on crossing, even though both parents are breeding true in regard to its absence. In a case, however, where the factors are not distributed equally among pollen and ovules, this unequal distribution may *in fact* prevent such a possibility, and this appears actually to be the case here. As yet no mating between two true-breeding singles has ever produced doubles. (For details of some of these cases see Report IV, Table III, p. 40.)

(**a**) General considerations in regard to singleness and doubleness apart from plastid character.

The requirements 1, 2, 3, stated above, which concern the general occurrence of singles and doubles apart from complications connected with plastid colour, would be met if we suppose

(1) That singleness—the dominant character—results from the presence of two factors (X and Y), doubleness from the absence of either or both.

(2) That in the eversporting forms these two factors are carried only *by the ovules* and exhibit partial gametic coupling[1]. The proportion of singles and doubles obtained points to a coupling either on a $7 : 1 : 1 : 7$ or on a $15 : 1 : 1 : 15$ basis. Breeding experiments on a much larger scale than it has yet been possible to attempt would be required to determine with certainty which term in the series represents the truth. But, as will shortly appear (see p. 324), certain results in which plastid character has also to be taken into account are more easily explained on the supposition of a $15 : 1 : 1 : 15$ series, and we may therefore adopt this value provisionally for the purpose of a working hypothesis.

On this view we may represent the eversporting zygote (so far as singleness and doubleness alone are concerned) thus

$$Xx \ Yy$$

and its gametes, where $2n$ are required to exhibit the whole series, in general terms thus[2]

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[1] Coupling of the kind here indicated was first described by Bateson and Punnett in the case of the Sweet Pea, where it was found that purple flower colour was partially coupled with long shape of pollen. (See Rep. Evol. Committee, III, 1906, p. 9, and IV, 1908, p. 3.) Several other instances of this kind are now known. For reference to some of the more recently investigated cases, see Bateson and Punnett, *Proc. Roy. Soc.* Series B, Vol. 84, 1911, p. 3.

[2] It is realised that the fact that the pollen of eversporting races appears only to carry doubleness merely proves the absence of X and Y *in combination* not of X alone or Y *alone*. The absence of either factor alone is deduced from the fact that all the singles of an eversporting race appear to behave similarly, which would not presumably be the case if some of the pollen carried X or Y and some did not. Were the pollen thus heterogeneous we should expect eversporting singles to be of two kinds, yielding different proportions of singles and doubles. We have no knowledge as to the cause of this inability on the part of the eversporting pollen to carry the factors X and Y. If we suppose that the quality maleness (M) in this case repels the factors X and Y, the assumption, though it accounts for the fact in question, carries us no further. It is almost unnecessary perhaps to add that when it is stated that the pollen is unable to carry a particular factor, the meaning which the statement is intended to convey is that the pollen is not carrying that factor in a form in which its presence can be detected.

Ovules	Pollen
$n-1$ XY	all xy
1 Xy	
1 xY	
$n-1$ xy	

or if n is taken as 16, thus

Ovules	Pollen
15 XY	all xy
1 Xy	
1 xY	
15 xy	

(**b**) Consideration of the relation of singleness and doubleness to plastid character.

All forms having colourless plastids, and breeding true in this respect, may be supposed to contain a factor W, and to be homozygous in respect of this factor. In true-breeding cream forms W is absent. In the sulphur-white race the case is more complex. The factor W, though present in some of the ovules, is evidently absent from the pollen, since matings with pure cream as ♀ yield only plants with cream plastids (see later p. 352, also Evol. Rep. IV. p. 39). Further there appears to be some complex relation between this factor W and the factors for singleness and doubleness, since, as previously stated, the sulphur-white race, even when self-bred, always gives a mixture of single whites and double creams with a small percentage only of double whites and apparently no single creams[1]. These results can be accounted for if we assume that in this form W is either coupled with, or repelled by, *one* of the two factors X or Y. The assumption that *repulsion* occurs can only be made to fit the results observed if other assumptions are also made involving further complexities; it will therefore be simpler to proceed on the hypothesis that the relation is one of coupling. We will suppose the coupling to be between W and X, we shall then

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[1] More than 2000 plants have been recorded, and none of the singles among them had cream plastids. The non-appearance of the single cream therefore seems hardly likely to be due to accident. Should this however eventually prove to be the case it would be unnecessary to assume the existence of any special relation between W and either X or Y (as described above), since the scheme of coupling described for the two factors X and Y extended to cover the case of *three independent* factors (X, Y and W) would give all four forms in the required proportion, viz. many single white and double creams, a few double whites and still fewer single creams.

express the composition of this and other eversporting forms more fully thus:

	Pure non-cream forms[1]		Sulphur-white race		Pure cream forms	
Zygote	$XxYyWW$		$XxYyWw$		$XxYyww$	
Gametes	ovules	pollen	ovules	pollen	ovules	pollen
	15 XYW	all xyW	15 XYW	all xyw	15 XYw	all xyw
	1 XyW		1 XyW		1 Xyw	
	1 xYW		1 xYw		1 xYw	
	15 xyW		15 xyw		15 xyw	

Expectation on self-fertilisation

480 single whites	480 single whites	480 single creams
544 double ,,	512 double creams	544 double ,,
	32 double whites	
	or	
7·5 single whites	7·5 single whites	7·5 single creams
8·5 double ,,	8·0 double creams	8·5 double ,,
	·5 double whites	

These formulae would give the uniform result of 7·5 singles : 8·5 doubles for all eversporting forms, and would explain the occurrence of a small percentage of double whites in addition to single whites and double creams, and the absence of single creams when sulphur-whites are self-fertilised. The fact that the number of these double whites is sometimes below, rarely above, the estimated proportion of ·5 in 16 or about 3 per cent. is an important point in favour of the adoption of 16 as the value for n rather than 8. Were a 7 : 1 : 1 : 7 series taken as representing the gametic output, the expectation in regard to double whites would be just twice the number given above.

We have now to see how far the assumptions made above in regard to the relations existing between the factors for plastid colour and for singleness and doubleness will satisfactorily explain the distribution of forms with white and cream plastids among the singles and doubles when the various eversporting forms are inter-crossed.

V. *Segregation in F_1 cross-breds derived from two eversporting forms, and statement of results obtained in F_2.*

As shown above (p. 320) matings between two eversporting forms were found to give a slight excess of doubles as in the case of self-fertilisation of either of the parents. This is in accordance with the

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[1] The term 'non-cream' is used to indicate any form with uncoloured plastids irrespective of the colour of the sap.

scheme suggested above (p. 323), according to which the distribution of the factors for singleness and doubleness is assumed to be the same for all eversporting forms. We should naturally expect that a condition which obtains in both parents would also hold good in their cross-bred offspring, and we may therefore conclude that, so far as the factors for singleness and doubleness are concerned, the general scheme of segregation in F_1 cross-breds derived from two eversporting forms will be the same as that put forward in the case of the parents (see p. 322).

The distribution of plastid colour needs further consideration, since in respect of this character reciprocal cross-breds from unions between eversporting cream and non-cream forms give different results. Matings of this type can be carried out in six different ways as shown below, where the unions 2, 4 and 6 are the reciprocals of 1, 3 and 5.

Mating	1	d-sulphur-white ♀	× d-non-cream ♂
,,	2	d-non-cream ♀	× d-sulphur-white ♂
,,	3	d-non-cream ♀	× d-cream ♂
,,	4	d-cream ♀	× d-non-cream ♂
,,	5	d-sulphur-white ♀	× d-cream ♂
,,	6	d-cream ♀	× d-sulphur-white ♂

The composition of the ovules and pollen uniting to produce the single plants in F_1 according to the scheme given above, together with a general statement of the results obtained in F_2 for those cases which have already been carried out, is given below.

	Constitution of the gametes uniting to produce the single plants in F_1		Results obtained in F_2			
Mating	Ovules	Pollen	Singles with white plastids	Singles with cream plastids	Doubles with white plastids	Doubles with cream plastids
1	XYW	xyW	many	none	many	none
2	XYW	xyw	(not yet carried out)			
3	XYW	xyw	many	none	none	many
4	XYw	xyW	{ (a) many	few	many	none
			{ (b) many	few	many	few (?)
5	XYW	xyw	(not yet carried out)			
6	XYw	xyw	(not yet carried out)			

Only three of these matings have as yet been carried to F_2. It is doubtful however whether the results of unions 2, 5 and 6, when available, will throw any further light on the relation existing between plastid colour and singleness and doubleness, since we may suppose

MATING 1. *Summary of results in* F_2.

Parental Types	Number of F_1 individuals used to produce F_2	Number of singles and doubles in F_2						Expectation on the supposition that F_1 yields 7·5 s. : 8·5 d.		Expectation on the supposition that F_1 yields 7 s. : 9 d.	
		Total singles	Total doubles	Singles with white plastids	Singles with cream plastids	Doubles with white plastids	Doubles with cream plastids	Singles	Doubles	Singles	Doubles
d-glabrous sulphur-white ♀ × *d*-glabrous red ♂	14	414	503	395	—	494	—	430	487	401	516
,, × *d*-glabrous azure ♂	28	269	415	246	—	402	—	321	363	299	385
,, × *d*-glabrous light purple ♂ ...	2	9	16	9	—	15	—	12	13	11	14
,, × *d*-glabrous white ♂	5	82	137	73	—	122	—	103	116	96	123
,, × *d*-hoary white (intermediate)¹ ♂	13	109	147	109	—	147	—	120	136	112	144
Totals	62	883	1218	832	—	1180	—	986	1115	919	1182

¹ So-called because the strains of this class are intermediate in *habit* between the annual and biennial forms.

that in case 2 the result will be the same as in case 3 which is already known; while in matings 5 and 6 the result will presumably be the same as if the seed parent had in each case been self-bred instead of cross-bred. We have then to consider the results in matings 1, 3 and 4 in the light of the assumptions made above.

Mating 1. d-sulphur-white ♀ × d-non-cream ♂.

Five different matings of this kind were made (see p. 326).

This type of mating gives only white plastids in F_2, a result fully in accord with expectation. For the sulphur-white ovules which carry creamness, by assumption, also carry doubleness; hence when this race is crossed with any non-cream form whose pollen carries doubleness, cream will not presumably reappear in any succeeding generation. It will have been bred out completely, though in the recessive condition, in the F_1 *non*-cream doubles. Thus only those sulphur-white ovules which carry the white plastid factor give rise to singles in F_1. These F_1 singles are therefore all homozygous as regards the factor W, since the mating will have been between XYW ovules and xyW pollen; segregation in their case may therefore be expected to proceed on the same lines as in a *pure-bred* d-race with uncoloured plastids, and to yield a similar proportion of singles and doubles. As regards the question whether a ratio of 7·5 s. : 8·5 d. or 7 s. : 9 d. more nearly represents the facts, it happens that the numbers obtained in this case agree better with the latter alternative (7 s. : 9 d.). It is just worth noting however that the mating in which the largest record was obtained, both absolutely and in proportion to the quantity of seed sown, and in which therefore the result might be supposed to be the most reliable, viz. the mating with d-glabrous red, leaves either alternative equally probable. In three out of the five matings the experiment was carried to F_3, where the complete breeding out of the cream was further confirmed, but where again the evidence is not quite decisive as between the two ratios. For, though the sum of the three totals gives 7 s. : 9 d., one of the two larger sowings gives almost exactly 7·5 s. : 8·5 d. The results are summarised below (see p. 328).

We may then conclude that in the unions of the form d-glabrous sulphur-white ♀ × d-glabrous non-cream ♂ segregation in single F_1 plants and in later self-bred generations is like that in any *pure-bred* eversporting glabrous form with white plastids.

22—2

MATING 1. *Summary of results in* F_3.

Parental Types	Number of F_2 individuals used to produce F_3	Number of singles and doubles in F_3						Expectation on the supposition that F_2 yields 75 s. : 85 d		Expectation on the supposition that F_1 yields 7 s. : 9 d	
		Total singles	Total doubles	Singles with white plastids	Singles with cream plastids	Doubles with white plastids	Doubles with cream plastids	Singles	Doubles	Singles	Doubles
d-glabrous sulphur-white ♀ × *d*-glabrous red ♂ ...	6	154	235	154	—	235	—	182	207	170	219
,, ,, × *d*-glabrous azure ♂ ...	13	199	221	155	—	203	—	197	223	184	236
,, ,, × *d*-glabrous light purple ♂ ...	1	6	6	6	—	6	—	6	6	5	7
Totals	20	359	462	315	—	444	—	385	436	359	462

MATING 3. *Summary of results.*

Parental Types	Number of F₁ individuals used to produce F₂	Number of singles and doubles in F₂						Expectation on the supposition that F₂ yields 7s. : 85d.		Expectation on the supposition that F₂ yields 7s. : 9d.	
		Total singles	Total doubles	Singles with white plastids	Singles with cream plastids	Doubles with white plastids	Doubles with cream plastids	Singles	Doubles	Singles	Doubles
d-glabrous red ♀ × d-glabrous cream ♂ (Plant B)[1] ...	12	241	258	237	—	—	258	234	265	218	281
" " (Plant H) ...	1	29	23	28	—	—	20	24	28	23	29
Totals	13	270	281	265	—	—	278	258	293	241	310

[1] Where cream is used the results are given separately for each individual merely for convenience in considering the composition of the cream material (see p. 314). In this case there is no reason to suppose that the slight excess of singles obtained from plant H in F₂ is more than an accidental variation from the usual result of a slight excess in the other direction.

Mating 3. *d*-glabrous non-cream ♀ × *d*-glabrous cream ♂.

Only one mating of this kind was made, two cream plants being employed as the pollen parents (see p. 329).

The totals from this mating were 270 singles and 281 doubles, a result which agrees with the view provisionally adopted that $7 + x : 9 - x$ rather than $7 : 9$ probably represents the true ratio of s. : d. All but 8 plants were flowered and the 543 individuals recorded included singles with white plastids and doubles with cream plastids, but the reciprocal combinations of whiteness with doubleness and singleness with creamness did not appear. Now in matings of this type all single F_1 plants will presumably be derived from the meeting of XYW ovules with *xyw* pollen, i.e. from unions in which all three dominant factors are carried by the ovules and none by the pollen. In other words the union is a union between the combination white plastid colour with singleness brought in by the female parent and creamness with doubleness brought in by the male. Since out of a total of 543 plants in F_2 all were either singles with white plastids or doubles with cream plastids, it follows that redistribution of the factors in such a way as to lead to the combination of singleness with creamness or of doubleness with whiteness either does not occur when segregation takes place, or it must occur very rarely. The above result seems to necessitate not only that the F_1 pollen should, as already inferred on other grounds (see p. 321), all carry doubleness, but also that it should all carry creamness. There is in fact a strong presumption that we have in these F_1 plants a condition similar to that obtaining in the sulphur-white race. In both cases the singles result from the union of the same combinations of factors (XYW ♀ × *xyw* ♂). If none of the pollen of the sulphur-white can carry the factors XYW although all three are present in the sulphur-white zygote, it need not surprise us if the same should hold good for an F_1 cross-bred of the same composition. The absence in F_2 of singles with cream plastids would thus be explained. The absence of doubles with white plastids would seem to show that the factor W must stand in some different relation to X and Y in the pure white race to what it does in the sulphur-white. In the present case W, which is introduced into the cross in combination with XY, appears only to occur in combination with XY in the gametes of F_1. If any gametic combination is formed in which W is dissociated from X or Y, such as is presumed to occur in the sulphur-white, it must evidently be rare, since no indication of such a gametic combination was apparent in an F_2 population numbering 543.

