REPORTS TO THE EVOLUTION COMMITTEE OF THE ROYAL SOCIETY.

REPORT II.

EXPERIMENTAL STUDIES IN THE PHYSIOLOGY OF HEREDITY.

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EXPERIMENTS WITH POULTRY.

By C. C. HURST, F.L.S.

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CORRIGENDA IN REPORT I.

Page 24, Table VI. The offspring of S. in. × S. ar. should stand under S. ar, instead of under T. in.

" 33, note ‡. After " purple " add " on fading."

" 34. The mark ‡ refers to note § on previous page.

" 68. In heading for " (R × D) " read " R × D."

" 71, Exp. 86. " Hoary " column, line 12, for " *br.* 28 " read " *br.* 8."

" 88, par. 5. For " more dingy" read " duller."

" 104, Exp. 37, and page 105, line 3. For " p. 140 " read " p. 96."

" 105. For " agree precisely, being 3·0 : 1 " read " are 2·7 : 1."

" 111, Exp. 51. For " Legh. 673 " read " Legh. 373."

" 115, Exp. 87. For " those " read " that."

Page 116, line 23. For " even " read " ever."

„ 123, par. 1. For " 76 and 77 " read " 80 and 81."

„ 131. The fanciers' view that the plain-head must be crest-bred is quite correct,
        because the heavy feathering (and perhaps skull-characters) are
        needed for a good crest.

„ 140. Mr. E. P. Boys-Smith has given us facts which make it very doubtful if
        the extension to goats is correct.

„ 160, note on Cupids, line 4. For " talls " read " Cupids."

Professor Weldon (' Biometrika,' II, p. 47) has pointed out that our reference
(Rep. I, p. 15, note) to the discovery by de Vries of " a wild specimen " of *Lychnis
vespertina* goes beyond the original account. Professor de Vries kindly replied to
our questions, that the glabrous plants came from seeds taken from wild plants
which were so far withered that their characters were not recognizable. Our
expression was therefore incorrect. The other criticisms made by Professor Weldon
appear to be based on misapprehensions.

INTRODUCTION.

This report is a continuation of Report I, 1902.   The experiments
were distributed as follows:—Those on *Datura, Matthiola, Salvia, Ranun-*
culus were done by E. R. Saunders; those on *Pisum* by W. Bateson and
H. Killby; on Sweet Pea by W. Bateson, E. R. Saunders, and
R. C. Punnett; on Poultry by W. Bateson with R. C. Punnett from
January, 1904.

The records are only complete to the end of 1903, but reference to
the work of 1904 is often necessary.

Part of the expense has been defrayed from funds received from the
Government Grant, and we have again to thank the Botanic Garden
Syndicate for the free use of an allotment.

Special attention may be called to the illustrations of reversion
following heterozygosis, and to consequent complications in the
application of Mendelian formulæ.   This is best seen in the case of
Stocks, where two glabrous types may unite to produce a hoary
heterozygote.   In another important group of cases the heterozygote
may assume either of two reversionary forms, one being a "total," and
the other a "half" reversion.

The facts as to Stocks give indications as to the special behaviour of
extracted recessives in a complex case, and similar evidence will be
provided by the Sweet Peas.

In the poultry the most novel results relate to "Walnut" or Malay
combs, where in special cases we meet the phenomenon of *four*
allelomorphs simultaneously segregated, and a definite example of true
synthesis occurs.

Disturbances caused by external influences are well exemplified in
the seed-characters of Peas, and though of less theoretical significance,
these facts are valuable as illustrating various sources of error.

"F_1" throughout designates the first filial generation resulting from
a cross.   "F_2" means the generation resulting from F_1 and, unless
qualified, means the offspring of $F_1 \times F_1$.   Other such terms are
urgently needed, *e.g.*, for the various offspring of DR × R, etc., but it
seems better to postpone the introduction of further symbols till their
use can be made strictly uniform (see Report I, p. 159, *note*).   "P"
means an original parent.

DATURA.

In the earlier report reference is made to a result recorded by Godron as following from the cross *D. Stramonium* ♀ × *D. Bertolonii* (= *Stramonium* v. *inermis*) ♂ in which the offspring were all *Bertolonii.* It is there suggested that this statement is possibly the result of an error either in description or experiment, since in all other cases of unions between the armed and unarmed races of *Stramonium* and *Tatula*, however mated, the armed character is dominant.* It so happened that we had not then used this particular union, but the reciprocal cross had been made, and had yielded armed and not unarmed offspring. The cross in question has since been made, and the offspring, 65 in number, were, in accordance with expectation, all armed.† This result confirms the view of Godron's statement expressed above, and shows that the reciprocal unions give identical results.

MATTHIOLA.

The experiments on *Matthiola* described in Report I have been continued, and the following is an account of the further results obtained.

Using a considerable number of types it was found that the inheritance for the most part followed simple Mendelian expectation, but there were certain definite groups of apparently unconformable cases, and also some scattered cases which seemed quite irregular. The investigation of these unconformable cases was a primary object.

In addition an attempt has been made to work out the laws of inheritance of colour, and to investigate the occurrence of double flowers, subjects which were only incidentally studied in the earlier experiments.

I. *The Apparently Unconformable Phenomena.*

A further study of these cases has proved that in many of them the inheritance is on ordinary Mendelian lines, and that the apparent discrepancy was due to the occurrence of an unexpected reversion. The later experiments bearing on these cases are dealt with in four sections numbered α, β, γ, δ.

* Report I, p. 24.
† This result is beyond question, since these armed cross-breds have now yielded offspring (F_2) showing the expected mixture of armed and unarmed individuals (46 armed, 15 unarmed).—[*Note added December*, 1904.]

(a) *Statement of Results.*

(α) *Experiments in the Form* $DR_1 \times R_2$.

The most interesting cases occurred in this group. The recessive character was glabrousness. From any mating DR × R an equality of D (hoary) and R (glabrous) offspring is the simplest expectation. Nevertheless in certain cases where the second recessive (R_2) differed in flower colour from R_1 used in the first cross, the offspring were *all D*, *viz.*, *hoary*. The possibility suggested itself that this aberrant result was due to the appearance of a *hoary* heterozygote as the result of the union of two *glabrous* gametes, and, however improbable such a supposition might be, it was not, as we pointed out,[*] yet excluded. Further experiment has shown that this is the true account. So long as R_1 and R_2 both belong to one of the sap-coloured types—red, flesh,[†] purple, claret, copper, etc., $DR_1 \times R_2$ gives the usual equality of D and R; but if one of these is sap-coloured and the other white or cream, or if the pair are white and cream respectively, $DR_1 \times R_2$ gives all hoary. (Report I, Table X).[‡]

Experiment I.—Of the new experiments in the form $DR_1 \times R_2$[§] the following three gave a simple Mendelian result.

		Offspring	
Colours of recessives.		Hoary.	Glabrous.
1. Red (br.)‖ R_1 and flesh (br.) R_2............		57	54
2. „ „ purple (gr.) R_2		32	22
3. „ „ claret (gr.) „		16	13
		105	89

The following six operations of the same kind representing as many different combinations of colours yielded 1105 offspring, of which *all except three were hoary.*

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* Report I, p. 86.

† *Flesh* is used here throughout for *pinkish-white* of the earlier experiments.

‡ In some experiments (*e.g.*, 87 and 88) an occasional recessive appeared, but these, in all probability, are due to accidental fertilisation.

§ In the previous Report (p. 10, note) attention is called to the fact that in the earlier experiments the breedings of cross-breds with pure types were almost all in the form of cross-bred ♀ × pure ♂. The proof of the differentiation of the germ cells of the cross-bred therefore rested almost entirely upon evidence drawn from the ovules. In order that the presumed differentiation of the ♂ germ cells should be similarly tested, the cross-breds in the present experiments were also used as pollen parents. In accordance with expectation the reciprocal unions yielded identical results.

‖ The letters in brackets refer to the colours of the seeds; br. = brown, gr. = green.

	Colours of recessives.			Offspring.	
				Hoary.	Glabrous.
4.	Cream (br.) R_1 and white (br.) R_2		......	315	1
5.	Red (br.) ,, ,, ,,		......	124	1
6.	,, ,, cream ,,		......	234	—
7.	Cream (br.) ,, flesh ,,		......	367	1
8.	,, ,, purple (gr.) R_2		......	31	—
9.	,, ,, claret ,,		......	31	—

The three glabrous which came from these matings were in all probability due to accidental fertilisation.

Seed colour alone gives no real indication of the behaviour of the recessives in these operations; for combinations in which the two recessives are brown-seeded occur in both groups (1, 4—7), as also do cases (2, 3, 8, 9) in which one recessive has green seeds and the other brown. The departure from the expected mixture of glabrous and hoary is always associated with the meeting either of a sap-coloured form with a white or a cream, or of white and cream with one another.

(β) *Experiments in the form* $DR_1 \times DR_2$.

Experiment 2.—Using cross-breds containing the same D (white *incana*), but different recessives, similar results were obtained.

(1) When R_1 was red and R_2 cream the offspring were   141 hoary.
(2)   ,,   cream ,, flesh   ,,   ,,   199 ,,
(3)   ,,   red   ,, flesh   ,,   ,,   157 ,, and
                                                        52 glabrous.

Here, again, the exceptional result followed in those cases where cream was introduced, and a precise Mendelian result when both recessives belonged to the sap-coloured group.   In all three cases alike the cross-breds were producing gametes carrying glabrousness, as shown by the results of self-fertilisation (pp. 16—18).

(γ) *Experiments in Crossing Two Glabrous Types*, $R_1 \times R_2$.

At the time of publication of the previous Report no crosses had been made between the various recessive types, nor could any information be obtained in support of the suggestion then tentatively put forward, viz., that a hoary form might be produced by the union of two dissimilar glabrous types.*   A large number of such crosses have now been made, and the results are recorded in the accompanying Table.

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* Report I, p. 86.

Table 1.—Results obtained from Unions between Glabrous Types of dissimilar Flower Colour.

These types were " wallflower-leaved " Ten-week Stocks, of which a collection was very kindly presented to us by Messrs. Haage and Schmidt, of Erfürt. To avoid confusion we have usually retained the descriptive terms used in the earlier Report to designate the various colours. The corresponding terms in Haage and Schmidt's catalogue are as follows :—

$$
\begin{array}{lll}
\text{Cream} & = \text{schwefelgelb H. and S.} \\
\text{Red} & = \text{carmoisin} & \text{,,} \\
\text{Light purple} & = \text{hellblau} & \text{,,} \\
\text{Very light purple} & = \text{lasurblau} & \text{,,} \\
\text{Dark purple} & = \text{dunkelblau} & \text{,,}
\end{array}
$$

Number of experiment.	Colour of glabrous parents.	Number of offspring.		Colour of offspring.
		Hoary.	Glabrous.	
3	White × cream and reciprocal ..	62	—	Purple.
4	White × red and reciprocal	43	—	,,
5	White × flesh	56	—	,, (paler).
6	White × copper...............	11	—	,,
7A	White × dark purple and reciprocal	32	—	,,
7B	Very light purple × white......	38	—	,, (paler).
8	Cream × red and reciprocal	88	—	Red.
9	Cream × flesh ,, ...	46	—	Rose.
10	Cream × copper ,, ...	25	—	Red.
11A	Dark purple × cream	31	—	Purple.
11B	Cream × light purple	22	—	,,
11C	Very light purple × cream......	3	—	,, (paler).
12	Flesh × dark purple	—	30	,, ,,
13	Flesh × copper and reciprocal...	—	32	Rose.
14	Flesh × red	—	27	,,
15	Red × dark purple and reciprocal	—	76	Purple.
16	Dark purple × light purple.....	—	33	,, (paler).

These results are perfectly concordant among themselves, and in complete harmony with those given under (α) and (β), to which they furnish the desired clue. For it appears that *when glabrous types of dissimilar flower colour are crossed together, the resulting offspring are all hoary or all glabrous, according to the particular combination of types employed.* When glabrous white and glabrous cream are crossed with each other or, so far as experiment has yet gone, with glabrous plants of any other colour, the offspring are *all hoary*, thus affording another example of the assumption of an atavistic character by a heterozygote.

This example, it may be noted, illustrates the rarer case of reversion in a structural character, most of those at present known being cases of reversion in colour. When the cross is between glabrous types, neither being white or cream, and both having the cell sap of some shade of red or purple, the offspring are *all glabrous*.

δ. *Extracted R × pure-bred R.*

Experiment 17.—The parentage of the individuals employed in these unions is most easily shown by the following diagram:—

White glabrous   Cream × White hoary   Cream
      type   glabrous. | (*incana*).   glabrous type.

F_1 Purple hoary.
                                  ×
                                 self.

F_2*   **White**   17A.   White   17A.   **White**   17B.   Cream
    glabrous. ♀   ×   glabrous   ×   **glabrous. ♀**   ×   glabrous
                         type. ♂   type. ♂

F_3 15 hoary.   71 hoary.   76 glabrous.
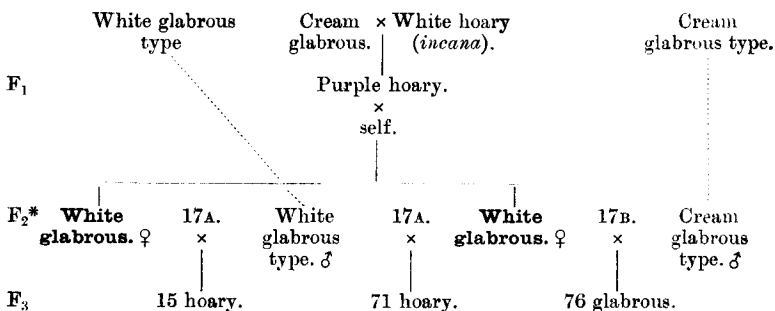
In one case (Experiment 17A) two " extracted" glabrous whites were crossed with a pure-bred glabrous white; *the* 86 *offspring (purple) were all hoary.* As stated in the earlier Report the F_2 generation in which the glabrous seed-parents came contained the expected number of recessives (roughly 1 in 4).† Such recessives are of two colours only, white and cream (see p. 18), and the numbers—48 white, 15 cream—suggest that possibly the whites may be of two kinds, the one pure, the other containing cream as a recessive.

[Note, added December, 1904.

This prediction has since been verified. Offspring were raised from 13 such extracted F_2 whites. Ten of these individuals bred pure, yielding altogether 106 whites, but no creams; the three remaining plants, among which was one of the two employed in Experiment 17, each yielded a mixture of whites and creams. Hence union of the white- and cream-bearing gametes of the cross-bred (F_1) evidently results in dominance of white, whereas in the case of pure-breds we had reversion to purple.]

Since all the F_3 individuals (86) were hoary, and since we must suppose that in any case some of the gametes of such " extracted" F_2 whites carry white only, it is evident that reversion to the hoary type

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* The coloured members of this family are here omitted.

may result even when the uniting gametes carry the same colour and surface character. The same deduction follows from the observations given under Experiment 2 (1) and (2), where both DR parents were giving off white glabrous gametes, as self-fertilisation proved (pp. 16—18).

In Experiment 17B the glabrous white seed-parent—one of the two used in Experiment 17A [and proved later to contain cream as a recessive, see dated note, p. 9] was crossed with a pure-bred, glabrous cream; *the offspring, 76 in number, were all glabrous*, and either white or cream in colour. Here, although the two recessive parents were coloured respectively white and cream, reversion to hoariness did not occur.

These two results throw a new light upon two somewhat similar experiments recorded in Report I (Experiments 79 and 80), and then regarded as puzzling and unexplained exceptions. In these two cases also the seed-parents were "extracted" glabrous whites. Their parentage was as follows :—An annual hoary white was crossed with a red recessive ; one of the resulting hoary cross-breds was then mated with a white recessive. The F_2 generation so bred, though for the most part hoary, contained a few recessives. A knowledge of the results obtained from such matings when *incana* is used as the hoary type, leads us to expect that such an F_2 generation would be *all* hoary, and in consequence to ask whether the above-mentioned recessives can have occurred as the result of accidental self-fertilisation. The total number of these recessives (9)* is large to attribute to an unnoticed source of error, nevertheless until a repetition of the experiments with an annual hoary has disproved this possibility, it must be admitted that such an explanation brings all four experiments most readily into line.

The further operations with two of these "extracted" recessives are shown below :—

Experiment 79 (Report I).   Experiment 80 (Report 1)

Extracted   ×   Pure-bred   ×   Extracted   ×   Pure-bred
white glabrous ♀.| glabrous white ♂.| glabrous white ♀.| glabrous cream ♂.

46 hoary, 1 glabrous.   30 hoary.   17 hoary.
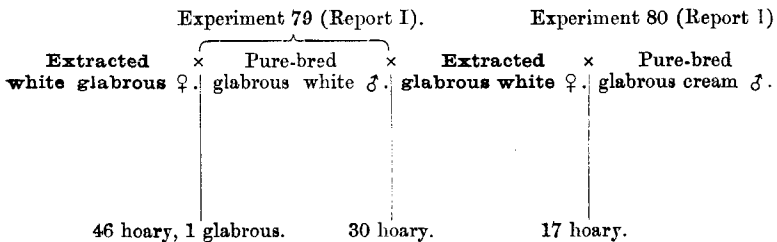
The diagram shows that with one exception (due in all likelihood to accident) the offspring of the matings between the "extracted" and the pure-bred recessives were all hoary. Here we have reversion not only when the "extracted" white is bred with a pure white (as in

* Report I, Experiment 63.

Experiment 17A), but also when it is bred with a pure cream (unlike Experiment 17B). *Taken together these results indicate that when an "extracted" white recessive is mated with a pure-bred recessive, which itself is either white or cream, reversion will occur in the succeeding generation provided that the pure-bred recessive does not belong to the recessive type introduced in the original cross.* The result is not affected if the pure-bred recessive and the extracted recessive are both similar in colour.

(b) Conclusions.

From what has been stated above in α, β, γ, it is clear that this diversity of result occurring alike in the operations $R_1 \times R_2$, $DR_1 \times R_2$, and $DR_1 \times DR_2$ is referable to the same complication. It appears that unions between two gametes carrying the recessive character glabrousness, in conjunction in the one with white or cream colour, and in the other with any colour except that of the gamete with which it unites, whether both are borne by pure-breds (γ), both by cross-breds (β), or one by a pure-bred and one by a cross-bred (α), produce reversionary (hoary) offspring. Whether this principle will be found to hold when similar unions are made between recessives, *both of which are "extracted,"* has yet to be determined. Conceivably the result may vary according as the recessives are "extracted" from cross-breds of like or unlike composition as has already been shown to be the case in δ, where the matings were between an "extracted" and a pure-bred recessive. So far only the albinos among the "extracted" recessives have been employed. In these cases reversion did not occur when the newly-introduced pure-bred recessive belonged to the same type as the recessive grandparent of the "extracted" albino. But when this was not the case, the F_3 offspring reverted to the hoary type. The evidence, in fact, indicates that given a recessive albino, extracted from a DR cross-bred, we require to know the colour of the R grandparent before we can predict the surface character of the offspring obtained by mating it with a pure-bred recessive. Further, it becomes clear that a difference of colour is not a necessary condition of reversion in all cases where two recessives are bred together; under certain circumstances, reversion to the dominant (hoary) form may occur when the recessives are alike in colour.

[Note, added December, 1904.

II. *Further Experiments with Recessives.*

(a) *Posterity of R_1R_2 Cross-breds.*

Offspring from these cross-breds were raised (α) by self-fertilisation; (β) by crossing back with R_1 or R_2; (γ) by a cross with R_3; (δ) by crossing with an R_2R_3 cross-bred.

$$(\alpha) \; R_1 R_2 \times Self.$$

In every case where $R_1 R_2$ was hoary (D), *i.e.*, in every case where F_1 had a white or cream parent, F_2 *was mixed hoary* (D) *and glabrous* (R). Though one might have anticipated equality of D and R, the actual result showed a constant excess of D. The numbers obtained in each case were as follows :—

Number of experiment.	Parents.	F_1.	F_2.	
			Hoary.	Glabrous.
18A	Cream R × white R................	All hoary	85	61
	Reciprocal................	,,	43	34
18B	Cream R × red R..................	,,	154	88
	Reciprocal	,,	4	2
18C	Cream R × flesh R.	,,	27	16
	Reciprocal.	,,	35	28
18D	Cream R × light purple R	,,	64	51
18E	Dark purple R × cream R......... .	,,	64	33
18F	White R × red R.................	,,	50	31
18G	White R × flesh R...............	,,	34	19
18H	White R × copper R	,,	41	28
18K	Dark purple R × white R..........	,,	44	25

This preponderance of hoary individuals can scarcely be accidental. In 18A and 18B the results indicate a certain amount of association or linking together of surface character with flower colour, the hoary character only appearing in conjunction with sap colours, the glabrous character only with white or cream. How far this complication may account for the irregular result is at present uncertain, since in other colour combinations the glabrous F_2 plants exhibit the same range of sap colours as the hoary, with white, or white and cream in addition. (For details of flower colour see p. 27.) No similar association of seed colour with surface character was apparent. Further consideration of these results is postponed until the evidence from F_3 is available.

In those cases, on the other hand, where $R_1 R_2$ was glabrous, *i.e.*, where both parents had been sap-coloured recessives, F_2 *was all glabrous*. One hundred and ten individuals were thus raised from various colour unions as shown below, and the results accord with simple Mendelian expectation :—

Number of experiment.	Parents.	F_1.	F_2.	
			Hoary.	Glabrous.
19A	Flesh R × red R	All glabrous.	—	5
19B	Copper R × flesh R..............	,,	—	25
19C	Flesh R × dark purple R	,,	—	32
19D	Dark purple R × red R..........	,,	—	25
19E	Dark purple R × light purple R ...	,,	—	23

(β). $R_1R_2 \times R_1$ and $R_1R_2 \times R_2$ when R_1R_2 is hoary, and either R_1 or R_2 is sap-coloured, the other being non-sap-coloured.

$$R_1R_2 \times R_1 \text{ or } \times R_2.$$

Sap-coloured R employed in both unions.   *Non-sap*-coloured R employed in both unions.

Number of experiment.	Colours of R types.	F_2.		Number of experiment.	Colours of R types.	F_2.	
		Hoary.	Glabrous.			Hoary.	Glabrous.
20A	(White × red) × red	21	14	21A	(White × red) × white..	11	11
20B	(White × flesh) × flesh..	26	33	21B	(White × flesh) × white.	10	9
20C	(Cream × red) × red .	14	8	21C	(Cream × red) × cream .	5	12
20D	(Cream × flesh) × flesh..	11	8	21D	(Cream × flesh) × cream	8	9
20E	(Dark purple × cream) × dark purple	6	18	21E	(Dark purple × cream) × cream	10	14
	Total	78	81		Total	44	55

In each pair of unions the same cross-bred was mated with R_1 and with R_2. A comparison of the numbers obtained in the separate matings suggests that the discrepancies are probably fortuitous, and do not indicate a real divergence from the simple expectation of equality of D and R. Adding together the results in each group of unions, we get the ratio 1 D : 1·03 R in the case of a cross back with the sap-coloured recessive, and 1 D : 1·25 R when the non-sap-coloured form was the one used in both crosses.

In the case of a repeated cross with white (Experiments 21A and 21B), there was a definite association of surface character with seed colour. The seeds were mixed green and brown. Green seeds gave rise to hoary, brown seeds to glabrous plants. This was not the case in the repeated crosses with cream where the seeds were either all

brown (Experiments 21c and 21d), or of more than two colours (Experiment 21e, where intermediates occurred). In the repeated crosses with sap colours, green seeds and brown seeds each yielded both surface characters.

(γ) $R_1R_2 \times R_3$ where R_1R_2 is Hoary.

The results in this case were also in agreement with expectation. When R_3 has coloured sap, F_2 *is mixed*, hoary and glabrous, in proportions approaching equality; when R_3 has uncoloured sap, F_2 *is all hoary*.

$$R_1R_2 \times R_3.$$

R₃ having coloured Sap.   R₃ having colourless Sap.

Number of experiment.	Colours of R.	F₂.		Number of experiment.	Colours of R.	F₂.	
		Hoary.	Glabrous.			Hoary.	Glabrous.
22	(White × red) × copper	12	15	26a	(White × red) × cream...	24	—
23	(White × red) × claret ..	3	4	26b	(White × flesh) × cream	31	—
24	(White × flesh) × red ...	13	20	26c	(Cream × flesh) × white	24	—
25	(Cream × flesh) × copper	9	7				

(δ) $R_1R_2 \times R_2R_3$ where R_1 alone has Colourless Sap.

Experiment 27.—The only mating of this kind was in the form (white R × red R) × (dark purple R × red R). F_2 showed the expected equality of D and R (20 hoary, 19 glabrous).

(b) Conclusions.

The results of breeding R_1R_2 cross-breds with any of the recessives R_1, R_2, R_3, or with a glabrous R_2R_3, are all in accord. In F_2, as in F_1, there is a sharp distinction between the results obtained from sap-coloured and non-sap-coloured forms. We can obtain at will an F_2 which is all hoary, or all glabrous, or hoary and glabrous mixed in approximately equal numbers, by employing recessives belonging to the appropriate group.]

III. Colour Inheritance.

The investigation of the laws determining colour inheritance present greater difficulties. Apart from the fact that with a larger number of categories the total number of observations is usually smaller (since it

is hardly possible to preserve every individual to maturity), the dis-
crimination of colour is rendered difficult, owing in part to the gradation
of shades which the corolla exhibits between unfolding and fading, and
in part to the almost universal occurrence of " flaking." These two
causes are likely to affect one's judgment of plants seen *en masse;* on
the other hand, a difference of shade is less easy to detect when single
flowers of individuals are compared.

Some account of the colours observed in various unions appears in
the earlier Report; but in those experiments the investigation of
colour was not the primary object. Only a relatively small number of
plants were flowered. The records, therefore, give *no indication of
the proportion,* and but little of the range of colours occurring in the
second (F_2) and later generations. In the present case the investiga-
tion was confined to experiments with a small number of authentic
types. The white flowered form of *incana* was used as the dominant
parent; the recessives were Ten-week Stocks with flowers white,
cream, purple, or some shade of red. *Incana* was also mated with
another dominant white strain (a hoary white Brompton Stock).

(a) *Colour of F_1 Cross-breds.*

When any of the above - mentioned recessives was bred with
white *incana*, the hoary F_1 cross-breds were all purple.* No differ-
ence in colour could be detected between the cross-bred plants
which had a white, cream, or red recessive parent. *All resembled the
purple-flowered type form of* incana. The cross-breds from the flesh-
coloured recessive were of a somewhat paler tint, but fading flowers
were as deeply coloured as those recently opened on the other cross-
breds. This difference of tint distinguishing the plants produced from
the cross *incana* × flesh-coloured recessive is also apparent when a
flesh-coloured recessive is bred with a recessive of another colour
(Table I, p. 8). Here, flesh-colour × white gave a purple paler than
that produced when white was crossed with cream, purple, red, or
copper-coloured forms ; again, flesh-colour crossed with cream, red, or
copper colour, gave rose, whereas cream with red or copper gave a full
red.

The colours of the R_1R_2 cross-breds is given in full in Table I
(p. 8).

The results may be summarised as follows :—

1. Purple in any combination yields a purple (Experiments 7, 11, 12,
15, 16).

2. Combinations of reddish colours give some shade of red
(Experiments 13, 14).

3. All combinations in which white was bred with non-white, give

* Report I, p. 46, Table.

purple, the heterozygotes being all hoary. In Experiment 7 the signi-
ficance of the purple is not clear, since purple is introduced in the
cross, but in Experiments 3 to 6 it is evident that we have reversion in
colour, as well as in surface character.

4. When cream is substituted for white there is again reversion in
surface character, but the reversionary purple does not appear
(Experiments 8 to 10 ; Experiment 11 is not in question for the reason
given above in the case of Experiment 7).

Cross-breds of the form D_1D_2 were obtained from the mating white
incana and white Brompton. In this case the parents were similar in
surface character and flower colour, but differed in habit. The cross-
breds showed no reversion in colour, but were white like both parents.

(b) *Colour of Posterity of DR Cross-breds.*

(a) *$DR_1 \times Self$ and $DR_1 \times R_1$.*

Cross-breds from *incana* by a recessive form were self-fertilised, and
also crossed back with the original recessive. In each case F_2 exhibited
the colours of both parents, and of the cross-breds (F_1); but when
cream was used as the recessive there appeared in addition to the cross-
bred and parental types at least one new distinct colour form, thus
indicating that a resolution had taken place.

The following were the actual numbers recorded :—

Case 1.—*When the Recessive was Red-flowered.*

Number of experiment.	Form of union.	Number and colour of individuals obtained in F_2 from a sample of fruits selected at random.							
		Total hoary.	Total glabrous.	Purple hoary.	White hoary.	Red hoary.	Purple glabrous.	White glabrous.	Red glabrous.
28A	DR × R	102	112	54*	—	48*	59*	—	53*
28B	DR × self	240	56	108	67	43	24	10	10

* The numbers marked with an asterisk are obtained by calculation from the
seed colour. Over 700 seeds had been harvested from 13 fruits on 6 individuals;
of these 349 were green and 365 intermediate in colour. Each colour gave rise to
both hoary and glabrous plants, but all individuals from green seeds were purple-
flowered, those from the intermediate seeds red. It is therefore possible to make a
prediction as to the colour of those individuals which did not flower, and such
glabrous and hoary plants are included in the numbers given above.

The simplest expectation in the case of the cross back with the original recessive is, as regards surface, equal numbers of hoary and glabrous plants : as regards colour, equal numbers of purple and red flowered individuals, the purples arising from the union of a red- with a white-bearing gamete, the reds from the union of two red-bearing gametes; and further, equal distribution of these two colours among the hoary and the glabrous groups. The results obtained fully confirm this supposition. For the expectation in every case being equality, the observed ratio of hoary to glabrous was 1 : 1·09; of red to purple 1 : 1·11; of the four different forms to one another 1·12 : 1·00 : 1·22 : 1·10.

In the case of self-fertilisation we should expect the appearance of six different forms, the three colours, red, purple, and white occurring in conjunction with hoariness and with glabrousness, the ratio of the colours in both cases being as 1 : 2 : 1. An approximation to the theoretical result though less close than in the previous case is clearly indicated. It was noted that the white flowered individuals were of a pure white, but the petals became tinged on fading, a phenomenon not uncommon in the pure-bred white *incana*. Among the red flowered plants there were slight variations in tint, some few individuals showing a bright crimson red, while the great majority were of a more carmine shade.

Case 2.—*When the Recessive was Flesh Coloured.*

Number of experiment.	Form of union.	Number and colour of individuals appearing in F_2							
		Total hoary.	Total glabrous.	Purple hoary.	Rose* hoary.	White hoary.	Purple glabrous.	Rose† glabrous.	White glabrous.
29	DR × self	65	20	15	25	9	3	8	5

Unfortunately no cross back with the original recessive was made in this case, and we have therefore only the rather small totals obtained from self-fertilisation. The results would presumably be the same as in the preceding case, with the substitution of pale shades for the full red and purple. As a fact, the ratio of hoary to glabrous was almost precisely 3 : 1, but the numbers as regards colour are not in accord

* The flesh colour of the recessive strain is represented in the F_2 individuals by a rather bluer tint (rose).

with expectation. In both the hoary and the glabrous lots there is a preponderance of rose, where we should have anticipated purple, the numbers being such as to suggest that the ratios are, for some unknown reason, reversed. Until further evidence is to hand it must remain doubtful whether the above numbers are too small to give a real indication of the actual ratios, or whether the result is in any way due to a breaking-up, such as seems certainly to occur in the third case described below. It may be noted in passing that were such decomposition to take place, and to result in the production of equal numbers of *two* kinds of pink-carrying gametes, which, meeting with the white gametes showed dominance in the one case and reversion to purple in the other, so that we should represent the proportions of the different gametes formed by the cross-bred as 2 White : 1 Pink A : 1 Pink B, then such reversal of the ratio of purple to pink would be in accordance with expectation, the proportions among both hoary and glabrous lots being 1 White : 2 Pink : 1 Purple. Possibly the appearance of rose instead of a true flesh colour in F_2 may also be accounted for in this way, but until the next generation has been raised the point must remain undecided.

Case 3.—*When the Recessive is Cream Coloured.*

Number of experiment.	Form of union.	Number and colour of individuals obtained in F_2 from a sample sowing in Experiment 20*a* and a full sowing in Experiment 20*b*.									
		Total hoary.	Total glabrous.	Purple hoary.	Purple c.e.* hoary.	Red hoary.	Red c.e.* hoary.	White hoary.	Cream hoary.	White glabrous.	Cream glabrous.
30A	DR × R	73	79	14	5	20	11	—	—	33	29
30B	DR × self	324	97	95	7	36	5	32	8	48	15

Both experiments are a repetition of some recorded in the earlier Report (Rep. I, p. 71, Table X, Experiment 86, and p. 74, Table XI, Experiment 93). In the case of *a cross back with the original recessive* ($DR_1 \times R_1$), reference to the earlier experiment shows a simple Mendelian result as regards surface character (297 hoary, 302 glabrous), but an irregular distribution of the three seed colours (green, brown, and intermediate), and want of strict association between

* c.e. = with cream eye; throughout the rest of the petal the plastid colour is obscured by the sap colour.

seed colour and surface character. In the present case the three seed colours were again obtained, and it was noted that the brown and green were respectively uniform in colour, and that the group of intermediates were somewhat graded in tint, the discontinuity between the brown and intermediates being sharper than between the intermediates and the green. No similar observation was recorded in the earlier experiment, and it is conceivable either that the seeds were less well ripened and the colours less well developed, or that the grading of the intermediates was less accurately observed. Be this as it may, the distribution of the seed colours in the present instance was more or less regular, the numbers approximating frequently in individual fruits, as well as in individual plants, to the proportion 1 green : 1 intermediate : 2 brown. Moreover, there was a strict association between seed colour and both surface character and flower colour. A sample sowing of all the seeds from three fruits—about 160—was made, and with one single exception, every seed classed as green or intermediate, gave rise to a hoary, and every brown to a glabrous individual. As regards flower colour every plant derived from a green seed was purple, every one from the intermediate seeds red, and from the brown seeds either white or cream. In the following columns the proportion of the seed colours in each of 23 fruits gathered from 4 individuals is shown, the total numbers are 325 green, 339 intermediate, 651 brown.

The inference from the sample sowing is that the total number of seeds would have produced 665 (664 + 1) hoary and 650 (651 – 1) glabrous plants, a sufficiently close approach to the Mendelian ratio 1D : 1R. Of the 73 hoary and 79 glabrous individuals actually obtained from the sowing, 112 have so far flowered; six different colour-forms appeared—purple, purple with cream eye, red, red with cream eye, cream, white. We have then the two parental colours (cream and white), the cross-bred colour (purple), and three other forms. Of these the two with cream eye have the peculiarity that, whereas other coloured forms become more or less streaked with white or "flaked," these show the purple or red streaked or patched with cream; they are, in fact, creams with sap colour added. Although the numbers obtained (see p. 18) are possibly too few to indicate the real proportions of the different forms, they offer several points of considerable interest. It will be noticed that all the glabrous individuals were either white or cream—the parental colours, the purple of the F_1 cross-breds and the novelties seen in the hoary plants were altogether absent; further that the two colours occurred in about equal numbers (29 and 33). Gametes carrying cream colour and glabrousness, and white colour and glabrousness were evidently produced by the cross-bred, and, we must suppose, in equal numbers. Union of the glabrous white gametes of the cross-bred with the glabrous cream gametes of the pure-bred pollen parent results, not in reversion to purple, as occurs when the corre-

Number and Colour of Seeds.