If the above account is correct, then so far as can be seen a similar result will ensue in the succeeding self-bred generations F_3, F_4, &c., since in each case the singles produced by self-pollination would appear to result from the meeting of XYW ovules and xyw pollen. The record obtained in F_3, so far as it goes, is entirely confirmatory. 54 families were raised and *all* included some doubles, a result which may be taken to establish the double-carrying character of all the F_1 pollen grains from which the F_2 parents were descended. The totals obtained in the whole number of F_3 families were 354 singles and 372 doubles. Only a few plants in each family were flowered; they proved to be again all singles with white plastids and doubles with cream plastids, thus confirming the results obtained in F_2.

We are thus led to conclude in regard to unions of the form d-non-cream ♀ × d-cream ♂: (1) That segregation in the male cells of the cross-breds exhibits the same peculiarity as in a sulphur-white, and that the pollen grains do not carry XYW, although all these three factors are present in the F_1 zygote. Thus the pollen of F_1 is similar to the pollen of the ♂ parent which was used to produce it. (2) That the factor for whiteness (W) which is brought into the pedigree by the ♀ parent in combination with X and Y remains in association with X and Y in the ♀ gametes of F_1. If exceptions occur in either case they must be extremely rare.

Mating 4. d-glabrous cream ♀ × d-glabrous and d-hoary non-cream ♂.

The matings were the converse of those just described, d-cream being here used as the ♀ parent, d-red as the ♂.

Three different crosses of this kind were made, three cream plants being used as male (see p. 332).

It will be convenient to consider the results under (*a*) and (*b*) separately, since it may be that the appearance of an F_2 single with cream plastids in (*b*)—a combination not recorded in (*a*)—is due to the impure nature of the cream plant used as the pollen parent in the (*b*) mating.

In matings of this type all single F_1 plants will presumably be derived from the union of XYw ovules with xyW pollen, so that in this case only X and Y are introduced by the female parent, W being brought in by the pollen. We may therefore assume that here W will be carried by at least some of the F_1 pollen, though whether by all, and if not by all, by what proportion, we cannot on purely *a priori* grounds

predict. Similarly we may suppose that some of the F_1 ovules which carry XY will lack W, though whether all will prove to be thus deficient we also cannot foretell.

MATING 4. *Summary of results.*

		Number of F_1 individuals used to produce F_2	Total singles	Total doubles	Singles with white plastids	Singles with cream plastids	Doubles with white plastids	Doubles with cream plastids
					Results obtained in F_2			
(a)	*d*-glabrous cream (Plant *H*) ♀ × *d*-glabrous red ♂	1	13	13	12	—	13	—
		same plant after 3 years	2	4	2	—	4	—
	,, ,, (Plant *G*) ♀ × *d*-glabrous red ♂	3	36	53	36	—	52	—
		1 of these after 3 years	94	141	79	—	110	—
	,, ,, (Plant *G*) ♀ × *d*-glabrous white ♂	2 after 2 years	97	175	56	—	149	—
	Totals in the case of the immediate sowings	—	49	66	48	—	65	—
	,, ,, ,, delayed sowings[1]	—	193	320	137	—	263	—
(b)	? *d*-glabrous cream ♀ (descendant of Plant *K*) × *d*-hoary white ♂ (intermediate strain)[2]	2 (after 3 years)	9	19	10	1	16	—

The experimental result was an F_2 of 49 s. and 66 d. in the case of the immediate sowings, and 193 s. and 320 d. in those that were delayed until the second or third year after harvesting. 513 plants were flowered and all had white plastids. Singles and doubles with cream plastids either do not occur, or if they are formed they must be present in very small numbers. We may therefore conclude that all (or all but very few) of the F_1 pollen grains must carry whiteness as well as doubleness. Thus both here and in the reciprocal type of cross, so far as experiment has yet gone, we find that the F_1 pollen appears to carry chiefly if not exclusively the particular combination of factors which is present in the pollen of the father. Although the F_1 zygote is heterozygous in regard to these factors, the allelomorphs brought in by the mother appear to be absent (or if not wanting altogether then very rare) in the male cells of the cross-bred. But if all (or almost all) the F_1 pollen is carrying W it is evident that the distribution of W among

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[1] See Appendix, note 1, p. 361.   [2] See note p. 326.

the ovules can only be certainly determined by breeding to F_3, since the result in F_2 will be the same (or almost the same) whatever be the proportion of ovules containing W to those lacking it.

We may surmise however from the behaviour of the cross-breds in the reciprocal union that most (if not all) of the ovules carrying single-ness will lack W, and conversely that W will be present in most (if not all) of those which carry doubleness. There seems in fact strong reason to suppose that in matings between eversporting forms of unlike plastid colour, the plastid colour allelomorphs are associated in F_1, chiefly or exclusively, the one with singleness the other with doubleness according as each is associated with singleness or doubleness in the germ cells which united to produce F_1.

The cream plant used as the seed-parent in experiment (b) was a descendant of plant K, an individual which yielded an excess of doubles on self-fertilisation but which nevertheless is under suspicion of not having been a genuine eversporting type, since some of its offspring were found to breed true to singleness (see p. 315). This being so, it is not improbable that this particular descendant of K was also not genuinely eversporting but some form of cross-bred. It is therefore at present uncertain whether we shall be right in ascribing the appearance of the one single with cream plastids in the case of the (b) mating to the spurious character of the cream plant used as the ♀ parent in this case, or whether we are to suppose that this form would also have appeared in the (a) results if a larger sowing had been made. For it is not certain that a total of $185 + 328 = 513$ plants, recorded when the cream plants G and H were used, is sufficiently large to exhibit the complete series in F_2.

We may then state the conclusions in regard to matings between eversporting forms thus:

1. Segregation in F_1 cross-breds from two eversporting forms follows the same course as in the eversporting parents, so far as the factors X and Y are concerned. (See above, p. 320, where it is shown that cross-breeding and inter-breeding between these forms give the same proportion of singles and doubles.)

2. If the eversporting parents are of unlike plastid colour, all or almost all the F_1 pollen carries the same allelomorph for plastid colour as the pollen which was used to produce F_1; similarly, the other member of the pair, which is borne only or chiefly by the ovules, is borne only or chiefly by those ovules carrying the same combination of factors as the ovule from which the F_1 plant in question was derived, viz. the

combination XY. Thus, where F_1 is derived from d-non-cream ♀ × d-cream ♂, all or almost all the F_1 pollen carries w, whereas W is carried only or chiefly by the ovules carrying XY. When, on the other hand, F_1 is derived from d-cream ♂ × d-non-cream ♀ it is W which is borne by all or almost all the pollen, and w only, or chiefly by the ovules carrying XY.

It remains to consider how far the scheme suggested will serve to explain the results obtained when eversporting forms are bred with *true-breeding* types.

VI.   *Constitution of the zygote and segregation in the pure-breeding (non-double-throwing) strains.*

The only information to be gained from the self-fertilisation of the pure-breeding forms is that they breed true to singleness and to plastid character. From this fact together with the evidence obtained from the testing of the ovules and pollen independently by crossing, which shows that the above result is not due to any complete coupling of the factors concerned with either kind of germ cell, it follows that all these forms are homozygous as regards X and Y: those with white plastids are also homozygous as regards the presence of W, those with cream plastids as regards its absence ($= w$). A detailed consideration of the results of crossing shows however that the simple formulae XYW and XYw do not fully express the complex relations existing between these pure-breeding strains and the eversporting forms when the two are inter-crossed. It is evident from the results of these matings that X and Y do not occur under the same conditions in the pure-breeding strains as in the eversporting forms; otherwise the results as regards the occurrence of doubles would presumably be the same when the XY ovule of a pure-breeding individual meets the xy pollen of an eversporting type, as when the XY ovule of an eversporting type is either fertilised with its own pollen or with that of any other eversporting form. But this is not the case, the percentage of doubles in the one case (pure-breeding × eversporting) being always very much fewer than in the other (eversporting × eversporting).

The results of matings between typical d- and *no-d*-strains in fact suggest that the resulting F_1 cross-breds are only able to form those gametic combinations of the $XxYy$ allelomorphs from which they themselves arose; if gametes are formed carrying different combinations of these factors, they must be extremely rare. Thus when an F_1

cross-bred has been produced by the union of germ cells carrying XY and xy respectively, it will again produce germs of XY and xy composition, but the combinations Xy and xY apparently do not occur. X and Y behave in fact as though they were coupled, a condition which we may represent thus $\widehat{XY}$. It will be well to point out that inability to throw doubles need not necessarily imply that an individual is homozygous in regard to the condition in which the factors XY are present. For we may suppose that if at any time an XY ovule of an eversporting form were by chance crossed with pollen from a pure-breeding single of $\widehat{XY}$ composition—a possibility which might easily come to pass now and again when the different strains are grown side by side in the open—we should at once get a zygote of $\widehat{XY}XY$ composition. This zygote and all its posterity would behave as any true-breeding single so long as self-fertilisation or inter-crossing among the offspring continued. The heterozygous nature of a certain proportion of the individuals would remain undetected and would be perpetuated indefinitely under these conditions. It would only become apparent if any of these individuals were crossed with an eversporting form; then the different proportion of doubles occurring in F_2 families derived from sister F_1 plants, on crossing with an eversporting form, would disclose the peculiar heterozygous nature of the nevertheless true-breeding parent.

Similarly it would seem that among true-breeding singles with white plastids some may have the factor W coupled in some or all the germ cells with the $\widehat{XY}$ group—a condition which may be indicated thus $\widehat{XYW}$—so that when such germ cells unite with an xyw ovule or pollen grain of an eversporting form the resulting F_1 cross-bred is unable to form the combinations XYw or xyW. In other cases on the other hand W appears not to be thus coupled, the results indicating a redistribution of the factors in the ordinary way. Individuals breeding true to singleness and to whiteness may therefore conceivably be of six different kinds, according as the factors X, Y, and W are wholly, partially, or not at all coupled in the zygote, as shown below.

Possible types of true-breeding singles with white plastids.

	Zygote Homozygous	Gametes
1	$XYWXYW$	all XYW
2	$\widehat{XY}W\widehat{XY}W$	all $\widehat{XY}W$
3	$\widehat{XYW}\widehat{XYW}$	all $\widehat{XYW}$

	Zygote Heterozygous	Gametes
4	$\widehat{XY}WXYW$	$\widehat{XYW}$ and XYW
5	$\widehat{XYW}XYW$	$\widehat{XYW}$ and XYW
6	$\widehat{XYW}\widehat{XYW}$	$\widehat{XYW}$ and $\widehat{XYW}$

VII. *Segregation in F_1 cross-breds derived from unions between ever-sporting and non-double-throwing forms, and statement of the results obtained in F_2.*

The various possible unions coming under this head are the following:

A.　Eversporting form employed as seed parent

Mating	1	d-cream ♀	× *no-d*-cream ♂
,,	2	d-non-cream ♀	× *no-d*-non-cream ♂
,,	3	d-cream ♀	× *no-d*-non-cream ♂
,,	4	d-non-cream ♀	× *no-d*-cream ♂
,,	5	d-sulphur-white ♀	× *no-d*-cream ♂
,,	6	d-sulphur-white ♀	× *no-d*-non-cream ♂

B.　Eversporting form employed as pollen parent

Mating	7	*no-d*-cream ♀	× d-cream ♂
,,	8	*no-d*-non-cream ♀	× d-non-cream ♂
,,	9	*no-d*-non-cream ♀	× d-cream ♂
,,	10	*no-d*-cream ♀	× d-non-cream ♂
,,	11	*no-d*-cream ♀	× d-sulphur-white ♂
,,	12	*no-d*-non-cream ♀	× d-sulphur-white ♂

In the case of matings 7—12 where the eversporting form is used as the pollen parent we may expect *every* F_1 family to yield doubles in F_2, whereas in the reciprocal unions (matings 1—6) *some* of the F_1 individuals may be expected to yield doubles and *some* to breed true to singleness. Reference to Tables IV and V will show that such was the case in each of the 8 types of union which have already been carried out.

With regard to the proportion of doubles occurring in those F_2 families which are mixed, it has been stated in the earlier accounts[1] that they occur in the proportion of the simple Mendelian recessive,

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[1] *loc. cit.*

viz. 1 in 4. This appears undoubtedly to be the case in the great majority of families, but there are a certain number of cases in which a considerably lower percentage of doubles was obtained, while occasionally the proportion was in excess of this amount. The cases in which the proportion of doubles is very small are so marked and, in some unions, of such frequent occurrence, that it seems clear that they cannot be regarded as other than genuine—that they must in fact represent a distinct ratio and not an extreme variation from the usual 3 s. : 1 d. On the other hand it seems highly probable that in the one or two cases where the proportion of doubles recorded is distinctly higher than 1 in 4 the excess is accidental.