Individual plants.			Individual fruits.		
Green.	Inter.	Brown.	Green.	Inter.	Brown.
110	114	193	16	15	30
			20	24	25
			21	14	27
			13	9	23
			15	22	26
			11	14	36
			14	16	27
48	77	124	16	16	31
			9	21	29
			15	19	31
			5	5	9
			9	16	24
58	62	106	12	21	22
			16	12	19
			15	13	32
			15	16	33
109	86	228	12	16	31
			17	13	42
			14	20	31
			15	10	38
			23	7	37
			18	6	27
			10	14	22
325	339	651			

sponding gametes of two pure-bred types unite (see Table I, Experiment 3), but in dominance of white. We may, in fact, expect that these whites will yield both white and cream plants in F_3, while the creams will breed true and produce only cream.*

[Note, added December, 1904.

This expectation has now been fulfilled. Separate sowings were made from 16 of these extracted whites, *and in every case F_3 showed a mixture of whites and creams.* On the other hand *an F_3 of creams only was obtained from six F_2 creams selected at random.*]

The hoary plants, on the contrary, show a total absence of both white and cream, a fact which indicates that the union of white and

* That creams can be bred from whites we already know, since it is a well-established fact that certain white strains habitually throw cream " doubles." In the hope of elucidating this and other points connected with the appearance of the cream colour, a histological investigation of the petals is now being made.

cream or even of cream and cream will give different results as regards colour according as the gametes are carrying these colours in conjunction with hoariness or with glabrousness. The appearance of an entirely new colour—red—suggests that a breaking-up of the constituent colours has occurred in the gametogenesis of the cross-bred. The evidence from the seed colours indicates that the red-flowered plants, whether self-coloured or with cream eye, will be equal in number to those with flowers wholly or partly purple, but the proportion of selfs to bicolours in each case is hardly to be gathered from the numbers at present available. We may, therefore, pass to a comparison of these results with those obtained from *self-fertilisation* of the cross-breds (Experiment 30B). Here the grading of the seed-colours was more continuous, and the sorted groups did not exhibit such a strict correlation with surface character and flower colour as to permit of sample sowings. A full sowing yielded the results given above (p. 18). The proportion of hoary to glabrous is almost precisely 3 to 1. The colours of the glabrous plants are similar to those obtained from the cross back with the original recessive, viz., cream and white only ; the ratio (almost exact) 3 : 1 suggesting as before that when the glabrous cream-and glabrous white-bearing gametes meet there is again dominance of white.* The hoary individuals exhibit the same colours as when the mating was of the form $DR_1 \times R_1$, and, in addition, white and cream. The last-mentioned form, we may presume, will breed true. From its appearance here we can scarcely doubt that the cross-bred is producing gametes carrying cream colour in conjunction with hoariness. The view that the results of unions of cream with cream will vary according as the gametes are also carrying the hoary or the glabrous character is thus further confirmed. [It will be remembered that when these very cross-breds were mated with a pure-bred glabrous cream, no hoary creams appeared.]

Here, as in the preceding case, it is doubtful whether the numbers are sufficiently large to give a reliable indication of the true ratios in the smaller groups of hoary plants. Moreover we do not yet know what forms the bicolours will produce. It must be borne in mind that flower colour in Stocks is due to the presence of colour, either in the cell sap, or in the plastids, or in both; white results from absence of colour in both these cell constituents. We can, therefore, classify these various colour forms under four heads as shown below where the + and − signs indicate presence and absence of colour respectively.

Now the original cross was between plants belonging to i and ii ; plastid colour behaves as a recessive character, all individuals in F_1 coming under iii. In F_2 we get the four possible combinations of the sap and plastid characters. In the case of i and ii we may probably

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* The actual proof is furnished in F_3 (see note, p. 9).

Totals in F_2.	i. − Sap. − Plastid.	ii. − Sap. + Plastid.	iii. + Sap. − Plastid.	iv. + Sap. + Plastid.
	White.	Cream.	Self-coloured reds and purples.	Reds and purples with cream eye.
Expt. 30A	33	29	34	16
„ 30B	80	23	131	12

accept the ratio 1 : 1 in Experiment 30A (DR × R) and 3 : 1 in 30B (DR × self). In the case of iii and iv the relation is probably less simple, and for elucidation of this point we must await further evidence.

Looking at the colour groups from another point of view, and taking sap colour alone into consideration we may class the selfs and bicolours together; we then have among the hoary individuals in 30B : 102 with purple sap, 41 with red sap, 32 white, 8 cream.

These numbers suggest the ratio 9 : 3 : 3 : 1, which would give 103·5 : 34·5 : 34·5 : 11·5, and though the result departs in some measure from this expectation, it is not impossible that this discrepancy may be fortuitous.

Tschermak,[*] crossing a white flowered strain of *M. glabra* with a deep blood-red coloured form of *incana* obtained in F_2 a mixed offspring in the proportion of 3 hoary coloured to 1 glabrous white (actual numbers 2249 and 845). The hoary individuals were divisible into four colour groups—pure violet, ash violet, pure rose, ash rose—the numbers indicating the ratio 9 : 3 : 3 : 1. Such a ratio we expect when two pairs of allelomorphic characters exhibit the phenomenon of simple Mendelian dominance, and in the present case this relation was deduced by Tschermak from the numbers he obtained in F_2 and further confirmed by his results in F_3. The pure colours were found to be dominant over the ash tints, the violet shades over the pink. Whether the corresponding ratio in our own experiments will be substantiated, and whether it is the outcome of such a simple Mendelian gametic ratio, can only be decided by further experiment.

Tschermak's observation leads to the important conclusion that certain of the F_2 individuals which exhibit a reversionary colour are homozygous, and will breed true; and, consequently, that in the gametogenesis of F_1, an actual synthesis has taken place. Our own experiments are not yet sufficiently advanced to give a clear indication on this point, though it is scarcely doubtful that the next generation will show this result.

As stated above (p. 21), the red colour obtained in these experi-

[*] 'Beihefte z. Bot. Centralb.,' 1903, Heft. 1.

ments (30A and 30B) is wholly new, and for the present we can form no certain opinion as to the components which combined to produce it. As possibly bearing upon this point, however, we may recall that on crossing a glabrous cream with a *white-flowered hoary Brompton Stock*, a similar red colour occurs in F_1 (Rep. I, Table, p. 46), a fact which suggests that certain gametes of the *incana* cross-breds, carrying *white* and *cream* respectively, may similarly unite to produce red where one might otherwise have expected reversion to purple.*

On the other hand, it may be that the *red* of the Brompton cross-breds is analogous with the *purple* of the *incana* cross-breds. The original Brompton Stocks were probably red, and the appearance of red in their crosses may be a reversion to this type just as the purple in the *incana* crosses is a reversion to the purple *incana*.

The following passage from Bradley lends support to this view:— "There are five Sorts of them (*i.e.*, Stocks) besides the Dwarf Kind or Annual Stock for Edgings. The White Flowering Kind, that with the Purple Flower, the strip'd Sort, the large Red Brompton Stock, and that Sort which blossoms the first year; of all which the Brompton Kind is esteem'd to be the best."† Again, Miller‡ gives "*Leucoium incanum majus coccineum*, the Greater Hoary Crimson Stock-July-flower, vulgarly called the Brumpton Stock," and in Loudon§ it appears under the name "*Matthiola coccinea*." It should, however, be noted that the appearance of red is not universal among Brompton cross-breds: though glabrous cream × hoary Brompton white yields red, glabrous white × the same type yields purple, whereas with *incana*, reversion to purple results from matings with any of the recessives employed. (The tint in the case of a flesh-coloured recessive is somewhat paler than in the other crosses.) As regards the origin of the cream form, we can find no precise statement. It was evidently known to Parkinson,‖ who speaks of *Leucoium sativum albido luteum simplex*, and adds "of no great regard, but only for rarity, and diversity from the rest."

$$(\beta)\ DR_1 \times R_2$$

Nine different combinations of recessives were employed in these unions (see pp. 6 and 7, Experiment 1). The colour results were as follows:—

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* For a more obvious case of two reversionary types *cf.* the case of Sweet Peas.
† 'New Improvements of Planting and Gardening, both Philosophical and Practical,' 1718, Ed. 2, pt. 2, p. 143; "Of Stock-July-Flowers."
‡ 'The Gardener's Dictionary,' 1731.
§ 'Encyclopædia of Plants,' 1829, p. 538.
‖ 'Paradisus,' 1629, p. 260.

Colour of recessives.	Colour of F_2 cross-breds.
1. Red R_1 and flesh R_2	45* pale purple, 70* rose.
2. Red R_1 and purple R_2	All purple (54).
3. Red R_1 and claret R_2	,, (6).
4. Cream R_1 and white R_2	,, (238).
5. Red R_1 and white R_2	120 purple, 3 red (? due to self-fertilisation).
6. Red R_1 and cream R_2	103* purple, 112* red.
7. Cream R_1 and flesh R_2	109* pale purple, 115* rose.
8. Cream R_1 and purple R_2	All purple (29).
9. Cream R_1 and claret R_2	,, (24).

These results may be summarised thus—

(i) When any shade of purple, whether a reddish purple or a true purple, was introduced in the cross as in 2, 3, 8, 9, F_2 was purple; in the cases where a true purple was used (2, 8), it is uncertain whether this colour in F_2 is due to dominance or reversion.

(ii) Reversion to purple occurred in both cases in which a white recessive was used. (In 5 the total included three reds, but these, in all probability, were the result of accidental fertilisation.) When the white was employed in conjunction with cream (4), the F_2 plants varied slightly in tint, but the series of colours which are borne by the gametes of the F_1 cross-breds, and which are manifested on self-fertilisation, vanish under the reversionary influence of the white recessive.

(iii) When cream is used in conjunction with some shade of red (6 and 7), the F_2 generation is mixed, one half only revert to purple, the other half are reddish, light or dark according as the other recessive was full red or flesh-coloured.

(iv) When both recessives were of some shade of red (1), the F_2 generation was again mixed, but the proportion of purple to red appears to be less than in the preceding case.†

(γ) $DR_1 \times DR_2$.

The colour results obtained when cross-breds containing the same dominant (white *incana*) and a different recessive were bred together, *i.e.*, when the experiments were of the form $DR_1 \times DR_2$, were as follows :—

Case 1.—(Red glabrous × white hoary) × (cream glabrous × white hoary). Experiment 31A. One hundred and forty-four seeds were

* The numbers marked thus * are calculated from the seed colours after a sample sowing has been made.

† For a similar deficiency of purple in F_2 when a flesh-coloured recessive was used, *cf.* Experiment 29, p. 17.

harvested from a single such cross-bred; 108 green, 36 intermediate, or precisely 3 : 1. As previously stated (p. 7), the 141 plants derived from these seeds were *all hoary;* in colour they were either red, purple, or white, the first mentioned being invariably derived from the intermediate seeds, the two latter from the green. The numbers actually obtained were 54 purple, 30 white, 21 red, a result which, taken together with the evidence of the seed colours, indicates the ratio of the three forms as 2 purple : 1 white : 1 red. Conceivably the purples arise from the union of gametes, carrying white and cream or white and red : the reds from a combination of the red and cream elements (compare Experiment 9, Table I) : the whites from the union of two white-bearing gametes, being probably homozygous.

Case 2.—(Cream glabrous × white hoary) × (flesh glabrous × white hoary). Experiment 31B. The results in this case are precisely analogous with those of the previous experiment, except that white-flowered individuals were obtained from the intermediate as well as from the green seeds, and that the coloured plants were of the paler shade of purple and of red characteristic of unions with the flesh-coloured form. The actual numbers were 50 pale purple, 25 white, 21 rose. Glabrous plants were again absent (see p. 7).

Case 3.—(Red glabrous × white hoary) × (flesh glabrous × white hoary). Experiment 31C. This experiment, it will be remembered, gave the expected proportion 3 hoary to 1 glabrous (see p. 7). The colour results, though less close in the case of the seeds, agree with those of the preceding experiment. There were 169 green seeds and 67 intermediates; both produced white and coloured plants. All three colours—purple, red, and white—appeared among both the hoary and the glabrous plants, the records from those which have already flowered indicating the same proportions as in the two preceding experiments (53 purple, 32 white, 25 red).

A comparison of these three cases discloses a point of considerable interest, but as yet not easy of explanation. All the three kinds of cross-breds employed owned the same father—a white *incana* plant —and all on *self-fertilisation* yielded a definite proportion of glabrous whites. Yet when they are *bred together* in each of the three possible ways *glabrous whites are wanting in two combinations out of the three—in the two in which cream is introduced as one of the recessives.* The mere fact that the uniting cross-breds contain different recessives is not in itself a sufficient explanation of this unexpected result, for in the one case (3) in which glabrous whites were obtained this was equally the case, the one cross-bred containing a flesh-coloured recessive, and the other a red. We can only suppose that the suppression of the glabrous whites is one more of the many peculiar features distinguishing cream from sap-coloured recessives in unions of this form. We appear to have definite evidence that when cream is employed in unions with *incana*

resolution or decomposition of the colour allelomorphs occurs, but whether such decomposition is in any way to be considered as the cause of the unexpected result referred to above, we have at present no means of determining.

[Note, added December, 1904.

(c) *Colour of Posterity of R_1R_2 Cross-breds.*

(α) $R_1R_2 \times$ *Self.*

(i) When R_1 and R_2 are the non-sap-coloured forms, white and cream (Experiment 18A).

In this case a definite association of the two characters, leaf surface and flower colour, was clearly apparent. As stated above (p. 12), F_2 showed a mixture of D (hoary) and R (glabrous), D being somewhat in excess. None of the glabrous individuals had sap-coloured flowers, all were either white or cream, the parental colours, the numbers (59 white, 16 cream) suggesting here, as elsewhere, the ratio 3 white to 1 cream. The hoary plants invariably had coloured sap; four distinct colour forms appeared, viz., purple, red, a terra-cotta or copper shade, and a livid blue or plum colour. The majority of the sap-coloured plants were self-coloured, but some individuals in each colour group showed the bicolour form with cream eye. One hundred and eighty-eight plants were flowered, the sap colours being distributed as follows :—

	Purple.	Red.	Plum.	Copper.	
Self	49	16	23	6	= 94 + sap − plastid.
Bicolour	9	5	3	2	= 19 + sap + plastid.
Total	58	21	26	8	

The numbers give no certain indication of the gametic formula in regard to flower colour. From seed colour we get no further clue; green seeds yield the blue shades (purple, plum); brown seeds the red shades, and white and cream; intermediates give both reds and blues. In regard to colour, as in the case of surface character, we must await the evidence from F_3.

(ii) When R_1 and R_2 belong respectively to the sap-coloured and the non-sap-coloured groups (Experiments 18B to 18K).

In four of these operations (Experiments 18B to 18E), cream was the non-sap-coloured type, in four others (Experiments 18F to 18K) white was used. In both sets of unions, where the numbers obtained were fairly large, the same range of sap-coloured forms was found in the glabrous as in the hoary plants; where this was not the case, it was evidently due to the smallness of the totals.

The colours crossed with cream were red, flesh, and light and
dark purple; thus, the unions were between $+$ sap $-$ plastid and
$-$ sap $+$ plastid. In three out of the four matings the sap and plastid
characters were redistributed in F_2, and gave all the four possible
combinations, viz., $+$ sap $-$ plastid (self sap-colours), $+$ sap $+$ plastid
(bicolours), $-$ sap $+$ plastid (cream), $-$ sap $-$ plastid (white). In the
fourth case cream has not yet appeared, but it can scarcely be doubted
that it would with a larger total. Thus, white may appear in F_2 as
the result of crossing, though both parents (P) be coloured. White
and cream only occurred in conjunction with glabrousness, but in these
unions definite association of surface character with particular colours
was limited to these two forms. No clear indication has yet been
obtained of the ratios of the various colours, or of the proportion of
selfs to bicolours. The following list shows the colour forms obtained
in each union :—

Colours of recessive parents.	Colours occurring in F_2.	
	a. Among both hoary and glabrous plants.	b. Among glabrous plants only.
Cream and red	Red (self and bicolour).	White and cream.
Cream and flesh	Various reds (self and bi-colour.	„ „
Cream and light purple .	Purple, red, rose (in each case self and bicolour).	„ „
Cream and dark purple .	Purple (self and bicolour), red (self and bicolour).	White (cream has not yet appeared).

The sap colours used in the unions with white were red, flesh, copper,
and dark purple. In these crosses, as in the matings with cream,
decomposition of the colour allelomorphs seems to occur, for in every
case F_2 showed a variety of sap-coloured forms. Here, also, white is
associated with the glabrous character. The colours obtained are
given below :—

Colours of recessive parents.	Colours occurring in F_2.	
	a. Probably among both hoary and glabrous plants.	b. Only among the glabrous plants.
White and red	Purple, plum, red, copper.	White.
White and flesh	Purple, rose, copper, flesh.	„
White and copper	Purple, plum, red, copper.	„
White and dark purple ..	Purple, plum.	„

The red colours were *always less numerous than the blue*, and one or another of these shades was wanting among the recessives in each of the first three combinations. In all probability these forms would appear in a more numerous offspring. At present the numbers are too small to give a reliable indication of the various ratios.

(β) $R_1R_2 \times R_1$, *and* $R_1R_2 \times R_2$ *where* R_1R_2 *is hoary, and either* R_1 *or* R_2 *is Non-sap-coloured, the other being a Sap-coloured Form.* (Experiments 20 and 21.)

The results of these operations are in harmony with those obtained from self-fertilisation of R_1R_2. A repeated cross with a non-sap-coloured form gave a *mixed* F_2 (sap-coloured and non-sap-coloured); with a sap-coloured form, an F_2 *all sap-coloured;* colourless sap was associated with the glabrous character. When R_1 was white, white was, as we should expect, the only non-sap-coloured form appearing in F_2; when R_1 was cream, both cream and white were obtained. Bi-colours only occurred when cream was used in both crosses. The following table shows the results in each case :—

(Experiment 20).

(*Sap*-coloured form employed in both unions.)

Colours of R types.	Colours occurring in F_2.	
	a. When hoary.	*b.* When glabrous.
(White × red) × red .. (White × flesh) × flesh..	Purple, reds (various). Pale purple, lilac, rose, flesh.	Purple, reds (various). Pale purple, lilac, rose, flesh.
(Cream × red) × red ... (Cream × flesh) × flesh (Dark purple × cream) × dark purple.	Red. Rose, flesh. Dark purple.	Red. Rose, flesh. Dark purple.

(Experiment 21).

(*Non-sap*-coloured form employed in both unions.)

Colours of R types.	Colours occurring in F_2.	
	a. When hoary.	*b.* When glabrous.
(White × red) × white .. (White × flesh) × white (Cream × red) × cream.. (Cream × flesh) × cream (Dark purple × cream) × cream.	Purple, plum. ,, Red bicolour.[1] Red bicolour, rose. Purple,[2] red, red bicolour.	White. ,, White, cream. ,, ,,

In all probability, one or two additional forms would appear if larger numbers were used, *e.g.*, red, perhaps, at [1], and purple bicolour at [2]. It is, however, evident, that in a repeated cross with a non-sap-coloured form, we have the same kind of association as in the case of $R_1R_2 \times$ self. Presence of sap colour is associated with the hoary character, absence of sap colour with glabrousness. When the repeated cross is with the sap-coloured form, we find the same range of sap colours in the glabrous as in the hoary plants.

(γ) $R_1R_2 \times R_3$ *when* R_1R_2 *is Hoary* (*Experiments* 22, *and* 24—26).

The results in six such operations were as follows :—

	Colours of R types.	Colours occurring in F_2.
i.	(White × red) × copper	Purple, red.
	(White × flesh) × red	Purple, various reds.
	(Cream × flesh) × copper........	Various reds.
ii.	(White × red) × cream	Purple, red.
	(White × flesh) × cream	Purple, various reds.
	(Cream × flesh) × white	Purple.

In all these unions, whether R_3 had coloured sap (as in i), or colourless sap (as in ii), F_2 was all sap coloured. (A single glabrous white, which appeared in one case, must be attributed to accident.) When F_2 showed a mixture of hoary and glabrous plants (i), the same variety of colour occurred in both groups. From the colours obtained in the last two matings, we may conclude that the results which follow from a particular combination of colours, may vary according to the order in which the colours are used.

(δ) $R_1R_2 \times R_2R_3$ (Experiment 27).

The mating (white × red) × (dark purple × red) gave purples and reds, in the ratio 3 : 1, in both the hoary (15 purple, 5 red) and the glabrous (15 purple, 4 red) groups.]

IV. *Frequency of Occurrence of Double Flowers.*

The occurrence of double flowers was recorded in the earlier experiments, but, as only a small percentage of plants were flowered, no statistical evidence of value was obtained on this point. The investigation of flower colour gave a convenient opportunity for fuller observation respecting doubling. Inasmuch as this feature is commonly supposed to depend largely on external conditions, it was not expected that the distribution would exhibit any obvious statistical regularity. Observation, however, has shown that doubling among the offspring of cross-breds may occur in proportions characteristic of ordinary

recessives; and there is little doubt that, in some cases, it is related to the single flower as recessive to dominant.

One feature of this case distinguishes it from the others with which we have dealt. In double Stocks the anthers and the pistil are not recognisable, and the centre of the flower is filled by a mass of petals. There is apparently petalody of both male and female organs, accompanied by reduplication or pleiomorphy,* but the precise morphology of the variation does not seem to be wholly clear. For the purpose of this discussion, the important point is that neither pollen nor ovules are present in the double flowers. Our experience agrees with that of almost all who have described this phenomenon in Stocks, that the variation is usually complete, intermediate conditions being only occasionally met with, and no mixture of doubles and singles having ever occurred on any individual plant.

It follows, therefore, that doubles must generally be the offspring of normal singles, and no double ever has a fully double ancestor in the direct line. In a pure race, therefore, the two forms probably constitute a pair of " *Mittel-rassen*," to use de Vries' term. In other words, the singles, though constantly selected, may continue to throw off doubles. Though, as will be immediately shown, the double Stock may behave to the single as a Mendelian recessive, the type individuals, which give off doubles, can scarcely be normal DR, since it is well known that as many as 80 per cent. of doubles, or even more, can sometimes be obtained on self-fertilisation, or fertilisation *inter se*.†

A brief note of the earlier references to doubling in Stocks has some value. From the nature of the case it is fairly certain that this doubling must have arisen in the past, as now, by mutation, and that no gradual selection can have been instrumental in its production. Though the earlier herbals devote much attention to Stocks, none that we have seen mention any double form. The first notice of double Stocks we have found occurs in Dodoens‡ who states that a form of Stock with a multiplicity of leaves in the flower is found in gardens, but it is extremely rare, since it is of the larger sort, flowering in spring, and requiring great care to prevent injury by cold in the winter months. Two years later Lobel and Pena§ give the further information that both Wallflowers and Stocks can be greatly improved by horti-

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* See Masters' ' Veg. Terat.,' 1869, especially appendix.

† Horticultural literature abounds with recipes for increasing the output of doubles in Stocks, and though the methods suggested often seem quite opposed to each other, the balance of evidence certainly favours the belief that the variation —viz., the production of gametes bearing this recessive character—may be promoted, if not caused by, environmental disturbance. Until critical experiments have been made, detailed discussion of these various statements is hardly profitable.

‡ 'Florum et coronariarum odoratarumque nonnullarum herbarum historia,' 1568.

§ 'Stirp. adv. nova,' 1570.

cultural treatment, and frequent transplantation, becoming double as a
Moss rose, but that they are then destitute of seeds. A figure of this
double form is introduced by Lobel into his 'Kruydtboeck' (1581), it
also occurs in Dodoens ('Pemptades Sex,' 1583), and is again used later
by Gerarde and others.

The seedlessness of double Stocks is mentioned by many authors of
the 16th and 17th centuries (see especially Parkinson*) who all agree
that doubles can only be raised from the seed of singles, none ever
referring to intermediate states.

Nevertheless Hill† has the following instruction for obtaining double
Stocks : "Let him select such single Stocks for Seed as are large, robust,
wellgrowing, and would naturally have a vast Multitude of Flowers;
and such as have in some Flowers somewhat above the proper Number
of Petals, five, six, or more: this is the first Tendency in Nature to
Doubleness; and this he should carefully watch for the farther
Improvement." One is inclined to regard this advice as based on
analogy rather than on practical experience, and of equal value with
another method much advocated, the planting of singles in close
proximity to doubles. Nevertheless, two writers, apparently inde-
pendent, in answer to an inquiry in 'The Floricultural Cabinet'
(1833, pp. 21, 89, 103) give precisely the same recommendation of
gradual selection, and the statement of the writers' experience has
every appearance of authenticity.

On the other hand, Chaté,‡ a French horticulturist, in whose family
the cultivation of Stocks had been practised for more than 50 years,
referring to this method of selection, writes that moderately good
results have been obtained by selection of plants as seed bearers which
show a fifth petal; that in the first year such plants have yielded
50 to 60 per cent. of doubles, but that in the second year the sowings
have only produced a small proportion. His own personal experience,
he adds, is that such plants are very rarely met with, and that it would
have been impossible to count on them for obtaining a supply of seeds.
The German cultivators are said to grow the seed plants in pots, with

* 'Paradisus,' 1629, p. 261 :—" But this you must understand withall, that those
plants that beare double flowers, doe beare no seede at all, and is very seldome
encreased by slipping or cutting, as the next kinde of double is : but the only way
to have double flowers any yeare, (for this kinde dyeth every winter, for the most
part, after it hath borne flowers, and seldome is preserved) is to save the seedes of
those plantes of this kinde that beare single flowers, for from that seede will rise,
some that will beare single, and some double flowers, which cannot bee distinguished
one from another, I meane which will be single and which double, untill you see
them in flower, or budde at the least. And this is the only way to preserve
this kinde : but of the seede of the former kinde was never known any double
flowers to arise, and therefore you must be carefull to marke this kinde from the
former."

† 'Eden,' p. 567, 1757.

‡ E. Chaté, ' Cult. prat. des Giroflées,' pp. 63, 80.

a minimum of water, thus obtaining 60 to 70 per cent. of doubles, while the French practice of removing the weaker branches, and sowing seed exclusively from the lower parts of the pods, is said to yield as many as 80 per cent.   The average yield in the case of sample sowings of seeds from the upper quarter of the siliqua was only 30 to 35 per cent. of doubles, from the remaining lower portion 75 to 80 per cent. were obtained.

Our observations are in full agreement with those of Chaté.   Flowers with one or two extra petals are occasionally seen.   In the present year, some thirty biennials growing in the open survived the winter, and several of these flowering in early spring produced scattered flowers with one or two extra petals.   Apart from these, only one or two instances have been observed, though in late autumn poor flowers may occasionally show petals deeply cleft.   In fact, doubles at the present day are obtained from normal singles, as recommended by the early writers on horticulture.

The evidence in regard to doubling was furnished by experiments, the results of which, in the case of surface character and flower colour, have already been given in detail.   As previously stated, the types employed were the white form of *incana* and glabrous Ten-week Stocks of various colours.   The tendency to produce doubles is a characteristic feature of the Ten-week races, which constantly yield singles and doubles mixed.   In white *incana*, on the other hand, this phenomenon was never seen, and in the wild plant it probably does not occur.* When the two are bred together in various ways the distribution of doubles was found to exhibit a distinct regularity.

The facts were as follows :—

No doubles occurred in F_1 when *incana* was bred with one of the Ten-week strains (whether $D \times R$ or $R \times D$).   Among such cross-breds it was not uncommon to find flowers with seven or eight stamens; this, however, is undoubtedly a wholly different phenomenon, and one which may have some interest in regard to the question of the origin of the Cruciferous androecium.

In the F_2 generation derived from the above, doubles were also absent when the mating was in the form $DR \times D$, or $D \times DR$.

The results obtained from the operations $DR_1 \times$ self, $DR_1 \times R_1$, $DR_1 \times DR_2$ and $DR_1 \times R_2$ are shown in the accompanying table :—

* A point of some interest; since it was in the biennial type, according to Dodoens, that doubles were first observed.

Table II, showing Distribution of Doubles in F₂ obtained from the Operations $DR_1 \times$ Self, $DR_1 \times R_1$, $DR_1 \times DR_2$, and $DR_1 \times R_2$.

Number of experiment.	Form of union.	DR individuals used in F_1.	Totals of singles and doubles.	Ratio of singles and doubles.	Total hoary	Total glabrous	Total purple	Total red	Total white	Purple hoary	Red hoary	White hoary	Purple glabrous	Red glabrous	White glabrous
30B	$DR_1 \times$ self when R_1 is cream	Plants A_1, A_2*	Single 241, Double —												
30A	$DR_1 \times R_1$ when B_1 is cream	,, A_1, A_3, A_8	Single 112, Double —												
31A, 31B	$DR_1 \times DR_2$ when R_1 is cream and R_2 has coloured sap	,, { $A_3 \times C_1$, $A_4 \times B_3$	Single 191, Double —												
1(4)	$DR_1 \times R_2$ when R_1 is cream and R_2 white	,, A_1, A_3 A_4, A_6 A_7	Single 238, Double —												
1(7), (8), (9)	,, when R_1 is cream and R_2 with coloured sap	,, A_2, A_3, A_5, A_8	Single 277, Double —												
1(5)	,, when R_1 has coloured sap and R_2 is white	Plant B_4	Single 120, Double —												
1(6)	,, when R_1 has coloured sap and R_2 is cream	Plants B_1, B_2, B_4	Single 215, Double —												
18B	$DR_1 \times$ self when R_1 is red	Plant B_2	Single 200, Double 66	3·0 : 1	172	28	101	39	60	87	32	53	14	7	7
19	,, when R_1 is flesh	,, C_1	Single 52, Double 15	3·4 : 1	50	16	35	14	17	25	11	14	10	3	3
18A	$DR_1 \times R_1$ when R_1 is red	Plants B_2, B_4	Single 97, Double 77	1·2 : 1	39†	13	14	24	12	11	10	7	3	5	5
31	$DR_1 \times DR_2$ when R_1 and R_2 are red and flesh respectively	Plant $B_2 \times C_1$	Single 84, Double 24	3·5 : 1	12	3	4	9	2	4	6	2	—	3	—
1(1)	$DR_1 \times R_2$ when R_1 and R_2 are red and flesh respectively	,, B_2	Single 115, Double —		49	48	51	46	—	25	24	—	26	22	—
1(2)	,, when R_1 and R_2 are red and purple respectively	Plants B_2, B_4	Single 30, Double 19	1·5 : 1	35	42	49	28	23	21	14	18	28	14	5
1(3)	,, when R_1 and R_2 are red and claret respectively	Plant B_2	Single 6, Double —		20	4	12	3	9	10	3	7	2	—	2

Analysis of totals. (columns: Total hoary, Total glabrous, Total purple, Total red, Total white, Purple hoary, Red hoary, White hoary, Purple glabrous, Red glabrous, White glabrous)

* Plants related as sisters are indicated by the same letter of the alphabet.

† In two of these 39 the colour was not recorded.

In each of the several operations mentioned above, two sets of DR_1 cross-breds were used; in the one the recessive component (R_1) was sap-coloured (red or flesh), in the other cream. In the case of each of these recessive strains only a single individual plant was used to produce the DR_1 cross-breds from which F_2 was derived. In the various unions made with cross-breds containing cream (those above the horizontal line in the table), eight such cross-breds were used (A$_1$ to A$_8$), and in no case were doubles obtained in F_2. This absence of doubles, more especially in cases when the cross-bred was self-fertilised, or mated with DR_2 individuals afterwards shown to be themselves capable of producing doubles, points to the conclusion that the cream parent of the F_1 cross-breds was not carrying doubleness as a normal recessive character. A like result followed the use of cream in Experiment 1 (6) where the plant used as R_2 was not the individual used in the preceding experiments as R_1. Here the plant B_2, a DR cross-bred from a red recessive, carrying doubleness as a hidden character, as shown by the results of self-fertilisation (see Experiment 18B), produced exclusively singles when bred with a cream recessive (R_2). It happened that a white recessive was only used in two unions, and in both as R_2 (Experiments 1 (4) (5)). In one of these matings (Experiment 1 (5)) the DR_1 cross-bred with which the white was bred was probably carrying the double character; in the others (Experiment 1 (4)), where the cross-breds were derived from a cream, we have already seen that this was probably not the case. In neither of these unions did doubles occur in F_2.

In the remaining unions, where R_1 was sap-coloured (red or flesh), only three DR cross-breds were used; the results show that certainly two, and probably all three, were carrying doubleness as a latent character. Two only (B_2, C_1), as it happened, were self-fertilised, and both yielded a mixture of singles and doubles, as also was the case when they were bred together. The third plant (B_4) was, however, used in two other operations, being mated again with R_1, and also with R_2; in each case doubles occurred, so that there is little doubt that in this character the third individual resembled the other two. In other cases, a cross back with a sap-coloured recessive led to a suppression of doubles, as e.g., in Experiment 1 (1), and thus, in all probability, the sap-coloured plant used as R_2 was not carrying doubleness.

In those unions where doubling occurred, the numbers indicate that this variation, which, from the nature of the case, cannot be exhibited either by the F_1 parents, or by the pure grand-parents, may appear in the F_2 generation in the proportions which we should expect in the case of a recessive character;* e.g., in the three cases where the expecta-

* Observations on some varieties of *Primula sinensis* seen at Messrs. Sutton's point to the same conclusion.

tion in regard to surface character is 3 hoary : 1 glabrous (Experiments 18B, 19, 31C); the ratio of normal to double flowers is 3·0 : 1, 3·4 : 1, and 3·5 : 1 respectively, the agreement being closest in the case where the totals are largest. Moreover, the doubles are fairly evenly distributed among the different kinds of offspring, so that, whether the grouping is according to surface character, or to flower colour, this ratio is generally indicated. In the one case, where the expectation is equality, the ratio is 1·2 : 1. Grouping the plants into the smaller categories, according to surface character and flower colour, it becomes clear that the expected equality in the case of the purples is almost precise, whereas, among the reds, both hoary and glabrous, the discrepancy is much greater, the ratio being about 1·5 to 1.

In the one combination where doubles resulted from the union $DR_1 \times R_2$ (Experiment 1 (2)), the ratio indicated was also 1·5 : 1. The question whether there is here a real deficiency of doubles, due to whatever cause, can scarcely be decided without further evidence.

The foregoing facts strongly suggest that, among the recessive strains, certain individuals only produce doubles, whereas others give rise exclusively to singles. The evidence, so far as it goes, further indicates that individuals carrying the double character occur frequently among the sap-coloured strains, but there is a slight presumption that the race of creams employed was not producing double-flowered offspring. White will be discussed later. These suggestions receive considerable support from the results obtained with the $R_1 R_2$ cross-breds. In these cases, however, the problem becomes more complex, and the results less easy of analysis. Here the particular constitution of *both* the parents must be taken into account. Conceivably one or both, or neither, may be producing doubles. Unfortunately, offspring by self-fertilisation were not raised separately from the various recessive individuals, and hence direct proof as to their behaviour in regard to doubling is not available. A further complication may be found to affect the result; it may be that interference owing to reversion may occur in regard to doubling, as we have already seen to be the case in surface character and flower colour.

Of the various unions in the form $R_1 \times R_2$ recorded in Table I, only three yielded doubles in F_1, viz., copper × cream (Experiment 10), very light purple × cream (Experiment 11C), and red × dark purple (Experiment 15). In Experiments 10 and 11C, the cream form employed was the strain known as Princess May, a form which, like the sap-coloured types, produces both singles and doubles true to colour.* The cream plants used in the other unions in Table I belonged, with one exception, to another race, and yielded no doubles in F_1. Most of

* Some whites breed true to colour in the singles, but throw cream-coloured doubles. Till lately such whites were the sole source of cream doubles.

the individuals of this other race were certainly single, but no com-
plete record of this character was made in this case, since no importance
was attached to the point at the time. But though it cannot be
affirmed with absolute certainty that no doubles occurred, it is most
probable that such was the fact. Further investigation of the
glabrous strains is now in progress, with a view to ascertaining how
large a proportion of the individuals in any strain produce doubles,
and whether the proportion of singles and doubles in each case is at all
constant. Until such individual breeding has been carried out in the
pure strains, and further crossing has given larger totals in the unions
where doubles occur, these cases cannot be further analysed.

Families derived from reciprocals have, so far, given uniform results.

[Note, added December, 1904.