It is the frequent occurrence of numbers approximating to the ratio 3 s. : 1 d. which suggests that, in the *no-d*-strains, the factors for singleness (X and Y) are so coupled that re-combination with x and y in the gametogenesis of F_1 cannot occur, in the manner described above for matings between two eversporting forms, where ovules with X and Y *uncoupled* meet xy pollen grains. This condition of singleness which is typical of non-double-throwing forms is, as stated above, conveniently represented thus $\widehat{XY}$: and since as regards singleness and doubleness, reciprocal heterozygotes of similar composition give similar results, we may write $\widehat{XY}$ for both the ovules and the pollen of a typical *no-d*-form. But, as explained above (p. 335), a single might breed true and yet not be pure-bred, a fact which should not be overlooked in considering any unexpected result in F_2. For in any cross between an eversporting and a true-breeding type, made in the form $d \; ♀ \times no\text{-}d \; ♂$, a certain number of the F_1 singles will have the composition $XY \; \widehat{XY}$; they will breed true to singleness, and on self-fertilisation will be indistinguishable from a pure-bred true-breeding single having the composition $\widehat{XY} \; \widehat{XY}$. But the *cross*-bred true-breeding single will presumably behave differently from a typical *pure*-bred single, when crossed with an eversporting form; since in the one mating the xy germ cells of the d-type will unite with certain germ cells in the *no-d*-type carrying an uncoupled XY group, and in the other, not. We have already seen that of the double-throwing plants assumed at first to be pure-bred eversporting, some were probably cross-bred[1], and it may well be that now and again the same may be found to be the case with a supposed type single. From such a true-breeding but

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[1] See pp. 313—317 where an account is given of the behaviour of commercial samples of the white and cream strains.

heterozygous single, when crossed with an eversporting form, we might well expect a proportion of the F_1 plants to yield a higher percentage of doubles than 1 d. : 3 s. Of such cases however we have as yet no certain example. It is otherwise however as regards those F_2 families which show a deficiency of doubles. Some of these cases, at least, seem beyond question, but until we have a fuller understanding of the real meaning of coupling it is difficult to obtain a clear insight into their cause.

The results seem to show that the lower proportion of doubles obtained from some F_1 cross-breds in matings where sister F_1 plants gave 3 s. : 1 d. cannot be considered in all cases as an effect due to *either one* of the parents apart from the other, but must be regarded as due to a *combination* of factors brought together by their union. It was found, for example, that the same true-breeding individual may give only the usual proportion of doubles (3 s. : 1 d.) in F_2 when crossed with one eversporting strain, but will show a marked deficiency of doubles in some families when crossed with another d-strain (see Table IV, where 6 F_1 derived from the union *no-d*-cream × *d*-azure all gave the usual proportion of double plants, while in F_2 from a mating with *d*-light purple, where the same cream individual had been used as the seed parent, one or two families indicated a marked deficiency of doubles). These facts suggest the possibility that the conditions which result in the production of a single or a double may, in some cases, be more complex than those represented in the simple formula hitherto employed, according to which the occurrence of a single is attributed to the presence of two factors (XY), the occurrence of a double to the absence of either or both. This may remain true, and yet it may also be that more than one such pair of factors exists, and that the presence of the two members of one *or* other pair will lead to the production of a single. The complementary distribution of the two members of a second pair ($X'Y'$) among some of the d- and *no-d*-strains respectively would lead to an increased production of singles in F_2 as the result of a union between a d- and a *no-d*-strain which happened to contain the complementary factors, if these factors are borne by ovules and pollen alike; whereas unions between two d-, or between two *no-d*-strains would be unaffected by the presence of one only of the second pair of factors. It is in fact difficult to see how otherwise results such as those obtained in mating 8 (see p. 341) are to be explained, since it seems hardly possible to suppose that the discrepancies can be due to a mere chance variation.

Details of the several matings.

i.   The parents are *alike* in plastid colour, and are homozygous as regards the allelomorph concerned (*W* or *w*).

Mating 1.   *d*-cream ♀ × *no-d*-cream ♂.   Not yet carried out.

Mating 7 (reciprocal cross).   *no-d*-cream ♀ × *d*-cream ♂.   Not yet carried out.

Mating 2.   *d*-non-cream ♀ × *no-d*-non-cream ♂.

As stated above (p. 336) the expectation in such cases is that of the F_1 plants, some will breed true to singleness, and some will yield both singles and doubles in F_2.   The results of several matings of this type have already been recorded[1].   More recently another experiment of this kind has been carried out on a considerably larger scale.   The two sets of results are summarised below:

Parental Types		Total number of F_1 plants tested	Number of F_1 plants which gave only singles in F_2	Number of F_1 plants which gave a mixture of singles and doubles in F_2
[2]*d*-glabrous red ♀	× *no-d*-hoary white (*incana*) ♂	1	0	1
[2]*d*-glabrous flesh ♀	× ,, ,, ,, ♂	1	0	1
[2]*d*-glabrous dark purple ♀	× *no-d*-glabrous white ♂	2	1	1
[2]*d*-glabrous copper ♀	× *no-d*-glabrous flesh ♂	1	0	1
[2]*d*-glabrous dark purple ♀	× *no-d*-glabrous light purple ♂	1	0	1
d-glabrous red ♀	× *no-d*-glabrous white ♂	25	16	9
	Totals	31	17	14

Altogether 31 F_1 *plants were tested;* 14 *yielded singles and doubles in* F_2 *while* 17 *gave only singles, where the expectation would be an almost corresponding excess the other way, i.e. a proportion of* 15 *breeding true :* 17 *which give doubles*[3]. *Experience has shown however in the case of another character, viz. hoariness and smoothness, that where the expectation is as near equality as in this case a corresponding excess on the wrong side is within the range of variation which we may expect.*

With regard to the *proportion* of singles and doubles in the mixed F_2 families it seems probable that the plants used as parents were true to type in constitution (viz. $XYxy$ and $\widehat{XY}\widehat{XY}$ respectively) and that the real ratio in every mixed family in F_2 was 3 s. : 1 d.   If we add

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[1]   Reports to the Evolution Committee.

[2]   Recorded in Report II, p. 37.

[3]   On the assumption, i.e. that the gametic series is on a 15 : 1 basis, see p. 322.

together the numbers obtained in the 9 mixed families in the last experiment (see Table V), we get a total of

371 s. and 115 d.,

where a ratio of 3 s. : 1 d. would give

364·5 s. : 121·5 d.

Though in two of the families the proportion of doubles was distinctly less than 1 in 4, it seems more likely, on the whole, that these are cases of accidental variation in the direction of deficiency from the ratio 3 s. : 1 d., than that they represent some considerably higher ratio such as evidently occurs in certain other matings. Assuming the constitution given above we may suppose that in the gametogenesis of F_1 an equal number among the pollen and the ovules carry the combinations $\widehat{XY}W$ and xyW (or XyW or xYW as the case may be). The gametic types would be simply expressed thus

Ovules	Pollen
$\widehat{XY}W$	$\widehat{XY}W$
xyW	xyW

in the case of an F_1 plant derived from an xy ovule, a corresponding substitution being made in the case of an F_1 plant derived from an Xy or an xY ovule. This being so, we should expect the same result in F_3 from the F_2 singles, as was obtained in F_2 from the F_1 plants; and this was the case. Of three F_2 sister plants which were self-fertilised, two gave a mixture in a proportion approximating to 3 s. : 1 d. (viz. 20 s., 9 d. and 5 s., 2 d. respectively) and one gave a family of 21 all single.

The F_2 families composed entirely of singles will have been produced by those F_1 plants which were derived from the union of XYW ovules and $\widehat{XY}W$ pollen. In all these families the double character will have been bred out completely, so that not only will doubles be absent in them, but they will be wanting in all later generations derived from such F_2 families. Confirmatory evidence of this fact was obtained both in F_3 and F_4, after which the experiment was brought to an end. The F_3 generation was raised from 41 self-fertilised F_2 plants belonging to 11 out of the 16 all-single families, and consisted of 898 plants all of which were single. In F_4 seven families numbering all together 77 individuals were again all single.

We may now consider the reciprocal cross.

Mating 8. no-d-non-cream ♀ × d-non-cream ♂.

The expectation in this case is that all F_1 plants will yield a mixture of singles and doubles in F_2.

A few experiments of this kind are given in the Evolution Reports, and others have been carried out since (see Table IV). The results in both cases are summarised below:

Parental Types		Total number of F_1 plants tested	Number of F_1 plants which gave only singles in F_2	Number of F_1 plants which gave a mixture of singles and doubles in F_2
[1] no-d-glabrous flesh ♀	× d-glabrous dark purple ♂	1	0	1
[1] no-d-glabrous white ♀	× d-glabrous copper ♂	1	0	1
[1] ,, ,, ♀	× d-glabrous red ♂	2	0	2
,, ,, ♀	× ,, ♂	46	0	46
no-d-hoary white (Brompton) ♀ ×	× ,, ♂	2	0	2
no-d-glabrous flesh ♀	× d-hoary white (intermediate) ♂ [2]	1	0	1
,, ,, ♀	× d-glabrous light purple ♂	7	0	7
	Totals	60	0	60

Altogether 60 F_1 *plants were self-fertilised and all gave a mixture of singles and doubles in* F_2. In the great majority of the families the ratio approximated to 3 s. : 1 d., in fact, in all but the last mating it can hardly be doubted that this represents the real ratio. If we take the case where the largest number of F_1 plants were bred from (as likely to furnish the most reliable result), and sum all the families (46) together, we get a total of 1640 s. and 505 d., where 1609 s. and 536 d. would have been an exact result. In the case of the mating between no-d-flesh and d-light purple however there is a very large deficiency of doubles in certain families, and it is evident that here some further complication is present. The question that arises is, whether this result is due to the particular constitution of *one* of the two parents, or whether it is the result of a combination of factors, some of which are brought in by the one parent, some by the other. This point is not easy to determine; on the whole, however, the evidence may be taken to point to the latter alternative, other factors being concerned besides X and Y in the manner suggested above (p. 338). The conclusions indicated by the series of results bearing on the point may be put thus:

1.   The no-d-glabrous flesh individual used as seed parent in the union with d-light purple did not happen to be employed in any other

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[1] Recorded in Report II, p. 37.

[2] See note, p. 326.

mating, but several sister plants gave a deficiency of doubles in several F_2 families when used either as seed or pollen parent in matings with various sulphur-whites—the only other d-form besides light purple with which flesh was crossed. Thus from one sister plant, used as the pollen parent to fertilise a particular sulphur-white, five F_2 families were obtained, composed as follows:

	Single	Double
	37	3
	30	3
	23	2
	24	5
	39	11
Totals	153	24

Now this particular sulphur-white was used in many matings. It gave a distinct excess of doubles, as we should expect, both when self-fertilised (viz. 5 s., 11 d.) and when crossed with pollen from five other eversporting forms, the seven F_1 families thus produced, comprising altogether 57 s., 95 d. 29 F_2 families raised from these latter matings gave a total of 418 s. and 597 d. We have therefore every reason to suppose that this particular sulphur-white was producing as large a proportion of ovules carrying doubleness as the typical eversporting plant. It therefore looks as though the deficiency observed in F_2 from the mating between flesh and this particular sulphur-white could not be attributed wholly to the sulphur-white. But if the flesh parent is partly or wholly responsible for the deficiency in this case, then we shall probably be right in regarding the flesh parent as similarly responsible in other matings where sister plants were employed.

2. On the other hand the d-glabrous light purple individual used as the pollen parent in the union with *no-d*-flesh was also similarly employed in matings with two *no-d*-cream individuals. In both these matings there was a distinct deficiency of doubles in F_2. Nine F_1 cross-breds in the one case gave 186 s. and 20 d., 5 F_1 cross-breds in the other gave 75 s. and 9 d. Now one of these same cream plants was also similarly used as the ♀ parent in a mating with d-glabrous azure, and here none of the F_2 families showed a deficiency, hence the cause of the deficiency in the mating between cream and light purple cannot be ascribed altogether to the cream, but must be due, wholly or in part, to the light purple individual which was used as the pollen parent in the mating with flesh as well as with cream.

3. These results can be harmonised on the assumption that in addition to X and Y a second pair of factors $X'Y'$ are concerned in the determination of singles and doubles, as suggested above (p. 338), and that these factors have a complementary distribution in some of the d- and no-d-strains[1]. Thus the presence of Y' in the no-d-strains flesh and cream, and of X' in d-sulphur-white and d-light purple but not in d-azure (in the case of those individuals used in these experiments), would mean a higher percentage of singles in F_2 than 3 s. : 1 d. after crossing the flesh or cream with the two d-forms, sulphur-white and light purple, but not after crossing with azure.

We get confirmatory evidence of the genuine nature of this high proportion of singles from the results in F_3. We should expect from analogy with simpler cases that F_2 would behave differently from F_1 in that not all the singles would yield a mixed offspring but that about one-third would prove to breed true to singleness. Those F_2 singles which yielded a mixture would presumably give the same proportions as the F_1 plants. This was found to be the case in the one kind of mating in which the experiment was carried to F_3. In the case of the mating no-d-glabrous flesh $\female \times d$-glabrous light purple $\male$, 14 F_2 singles were self-fertilised to produce F_3. Disregarding one family of 8 singles as indecisive we find that among the remaining 13 families 4 were composed entirely of singles, and 9 included a mixture of singles and doubles; in two cases a proportion of about 3 s. : 1 d. was recorded, in the other 7 the proportion of singles was considerably higher.

ii. The parents are of *unlike* plastid colour; each is homozygous in the allelomorph concerned (W or w).

In these cases we have to consider not only the *total* number of singles and doubles obtained, but also the *proportion* of each form having white and cream plastids respectively.

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[1] A somewhat similar case in which the recessive form was found to occur in an extremely small proportion in F_2, owing to the presence of several factors in F_1, any one of which *alone* sufficed to produce the dominant form, has already been investigated and fully described by Nilsson-Ehle. This observer finds that if two wheats are crossed together one having red grains and the other white, plants with white grains only occur in F_2 in the proportion of 1 in 64. This, he explains, is due to the existence in the red wheat of three factors (R_1, R_2, R_3), the presence of any *one* of which will suffice to render the grain red. Hence only those F_2 plants in which *all three* factors are absent will have white grains, and these will only occur in the proportion of 1 in 64. (See Nilsson-Ehle, *Kreuzungsuntersuchungen an Hafer und Weizen*, Lund, 1909.) The Stocks appear to offer a parallel but more complex case, as in this instance *pairs* of factors instead of *single* factors are concerned.

Mating 3. *d*-cream ♀ × *no-d*-non-cream ♂.

Summary of results. For details see Table V.

Only one kind of mating of this type was made, viz. *d*-glabrous cream ♀ × *no-d*-glabrous white ♂. The *d*-cream plant *M* as ♀ was crossed with the *no-d*-white plant *J* as ♂, and two *F*₁ descendants of the *d*-cream plant *K* as ♀ were crossed with an *F*₁ descendant of plant *J* as ♂ (see pp. 314—317 and Table II). Now plant *K*, it will be recalled, was a sporting cream which gave excess of doubles, but which was under suspicion of being a *cross-bred* cream since some of its offspring appeared to breed true to singleness. At present therefore we must accept the results obtained from this plant with some reserve until they have been confirmed with material that is beyond question.

In accordance with expectation some *F*₁ families gave a mixture of singles and doubles, others bred true to singleness. In the mixed *F*₂ families the proportion of singles and doubles was evidently 3 s. : 1 d. with one doubtful exception; the bulk of the plants were singles with white plastids and doubles with cream plastids, the former being in excess, but a small proportion of singles with cream plastids, and doubles with white plastids occurred in some cases. The *F*₂ families containing only singles were composed almost exclusively of non-creams, only 7 individuals in a total of 420 having cream plastids; these 7 occurred in 2 *F*₂ families derived from the suspected cream.