The posterity of the R_1R_2 cross-breds gave the following results.
(See p. 37.)

Consideration of the results in the F_2 generation reveals several
points of interest.

(1) In each case where R_1 and R_2 were both sap-coloured, the opera-
tion $R_1R_2 \times$ self gave doubles in F_2, the proportion being highest in
the case of the one mating* which had also produced them in F_1. It
seems by no means improbable that when doubling occurs in F_1 as
well as F_2, both recessive parents will be found to be carrying the
latent character, but that when the doubles occur only in F_2 one
parent alone will produce doubles on self-fertilisation.

(2) In several experiments where a cream not belonging to the
Princess May race had been used, no doubles resulted in F_2, when the
F_1 cross-breds were self-fertilised. In the two matings in which this
was not the case, the doubles were found only among the white and
sap-coloured plants; the creams and the bicolors were all single, thus
indicating a certain antagonistic relation in these cases between plastid
colour and doubling. These results confirm the suggestion already
put forward that the creams not belonging to the Princess May race
were producing only singles. We can hardly attribute to mere
coincidence—to the accidental choice, for various unions in various
years, of certain individuals, which happened not to be producing
doubles, though others of the race were—facts such as the following:
(1) that no doubles were obtained either in F_2 from those bred with
incana, or in F_1 from those bred with another recessive; (2) that in F_2
from (cream $R \times$ non-cream $R) \times$ self, doubles, when they occurred, were
confined to the non-cream plants.

(3) In the one experiment of the form $R_1R_2 \times$ self in which a
Princess May cream was used, the distribution was strikingly
reversed.

* See p. 35.

R$_1$R$_2$ × self (Experiments 18, 19).

Colour of R parents.	Individuals used in F$_1$.	Total single.	Total double.	Proportion of singles and doubles in F$_2$.							
				+Sap −plastid.		+Sap +plastid.		−Sap −plastid.		−Sap +plastid.	
				Single.	Double.	Single.	Double.	Single.	Double.	Single.	Double.
White$_6$ × cream$_5$	Plant A	75	—	—	—	—	—	—	—	—	—
White$_6$ × flesh	,, B	45	—	—	—	—	—	—	—	—	—
Dark purple × white	,, C	16	14	—	10	—	—	—	4	—	—
	,, C'	33	1	31	1 (H)	—	—	2	—	—	—
White$_6$ × red	,, D	8	10	7	10 (H)	—	—	1	—	—	—
	,, D'	37	19	29	13	—	—	8	6	—	—
White$_8$ × copper	,, E	48	—	36	—	—	—	12	—	—	—
Cream$_5$ × white$_1$	,, F	110	—	—	—	—	—	—	—	—	—
Dark purple × cream$_5$	,, G	88	—	—	—	—	—	—	—	—	—
Cream$_1$ × flesh	,, H	25	—	—	—	—	—	—	—	—	—
Cream$_3$ × red	,, I	130	58	82	47	24	—	20	11	4	—
Cream$_6$ × light purple	,, K	73	42	41	37	10	—	17	5	5	—
Flesh × cream (Princess May)	,, L	44	16	33	—	1	12	10	1	—	3
Copper × flesh	,, M	20	2	—	—	—	—	—	—	—	—
Flesh × dark purple	,, N	28	8	—	—	—	—	—	—	—	—
Red × dark purple	,, O	16	9	—	—	—	—	—	—	—	—
Dark purple × light purple	,, P	20	3	—	—	—	—	—	—	—	—

(H) = hoary.

$R_1R_2 \times R_1$, $R_1R_2 \times R_2$, $R_1R_2 \times R_3$, and $R_1R_2 \times R_2R_3$ (Experiments 20—27).

Form of union.	Individuals used in F_1.	Total single.	Total double.
(White × red) × red	D′	21	14
„ × copper	D′	13	10
„ × white	D′	22	—·
„ × cream...................	D″	12	—
(White × flesh) × flesh................ {	B	16	—
	B′	39	—
„ × red	B′	32	—
„ × white	B′	18	—·
„ × cream	B	21	—
(Cream × red) × red........	I′	9	18
„ × cream	I′	16	—
(Cream × flesh) × flesh...............	H′	19	—
„ × copper	H′	16	—
„ × white	H	24	—
„ × cream	H	17	—
(Dark purple × cream) × dark purple	G′	24	—
„ × cream	G′	23	—
(White × red) × (red × dark purple)	D × G′	38	5

Doubles occurred in F_2, but with one exception they were confined to the plants with coloured plastids (cream and bicolor), none appeared among the sap-coloured selfs, the one exception being a white. As previously mentioned, white commonly occurs in F_2 from a cross between cream and sap-coloured recessives, for the plastid- and sap-characters are recombined in the gametogenesis of F_1.

(4) With regard to the interpretation of the results obtained with the white race there is more uncertainty, as we have as yet no evidence from the *incana* cross-breds. Doubles were absent in F_2 raised from four self-fertilised cross-breds (A, B, C, and F), to produce which certainly two and probably three white individuals were used. Two of the cross-breds were obtained from matings between white and cream, two from white × sap-colours. In these cases the character of the whites has to be inferred from the behaviour of only four of their gametes. Again, we have seen that an *incana* cross-bred (Table II, plant B_4) which yielded doubles on two occasions when crossed with sap-colours, produced none when crossed with a white: here a numerous F_2 offspring represent as many gametes of the recessive white. On the other hand, four other R_1R_2 cross-breds (C′, D, D′, E), derived from unions between white and sap-colours produced doubles, C′ being own sister to C which gave none. In the case of C′ and E the doubles were distributed alike among hoary and glabrous, coloured and white plants, whereas in the case of the two sister cross-breds, D and D′, the doubles

only appeared among the hoary, and therefore coloured plants. The evidence points here as in some previous cases to an association or coupling of doubling with another character. If experiments on a larger scale should confirm these results, then any hypothesis concerning the production of doubles on crossing recessives must take into account the following possibilities: (1) absence of doubles; (2) occurrence of doubles in all categories; (3) occurrence of doubles in certain categories only. The fact that of sister cross-breds one may give rise to doubles, and another not, indicates differentiation (as regards doubling) among the germ cells of one individual, since here interference owing to reversion can scarcely be in question. Whether the three kinds of results observed in F_2 can be satisfactorily accounted for on the supposition that of the recessive parents, one, or both, or neither may be producing doubles, and that when a mixture of singles and doubles occurs, there is a corresponding differentiation among the germ cells of the individual producing them, is not altogether clear. We can, therefore, form no final conclusion as to the behaviour of the white race in regard to doubling, since it remains uncertain whether, when doubles occurred, they are to be regarded as derived from both parents, or only from the non-white, though at present the evidence favours the latter view.

(5) The F_2 generation obtained from a cross back with one of the parent strains showed an absence of doubles when the recessive bred with F_1 was the non-sap-coloured form. When the sap-coloured type was introduced twice the results varied, some cross-breds gave doubles, others not. If the suppositions mentioned in (4) are correct, this is to be expected.]

V. *Experiments with* M. sinuata.

'Curtis's Botanical Magazine' for 1900 contains a coloured figure of a white-flowered glabrous variety of *M. sinuata*, together with the following statement :—" *M. sinuata v. oyensis* is a native of the Ile d'Yeu off the coast of La Vendée, where it grows associated with the typical form." It is described as "an annual or biennial branching green herb, 1 to 2 feet high, somewhat sparsely furnished with stalked glands on the stems, leaves, calyces, and pods, but quite destitute of the dense felt-like greyish tomentum characteristic of typical *M. sinuata.*" Specimens of this variety, raised in the Botanic Garden, were kindly placed at our disposal by Mr. Lynch. Reciprocal crosses were made between the variety and the type form which occurs wild on the south and west coasts of England. Unfortunately the attempt to rear vigorous healthy plants of the type form was unsuccessful. Some few plants produced flowers which furnished a supply of pollen, but they invariably perished before setting fruit; the cross-breds obtained were, therefore, all from the mating var. ♀ × type ♂. These

cross-breds—one family of twelve plants—were covered with a tomentum, and were indistinguishable from the type form. Here, as in the similar experiments with *incana*, the hoary character is dominant.

Matings between the glabrous variety of *sinuata* and *incana* showed considerable sterility. A few good seeds were obtained, from which three cross-breds were raised. These plants have not yet flowered. In regard to leaf outline and character of the tomentum, they showed a condition intermediate between the type forms of the parent species. The stalked glands, characteristic of *sinuata*, were absent; evidently gland-formation behaves as a recessive character on crossing with the non-glandular *incana*.

VI. *Summary of Conclusions from Experiments with Matthiola.*

1. Various matings of Stocks yield heterozygotes which are reversionary, and the occurrence of such reversion may interfere with the appearance of a recessive character.

2. Such interference with regard to the recessive character glabrousness occurs in all unions of the form $R_1 \times R_2$, $DR_1 \times R_2$, and $DR_1 \times DR_2$[*] when either or both of the recessives is a type with uncoloured sap (*i.e.*, a white or cream); in such cases all the resulting cross-breds are hoary.

3. Curious specific results affecting physiologically distinct characters follow the use of specific types, which, so far, seem to differ in flower colour alone. Whether the presence of these dissimilar colours in reality causes the difference in results is still unknown, and it is not impossible that the essential distinction may be some quality with which the flower colour happens to be associated.

4. The union of certain allelomorphic characters, when these are carried by the gametes of pure-bred types, may give rise to reversionary forms, whereas when the same combination of characters is made by the union of the gametes of cross-breds, such reversion does not always occur. In certain cases it may be altogether wanting, or it may occur in one character and not in another, or in other cases, again, the two kinds of unions may produce similar results. Illustrations of such cases may be briefly stated thus: (1) Pure-bred glabrous white × pure-bred glabrous red produces *hoary purple*, but a cross-bred gamete carrying white colour and glabrousness meeting either a pure-bred, or a cross-bred sister gamete carrying red colour and glabrousness gave *glabrous purple*. *In the former case there is reversion both in surface character and colour ; in the latter the two characters are dissociated, and reversion occurs in the one (colour) and not in the other (surface*

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[*] D and R are used throughout to denote the dominant character hoariness and the recessive character glabrousness.

character) (see Experiments 4, 28A, 28B): (2) Pure-bred glabrous white × pure-bred glabrous cream also produces *hoary purple*, but a cross-bred gamete carrying whiteness in conjunction with glabrousness, on meeting either a pure-bred, or a cross-bred sister gamete carrying cream colour and glabrousness yielded *glabrous white*. *Here, also, there is in the former case reversion in both characters ; in the latter it occurs in neither. Instead, white is now dominant over cream, and the glabrous character is inherited* (see Experiments 3, 30A, 30B). (3) When certain DR cross-breds containing different recessives as, *e.g.*, cream and red, are mated together (gametes carrying these two colours + glabrousness presumably meeting each other), *the result of such union is certainly as regards surface character and possibly also as regards colour, the same as when similarly coloured pure-bred recessive types are bred together* (see Experiments 8 and 31A, where cream glabrous × red glabrous appears to give red hoary in both cases).

5. Cross-breds containing the same dominant (white *incana*), but a different recessive, produce, at least, one set of gametes which are carrying a similar combination of recessive characters (whiteness and glabrousness). When such cross-breds were bred together, and when, therefore, these particular recessive gametes must have met, such unions produced either (1) individuals exhibiting this same combination of recessive characters (viz., whiteness and glabrousness), or (2) individuals which, whatever may prove to be their colour,* reverted to the dominant (hoary) type in surface character. In (1) both cross-breds contained a sap-coloured recessive, and in (2) one contained a sap-coloured and the other a cream-coloured recessive, see Experiments 21A, 21B, where

(Red glabrous × white hoary) × (Cream glabrous × white hoary) and (Cream glabrous × white hoary) × (Flesh glabrous × white hoary)

gave no white recessives : whereas in 21C

(Red glabrous × white hoary) × (Flesh glabrous × white hoary)

yielded the expected proportion. It happened that no matings were made with cross-breds containing a white recessive. Had such cross-breds been used, it is probable that the result in this respect would have been similar to those obtained with cream, and that here as elsewhere the general rule holds that the one result follows when two sap-coloured recessives are employed, and the other when sap colour is absent in one or both of the recessives.

6. When extracted recessives are mated with pure-bred recessives, the result is dependent not merely upon the visible characters of the

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* Whether these individuals were among the white-flowered dominants cannot be certainly determined until the results in F_3 have shown which of the colours obtained in F_2 were produced by these particular gametes.

" extracted " plant and of the pure-bred race, but also upon the composition of the cross-bred from which the recessive in question is extracted: *e.g.*, a glabrous white extracted from a DR cross-bred containing a cream recessive, when mated with a pure-bred cream recessive, gave a glabrous offspring; but a glabrous white extracted from a cross-bred which did not contain cream, when similarly mated, yielded hoary plants. These diverse results were obtained from what appear to be precisely similar pairs of whites and creams; nevertheless, the result varied according as the new recessive was or was not similar to the one introduced in the original cross. A parallel result occurs when an " extracted " glabrous white derived from a DR cross-bred, where R is cream, was bred with a pure-bred glabrous white; the plants obtained were all hoary. Here, again, reversion occurred when the newly-introduced recessive differed in colour from the original R.[*] (A separate experiment in which this relation appeared not to hold was open to suspicion of error on other grounds.) We thus arrive at the result that two apparently similar recessive parents may produce offspring unlike themselves.

For comparison the following table exhibits the results which we know to occur when certain *pure-bred* types are intercrossed, and those which apparently take place when one or both of the meeting gametes is derived from a *cross-bred*.

Combinations of allelomorphs borne by the uniting gametes.	Results known to occur when both gametes are from pure-breds.	Results indicated.	
		1. When one gamete is from a pure-bred and one from a cross-bred.	2. When both gametes are from cross-breds.
White glabrous and cream glabrous.	Purple hoary (Experiment 3).	White glabrous (Experiment 30A) (colour unknown), hoary (Experiment 80, Report I).	White glabrous (Experiment 30B), purple hoary (Experiment 31A).
White glabrous and red glabrous.	Purple hoary (Experiment 4).	Purple glabrous (Experiment 28A).	Purple glabrous (Experiments 28B, 31C).
White glabrous and white glabrous.	White glabrous.	(Colour unknown) hoary (Experiment 17A).	White glabrous (Experiment 31C), white hoary (Experiment 31A).
White hoary and white glabrous.	Purple hoary (Experiment 19, Report 1).	—	White hoary (Experiments 30B, 31A, 31B, 31C).
Cream hoary and cream glabrous.	—	Non-cream hoary (Experiment 30A).	Cream hoary (unnumbered experiment).

[*] Parallel experiments with sap-coloured recessives have not yet been made.

The conclusion that the meeting of the gametes in the several experiments, was that given in this table, is arrived at by a tentative analysis of each case. The experimental analysis has not yet proceeded far enough to enable us to state the precise cause of the dissimilarity of results in certain cases. There is, however, little doubt that further experiments will bring the whole into one uniform system, as has already been done for other results in F_2, some of which, at first sight, seemed similarly aberrant.

7. Doubling frequently behaves as a Mendelian recessive, and may show definite association with physiologically distinct characters. The evidence strongly suggests that certain Ten-week recessive types produce exclusively singles (some cream and perhaps some white races), and that others (notably the sap-coloured forms and the cream strain, Princess May), constantly yield singles and doubles mixed. Among these latter there is probably differentiation in regard to doubling, not only among the several individuals of any race, but also among the several gametes of one individual.

8. The differentiation previously established for the female gametes of cross-breds is equally true of the male.

9. The hoary character appears in F_1 when the type form of *sinuata* and the white-flowered glabrous variety *oyensis* are bred together. The relation of hoariness to glabrousness is here as in *incana*, that of dominant to recessive.

The stalked glands characteristic of *sinuata* (both type and variety), disappeared when *incana* and *oyensis* were crossed together. Gland formation evidently behaves as a recessive character when *sinuata* is crossed with the non-glandular *incana*.

10. We have now an explanation of many of the experiments which in the earlier Report were classed as aberrant (see Report I, Tables XIV and XV), and now appear to be due to unexpected reversion in the heterozygote. We thus account for the two experiments (79 and 80 in Table XIV), previously regarded as aberrant, in which dominant offspring were produced when the expectation was all R. On the supposition (already discussed in Report I, p. 81), that the group of 9 experiments in the same Table, where some recessives occurred when the expectation was all D, are probably to be explained as cases of the " false hybridism " of Millardet, we have left only a single result (Experiment 10), in Table XIV, which appears to be at variance with the Mendelian account. In this case the aberrant result occurred when a half-hoary strain was used as the dominant type, and no further experiments with this strain having yet been made, this one result still remains unexplained. Of the aberrant cases where the expectation was a mixed offspring (Table XV), many can now be similarly brought into line. Nine of these cases occurred in experiments where the expected result was 1 D : 1 R; of these only two

remain unaccounted for. In one of these (Experiment 73B), the exceptional result was obtained from only one individual, while 7 others gave a Mendelian result (Experiment 73A); it seems, therefore, not impossible that this exceptional result may have been due to the selection of a seed-parent in the final cross, which was not really a DR but a DD produced by accidental self-fertilisation. With regard to the other (Experiment 60), we have as yet nothing further to state, this being another experiment in which the half-hoary strain was employed. For the same reason further comment is deferred respecting most of the cases which occurred where the expectation was 3 D : 1 R, and in which either a half-hoary, or a fully hoary annual type was employed. The other cases in this group are possibly due either to the same cause as that suggested in the case of Experiment 73B (Experiment 100A); or, where the deviation from expectation consists in a deficiency and not a complete absence of recessives, to some disturbance affecting the usual symmetrical distribution of the gametes (Experiments 95, 96, 107A).

SALVIA HORMINUM.

This species was chosen for experiment as offering a good case of a character with three well-marked contrary or alternative forms. The wild plant is found in the Mediterranean region, and is remarkable for the coloured bracts which terminate the stem axes. It is described as occurring wild under two forms,* in the one the flowers and terminal bracts are coloured violet, in the other pink; a third (albino) form with bracts and flowers white is in cultivation. All three strains breed true.

Of previous records of cross-breeding experiments with this species we have those of H. Hoffmann.† From crosses between the two coloured forms he obtained the following results:—(1) a mixed offspring in F_1, the individuals being similar in colour to one or other parent, none being intermediate in tint; (2) a second generation (F_2), also frequently mixed, whether derived from violet or from pink seed-parents.

Details of the experiments are not given; we are not told whether emasculation was performed in the first cross or not, nor whether any other precaution against chance cross-fertilisation was taken beyond placing the plants in a room. It is, however, stated that in the later generations the possibility of such cross-fertilisation was not definitely excluded. In the light of the results about to be described it seems clear that little value can be attached to Hoffmann's numbers. The mixed result obtained by him in F_1 may probably be explained by

* Engler u. Prantl, 'Die Natür. Pflanz.,' vol. 4, 3a, p. 274.
† 'B. Z.,' 1887, Band 45, p. 755.

the supposition that the violet plants were not pure but cross-breds, while the fact that in F_2 both pink and violet plants were obtained from pink seed-parents, must undoubtedly be attributed to crossing.

In the present experiments the method of procedure was as follows:—the plants for convenience of handling were grown singly in pots and covered with muslin. In the earlier experiments some unemasculated flowers were allowed to open under cover with those prepared for crossing, but in the crosses made in the second year this possible source of error was avoided. The manipulation of the flowers was somewhat troublesome; both emasculation and pollination were carried out under a lens. Emasculation was performed before the corolla exceeded the calyx tube in length. Careful handling is necessary as the buds break somewhat readily from their pedicels. By holding steady the free end of the bud, the calyx tube can safely be slit backwards, and a window made in the side of the hood of the corolla; through this opening the stamens are at this stage easily withdrawn bodily by gently gripping the filaments at the point of curvature. Pollination was effected by inserting the stigmas into the slit of a ripe detached anther, but although a number of pollen grains were often observed to be adhering to the stigmatic branches, the full complement of seeds (four), was not very often obtained from artificially fertilised flowers.

Some 20 plants of the three forms were raised from seed; of these all came true to the specified colour except two, which should have been pink but were violet. The suspicion that these two individuals would prove to be cross-breds was fully confirmed later, for both gave rise to a mixed offspring of violet and pink; the remaining plants bred true to colour on self-fertilisation.

In the following account the expressions V_1, V_2, P_1, P_2, W_1, W_2, etc., will conveniently distinguish the different individuals according to their colour.

(*a*) From the accompanying Table (see p. 46) it is seen that in each of the four unions $W \times V$, $V \times W$, $P \times V$, and $V \times P$ the result is the same: the offspring are all violet; pink and white are thus both recessive to violet. Moreover, the violet colour of the cross-breds is indistinguishable from that of the pure form.

(*b*) In the unions between the pink and white strains, however, the results appear less concordant; the majority of the offspring are again violet, but in one mating (Experiment 5) the offspring were mixed, and included three whites, and in another (Experiment 6B) the five offspring obtained were all pink. In view of the fact that from every union except No. 5 a uniform result was obtained, it is scarcely possible to doubt that the mixture in this case is attributable to accident, and that the three whites were either accidental selfs or strays. With regard to Experiment 6B, the supposition at the time was that here, also, some

Table I.—Offspring obtained from Reciprocal Crosses between the Three Different Forms.

Date.	Number of experiment.	Parentage.	Offspring.		
			V.	P.	W.
1901	1	$W_1 \times K$	2		
		$W_1 \times V_4$	14		
		$W_2 \times V_4$	3		
		$W_3 \times V_4$	6		
		$W_4 \times V_6$	1		
	2	$V_7 \times W_1$	3		
		$V_7 \times W_4$	2		
	3	$P_1 \times V_4$	3		
		$P_1 \times V_7$	3		
		$P_4 \times V_7$	1		
	4	$V_1 \times P_2$	10		
	5	$W_1 \times P_1$	13		3
	6A	$P_1 \times W_1$	6		
		$P_1 \times W_3$	10		
	6B	$P_4 \times W_2$		5	
1902	7	$(W_4 \times \text{self}) \times (P_4 \times \text{self})$	2		
	8	$(P_1 \times \text{self}) \times (W_3 \times \text{self})$	18		
		$(P_1 \times \text{self}) \times (W_4 \times \text{self})$	7		

unknown error had occurred either in marking the particular flowers crossed, or in gathering the seed, and that the five pink plants must have resulted from self-fertilisation. If this view were correct, and if, therefore, from the results of Experiments 5 and 6A we might conclude that a cross between pink and white would always produce violet, it followed that *any* white or pink plant could be regarded as pure, that a pink could not be obtained from a white, nor a white from a pink (except as a variation *de novo*), and that unions in which any one of these five pink plants was employed should give the same results as similar unions in which other pink individuals were used. If, on the other hand, the five pinks did actually result from the union $P_4 \times W_2$, it is clear that *pink* plants might be cross-breds, that a pink could be obtained from a white, and probably, therefore, conversely a white from a pink; that unions with one of these five cross-breds would give results different from those obtained when a pure-bred pink was employed; and, further, that the result of a first cross between a white and a pink will vary with the individuals employed. In order to settle the point in question some of the five pink plants were used in several

later unions instead of pink individuals *known* to have resulted from the self-fertilisation of pink parents. The difference of result in the two cases (compare Experiments 7 and 8 with Experiments 24A, 24B, 25A, 25B) fully disposes of any suspicion of experimental error in the earlier cross, and proves beyond doubt that the five pinks of Experiment 6B were genuine cross-breds. For when whites and pinks known to be pure-bred were crossed together (Experiments 7 and 8), the offspring, twenty-seven in number, were all violet, a result entirely in agreement with that obtained in Experiment 6A, and, we may suppose, in Experiment 5 also. But when similar pure-bred whites were crossed with the supposed pure pinks of Experiment 6B, the offspring, which were mixed, always included some whites, thus again indicating that the pink parent was not pure, but PW in composition. If yet further evidence were needed to substantiate this view, it is afforded by the experiments recorded in Table II, which were designed to test the point as to whether white plants could be obtained from pink, or *vice versâ*. For this purpose a large number of seeds were

Table II.—Offspring obtained from Chance Fertilisation of (*a*) Pure-bred Whites, (*b*) Pure-bred Pinks, (*c*) Pink Cross-breds, which were left Uncovered.

	Number of experiment.	Parentage.	Number of seed parents.	Offspring.		
				V.	P.	W.
(*a*)...	9	$(W_1 \times$ self$) \times$?	2	106	—	147
		$(W_2 \times$ self$) \times$?	1	77	3	54
		$(W_3 \times$ self$) \times$?	1	30	—	34
		$(W_4 \times$ self$) \times$?	2	152	—	175
		$(W_1 \times$ self$) \times$?⎫ $(W_2 \times$ self$) \times$?⎪ $(W_3 \times$ self$) \times$?⎬ $(W_4 \times$ self$) \times$?⎭	?	220	2	293
(*b*)...	10	$(P_1 \times$ self$) \times$?	3	56	81	—
		$(P_4 \times$ self$) \times$?	2	28	50	—
(*c*)...	11	$(P_4 \times W_2) \times$?	3	50	186	29

collected from various pure-bred white and pink plants, and from three of the five pinks of Experiment 6B, all having been grown under conditions which exposed them to the possibility of being crossed both with the pure types and with cross-breds. In order to avoid any chance of error through the germination of stray seeds the experiment was duplicated; some plants were raised in the Botanic Garden allotment, and others away from Cambridge. In the new localities seeds from white plants only, or from pink plants only, were sown in

each garden.* In every case the results showed that the expose(
plants must have been cross-fertilised to some extent, for all th(
different sets of offspring were mixed. In the case of the pure-brec
pinks (Experiment 10), they were violet and pink (131 P, 84 V), bu
in accordance with expectation none were white. In the case of th(
three pinks of Experiment 6B, the offspring were also mixed (Experi
ment 11), but here all three colours appeared (186 P, 50 V, 29 W), anc
we thus have further proof that the five plants of Experiment 6B wer(
genuine cross-breds, that in certain cases P × W shows dominance of P
and that such pink cross-breds will again yield whites (presumably
both on self-fertilisation and on fertilisation with whites).

Since it is evident that some white and pink plants, when crossed
together, yield only violet offspring, while others, when thus crossed,
produce pinks, it becomes important to know whether we can recognise
these different kinds of individuals, and so predict their behaviour in
any given union. It will be noticed that neither of the two parents
of the five pink cross-breds (P_4 and W_2) happened to have been used
in the other matings of pinks and whites (see Table I). The only
further piece of information which the Table affords is the fact that,
although P_4, when crossed with white, gave pink, the offspring of P_4,
by self-fertilisation, when thus crossed, produced violet plants. In
this connection, the results obtained in Experiment 9 are of consider-
able interest. In this experiment, offspring by self-fertilisation of the
various white plants used in the crosses with pinks and violets were
not covered, and fertilisation was left to chance. Crossing evidently
occurred, for, in every case, the next generation was mixed ; the total
number of plants obtained were 585 V, 703 W, and 5 P. Now it is
conceivable that these five pinks were all descended from W_2 ; three
certainly were, and the remaining two came from a mixed lot of seeds,
some of which were gathered from W_2—the individual which crossed
with P_4 yielded pink offspring. Even if this were so, however, it is
surprising that, with random fertilisation, the number of pinks should
be so small as compared with the violets obtained from the same plant.
An error, due to germination of stray seeds, is here out of the question,
for the five pinks occurred among the plants raised away from Cam-
bridge ; the only possible source of error would be in harvesting, but,
as this is not very probable, the result must be considered as it stands.
Putting all the facts together, we have
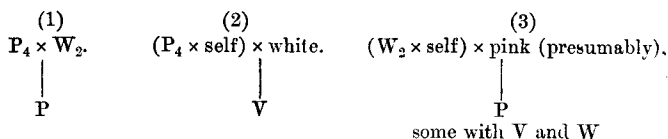
$$
\begin{array}{ccc}
(1) & (2) & (3) \\
P_4 \times W_2. & (P_4 \times \text{self}) \times \text{white.} & (W_2 \times \text{self}) \times \text{pink (presumably).} \\
| & | & | \\
P & V & P \\
& & \text{some with V and W}
\end{array}
$$

Of the ancestry of the individuals, P_4, W_2, we know nothing, they may have been derived from pure parents, or "extracted" from cross-breds. Now we already know cases in Stocks and Sweet Peas among plants, and in mice among animals, where "extracted" individuals behave differently from the pure-breds which they resemble. In the case of Stocks, we know that pure-bred glabrous white × pure-bred glabrous cream yields purple hoary, but "extracted" glabrous white × pure-bred glabrous cream may give glabrous plants with colourless sap. Again, in the white-flowered Sweet Pea, known as Emily Henderson, there are two forms, with round and long pollen respectively. A cross between the two produces Purple Invincible with long pollen, which, when self-fertilised, yields again, besides a variety of other types, white-flowered plants, with long pollen, and others with round pollen. As far as our experience has gone, such extracted "long" and "round" whites give whites (long) and no reversion to purple.* The suggestion here made is that the Salvia result may possibly be analogous with that in the Stock and the Sweet Pea; that, in Experiments 5 and 6A, the cross was between individuals, either or both of which were pure-bred, but that in Experiment 6B, it happened to be between individuals, both of which were "extracted." If such were the case, the occurrence of reversion to violet in the former cross, and of dominance of pink in the latter, would only be in accordance with what we already know in other instances. Until we have before us the evidence from unions between individuals known to be "extracted" —experiments which are in progress—no more definite statement can be made.

Unfortunately, nothing can be ascertained regarding the composition of the five pinks of Experiment 9, since all plants obtained in this experiment were destroyed as soon as recorded. Nor can the supposition that the seed-parent of these plants (W_2 × self) may have been crossed with an "extracted" pink—the only explanation which suggests itself—be immediately tested, since, as yet, we know nothing of the results of such unions. We cannot foretell whether the offspring of "extracted" parents will behave like such parents or like pure-breds, in the cases where the two differ, nor whether such offspring will yield a mixture of the two kinds of individuals, though the evidence of Experiment 9, so far as it goes, is against the second alternative.

All the six kinds of violet-coloured cross-breds in accordance with expectation yielded a mixed offspring when self-fertilised or fertilised *inter se*. When the original union had been between violet and pink or between violet and white, the colours exhibited by the F_2 generation were those of the original parents, violet and pink only in the former

* For a fuller account of these results, see pp. 82 and 96.

Table III.—Offspring obtained from Violet Cross-breds by Self-fertilisation or Fertilisation *inter se.*

Number of experiment.	Parentage.	Number of seed-parents.	Offspring.		
			V.	P.	W.
12	(W × V) × self or *inter se*	1	24	—	7
13	(V × W) × ,,	4	26	—	17
14	(P × V) × ,,	1	45	20	—
15	(V × P) × ,,	7	775	245	—
16	(W × P) × ,,	2	59	25	34
17	(P × W) × ,,	12	255	92	114

case, violet and white only in the latter. In Experiment 15 when a large sowing had been made and more than 1,000 plants flowered, the numbers obtained are in good agreement with expectation, the ratio of violet to pink being as 3·1 : 1 instead of 3 : 1. In the reciprocal cross (Experiment 14) very much smaller numbers were recorded, and the result showed a slight excess of recessives. In the two experiments where the cross was between violet and white, the numbers were smaller still; in the one case (Experiment 12) the result was almost exact (24 V : 7 W), but in the reciprocal (Experiment 13) the number of recessives was much too high (26 V : 17 W).

The two remaining experiments (Experiments 16, 17) are cases in which we should *a priori* expect that all three colours would appear in the F_2 generation in the ratio 1 P : 2 V : 1 W, and further that such pinks and whites would henceforth breed true, but that the violet plants would prove to be cross-breds and yield a mixed offspring in the next generation. We should, in fact, be dealing with a case of simple reversion unaccompanied by the complication of disintegration or resolution of the allelomorphs, a case, therefore, in which we can distinguish among the F_2 individuals the cross-breds from the two parental forms. The facts observed will be seen to agree well with expectation. Self-fertilisation of the violet-coloured PW cross-breds yielded all three forms, the ratios obtained in the reciprocal crosses being respectively ·72 P : 2 V : ·89 W and ·84 P : 2 V : 1·1 W.

When violet-coloured cross-breds of whatever composition are crossed back with an original parental form, such parental form not being violet, the expectation is that the offspring will be mixed, of two colours in equal numbers, half being violet and half the colour of the form introduced in both unions. In two or three cases the numbers obtained were very small, in Experiments 20 and 21 too small probably to be conclusive, the offspring which were all violet being only two in the one case and only six in the other. That a mixed offspring would

Table IV.—Offspring obtained from Violet Cross-breds, by crossing back with one of the original Parent Forms, such Parent Form not being Violet.

Number of experiment.	Parentage.	Number of seed parents.	Offspring.		
			V.	P.	W,
18	(W × V) × W	5	16	—	17
19	(V × W) × W	1	5	—	1
20	(P × V) × P	1	2	—	—
21	(V × P) × P	1	6	—	—
22	(P × W) × P	2	2	6	—
23	(P × W) × W	2	14	—	9

undoubtedly have been obtained if a larger number had been raised we may safely conclude from the fact that the same cross-breds when self-fertilised (Experiments 14 and 15) did yield both parental forms. In the other cases the offspring showed the two anticipated colours, and though generally in unequal proportions, the discrepancies are not greater than might be expected to occur with such small totals.

From the very definite and comparatively simple symmetrical grouping of the ovules and flowers in this species—four ovules to each flower and six flowers to each whorl (verticillaster) it was hoped that some indication of a definite symmetrical disposition of the different kinds of female gametes in the cross-bred might be obtained. With this end in view all the flowers of several consecutive whorls of a cross-bred were crossed back with the original recessive form, the order in which the flowers opened was noted,* and the seeds of each were harvested and sown separately. The experiment requires that every ovule should be fertilised, that every seed should germinate, and that every seedling should reach maturity. Unfortunately, however, the full number of seeds is not often produced in artificial fertilisation, and no sufficiently continuous record was obtained. Only in some half-dozen isolated instances was the experiment successful; the results from these particular flowers showed that in one case all four ovules were recessive, in another two were dominant and two recessive; in two cases three were dominant and one recessive, and in two cases one was dominant and three recessive. It is thus evident that if the individual cross-bred produces, as we have reason to believe, equal numbers of allelomorphic ovules, this equality is not necessarily bound up with a corresponding equality of distribution in each individual flower.

* Of the two axillary cymes composing each whorl, the central flowers usually open simultaneously and before the younger lateral flowers; these latter, in fact, do not generally unfold until after the central flowers of some of the higher nodes are open.

Table V.—Offspring obtained from Reciprocal Unions between Pure-
bred Whites and Pink Cross-breds.

Number of experiment.	Parentage.	Number of seed parents.	Offspring.		
			V.	P.	W.
24A	(W₁ × self) × P cross-bred	3	16	—	16
24B	(W₄ × self) × P cross-bred	2	12	—	7
25A	P cross-bred × (W₃ × self)	2	10	—	7
25B	P cross-bred × (W₄ × self)	1	4	—	2

In the case where P × W yields V we have seen that the result of
the cross PW × W is a mixed offspring, half violet, half white
(Experiment 23), but in a case where P × W yields P, what are we to
expect from a union between such cross-breds and pure-bred whites ?
A mixed offspring, of which half will be white, arising from the
meeting of the white-bearing gametes of the pure form with the
similar gametes of the cross-bred, we may perhaps predict, but what
will be the colour produced when these same gametes unite with the
pink-bearing gametes of the cross-bred ?

According to the results of Experiments 24A, 24B, 25A, 25B, such
unions yield violet, for the mixed offspring obtained was composed of
about the expected proportion of white and coloured individuals (half-
and-half), the coloured plants being all violet. Until we know more
of the behaviour of "extracted," as compared with pure-bred indi-
viduals, it is impossible to say whether the above result would always
follow when such pink cross-breds are mated with a white form, or
whether by union with an "extracted" albino a mixed offspring would
not be obtained, consisting of equal numbers of pinks and whites,
instead of violets and whites.

Table VI.—Results obtained when Offspring of a Cross between the
Dominant (Violet) Type and one Recessive Form are Crossed
with the other Recessive Form.