Altogether 26 *F*₁ plants were self-fertilised to produce *F*₂. 14 of the *F*₂ families were mixed, 12 were composed only of singles. Although two or three of these latter families are too small to put their purity beyond doubt, and may therefore possibly cause the percentage of all-single families to appear slightly higher than it actually is, the result as it stands cannot be far from the truth, and agrees well with the expectation of $7 + x$ breeding true to $9 - x$ giving both singles and doubles.

In the case of the *mixed* *F*₂ families, the *F*₁ parent was presumably derived from the union of

$$xyw$$
or Xyw
or xYw ovules with $\widehat{XYW}$ pollen

and a scheme of gametogenesis which would give the observed result, where all four forms occurred in *F*₂, might be imagined thus in the

first case, the appropriate substitutions being made for the alternative cases :

Ovules	Pollen
$n-1$ $\widehat{XY}W$	$n-1$ $\widehat{XY}W$
1 xyW	1 xyW
1 $\widehat{XY}w$	1 $\widehat{XY}w$
$n-1$ xyw	$n-1$ xyw

where the distribution of $\widehat{XY}$, xy, W and w is the same among ovules and pollen, but where partial coupling between the plastid colour factor and the factors for singleness and doubleness occurs in such a way, that the two most frequently occurring terms in the series represent the combinations received from the parents, the two rarer terms the recombinations of these factors.

The conception that heterozygotes containing the same components, but having received these components combined in different ways, may form different gametic series has recently been put forward by Bateson and Punnett[1] in explanation of certain facts observed in the course of their experiments with the Sweet Pea. In certain cases where two separate pairs of allelomorphs are concerned, and where particular combinations occurred in the gametic series with greater frequency than others, they found that the results obtained would be explained if it is assumed that a heterozygote of composition $AaBb$, which has been built up of the combinations AB and ab, again forms chiefly the gametes AB and ab, only comparatively few in the series being Ab or aB in composition. Whereas in an $AaBb$ heterozygote, which has received A from one parent and B from the other, Ab and aB are the more frequent, AB and ab the less frequent terms in the series. In Stocks a parallel case may be found in the type of union now under consideration, viz. those in which the parents are of *unlike* plastid colour, each being homozygous in the allelomorph concerned (W or w), and in which the one is an *eversporting*, the other a *true-breeding* single. Since two factors X, Y (or $X'Y'$) are required to produce singleness, we are here concerned altogether with three factors, viz. X, Y and W, but X and Y being linked together in the true-breeding single, the two behave as a single allelomorph. When an $\widehat{XY}xyWw$ heterozygote has received these components in the combinations $\widehat{XY}W$ and xyw (as in

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[1] *Proc. Roy. Soc.* Series B, Vol. 84, p. 3, 1911.

the case *no-d*-non-cream × *d*-cream), $\widehat{XYW}$ and xyw are the more frequent, $\widehat{XYw}$ and xyW the rarer terms in the gametic series. If, on the other hand, the $\widehat{XYxy}Ww$ heterozygote has been built up from $\widehat{XYw}$ and xyW (as in the case *no-d*-cream × *d*-non-cream), then $\widehat{XYw}$ and xyW gametes are chiefly formed, those of $\widehat{XYW}$ and xyw composition being comparatively rare. The same scheme of coupling, as already shown, holds in regard to the *female* germs when the eversporting single is *self*-fertilised, but here the symmetry of the gametic series is disturbed by the fact that the male germs are unable to carry either of the dominant factors X or Y. Every eversporting single is an $Xx Yy$ heterozygote and is built up from the combinations XY and xy. In gametogenesis XY and xy ovules are chiefly formed, only comparatively few, we may conclude, are Xy and xY in composition, though direct proof in this case is not as yet possible. For since all doubles are sterile we cannot apply the breeding test, and at present therefore we are unable to demonstrate differences of composition between the doubles derived from Xy, xY and xy ovules respectively.

We may now consider the results of the present experiment in detail. If we accept the results as they stand, with the reserve mentioned above, and compare the totals obtained from the 14 mixed families with the results which would follow from gametogenesis on the lines suggested above, we get:

	Singles with white plastids	Singles with cream plastids	Doubles with white plastids	Doubles with cream plastids
Observed result	457	7	10	140
Calculated result if $n=16$ ...	442	18·5	18·5	135
,, ,, if $n=32$ ...	451	9·5	9·5	144

This latter result agrees very closely with that obtained experimentally. If we take the recorded result to be an *average* sample of F_2, it appears that in F_1 n may have the value 32, whereas in the eversporting parent, as previously stated, n probably $= 16$. In several of the smaller families the two rarer forms were not recorded, but, on the whole, it seems probable that their absence in these cases is accidental and is to be accounted for by the small size of the F_2 family. For the largest family in which these two forms were absent numbered only 32, and on the present supposition the expectation for both forms is less than 1 in 64, and even with the lower value for n would not be quite as high as 1 in 32. It may be worth while to note that the occurrence of even

larger F_2 families composed entirely of singles with white plastids and doubles with cream plastids would present no serious difficulty on the present view. Segregation in these cases might be in accordance with some higher term in the series. For with each successively higher value for n the difference in the proportion of the two more frequent forms (singles with white plastids and doubles with cream plastids) would be so slight, that it would not be practically appreciable in experiments on the present scale; whereas the proportion of the two rarer terms (doubles with white plastids and singles with cream plastids) would be successively reduced by about one-half, and hence in small families it would be unlikely that they would be recorded. If the value for n were sufficiently high the coupling would appear to be complete, and these two forms would then appear to be altogether wanting. Or again a like result would follow if the *no-d* parent were by chance a form in which W was linked with $\widehat{XY}$ in some of the germs (see above p. 335). In this case we should expect the F_1 plants derived from the $\widehat{XYW}$ germ cells to give F_2 families composed of only the two forms—singles with white plastids and doubles with cream plastids— while those derived from $\widehat{XY}W$ gametes would yield the F_2 families which include all four types.

The *all-single* F_2 families will be produced by the F_1 plants derived from the XYw ovules. These cross-breds will naturally breed true to singleness. In all these F_2 families we find either absence, or a marked deficiency of individuals with cream plastids. This deficiency recalls a similar result obtained in an earlier experiment where the parents, *both* in this case eversporting, were of unlike plastid colour, *d*-cream being used as ♀, *d*-non-cream as ♂. In this latter case XYw ovules were also fertilised by pollen carrying W, and here a single with cream plastids was obtained in F_2 when a descendant of plant K was used, but not when other cream individuals were employed. We may suppose that the distribution of W among the F_1 pollen grains will be the same in both crosses (see p. 332, where this point is discussed). In the present case, among 10 families which included a total of 279 individuals none had cream plastids; in the two remaining families 7 plants with cream plastids were recorded in a total of 141, but these 7 are not beyond suspicion, since some doubt exists as to the genuine eversporting nature of the cream parent (a descendant of plant K).

To sum up; we find that the union *d*-cream ♀ × *no-d*-non-cream ♂ gave, in accordance with expectation, some all-single-families, and some

mixed families with a proportion of 3 s. : 1 d. We may suppose (1) that in F_2 families containing doubles all the four possible forms will occur if in the non-double-throwing ♂ parent W is not coupled with XY, but that only the two parental forms will occur if W is linked with $\widehat{XY}$; (2) that the small number of singles with cream plastids and doubles with white plastids is due to partial coupling in the F_1 gametes such that W and w occur much more frequently in combination with the factors with which they are associated in the parents than in other combinations: (3) that in F_1 cross-breds producing the all-single F_2 families, all or most of the pollen must carry W, as has already been seen to be the case when d-non-cream is used as the ♂ parent instead of *no-d*-non-cream.

Mating 9. *no-d*-non-cream ♀ × *d*-cream ♂.

This reciprocal cross was made with the same two strains.

Summary of results. For details see Table IV.

A true-breeding single glabrous white was crossed with pollen from a double-throwing glabrous cream (plant *H*, see p. 314). Only four of the F_1 plants were tested; *each in accordance with expectation gave a mixture of singles and doubles in F_2*. All four forms occurred, though all were not recorded in each family. Singles with white plastids and doubles with cream plastids were obtained from each of the F_1 cross-breds, the former being in excess, but the other two forms were present in such small numbers that larger sowings would be necessary to determine whether their absence in the families in which they were not recorded was real, or not. Quite possibly it is merely accidental. In two of the families the total number of singles and doubles approximated to 3 s. : 1 d.: in the other two the proportion of doubles was less, but the deficiency is not so great (about 1 d. : 6 s.) as to render it beyond doubt that it is to be regarded as genuine.

In this form of mating F_1 is presumably produced by the union of $\widehat{XY}W$ ovules with *xyw* pollen. If gametogenesis follows the same course as in the reciprocal mating where the union is between *xyw* ovules and $\widehat{XY}W$ pollen (see above, p. 344), then, taking the two families in the present case where experiment gave the expected proportion of 3 s. : 1 d., we should expect a total of

	Singles with white plastids	Singles with cream plastids	Doubles with white plastids	Doubles with cream plastids
	117	2·5 (nearly)	2·5 (nearly)	37
where	122	3	1	33

were actually observed. The agreement between the observed and calculated results is so close that we may conclude that the same gametic series is formed by the reciprocal cross-breds (xyw ♀ × $\widehat{XYW}$ ♂) of the present mating and ($\widehat{XYW}$ ♀ × xyw ♂) of mating 3. If n has the same value in each of the F_1 plants, and if in the present mating the non-double-throwing parent is homozygous in $\widehat{XYW}$, we must suppose that the absence of the two rarer forms in the two families mentioned above is a chance variation.

Mating 4. d-non-cream ♀ × no-d-cream ♂. Not yet carried out.

Mating 10. Reciprocal cross. no-d-cream ♀ × d-non-cream ♂. Summary of results. For details see Table IV.

Five kinds of matings of this type were carried out, viz.,

no-d-glabrous cream ♀ × d-hoary white (intermediate) ♂[1].
     ,,   ,,   ♀ × d-glabrous white ♂.
     ,,   ,,   ♀ × d-glabrous red ♂.
     ,,   ,,   ♀ × d-glabrous azure ♂.
     ,,   ,,   ♀ × d-glabrous light purple ♂.

72 F_2 families were raised, all of which included some doubles, the proportion varying from 3 s. : 1 d. to a very much higher proportion of singles. *A point of special interest in this group of matings is that no doubles with cream plastids were recorded in an F_2 generation numbering more than* 3000. That is to say, in no case in which a non-double-throwing cream has been employed in a mating with an eversporting non-cream form has it yet been found possible to obtain the combination of creamness with doubleness in F_2, though a considerable number of the *single* F_2 plants have cream plastids. The total numbers obtained were:

         1666 singles with white plastids
         773 doubles ,,   ,,   ,,
         790 singles   ,,   cream   ,,

or about twice as many of the form with both dominant characters as of either of those exhibiting one dominant and one recessive character.

In matings of this type F_1 is presumably derived from the union of $\widehat{XYW}$ ovules with xyW pollen. Now if the two kinds of germ cells which united to produce F_1 were formed again by F_1 without any redistribution of the factors for plastid colour and for singleness and

[1] See note, p. 326.

doubleness, the result would be entirely in agreement qualitatively with that actually observed, and not very different from it quantitatively. For where

sw.	dw.	sc.	
1615	807	807	would have been an exact result,
1666	773	790	were actually observed.

But it seems doubtful whether the case is in reality quite so simple as this, for the proportion of the three forms occurring in the different F_2 families was not as uniform as on the above scheme we should expect it to be, the deficiency of plants with cream plastids in some cases being too great to be reasonably regarded as an accidental variation from the ratio 3 white : 1 cream. On the supposition that the repulsion in F_1 between $\widehat{XY}$ and W is complete for both kinds of germ cells, we get

Ovules	Pollen
$\widehat{XY}w$	$\widehat{XY}w$
$xy\,W$	$xy\,W$

It follows that all the F_2 singles with white plastids should be heterozygous both as regards singleness and doubleness and also as regards plastid colour. Out of 108 such F_2 singles derived as follows:

70 from the mating between *no-d*-cream ♀ × *d*-light purple ♂
18   ,,   ,,   ♀ × *d*-white ♂
20   ,,   ,,   ♀ × *d*-red ♂

which were tested, 90 (viz. 61, 15 and 14 from the three matings respectively) have already proved to be heterozygous as regards singleness and doubleness. In the other 18 families doubles were not recorded, but the numbers, none of which exceeded 11, are too small to be regarded as decisively indicating that the F_2 parent was unable to produce doubles. So far, then, the evidence presents no difficulty in the way of the above supposition. But only 79 of these families (viz. 55, 12 and 12 from the three matings respectively) included plants with cream plastids; and although the numbers in the other 29 families in which they were lacking were mostly too small to be conclusive, the fact that in one case as many as 40 singles were recorded, all with white plastids, leaves it doubtful whether some of the F_2 plants may not be breeding true to whiteness, and consequently, whether some F_1 gametes may not be carrying the combination $\widehat{XY}W$. If any such are formed they must evidently however constitute only

a small proportion of the whole number of gametes. On the supposition that the repulsion is only partial we might expect recombination thus:

Ovules	Pollen
$n-1$ $\widehat{XY}w$	$n-1$ $\widehat{XY}w$
1 $\widehat{XY}W$	1 $\widehat{XY}W$
1 xyw	1 xyw
$n-1$ xyW	$n-1$ xyW

This would give a result in F_2 almost precisely similar to that produced by complete repulsion, except that there would be in addition to the three forms given above a proportion of rather less than 1 in 1000 of doubles with cream plastids, if $n = 16$; or rather more than 1 in 4000 if $n = 32$. The difficulty of distinguishing between these two possibilities will be apparent from an examination of the figures given below, where the composition of the resulting F_2 generations is compared in detail in the two cases.

		Coupling partial $n=16$	Coupling complete	Coupling partial $n=32$	Coupling complete
Singles, plastids white	...	513	512	2049	2048
Singles, plastids cream	...	255	256	1023	1024
Doubles, plastids white	...	255	256	1023	1024
Doubles, plastids cream	...	1	0	1	0
Totals	...	1024	1024	4096	4096

As between complete repulsion on the one hand, or partial repulsion on either a 15 : 1 or a 31 : 1 basis on the other, the evidence therefore is not absolutely clear. If the former assumption (coupling complete) should prove correct, then, as stated above, all F_2 singles with white plastids should prove heterozygous in singleness and doubleness and also in plastid character; while all the singles with cream plastids should be homozygous in both characters: further, the observed absence of doubles with cream plastids will be absolute. If on the other hand the repulsion is partial, then certain of the F_2 singles with white plastids will breed true both to singleness and to whiteness, others to singleness though not to whiteness, others to whiteness though not to singleness, while others again will be heterozygous as regards both characters: similarly some of the singles with cream plastids will prove to be breeding pure to singleness, others not. In this case it must be supposed that with a larger count in F_2 an occasional double with cream plastids would appear. The available evidence from the F_3

generation leaves the question still undecided. 38 F_2 singles with cream plastids were tested, 33 from the mating with d-light purple and 5 from that with d-red; none yielded doubles in F_3. So far as it goes this fact is against the view that the repulsion is only partial, but again it is doubtful whether the experiment is on a sufficient scale for the result to be regarded as conclusive.

iii. One parent is homozygous and the other heterozygous in regard to plastid colour.

Mating 5. d-sulphur-white ♀ × *no-d*-cream ♂. Not yet carried to F_2.

Mating 11. Reciprocal cross, *no-d*-cream ♀ × d-sulphur-white ♂.

46 F_3 *families were raised, and doubles were obtained in all but one.* The probability that this all-single family was not derived from a cross-bred has already been discussed (see p. 310).

As we should expect, the F_2 generation all have cream plastids, for F_1 had cream plastids, being derived presumably from the union of $\widehat{XYw}$ ovules with *xyw* pollen. The proportion of singles and doubles in F_2 approximates in many cases to the ratio 3 s. : 1 d. In those families in which the doubles amount to *more* than 1 in 4 it is doubtful whether the excess observed is real, but among some at least of those in which the proportion is *less* than 1 in 4 the deficiency is probably genuine (see Table IV). An explanation of these cases has already been suggested (see p. 338), the supposition being (as in the case of Mating 10) that we are here dealing with the additional pair of factors $X'Y'$, X' occurring in the one parent and Y' in the other, the union of the two producing a higher percentage of singles than is the case where X and Y alone are concerned. We shall therefore express the composition of the germ cells uniting to produce F_1 more fully thus

$$X Y X'w \text{ ♀} \times xy Y'w \text{ ♂}.$$

Mating 6. d-sulphur-white ♀ × *no-d*-non-cream ♂.

Four kinds of unions of this type were made, viz.

d-sulphur-white ♀ × *no-d*-hoary white (*incana*) ♂.
    „   ♀ × *no-d*-hoary red (Brompton) ♂.
    „   ♀ × *no-d*-glabrous white ♂.
    „   ♀ × *no-d*-glabrous flesh ♂.

We may suppose that in this class of unions there will be at least four different types of plants in F_1, and therefore that there will be

different types of families in F_2. We may state the expectation in general terms thus:

(*a*) Nearly half the F_1 plants will be derived from the union of $\overparen{XYW}$ ovules with $\overparen{XYW}$ pollen; these will give only singles in F_2, all with white plastids.

(*b*) A small percentage of the F_1 plants will be derived from the union of $\overparen{XyW}$ ovules with $\overparen{XYW}$ pollen, and these should give a mixture of singles and doubles both with white plastids.

(*c*) Half of the F_1 plants will be derived from the union of xYw or xyw ovules with $\overparen{XYW}$ pollen, and these may be expected to give all four forms in F_2 (i.e. singles and doubles with white plastids and singles and doubles with cream plastids).

The results obtained may be summarised thus (for details see Table V).

A total of 128 F_2 families were raised, composed as follows:

(1) 65 families were composed entirely of singles with white plastids. Of these no doubt some should be disregarded on account of the small number of plants recorded. Leaving out of account all families of less than 10 individuals there remain 46, representing a total of 1303 individuals all single and all with white plastids (see paragraph (*a*) above).

(2) 63 families included a mixture of singles and doubles.

(α) Two of these contained only plants with white plastids, but in both the numbers were small and included only one double, so that although they *may* represent the type of family given above under (*b*) the evidence is insufficient for proof.

(β) 11 families included all four forms, singles with white plastids and doubles with cream plastids being largely in excess.

(γ) Of the remaining 50 double-coutaining families there were 22 in which singles with cream plastids and 2 in which doubles with white plastids were absent (the other three forms being present in each case); and 26 in which singles with white plastids and doubles with cream plastids only were present.

If we apply the same reasoning here as in the case of Mating 3, where *d*-cream was used instead of *d*-sulphur-white (see p. 344), we shall conclude that many (? all) of these 50 families would yield the missing forms if a larger sowing were made. For here as in the earlier case the great majority of the double-throwing cross-breds will be derived from the mating of xyw ovules and $\overparen{XYW}$ pollen; recombination

together with partial coupling of the factors for singleness and double-
ness and for plastid colour, giving, as previously stated (p. 346), both the
rarer forms in the proportion of only about 1 in 33 if $n = 16$, or 1 in 65
if $n = 32$, may well account for their apparent absence in a large number
of families in the present experiment. There seems in fact no reason
to doubt that, so far as the factors X, Y, W are concerned, the same
relation holds in both matings. But in the present case it seems
probable that in two of the unions another pair of factors come into
play, one member of this pair being present in the sulphur-white, the
other in *no-d*-flesh, and also apparently in *no-d*-white, but not probably
in either *incana* or the Brompton strain. The effect of the presence
of these additional factors in any F_1 cross-bred will be to raise the pro-
portion of singles in the F_2 family derived from this cross-bred as
described in Mating 11. Only in this way does it seem possible to
explain the frequent high percentage of singles in the F_2 families
where the two ten-week strains were employed, when other forms
such as the two biennials gave the expected 3 s. : 1 d. The genuine-
ness of these results is confirmed by those obtained in the reciprocal
union.

Mating 12. Reciprocal cross. *no-d*-non-cream ♀ × *d*-sulphur-
white ♂. (For details see Table IV.)

Two kinds of mating of this form were carried out, *no-d*-hoary
Brompton white being used as the seed parent in the one case,
no-d-glabrous flesh in the other. All four forms appeared in F_2,
singles with white plastids and doubles with cream plastids greatly
preponderating; in many families in fact only these two forms were
recorded. The proportion of singles and doubles in the large F_2 families
derived from the Brompton white was evidently 3 s. : 1 d. The families
derived from the *no-d*-flesh are mostly of small size. In some no doubt
the ratio is also 3 s. : 1 d. but in others there appears to be a distinct
excess of singles as in the reciprocal cross (see above). Altogether
48 F_2 families were raised and doubles were recorded in 46; the larger
of the two remaining families consisted of 17 singles, the smaller of only
8; both were derived from the *no-d*-flesh parent. As there is every
reason to suppose that *every* F_1 derived from the union *no-d* ♀ × *d* ♂
will produce doubles, and as the proportion of doubles in one or two
sister families is even less than 1 in 17, we may reasonably conclude
that a larger sowing would have given the expected mixture in these
cases also.

Summary of results of cross-breeding.

If we now put together the whole body of evidence obtained from unions between true-breeding and eversporting forms we may summarise the results as follows:

From those matings in which the eversporting form was used as ♀ 185 F_2 families were raised; 91 showed a mixture of singles and doubles, 94 were composed of singles only. This latter total no doubt appears larger than it is in reality through the fact that some families are probably included in it, which, if a larger sowing had been made, would have been found to contain some doubles. As however it is not possible to tell exactly how many of these smaller all-single families should be disregarded, the totals are given as they stand. But we may take the results as fully establishing the fact that when the eversporting form is used as ♀ in matings with a true-breeding strain, some F_2 families will be mixed and some all single; and that the proportion of the all-single to the mixed will be the same as the proportion of single-to double-carrying ovules in the ♀ parent, viz. $7 + x$ single : $9 - x$ double where x is less than 1.

From the reciprocal form of mating 230 F_2 families were obtained and doubles were recorded in 227. In two at least of these exceptions the evidence in regard to the seeming absence of doubles cannot be regarded as conclusive, and it may be that in the remaining case the same explanation also holds good; or, it may be that this family did not arise from a cross at all, but was the result of accidental self-fertilisation which in this case would not betray itself in F_1.

When one of the parents in these unions is homozygous in W (plastids white) and the other in w (plastids cream) the proportion of F_2 singles and doubles having white and cream plastids respectively indicates that in almost all the F_1 gametes, whether pollen or ovules, each of the allelomorphs W and w is associated chiefly with the particular combination of factors for singleness and doubleness with which it was combined in the ovule or pollen grain used to produce F_1. Thus in a mating between no-d-white and d-cream, W is borne for the most part by those F_1 gametes carrying XY, w by those carrying xy. Conversely when the mating is between d-white and no-d-cream it is W which is carried almost entirely by the XY gametes, w by those of xy composition.

VIII. *Summary.*

In the preceding pages an attempt has been made to work out a scheme which will account for the behaviour, so far as we know it at present, of various races of Stocks in regard to the two characters, colour of plastids and production of doubles. The results have already shown that the relationship of the various factors concerned is by no means simple, but it is not unlikely that as more facts come to light still further complications will become apparent. It may be claimed however that the scheme as it stands affords a useful working hypothesis enabling us to grasp a complicated series of facts; moreover it is one which can be tested in detail by further experiment on definite lines. A solution which enables us to fit together so many pieces of the puzzle must, one cannot but believe, prove to be substantially correct.

We may therefore venture to add to the conclusions already formulated on pp. 321—324 the following general statements:

(1) All sap-coloured races of Ten Week Stocks so far investigated (i.e. azure, light purple, dark purple, marine blue, flesh, copper, red) and the two non-sap-coloured forms pure white and cream can occur under two forms, a pure-breeding form and an eversporting form.

(2) The sulphur-white race—a race which is peculiar in being eversporting in regard to plastid colour as well as in regard to doubleness—is only known in the double-throwing form. It produces single whites, double creams and a small percentage of double whites.

(3) Every individual in an eversporting strain yields doubles in excess; the proportion may be stated as $7 + x$ single to $9 - x$ double where x is less than 1.

(4) All the pollen grains of such strains appear to carry doubleness: that is to say, in these strains the distribution of the factors for single-ness (X and Y) is limited to the gametes of one sex.

(5) The ovules in every individual belonging to these strains are mixed, the proportion of those carrying singleness and doubleness is presumably the same as the proportion of singles and doubles among the offspring, since the pollen is uniform.

(6) The proportion of $7 + x$ single to $9 - x$ double is most easily explained on the supposition (1) that two factors at least are con-cerned (X and Y), (2) that the zygote is heterozygous in regard to both, and (3) that in the case of the *ovules* these factors show partial coupling of the kind with which we are already familiar in the Sweet

Pea[1]. Though, however, the scheme of coupling is based on the same principle in the two cases, there is in the Stocks an additional complexity owing to the limitation of the power of carrying these factors to the gametes of the female sex.

(6 *a*) The scheme of coupling is such that the combinations of the allelomorphs $XxYy$ carried by almost all the ovules in an eversporting individual are the combinations borne respectively by the male and female germs which united to produce that individual; the rarer terms in the series are those which represent recombinations of these factors, one factor in the recombination being derived from the male parent, the other from the female. The number of gametes required to exhibit the whole series being taken as $2n$, we may represent the gametic series in the eversporting forms in general terms thus:

$$
\begin{array}{cc}
\text{Ovules} & \text{Pollen} \\
n-1 \;\; XY & \text{all} \;\; xy \\
1 \;\; Xy & \\
1 \;\; xY & \\
n-1 \;\; xy &
\end{array}
$$

where XY represent factors, required for singleness, and where the zygote has arisen from the union of an XY ovule with an xy pollen grain. The value for n is probably 15 for the type forms though in some cross-breds it may be 31 (or possibly some higher term in the series).

(6 *b*) The above formula holds good for all the eversporting strains investigated, hence when no further complications arise the proportion of doubles remains the same whether these strains are self-fertilised or inter-crossed. Thus we are able to understand how it is that these eversporting strains produce a constant excess of the recessive (double) form. The only other instance of the kind, at present known, that seems in any way comparable, is that of one of de Vries' Oenothera hybrids—a tall form which gave an excess of dwarfs[2].

(7) Singleness in the pure-bred, non-double-throwing single is due to the presence of the same two factors (X and Y), but in these strains these two factors are linked together ($\widehat{XY}$), so that when this type of single is crossed with an eversporting form recombinations of the two pairs of allelomorph do not occur.

(8) In addition to the pair of factors referred to under (6) and (7),

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[1] See note, p. 322. [2] *Ber. der Deut. Bot. Gesell.* Bd. xxvi. *a*, 1908. p. 667.

which are present in *all* the strains, there appears to be a second pair of factors ($X'Y'$), the presence of which also renders the zygote single. One member of this second pair appears to occur in some but not all of the pure single strains, the other in some but not all of the double-throwing strains.

(9) The effect of the coupling mentioned under (7) is that when only the pair of factors common to all the strains is present (XY), the mixed F_2 families from a cross between the non-double-throwing pure-bred and the eversporting single contain a proportion of about 3 s. : 1 d.

(10) When a similar cross is made between forms which contain in addition one member of the second pair of factors mentioned under (8), the distribution of the members of the second pair being complementary, some of the mixed F_2 families again show a proportion of about 3 s. : 1 d., but in others the proportion of singles is considerably higher.

(11) White plastids result from the presence of a factor (W), cream plastids from absence of the same factor (w).

(12) Pure white or cream races are homozygous in W and w respectively, but the sulphur-white race is heterozygous in regard to this factor which is present in some only of the ovules and absent altogether from the pollen; moreover in this latter race W appears to be coupled with one of the factors required for singleness. We may represent the gametic series in this sulphur-white race thus:

$$
\begin{array}{lll}
\text{Ovules} & & \text{Pollen} \\
n-1 \ \ \widehat{X\,Y\,W} & & \text{all } xyw \\
1 \ \ \widehat{X\,y\,W} & & \\
1 \ \ xYw & & \\
n-1 \ \ xyw & &
\end{array}
$$

(13) The distribution of the allelomorphs W and w among the gametes of F_1, where the parents are of unlike plastid colour, appears to depend upon the conditions under which the plastid colour factor is introduced into the cross, i.e., whether by the male or the female germ, and whether in combination with singleness or doubleness.