Number of experiment.	Parentage.	Number of of seed parents.	Offspring.		
			V.	P.	W.
26	(W × V) × P	1	3		
27	(V × W) × P	1	4		
28	(P × V) × W	2	10		
29	(V × P) × W	1	2		

In Table VI are given the results obtained from operations of the form $DR_1 \times R_2$. The total number of plants raised was 19, and all were violet, a result completely in harmony with expectation, since on the supposition that we are right in attributing the exceptional result in Experiment 6B to the use of an " extracted " in place of a pure-bred plant, we may conclude *that a cross in any form between two types of unlike colour will produce the same colour result, viz., violet.*

Summary of Conclusions from Experiments on Salvia Horminum.

1. The results obtained from reciprocal crosses between the different forms entirely support Mendel's conception of germ purity.

2. Of the three strains, violet, pink, and white, the two latter are both recessive to the first-mentioned form. Cross unions between violet and either of the other colours exhibit the simple Mendelian phenomenon of dominance in F_1 and segregation of the two parental forms in F_2, the proportions approaching the Mendelian ratios in cases where fairly large numbers are recorded.

3. Cross unions between the two recessive forms in one instance showed dominance of pink, and in the others reversion to violet. In explanation of these diverse results it is suggested that dominance of pink occurs when both the parents are " extracted," but that otherwise there is reversion to violet.

[Compare the results obtained with the Sweet Pea "Emily Henderson " and with Stocks.]

4. The violet cross-breds resulting from unions between pinks and whites yield all three forms in the next generation in the ratio 1 P : 2 V : 1 W; the F_2 cross-breds are thus distinguishable from both the extracted types. The pink cross-breds (formed presumably when an "extracted" pink is crossed with an "extracted" white) yield only the two parental forms—pink and white.

5. When a cross-bred produced by mating the dominant (violet) type with one of the recessive forms, is crossed with the other recessive form, *i.e.*, in operations of the form $DR_1 \times R_2$, the offspring, in accordance with expectation, are all violet.

RANUNCULUS ARVENSIS.

This species occurs under three forms. In the only British type the carpels are covered with numerous long spines ; in the var. *tuberculatus* the spines are replaced by obtuse tubercles, while in the third form, var. *inermis*, the veins form anastomosing ridges which are unarmed. All three forms are described by Koch,* who mentions Bonn as a ocality where the unarmed variety is to be met with, adding, how-

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* ' Syn. Flor. ger. et helvet.,' éd. 1, 1837, p. 18.

ever, that it is very rare.   Godron* states that he had been accustomed
for several years to find *inermis* in a field at la Malgrange, near Nancy,
but up to that time it had only been recorded from the environs of
Bonn, and was extremely rare, whereas the armed variety *tuberculatus*
was less uncommon.   These forms had also been noticed in the corn-
fields around Nancy by an earlier observer.†

R. arvensis was another of the many species used by Hoffmann‡ in
his cross-breeding experiments, and here, as in *Salvia Horminum*, the
want of uniformity in his results suggested the possibility of experi-
mental error (as he himself realised), and the likelihood that a
repetition of the experiments would yield a constant result.   This has
in fact proved to be the case.

The plants used in our experiments were a single stray individual of
the type form found growing in the allotment, and some half-a-dozen
specimens of each of the two varieties (*tuberculatus* and *inermis*) obtained
through the kindness of Mr. Lynch from the Botanic Garden at
Bonn.   Each individual was covered separately with muslin.   No
flowers were allowed to expand under cover with those to be crossed,
and the latter were emasculated before dehiscence of the anthers.

Reciprocal unions between *inermis* and either of the armed types
gave very similar results.   From various matings 29 plants were
raised, and all bore armed fruits, not one in more than 2000
harvested being destitute of spines or tubercles.   There appeared to
be a considerable degree of sterility, for the total number of cross-breds
represented an average of less than one individual from each mating.
Details of the crosses are given below :—

Parentage.	Number of offspring.	
	With armed fruits.	With unarmed fruits.
Inermis A × *tuberculatus* 1	1	None
,, D × ,, 1	1	,,
,, D × ,, 6	2	,,
,, D × type plant	4	,,
Tuberculatus 1 × *inermis* C	8	,,
,, 4 × ,, C	8	,,
,, 5 × ,, C	4	,,
,, 6 × ,, C	1	,,
Total	29	

* 'Mém. Acad. Stanisl.,' 1864, p. 214; also 'Flore de Lorraine,' éd. 2, 1857,
t. 1, p. 22.

† Suard, "Catalogue des Plantes vasculaires du département de la Meurthe," in
'Statistique historique et administrative,' by H. Lapage, Nancy, 1843, 1re partie,
p. 142.

‡ 'B. Z.,' 1884, Bd. 42, p. 243.∣

In the case of the union between *inermis* and the type form, the fruits of the cross-breds were indistinguishable from those of the armed parent, the carpels being furnished with numerous spines, often hooked, and of varying size, the largest measuring as much as ⅛th of an inch. In the matings between *inermis* and *tuberculatus* the resulting fruits were intermediate between those of *tuberculatus* and the type form ; numerous spines were present as well as tubercles, but the degree of prickliness was a little less than in the previous case. We have then in unions between the unarmed and the two armed races, in the one case dominance of, and in the other imperfect reversion to the type (spined) form, in both cases the unarmed character is recessive.

Now Hoffmann's results were as follows : from two matings of type (*muricatus*) × *inermis*, dominance of type form (three plants); from three reciprocal matings dominance again in one case (two plants), and in each of the two others the appearance of the recessive form (one plant). Hoffmann remarks that the result in these two latter cases may be due either to reversion to the mother form or to unobserved fertilisation. Our own experiments indicate that the latter interpretation is probably correct.

PEAS (*Pisum sativum*).

(Experiments made by W. BATESON and MISS KILLBY.)

Though Mendel's results have been amply confirmed by Tschermak and Correns, experiments with *Pisum* were made partly from a desire to witness the classical phenomena and partly in the hope of elucidating certain obscure points. Tschermak's second and third papers, which have appeared since we began Peas, have provided much information on several of these points, and our work is thus largely confirmatory of his. In addition we have investigated the peculiarities of cotyledon colour in types which, like Telephone, are often piebald, and we are able to add some facts on the properties of " indent " types. Experiments were made to test whether geitonogamy has any effect in weakening dominance. On this point our results were entirely negative, and it seems clear that no such effect is produced.

Cases of irregularity in dominance seemed also worth investigating, and the possibility that departures from the expected F_2 ratios might not be purely fortuitous, was a special subject of inquiry.

The occurrence of degenerate " rogues " among high-class Peas raises important problems in variation and heredity, and experiments on the subject are in progress.

The net result of our work tends to the conclusion that Mendelian

principles in regard to heredity in Peas are capable of an application more literal than at first seemed likely.   Difficulties based on the supposed variability of the seed characters in the type have proved to be small, and it is doubtful whether there are any genuine " exceptions " which cannot be traced to interference of conditions or mistakes.

Crossing began in 1901.   This season was good, and 1902, in which most of the F_1 plants ripened, was fairly good at first, though later the weather broke, and harvesting of late sorts had to be done in the wet. The summer of 1903 began with late frosts in May and June, and was the wettest on record.   Total loss of the crop was expected by English growers, and badly coloured samples were common.

In such a season the colour is dull and the seed-characters indeterminate.

The Pure Types.

The first supply was selected from a fine set of samples kindly sent by Messrs. Vilmorin, Andrieux and Co.   Others were afterwards obtained from various sources, chiefly from Messrs. Sutton and Sons. I take this opportunity of expressing my thanks to Mr. Arthur Sutton for much assistance, and especially for opportunities of studying several types on a large scale.

In the course of the work much information about these various types was obtained which cannot be included here.   N. de B. is very similar to Buchsbaum used by Tschermak.   It exists in the *sans parchemin* form as *nain hâtif Breton*.   Some types exist in both pointed and stumpy forms, *e.g.*, Perpetual (ptd.) and Continuity (stp.). " Round " applied to seeds does not mean that the seeds are spherical but that they are smooth.   F. B., for instance, is squared by pressure.

THE CHARACTERS AND THEIR BEHAVIOUR ON CROSSING.

Cotyledon Colours.

Peas are often classified on their appearance as white or yellow, blue, green, grey.   The appearances may be due to the colour of the cotyledons, or of the skins, or both, and therefore such a classification must be used cautiously.   The *cotyledon colour* taken alone may present a variety of colours, as follows :—

(1) *Yellow*, as in N. de B., Serp., Sabre, B. Q., Purp., etc.

(2) *Green* as in F. B., B. P., L.'s A., etc.   Among the yellows Purp. is perhaps the deepest, and among the greens, perhaps B. P. is the deepest green, but practically the true yellows and greens may be regarded as two uniform types.

(3) *Piebald, tinged or yellowed*, as American Wonder, William I, and Telephone.

List of the Pure Types used in Crosses.

Name.	Abbreviation.	Seed-characters.			Height in feet.	Pods.	Flower colour.	Notes.
		Cotyledons.		Skin.				
		Colour	Shape.					
Très nain de Bretagne	N. de B.	y.	rd.	wh., tpt.	dwf., 2½—3	stp.	White	Seed v. small; cots. sometimes greenish.
Serpette nain blanc ..	Serp.	y.	wr.	wh., opaque	dwf., 1½—2½	ptd.	"	Skin has brown spots in pits, often bursts here.
Blue Peter	B. P.	g.	rd.	tpt.	dwf., about 3	stp.	"	Often bursts.
Fillbasket	F. B.	g.	rd.	Green, opaque	½ dwf., 3½—4¼	ptd.	"	Seeds squared by pressure.
Sabre	—	y.	rd.	Greenish, tpt.	Tall, about 5	stp. (?)	"	Shape of pods unique, curving to suture-side.
Express	Exp.	g.	rd.	tpt.	Tall, 3¾—5½	stp.	"	Height irregular, but always "tall" in habit.
Victoria (marrow) ...	Vict.	y.	rd.	wh., tpt.	Tall, 5—6	stp.	"	Very late; seeds often pitted.
Laxton's Alpha......	L.'s A.	g.	wr.	tpt.	", 5—7⅓	ptd.	"	Cots. rather liable to tinge.
British Queen.......	B. Q.	y.	wr.	wh.-greenish	Tall, 5—6	stp.	"	Very late.
Telephone..........	Tph.	g. tinges	wr.	g. tinges	Tall, 5—6	ptd.	"	Seeds usually turn piebald or yellow unless protected.
Early Giant	E. G.	y.	wr.	wh.-green-ish, opaque	Tall, 5—5½	ptd.	"	
Purple Sugar Pea....	Purp.	y.	ind.	gr.-br.	Tall, 6—7	s. par.	Purple	Skin-colour irregular; axils purple.
Debarbieux.........	Deb.	y.	Flat, smooth	purple spots —	½ dwf., 3—3¾	s. par.	White	Size of seeds irregular.
"Irish" Mummy.....	Irish	y.	rd.	Maple	Tall, 6—7	stp.	Salmon	Fasciated top of stem, stand. wh., wgs. pale red, axils red.
Field Pea...........	F. P.	y.	ind.	Green-brown	Tall, 5—6	stp.	Purple	Seed skin darkens with age, with faint traces of purple spots.
Maple..............		y.	rd.	Maple	"	stp.	"	

y., yellow; g., green; rd., round; wr., wrinkled; ind., indented; tpt., transparent; dwf., dwarf; stp., stumpy end; ptd., pointed end; s. par., *sans parchemin*: all pods inflated except s. par. sorts. All with coloured flowers have dark axils. Salmon flowers go with red, purple flowers with purple axils.

Uniformity of Types: the Piebald Seeds.

In a fine year samples of yellows or greens picked from healthy plants as soon as the pods are ripe are very uniform in colour. The difficulties which Professor Weldon has suggested may arise from variability, are not commonly experienced. If, however, the weather is bad, certain yellows (*e.g.* N. de B.) are liable to give some greenish seeds; and some of the greens (especially L.'s A.) will always give a proportion of piebald with even a few yellow seeds if the pods are left on the plant till all are ripe.

Two kinds of impure colours have, therefore, to be considered. (1) Yellows which have remained greenish; (2) Greens which have become tinged with yellow. In neither case did selection of the discoloured seeds have the slightest effect on the colour of the offspring, and the evidence strongly indicates that the departure from type is in each case produced by external influences; (1) being due to failure to ripen properly, (2) to bleaching after ripening.

In this connection the normally piebald types are important. Before trial I supposed, with Professor Weldon, that such peas were really "mosaics" of yellow and green, and I, therefore, hoped that they could be used to elucidate the inheritance of a mosaic character. This proved to be a mistake, and the piebald types are evidently green Peas, which are peculiarly liable to tinge. The difference is not due to a mosaicism of yellow and green characters (in the sense in which, for instance, a Carnation may be a mosaic of colour and whiteness), but to the peculiar instability of the green pigment in these types. ,

All Peas, of course, are green before ripening. Yellow varieties turn yellow *before they are hard.* Piebald varieties, however, may be still green *after they are hard,* and have—in wrinkled types—assumed the wrinkled form. If then gathered, and put in a dark and dry place, they, for the most part, stay green, but if exposed to the light they quickly tinge *on the exposed surface.*

All green Peas will tinge if exposed to the sunlight, especially when freshly gathered, but the piebald types change with much greater rapidity than the ordinary green types. Exposure to moisture has a similar effect. In piebald types, though the older pods contain piebald or even yellow seeds, those in the younger pods on the same plants are still green, though hard. The discoloration is much delayed if the pods are picked, and left unopened.

Another indication of the same kind is the fact that if piebald seeds are examined in the pods it will be found that those in one pod are tinged on *the same surface.* Examination *in situ* frequently shows that the tinging is towards that surface of the pod which is most exposed to weather, and especially to the sun.

The facts here given regarding types commonly piebald hold also

for the exceptional piebald seeds of green types, and their departure
from the normal green is a direct result of external causes, partly, and
perhaps entirely, preventible.

It is, however, true that the degree of susceptibility varies from type
to type, and it is possible there may be some variation in this respect
between individuals, but no clear positive evidence to this effect was
obtained. There is a notable difference between tinged seeds of
normally piebald types and those of normally green types, in the fact
that while the former germinate as well as green seeds of the same
type, the latter show a marked loss of vitality. Tinged seeds of
Laxton's Alpha, for instance, though they germinate well enough, if
sown at once, scarcely produce any plants if kept till the following
March, and those that do grow are feeble. If the seeds are taken up
and examined, after being in the ground about 20 days, they are found
to be half rotten, and infested with dipterous larvæ, and there is little
doubt that the tinging indicates partial death of the tissue. Tinged
seeds of Blue Peter were less seriously affected by tinging, and a March
sowing of tinged seeds gave plants as good as those from green seeds.
In the following year, however, the tinged seeds were dead, though the
green ones were still able to germinate freely. This special vitality
may be connected with the fact that in Blue Peter the green colour
extends deep into the cotyledon, while in Laxton's Alpha, for instance,
it is shallower.

In all cases tinged seeds that did grow gave plants with no more
tinged seeds than any others of the same type. Numerous experiments
were made on these points, which are not worth recording in detail.

The occurrence of tinging, sometimes so complete as to make the seed
pass for yellow, is the origin of the numerous statements as to the
great "variability" of Telephone in cotyledon-colour. I have seen a
sample of Telephone consisting of a great majority of piebald seeds,
some greens and some "yellows"; but all sown, even the yellowest,
gave the true Telephone type, viz., green seeds liable to tinge after
hardening. Another sample, in addition to the above sorts, contained
one genuine yellow, which bore yellow seeds only, and behaved as a
pure yellow in crosses made with it.* The belief, therefore, that both
yellows and greens may each give the other arises from neglect of the
distinction between natural yellows, and yellows produced by tinging.
Separate harvesting makes this clear at once.

In some varieties (*e.g.*, Sutton's Nonpareil), true yellow cotyledons
are about as common as green ones, a clear proof that the original
plant selected for the type was heterozygous in this respect. These
various facts show how necessary it is in experiments with such types
to number each plant used in crossing, and to examine its seeds when
ripe in order to be sure that it came true to type. We have next to

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* Doubtless a stray.

consider whether the susceptibility to tinging indicates failure of segregation. If so, we should regard the piebald types as in a neutral state between yellow and green.

Experimental evidence, as far as it goes, is quite unfavourable to this view.

When the yellow types ripen, the green colour is changed to yellow, and the same occurs when the piebald types assume the parti-coloured condition; but though the processes may be thus similar it is unlikely that they are identical, and it is almost certain that the latter change is not merely an incomplete manifestation of the phenomenon which is completed in yellow types. It is interesting to note that of the few recorded cases of failure in dominance of yellow most have occurred when Telephone was used. To Tschermak's cases I am able to add the following: Nain de Bretagne × Telephone, giving 4 distinctly green* though slightly yellowish seeds (v. infra), the only exception of the kind we have seen. Such a coincidence can scarcely be purely fortuitous, and though the exceptions are rare and irregular, I think they may be taken as indicating a real peculiarity in the piebald type. But in any case since the departure from the normal result, is in the direction of *green*, such evidence is opposed to the view that Telephone's qualities are due to a share of yellowness.

Until the chemistry of these colour-changes is investigated further discussion is hardly possible.

Generally, however, crosses between yellow types and piebald give a normal yellow F_1. In F_2 I have not found the greens less sharply defined from the yellows than when pure green types are used. Crosses between green types and piebald in our experiments gave green F_1, but in some cases many tinged seeds occurred in F_2 mixed with greens, and it was clear that the instability of the green of Telephone had reappeared. Whether segregation of this character (liability to tinging), occurred or not, cannot be stated until F_3 is grown.

Crosses between two *green* varieties gave F_1 seeds distinctly tinged with yellow four times. I supposed, at first, that there might be a case of heterozygous reversion, but the fact that the yellowest failed to germinate at all, and that only three out of nine grew, showed rather that the tinging here also was a morbid change. Those that did grow gave normal greens.

SEED-SKINS.

There are many types of skins, differing in thickness, opacity, and pigmentation. The last is an important character for our purposes.

* These seeds, however, gave a normal Mendelian F_2. Another similar cross gave 1 yellow F_1, and a reciprocal gave 4 yellow. Nain de Bretagne, as stated

Some coats are practically unpigmented and transparent. (Exp., L.'s A., N. de B.).   Of pigmented skins there are four chief types :—

(1) Yellowish- or greenish-white (Serp., B. Q.).

(2) *Green, deep (F. B.), or pale (Telephone).*   The green skins, like the green cotyledons, may bleach on ripening, especially in sorts liable to go piebald.   Fillbasket rarely bleaches.

(3) "Greys," namely dull green to brick-red (purple flowered Sugar Peas), usually with a variable amount of purple specks which are obliterated in the redder skins.   The redness is merely a matter of exposure to sun in ripening, or to moisture.   It is often unilateral. In dull years scarcely any go red, except those that have got wet and are decaying on the surface.   The colour gets browner with age. They are called " grey " from the colour after boiling.

(4) " Maples " (*perdrix*), viz., bright brown anastomosing lines and patches of pigment on yellowish ground, always associated with coloured flowers, either purple or salmon, according to the type.

Yellow cotyledons are not often in green skins but occasionally they are.

The skins are important, first, in connection with the phenomenon of " Xenia," viz., a change in a maternal tissue—here the skin—when foreign pollen is introduced.   The genuineness of the phenomenon has been questioned, but though capricious it is not rare.   It can only be seen when the skin of the seed parent contains a pigment which *can* be transformed.   Non-pigmented skins show no xenia.   White-skinned seeds sometimes are slightly greenish in crossed seeds, but this cannot be held to be xenia unless it be proved that the change is not merely an arrest of development due to interference.

If, however, a green-skinned Pea with green cotyledons be fertilised with pollen of a yellow cotyledoned type, xenia is often seen in the change of skin colour from green to yellow, associated with the similar change of the enclosed cotyledons.   Sometimes, however, the skin does not change and it is pretty clear that, for the effect to be produced, the conditions (presumably the degree of moisture), must be exactly right.   I have had excellent cases of xenia in Fillbasket and in green Telephone when fertilized by yellow types.

In grey Peas size and number of purple specks may vary considerably both from plant to plant and from pod to pod.[*]

The general uniformity of seeds in each pod is striking, and raises the important question whether there is actual differentiation between pods on the same plant.

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above, not rarely gives greenish seeds like Buchsbaum, a very similar type which provided some of Tschermak's exceptions.   It is not impossible that the greenness in F_1 was due to bad ripening consequent on the operation.

[*] Hence the apparent increase in purple spotting in the skins of artificially crossed seeds cannot confidently be attributed to xenia (see later).

The influence of exposure is, however, so great, that it is difficult to know how much of this apparent differentiation is really due to difference of conditions. Correns has expressed the view that in cross-bred plants (from a "grey" parent), the differentiation indicates some failure of dominance, but I have been unable as yet to find greater differentiation between pods on cross-bred plants than on the pure-bred, and I am disposed to think that difference of conditions is the chief and probably the only factor to which such ·differentiation is due.

As regards dominance, crosses between "greys" and all other sorts except maple show ordinary dominance of "grey." Transparent skins crossed with opaque green or white skins give various results, but never, so far as I have seen, a really opaque skin. The heterozygote skin may be fully transparent, or to some extent, pigmented, and then intermediate in character ; but as Telephone and Fillbasket were the only opaque greens used, no general statement can be confidently made. It should, however, be understood that the opacity of skin is too indefinite a character for these purposes. Crosses between two opaque skins gave opaque skins always.

Maple skins gave some valuable results. Laxton crossed Ringleader (skin, from descriptions, white or faintly greenish), with maple, and the F_1 skins were either maple (doubtless with minute purple specks), or various shades of *full purple*. In subsequent generations he describes complex results, amongst others, the occurrence of some *white-skinned* seeds on purple-flowered plants. If the description is correct this would indicate very remarkable segregation of pods. To investigate the question we crossed (1902) maple with Nain de Bretagne, British Queen, and Victoria Marrow, all yellow in cotyledon and whitish yellow in skins (British Queen opaque, the others nearly transparent). Ringleader was not available. The first two crosses bore seeds in F_1 (1903), having skins *maple with purple specks*. Neither parent has any definite purple specks,* though maple has purple flowers and purple marks in axils. This, therefore, is a case of a new and probably reversionary character appearing in heterozygosis. The F_1 skins from the Victoria Marrow cross were plain maples, with no more purple spotting than maple, showing ordinary dominance only. The maple ♀ was the same which, with another ♂, gave full purple spots.

Tschermak records similar purple spotting in F_1 skins from several crosses† made between certain unspotted types of *Pisum arvense* and ordinary Peas with colourless skins, especially Victoria, by Dr. Tedin

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* Minute examination has shown very small spots in occasional maple seeds, which are faint indications of purple specks.

† Correns has also seen a similar case. Tschermak has found the same phenomenon in *Phaseolus*.

at the Svalöf Station, and interprets them, no doubt rightly, as examples of reversion on crossing.

The purple spotting was curiously specific in its occurrence, and seems to be a property of certain matings. (For details, see the original.) Two cases are especially noteworthy in which Victoria, used as *mother*, gave with two unspotted types *P. arvense*, purple-spotted F_1 skins, while the skins of the reciprocal crosses were without the purple spots. Our case of maple ♀ × Victoria·♂ similarly gave no strong purple spots. As it is most important to determine the relation of dominance to reversion, it is to be hoped that these cases may be further investigated in order to decide whether the difference between the cases is due to properties of the individuals or of the types.

In 1901 a cross was made between ♀ purple Sugar-Pea (skin "grey" with purple specks) and a form of maple known as the "Irish" pea ("mummy" habit, salmon-flowered, round seeds and maple skins). F_1 skins, 1902, were maple with purple specks, showing simultaneous presence of both parental characters. There were four such plants. One of them, near the top of the plant, bore a few pods with *deep purple* seed-skins like those described by Laxton. In some pods all skins were purple ; in two pods normal and purple were both present ; one skin was half purple and half maple, with purple specks. A preliminary sowing of these two sorts of seeds was made. Qualitatively, F_2 plants had skins of four kinds : (1) "Grey," viz., brownish, with purple specks ; (2) maple with purple specks ; (3) maple ; (4) in one plant, no mapling, and purple specks no stronger than in maple. F_2 plants from purple F_1 skins did not differ in any way from the rest. One pod only (on F_2) contained three maple seeds *with purple skins*. The number of plants in each class was not recorded, but in view of the result, the case will now be followed up. The maple and purple pigments are in different layers and must be of distinct physiological origin. The allelomorphs must be maple, non-maple, purple, non-purple ; and the plant (4) presumably represents the two negatives. (*Cp.* cases of white in F_2 from sap-colour × cream in Sweet-Pea, p. 86, and Stocks, p. 27.) In view of the result with colourless skins, the possibility that the purple specking may be reversionary, must also be remembered in classifying F_2, etc.

Tschermak also obtained several of the full-purple-skinned seeds from Express × Graue Riesen. They were distributed sporadically (as in Laxton's cases and in our own). Of sixteen sown by him, only one gave a plant bearing some purple-skinned seeds, which were again sporadically distributed, some pods containing only such deep purples, others containing normal purple-specked seeds.

Tschermak's experiment proves that the maple character is not essential to the production of the fully purple skins. The evidence, as a whole, seems to indicate that the occurrence of such skins is due

to some special conditions and not to any transmissible character. The distribution on the plants proves that it is not merely due to heterozygosis, as I had previously supposed. Nevertheless, the condition is, I believe, never seen in pure-bred purple-specked seeds, and an increase, generally slight, in purple specking is not rare in crosses from such types. I found that the purple colour is easily extracted by boiling, and the normal maple markings are then apparent *and normal*.

Shape and Size of Seeds.

These two characters are not readily separable. Shape is made up of at least two factors, of which the chief is evidently the state of the reserve material. Peas are readily classified as follows:—

(1) *Round*, viz., cotyledons smooth, as Express, Nain de Bretagne, Victoria Marrow, Blue Peter, Fillbasket.

(2) *Indent*, cotyledons with rounded depressions, as the purple Sugar Pea (*Graue Riesen*) and Field Pea.

(3) *Wrinkled*, cotyledons irregularly corrugated, as Laxton's Alpha, Serpette Nain Blanc, Telephone, Veitch's Perfection.

Many kinds (*e.g.*, William the First) contain a mixture of round seeds, intermediates between round and wrinkled, and apparently fully wrinkled. But just as in the case of colour, piebalds are not really intermediate between yellow and green, so here it is found that in these mixed types the wrinkling is spurious. Mr. R. P. Gregory[*] has shown that the starch grains in round and indent Peas are large, and in wrinkled Peas very small, and frequently compound. "Intermediates" have starch of the "round" type, and it is doubtful whether any genuine intermediate exists. The same is true of the apparent intermediates seen in F_2, which also are of the spurious kind. These are spoken of as "pitted" seeds.

Indent Peas have peculiar properties, and must be carefully distinguished from both sorts. Confusion has already arisen from neglect of this distinction. Their starch is of the "round" type. The chemical nature of these differences is still unknown, though possibly conversion has taken place in the starch of wrinkled types.[†]

Pitted seeds may occur in any round type, but are specially common in some, *e.g.*, Victoria. When they occur *they are generally associated in pods*. Selection of such seeds does not usually lead to any departure from type, and there is no doubt that, as a rule at least, the change

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[*] 'New Phytologist,' vol. 2, 1903, p. 226.

[†] Denaiffe ('Pois Potagers,' p. 8) points out that at the same stage of maturity, before they shrink, wrinkled types contain a much greater proportion of water than round ones, and conversely that when dry they can take up much more water than the round. To the former fact is of course due the fact that wrinkled Peas are still tender at a stage when the round are hardening.

is due to conditions.* Occasionally, especially in a bad season, there is so much pitting that F_2 seeds cannot be sorted without histological examination.†

Wrinkled seeds show an almost absolute uniformity, apart from the question of rogues and sporting.

Round × round always gave round F_1, and wrinkled × wrinkled always gave wrinkled F_1. In crosses between round and wrinkled, no genuine exception to dominance of round occurred. Cases of slight dimpling occurred, but these gave ordinary Mendelian F_2. In one case all seeds were wrinkled, but these proved to be self-fertilised.

Indent Peas, fertilised by wrinkled types, do not change their shape, but wrinkled, fertilised by indent, give a *round* F_1. F_2 from both such crosses consists of indents and wrinkleds (mixed in the pods just as in ordinary F_2 from round × wrinkled), doubtless as $3:1$, but as the difference between the types is rather elusory, the classification cannot be exactly made. Wrinkled seeds, selected from F_2, gave pure wrinkled F_3.

Indent × round gives indent F_1, and round × indent gives round F_1. The shape, therefore, is here, though an embryonic feature, decided by the maternal plant just as much as the seed-coat. *All F_2 seeds from* BOTH *these crosses are, nevertheless, indent,* showing indent as a dominant character (similarly " maternal "). In F_3, however, some plants have exclusively indent, and some have exclusively round seeds, showing the reappearance of the round—here recessive—character as a maternal property. The meaning of this peculiarity is not obvious, but it must not be confused with difference between reciprocals. The statistical proportions are presumably the normal $3:1$, but, as only sample sowings were made to test the qualitative result, no statement as to the ratio can be made.

Our results also with maple and indent are practically the same, *mutatis mutandis,* as Tschermak's on Graue Riesen (indent) crossed with several white-flowered round sorts. In all these cases he got uniform (indent) F_2 seeds, while these F_2 plants bore F_3 seeds, either indent or round, without mixture on individual plants. Just as in Laxton's experiment, *the round seeds were peculiar to white-flowered plants,* and consequently were in unpigmented (strictly " non-grey ") skins, while the indents were all on purple-flowered plants in " grey " skins.‡

* The existence of such a type as William I shows that liability to pitting must sometimes be a transmissible character; but even then it is very irregular, and clearly dependent on conditions.

† It is presumably to such appearances that Mendel refers when he says that weakly plants often give uncertain results; and unless the pods be examined separately, great confusion may be introduced by such cases, and numerous contradictory observations might be made.

‡ [Fillb. × purple sugar has since behaved similarly. The statement (Mendel's Principles, p. 156) that Debarbieux × behaves thus is incorrect. It was based on

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Similarly, in our case, all the round F_3 seeds were in maple skins, *without* purple spots ; but the indents had *either* maple-purple-spotted skins, *or* spotted skins without maple marks. No mixture of these seed or skin-characters was seen on any plant, and Laxton's observation of such segregation *by pods* is as yet unconfirmed.

Tschermak's use of " *schwach gerunzelte,*" in application to indents, has led to the supposition that the character " wrinkledness," is here dominant over round ; but the fact that indent must be distinguished from both is abundantly clear, especially in the results of crossing indents with a genuine wrinkled type.

In connection with the reversionary appearance of purple spots in the skins, Tschermak observed on several occasions seeds which are described as *wrinkled* in F_2 (borne by F_1 plants), resulting from some of his crosses between various *arvense* forms and Victoria. As he interprets this also as reversionary, like the spotting, " wrinkled " may be presumed here also to mean *indent*, and not *pitted*. We have not seen this interesting result in our crosses, and the only cases in which it could conceivably have occurred, were those of Maple × Victoria or × Nain de Bretagne. In both these cases F_2 seeds were round.

There are several features of shape that would require much space for adequate treatment. It is likely, also, that certain types, both of round and wrinkled, have other peculiar physiological properties, which ought to be carefully examined. To these only a bare reference can be made. The most striking concerns the difference between what may be roughly called *small* and *large* seeds. There are round and wrinkled of both sorts. Generally speaking, when large and small are crossed, the size of F_2 seeds is intermediate, but I have seen a case suggesting segregation in these characters.* When a large wrinkled green, like Telephone, is crossed with a small round yellow, like Nain de Bretagne, the green wrinkleds in F_2 are not in the least like the original Telephone, being smaller and quite different in shape. Mr. R. H. Lock, crossing a small round native Pea at Peradeniya (Ceylon) with Telephone, has seen a similar result, and, as he pointed out to me (*in litt.*), " shape " cannot be treated as *one* character, but may depend on a combination of many. In all such cases, the wrinkled seeds, for instance in F_2, have a general resemblance to each other, showing again a peculiarity of shape as a maternal character, comparable with that seen in indent Peas. There cannot be any doubt that, when the F_3 seeds are formed, the Telephone shape will reappear as characteristic of individual *plants*.

In most types and cross-breds, individual *pods* sometimes occur, which contain only *very small* uniform seeds, about half the normal size. This

F_1 appearances, but F_2 proved that nothing abnormal occurred. In all abnormal *Pisum* cases, a *dark* seed-skin is present. Note, February, 1905.]

* The next generation (F_3) was unfortunately lost.

phenomenon is met with also in Sweet Peas. It has nothing to do with crowding, as the pod is almost empty and flat, though of the usual length and width. When two pods are on one peduncle, I believe it is always the case that, if either contains such small seeds, both do.* No cause can be suggested for this phenomenon. There is no appearance of unhealthiness in the pod or the peduncle. The occurrence is frequent on thoroughly fine plants. These curious "small" seeds did not germinate less well than normal ones, and they produced perfectly normal plants of good size, with normal seeds.

Shape of Pod.

Mendel found the hard pod, with a tough lining membrane, dominant over the *sans parchemin,* or *sugar-pod,* which is without such a membrane. Our experience has been that, though pods of F_1 are never *sans parchemin,* they are decidedly less hard than the hard type, and might sometimes be almost described as intermediate in character. F_2 showed the normal segregation, with the exception of a single plant, which bore pods, some of which would pass for inflated, while others were of the constricted type. Unfortunately, the development of the "parchment" was not examined in this case.

There is great diversity in the shapes characterising the pods of various types, but they may be roughly classified into those known as "stumpy," which, when the pod is full, have a blunt rounded end, and those which are *pointed.* We have found the former always dominant over the latter, and F_2 segregates normally. This observation of the dominance of the stumpy over the pointed types is in agreement with the similar results obtained by Tschermak, and will almost certainly prove to be of wide general application, and of value to the practical breeder.

Height.

This character is liable to considerable fluctuations, which in great measure are due to conditions, especially to difference in preparing the soil, manure, season, etc. Injury to the cotyledons or to the young plant has a marked effect on the height.† The tall types, moreover, are probably not really "pure" in respect of height, but might be subdivided into "*reine Linien.*"‡

* In all cases of noticeable peculiarities distinguishing the seeds of individual pods, paired pods are generally alike in their peculiarity, whether of colour, shape, or size.

† Experiments on this question have been made by Dimon, 'Biol. Bull.,' vol. 2, 1901, p. 209.

‡ *Cf.* Johannsen, 'Erblichkeit in Populationen und in reinen Linien,' Jena, 1903.

Hence it is clear that height is not a character well-suited to these experiments, and reliable results can only be got when extreme types are used.

Peas are usually classified as tall, half-dwarf, and dwarf, and though plants occur of all intermediate heights, the terms are fairly distinctive and easy to apply.

Dwarf Peas range from about 1 to 3 feet ;

Half-dwarf, about 4 feet ;

Tall, about 5 feet and upwards.

The distinction between tall and the rest is a definite one, and it would scarcely be possible to hesitate as to whether a plant belongs to the tall class from the time it is 6 inches high. At this stage, when rapid elongation begins, the talls form relatively long internodes, beginning from about the 4th or 5th. The stem also in the dwarfs and half-dwarfs bends stiffly at each node, forming a zigzag, while the talls are much straighter and more flexible. In talls, moreover, the root is much longer. These distinctions in habit are almost more characteristic of the classes than the actual heights.

The distinction between the dwarfs and half-dwarfs is not nearly so sharp as between them and the talls. The heights of the types taken here in almost every case greatly exceeded those given in the books for these types, being sometimes double. Our plants were grown singly, well manured, and measured on the stretch when growth had ceased. The indications in the books, I imagine, refer to the heights of the plants, sown in drills, at the time of cropping. Many types, especially dwarfs, when mature, have the lower part of the stem more or less horizontal, and this would not be reckoned in stating the height for cultural purposes.