(*a*) When the union is between two eversporting forms, and when W is introduced on the female side in combination with XY (XYW ovules) and w on the male side with xy (xyw pollen) as in the cross *d*-white ♀ × *d*-cream ♂, all the F_1 pollen appears to carry creamness (w) as well as doubleness (xy) like the pollen of the ♂ parent: and

all the F_1 ovules carrying singleness (XY) appear to carry whiteness (W) like the ovules from which F_1 is itself derived; while of those F_1 ovules which carry doubleness all (or almost all) lack W. If it should be confirmed that only the two parental forms (singles with white plastids and doubles with cream plastids) occur in F_2, then "all" will presumably be correct in each of the above cases; but if, as analogy with other cases suggests, the factor W shows not *complete* but *partial* coupling, of the same nature as that described under (6 a) for the factors X and Y, then we may expect that of the F_2 ovules carrying doubleness *almost* but not *quite* all will lack W, and that in a large sowing in F_2 a few doubles with white plastids will occur. In the event of this latter alternative proving true we should be able to synthesise the sulphur-white form afresh from true-breeding whites and creams. For the F_2 single from d-non-cream $\times$ d-cream is formed from the union of the same combinations of factors as was F_1, and will presumably therefore repeat the same gametic series. Hence if the appropriate single white be selected in F_2 it may be expected to behave like a pure-bred sulphur-white.

(*b*) In the reciprocal cross where single F_1 plants are derived from the union XYw ovules and xyW pollen a corresponding but reversed distribution of the plastid colour factor explains the observed results. Here W is introduced into the pedigree on the male side and is evidently borne by all (or almost all) the germ cells of one sex—no doubt the male—in F_1. Since the presence of the dominant allelomorph in all or nearly all the germ cells of one sex produces a constant or almost constant result in F_2 whatever the distribution of this factor among the germ cells of the other sex, we are unable merely from the F_2 result to infer the distribution of W among the ovules. But we may suppose from analogy that all (probably) of the ovules carrying creamness will carry singleness, and that nearly all those carrying doubleness will carry whiteness.

(*c*) When crossing occurs between two forms of unlike plastid colour, one of which is an eversporting, the other a non-double-throwing single, the distribution of the allelomorphs W and w appears to be different in the F_1 singles which are *heterozygous* in regard to singleness from that in the singles which are *homozygous* in this respect. In the *heterozygous* singles, which here have the constitution $\widehat{XY}xyWw$, recombination of the four components $\widehat{XY}$, xy, W, and w occurs in the same manner as described above under (6 a) for the four

separate allelomorphs X, Y, x and y, but with this difference, that in this case the same gametic series occurs among both male and female gametes. That is to say the majority of *both ovules and pollen in* F_1 exhibit the combinations occurring in the ovule and the pollen grain which united to produce F_1; the rarer terms in the series are represented by the recombinations of the two sets of factors. Thus when the mating is between single white from a *no-d*-strain of the form $\widehat{XY}W$ and double cream (xyw) we shall represent the gametic series in F_1 thus:

Ovules	Pollen
$n-1$ $\widehat{XY}W$	$n-1$ $\widehat{XY}W$
1 $\widehat{XY}w$	1 $\widehat{XY}w$
1 xyW	1 xyW
$n-1$ xyw	$n-1$ xyw

When on the other hand single cream and double white of the form ($\widehat{XY}w$) and (xyW) unite to produce F_1 the gametic series will be as follows:

Ovules	Pollen
$n-1$ $\widehat{XY}w$	$n-1$ $\widehat{XY}w$
1 $\widehat{XY}W$	1 $\widehat{XY}W$
1 xyw	1 xyw
$n-1$ xyW	$n-1$ xyW

In the first case F_2 is composed chiefly of singles with white and doubles with cream plastids, the other two forms, doubles with white and singles with cream plastids, being scarce.

In the second case, on the other hand, doubles with cream plastids, if they occur, must be extremely rare (none have as yet been recorded, though possibly they would occur in a larger sowing); doubles with white plastids and singles with cream plastids are fairly numerous, and singles with white plastids abundant. In the sister F_1 singles which are *homozygous* in regard to singleness ($\widehat{XYXY}Ww$) the distribution of the plastid colour factor must be such that all or nearly all the gametes of one sex carry W. Possibly the plastid colour factor W is here associated with the gametes of one or other sex according as it is brought in on the male or female side, as described above in the case where *both* parents are eversporting in regard to doubleness (see 13 *a* and *b*).

APPENDIX

NOTE 1. ON THE RELATIVE VIABILITY OF SEEDS GIVING RISE TO SINGLES AND DOUBLES

The belief that in Stocks a larger proportion of doubles can be obtained from old seed than from seed recently harvested is one of long-standing, but it appears to be rather of the nature of a tradition than of an opinion founded on a knowledge of definite facts. Discussing this point in his paper entitled "Beiträge zur Kenntniss gefüllte Blüthen" Goebel[1] refers to a treatise by F. A. H. Thiele which shows that the above view was current at the beginning of the last century. Thiele[2], as Goebel tells us, was seeking an answer to the questions how can one obtain Stock seed which will produce a high proportion of doubles and how can one recognise this seed? à propos to the former inquiry he mentions among other traditions current at that time the view that the older the seed the more doubles does it yield. Commenting on this statement Goebel adds that though unsupported by experiment it may very well prove to be the case, and might be explained on the supposition that in course of time more and more seeds which would have produced singles lose their power of germinating.

Chaté, a French horticulturist, in a treatise on the cultivation of Stocks, the culture of which had been carried on in his family for more than 50 years, expresses himself on this point as follows: Experiment has shown that seeds two years old give more doubles than seeds one year old. In proportion as the seeds get old their power of doubling increases, whilst the power of germinating diminishes[3]. Although Chaté here states that his view is based on experiment, it seems clear that he did not recognise the possibility that the character of the flower may already be pre-determined in the seed, and that his suggestion that a seed which would have produced a double may, if kept, eventually give rise to a single, is not a true explanation of the facts.

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[1] *Pringsheims Jahrbuch*, Band XVII. p. 285, 1886.

[2] *Prediger zu Pitzerwitz bei Kyritz in Pommern*, Cöslin, 1825.

[3] *Culture pratique des Giroflées.* Paris, N.D.

The present series of experiments has made it abundantly clear that singleness or doubleness in the flower is a character which is dependent solely upon the constitution of the germ cells from which it arose; that it is in fact already determined in the seed, and is entirely independent of external conditions. Though the present results have disproved the interpretation, they have confirmed the fact observed by Thiele, Chaté and others that the proportion of doubles obtained from old seed is often higher than that given by seed more recently harvested. They have also furnished incidentally a certain amount of evidence as to the relative viability of the seeds giving rise to singles and doubles respectively, and also as to the possibility of identifying those which give doubles.

(a)　*Viability.*

Although critical experiments on a very large scale, and specially designed to this end, would be required to show the relative rates at which the progressive loss in germinating power occurs among seeds destined to give rise to singles and doubles respectively, the evidence already available points strongly to the conclusion that in any lot of seed which has been kept until the bulk of it is no longer capable of germination the surviving remnant will be mostly if not exclusively composed of those yielding doubles[1]. The effect of this greater viability

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[1] It is perhaps hardly necessary to state that the time during which the seeds retain their vitality varies greatly with the quality of the seed. Cent. per cent. germination was obtained in some cases after the lapse of three years; even after seven years—the longest period over which sample sowings from any one lot of seed were extended—a few still retained their vitality. On the other hand badly ripened seed sometimes failed altogether to germinate after three, or even two years.

In considering the results of repeated sowings made after a considerable lapse of time the following point must be borne in mind. Where only a small number of seedlings are obtained, it may be that all or most of the seeds in one or two better ripened pods have retained their vitality while those belonging to all the other pods have died; or on the other hand it may be that only a seed here and there in each of several pods has survived. In the former case the original ratio of single to double will presumably be unchanged; only in the latter case are we concerned with the question of a differential death-rate. Unless the seed is unmistakeably of uniform quality, it is therefore desirable, in experiments designed to test this point, that the seed of individual fruits should be sown separately, though this method of procedure necessarily entails much waste of space when very few of the seeds still survive. When the further fact is taken into account that single fruits are often found not to afford average samples it will be seen that any comparative experiment will be of little value unless carried out on a very considerable scale. Furthermore only those cases should be taken into account in which all or most of the remnant which germinated survived to flower. Where the number of plants involved is in any case very small, the loss of several individuals before the flowering stage may render the result quite untrustworthy.

of seeds producing doubles is that in cases where sowings are made from seed which has been kept for some seasons, a certain error is likely to be introduced in the direction of making the proportion of doubles appear greater than it actually is, the variations from the theoretical result in the case of old sowings being always in the same direction. The fact that this increase in the proportion of doubles may be obtained from a sample of quite good seed, after it has been kept, shows that it cannot be attributed to a particular distribution of the double-carrying ovules in different regions of the pod, such e.g. as that those occurring in the distal region give rise to fewer doubles than those occurring in the basal part, since in the case of Stocks *all or nearly all* the ovules in each pod are naturally fertilised under favourable conditions; hence a sample of loose seed is likely to represent all regions equally. Moreover, direct experiment by means of halving the pods transversely and sowing the seeds from the upper and lower halves separately gave no indication of any such unequal distribution.

Subjoined are some of the more striking instances in which the greater viability of the seeds which give rise to doubles is plainly manifest.

i. In 1904 a glabrous dark purple plant gave a family of 11 single and 5 double. This excess of singles was probably accidental since the plant appears to have been a true eversporting individual, and no doubt with a larger sowing would have given the usual preponderance of doubles.

In 1908 about 400 seeds from 9 of the F_1 singles were sown : 44 germinated of which 35 lived to flower, 8 being single and 27 double. The families were composed as follows :

Family 1.		16 seeds sown.		5 germinated		all 5 plants were double
,, 2.	16	,,	,,	3	,,	all 3 plants ,, ,,
,, 3.	19	,,	,,	3	,,	2 were double, 1 died before flowering
,, 4.	228	,,	,,	33	,,	17 were double, 8 died before flowering, and 8 were single

The seeds from the 5 other F_1 plants gave no result.

In 1909, 30 seeds from one of the F_2 singles were sown, only 1 germinated and this proved to be a double.

In 1910, > 130 seeds from another F_2 single were sown ; 21 germinated, all of which lived to flower ; 7 were single and 14 double.

ii. In 1907 a glabrous white plant yielded an F_1 of 83 singles and 100 doubles.

In 1908, 30 more seeds of this plant were sown; only 2 germinated; both were double.

In 1909, 47 more seeds were sown; only 7 germinated and again all were double.

Of 5 seeds, harvested also in 1906, from a sister plant, but not sown till 1909, only 2 germinated and both produced doubles.

In 1908 nearly 200 seeds harvested from 5 of the F_1 singles were sown; 40 germinated of which 27 lived to flower, 5 being single and 22 double. The families were composed as follows:

Family 1.	> 30 seeds sown.		1 germinated and produced a double		
,, 2.	34 ,,	,,	12	,,	8 were double, 4 died before flowering
,, 3.	33 ,,	,,	15	,,	8 were double, 4 died before flowering and 3 were single
,, 4.	30 ,,	,,	12	,,	5 were double, 5 died before flowering and 2 were single

All the seeds from the fifth F_1 plant failed to germinate.

In 1910, 85 more seeds from 3 of these same F_1 plants were sown, but none germinated.

About 500 seeds from 20 others among the F_1 singles gave a total of 79 singles and 114 doubles. Here the proportion of seeds still capable of germination, though less than 50 per cent., was considerably greater than in the lot sown in 1908, and the result is not very different from what we should expect had the seeds been sown in the season following that in which they were harvested. From this and other facts it is evident that the length of time during which the seeds retain their power of germinating is not fixed but depends probably on the quality of the seed in the first instance, and on the conditions under which it is kept.

iii. In 1908, 69 seeds of a sulphur-white which had been harvested in 1906 gave 23 singles and 32 doubles.

In 1910, 128 more seeds were sown; only 5 germinated of which 4 lived to flower: all were double.

A similar increase in the proportion of doubles was observed in many cases where the seed was originally of bad quality, and where only a small percentage germinated even when sown the following season. This is well shown in the case of the two type forms from which the largest sowings were made in 1910. Owing to a bad season in 1909 a great deal of the seed harvested was of miserable quality and a large proportion failed to germinate. Though no real line of

division exists, since all grades occur, some arbitrary classification must be made for the purpose of comparison, and the line is therefore drawn between those pods where at least half the number of seeds sown germinated, and those in which less than half proved to be good. The results may be summarised thus:

Type	Number of seeds sown where less than half germinated	Number of seeds which germinated	Number of singles	Number of doubles	Number of seeds sown where at least half germinated	Number of seeds which germinated	Number of singles	Number of doubles
Marine blue	744	161	42	108	238	162	67	71
Light purple	790	237	85	125	1439	1040	447	494

In both cases the fruits containing the less good seed have given a higher percentage of doubles.

As to the proportion of doubles actually obtainable from the various types the numbers quoted in seed catalogues range from about 50 per cent. to as much as 90 per cent. In the case of the Erfurt Ten Week strains from 60 to 75 per cent. is given. This is a rather higher proportion than was found to occur in the breedings here described, where the *average* ranged between 53 and 57 per cent., though a considerably higher proportion might now and again be obtained in individual sowings. Chaté[1] believed his experiments to show that a larger percentage of doubles could be obtained from the pods on the main stem and from the lower ones on the primary laterals than from those on the laterals of a higher order; and similarly from the seeds from the lower region of a pod as compared with the upper: the difference is given as 20 per cent. only of doubles from branches of a higher order as compared with 65 per cent. from those of a lower order, and 30 to 35 per cent. from the upper region of the pods as compared with 75 to 80 per cent. from the lower region. These two latter numbers would give an average of 55 per cent. for the fruit as a whole, which agrees very closely with the observations contained in the present paper, and with the average which the theoretical considerations here advanced would lead us to expect. No indication of the aggregation of seeds giving rise to doubles in definite regions of the fruit was obtained, although a number of observations were made with a view to testing this point. 68 pods belonging to three different strains (red, marine blue, and Princess May) were halved transversely, the seeds from the upper and lower halves being sown separately. The same result was

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[1] *loc. cit.* p. 79.

obtained as in the case where the seeds were sorted according to shape (see below). Sometimes a higher proportion of doubles would be obtained from the lower half, sometimes from the upper, making it evident that no constant difference exists in the two regions with regard to the distribution of the two kinds of seed. It seems in fact probable that the distribution observed by Chaté was accidental, and not the result of any general arrangement throughout the individual.