The position of the lowest flower is independent of the height, but is fairly constant in each type.*

The absolute height and the position of the first flower are liable to show deviations if the seedlings are injured by birds, or otherwise, and I have little doubt that the chief irregularities in the direction of reduction in height are all due to this cause. No tall type ever gave a plant which could be mistaken for a half-dwarf, nor did the latter ever give a tall, with the exception of a single plant in a row of Eureka, a variety not used in these crosses.

Of all crosses between talls and dwarfs or half-dwarfs, none presented

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* Economically this character is important, because low flowers, beginning at about the 7th node, indicate precocity, while high flowers, beginning at about the 12th to 20th nodes, indicate lateness. It is difficult to count the nodes with absolute accuracy. Many records on this character were made, but are omitted to save space. Crosses between low flower and high flower often give an F_1 intermediate in this respect, but definite dominance of very high flower and extreme lateness was also seen (*e.g.*, British Queen).

the dwarf habit. In one case (Serpette × Express) two plants were raised which were much shorter than the reciprocals, but they were noted as weakly plants, and they had none of the dwarf character. I attribute their shortness to some unhealthiness or injury. The same applies to three plants from Laxton's Alpha × Serpette. With the exception of a few cases of this kind, F_1 plants were tall, and frequently much taller than their tall parent. The increased height of the heterozygotes was most marked in Laxton's Alpha × Blue Peter, and in crosses with the purple Sugar-Pea.

Crosses between dwarfs and half-dwarfs gave commonly an intermediate result as regards height, and in all cases the characteristic zig-zag habit was retained. No tall plants came from such crosses.

The 1903 sowings suffered greatly from the late frosts, and several lots were much injured by birds. The Telephone crosses were more attacked than any others, and the irregularity in their heights is without doubt due to this cause. Many of them were completely destroyed, and some of those which grew had every leaf picked off in April.

Importance would attach to the question whether half-dwarf segregates from dwarf, as the case is typical of many natural phenomena of heredity. No sufficient opportunity of testing the point has occurred, for an exceptionally favourable season and uniform conditions would be needed in order to study such small differences. Such evidence as exists is slightly in favour of non-segregation. [*Note added February*, 1905. In 1904 a striking case of intensification of dwarfness was seen. Fillb. (half-dwf.) × purple sugar (v. tall) gave F_2 8 tall, 2 half-dwf., 2 extreme dwf.]

The Order of F_2 Seeds in the Pods.

Great labour was devoted to the solution of this question, and many plants were mapped throughout in the hope of detecting an order in the distribution of the seeds. Numerous crosses of F_1 plants with pure recessives were made for the same purpose. No regularity, however, was found. The presumption that some order exists is so strong, *à priori*, that I am disposed to think that the process of oögenesis in which the dominant or recessive character of the egg-cell is determined must be liable to disturbance by accidents.

The Nature of " Rogues."

Even under careful selection, occasional " rogues," or untrue plants appear, and their existence constitutes a most important problem. With Mr. Arthur Sutton's help I have begun to investigate this question, and though little has so far been discovered, the matter must be alluded to as bearing on the question of purity of strain.

Rogues may occur in any type, but are much commoner in some

than in others.   Some of these are merely recurring recessives and call for no discussion, but a certain number are *dominants* appearing in recessive strains.   Of these, many are traceable to imperfect selection of the type-seeds.   For instance, in Veitch's Perfection a round rogue is very common.   This is primarily due to *pitted* seeds of the rogue passing for *wrinkled* seeds of the type.

On minute inspection such seeds can be recognised.   They give the usual round seeded rogue, and I find this is an ordinary dominant when crossed with the type.

The question then arises whether *all* rogues are similarly due to imperfect sorting, or to recurrence of recessives, but the balance of evidence is scarcely favourable to this view.

Some rogues are so primitive in habit that it is very unlikely they can be recessive, and their seeds are sometimes so characteristic that it is almost impossible they can get passed over in the fairly rigorous hand-picking to which Peas are subjected.   We are, therefore, in all probability, here confronted with a problem of original variation.   To investigate it the seeds of individual plants must be separately sown on a large scale, and the attention of experimenters is called to this attractive inquiry.   The first question is to decide whether the wild rogues are given off by a few plants only, as seems likely, and if so, to determine their distribution on these parent plants.

If it appears that the rogues are merely recurring recessives, or due to imperfect sorting, it should be possible to get rid of them once for all.

Wiegmann ('Bastarderz. im Pflanzenreiche,' 1828, p. 14) states that he saw a natural cross between *Pisum* and *Vicia*.   Such a statement needs confirmation.   I have seen but one case of a suspected natural cross on *Pisum*, and I incline to think it was a pod which I had myself crossed, and omitted to label.

NUMERICAL RESULTS (F₂ seeds).

Table I.—Yellow and Green.

No.	♀.	♂.	Height in feet.	Yell.	Green.	Dubious.
			Wrinkled.			
17*a*, 1	L.'s A.	Serp.	About 7	77	26	2
2			,,	84	21	
3			,,	116	28	
4			,,	57	21	
5			,,	138	44	
17*b*, 1	,,	,,	6¾	96	31	
2			6	56	17	
3			6½	90	33	

Table I.—Yellow and Green—*contd.*

No.	♀.	♂.	Height in feet.	Yell.	Green.	Dubious.
12, 1	L.'s A.	Serp.	5	Lost		
2			$6\frac{3}{4}$	76	22	
3			$5\frac{1}{4}$	51	16	7
13, 1	„	„	3	19	7	
2			$4\frac{1}{4}$	20	8	1
3			7	67	18	2
4			$4\frac{1}{4}$	4	2	
17c, 1	Serp.	L.'s A.	$4\frac{1}{2}$	47	9	2
2			$5\frac{1}{2}$	42	16	
3			$5\frac{1}{4}$	60	9	
23, 1	Teleph.	E. Gt.	4	19	5	
2			$4\frac{1}{4}$	26	11	
3			4	23	7	
24, 1	E. Gt.	Teleph.	$3\frac{3}{4}$	15	10	
2			$5\frac{1}{2}$	53	22	
25, 1—3 mixed.	„	„	3	31	10	3

Round.

No.	♀.	♂.	Height in feet.	Yell.	Green.	Dubious.
14, 1	Vict.	F.B.	7	141	46	
2			7	93	38	
3			$6\frac{3}{4}$	138	53	
4			5 +	77	32	
5			$6\frac{1}{2}$	58	16	3
29a, 1	F. B.	Deb.	$4—4\frac{1}{2}$	298	79	
2			„	10	2	
3			„	163	66	3
29b, 1	„	„	$4\frac{3}{4}$	173	72	2
2			4	107	35	
31a, 1	„	N. de B.	$3\frac{3}{4}$	111	41	
2			„	69	21	
3			„	145	44	
4			„	197	64	
5			„	91	30	
6			„	162	54	
31b, 1	„	„	$3\frac{1}{2}$	67	24	1
2			„	97	36	1
3			„	70	14	8
4			„	49	25	2
+ Loose seeds.				16	7	
2, 1	„	„	Not recorded.	31	15	1
2				92	34	2
3				77	29	1

Table I.—Yellow and Green—*contd.*

No.	♀.	♂.	Height in feet.	Yell.	Green.	Dubious.
K1, 1	F. B.	N. de B.		40	12	
2				8	1	+ *
3				8	1	+
4				4	.2	
5				13	6	+
6				35	13	
K2, 1	,,	,,		15	2	+
2				27	20	+
3				9	3	+
4			1¾—3 ft. (17 plants being 2—2½).	7	5	+
5				35	13	
6				44	16	+
K3, 1	,,	,,		65	14	+
2				12	2	
3				18	5	
4				19	5	+
5				10	4	
K4, 1	,,	,,	2—2½	15	5	+
2			,,	13	7	
5, 1	N. de B.	F. B.	3	111	46	3
2			2¾	69	18	3
3			2¼	23	12	
37, 1	B. P.	Deb.	3¾	55	24	
2			4	32	20	1
K5, 1	Sabre	Exp.		70	27	
2				44	16	
3				13	2	
4				81	26	2
5				100	32	
6				75	29	
7				34	4	
K6, 1	,,	,,	2¾—5¼ (9 being between 4 and 5 ft.).	24	14	
2				95	37	
3				12	4	3
4				13	6	
5				49	17	
6				83	20	
7				41	13	
K7, 1	Exp.	Sabre	5¾	74	32	
2			6¾	89	24	

Total   5321   1804

Ratio, 2·95 : 1

* + means many seeds shed before gathering.

Table II.—Round and Wrinkled.

No.	Green. ♀.	Green. ♂.	Height in feet.	Round.	Wrinkled.	Dubious.
18a	L.'s A.	Exp.	5	73	20	5
K8, 1	,,	,,	about 3	32	9	+
2			,,	30	10	
18b, 1	Exp.	L.'s A.	$5\frac{1}{2}$	70	28	
2			$4\frac{1}{4}$	28	7	
3			$3\frac{1}{2}$	14	2	
4			$4\frac{3}{4}$	67	17	
5			5	73	25	
18c, 1	,,	,,	6	81	28	1
2			$5\frac{1}{2}$	46	14	
3			5	40	12	
4			$3\frac{3}{4}$	34	11	
18d, 1	,,	,,	about 6	88	20	
2			,,	60	28	1
3			,,	114	46	1
4			,,	102	38	
5			,,	61	15	
18e, 1	,,	,,	about 7	95	37	
2			,,	87	40	
3	.	.	,,	53	19	1
4			,,	69	25	5
5			,,	76	33	1
6			,,	40	9	
K9, 1	,,	,,	about 4	18	6	+
2			,,	21	6	+
3			,,	21	9	+
19, 1	L.'s A.	B. P.	6	104	28	
2			7	134	35	
3			$7\frac{1}{4}$	96	21	2
4			$6\frac{1}{2}$	107	32	
K10	,,	,,	Tall	23	6	
20b, 1	,,	F. B.	7	88	21	
2			$7\frac{1}{2}$	70	29	
3			$6\frac{1}{2}$	26	11	
4			$7\frac{1}{2}$	67	14	+ ?
*20c, 1	F. B.	L.'s A.	7	39	18	
3			$8\frac{1}{4}$	79	37	
4			$8\frac{1}{2}$	78	31	
5			9	120	40	
6			$8\frac{1}{4}$	98	39	

* 20c, 2 proved to be self-fertilised.

Table II.—Round and Wrinkled—*contd.*

No.	♀.	♂.	Height. in feet.	Round.	Wrinkled.	Dubious.
27, 1	Deb.	Serp.	$2\frac{1}{2}$	6	1	
2			4		Lost	
3			$3\frac{1}{4}$	25	6	1
4				30	9	4
5				57	26	
*35, 1	B. Q.	N. de B.	about $6\frac{1}{4}$	253	92	15
2			,,	108	22	2
3	(a branch only)	,,		50	13	3
4		,,		151	45	
K11, 1	Serp.	Sabre	$3\frac{1}{2}$	32	12	
2			4	16	2	
3			$4\frac{1}{4}$	38	8	
K12, 1	,,	N. de B.	2—$2\frac{1}{2}$	42	14	
2			,,	49	15	
3			,,	6	0	
4			,,	16	9	+
5			,,	70	24	
18, 1—5	F. B.	Teleph.		332	119	25
19, 1	,,	,,	7	55	22	4
2			$6\frac{3}{4}$	66	24	2
3			5	69	· 20	
20, 1	,,	,,	$4\frac{1}{2}$	23	9	3
2			$4\frac{1}{4}$	4	2	
28	,,	,,	5	32	9	1
21	Exp.	,,	$7\frac{1}{2}$	94†	29	6

Total   4246   1408

Ratio, 3·02 : 1

Table III.—Yellow Wrinkled and Green Round.

No.	♀.	♂.	Height in feet.	yr.	yw.	gr.	gw.	Dubious.
16a, 1	Serp.	Exp.	$2\frac{3}{4}$	20	10	6	2	
2			$3\frac{3}{4}$	21	9	11	4	
16b, 1	Exp.	Serp.	$6\frac{1}{2}$	96	37	28	6	34‡
2			$6\frac{1}{4}$	70	17	15	5	2
3			$5\frac{3}{4}$	69	19	27	3	2
4			$6\frac{1}{4}$	131	45	44	9	13
5			6 +	83	32	24	8	11
6			$5\frac{3}{4}$	74	33	23	10	6

* 1 proves to be self-fertilised.
† Much pitting.
‡ Shapes doubtful : 24 y., 10 g.

Table III.—Yellow Wrinkled and Green Round—*contd.*

No.	♀.	♂.	Height in feet.	yr.	yw.	gr.	gw.	Dubious.
16c, 1	Exp.	Serp.		110	45	37	19	3
2				52	12	17	3	1
3				83	26	11	11	5
16d, 1	,,	,,	4	58	13	29	5	1
2			5	79	23	25	10	4
3			5	41	11	10	2	
4			5	65	13	26	4	1
5			6¼	56	15	11	3	16
7	,,	,,	about 3¼	16	9	7	1	2
8			5¼	42	11	12	5	4
11, 1	,,	,,	5	49	20	16	10	7
2			2	11	3	7	1	
3			5			lost		
9, 1—3	,,	,,		94	31	26	15	14
32a, 1	F. B.	,,*	3½	142	40	48	7	19
32b, 1	,,	,,	3—3½	53	19	20	7	4
2			,,	53	18	28	2	7
3			,,	85	23	27	5	8
4			,,	54	12	26	10	3
5			,,	53	22	13	7	3
32c, 1	,,	,,	,,	16	10	7	1	
2			4	65	20	28	10	8
3			4	98	35	38	10	1
4			4¼	87	36	25	10	2
5			3¾	18	2	5	2	2
6			4¼	74	27	30	9	5+
7			4¼	91	33	42	9	5
32d, 1	,,	,,	about 4	67	23	27	2	1
2			,,	80	23	21	6	9
3			,,	62	23	21	5	11
4			,,	68	17	18	6	
5			,,	45	24	15	1	6
6			,,	47	14	12	1	1
7			,,	77	17	26	10	4
32e, 1	,,	,,	,,	98	40	29	4	2
2			,,	55	13	11	6	1
3			,,	76	23	19	9	17
4			,,	38	18	16	3	1
5			,,	67	22	23	7	4
6			,,	75	30	15	6	

* This combination gave a very uniform height.

Table III.—Yellow Wrinkled and Green Round—*contd.*

No.	♀.	♂.	Height in feet.	yr.	yw.	gr.	gw.	Dubious.
32f, 1	F. B.	Serp.	3½	61	27	18	4	3
2			,,	107	26	20	9	6
3			,,	82	27	23	7	7
1, 1	,,	,,	3¼	70	24	30	6	2
2			3½	175	65	68	21	13
3			,,	32	8	14	2	9
4			,,	37	23	13	9	3
30, 1	,,	Tph. yell.	3½	17	6	6	2	1 ⎫
2			3¾	12	4	4	0	3 ⎬ V. poor.
3			,,	8	6	3	0	⎭
34, 1	B. P.	Serp.	2½	27	11	8	0	
2			,,	34	6	11	4	
3			2¾	40	7	11	1	
4, 1	Serp.	B. P.*		42	16	17	9	2
2				77	27	28	5	
3				53	21	16	4	
4				37	12	11	4	

Yellow Round and Green Wrinkled.

No.	♀.	♂.	Height in feet.	yr.	yw.	gr.	gw.	Dubious.
15† 1	N. de B.	Teleph.	6	50	13	17	4	7
2			6½	75	18	14	7	6
3			6½	31	11	12	3	20
17	,,	,,	7	60	22	31	8	6
29, 1	Teleph.	N. de B.	4	28	8	14	4	1
2			5	24	6	4	2	3
3			3	6	2	2	0	
K13, 1	Sabre	L.'s A.	⎫	88	44	37	7	
2				25	11	10	1	
3				14	8	8	0	
4				74	21	16	5	1
K14, 1	,,	,,	4 ft. 10 in. to 6 ft. 3 in.	22	16	4	2	2
2				74	18	29	4	
3				47	21	12	5	2
4				71	28	18	12	
5				85	23	31	8	
6				18	8	8	4	
7				47	19	16	7	
8				52	14	13	7	1
K15, 1	L.'s A.	Sabre		19	0	10	2	
2				15	6	4	3	
3			⎭	26	5	8	5	
Total ...				4926	1656	1621	478	

* Tinging and pitting.   † In this case the F_1 seeds were greenish (p. 60).

Taking the whole mass of seed results in F₂, involving one pair of allelomorphs, there were :—

<blockquote>
5321 yellow, 1804 green, giving the ratio ...... 2·95 : 1
4246 round, 1408 wrinkled   ,,   ,, ... 3·02 : 1,
</blockquote>

where 3·0 is expected. The ratios found in individual plants, 62 for shape and 85 for colour, are not enough for full discussion, and a study of them does not, so far, suggest the presence of any definite disturbing factor.

In the seed-results where two pairs of allelomorphs, shape and colour, are considered, the totals are :—

rd. yell.	wr. yell.	rd. green.	wr. green.
4926	1656	1621	478
4878	*1626*	*1626*	*542*

the expectation being shown in italics. The deficiency of wrinkled green is noticeable. Of the seeds classed as "dubious" (generally exclusive of dead seeds) the majority could be sorted either as regards shape or colour, but these details are not worth printing. The case of 16 *b*1, is interesting, as in it there were 34 seeds (24 y, 10 g), which could not be sorted with confidence in regard to *shape*. They were mostly the produce of certain pods which contained exclusively "pitted" seeds. As stated above, this appearance is due to some unknown somatic disturbance, and has nothing to do with transmission. The net deficiency of green wrinkled seeds is probably due to a slightly greater tendency to tinge, or to burst, owing to which a larger proportion have been consigned to the "dubious" class, or have been rejected as dead.

Various F₂ green seeds and wrinkled seeds were sown and gave exclusively recessive seeds, nothing new being observed. Particular attention was paid to these tests in the case of F₂ from crosses with the Purple Sugar Pea × a wrinkled green (L.'s A.), the case not having been investigated before. The behaviour of the recessive was normal throughout. The dominants were DD or DR as usual.

The statements as to the behaviour of the coloured-flowered types in their crosses are founded on the following original crosses and their descendants :—

	Pods.	Seeds.
L.'s A. × Purp. .... · 1		4
Recip. 1		5
Exp. × Purp. 1		5
B. P. × ,, ... 1		6
Deb. × ,, ... 1		1
Purp. × N. de B. 2		10
,, × Irish.................. 1		4

	Pods.	Seeds.
Purp. × F. B.	1	6
,, × Teleph................	1	1
Recip.	1	2
Teleph. × F. P.	1	7
Maple × Purp.	1	1
,, × Vict.	1	8
,, × B. Q.	1	5
,, × N. de B.	2	7
,, × B. Q.	1	6
Recip.	2	10
Purp. × Sabre	3	16
Recip.	3	16
B. Q. × Purp.	2	7

Correct F_2 numbers for seed-colour could not be given without peeling, or for shape without sowing. There is no reason to suppose that they are of special interest. As explained, the *plant* characters of F_2, etc., are important, and these will be followed up.

Summary of Evidence on Peas.

The evidence, for the most part, is confirmatory of that of Mendel and others. The following points are noteworthy.

1. F_1 from tall × dwarf or × half-dwarf was always tall, often greatly exceeding the original " tall " in height, but from dwarf × half-dwarf it is usually intermediate, and was never tall. The character, height, is liable to great fluctuations, largely due to conditions and injury, perhaps also to mixture of types. " Tall " segregates from dwarf, as is well known, but it is not yet certain that half-dwarf segregates from dwarf.

2. *Seed Characters* (*a*) *Colour*.—Tinged and piebald cotyledons must not be treated as genetic characters " intermediate " between yellow and green, nor are they mosaics. The yellow in them results from external conditions, being sometimes morbid, sometimes natural. Susceptibility to such changes in some green types is common, in others rare. To dominance of yellow one dubious exception was seen, which, nevertheless, gave a normal F_2.

(*b*) *Shape*.—" Round " was always dominant over " wrinkled." " Indent " is quite distinct from " wrinkled " and from " round." Crossed with wrinkled, the indent type behaves as round. Crossed with round it behaves as a maternal or *plant* character, being dominant in F_1 plants. In gametogenesis it segregates from round, but indent can only appear in association with a coloured seed-coat (and flowers). On the other hand " round " though segregated cannot appear in the seeds borne by F_1. A similar case has been seen by Mr. R. H. Biffen.

When Polish wheat is crossed with Rivet, the F_2 seeds are of inter-mediate length, though doubtless the F_2 plants will bear respectively long, intermediate, and short seeds.*

True wrinkling is always associated with, and probably depends on a peculiar condition of the reserve materials, of which the small and compound starch grains are the visible indication (Gregory). From this the pitting and spurious wrinkling, sometimes common in round types and in F_2 from crosses, must be distinguished. Spurious wrinkling is evidently due to conditions, though special susceptibility to it is probably transmissible (*cf.* William I, p. 65). Nevertheless, no difference could be seen in the offspring of extremes in this variety.

(*c*) *Seed-coat.*—Greys and browns associated with coloured flower are always dominant. Crossed with whites they occasionally *give " rever-sionary " F_1 with purple spots*, though neither parent has such spots. The deep purple coat occasionally seen on such seeds is probably due to conditions and has not been seen to be transmitted.

3. The common application of the term " variable " to the shapes and colours of Peas rests on a misconception. No case of variation in either respect has been observed, which has borne critical investigation.

The statement that variation occurs in these characters is founded on observation of somatic differences, or on results of crossing mis-understood. There is no evidence that the colour or the shape can be changed by selecting these somatic differences.

On the other hand, at various points of time, such variations must have taken place; the green has arisen from the yellow, and the wrinkled from the round. There is no reason for supposing that these changes were due to progressive selection, and it is practically certain that they were discontinuous. Whether the " rogues " now occurring in many types are true variations is uncertain. Many of them certainly are not, others possibly are.

4. *Exceptions.*—Writing, in 1902, I was disposed to believe that genuine exceptions to the dominance of yellow cotyledons or of round-ness, and to the purity of segregation of these allelomorphs from their recessives, might be not infrequent. Experience has shown that such exceptions are in any case very rare, and it is doubtful whether there are any which cannot be referred either to mistakes or to inter-ference of external conditions.

We are probably right in declaring that when true yellow is crossed with true green, or true smooth cotyledons with true wrinkled, yellow and smooth are always dominant if the external conditions are the same.†

* Now described in full; Biffen, 'Jour. Agr. Sci.,' I., 1905.

† [Since this was written, Tschermak has given further details (' Zt. landw. Versuchsw., 1904 ') of cases giving exceptional results after F_2. It is conceivable that a true anomaly of segregation was involved in some of these, but it seems

5. All the characters studied are independent and separately transferable, with the following exceptions. Flower colour and axil colour and "grey" or "maple" seed-coat are not usually separable, but Tschermak has seen a form with flowers coloured and axils plain.

Indent shape seems to be inseparable from the seed-coats proper to coloured flowers. It may nevertheless segregate, both from round shape and from wrinkled.

SWEET PEA (*Lathyrus odoratus*).

(Experiments carried out by W. Bateson, E. R. Saunders, and R. C. Punnett (in 1904).)*

Types of Pollen.

After the the re-discovery of Mendel's work it seemed desirable to use varieties differing in a pollen-character. Searching for such forms, it was found in October, 1900, that the Sweet Pea, Emily Henderson (referred to as E. H.), a pure white var., usually has pollen distinct from that of normal vars. When dry it is irregularly kidney-shaped or *round*, while normal pollen is long with straight sides. Treated with reagents normal pollen swells to an *elliptical* shape with a distinct long axis, and shows *three* pores set evenly round the short circumference. Round pollen thus treated becomes nearly *spherical*, and usually has only *two* pores. These pores are sometimes placed at two poles, but not rarely are asymmetrically placed, in which case one may be larger than the other. Grains with only *one* pore occur in round pollen. In E. H. these are rare, but in some of the later derivatives they may be fairly common, and even constituted the majority in a few plants. Lastly, grains which, though round, are three-pored, are not very uncommon.

Extensive search among plants of many natural orders has revealed no similar case. Variation in number of pores is not rare, *e.g.*, in some Violas and Tropæolum, where two-pored and even one-pored grains may occur among the normal three-pored, but no variety was found characterised by an abnormal pollen.†

The round pollen was discovered in a short row of E. H., sown without any thought of experiment, which had survived into late autumn. Seed of this row was collected promiscuously, the importance of the subject not being realised. In 1901, when experiments were contemplated, this seed was examined, and it was found to contain some *black*-skinned seeds mixed with the drab or *light*-skinned seeds proper to all truly white varieties. The *black* seeds proved that at least one of the original row had been a coloured plant. But since the seed came from a Sweet-Pea specialist, all blacks would certainly have been picked out from the seed supplied. Therefore it is certain that the coloured plant or plants were "rogues," *i.e.*, offspring of a white or normal mother-plant. The nature of such rogues we shall presently discuss.

Besides the home-grown seed, other samples of E. H. were obtained from various firms. These were all found to give, together with "round" plants, a variable number, which, though otherwise identical with E. H., had normal *long* pollen. Such longs are usually a minority, but samples have been seen in which longs were as common as round.

With the exception of E. H. the ordinary tall varieties of Sweet Peas are apparently all long-pollened, but among the dwarf procumbent varieties called *Cupids*, rounds are common, white Cupids in particular being almost always round.

The half-dwarf or "bush" variety, known as Mont Blanc or New Early White also frequently has round pollen. Both this and white Cupid are very like E. H. in other respects, and there is every probability that they were derived directly from it.*

In 1901, a large number of crosses were made between the long and round E. H. and between each of them and certain coloured types. Of these, many failed, but a good number of F_1 plants were produced.

In all F_1 plants the pollen is long, and experience has shown that the characters long and round generally behave as Mendelian dominant and recessive plant-characters.

Mixed Pollens.—Round grains are never found on "long" plants, and never occurred in F_1. But in subsequent generations an apparently genuine mixture of characteristic long grains among pollen otherwise round, was seen in occasional plants, and was proved to occur even in individual anthers. These "mixed" plants may have amounted to about 2 per cent. of later generations, and sometimes were associated in particular families. Such mixture must be distinguished from the occurrence of three-pored round grains in normal round pollen. The true mixture is not only rare but very capricious in occurrence, and

* As one grows familiar with pollens, other classes become recognisable in addition to round and longs. For the present such further subdivision is not attempted. With practice it is likely that some types at least could be recognised by their pollens.

plants showing mixture in an occasional flower may have in most flowers only round pollen.   As the mixed cannot be certainly distinguished from the round, they are all counted together for the present as round.

Rounds, being recessive in that character, give, left to nature, rounds only, except for an occasional " rogue " such as may occur in any type. Seed from many putative " mixed " plants was saved, but in only one case (offspring of a " rogue ") did a distinct proportion of longs appear (14 long, 52 round), which were not merely " rogues."

Longs, with the rarest exceptions (which are probably due to error, see p. 92), give either longs only, or longs and rounds approaching the ratio 3 : 1.

Before experiment it seemed just possible that F_1 would visibly exhibit the underlying gametic differentiation, as a mixture of longs and rounds, but the evidence so far is very decidedly against this view, and it is certain that such mixture, though having doubtless a distinct significance, is a very rare and exceptional phenomenon.

Our evidence indicates that the shape of the pollen grain and the number of pores is a zygotic and not a gametic character, just as seed-coat is.   Mr. R. P. Gregory has made careful studies of the maturation-processes in various types, but, so far, has found no difference between the pollen-formation in long and round.

The pollen-characters having—with a few exceptions—a simple Mendelian behaviour, the importance of the work relates almost entirely to colour-inheritance, but before introducing this subject two other structural characters may be referred to.

Cupids.—These are dwarf procumbent plants, making no erect stem. Their leaves are a peculiar dark green.   They behave as simple recessives. F_1 from Cupid × tall is tall. F_2 gives 3 tall : 1 Cupid. The actual numbers seen were 693 tall, 215 Cupids, or 3·22 : 1. Cupids left to Nature give, as a rule, Cupids only.   An exception to this was seen at Messrs. Sutton's, in the fact that Cupids Mme. Carnot (blue), F_3 from white Cupid × Mme. Carnot, gave 2 white Cupid, 24 Cupid Mme. Carnot, *and* 12 *tall blue-purples*.   There can be little doubt that these latter were due to crossing by *Megachile* (see " rogues," p. 95).   In 1904 they gave normal F_2 families.

Cupids are difficult to seed.   They not rarely have deficiency of pollen, and, consequently, must be very liable to get crossed.   Moreover, they often amputate their flowers at the pedicel-joint.   Other types do this sometimes, a whole plant being occasionally thus affected. Probably this also is a recessive character.   Cupids frequently have round pollen, and there is little doubt that the white Cupid, one of the first Cupids—if not the first—came as a mutation from E. H.   The other Cupids have been obtained by crossing Cupid with various tall types, of which most of the best known are now to be had as Cupids.

The Cupid habit can thus be combined in F_2, or later, with any previously existing colour, according to the ordinary Mendelian principles.

" *Snapdragon* " *Types.*—In these the standard is tucked in, forming a hood, like the flower of *Linaria*. This is a recessive character. F_1 has standard erect, or very slightly hooded, like the hooded types (*e.g.*, Blanche Burpee). F_2 gives 3 erect : 1 " snapdragon." Numbers observed erect, 246 ; "snapdragon," 77 ; or 3·02 : 1.

It is nearly certain that the hooding of ordinary hooded types is a similar recessive, though actual counts have not been made. Though in F_2 the segregation of the " snapdragon " character from the erect standard is complete, an intermediate state is possible.

Salvation Lassie is almost exactly intermediate between a true " snapdragon " such as Red Riding Hood, and the type. The fact, here well illustrated, that an intermediate type may, on occasion, come into existence (whether by mutation or crossing), though the two extremes habitually segregate, is one of great theoretical significance.

[Attention is called to the " Snapdragon " types as good subjects for experiments demanding a plant practically above suspicion of any possibility of crossing by insects.]

Colour.

Through the great kindness of Messrs. Sutton and Sons we have been permitted to study, year by year, the long series of Sweet Pea crosses made by them. This privilege has been most valuable, enabling us to make acquaintance with the phenomena of heredity in Sweet Peas on an ample scale, and to direct our own experiments in the light of the experience gained at Reading. We take this opportunity of acknowledging our great indebtedness to Messrs. Sutton and their staff for the constant help they have afforded us in placing their crops and records in the freest way at our disposal.

At the present time there are more than a hundred colour-types in Sweet Peas. The colours are of two kinds : (1) those due to cell-sap colour, ranging through chocolate, purple, blue, red, pink ; (2) yellow, due to presence of coloured plastids, here spoken of as *cream ;* or to various combinations of (1) and (2).

Besides flower-colour the plants may differ in colour of axils, which are either red, here called dark axil (*dk. ax.*), or simply green, here called light axil (*lt. ax.*).

The phenomena are greatly complicated by the occurrence of reversion, and various processes of resolution and disintegration ; but, speaking generally, white is a recessive to sap-colour, cream is recessive to non-cream, and lt. ax. to dk. ax. Therefore, cream is always homozygous. White × any sap-coloured type has, so far, always given

a reversionary F_1 (excepting 1 case of magenta self "Her Majesty"), and white by white has always given reversionary F_1 when "pure" parents, with long and round pollen respectively, were used.* The results from pure-bred cream types, without sap-colour, crossed with white are not yet known. Crosses between two sap-coloured types give complex results and are only referred to incidentally in this paper.

The reversionary F_1 may present one of two forms. It may either revert totally to the original *purple* type, or it may be the *red bicolor* known as Painted Lady (P. L.). The two are never mixed together in F_1 families. The axils may or may not revert to the dark type.

The wild purple type is common in Sicily, and through Dr. S. F. Harmer we have received valuable information respecting it from Professor Gojacono and Mr. Whitaker, who have most kindly sent a dried flower. This agrees exactly with the ordinary purple F_1. Professor Gojacono also tells us that the red bicolor is occasionally found wild, but he has never seen a white wild. The P. L. form is also stated to have been originally brought into cultivation from Ceylon.†

The purple is still sometimes grown as "Purple Invincible." The P. L. is grown under several names, each type presenting slight differences chiefly in tint of wings, ranging to magenta, when it is known as "Miss Hunt." An early type, "Earliest of All" × Mont Blanc, round, gave ordinary dominance with a fairly simple Mendelian F_2 (about 40 P.L. various tints and 11 white + 2 purple "rogues"), seen at Messrs. Sutton's.

The existence of two reversionary types, the one a total, the other a "half" reversion, is important, and leads to various complications.

CROSSES (F_1).

So far in our crosses white *long* × coloured has given purple F_1; and white *round* × red *sap-coloured* has given P. L., but × blue sap-coloured gives purple.

White long × white round sometimes gives purple, sometimes P. L. No F_1 family ever contained a mixture of these, but the factors which decide whether the reversion is total, or half, are still unknown.

Purple F_1 presents various minor differences according to the coloured type used, some having blue, others purple wings. A form flaked with red-purple occasionally appears, and once F_1 was striped with white something like "Grey Friar."

* Extracted whites have a different behaviour.

† *Cf.* Burmann, 'Thes. Zeylanicus." This is clearly Painted Lady, but as Trimen mentions no Lathyrus in his 'Flora of Ceylon,' there is grave doubt as to the original record. Mr. R. H. Lock, as the result of inquiries made at Peradeniya, writes that he can hear of no such plant native in Ceylon.

Similarly the F_1 P. L. ranges from the common form with white or pale pink wings to Miss Hunt, and in this respect individuals may differ in the same family. Considerable differences in these minor respects may occur between flowers on the same plant. Late flowers are often flaked and irregular in colour.

The following list shows the evidence as to F_1 obtained in 1901 and 1902 (put together to save space. Of course the former only have reached F_2). As reciprocals have hitherto been alike, they also are not distinguished from each other.

pur., purple ; pk., pink ; cr., cream ; choc., chocolate ; td. wh., tinged white ; wh., white.

I. *White long × white round—*

Parents.	F_1.	Families.
E. H. long and round	29 pur. dk. ax.	9
„ „	1 P. L. dk. ax	1
Blanche Burpee × E. H. red......	3 pur. dk. ax.	2
„ „ „	14 P. L. lt. ax.	3

II. *Whites of similar pollen—*

E. H. round × ditto	3 wh. rd.	3
Bl. Burpee × E. H. long	9 wh. long	3

III. *White long × cream—*

E. H. long × cream long	3 pur. dk. ax.	1

(The cream was saved from an extracted F_2 cream, proved pure on selfing, giving about 200 cream + 1 P. L. and 1 white, regarded as rogues.)

IV. *White long × red sap-colour, with or without cream.*

The following types were used. The first figure gives the number of plants, the second the number of families. F_1 purple, unless otherwise stated. All dk. ax.

Venus, pk. cr., 1, (1); Her Majesty, 1, (1): Lovely, pk., 24, (7); Queen Victoria, pk. tinged, cr., 13, (4); Lottie Hutchins, flaked pink 1 F_1, striped pur.; Salopian, red, 1; Gorgeous, red cr., 1; F. Bouverie, pk., 3 (1); Sadie Burpee, black-seeded, tinged wh., 7 (2); Firefly, red, 17·1, (3); Lady Penzance, pk., 1.

In above cases, E. H. long was the white parent. In addition Bl. Burpee white long × Sadie Burpee black-seeded, tinged white, gave 1 purple. Once Bl. Burpee ♀ × Mrs. Sankey ♂, very like Sadie Burpee used in last cross, gave 3 *whites*, but these, being quite exceptional, are for the present suspected of being accidental self-fertilisations.

V. *White long* × *blue or purple sap-colour.*

E. H. long × Navy Blue, peculiar clear blue, lt. ax., gave 3 dark purple, slightly dk. ax. (1); Black Knight (choc. purple) × E. H. long gave 5 purple dk. ax. (1).

VI. *White round (E. H.)* × *red sap-coloured, with or without cream.*

F_1 was P. L. in all cases.