(*b*) *On the possibility of distinguishing the seeds giving rise to singles and doubles respectively.*

In several papers by earlier writers, treating of Stocks, we find the statement repeated that more doubles are obtained from the lumpy irregular-shaped seeds than from the typical regular disc-shaped seeds. No figures are quoted in support of this view, which is probably the outcome of an association of ideas rather than of critical experiments, which would need to be carried out on a considerable scale in order to allow for any disturbing effect due to the frequent marked irregularity of distribution which has already been noted. So far no indication has been observed of any connection between the shape of the seed and the character of the flower. The glabrous-red race being one in which many lumpy or irregular seeds constantly occur, the seeds from a certain number of pods belonging to this race were sorted according to shape, the flat seeds being sown separately in one lot, the irregular-shaped seeds in another. It was found that cases where more doubles were obtained from the flat seeds were about as numerous as those where the reverse was true, and that so evenly did the variations in the one direction balance those in the opposite direction that the ratio obtained from the totals in the two cases was almost identical. Thus in 1906 the seeds of 10 pods of the red race were sorted before sowing. The results were:

From the flat seeds a total of 65 singles and 93 doubles or 1 : 1·43
     ,,   lumpy   ,,   19   ,,   28   ,,   1 : 1·47

Similar sowings in other years gave similar results.

It seems much more probable that the irregular shape of the seeds is connected with the way in which they are packed in the pod. In the case of the cream race Princess May, and of a certain strain of sulphur-whites, the pods are often some inches in length. The seeds are borne at some distance from one another, and although a pod may contain from 60 to 70 or even more, they do not overlap. They are so regular

in shape that a lumpy seed can only be found now and again. In the glabrous red, on the other hand, the pods are so short that though very much fewer in number the ripe seeds are crowded together. Yet the same proportion of doubles is obtained from each of the three strains.

We may therefore conclude that no system of selection based on the shape of the seed will enable us to obtain a proportion of doubles which is constantly above the average. In the case of certain sulphur-whites however it is quite possible by sorting the seeds according to *colour* to separate almost completely those giving rise to singles from those producing doubles. The present experiments have shown that there are at least two types of sulphur-white on the market, one in which the seeds are small, brown, often irregular in shape, and indistinguishable in appearance from those of a true-breeding white; the other in which the seeds are very regular, larger, of a lighter yellowish colour, and similar to those of the cream race Princess May. These two types have no doubt a different origin, and are different in constitution (see later, p. 370). In the case of the type with the yellow seeds it was found possible in well ripened pods to sort the very yellow seeds which give rise to the creams which are all double from the less yellow seeds which give rise to whites of which nearly all are single. The following result will show the degree of accuracy which can be reached by this method.

Of 81 seeds taken from one pod

48 were expected to give rise to creams	33 to whites
38 germinated	27 germinated
34 flowered	26 flowered
30 were cream doubles	24 were white and all single
4 were white and all single	2 were cream doubles

Of 72 seeds taken from another pod

44 were expected to give rise to creams	28 to whites
28 germinated	25 germinated
28 flowered	16 flowered
27 were cream doubles	16 were white (15 single, 1 double)
1 was white and single	0 were cream

Thus of the 60 doubles which were obtained 57 were recognised by the seed-colour; of the whites 5 were wrongly classed as probable creams, but the remaining 40 were correctly identified, and 39 proved to be single. A very slight error must however always remain in sorting the singles from doubles, since the rare double white is not distinguishable in seed-colour from a single white.

NOTE 2.   ON THE INHERITANCE OF THE BRANCHED AND
THE UNBRANCHED HABIT.

Most races of Stocks branch freely, and in the case of biennial types
form large bushy plants.   Of the various sorts used in the present
experiments the Ten Week strains all have the branched habit, as have
also among the biennials, *incana* and the Brompton strains raised by
Continental growers.   The typical English Brompton is on the other
hand *un*branched, the single stout stem being prolonged above the
region of the leaves as a simple raceme.   Both leaves and fruits in this
type are thick and somewhat fleshy.   The unbranched habit is recessive
to the branched.   When a cross is made between an English type of
Brompton and a branched form the F_1 cross-breds are bushy plants like
incana.   In F_2 the pure Brompton habit reappears in a proportion of
the plants.   The sorting of the F_2 plants is rendered difficult owing to
the fact that the formation of branches can no doubt be induced by a
variety of causes producing a check in growth.   An injury to the
terminal bud or to the roots may cause a check in the growth of the
main axis and lead to the development of one or more axillary buds
which otherwise would have remained dormant.   Injuries of this kind,
resulting in a check to growth, are very likely to occur when the young
plants are planted out, and hence in a strict count a certain number
of individuals are likely to be classed as normally producing branches
which in fact only do so owing to unfavourable conditions, or to accident ;
thus the proportion of individuals inheriting the unbranched habit is
likely to appear less than it actually is.   In the one mating in which
an English Brompton stock was crossed with a branched form 394 plants
were raised in F_2.   Of these 66 were recorded as typical Brompton
plants and 31 others as being unbranched except for a single lateral.
These numbers suggest that the true proportion of plants inheriting
the unbranched habit in F_2 is probably 1 in 4 as in the ordinary case
of a simple recessive.

The characteristic appearance of the unbranched as compared with
a branched type is shown in the accompanying figures showing two
of the F_2 plants derived from a cross between an English Brompton
and a branched Ten Week strain.   (Fig. 1 shows the branched, fig. 2 the
unbranched habit.)   The photographs were taken at the end of the
season when the plants were in fruit and the leaves had fallen.   In the
F_2 generation the Brompton plants presented a very curious appearance,
the single stem in many cases reaching a height of from 3 to $3\frac{1}{2}$ feet.
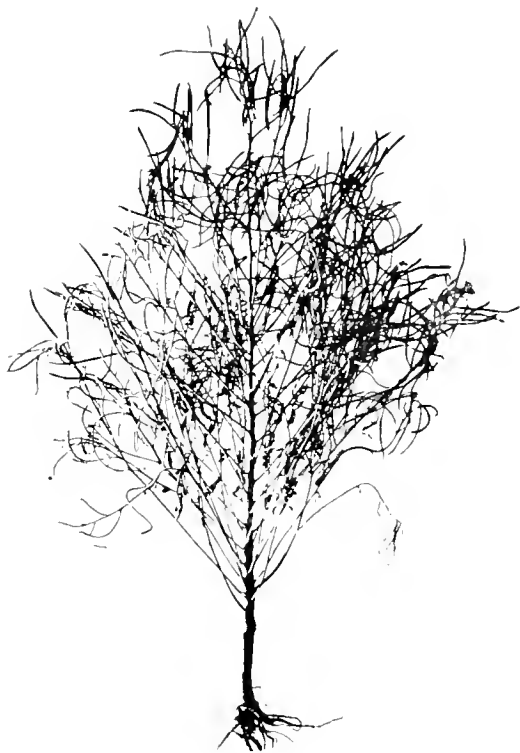
Fig. 1.   Fig. 2.

NOTE 3.   ON CERTAIN SAP-COLOURS NOT DEALT WITH IN THE EARLIER
    ACCOUNTS, AND ON THE CONSTITUTION OF THE SULPHUR-WHITE
    RACE.

Sap-colours.

Rose is obtained from unions where the colour factors C and R are
present together with a factor for paleness, provided the blue factor B
is absent from at least one of the parents.   Hence it is obtained when
flesh or a certain type of sulphur-white (type 1 of p. 367) is crossed with
any form which gives a coloured F_1.   If both parents lack B then it
appears in F_1, but if one or other contain B it does not occur till F_2.
Thus when sulphur-white type 1 was crossed with red, flesh, cream, or
Brompton white, F_1 was rose; whereas when bred with azure or light
purple the rose colour only appeared in certain plants in F_2.   Owing

to the presence of the B factor, azure and light purple can never give rose in the first generation, but in any mating with a b-form they will presumably give it in F_2.

Rose is epistatic both to the deeper colours carmine and crimson, and to the purer red shades flesh and terra-cotta.

Lilac is a somewhat bluish pink form, the blue tinge becoming more marked on fading. It occurs in F_2 from certain unions where flesh is used, as, e.g. flesh × light purple or white *incana*. Its position in the colour series has not yet been determined owing to the failure of the crop in 1910.

Terra-cotta (? Rothbraun of German catalogues) is a full pure colour. So far it has only been obtained in F_2 from matings between flesh and sulphur-white or cream. It is recessive to flesh, and possibly stands at the hypostatic end of the scale of the pure reds as copper probably does of the impure series.

Carmine and Crimson. These full red colours have hitherto been spoken of collectively as "red." But carmine certainly includes three distinct shades, and crimson probably more than one. The two colour groups together form a very closely graduated series, and a full analysis of these shades has not been attempted. When, as here, a considerable deepening of the colour occurs between the unfolding and the fading of the flower, the range of shades exhibited by individuals of a pale grade may overlap those of an intermediate class, and so on up the scale, thus increasing the difficulty of sorting.

The same difficulty is met with among some grades in the blue series, but the three main classes, dark purple, light purple and azure or very light purple, are easily distinguished. *Marine blue* is a larger-flowered form, in range of tint between unfolding and fading covering almost those of azure and light purple together. The two paler forms azure and marine blue, differ from the more deeply coloured purple types in having brown and not green seeds.

Constitution of the sulphur-white race.

All sulphur-whites were found to behave alike when self-fertilised, in giving a mixture of white singles and cream doubles; all probably also give a small percentage of white doubles. When bred with other glabrous forms the results varied according to the type of sulphur-white employed. Seed supplied by Messrs Haage and Schmidt proved to belong to the second type described above (p. 367, seeds yellow, large, regular). The plants crossed with glabrous cream gave F_1 all glabrous, and either all cream or mixed white and cream, according as the

sulphur-white was used as $\male$ or $\female$. When crossed with glabrous white or glabrous sap-coloured strains F_1 was hoary and sap-coloured. If a full sap-colour as e.g. red was used, a full colour was obtained in F_1. This type of sulphur-white contains the hoary factor K[1], and one of the two factors C and R necessary for the production of sap-colour; the one present must be the one which occurs in Princess May ($= R$). The other colour factor (C) and the factor which turns red blue (B) are both absent. We can therefore express the composition of this type of sulphur-white thus—$bcRK$. The seed obtained from Herr Benary showed the characteristics described under type 1 (p. 367, seeds small, brown, irregular). This form evidently has the composition $bCrK$, and has also a factor causing paleness, so that in a cross a full sap-colour carried by the other parent becomes pale in F_1. This type when bred with glabrous cream or a glabrous sap-coloured form gives F_1 all hoary sap-coloured; with glabrous white on the other hand it gives F_1 all glabrous white. Bred together these two sulphur-whites should give a sap-coloured hoary F_1 of a pale red colour ($=$ rose). It was hoped that plants from this mating would have been raised this year, but unfortunately owing to the bad season in 1910 no good seed was obtained. Indirect proof however is already forthcoming, for a mating in the form

[sulphur-white (type 2) × glabrous red] × sulphur-white (type 1)

gave *all rose hoary* (217); whereas the mating

[sulphur-white (type 2) × glabrous red] × sulphur-white (type 2)

gave the expected result—half the offspring being red hoary and half white smooth.

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[1] See Evolution Report IV. p. 36.

TABLE III.

Showing the composition of the self-bred families raised among various Ten Week strains.

Glabrous red (87 families)

Single	Double	Single	Double	Single	Double	Single	Double	Single	Double	Single	Double
13	9	10	16	3	7	2	4	2	4	6	17
17	24	—	9	45	48	9	5	3	2	109	131
13	13	13	32	2	6	15	23	—	1	130	119
10	21	—	3	10	9	5	4	13	18	3	9*
15	24	24	19	49	58	16	20	6	9	93	102
9	23	18	19	45	53	4	9	—	4	14	15
6	2	57	55	10	12	11	20	5	3	19	25
3	10	—	1	31	26	24	32	3	3	74	73
18	18	45	60	8	12	12	22	16	39	7	14
3	1	—	2	5	9	15	20	8	32	59	81
28	33	3	1	4	4	33	29	10	16	23	8
25	33	29	52	2	3	13	24	30	40	56	74
18	24	6	5	2	5	11	33	7	8		
39	45	42	42	9	16	23	43	18	13		
9	16	4	6	—	4	31	41	3	11		

Glabrous sulphur-white (62 families)

Single	Double	Single	Double	Single	Double	Single	Double	Single	Double
13	18	11	13	6	7	1	2	51	76
7	9	55	86	3	4	1	1	2	7
16	23	5	21	5	6	3	4	5	5
25	34	92	118	5	3	3	5	1	2
16	25	24	38	2	4	5	6		
12	32	8	23	1	2	—	25*		
5	11	15	21	2	3	8	14*		
8	7	?	8	3	5	10	34*		
22	33	6	2	5	4	11	19		
52	65	4	6	1	4	6	2		
24	30	2	10	—	3	6	11		
11	13	2	5	6	1	1	2		

Glabrous light purple (54 families)

Single	Double	Single	Double	Single	Double	Single	Double	Single	Double	Single	Double
16	25	5	4	—	4	2	3	19	37	10	9
26	41	—	1	2	1	—	2	28	32	23	22
2	2	1	4	—	1	5	4	14	15	39	34
5	5	2	1	2	2	21	24	27	27	32	36
6	2	—	1	1	1	9	23	5	4	13	21
7	2	—	5	9	8	15	14	23	54	19	38
4	4	3	4	17	18	3	6	43	41	103	83
2	5	1	2	12	23	5	9	16	20	35	35
1	2	—	1	1	1	2	2	8	9	67	88
5	5										
12*?											
4*?											

Glabrous azure (16 families)

Single	Double	Single	Double	Single	Double	Single	Double	Single	Double
52	38*	7	6	30	40	10	14	27	37
81	94	11	14	5	4	51	67	7	8
70	70	3	4	29	27	6	7	2	4
—	3	—	1						

Glabrous marine blue (22 families)

Single	Double	Single	Double	Single	Double	Single	Double	Single	Double
11	5	7	14	1	3	10	12	2	5
—	5*	11	14	—	1	3	7	7	12
		3	3	—	2	2	6	8	10
		—	3	4	4	4	7	13	19

Glabrous dark purple (7 families)

Single	Double	Single	Double	Single	Double	Single	Double
—	2*	—	3*	8	17*	—	1

Hoary azure (6 families)

Single	Double	Single	Double	Single	Double	Single	Double
31	44	6	7	16	19	4	12

Glabrous copper (1 family)

Single	Double	Single	Double
2	4	7	7

Glabrous flesh (2 families)

Single	Double
9	10
2	8

* Records marked with an asterisk were obtained from delayed sowings (see Appendix, Note 1).

TABLE IV.