Venus, pk. cr., 13, (6); Queen Victoria, tinged cream, 15, (3); Sadie Burpee, tinged wh., 1; Prince of Wales, carmine, 4, (1); Firefly and Mars, reds, not distinguished, 27, (6); Lady Penzance, pk., 5, (2);

VII. *White round (E. H.)* × *blue or purple sap-coloured.*

F_1 purple in all cases.

Navy Blue, blue, lt. ax., 2 lt. ax., (1); Black Knight, choc.-purple, 4 (1); Countess Cadogan, blue-purple, 7 dk. ax. (1); Stanley, rather irregular, purple to choc.-purple, 1; Countess Radnor, lavender, 2, (1).

In some of the above crosses there is reversion to dark axil, but in others, reversion in flower-colour occurs without any change to dark axil.

$$F_2.$$

Except in the case of simple dominance given above (p. 84), F_2 results are all complex and cannot be fully understood till F_3 and F_4 are grown. In all cases of reversion a more or less numerous series of new types appears in F_2. Generally speaking (from white × sap-colour), white reappears in the proportion of 1 white to 3 sap-coloured (actually 379 to 1245, 1 : 3·29).

In one family, Venus × E. H. rd., two F_2 gave *no* white (in 64 F_2 plants). The evidence points to some mistake having been made in that case, and suggests that these plants were really DD in sap-colour. These 64 are omitted from total. Nevertheless there were certain distinct irregularities when Venus was used, and it is not impossible that some of these effects may be really due to monolepsis or to failure of segregation. As cream is recessive to non-cream, *untinged* creams must be added to the whites and this is done in total given.

At Messrs. Sutton's cases were seen of the appearance of true *whites* in F_2 from Mrs. Eckford (a pure cream with light axils and seed-skin), crossed with three different coloured types, viz., Her Majesty (magenta), Countess Radnor (lavender), and Queen of Pinks (pink, ? with cream). Mrs. Eckford is a pure cream, viz., a white + coloured plastids. A similar appearance of whites occurred in Stocks (see p. 27), and evidently is due to recombination of the characters no sap-colour with uncoloured plastids, according to the ordinary

scheme for di-hybrids. The only difficulty lies in the case of Queen of Pinks, which *looks* as if it had coloured plastids. Presumably this appearance is misleading. Mrs. Eckford × Queen Victoria (tinged cream) of course gives no whites in F_2, for both parents have cream.

The coloured offspring in F_2 are generally capable of being classified and sorted into types without much difficulty, though, from the fact that the nature of cream was not understood when the work began, some want of uniformity was introduced. The following is a list of the types which constantly recur :—

		Standard.	Wings.
(1)	*Purple*.........	Choc.-purple.	Blue, or purple.
(2)	*Picotee*.........	White edged with purple or red.	White edged with blue.
(3)	*Painted Lady.*	Red.	White to pink.

This ranges to Miss Hunt, which has magenta wings, from which it cannot be always distinguished.

(4) *Tinged white.*—White with faint red tinge, especially at base of standard.

As picotee flowers fade the standard becomes suffused with red,[*] and may then be easily mistaken for P. L., though the buds distinguish the two at once, picotee being whitish, while P. L. is red. P. L. and tinged white, on the contrary, grow paler with age. The latter is a much diluted P. L., standing to it much as picotee does to purple.

The following also occur in certain matings :—

(5) *Her Majesty.*—Self-magenta.

(6) *Pink P. L.*—A distinct but rather irregular class in which the prevailing colour is pink, not red.

As regards the valency of these colours the evidence so far indicates that—

(1) May contain or be dominant over all
(2)   ,,   ,,   ,,   (4) and *white.*
(3)   ,,   ,,   ,,   ,,
(4)   ,,   ,,   ,,   white only.

It is noticeable that (2) has not, so far, given (3). This evidence, however, has not been derived from actual F_2 plants of known origin, but from specimens of these types raised from "rogues." It is probably a fair indication, nevertheless.[†]

Where cream has been introduced, all the red types (3), (4), (6) may have cream in addition, and the same is probably true of types (1)

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[*] Such suffusion on fading is common in picotee varieties, *e.g.*, red picotee tulips, and Shirley Poppies.

[†] Fully confirmed in 1904.

(2) and (5) also, though in them cream is not so easily detected.   The type Queen Victoria, spoken of below, may be regarded as (4) with cream added.

Any of the coloured types may have either dark or light axil ; but a genuine white or cream untinged, has a green pedicel, with the axils light (and a pale seed-skin).

Distribution of Pollens in F_2.

When a round pollened parent (P) is used, any F_2 type may have either round or long pollen, but the proportion of long to round individuals differs greatly in different types.

At the present time it is scarcely profitable to suggest gametic formulæ for any of these families.   This can only be attempted when F_3 has been grown, and it is known which are homo- and which hetero-zygous, what types each may contain, etc.   In several cases, however, the F_2 statistics make it almost certain that actual flower-colour-bearing gametes of several types may be produced by F_1 plants even when both parents were white, and there is no doubt that gametes bearing dark axil may be produced by the F_1 from two light-axilled types (probably an illustration of the phenomenon seen by Cuénot in mice).

In several cases the numbers indicate that F_1 plants, though own sisters, do not have precisely the same gametic formulæ.   This is well seen in the case of E. H. round × E. H. long, where the discrepancies between individual F_2 families were too great to be fortuitous.   This fact proves either (1) that there was heterogeneity in the gametes of the original parents, which is very possible; or (2) that the process by which gametic differentiation arises is liable to disturbance; or (3) that irregularities occur in fertilisation.   Possibly all these factors contribute to the result, but the chief cause is probably to be sought in (1) and (2).

To settle these questions a great range of observations will be required, and for the present we must be content to deal with the simpler cases.   The F_2 families are now given in order, first from a purple F_1, then from a P. L. F_1 ($l. = $ long : $r. = $ round).

I. FROM F_1 PURPLE.

(1) *From E. H., Long × E. H., Round.*
(White × White).
(9 families).

651 plants flowered in F_2 from 9 F_1 plants.   Of these, 14 were imperfectly recorded.*   Omitting these, 637 remain.

* Viz., 1 pur. *l.*, 8 pic. *l.*, 3 P. L. *r.*, axils unrecorded ; 1 pur. dk. ax. and 1 white, pollen unrecorded.

Purple	*l.*,	dk. ax.	176		P. L.	*l.*,	dk. ax.	10
		lt. ,,	45				lt. ,,	6
,,	*r.*,	dk. ,,	11		,,	*r.*,	dk. ,,	23
		lt. ,,	2				lt. ,,	17
Picotee	*l.*,	dk. ,,	39		Td. wh.	*l.*,	dk. ,,	2
		lt. ,,	15				lt. ,,	3
,,	*r.*,	dk. ,,	7		,,	*r.*,	dk. ,,	5
		lt. ,,	1				lt. ,,	7

$$\text{White } l. \quad 195$$
$$r. \quad 73$$

Neglecting axils there were 649, with pollens as follows :—

Purple   *l.*   222   or *17·0 : 1*   P. L.   *l.*   16   or *1 : 2·7*
   ,,   *r.*   13   ,,   *r.*   43

Picotee   *l.*   62   or *7·7 : 1*   Td. wh.   *l.*   5   or *1 : 2·4*
   ,,   *r.*   8   ,,   *r.*   12

White   *l.*   195   or *2·7 : 1*
  ,,   *r.*   73

The peculiarities of this distribution are without doubt significant. Taken together there are 500 long, 149 round, or 3·36 : 1 ; and 382 coloured, 269 white, or 1·42 : 1. The last figures indicate some complication.

Since the original parents were both white, the simplest expectation is equality of white and coloured. It is, therefore, almost certain that the excess of coloured is due to production of colour gametes. This, however, cannot have been uniform in all families. An analysis showed that of the 9 F_1, five gave an approach to equality* of white and coloured, and the great excess of coloured was all in four families.

In the purples and picotees *long*-pollened plants are in excess. The facts suggest that of purples about 1 in 16 is round, and of picotees about 1 in 8. But the P. L. and Td. wh. always have *round*-pollened plants in excess, probably as about 3 : 1. *There is, therefore, some coupling of pollen-shape and colours.*

The fundamental question to what extent the colours in F_2 depend on heterozygosis, being as yet unanswered, a full analysis is impossible. Meanwhile, it may be noted that the distribution shows that the gametes cannot be merely whites of two kinds in equal numbers (which might, perhaps, be expected), nor can there be an equality of coloured and white, but the actual composition must be

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* A similar F_2 family was kindly recorded at Reading by Miss Hart-Davis, but as in it the picotees, P. L., and tinged whites were not distinguished from each other, these numbers are only available for the rougher statistics. In it there were 75 coloured long, 12 coloured round, 63 white long, 29 white round, *i.e.*, 92 coloured, 87 white, or approximate equality ; 138 long and 41 round, or 3·3 : 1.

something between these two. It is, moreover, almost certain that one of the coloured gametes is such as to produce picotee and tinged white at least.

$F_1 \times$ *Types.*—A few matings of purple F_1 with the parental types have been made. These, so far, have given the following totals :—

F_1 with E. H., rd., gave 2 purple, 1 P. L., 2 white, all long,
and 1 P. L., 6 white, all round.

F_1 with E. H., long, gave 6 purple, 4 picotee, 3 white, all long. The details will be given when this part of the work is further advanced.

(2) *From Firefly* × *E.H., long.*

(*Red* × *White.*)

Firefly is a red self, axils usually light. It is scarcely if at all distinct from Mars, and the two are not separated here. The purple F_1 is the same as that formed in (I) above, from two whites. Five F_1 gave 299 F_2 plants, 64 white, 235 coloured. To these we can add a family of 140, recorded by Miss Hart-Davies, at Reading, viz., 33 white, 107 coloured ; in all, 97 white, 342 coloured, or 1 : 3·5. Of the coloured, 269 were purple, 73 red, or about 7 : 2.

The Cambridge crop was further subdivided as follows :—

Purple.............................	149	6⎫ 7⎫		149·4
Purple to Black Knight	35	1⎭ ⎬9		24·9
P. L.	29	1⎫ 2⎭		24·9
Miss Hunt to Firefly............	22	1⎭		24·9
White..................	64	3		74·7

The figures in italics show the ratio that the observed statistics suggest, and the expectation on that ratio. The two classes of purple and the two classes of reds cannot be subdivided with precision. The deficiency of whites is perhaps noteworthy.

A remarkable feature is the *almost total disappearance of Firefly*, and the same occurred (p. 93) in F_2 from the P. L. F_1 of Firefly × E. H., round. Special interest also attaches to the appearance of Black Knight. Intensification of a character, in this case colour, in some members of F_2 not rarely follows a cross with a type destitute of that character— in this case albino.

This phenomenon has played a great part in the evolution of domesticated varieties. We may, perhaps, conjecture that the deep claret Cyclamen, "Vulcan," arose in this way, but this peculiar segregation occurs with other classes of characters also. Where F_1 is P. L., no Black Knight or other purple appears in F_2.*

* Unless two rogues are so regarded.

Axil.—The axil of the Firefly used was not recorded, but there is scarcely a doubt it was light. F_1 was dark, and of the coloured plants in F_2, 230 were dark, 110 light, in addition to the 97 white.

(3) *E. H., long* × *Lady Penzance.*

(*White* × *Red-pink, Axils light.*)

Appearance of Sterility.—One F_1 only, purple, with purple (*not* blue) wings: axils dark. In F_2, 227 plants; a remarkable family for the reason that it contained a large proportion of plants in which the male organs, at least, were *sterile.* These anthers were in various states of imperfection, some small, others of fair size, but withered, or " contabescent," to use Darwin's term.

The female organs of these plants may have been normal,* for a few seeds formed on some, presumably fertilised by *Megachile.* Artificial fertilisations all failed, but they were made after the bad weather set in, and the fact therefore proves nothing. One plant recorded early in the season as contabescent, afterwards produced both pollen and seeds, and is therefore counted as fertile. No other doubtful plant was found. The presumption seems to be that only the male organs were affected.†

Among the coloured plants the sterility was almost entirely confined to those which had *light* axils. Of 53 sterile plants, 12 were white, and of the 41 coloured, only two had dark axils. Conversely, of 126 coloured and fertile only five had really light axils (including the plant named above), two had axils faintly coloured, and 48 were white.

Altogether there were 173 fertile. 54 sterile, or 3·25 : 1, a ratio which makes it probable that this sterility is a recessive character transmitted in Mendelian fashion.‡

Altogether there were 60 white, 167 coloured, or 1 : 2·78.

The case is of importance in another way. In this, as in some others, the coloured dark axil to coloured light axil are about 3 : 1, excluding the whites. Therefore it is likely that the whites themselves consist of two classes, those which would have dark axils *if the flowers were coloured,* and the rest. Here we should therefore expect fertile, *i.e.,* " potentially " dark axil whites—to be to the sterile whites, *i.e.,* the

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* A case of contabescent anthers in *Primula sinensis* had female organs perfectly fertile.

† In 1904 artificial fertilisations of such plants succeeded.

‡ The occurrence of extensive and similar sterility was seen in one other family, which gave 44 fertile, 19 sterile, coloured 49, white 14. The incidence of sterility was almost exactly as in the case given above, the coloured plants with *light* axils being almost all sterile. Unfortunately there was some error in the labelling of this family, and as its origin cannot be given with certainty, we are obliged to neglect it.

light axil whites, as 3 : 1.   They are as 4 : 1 (48, and 12) which, though somewhat out, indicates clearly enough the existence of the two expected classes.   The fact will illustrate the probability that the white in F_2 from such a mating as E. H., long × E. H., round, may again consist of two classes (both in longs and rounds), and that different breeding results may be expected from each.   In all likelihood it is to the existence of such differences among albinos that many observed complexities are due.

Contabescent anthers were seen from time to time in many families, though commonly confined to individual flowers.   This sporadic sterility has not been particularly studied.

It is interesting to compare this example of the definite appearance of sterility, at least on the male side, with the familiar occurrence of sterility in cross-breds.   Such a phenomenon has often been supposed to indicate remoteness of kinship, yet here a closely comparable effect occurs in F_2 as the result of a cross between two types which must be very nearly related.

Mr. Gregory in a careful examination of the pollen-genesis, found that the divisions were normal up to the reduction-division, when the chromosomes form shapeless knots and entanglements, failing to divide.[*]

II. From F_1 Painted Lady (Red and White).

(1) *From Blanche Burpee × E. H., Round.*
(*White × White.*)

F_1, ordinary P. L. : axils light, 10 plants.

F_2, 272 plants (of which 41 were raised and recorded at Reading). They were distributed thus :—

Coloured long.	White long.	Coloured round.	White round.
116	83	41	32

This gives 199 long to 73 round, and 157 coloured to 115 white. From these figures it is practically certain that there have been some coloured gametes produced by F_2, but how many and of what kind cannot yet be stated.

The coloured plants were all P. L., ranging to Miss Hunt, except 5 Her Majesty and 3 rogues not reckoned.

In addition to the above, 1 F_1 plant gave at Reading an entirely aberrant result, 53 long, 2 reckoned as round, and 2 uncertain. Until such a result is confirmed we regard it as probably due to some error.

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[*] ‘Roy. Soc. Proc.,’ 1904, vol. 73, p. 91.

(2) *From Lady Penzance* × *E. H., round.*

(*Red-pink, Light Axil* × *White.*)

F₁ ordinary Painted Lady, light axils: 5 plants from 2 pods.

172 F₂ plants from 4 F₁ plants, 46 white, 126 coloured, viz., 1 : 2·7. The coloured plants were chiefly Painted Lady (83) and a certain number of pink Painted Lady (23). There were 17 others distributed among various coloured sorts, including 3 picotees (from 1 plant, ? rogues) which are unexpected. Only 1 plant of Lady Penzance appeared.

Result may be summarized thus :—

P. L.	Other colours.	White.	
83	43	46	

Coloured long.	Coloured round.	White long.	White round.
89	37	36	10
9	*3*	*3*	*1*
96·7	*32·2*	*32·2*	*10.7*

But though grouped thus roughly the result is simple, it must be remembered that undoubtedly several types of colour gametes have arisen, and there are many complexities to be subsequently considered. Lady Penzance is the variety which gave the sterile plants in F₂ from E. H. long (p. 91).

(3) *From Firefly* × *E. H., Round.*

(*Red* × *White.*)

F₁ ordinary P. L. Firefly usually has light axils, but some have dark. In the original parents this point was not noted. Probably one was DR in dark axils, for 4 F₁ from it had dark axils and 2 had light. Axils apart, the families presented no differences, so all are put together.

Of 943 plants 209 were white, 734 coloured, or 1 : 3·51; 205 were round or mixed, 658 long, 1 : 3·2 (rest not done). In this case the "mixed" were comparatively frequent.

The following is a summary of the fully recorded plants :—

Coloured long.	Coloured round.	White long.	White round.
480	144	132	45
9	*3*	*3*	*1*
450	*150*	*150*	*50*

The italic figures show the expectation on the simple hypothesis of 9 : 3 : 3 : 1, and though there is an approach to these numbers it is pretty clear that there is some disturbance not accounted for.

The coloured forms were mostly P. L. (360 long, 122 round), 98 were

Miss Hunt (78 long, 20 round), of which 18 longs were somewhat like the magenta Her Majesty. Only 24 long and 2 round in any way resembled Firefly, and several of these were not very different from ordinary Miss Hunt. Firefly is therefore almost entirely disintegrated.

<center>(4) From Queen Victoria × E. H., Round.</center>
<center>(Tinged Cream, Axils Dark × White.)</center>

F_1, 8 plants P. L. (1 with some magenta in wings): all dark axils.

F_2, 270 plants, namely, 38 white, 23 cream without sap-colour, and 209 with sap-colour, of which 89 were creams. As regards pollen the grouping was as follows:—

<pre>
                                    Uncoloured sap.
                          ┌──────────────┴──────────────┐
    Coloured sap.   Cream.   White.
  ┌──────┴──────┐   ┌─────┴─────┐   ┌─────┴─────┐
  Long.   Round.   Long.   Round.   Long   Round.
  151   58   14   9   35   3
    └────┬────┘   └───┬───┘   └───┬───┘
       209   23   38
        3   └──────────┬──────────┘
      202·5   61
                                         1
                                       67·5
</pre>
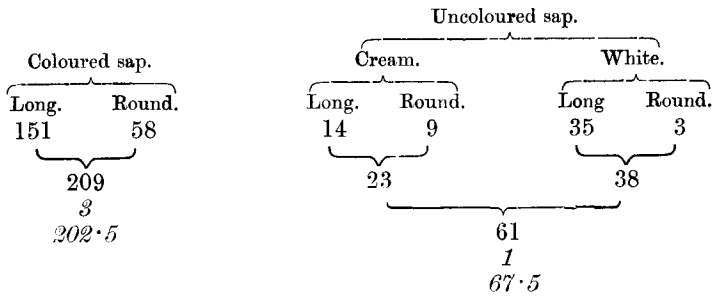
Long to round are, therefore, 200 to 70, 2·8 : 1.

Thus far there is great simplicity in the arrangement, but several underlying complications must be noticed. There is an unaccountable scarcity of round whites. The whites without cream are only 38, to 23 with cream, where 3 : 1 would naturally be expected. Moreover, the whole number of non-cream is 158, cream being 112, showing that a similar proportion, about 1·5, exists in the whole group.

There was a good deal of overlapping between the colours, and all cream types are somewhat difficult to classify strictly, but the following table shows the proportions approximately. Besides P. L. there appeared a pink (quite distinct from the red P. L.), and some of a peculiar pinkish cream resembling " Venus." The numbers suggest that Venus is the pink + cream. Only 7 Queen Victoria came in F_2.

P. L. no cr.		P. L. cr.		pk. P. L.		Near Venus.	
l.	r.	l.	r.	l.	r.	l.	r.
57	28	35	13	31	4	21	13

Q. Vict.		White.		Cream (no tinge).	
l.	r.	l.	r.	l.	r.
7	0	35	3	14	9

(5) *From Venus* × *E. H., Round.*

Venus is pinkish cream of a peculiar shade, axils usually light. The four families which have reached F_2 showed such individual peculiarities (in addition to that described in F_1) that they could only be described at length. Moreover, there is a strong suspicion that the original sample of Venus used contained a mixture. All the E. H., round, used as fathers, were from the same stock of seed, but the number of plants used is not known.

The most aberrant results were seen in the case where F_1 consisted of 3 Miss Hunt (p. 87). Of these, one gave no white and no round in F_2. The second gave 12 white, 36 coloured, but no round. The third gave 37 long, 13 round, but no white. It is scarcely doubtful that some cross-bred was accidentally used as the original father, and that the record is wrong.

The other three families, though each showing peculiarities, have several points in common. Together they gave 283 long, 81 round (3·5 : 1); 267 sap-coloured, 97 uncoloured (12 being cream, 85 white); and the same distribution, 267 non-cream, 97 cream (2·75 : 1). The coloured plants were various reds and pinks, with or without cream, about 50 approaching Venus. In this case it is evident that non-cream behaves as an ordinary dominant to cream.

Behaviour of Extracted Whites.

Investigation of this subject has so far been insufficient, and we have to rely on evidence derived from the use of whites extracted from "rogues." All the facts observed point to the conclusion that extracted whites, whether long or round, give only *white* when bred together. Details will be given when more experiments have been made, but in view of this result, it is conceivable that all the coloured in F_2 from two whites are due to the production of colour-bearing gametes by F_1.

Accidental Cross-Fertilisation : "*Rogues.*"

It is not doubtful that *L. odoratus* is, as a rule, self-fertilised, but the question whether it is ever crossed has been often discussed by Darwin and others. Our experience is that hive-bees and *Bombi* when they visit it, which they do not habitually do, almost always go to the base of the flower, working at the side. The leaf-cutter (*Megachile*), on the contrary, *habitually* visits Sweet Peas, partly for honey, but especially for pollen. This insect settles on the keel, depresses it with the hind legs, and with them scrapes up the pollen off the stigma, plastering it on its abdomen.

This operation obviously gives a risk of crossing.* But as the anthers dehisce before the bud opens, the risk is greatly reduced, for fertilisation is probably begun, if not completed, before the cross can be made. If, however, from any cause the pollen is defective, crossing becomes probable. Such deficiency certainly occurs sometimes. Apart from the want of pollen regularly occurring in certain plants described above, flowers without pollen are from time to time seen on seemingly normal plants. If in these the female parts are perfect, crossing must be expected.

Secondly, careful trials proved that the round pollen of E. H. is not ready to germinate in sugar solution when the flower begins to unfold, an age at which long pollen germinates freely, and it is almost certain, therefore, that these round whites are exceptionally liable to crossing. Our experience has been that "rogues" (purples or P. L.) do occur much more often in round E. H. than in long, and there is a presumption that they are crosses. Mr. Leonard Sutton kindly made inquiry from growers in California, where most of the Sweet Pea seed is raised, but they had no such experience of E. H. It should be remembered, however, that they would be growing many acres of a sort together, and *Megachile* may, perhaps, not occur in that country.

All varieties of Sweet Peas give occasional "rogues," which are often either purples or P. L. On the whole it seems likely that they are all crosses, but the possibility that they are due to more profound causes must be remembered. In our own work F_2 consists partly of plants selfed under cover and partly of seed set exposed. Among the former no unexpected plant has occurred, but among the latter there has been a trifling percentage—about 1 or 2—of plants which can hardly be supposed to be normally produced, e.g., purple in offspring of whites, P. L.'s, or creams.

These were all recorded, but are neglected in this account. A trifling error is doubtless introduced by the presence of an occasional P. L. "rogue" which cannot be recognised as such.

In all crossing it is most important that the pollen should be taken either from an unopened flower or from covered flowers. In fine weather the pollen of open flowers may naturally have been mixed by *Megachile*. This condition latterly has been strictly obeyed, but the necessity was not sufficiently appreciated in the original crosses of 1901.

Summary of Evidence and Discussion of Results in Sweet Peas.

1. The characters "long pollen" and "round pollen" usually behave as ordinary plant characters, being dominant and recessive respec-

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* In some years (e.g., 1903) the minute beetle *Meligethes* abounds in Sweet Pea flowers. It is not known whether it travels from flower to flower, or whether it is capable of crossing. Flowers containing *Meligethes* were not used for fertilisations.

tively. Long grains are occasionally seen on "round" plants, but as yet only one plant bearing round pollen has been found to give any "long" plants on self-fertilisation.

2. White flower-colour is recessive to all sap-colours.

3. The character, coloured plastids, giving a cream-colour, is recessive to absence of colour in the plastids; consequently, cream is recessive to white.

4. Light axil commonly behaves as a simple recessive to dark axil. The figures frequently show that the result 3 dark : 1 light appears in the *coloured* plants alone, whites never having dark axil, thence it might be suggested that there is a correlation or "coupling" between light axil and white. This would pre-suppose an asymmetrical distribution of axil-colours among the gametes. The facts may be more satisfactorily expressed by inverting the conception thus: in order that the dark axil may appear, the allelomorph to which it is potentially due must be introduced into the same zygote as the allelomorph of sap-colour. We should then recognise *two* classes of whites (both long and round), one which contained the dark axil allelomorph and one without it. The very important case of F_2 from Lady Penzance (p. 91), practically proves that this view is correct, for there sterility of the anthers probably indicates the white plants without the dark axil allelomorph. It is not improbable that such a distinction between different whites is a factor, if not the factor, which determines the reversion to purple *or* to Painted Lady. It should not be impossible to test this suggestion experimentally, for the statistics of F_1 from whites in that family should settle the question.

5. In crosses with white, F_1 generally reverts either to the original purple, or to the red bicolour, Painted Lady, which is also known to be a primitive type. The reversion may or may not affect axil-colour. The most striking cases are those in which one or other of these reversions occurs as the result of crossing white, pollen long, with white, pollen round. As yet Painted Lady has only come once as F_1 from the two Hendersons, but the occurrence of purple sometimes and Painted Lady sometimes from Bl. Burpee (white) × E. Henderson, round, proves that two whites, apparently identical, may give either of these reversionary forms—of which one may be called a *whole*, and the other a *half*-reversion.

6. The long E. H. may naturally be supposed to be, in origin at least, an extracted recessive, though, perhaps several generations old. A chance cross on E. H. would give black F_2 seed and this would usually be rejected; but if any of it were sown, white plants might arise and henceforth pass for pure E. H. Such plants would be 3 longs to 1 round.

Nevertheless, the phenomenon of reversion is not much elucidated by this consideration; for the reversion is not to any type with which

a cross is likely to have happened, but to one or other of the two
primitive types. The evidence from Blanche Burpee, also, is unfavour-
able to this supposition, for it also gives either purple or P. L. when
crossed with E. H., round, while × E. H., long, it has so far given whites
only.

7. Though the reversion occurs when the long white is crossed
with the round white, it must be remembered that the fact does
not prove that it is the meeting of these differences in one zygote
which " causes " the reversion. On the contrary, the numbers in F_2
show plainly that there may be *white* heterozygotes of long and round
(proved in 1904), and it is almost certain that it is the meeting of some
other qualitative differences which determines the reversion.

8. In all the cases where F_1 is reversionary, a complex disintegration
and recombination of characters takes place on gameto-genesis, leading
to the formation of new zygotic types. Until F_3 is reached it is
impossible to say which of these are homo- and which hetero-zygous.
It is therefore still uncertain to what extent the coloured types in F_2
owe their colour to the creation of coloured gametes in cases where
both pure types were white.

[Note added December, 1904.

Sowings from the F_2 plants, produced by E. H., long × E. H., round,
showed that at least 8 types of purple F_2 plants exist, each type having
a different F_3. Some purples breed true, proving that there is a real
gametic synthesis of purple. The P. L. plants of F_2 can give no purples,
but may breed true. The picotees may give whites, or tinged whites,
or may breed true, but give no purples or P. L. Tinged whites may
breed true, or may give whites only, in addition. All whites, creams,
and round-pollened F_2 plants, of course, breed true to those characters.
At least four types of colour-gametes may be formed by F_1.

The Black Knights (deep chocolate-purple), which occurred as new
forms in F_2 from Firefly (red) × E. H., long, have also bred true.]

9. After the break-up of the parental characters in F_1 from white
× colour the re-constitution of the gametes may evidently proceed
on different plans in the various cases, but the number of whites (more
strictly plants with uncoloured cell-sap), averages about 1 in 4—the
total being 570 white, 1846 coloured, or 1 : 3·24.

The coloured parent in the cases examined was almost entirely
broken up, and only reappeared occasionally in F_2.

10. When both parents are white and F_1 is coloured, the evidence
shows that after total reversion to purple the half-reversion forms
appear in F_2; but when F_1 is a half-reversion the converse does not
occur. Gametes bearing colour are formed in the first and probably

in the second case also. The number and characters of these are as yet unknown, but it is clear that great fluctuations occur.

11. The "Cupid" (dwarf procumbent), and the "Snapdragon" shape of flower are ordinary Mendelian recessives to the normal.

POULTRY.

(Experiments made by W. BATESON and R. C. PUNNETT.)

The following table shows the results obtained respecting comb characters and extra toes. The numbers prefixed to the experiments enable the reader to trace the relationships in the case of all cross-bred birds. To save space the relationships of the pure-bred birds are not given. No case was seen in which this was found to influence the result. Slight and equivocal indications of a change of "prepotency" due to in-breeding were mentioned in Report I. Fuller experience strongly suggests that these appearances were due to accidental fluctuations.

In the tables, DR is F_1, $\dfrac{DR}{2}$, $\dfrac{DD}{2}$, are, respectively, heterozygous and homozygous dominants in F_2.

$\dfrac{R}{2}$ is extracted recessive in F_2.

The asterisk (*) means that the bird had some special origin, which can be ascertained from the breeding. R*, for instance, may mean R from DR × R, or R appearing in F_1 (see Report I, p. 116), etc. These distinctions must be indicated, but they do not seem to affect the results.

p.p., r.r., mean that the bird was proved to be pure pea or pure rose ; i.r., i.p. and p.s., that it was proved to contain single.

Doub. means the longitudinally *split single*, described later.

r.p. is the rose-pea, or "walnut" comb, whether natural (Malay) or artificial.

The same bird is given as DD in its matings with a single, and as r.r. or p.p., in its matings with one of the dominants.

1902.

Pen.	Exp. No.	♀	Origin (♀)	Cb.	Ft.	Used in exp.	♂	Origin (♂)	Cb.	Ft.	Used in exp.	Nature of mating (Combs)	r.	r.p.	p.	s.	Dubious	Nature of mating (Feet)	e.	½ e.	No e.
1	89	27	5	p.			new Br. L.		s.			DR × R			7	15		DR × R	10		14
	90	91	5	p.			„ Br. L.		„			R* × R		5	12	21		D × R	26		34
2	91	540	73	s.			W. L. 59	I. G.	„	„		r.r. × p.p.				22		R × D	20	2	20
3	92	523	77	r.	„	26	531	Dor.	r.	„	151 and 152	p. × r.r.		18		59					2
4	93	122	Dor.	p.	„	152 and 186	„	„	p.	„											
	94	664	I. G.				„	„													
5	95	586	Br. L.	s.		151 and 176	„	„	„	„		R × D	45					„	45		2
	93	47	W. L.	„			„	„	„	„		„	33					„	34		1
	97	547	„	„			579	36	p.	„	165 and 193	R × DR/2	28		13	21		„	28	2	
5	98	483	„	p.			„	„	„	„		?p.p. × p.s. R/2 × R/2			8		38	R × (DR)/2	18		20
	98a	384	I. G.	s.			464	85	s.	no e.											
6	99	472	40	r.	no e.	179 and 121	„	„	„	„	DR/2 × R/2	11			9		„	11		10
	100	530	38																		

No.				ref.				ref.	Cross			Cross			
101	565	W.L. a.		167					$R \times \dfrac{R}{2}$	8	52	$R \times \dfrac{(DR)}{2}$	30		29
102	493	85 r.		178					$\dfrac{DR}{2} \times \dfrac{R}{2}$	36	5	$\dfrac{DR}{2} \times R$	1	1	10
8 103	440	38 e. s.		157	435	82			$\dfrac{DD}{2} \times R^*$		22	$DR \times R$	25		16
104	317 ♀s.	70 s.		68	608	65		64 to 67	$R^* \times R^*$	4 doubs.	131	$DR \times R$	7		13
9 105	4 ♀s.	74 p.		77, 158, and 117	419	I.G.			$R^* \times R^*$		1	„	58	8	68
10 106	416	I.G. s.		122					i.p. × i.p.	2	5				
107	378	W.L. s.							R × i.p.	9					
108	372	„							„	7	4				
109	114	„							$DD„ \times$ i.p.	9	11				
110	644	I.G. p.		78		„ p.			i.r. × i.p.	25			[644 was (W.L.×I.G.)×I.G.]		
111	262	Dor. r.			558	W.L. s.		145 to 147	$DR \times R$	3	2	$D \times R$	11	1	24
11 112	607	25								23	16	$DR \times R$	15		
113	511	85							$\dfrac{DD}{2} \times R$	36	15	$\dfrac{DR}{2} \times R$	24		13
118a	85	24							$DR \times R$	19	30	$DR \times R$	16	1	20
114	534	25							$DR„ \times R$	25		„	19		36
12 115	453	85	no e.		G. Dor.	e. s.		158 to 161	$\dfrac{DR}{2} \times R$	21	24	$\dfrac{R}{2} \times D$	41	3	2
116	520	85	e.						$\dfrac{R}{2} \times R$		34	$\dfrac{DR}{2} \; ? \times D$	29		3
117	378	W.L.		77, 158, and 107 159					$R \times R$		37	$R \times D$	37		3
118	590	72	r. e.						$DR \times R$	12	18	$? \times D$	31		

1902—*continued.*

Pen. Exp. No.	♀	♀ Origin (numbers refer to expts.)	♀ Cb.	♀ Ft.	♀ Used in exp.	♂	♂ Origin (numbers refer to expts.)	♂ Cb.	♂ Ft.	♂ Used in exp.	Nature of mating	Combs. Offspring r.	r.p.	p.	s.	Dubious.	Nature of mating	Feet. Offspring e.	½ e.	No e.
14 119	450	85	s.	e.		560	38	s.	e.		$\frac{R}{2} \times \frac{R}{2}$				20		$\frac{DR}{2} \times \frac{DR}{2}$	12	1	8
120	452	85	„	„	155	„	„	„	„		„				14		„	11		3
17 121	530	38	r.	no e.	100 and 179	544	„	r.	no e.		$\frac{DR}{2} \times \frac{DD}{2}$			26			$\frac{R}{2} \times \frac{R}{2}$			27
122	372	W. L.	s.		108	„	„	„	„		$R \times \frac{DD}{2}$			39			$R \times \frac{R}{2}$			45
123	683	51	p.			„	„	„	„		$p.s. \times \frac{r.r.}{2}$			36			„			44
123a	514	85	r.	e.		„	„	„	„		$? \times RR$			6			$?\frac{DD}{2} \times \frac{R}{2}$	7		
18 124	{ 61 63	29	„	„	37	667	22a	p.		178 to 180	$r.s. \times p.s.$			68	24		$DR \times R$	43	4	48
125	4 ♀s.	17	p.		34	471	I. G.	„	„		$DR \times DR$		43							
19 126	546	W. L.	s.		174	„	„	„	„		$R \times D$		37		16					
127	463	I. G.	„		143	„	„	„	„				42							
128	529		p.		153	„	„	p.	„		$i.p. \times p.p.$		6			2				

										Cross			Cross			
20 129	573	38	s.	181	552	38	s.	e.		$\frac{R}{2} \times \frac{R}{2}$	43		$\frac{DR}{2} \times \frac{DR}{2}$	39		8
130	151	58	p.	81	,,	,,	,,	,,		$DR \times \frac{R}{2}$	42	42	$R \times \frac{DR}{2}$	44		41
21 131	508	86	s. no e.	146	488	86	,,	min. e.	183	$R^* \times R^*$	36		$\frac{R^*}{2} \times \frac{DR^*}{2}$	12	3	21
132	631	77	e.		,,	,,	,,	,,		,,	56		$DR \times \frac{DR^*}{2}$	41	1	21
133	532	86	,,		,,	,,	,,	,,		,,	41		$\frac{DR}{2} \times \frac{DR^*}{2}$	32	3	9
23 134	234	16	p.	160 and 185	461	85	r.	no e.	184 to 187	$p.s. \times \frac{r.r.}{2}$	} 33		$R \times \frac{(DR)}{2}$	17	1	17
135	609	19	,,	184	,,	,,	,,	,,		,,	} 8		,,	6		5
136	527 W.L.	W.L.	s.		,,	,,	,,	,,		$R \times \frac{DD}{2}$	21		,,	10		13
137	47	15	p.	192	,,	,,	,,	,,	192	$p.s. \times r.r.$	} 12		,,	7		4
24 138	2♀s.	51	s.		608	65	s.	e.		$R^* \times R^*$	60		$DR \times DR$	76	5	32
25 139	3♀s.	75	,,		638	75	r.			$R^* \times DR$	36	4				
27 140	47	W.L.	:		651	63	p.			$R \times DR$	46	6				
141	547	..	:		Eg.♂ doub.	doub.	,,			,,	5					
28 142	2♀s. Egyp. doub.	..									3					
											28 doub.					

1903.

Pen. Exp. No.	Origin (numbers refer to expts.) ♀	Cb.	Ft.	Used in exp.	♂	Origin	Cb.	Ft.	Used in exp.	Nature of mating (Combs.)	r.	r.p.	p.	s.	Dubious	Nature of mating (Feet.)	e.	½ c.	No e.
1 143	463	W.L.	s.	127 and 191	Eg.	W.L.	doub.	no e.		$\dfrac{DR*}{2} \times R$	37 split								
144	4 ♀ s.	Eg.	doub.	c.	"		"	"		"	35		10	12		DR* × R	13	Mixed	9
2 145	876	124	p.	e.	558	W.L.	s.	"	112 to 114										
146	508	86	s.	no e.	"		"	"	131	R* × R	9			27		R* × R	14		29
147	983	103	r.	e.	"	Andal.	"	"		DR* × R			4	16		DR′ × R			11
3 148	79	111	p.	"	"		"	"		"				5		DR × R	4		5
149	498	40	s.		"		"	"		$\dfrac{R}{2} \times R$				25					
150	16	Mal.	r.p.						95 and 176	r.p. × s.									
4 151	586	Br.L.	s.		531	W. Dor.	r.	e.	94 to 97	R × D	18	5	3			R × D	19		
152	664	I.G.	p.		"		"	"	94 and 186	p. × r.r.	? 1	16				"	16	1	
153	529	?	?		915	90	p.	"	128	i.p. × r.r.	1	1							
5 154	939	90	s.		"		"	"	90	R* × DR			30	36			8	1	8
155	452	85	"	"	"		"	"	120	$\dfrac{R}{2} \times DR$			8	7	1	$\dfrac{DR}{2} \times R$			

	984	134	r.		? DR*/2 × DR*/2	51	24		DR* × DR*	40	1	35
6 156	969 134	"	r.	103	DD/2 × DR*/2	5			DR/2 × DR*			2
	833 " 137				R* × R*							
	906 137											
157	440 38	"	"		R × R		63		*Mixed*	3	2	7]
11 157a	4 ? s. 115–	s.								[54		
12 158	378 W.L. 116	"	"	77, 107, and 191		10	10		R × D	10		
							3	1				
159	590 72	r.		118	DR × R	6	4		? × D	10		31
160	609 19	p.		135	"		3		R × D	7		33
				and 185		9	10			18	1	35
13 161	17 Mal. r.p.			172	r.p. × s.	10	4		DR"×DR			
162	881 137	"			r.p. × r.p.	11	13		R × DR	14		11
163	9 W.L.	s.		98	s. × r.p.	17	8		"	13		1
164	956 Br.L.	"		and	"		16		"	30	4	23
165	483 W.L.	"		193	"		16					14
166	548 "	"		101	"	5+	8		"	7		14
166a	710 "	"			"	1	1		"	2		14
15 167	565 "	"			"	16	11		"	34	2	1
168	Br.L.	"			"	2	12		"	7	1	
169	Buff. Legh.	"			"	7	8		"	12		
170	Blk-red Game "	"			"	7	6		"	14		
171	16 Mal. r.p.				r.p. × r.p.	1	1		"	5		
172	881 137 " e.		no e.	162	"	16	12		DR* × DR	73	8	20
	887 135					22	22					
17 173	844 124 "	s.		126	s. × r.p.	1	0		R* × R*			19
174	546 W.L.	s.			"	22	21		R × R*			75

† Includes 1 *double* r.c.

1903—continued.

Pen.	Exp. no.	♀	Origin (♀)	Cb. (♀)	Ft. (♀)	Used in exp. (♀)	♂	Origin (♂)	Cb. (♂)	Ft. (♂)	Used in exp. (♂)	Nature of mating (Combs.)	r.	r.p.	p.	s.	Dubious	Nature of mating (Feet.)	e.	½ e.	No e.
	175	985	134	r.p.	no e.	95	855	137	r.p.	no e.		r.p. × r.p.	9	24	12	4		R* × R*			47
	176	586	Br. L.	s.		and 151	,,	,,	,,	,,		s. × r.p.	6	14	9	11		R × R*			40
	176ia	3	,,	s.			,,	,,	,,	,,		,,	21	11	10	17	1 doub.	,,			60
	176b	853	W. L.	s.	e.	195	,,	,,	,,	,,		,,	17	10	7	8		,,			42
18	177	{760, 849}	105	doub.	no e.	194	799	Br. L.	s.			doub. × s.	50 doub.			20		Mixed	[15	3	52]
19	178	493	85	r.	no e.	102	471	I. G.	p.		126 to 128	r.s. × p.p.		12	16			$\dfrac{R}{2} \times R$			28
	179	530	38	,,	,,	100 and 121	,,	,,	,,	,,		,,		21	14			,,			35
	180	777	100	,,	,,		,,	,,	,,	,,		,,		50	41			$\dfrac{R*}{3} \times R$			92
20	181	573	38	s.	e.	129	867	105	doub.	,,		s. × doub.	9 doub.			23		$\dfrac{DR}{2} \times R$	12		17
	182	849	105	doub.	no e.		,,	,,	,,	,,		,,	27	,,		30		R* × R			57
21	183	938	90	s.			488	86	s.	min. e.	131 to 133	R* × R*				34		$R \times \dfrac{DR*}{2}$	18		18

						R×$\frac{\dot{D}D}{2}$					R×$\frac{(\dot{D}R)}{2}$			
23 184	527 W.L.	"	136	461	85	r. no e. 134 to 137		9			1		4	1	5
185	609 19 p.	135 and 160	"	"	"	p.s.×$\frac{r.r.}{2}$	10 *13	3	2		"	7		16
186	664 I.G. "	94 and 152	"	"	"	p.p.×$\frac{r.r.}{2}$	10				"	4		6
187	649 63 p.		"	"	"	p.s.×$\frac{r.r.}{2}$	10 17				"	10		16
24 188	new 8 W.L. s.		Mal.		r.p.	s.×rp.	1 4 3 2				?.	0	2	8
189	Buff. Legh. "		"		"	"	6 7 8 8							
190	796 90 "		"		"	"	10 8 8 9							
191	{378 463} W.L. "	77, 107, and 127	"		"	"	4 3 1 1							
25 192	3♀s. 75 e.	139	638	75	r. e. 139	R*×DR / s.×doub. 3 doub.	100	110 5			DR×DR R×R*	133	8	72 8
27 193	483 W.L. "	98 and 165	866	105	doub. no e.									8
194	849 105 doub. no e.	177	"	"	"	doub.×doub. "	30 19	16 10			R*×R* DR*×R*	8	2	47 19
195	760 105 e.	177	"	"	"									

DISCUSSION OF RESULTS.

I. *Comb-characters.*

DR birds, r. or p., produced in various ways, bred with R birds (s.c.) of various origins gave 449 D to 469 R. DR × DR gave a total of 211 D to 83 R. These totals* are not very far from the 1 D : 1 R or 3 D : 1 R severally expected. Individually, however, there are some wide departures from these expectations, and it is practically certain that in several cases there was distinct numerical inequality of D and R gametes, as seen in the case of Peas and elsewhere. On the other hand there is no indication that DR individuals themselves are capable of subdivision into classes, and all the figures available point to a monomorphic distribution of the aberrant individuals round the mean case of equality in output of D and R. There is also distinct evidence that the proportional output of D and R may change at different times in the life of the same individual. There is, as yet, no clear case, unfortunately, in which a DR ♂ giving an aberrant number with one s.c. ♀ was simultaneously bred with another s.c. ♀. It is practically certain, nevertheless, that the irregularity did not, in any way, depend on the recessives, for the same bird often gave regular numbers with 1 DR and aberrant numbers with another. In these comments it is assumed that no gametic selection occurs.

"Extraction" had no influence on the proportions, as may be seen from the table.

An example of a ♀ extracted pure
   dominant (rose) occurs in .... Experiment 103 and 157
Another, ditto ....   ,,   113
An example of a ♂ extracted pure
   dominant (rose) occurs in ....   ,,   121—123A
Another, ditto ....   ,,   134—137
Another, ditto ....   ,,   184—187

Very few F_2 p.c. birds have been tested, and, as it happens, no case of pure extracted dominant F_2 has been met with, but ♀ 644 from DR × D was, however, a pure DD (Experiment 110).

Purity of Recessive (Single) Comb.—Singles of various origins, derived in several ways from rose and from pea crosses, when mated together, have never given either rose or pea. In all, such matings have given 800 singles. In one case (Experiment 105) *four specimens of a new form of comb* appeared, together with 131 singles (included in total just given).

This mating was made of 4 F_1 recessive ♀'s from a "non-Mendelian"

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* They include chicks kindly bred by Mr. Assheton (not given in the table) from birds raised in Experiment 33, as follows : DR × R, 16 r. 6 s. DR × DR, 36 r., 16 s.

or mixed F_1 from rose-comb, bred with a similar F_1 recessive ♂ from pea-comb. In the four mutational birds the combs were imperfectly split posteriorly (see p. 113). These must be regarded as *illustrations of* that twinning or duplicity which has been observed in so many median organs. A similar case of posterior duplicity in a rose-comb* came in Experiment 166. Such double "single" combs are not very rare in fowls, but are not found in any recognised breed, the Houdan "leaf" comb being, in some ways, distinct.

Relation of Rose to Pea Comb.—In 1902 this inquiry was begun by crossing DR rose-combs with DR pea-combs (Experiment 124). These birds may respectively be called r.s. and p.s. They gave, as was expected, four types of comb, viz., s.s. singles, r.s. roses, p.s. peas, and finally r.p. combs, the latter being a type not before seen in the course of the work.† It is characteristic of their comb that it is wide like a rose, though much less papillose and with no posterior point or "pike"; but the most singular feature of it is the *presence of small bristles or minute feathers on the posterior third.* Often these feathers form a narrow band crossing the comb from side to side in front of the posterior third. Sometimes, however, there is no definite band, but the feathers are either generally distributed over the back or on the posterior sides of the comb. No such bristles or feathers ever occur on singles, roses, or peas. Their existence raises a morphological problem of some interest, but this cannot be treated as yet. In front of the feathered part of the comb is often a well-marked transverse groove. On approaching maturity the part anterior to the groove generally widens out (especially in males) and becomes corrugated, the posterior part remaining narrow and flat.

This peculiar comb is the structure known as the "walnut" comb, proper to Malays and to no other breed of fowls. As stated, it was here first formed indirectly by crossing r.s. × p.s. and it has since been made directly by breeding both pure r. and extracted F_2 r.r. with pure p. Sometimes it is distinctly larger than in pure Malays, but the artificial walnut comb is often indistinguishable from the pure Malay type.

The results from the "artificial" walnut combs were as follows. Three such r.p. ♂'s were bred through the season of 1903 with various s.c. birds (Experiments 163—170, 174, 176, 176A—B), and gave—

	r.p	r.	p.	s.
	139	142	112	141 + 2 doubtful.
Simple expectation ...	*133*	*133*	*133*	*133*

* In 1904 a case of partial duplicity in a pea-comb has occurred. A split s.c. like the mutational form occurred also in Experiment 176A.

† The features of the 3 forms of dominant were not satisfactorily distinguished in the earlier chicks from Experiment 124. They are therefore given collectively as 68 r., rp., p. and 24 s.

Four " artificial " r.p. ♀'s with similar ♂'s gave (Experiments 162,
172 and 173, 175)—

	r.p.	r.	p.	s.
	95	26	38	16
Simple expectation.........	*99*	*33*	*33*	*11*

We have, therefore, in the first case a fair approach to equality, and
in the second, figures not very far removed from 9 : 3 : 3 : 1. It is,
therefore, clear that the artificial r.p. birds were giving off approximately
equal numbers of gametes, r.p., r., p., s. The individual results show
some irregularities, especially 176B, which gave 10, 17, 7, 8, but the
average result is unmistakable.

These facts show two points of interest, first, that some gametes are
bearing r.p. *unsegregated ;* secondly, that s. is evidently present though
it is presumed that in the parental gametes of the r.s. and p.s. birds
the s. elements had been eliminated by segregation.

At first sight it seemed that the presence of s. indicated a failure of
segregation. Further experiment, however, has shown that r.p. birds
raised from *pure* r. and *pure* p. birds are in exactly the same condition
as those raised from r.s. × p.s. This latter observation, which will be
described with the work of 1904, proves that s. gametes may in some
way be formed by resolution of the product of the cross r. × p.

The next step was to investigate the properties of the true Malay
walnut, or natural r.p. comb, and especially to determine whether it
could be resolved into r. and p. Mr. Edgar Branford, of Woodbridge,
who has a long experience of the breed, was kind enough to give much
help in this matter, and further assistance was also received from
Mr. Wootten, a breeder of White Malays. It appears that Malays
bred *inter se* sometimes produce true peas as well as the normal walnut.
Occasionally in certain strains peas come often, but generally speaking
they are uncommon. Whether pure Malays ever throw actual roses or
singles is not quite certain, but if they do, these occurrences must be
excessively rare.

A pure black-red Malay ♂ and two pullets were obtained from
Mr. Branford. The ♂ had been used by him in 1902 with pure hens,
and certainly then gave no rose or single, though possibly occasional peas.

The Malay ♂ was bred with 5 s.c. hens of various origins and gave
(Experiments 188–191).

r.p.	r.	p.	s.
22	21	20	20

the equality of the four types of gamete being evident. The Malay
hens are notoriously bad layers and only gave small totals. Each was
bred with a s.c. cock and the result was

r.p.	p.
14	13, no true r.c. or s.c.

Of the pea-combs, 3 were of the high, intermediate type, inclining to s.c., but none was a true s.c. Of the r.p. group, 1 on hatching was regarded as an irregular rose, but it developed into a fairly ordinary type of walnut comb, though having two rather prominent knobs behind.

In Experiment 171 a Malay ♀ is recorded as giving × artificial r.p. ♂, 3 r.p., 1 r, 1 p., 1 s. The r. was irregular, and the s. was very low. In the light of later experience, it is perhaps possible that both were wrongly classified. Both were dead in the shell, and at that date the distinctions were not familiar to us.

In these results there are still certain points obscure. The "artificial" r.p. birds are giving off the four types of gamete. Therefore there must be five types of r.p. comb possible, namely r. × p., r.p. × r.p., r.p. × r., r.p. × p., r.p. × s.; but owing to the fact stated above, that s. may be created afresh by at least one of the combinations into which it does not directly enter, the subsequent analysis becomes very complex.

A further difficulty is suggested by the behaviour of the natural r.p. Though the ♂ r.p. with s. ♀'s gave the four forms in equal numbers, it is practically certain that in Malay breeding, if r.c. and s.c. are ever seen, they are excessive rarities ; whereas if there were gametic equality on both sides, 3 in 16 should be r.c., and 1 in 16 should be s.c. For some time the conclusion seemed irresistible that the appearance of these forms on crossing with s. must be due to some imperfection of fertilisation, leading to a partial monolepsis,* and this account was provisionally adopted. At that time the difference between reciprocal crosses was not fully appreciated ; but after a critical study of their material it is more likely that the true explanation lies in a difference of constitution between the ♂'s and ♀'s.

It is possible that only ♂'s with walnut combs produce all four kinds of gamete, r.p., r., p., s., other males giving only r.p., or r.p. and p., or r.p. and r. ; while r.p. ♀'s give either r.p. and p., or r.p. only. If this conclusion is substantiated, it will be possible to give a complete account of this curious case.

[Note added December, 1904.

Extensive inquiry among Malay breeders has now made it practically certain that real rose or single combs do not occur among Malays when bred pure. The problem created by their absence must still be regarded as unsolved.

We have examined the combs of a great number of Malays in the best strains of the West of England. The males evidently present two

* See Report I, p. 155.

fairly distinct types: (1) Saddle-shaped, more or less papillose in front; (2) a narrower comb, in which the " working " is in the form of corrugations. Probably it is only the former (1) which gives off rose; but as such birds are freely used for breeding, the entire absence of rose-combed chicks cannot be attributed to selection of males of type (2) exclusively.

The work of 1904 has shown that 2 ordinary r.p. Malay ♂'s were r.p., p., and a Malay Bantam ♂ was r.p., r. Two ordinary r.p. Malay ♀'s proved to be r.p., r.p., and one proved to be r.p. p. One such ♀, however, is recorded as having given (× s.c. ♂), 1 r.c., and 2 s.c. chicks, besides 1 p.c. and 1 r.p. On the hypothesis suggested in the text, this should be impossible. Unfortunately there is an element of uncertainty in these particular records, and until this ♀ has been tested again the question must be left undecided. Two Malay Bantam ♀'s proved to be r.p. r.p.]

Experiment 156 proves that r. birds derived from r.s. and p.s. carry only r. (or r. and s.), p. having been excluded. The work of 1904 similarly has proved that s. from s. × r.p., whether natural or artificial, is also pure ; and that r. or p. from combinations of any r.p. × s. are similarly free from p. or from r. respectively.

Finally, by the mating of two r.p. birds (bred from r.s. × p.s.), at least one homozygous r.p. has been produced, proving that here an actual synthesis of r. with p. has been effected. The facts may be set out thus
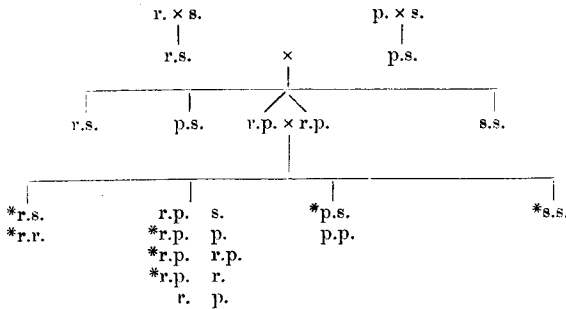
The asterisk (*) marks the combinations already met with experimentally.

Mixed F_1 from $R \times S$ and $P \times S$.

The meaning of these mixtures was discussed in Report I, p. 116, and the applicability of two hypotheses was considered. The further course of the inquiry has all tended to disprove the second hypothesis, which supposed a failure of dominance in the R birds of F_1. Such birds and their posterity have behaved as pure R, except for the production of the four split-comb birds in Experiment 105.

Further evidence on this question is provided by Experiments 126–7, in which 471 ♂ was proved pure p. though he came from 17 ♀ × Gr. ♂ which *both* gave mixed F_1 (Experiments 49–51 and 46–8). Therefore, whatever the "impure" character may be, a pure dominant may be segregrated from it.

Next there is the important result seen in Experiment 111. Dork. ♀, 262, was raised from "impure" parents K ♀ × K ♂ (Report I, p. 114). She was proved "impure" in Experiment 78, and in Experiment 111 by I. G., 419 ♂ (proved "impure" in Experiments 64–7 and 107–9), she gave 5 r., 2 r.p., 3 p., 2 s. Singles are thus produced from impure rose × impure pea, though each of these can have had no s.c. ancestor for an indefinite number of generations.

Taken in connection with the fact that s.c. gametes may be formed by F_1 from pure r. × pure p., it is difficult to resist the conclusion that an impure r. or p. is really a bird in the condition of one of de Vries' "*Halb-rassen*" and is giving off an unknown proportion of a second gamete, here s.c. Such a conclusion harmonizes well with the fact given in Report I, p. 116, *Note*, that a pure strain of r.c. occasionally throws a s.c. bird, and that when fresh blood is introduced, the proportion of s.c.'s greatly increases. These facts have perhaps a bearing on the behaviour of the Malay r.p. just described, but the exact relation of the two sets of phenomena is not yet clear.

The attempt to increase the proportion of s.c. in mixed F_1 by inbreeding the s.c. parent has failed in the case of White Legh., owing to the strain becoming delicate and dying out. The Br. Legh. strain, though persistently inbred, has developed no such delicacy, but no result of the kind has been witnessed in the case of combs (all the Br. L. birds in the Tables not marked "new" belong to the inbred strain). In the case of the foot-character it is just possible that there is a positive effect of this nature.

SPLIT S.C.

The behaviour of these mutational forms has been imperfectly studied, and thus far is quite anomalous (see Experiments 181, 182, 193 to 195). In 182 we have split × split giving approximate equality, 27 split to 30 s., but the same split ♀ × another split ♂ gave 30 split to 16 s.c. It is probable that the dominance of the split comb is very irregular. To investigate the behaviour of an established split comb we received through the great kindness of Mr. Stanley Flower, specimens of split-combed fowls from Cairo, mentioned in the writings of Mr. F. Finn. The fowls were common bazaar birds and have presumably not been selectively mated. The comb is not unlike that of our own splits, but the separation was greatest *posteriorly* instead of anteriorly. This proved to be a distinct dominant over s.c. and nothing novel has yet

been obtained respecting it. The experiments are being continued to test certain questions as to cresting and will be given in detail hereafter.

II. *Extra Toes.*

As was described in Rep. I (Experiment 88 and pp. 119 and 129), the normal foot, though commonly recessive, may sometimes *dominate* over the extra-toe character, and this heterozygote may give equality when bred with recessives, just as if it were an ordinary DR. The investigation of subsequent generations, therefore, becomes very complex, though the gametic segregation of the characters can be demonstrated with fair certainty. Having these difficulties in view, the experiments were arranged primarily with regard to the more amenable problems of the combs, the feet being studied only incidentally.

From the fact that the no-e.t. character may dominate, we must expect that on an average the departures from simple Mendelian expectation will be in the direction of excess of no-e.t. birds, and this is the case, various forms of DR × R giving in all

	Both e.	1 e.	no e.
1902	399	18	456
1903	240	12	307
	639	30	763

Adding the 30 cases of 1 e.t., there were, therefore, only 669 e.t. birds to 763 no e.t. Similarly, various forms of DR × DR gave in all 412 e.t., 27 halves, 212 no e.t.; the cases of 2 or 1 e.t. together give only 439 to 212 no e.t., or 2·07 : 1.

There can be no doubt that the excess of recessives is due to the occasional dominance of the no e.t. character.

One ♂, 544, and one ♀, 530, without e.t., from Experiment 38 (unmixed F₁ group), and one ♀, 493, from Experiment 85 (mixed F₁ group) were proved to be pure recessives in that character. A similar ♀ (from ♀ 493 × no-e.t. ♂ 464, which was proved to be heterozygous in that character) was similarly proved to be pure. Collectively, these recessives gave 271 birds without trace of e.t. (Experiments 121 to 123, 178 to 180). The ♀, 508, from Experiment 86 was similarly a pure recessive (Experiments 146 and 131).

In addition to ♂ 305 (Rep. I, p. 118), two other birds (464, 461) without e.t. have proved themselves to be ordinary heterozygotes in respect of foot-character (Experiments 99 to 102, 134 to 137, 184 to 187). In one case also a ♂, 488, which had, on hatching, been counted as no e.t., was afterwards found to have each hallux slightly thickened, with a *minute extra nail* pressed to the normal on one foot. This bird also behaved like an ordinary DR (Experiments 131 to 133).

In the case of the ♂, 461, just mentioned, the output of e.t. and no-e.t. gametes (or conceivably the dominance) differed greatly in the 2 years. In 1902, with various no-e.t. ♀'s, he gave (Experiments 134 to 137) 40 e.t., 1 half, 39 no e.t., but in 1903 (Experiments 184 to 187) he gave 25 e.t., 1 half, 43 no e.t., a striking excess of recessives. Similar changes at different periods have been seen in other cases, though less pronounced.

We are led to the conclusion that if an individual be heterozygous, there is no direct relation between the somatic character it presents and the gametic output. Nevertheless, it would be expected that since a no-e.t. "DR" shows dominance of that character, similar aberration of dominance might appear in its offspring. Thus far, however, only a slight indication of such a result has been found. Taking, for instance, the various cases of DR × R, the totals from the mixed F_1 group gave 335 e.t. or 1 e.t., to 339 no e.t. ; and from the unmixed F_1 group 334 e.t. or 1 e.t., to 364 no e.t. The difference of about 10 per cent. may well be due to this cause, but it is scarcely emphatic enough to make the point clear in view of the fact that the departures from equality occurred in both groups in both directions without any striking disparity.

Amongst the various forms of mating indicated by DR × R, the cases were distributed as follows :—

		e.t.	½ e.	no e.
(1)	DR × R	336	21	439
(2)	$\dfrac{(DR)}{2}$ × R.........	125	3	151
(3)	$\dfrac{DR}{2}$ × R	113	1	95
(4)	R × DR*	18	—	18
(5)	$\dfrac{R^*}{2}$ × $\dfrac{DR^*}{2}$	12	3	21
(6)	DR* × R*	35	2	39
		639	30	763

Here DR is the ordinary F_1. $\dfrac{(DR)}{2}$ indicates F_2 birds with no e.t., but heterozygous. $\dfrac{DR}{2}$ is the heterozygous e.t. form in F_2. DR* a dominant heterozygote otherwise produced (see tables). R the pure-bred no e.t. R* a pure no e.t., otherwise produced.

There is an obvious suggestion that the different results in (2) and (3) may be due to the dominance of the no e.t. in (2), but the general run of the results is too irregular to warrant much confidence on the point, especially in view of the equality (77, 1, 78) given in Experi-

ment 88 by an F_1 no-e.t. bird. Similarly, the material is too hetero-geneous to indicate the average ratio of dominant no-e.t. gametes to recessive no e.t., though, presumably, there is an underlying regularity here also.

Among dominants in F_2, 3 ♂'s and 6 ♀'s proved to be DR and none DD,[*] but of these only 3 ♀'s had the toes sufficiently well-marked to be possible DD, having been selected for comb characters. One or more ♀'s in Experiment 157A (from DR × D) were presumably DD, but they were not separately tested.

It should be noticed that the Silver-grey Dorking ♂ in Pen 12, 1902, though of the purest strain attainable, threw 8 no e.t. in 149 chicks. In 1903, however, the same ♂ gave 45 chicks, all e.t. (for hens see table). From our experience and from such information as has been received from breeders, an occasional no-e.t. chick is given off from time to time by the purest strains, and must be regarded as comparable with the " *semi-latent* " characters of de Vries.[†] It need scarcely be said that no parent without full-sized extra toes can have been used in such a strain for an indefinite number of generations.

An anomalous case also occurred (Experiment 188) in which a Wh. Legh. ♀ × Malay ♂ gave 2 chicks (out of 10), having 1 e.t. each. The ♀ was given to me by Mr. Lister-Kay, and belonged to his famous strain. It seems likely that this must be regarded as an original variation.

Slight feathering on the shanks has also from time to time been seen in birds from the Dorking crosses, but this has not been followed up.

III. *Colour.*

The colour phenomena are in several respects complex, though the general behaviour is fairly simple. As stated in Rep. I, F_2 from white (Leghorn or Dorking) × brown (Ind. Game or Br. Legh.) consists of about 3 light : 1 dark. The *light* class is made up of pure white birds, white birds with "ticks" (barred or plain), and from Br. Legh. × Wh. Dork.—some pile, viz., yellow or chestnut and white. No true pile has yet come from Ind. Game and White, though ♂'s in F_2 (and F_1) often have red or yellow splashes as well as dark ticks.

The *dark* class consists of brown birds, somewhat like the parent, cuckoos, and blacks. Each kind may have an irregular amount of white. Three ♀'s (F_2 from Br. Legh. × Wh. Dork.) have appeared of the brown type, *spangled* more or less regularly with white, having the coloration of Spangled Old English Game. From the same mating also a few true Silver-grey or Duckwing hens came in F_2, but hitherto no ♂.

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[*] Unless 514 (Experiment 123A) be such a bird, she gave only 7 chicks, all e.t.

[†] (Mut., I, p. 424; compare case of s.c. from r.c., p. 113).

Some, at least, of these F_2 types must be regarded as resolved forms. Their properties are being gradually worked out, and for the present a detailed account is deferred.

The following points have been made out since the last Report :—

The unticked birds are sometimes in great excess over the ticked.

The ratio of light to dark is very constantly about 3 : 1, the present totals (1903), counting pile as light, being 537 : 173, or, adding Experiment 130, p. 103, 603 : 187. DR × white gives, with great constancy, about 1 : 1, the totals being 210 light : 215 dark.

A pure white F_2 ♀ × similar ♂ gave (Experiment 131) 36 light without ticks ; and with a pure white ♂ (Experiment 146) she gave 27 without ticks.

One (if not both) of the F_2 whites was, therefore, pure DD in white.

All dark birds in F_2 bred together, or with other dark birds, gave exclusively dark birds.

Two Silver-grey hens, mentioned above, were bred with a pure Duck-wing or Silver-grey Dorking, no such ♂ having come in F_2. They gave (F_3) 78 Silver-grey chicks. Of these, again, 4 ♀'s, bred with own brother, gave, in 1903, 63 Silver-grey chicks. Most of these were typical Silver-greys, but a few had white splashes or were a little light in colour. The original F_2 Silver-greys must, therefore, have been, as anticipated, homozygous in respect of that colour.*

There can be little doubt that the spangled type is similarly homozygous.

Dominance of White and Exceptional Cases.

Among the many hundreds bred from a pure white parent with coloured or DR birds, only two are recorded as having come dark. Of these, one was probably due to a mistake in marking the egg. The second *may* have been referable to the same cause, but there is no definite reason for doubt in this case. For the present, both cases should be counted as exceptions.

The subsequent breeding has proved that each of the 3 Cr., White Dorking birds (Rep. I, p. 93), were impure in whiteness, being in all probability DR of white over some colour.† The K. White Dorkings, however, were pure.

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* In F_4 one pied bird, White and Silver-grey, has occurred. Whether such birds ever come in pure Silver-grey strains we do not know.

In F_2, from Brown Leghorn × White Leghorn, two Silver-greys have now come, proving therefore that such birds in Brown Legh. × Wh. Dorking are not simply attributable to Grey Dorking ancestry in the case of White Dorking.

† Later experiments have shown that a pure race of *white with minute ticks*, usually one or two, when crossed with colour gives *dark* F_1. Hence the Cr. birds probably were heterozygotes of white × ticked white. February, 1905.

As regards the Cr. birds, the proof was as follows:—

Cr. 121 ♀ put up a buff feather in each wing on the second moult. By a Brown Leghorn ♂, she gave 4 dark, 3 with buff down (not reared), 1 pile, 10 light, 2 recorded as doubtfully light. Two of the dark and the pile were the only ones reared.

Cr. 122 ♀ was never seen to show a coloured feather. Nevertheless, by an Ind. Game ♂ (Experiment 93) she gave 2 dark, 3 light. These were the "exceptions" mentioned in Rep. I, p. 141, *Note*.

Cr. ♂ never showed a coloured feather. He was never bred with a coloured hen directly, but as stated (Rep. I, Experiment 38), six— then unexpected—dark chicks came in 102 F_2 by him out of White Leghorn ♀. These F_2 were from 3 ♀'s.

There is, therefore, no doubt that all three birds were heterozygous in colour, and the ♂ in Experiment 38 with one or more of the 3 F_1 hens was similarly heterozygous. Consequently, the darks from 122 ♀ should not have been counted as exceptional. Unfortunately, only one mating between the three Cr. birds was made, viz., 122 ♀ × Cr. ♂, producing 6 chicks. None were dark, but 2 only were reared, both white, without ticks, so far as is known.

One of the F_2 just named was used as ♂ with DR ♀ 151 (see Experiment 81), and gave (Experiment 130) 66 light, 14 dark, where the simple expectation is 60 : 20.

The conclusion from these facts is that a bird may be heterozygous though no coloured feather is to be found, and the various supposed exceptions disappear. A similar explanation, no doubt, would hold in respect of the at-first-sight anomalous result in Experiment 40.

The excess of unticked birds over ticked in F_2 from brown × white obviously points to the same conclusion.

Heterozygous Nature of Blue in Andalusians.

In the last Report (p. 131) we stated that the Andalusian colour is probably heterozygous, inasmuch as it is alleged never to breed true. By the courtesy of Mrs. Blacket Gill, one of the leading fanciers of this breed, the information was given that up to the date of inquiry in 1902, her birds had given 17 white-splashed, 36 blues, 22 blacks. Birds were subsequently obtained from her as follows: a white-splashed ♀, a black ♀, a blue ♂.

By the blue ♂ the white ♀ gave 34 blue, 20 white-splashed, and the black ♀ gave 27 blue, 19 black. In each case the result is qualitatively what would be expected if the blue is a heterozygote of black × splashed white; but whether the departure from equality indicates that some gametes bear the unsegregated blue, or may merely be taken as individual irregularities, cannot yet be stated.

The same blue cock was bred with a black hen from Experiment 40

(in which the dark birds were unexpected), F₂, from White Wyandotte × Wh. Legh., giving as offspring 10 black, 15 slaty black to bluish. Hence, therefore, it is evident that the black ♀ was a homozygous black. The 10 blacks are the result of the union of the black gametes from the Andalusian ♂ with those of the ♀, and the 15 slaty resulted from the meeting of the black of the hen with the white-splashed from the Andalusian.

NOTES ON THE PROGRESS OF MENDELIAN STUDIES.

During the 2 years that have passed since the publication of Report I the growth of Mendelian literature has been so rapid that it is impossible to give any adequate summary here. We can only specify the more significant results of recent work.

New Mendelian Cases.—The valuable memoir of Coutagne* on heredity in the silkworm, written without a knowledge of Mendel, shows that several of the characters studied have a Mendelian inheritance. Of the larval characters both black colour and transverse striping are evidently dominants to the normal whitish colour. In most of the cases white silk is dominant to yellow silk, one race presenting an exception to this rule. An artificial race of dark moths also showed a partial dominance (with some blending) over the normal light colour. This dark race was made by the use of two dark males which seem to have arisen as a sport. These were bred (1889) with the brownest females which could be found in a normal race, and from the offspring a dark race was produced by selection in about 5 years.

In the case of each of these characters the gametic segregation was evidently complete or almost complete, and the purity of the recessives at least was established in numerous experiments. Apart from cases of mixture of DR and DD, some irregularities are noticeable, but the general course of the inheritance is quite clear. Three larvæ were seen which were black on one side and white on the other, an important phenomenon occasionally seen in discontinuous variations of Lepidoptera, comparable, no doubt, with gynandromorphism.

In contrast with Mendelian inheritance of these discontinuous characters, the character, called by Coutagne, *richesse de soie* shows, to all appearances, continuous variation and a non-Mendelian inheritance, not undergoing any sharp gametic segregation, and being capable of intensification by gradual selection. It is likely that this quality depends on numerous factors.†

* ' L'hérédité chez les Vers à Soie. Bull. Sci., Fr. and Belg.,' 1902, vol. 37.

† Coutagne's memoir contains very many facts of great importance which cannot be referred to here. The attention of students of evolution is also called to the same author's "Recherches sur le Polymorphisme des Mollusques de France," 'Soc. Agric. Sc. Ind. de Lyon, 1895,' a treatise of altogether exceptional value on the interrelations of varieties and the significance of locality.