Showing the number of singles and doubles obtained in F_2 families derived from matings of the form no-d ♀ × d ♂.

no-d-glabrous white ♀ / d-glabrous red ♂

Single	Double	Single	Double
16	8	21	7
3	1	46	18
18	8	43	14
20	7	20	6
7	9	51	19
16	9	15	6
13	6	47	16
17	2	53	21
20	3	37	9
25	4	15	6
28	8	41	13
37	9	35	9
42	13	24	6
44	10	41	16
13	5	44	12
40	12	50	13
27	10	27	13
18	8	32	8
37	8	59	26
66	22	47	21
5	2	28	2
65	20	24	6
111	39	69	18

no-d-hoary white (Brompton) ♀ / d-glabrous red ♂

Single	Double	Single	Double
42	21	44	13

no-d-glabrous flesh ♀ / d-hoary white (intermediate) ♂ [1]

Single	Double
54	15

no-d-glabrous flesh ♀ / d-glabrous light purple ♂

Single	Double	Single	Double
208	12	64	6
116	7	92	5
26	1	58	5
60	2		

no-d-hoary white (Brompton) ♀ / d-sulphur white ♂

Single	Double	Single	Double
37	11	29	8
38	16	1	1
11	5	139	33
125	39		

no-d-glabrous white ♀ / d-glabrous cream ♂

Single	Double	Single	Double
72	13	48	14
84	14	84	29

no-d-glabrous flesh ♀ / d-sulphur white ♂

Single	Double	Single	Double
2	1	9	2
9	1	17	—
8	3	3	6
23	7	7	1
3	3	14	1
1	1	1	1
8	1	7	3
8	2	7	2
37	1	4	3
6	1	10	3
19	3	40	2
11	2	6	1
21	4	9	1
3	2	6	5
7	2	7	1
18	1	6	1
8	—	10	2
26	6	4	3
17	1	19	7
28	6	38	6
		19	8

no-d-glabrous cream ♀ / d-hoary white (intermediate) ♂ [1]

Single	Double	Single	Double
21	8	21	4
8	2	8	2

no-d-glabrous cream ♀ / d-glabrous white ♂

Single	Double	Single	Double
—	1	6	1
5	6	8	4
9	3	8	2
7	2	73	26
9	1		

no-d-glabrous cream ♀ / d-glabrous light purple ♂

Single	Double	Single	Double
242	81	6	1
118	43	13	4
107	87	47	6
167	85	32	1
6	7	12	1
5	2	3	4
11	2	53	1
26	3	8	1
6	1	5	2
33	1	5	1

no-d-glabrous cream ♀ / d-glabrous azure ♂

Single	Double	Single	Double
41	22	23	8
148	62	14	12
14	5	12	4

no-d-glabrous cream ♀ / d-sulphur white ♂

Single	Double	Single	Double
64	15	24	11
55	11	25	3
12	1	22	6
16	6	14	3
21	7	17	3
20	5	20	4
6	1	8	6
29	7	8	4
32	8	7	1
50	5	11	3
?[33	—]	12	2
7	1	10	3
10	2	12	1
18	5	23	4
43	5	8	1
11	2	9	7
20	6	3	2
31	6	11	2
5	2	29	6
17	6	9	4
9	2	10	3
21	9	19	3
19	4	21	3

no-d-glabrous cream ♀ / d-glabrous red ♂

Single	Double	Single	Double
28	11	17	9
44	12	42	6
56	9	38	22
47	17	43	15
57	12	45	10
43	6	54	11
72	30	55	11
57	17	53	15
77	21	32	9
40	9	59	16
49	18	33	3
50	5	49	14
54	12	41	10
41	21	41	12
50	12	44	20
44	11	43	11
47	5		

[1] See note, p. 326.

TABLE V.

Showing the number of singles and doubles obtained in F_2 families derived from matings of the form $d ♀ \times no\text{-}d ♂$. In this case some of the families will contain doubles and some will be all-single. [The all-single families in each mating are arranged on the left, the mixed families on the right.]

d-glabrous red ♀ / no-d-glabrous white ♂

Single	Double	Single	Double
47	—	18	6
30	—	32	6
46	—	32	15
46	—	50	11
14	—	50	16
69	—	40	8
26	—	34	16
70	—	44	18
23	—	39	13
63	—		
35	—		
27	—		
52	—		
58	—		
65	—		
33	—		

d-sulphur white ♀ / no-d-hoary white (incana) ♂

Single	Double	Single	Double
49	—	76	21
11	—		
11	—		
6	—		

d-sulphur white ♀ / no-d-red hoary (Brompton) ♂

Single	Double	Single	Double
137	—	156	29
		132	33

d-glabrous cream ♀ / no-d-glabrous white ♂

Single	Double	Single	Double
36	—	42	7
79	—	10	3
55	—	8	4
20	—	6	4
15	—	5	2
30	—	29	3
83	—	1	1
58	—	7	1
17	—	1	1
20	—	6	2
7	—	66	27
8	—	93	23
9	—	99	32
		138	39
		13	6

d-sulphur white ♀ / no-d-glabrous flesh ♂

Single	Double	Single	Double
27	—	47	4
31	—	20	5
20	—	42	7
24	—	29	5
11	—	19	9
13	—	10	2
51	—	39	2
21	—	37	3
70	—	38	3
12	—	37	3
59	—	30	3
60	—	23	2
24	—	24	5
43	—	39	11
17	—	11	2
27	—	30	1
32	—	9	1
32	—	8	1
29	—	5	1
26	—	86	17
14	—	114	17
34	—	23	7
10	—	120	28
19	—	54	10
12	—	32	7
18	—	23	5
		37	4
		22	3
		61	7
		60	13
		87	7
		13	2
		33	7
		25	3
		36	7
		48	7
		13	6
		42	7

d-sulphur white ♀ / no-d-glabrous white ♂

Single	Double	Single	Double
10	—	124	24
23	—	64	16
21	—	86	9
19	—	35	5
18	—	20	9
10	—	25	3
19	—	75	5
16	—	19	2
18	—	45	7
24	—	17	3
21	—	116	22
16	—	16	3
10	—	92	30
10	—	99	24
57	—	39	7
5	—	37	5
5	—	45	3
9	—	31	9
7	—	71	4
2	—	8	1
5	—	10	1
7	—	13	1
1	—		
3	—		
1	—		
80	—		

TABLE VI.

Showing the number of singles and doubles obtained in 50 F_1 families derived from matings between two ever-sporting forms. (See p. 319.)

Single	Double
2	5
—	1
2	2
3	11
11	7
2	14
1	8
56	52
3	2
25	31
63	78
10	13
14	17
18	16
14	13
9	8
8	18
14	23
8	7
—	1
—	1
7	12
8	13
11	16
5	6
8	12
71	86
3	4
3	2
8	13
5	9
8	18
9	10
22	29
6	11
18	25
18	17
4	7
9	12
7	8
18	21
3	4
14	19
1	12
1	11
9	8
2	3
23	24
14	7
8	7

TABLE VII.

Showing the number of singles and doubles obtained in 81 F_2 families when the F_1 cross-breds from matings between two eversporting forms are self-fertilised. (See p. 324.)

Single	Double	Single	Double
24	24	5	6
29	18	39	60
5	12	6	9
36	44	16	15
9	17	35	45
40	26	3	2
19	25	6	8
13	19	3	4
22	13	7	13
10	23	1	1
20	16	—	2
14	21	6	9
29	23	—	4
74	81	1	1
7	4	8	15
3	8	20	23
31	53	5	4
56	65	—	2
4	4	41	86
22	22	16	22
28	37	12	16
65	61	6	16
2	7	22	24
28	40	24	18
30	38	1	1
7	13	3	14
57	70	—	4
5	20	2	7
5	11	5	4
5	12	24	28
4	13	6	7
3	7	3	7
10	21	1	1
29	33	(13	13)
5	15	(*2	4)
5	6	7	20
6	8	(12	17)
4	8	(*94	141)
4	6	17	16
7	12	*85	146
37	53	*12	29
13	12		

TABLE VIII.

Showing the number of singles and doubles obtained in 35 F_2 families when F_1 cross-breds from matings between two eversporting forms were crossed back with one of the eversporting parents. (See p. 319.)

Single	Double
4	2
44	48
11	8
9	12
8	6
3	3
33	37
16	28
30	36
3	3
20	30
10	12
18	19
11	18
23	37
18	9
16	14
10	3
—	1
—	11
9	13
17	29
7	9
9	6
11	8
11	14
5	2
3	3
9	17
8	11
8	7
12	19
9	11
9	13
4	6

* Records marked with an asterisk were obtained from delayed sowings (see Appendix, Note 1). Below are shown the matings from which the above families were derived.

Fam.		
1–2	cream	× white
3–4	,,	× red
5–7	red	× cream
8–11	,,	× sulphur-white
12–19	sulphur-white	× white(hoary)
20–40	,,	,, × red
41	,,	,, × white
42–44	,,	,, × azure
45	,,	,, × light purple
46	azure(hoary)	× sulphur-white
47	flesh	× azure
48	azure	× red
49	light purple	× ,, light purple
50	red	× light purple

Fam.		
1–13	red	× cream
14–27	sulphur-white	× red
28–55	,,	,, × azure
56–57	,,	,, × light purple
58–62	,,	,, × white
63–75	,,	,, × white(hoary)
76–79	cream	× red
80–81	,,	· white

Fam.	
1–2	red × (red × sulph.-wh.)
3–5	,, × (sulph.-wh. × red)
6	(sulph.-wh. × red) × red
7–31	,, ,, × sulph.-wh.
32–33	(red × sulph.-wh.) × sulph.-wh.
34–35	(cream × sulph.-wh.) × red

# NOTE ON THE INHERITANCE OF CHARACTERS IN WHICH DOMINANCE APPEARS TO BE INFLUENCED BY SEX.

By L. DONCASTER, M.A.

Fellow of King's College, Cambridge.

A NUMBER of cases have been described, in which it appears that a character is dominant in one sex, recessive in the other. Such cases fall into two categories, according to whether the character concerned is inherited in the normal Mendelian manner, or is sex-limited in its inheritance. Examples of the former type are the horned character in sheep (horns dominant in the male[1]), and probably the white colour in the butterfly *Colias* (white dominant in the female[2]); of the sex-limited type examples are colour-blindness, hereditary nystagmus and haemophilia in man, and probably the orange colour in cats[3]. In the latter class it has frequently been stated that the character concerned is dominant in the male, recessive in the female. Taking colour-blindness as an example, we find the following facts. A colour-blind man married to a normal woman has usually only normal offspring; his sons do not transmit the affection, but his daughters transmit it to some of their male children, as in the following scheme:

   ♂ colour-blind man

   ♂ normal man

   ♀ normal woman.
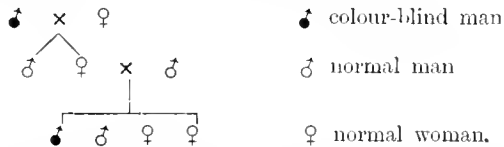
A colour-blind man married to the normal daughter of a colour-blind man may have colour-blind daughters as well as sons, thus:

---
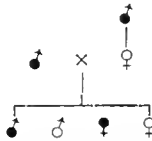
[1] Wood, *Journ. Agric. Science*, III. 1909, p. 145.

[2] Gerould, *Amer. Naturalist*, 45. 1911, p. 257. In this case there is the complication that homozygous white females have not been observed.

[3] Doncaster, *Proc. Camb. Phil. Soc.* XIII. 1905, p. 35. Since the publication of that paper I have obtained evidence, not yet conclusive, that the inheritance of the orange colour is sex-limited. Experiments to test this more fully are being made.

The explanation commonly given of these facts has been that colour-blindness is dominant in the male, recessive in the female, so that the male heterozygote is colour-blind, the female heterozygote normal; a colour-blind woman can thus arise only when the affection is inherited from both parents. It is also evident that the affected male transmits the factor for the disease only to his daughters; the heterozygous female, however, transmits to some of the offspring of both sexes. This sex-limitation of the transmission makes a different explanation possible, which is also more in accord with other cases of sex-limited inheritance.

Since the male transmits the factor for colour-blindness only to his daughters, it must be assumed that the male in this case is heterozygous for the sex-determiner. In former papers I have suggested that if maleness is determined by a factor $\male$, femaleness by a factor $\female$ epistatic to $\male$ when both are present, then a male individual may be represented $\male O$, a female $\male \female$; i.e. that both sexes are heterozygous for sex-determiners, with selective fertilisation between $\male$-bearing eggs and O-bearing spermatozoa, and between $\female$-bearing eggs and $\male$-bearing spermatozoa[1]. If we adopt this scheme as a working hypothesis, and then represent normal sight by N, colour-blindness by absence or modification of $N (= n)$, and further suppose that N can only be borne by gametes containing a sex-determiner ($\male$ or $\female$, not O), we obtain the observed results.

	Parents	$n\,\male\;O$ (affected male)		$N\,\male\;N\,\female$ (normal female)	
	gametes	$n\,\male\,,\,O$		$N\,\male\,,\,N\,\female$	
	F_1	$N\,\male\;O$ (normal male)	$\times$	$n\,\male\;N\,\female$ (normal female heterozygous)	
	gametes	$N\,\male\,,\,O$		$n\,\male\,,\,N\,\female$ $N\,\male\,,\,n\,\female$	
F_2	$n\,\male\;O$ (affected male)	$N\,\male\;O$ (normal male)	$N\,\male\;n\,\female$ (normal female heterozygous)	$N\,\male\;N\,\female$ (normal female)
	$n\,\male\;O$ (affected male)	$\times$	$N\,\male\;n\,\female$ (heterozygous female)	
gametes	$n\,\male\,,\,O$		$N\,\male\,,\,n\,\female$ $n\,\male\,,\,N\,\female$	
	$n\,\male\;O$ (affected male)	$N\,\male\;O$ (normal male)	$n\,\male\;n\,\female$ (affected female)	$n\,\male\;N\,\female$ (normal female heterozygous)

[1] *Proc. Roy. Soc.* B. 82. 1910, p. 88, B. 83. 1911, p. 476. My reasons for continuing to prefer this scheme to that of the American writers, who represent the male as XO, the female XX, will be given in a subsequent paper on the same subject. The argument in the present case applies equally to both schemes.

This scheme is exactly comparable with T. H. Morgan's results on the inheritance of the white eye in *Drosophila*[1], in which no suggestion of alternative dominance has ever been made ; if N represents the factor for red eye and n its absence (white eye), the scheme does as well for *Drosophila* as for human colour-blindness.

The scheme here outlined will apply to all cases of a character apparently dominant in one sex only and also sex-limited in its transmission by that sex (with the possible exception of the orange colour in cats, the inheritance of which is not adequately known). It will not apply to cases which show no sex-limitation in inheritance (e.g. horns of sheep) ; in these it must probably be supposed that a sex-limited modifying factor is present in one sex.

[1] Morgan, *Science*, 32. 1910, p. 120; *American Naturalist*, 45. 1911, p. 65.

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