A peculiar case of recessive variety, generally female, has been pointed out by Doncaster* in the case of *Abraxas grossulariata* var. *lacticolor* on the experimental evidence obtained by G. H. Raynor.

From the records of former experimenters there could be little doubt that the long-styled form in *Primula* is recessive to the short-styled, and experiments in progress (begun by W. Bateson in conjunction with R. P. Gregory) have confirmed this view. It is, however, doubtful as yet whether any *pure* short-styled plants exist, F_1 being a mixture of longs and shorts, of which the longs breed true. Whether the mixture is due to heterozygosis in the thrums used, or to a perpetual production of long-style gametes as a *Halb-rasse* by the short-styled plants, is not quite certain.† Horticulturists have decreed that the pin-eye is the correct form of *P. sinensis*, but all Auriculas and Polyanthuses must be thrums. Owing to the recessive nature of the long style, the short style has been totally eliminated from most English collections of *sinensis*, and now is only to be procured with difficulty. But there is apparently no *Auricula* or *Polyanthus* which breeds true to thrum eye, though such strains would certainly be in demand. Hence we are led to infer that the persistent appearance of the pin-eye is due to a perpetual output of recessive gametes by the thrums (see later paragraph on Sex, p. 128). The homostyled type which is also characterised by a great extension of the yellow centre or eye is recessive to both long and short style. For continued opportunities of studying the breeding of *P. sinensis* at Reading we are greatly indebted to Messrs. Sutton & Sons. A detailed account of these observations will be prepared later. Further observation has confirmed the statement in Report I that the fern-leaved type is recessive to the palm-leaved, segregating from it perfectly, with very rare exceptions. The green stem is similarly recessive to reddish stem, but the deep red stem is also recessive to the reddish. The curious form known as "ivy-leaved" is also a recessive to palmate leaf, segregating perfectly from it. *Double* flowers constitute a recessive character, as in Stocks (see p. 33).

As regards colour inheritance there are some complications not fully explored. Pure white on a green stem is almost certainly recessive to all colours, but the white strains on coloured stems may sometimes give white F_1, even when the other parent is a fully coloured type. On this point the evidence is not altogether consistent, and more inquiry is needed. It is possible that the presence or absence of colour in the stem affects the result.

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* 'Ent. Rec.,' 1903, vol. 15, p. 142.

† From the later evidence there is little doubt that pure short-styled plants exist. February, 1905.

Blue may be almost entirely broken up on crossing, rarely reappearing in F₂, probably as 1 in 16.

The case of certain pink-flaked and mauve-flaked types is of more practical importance. The pink is recessive and breeds true at once. The mauves, on the other hand, may throw pinks. Savings from individual plants showed that some are pure or DD mauves and others are heterozygotes of mauve and pink. A pure strain of mauves may be immediately obtained by saving from a homozygous mauve.

The work of Biffen has greatly extended the application of Mendelian principles in the case of wheat (see 'Jour. Agric. Sci.,' I).

Castle* has found the rough, "rosetted" or "Abyssian" condition of the coat in guinea-pigs dominant over the normal smooth coat, and that the Angora coat is recessive to the normal in both rabbits and guinea-pigs.

We are indebted to Mrs. Staples-Browne, of Bampton, for a game Bantam cock and two hens bred from ♀ brown-red × ♂ black-red, both believed to be pure. All three are very near the brown-red in colour. The two hens have the purple or "gipsy" face of the brown-red, almost, if not quite as well developed as pure brown-reds. The cock's face, though showing a tinge of purple, is more nearly the ordinary red. This dominance of so novel a character as brown-red and purple face is somewhat exceptional. In their down the F₁ chicks are said to have been very dark, thus also resembling the brown breasted.

The paper just published by A. Lang contains evidence, which as the author states, goes far to show that the well-known discontinuity between the banded and bandless *Helix hortensis* depends on Mendelian segregation.† The bandless character is dominant.

The poultry cases here related illustrate the simultaneous segregation of *four* allelomorphic comb-characters.

Biffen (*loc. cit.*) has found *primâ facie* evidence for the belief that in wheat, power of resisting rust is a recessive character. The remarkable case referred to by Orton‡ in cotton seems rather to indicate that resistance to the wilt disease is a dominant character.

Reversion.—When F₁ presents a character distinct from that of either parent, it is not rarely reversionary. In addition to the cases hitherto noticed, an interesting one was exhibited by Hurst at the Southport Meeting of the British Association, white Angora rabbit × Belgian hare giving F₁ grey like a wild rabbit. These experiments are in progress and will be published hereafter.

The cases given above respecting Sweet Peas are of a somewhat distinct type, as in them two entirely white or "albino" plants gave

* 'Science,' N.S., vol. 18, 1903.
† 'Festsch. z. Siebzigsten Geburtstage v. E. Haeckel,' 1904, pp. 482, 503.
‡ 'U.S. Dep. of Agric. Bull.,' No. 27, 1900.

a coloured reversion, which in some families was complete, to the wild purple type, and in other families took the form of " half-reversion " to the red bicolour " Painted Lady " type. This is a well-known and ancient type of the cultivated flower, said to occur wild in Sicily.

The appearance of hoary F_1 as the result of crossing certain glabrous Stocks is one of the few examples of reversion in a "structural" character as distinguished from colour (see later, p. 124).

Special interest attaches to the behaviour of yellow flowers in their crosses. It is to be remembered that yellow may be due to various physiological types of pigmentation, and the evidence is complicated by the frequent occurrence of reversion in F_1. Cream Stocks and white for instance, give purple F_1. Cream Sweet Peas may do the same. Correns* found that in *Mirabilis jalapa* yellow and white always gives red. The evidence from generations of Sweet Peas and Stocks later than F_2 plainly shows that there may also be simple dominance of *white*, viz., no *coloured* plastids, over cream, or coloured plastids. Correns states that in his *Mirabilis* F_1 there was no trace of yellow (except a spot in a mosaic). Mr. Lynch has called our attention to the case of *Begonia Weltonensis* (pink), from *B. Sutherlandi* (orange), and *B. Dregei* (white), which is perhaps comparable. Before the relations of these dissimilar illustrations can be compared, the nature of the yellow in each case must be determined. In the Begonia case it is not impossible that the pink of the hybrid is due to dominance of the sap-colour from *Sutherlandi* while its chromoplastic yellow is recessive.

Monolepsis.—In considering this subject (Report I, p. 155), we were not aware that a suggestion very similar to our own had been proposed by Giard.† Further information respecting Orchid cases was given by Hurst.‡ In connection with Millardet's original observation on the Strawberry, a record of Andrew Knight§ respecting a case in the Strawberry, possibly of a similar nature, is interesting. Further information as to the phenomenon is greatly to be desired, and it is unfortunate that the recorded cases relate to subjects, which for various reasons are difficult to experiment with.

Mixture of forms in F_1.—In certain cases two types which each breed true separately, give, on crossing, individuals of two or more kinds. If this complication is not determined by sexual dimorphism, one or other of the two pure types must, in reality, be giving off more than one type of gamete. There are then two possibilities only. Either the difference between these types of gamete lies in the characters

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* ' Ber. Deut. Bot. Ges.,' vol. 20, 1903, p. 605.

† See especially Giard, ' C.R. Soc. Biol.,' 1903, vol. 55, p. 779, and ' Cinquante-naire Soc. Biol.,' p. 12.

‡ ' Gard. Chron.,' 1903, ii, p. 227.

§ ' Trans. Hort. Soc.,' vol. 5, 1824, p. 294.

with which they are endowed in gameto-genesis, or in the manner in which they are affected by fertilisation. In the former case we must conceive of the gametes of the parental type A being, in reality, xA and yA ; in the latter they may be called xyA, but on fertilisation with some other pure type there is a partial monolepsis, by which on fertilisation with B, sometimes the result is xAB, and sometimes yAB, and not always $xyAB$. Up to the present time there is no case which can be positively declared to be of the latter class, but as monolepsis certainly occurs in the complete form, the possibility of partial monolepsis should not be forgotten. For a long time it seemed that the phenomena seen in Malay crosses must point to this interpretation, but further experience is not favourable to that suggestion.

In most of the recorded instances of mixed F_1 there is now no doubt that the first is the true account. In discussing the results of Crampe attention was called* to the possibility that the dissimilarity between two F_1 forms from " pure " parents might turn on a hidden distinction *either* between the different albinos, *or* between the different coloured parents, and that in certain cases of Parsons the distinction was certainly in the albinos, most giving pied offspring while self-coloured F_1 came from others.

At this point the recent paper of Cuénot† marks a very important advance. Mixed F_1 has been several times recorded in mice, some families containing blacks and greys, though the parents in each case seemed to be pure. It had appeared to us that here the probable interpretation lay in impurity of the coloured parents, but Cuénot has now proved that albinos extracted from the several colours will give those colours on crossing with coloured types.

Still more significant is his proof that by crossing albinos of different extraction the allelomorphs determining the various colours *will them-selves segregate* in the gametogenesis of the albino in ordinary Mendelian fashion. For example, albino *ex* yellow bred with albino *ex* black gives a heterozygous albino whose gametes are in equal numbers bearers of the factors which determine to black or to yellow respectively. When such an albino breeds with a pure colour-type, a mixed F_1 may result. As he points out, this fact disposes of various outstanding difficulties met with by Darbishire and others. The appearance of the two reversion types in Sweet Pea is almost certainly determined by similar factors, though the proof can only appear next season.

[Note added December, 1904.

Tschermak‡ had previously brought forward a large mass of facts of a similar nature, and (in view of Cuénot's evidence) his account is

* W. Bateson, ' P.Z.S.,' 1903, ii, pp. 78 and 84.
† Cuénot, 'Arch. Zool. exp. et gén., Notes et Rev.,' 1904, vol. 11, pp. 45 to 56.
‡ ' Beihefte zum Bot. Cbltt.,' vol. 16, 1903, Heft. 1.

clearly correct, applying perhaps to all cases where F_2 gives the ratio $9 : 3 : 3 + 1$. It is, however, doubtful whether we should speak of such factors as " latent." It is rather that an element is present which when it meets another element produces a certain character in the fertilised result. This is not the character which was latent. As stated later, there is still a case, that of hoariness resulting from the crossing of glabrous Stocks, to which no adaptation of this simple view is yet applicable.]

Peculiarities of Extracted Types.—In addition to the fact observed by Cuénot that an extracted type (*e.g.*, albino) may carry on segregable determinants, whereby the individuals may, in reality, differ from each other, though outwardly alike, there are other specific properties of extracted types which call for notice. At an early stage in the inquiry it was remarked that though gametic unions between certain pure types give reversion, unions between extracted gametes, ostensibly similar to the pure ones, give no reversion. This has now been seen most clearly in Sweet Peas where, so far, two dissimilar recessives (long white × round white) of the same extraction, crossed together, give no reversion, though the plants used are indistinguishable from the two original types which gave the reversion. Moreover, in Stocks when one such extracted is crossed with one of the *original* pure types, there is no reversion, though a *new* pure type may cause the reversion again. Conversely, in Stocks, $DR_1 \times DR_2$, where D is a white hoary, may give some glabrous, while $DR_1 \times DR_3$ give only hoary.

These phenomena must be distinguished from that described by Cuénot; for in the cases now under consideration the quality which determines or prevents the reversion is apparently common to all the sister cross-breds and does not depend on any segregable or allelomorphic character. Therefore, though the process, so far as we yet know is quite specific in its results, it is not Mendelian. In view of these facts the nature of the reversionary forms in F_2 is often problematical. The relation of the two phenomena is a question which only the later generations can solve.

With the facts just described, may be compared the results obtained in Stocks, where among the glabrous types, not only white × red, and cream × red give reversion to hoary, but the same reversion occurs when white is crossed with cream. Therefore, the reversion cannot be regarded as merely due to the meeting of a pair of elements, of which one is borne by each type, but it must have some more complex causation.

Resolution and Disintegration : Synthesis.—The conception of resolution applies properly only to those cases where a character appearing in F_2 is constituted by the breaking up of the compound allelomorphs of the original parents, the term disintegration being reserved for cases when

the integrity of an allelomorph is impaired and segregation is incomplete. Thus the occurrence of homozygous types in F_2 made as a blending or mosaic of the original parental allelomorphs is an indication of disintegration. For instance, the white-spangled types seen in F_2 from Brown Leghorn × white, and certain chequered types, similarly produced, must be regarded as acquiring their colour from the coloured parent, and their white from the white parent, which is then disintegrated.

In view of Cuénot's evidence great care will be needed in discriminating these various cases. The uniformity of F_1 will generally be a guide to the nature of the case, but at least the homozygous nature of the F_2 type in question must be tested in each instance. It is not inconceivable that, owing to dominance and other peculiarities of heterozygosis, F_1 may be uniform though the gametes of one or other parent are not so, and a spurious appearance of resolution may thus appear in F_2. In such cases sensible uniformity in the statistical composition of F_2, together with proof of homozygosis of resolved forms, will furnish the only reliable criterion as to real resolution in F_1.

It should be especially noted that the phenomenon detected by Cuénot, while simplifying some cases, formerly interpreted as resolution, does not provide a substitute for that conception; for, to go no further, we still have to deal with cases where one of the original pure types practically disappears from F_2, etc., having evidently been entirely or almost entirely broken up in the gametogenesis of F_1 (*e.g.*, blue flowercolour in *Primula sinensis*, the red of some sweet peas, pp. 121 and 90).

As to the statistical relations of the products of resolution there is, as yet, no evidence which is quite satisfactory, and it is clear that several types of cases occur. The case of *Antirrhinum* studied by de Vries* seems to be peculiar in the fact that, on crossing red × white only 1 white in 16 appeared in F_2.†

An intensification of one of the pure parental characters is not rare in some members of F_2 where resolution occurs. Perhaps the most striking illustration is that seen by Biffen (*loc. cit.*, p. 31) in the case of lax ear in Wheat. A similar case in colour is given, p. 90.

Tschermak's‡ cases of resolution in *Matthiola* are, thus far, the most fully studied, F_3 having been already reached. They give valuable indications as to the statistical relations in a case where resolution

* 'Mutationstheorie,' vol. 2. p. 198.

† [*Note added December*, 1904.—In 'Camb. Phil. Soc. Proc.,' vol. 12, p. 50, I suggested that this result might be attained if F_1 produced 4 types of gametes in equal numbers. Mr. R. H. Lock has pointed out to me that the case may very probably be regarded as an *actual* example of " di-hybridism." If this proves to be true there is then no resolution or synthesis to be reckoned with, and the original red would not be, gametically, a compound character.—W. B.]

‡ 'Beihefte z. Bot. Cbltt.,' 1903, vol. 16, p. 18.

follows on reversion in F_1; though, for this reason, the precise interpretation of the phenomena is somewhat obscure.

All the available facts support the expectation that a symmetry will be found to prevail in the distribution of the resolved characters comparable with that occurring in the case of unresolved characters in ordinary mono-hybrids.

It is desirable that the term synthesis should be restricted in heredity to the permanent union of component allelomorphs to form a compound allelomorph which breeds true without segregation. Such an example is seen in the case of the " walnut " (r.p.) comb, produced by crossing rose-comb with pea-comb. The F_1 comb, thus artificially formed, may be scarcely, if at all distinguishable from the natural "walnut" comb of the Malay breed. F_1 produces four types of gametes (probably in equal numbers), r.p., r., p., s. Among the F_2 types there are, therefore, some birds formed by r.p. × r.p., and the evidence (1904) proves that some, at least, of these are then really synthetic r.p., breeding true to that character.

Tschermak's discovery that after the production of reversionary purple F_1 in *Matthiola*, certain purples appear in F_2 which seem capable of breeding true, probably points to a similar permanent synthesis.* Here, however, a complex resolution has evidently taken place, and possibly these cases may prove to be analogous with the production of various homozygotes after resolution; for the degree to which the compound allelomorphs of the new forms derive elements from both pure types is not yet determined.

Heterozygous Breeds.—As an illustration of a breed permanently heterozygous, the Andalusian fowl was given tentatively in Rep. I. Experiments have now shown that this is the true account. The blue Andalusian gives off gametes, black and white-splashed. The blue is formed by heterozygosis of these two, but the black and the white-splashed birds, produced by mating blues together, are homozygous and generally breed true. Further study of the Giant Lavender, *Primula sinensis*,† has confirmed the view that this also is a heterozygote of magenta and white-tinged, offering an exact parallel to the Anda-

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* [*Note added December*, 1904.—Our later results with Sweet Peas prove that there also a synthesis has occurred, forming purple-bearing gametes, and bicolour-bearing gametes. A strain of pure purple and of pure bicolours can thus be produced from F_2 made by white × white. The same is true for the picotee and tinged white types in F_2.

Darbishire's results ('Biometrika,' vol. 3, Part 1, pp. 24, 25) are without doubt capable of a similar explanation. Some of the greys in F_2 and later generations are evidently in composition grey × grey or some other colour. The deficiency of albinos in the matings where such greys were used is therefore in harmony with the facts seen in Sweet Peas, Stocks, etc., as must appear at once when the offspring of each individual are made separately traceable in the Tables.]

† W. Bateson, ' Mendel's Principles of Heredity,' 1902, p. 182.

lusian. In each case there is, however, a doubt as to whether the white-splashed or tinged may not, in certain cases, subsequently segregate into a purer white and a form more distinctly coloured, possibilities which require further investigation.

Sex.—In Report I we indicated the possibility that sex may be ultimately a phenomenon of gametic segregation comparable with that seen in ordinary Mendelian cases. In an interesting essay, Castle* has greatly amplified this suggestion, and has shown reasons for believing that the segregation of male spermatozoon from female spermatozoon and of male ovum from female ovum may occur at the reduction-division in gametogenesis. While admitting the likelihood of this suggestion, we feel that for the present it should be received with caution. In particular, we doubt the conclusion that *both* ova and spermatozoa (after a reduction-division) are always bearers of either the male or the female character. It seems more likely that special cases will present special phenomena in this respect. As yet the evidence most applicable to the decision of the question is thus derived from those reciprocal crosses which give dissimilar results, and in view of the idiosyncrasies of these cases, we incline to expect that sometimes the male element, sometimes the female, will be found to be responsible for sexual differentiation, and that the similar differentiation of both elements is not likely to be universal. For instance, if the case of Malays, already discussed (p. 111), be shown to bear the suggested interpretation, it is evident that the gametes of one sex alone, probably the male, and not both, will determine the sex of the offspring. One sex must then be regarded as a "Halbrasse" of the other, just as long style may, perhaps, be of short style in Primula.

The evidence of Correns† as to Bryony crosses has a direct bearing on this question. Using *Bryonia alba* ♀ as seed-plant and *B. dioica* as male, he obtained offspring all diœcious (with a doubtful exception). As he states, this fact points to the segregation of the sex-determinants among the male cells of *Bryonia*. The result of the reciprocal cross will be awaited with interest.

Gärtner,‡ however, using ♀ *Lychnis diurna* × ♂ *L. flos cuculi* (♀) also obtained F_1 all diœcious, males and females, pointing to sex-segregation among the egg-cells of the mother. In each of these cases, unfortunately, the problem is complicated by the appearance of sterility in F_1, and in the case of ♀ *L. diurna* × ♂ *Silene noctiflora* (♀) the results were somewhat ambiguous.§

A case that may be used for the elucidation of this problem is that

* 'Bull. Harvard Mus.,' vol. 40, 1903.
† 'Ber. Deut. Bot. Ges.,' 1903, vol. 21, p. 195.
‡ 'Bastarderzeugung,' p. 49.
§ *Ibid.*, p. 287.

of the Cinnamon Canary, recently described by Norduijn,* who has most kindly given us much supplementary information. As to the essential facts, Canary-breeders seem to be agreed. The Canary has two forms which are both in a sense albinos, the yellow and the cinnamon. The latter, in the nestling stage at least, has red eyes, which subsequently darken, but red eyes may occur also in yellows. When green (viz., non-albino) ♀'s are crossed with cinnamon ♂'s, both greens and cinnamons are produced, of which the males are always and the females sometimes green, but *the cinnamons are invariably female.* From the reciprocal cross the young are always green.

The F_1 males from cinnamon ♂, when bred with green or yellow ♀'s, may again produce cinnamons which are exclusively ♀. The interpretation of this case is still quite obscure, but attention is called to it as a most important subject of experiment. The facts strongly suggest that there is here some phenomenon of gametic coupling† of the female sex-character with cinnamon. When yellows are used the results are complicated by the appearance of reversionary heterozygotes, green or green-marked.

Castle is doubtless right in the view that marked inequalities observed in the distribution of characters between the sexes after crossing are due to some similar coupling of a sex-character with some allelomorphs,‡ and the investigation of these cases will probably much elucidate the real nature of sexual differentiation. The phenomenon of sex is possibly comparable in some aspects with that of the "*Mittelrassen*" of de Vries, the production of one form being, in gametogenesis, constantly accompanied by the production of a second.

In the sweet-peas with sterile anthers we have a phenomenon which may be described by a slight stretch of language as Mendelian segregation of a female from a hermaphrodite (see p. 91).

Disturbances, due to sex, have been met with by several observers, a particularly striking one being recorded by Hurst (p. 148).

The Moment of Segregation.—The balance of evidence is in favour of the belief that gametic segregation takes place at the reduction-division, but no crucial test is yet forthcoming. The new evidence as to the individuality of the chromosomes and the discovery that a true transverse division occurs in the chromosomes of plants at reduction

* 'Album der Natuur,' 1903, p. 71. See also Blakiston, Swaysland, and Wiener, 'The Canary Book,' Jerome, 'Canary Breeding,' 1896, etc.

† In Report I, we took exception to Correns' use of the term "conjugation" to denote this association of characters, preferring the word "correlation" already in use. Experience, however, has shown that, owing to the special uses of correlation now prevalent, the term here leads to confusion. No such objection attaches to the words "coupling" or "coupled," also introduced by Correns in the same sense, which in future we propose to adopt.

‡ For a case of a curious distribution of such varieties in a wild form, see the case of the beetle, *Gonioctena variabilis*, W. Bateson, 'P.Z.S.,' 1895, p. 850.

ale clearly favourable to the hypothesis that the reduction-division is the critical moment. A fact which rather suggests that segregation occurs at some earlier dichotomy, is the irregularity of the individual F_2 ratios (*cf.* pp. 88 and 108) in certain cases (*e.g.*, Poultry), which strongly contrast with the extreme regularity of these ratios in the case of wheat, for example (Biffen), or maize (Lock).

Up to the present time the attempt to discover an order in the occurrence of the gametes, bearing either of a pair of allelomorphs, has led to negative results. The case of *Pisum* seemed not unpromising for this inquiry, but a considerable number of pollinations of DR plants with R pollen has, so far, failed to show that the D and R ovules are arranged in any definite pattern or order, but as conceivably more than one plant* may have to be taken into account, the recognition of the arrangement may be a very difficult matter.

As to the factors which determine the retention or exclusion of any character in the case of any germ-cell, no suggestion has yet been made. It is not impossible that this may be influenced by some factor easily disturbed by environmental influences, so far, at least, as the egg-cell is concerned. To take a crude illustration, if gravitation effected the result, the regularity of the order might be obliterated by the action of the wind at the moment of segregation. Improbable as this particular suggestion obviously is, it is, perhaps, to some irregularity of a similar nature that the want of a visible order may be due.

The relation of *gametic* differentiation to the normal differentiation between *somatic* parts of the same body is one which, sooner or later, will call for consideration. There are besides many examples of differentiation between somatic organs manifesting itself in bud-sports, where the differentiating pair of characters are such as we elsewhere know to be an allelomorphic pair.

Statistical Consequences of Mendelian Heredity.—This subject has been discussed by Yule† and by Pearson.‡ In Rep. I, p. 158, we suggested "that Galton's law may be a representation of particular groups of cases which are, in fact, Mendelian," in the sense that the gametes are pure. The analysis carried out by Yule points to a similar conclusion, if the phenomena of dominance and special consequences of heterozygosis are neglected. Pearson's conclusion that various phenomena of inheritance studied by him are incompatible with Mendelian expectation is open to the objection that many of his characters are obviously

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* For example, there is every likelihood that the seeds from the right and left carpellary edges are antidromic, though all stigmas turn to the flower's right (see Macloskie, 'Am. Nat.,' November, 1895).

† 'New Phytologist,' 1902, vol. 1.

‡ 'Phil. Trans.,' 1904, 203 A, p. 53, and 'Roy. Soc. Proc.,' 1904, vol. 73, p. 262.

liable to such great disturbances from the interference of conditions that the operations of heredity alone must be largely obliterated. In other classes of cases to which he refers (various colour phenomena) no sufficient analysis is yet provided, and in such a field comprehensive statistics are an inadequate indication as to the underlying physiological processes.

The experiments of Johannsen* have made an important contribution to this part of the inquiry. Taking self-fertilised beans (*Phaseolus*) he found indications that the number of "pure lines" in respect of seed-weight was very considerable. Hence we may suppose with some confidence that segregation, in respect of this character, deals with units which, though small, have a sensible size. It is to be hoped that others will be attracted to this fruitful method of research.

General.—As the results of experiments now in progress here and elsewhere will soon clear up many doubtful points, we propose to defer a general survey of the subject. Certain conclusions of significance are, nevertheless, obvious.

The solution of the various problems of heredity is now seen to depend primarily on a study of the process of segregation in gametogenesis, and secondarily on a determination of the specific consequences of the union of gametes of the various types in fertilisation. These questions can be answered only by a minute experimental analysis, and little advance can be expected from study of the phenomena in the mass by comprehensive statistical methods, however appropriate such treatment may have seemed in the absence of any knowledge of the physiological processes which constitute heredity.

In a large and rapidly increasing number of cases, it is known that segregation of characters is sensibly complete, the characters being thus allelomorphic and the gametes bearing them pure. Such allelomorphism may apparently subsist in the case of any character of animals or plants. Though naturally the phenomenon is more easily demonstrated for some characters than others, any one who conducts breeding experiments can perceive frequent indications of the prevalence of segregation in numberless dissimilar characters.

In fowls, for instance, there is no reasonable doubt that such features as late or early feathering, shortness of wing-quills and tail, peculiar qualities of voice, forms of constitutional weakness, follow rules closely similar to those detected in features more amenable to critical study. There is no reason to suppose that physiological distinctions, such as liability to disease (*cf.* p. 121, and Biffen, *loc. cit.* p. 40), late and early ripening (Biffen, p. 34), certain forms of sterility (see p. 91), and so forth, will be exempt from the operation of these rules. There are already indications, moreover, that such features may be

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* Erblichkeit in Populationen,' Jena, 1903.

gametically coupled with others more easy to deal with, for example, certain types of pigmentation.

On the other hand, it has been asserted that certain experiments have demonstrated that gametic purity does not occur in cases where its presence might be expected, *e.g.*, the colours of mice.* It appears to us, however, that the analysis of these cases is as yet materially imperfect. The evidence in the case of *Matthiola*, for instance, shows that many complexities have to be considered before such negative propositions can be established.

Especially in dealing with extracted types caution is needed. Difference between the behaviour of an extracted and an originally pure type may evidently be caused by the presence of various determining characters, which though imperceptible until a cross is made, may modify the result. Nevertheless, these hidden characters may themselves be allelomorphic to each other in a simple Mendelian fashion (Cuénot), and the phenomena may illustrate gametic purity in the strictest sense.

Irregularities resulting from the direct action of conditions may also obscure the simplicity of the result, and mistakes of interpretation may easily occur through want of attention to this fact (*cf.* Peas, pp. 58 and 64).

EXPERIMENTS WITH POULTRY.

By CHARLES C. HURST, F.L.S., Burbage, Leicestershire.

These experiments were designed in 1901, to test the Mendelian principles of heredity. Four pure breeds were selected for experimental crossing, viz., White Leghorn, Houdan, Black Hamburgh, and Buff Cochin.

PURE BREEDS (P_1).

White Leghorn.—The chief characters of the breed are, clear white plumage, large single comb, four toes on each foot and yellow shanks quite free from feathers. The white plumage often acquires a yellowish tint when exposed to the sun, but the birds always moult out clear white. The down of the chick is at first yellowish white, afterwards becoming clear white. The large single comb, erect in the cock, and falling over to one side in the hen, consists of a single lobe, extending beyond the back of the head, with four to five deep and even serrations. The deep yellow shanks become lighter with age. The hens lay white eggs, as a rule, and do not sit.

Houdan.—The chief characters of the breed are, black plumage

* Darbishire, 'Biometrika,' vol. 3, p. 1, *passim.*

ticked or mottled with white, large crest, beard, and muffling, leaf comb, 5 toes on each foot, white shanks spotted with blue-black, usually free from feathers. This breed has an abnormal protuberance of the skull with cavernous nostrils, both of which appear to be correlated with the large crest.* The plumage is a dull blue-black shaded with brown; the white markings are irregular in size and distribution, varying from a few white ticks in the dark birds to clear white feathers in the flights and crest of the light ones. The down of the chick is clear black above with white head and underparts irregularly mottled with black. The leaf comb is an irregular structure consisting of 2 single serrated lobes spread out somewhat like the leaves of an open book, and joined at the base by a mulberry-shaped process; it is always large in the cock and small in the hen, and varies considerably in detail in individual birds, though unmistakably different from any other kind of comb. The ideal leaf comb of the fancier has been likened to a butterfly with open wings. The extra-toe is usually a distinct digit, curving gently upwards, sometimes it is imperfect and even joined to the hallux. The pigmentation of the white shanks is variable, in some cases there are a few small spots, while in others the spots are so numerous and suffused that the shanks appear to be blue-black rather than white. The shanks are usually free from feathers, but sometimes birds appear with a few traces of feathers on the upper part of the shanks. The crest varies in size in individual birds. The hens lay white eggs and do not sit.

Black Hamburgh.—The chief characters of the breed are, black plumage, rose comb, 4 toes on each foot, and blue-black shanks, quite free from feathers. The black plumage has a lustrous green sheen. The down of the chick is clear black above with whitish throat and underparts, but the white disappears with maturity, leaving the bird clear black. The rose comb has a flat surface covered with a large number of small points, it is squared in front, gradually tapering back-wards to a long spike or peak. The breed is small in size, close-feathered, with a neat and active carriage. The hens lay pure white eggs and do not sit.

Buff Cochin.—The chief characters of the breed are, buff plumage, small single comb, 4 toes on each foot, and yellow shanks heavily feathered down to the toes. The buff plumage varies considerably in individual birds, and also with age; the shades range from lemon to cinnamon, some of the darker cocks having quite a red tinge in their hackles and saddle feathers; black or brown feathers in the tail, white feathers in the flights, and mealy or white speckled birds are often seen in the most carefully selected strains. The down of the chick varies from light to dark buff, shaded with creamy white. The small single comb is erect in both sexes and very small in the hen. The

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* *Cf.* Darwin, 'Animals and Plants,' vol. 1, p. 275, 2nd ed., 1893.

shank-feathering varies in length and number of feathers in individual birds. The hens lay dark brown eggs, and frequently want to sit. The breed is large in size, with loose, fluffy feathers and heavy limbs.

The above observations were obtained by the personal examination of more than 2000 birds of the pure breeds concerned, and in the particular strains from which the stock birds, used in these experiments, were derived.

<div align="center">FIRST CROSSES (F₁).</div>

<div align="center">*Experiment* 1.—*White Leghorn* ♀ × *Houdan* ♂.</div>

In 1902 12 White Leghorn hens were mated with a dark Houdan cockerel; eggs from this pen produced 105 chicks with the following characters :—

COMB.—*Single* ♀ × *Leaf* ♂ gave all with variable leaf combs; of these, 9 were apparently full leafs, and 96 were split leafs, having a single lobe in front split into 2 more or less concave lobes behind; there were no single combs.

DOWN.—*White* ♀ × *Black* ♂ gave 94 whites and 11 blacks; of these, 22 were apparently clear white, 72 white ticked with black, 1 black with white head, and 10 black, ticked with white. In each case the tickings were slight and inextensive, so that in the ground colour the distinction between white and black was marked and discontinuous. In the first plumage all except two of the clear whites developed black ticks, similar to those that were born ticked; the blacks developed into 6 blacks and 5 " cuckoos," 5 of the blacks were slightly ticked with white in the crest only, and in their plumage were indistinguishable from the Crève-cœur breed, the other black developed into a typical light Houdan; the 5 cuckoos were grey-white, barred with blue-black, with odd black or white feathers; both the blacks and the cuckoos were distinctly shaded with brown. Curiously enough the 6 blacks were all pullets and the 5 cuckoos all cockerels !

FEET.—*No-extra-toe* ♀ × *Extra-toe* ♂ gave 103 with e.t., and 2 with no e.t. ; of these, 23 had the e.t. apparently perfect on both feet, 70 had e.t. in all stages from the almost perfect e.t. down to the mere duplication of the nail, 6 had e.t. on one foot only, while 4 had 4 toes on each foot, but in each case the hallux was elongated with extra joints, all these various states indicating digital proliferation are counted as e.t. The 2 chicks with no e.t. were apparently normal with no trace of e.t.

SHANK FEATHERING.—*Clear* ♀ × *Clear* ♂ gave 103 with clear shanks and 2 with a few traces of feathers on the upper part of the shanks ; both the latter were cockerels, and one was also exceptional in having cuckoo plumage and no e.t.

SHANK COLOUR.—*Yellow* ♀ × *White* ♂ gave all with white shanks, more or less pigmented with blue-black; the cockerels without excep

tion had very little pigment, while the pullets, with 4 exceptions, had a large amount, and at a distance appeared more blue than white in their shanks. There were no yellow shanks nor any tinged with yellow.

EGG COLOUR.—*White* ♀ × *White* ♂ gave all with white eggs.

CREST.—*Clear* ♀ × *Crested* ♂ gave all crested, but in every case the size of the crest, in both length and number of feathers, was reduced to about one-half.

BROODINESS.—*Non-Sitting* ♀ × *Non-Sitting* ♂ gave all non-sitters.

Experiment 2.—White Leghorn ♀ × Black Hamburgh ♂.

In 1903 10 White Leghorn hens were mated with a Black Hamburgh cock; eggs from this pen produced 57 chicks with the following characters :—

COMB.—*Single* ♀ × *Rose* ♂ gave all rose combs with no trace of the single comb.

DOWN.—*White* ♀ × *Black* ♂ gave 49 whites and 8 blacks; of these, 1 was apparently clear white, 48 white ticked with black, and 8 black with whitish throats.

FEET.—*No-e.t.* ♀ × *No-e.t.* ♂ gave all with no trace of e.t.

SHANK FEATHERING.—*Clear* ♀ × *Clear* ♂ gave all clear with no trace of feathers. These chicks were not reared for the observation of their mature characters.

Experiment 3.—White Leghorn ♀ × Buff Cochin ♂.

In 1903 12 White Leghorn pullets were mated with a Buff Cochin cockerel; eggs from this pen produced 60 chicks with the following characters :—

COMB.—*Single* ♀ × *single* ♂ gave all with single combs.

DOWN.—*White* ♀ × *Buff* ♂ gave 53 whites and 7 buffs; of these 2 were apparently clear white, 51 white patched with buff and brown, chiefly on the head, neck and breast (18 of these had also odd black ticks); the 7 buffs were all more or less patched white.

FEET.—*No-e.t.* ♀ × *No-e.t.* ♂ gave all with no trace of e.t.

SHANK FEATHERING.—*Clear* ♀ × *Feathered* ♂ gave all with feathered shanks, but in every case the length and number of feathers was reduced to about one-half.

Experiment 4.—Black Hamburgh ♀ × Houdan ♂.

In 1903, late in the season, one Black Hamburgh hen was mated with a light Houdan cockerel, and only 6 chicks were hatched, with the following characters :—

COMB.—*Rose* ♀ × *Leaf* ♂ gave all rose combs, but they were

irregular, inasmuch as the usual long peak of the pure rose was replaced by two shorter ones.

DOWN.—*Black* ♀ × *black* ♂ gave all blacks with white heads.

FEET.—*No-e.t.* ♀ × *E.t.* ♀ gave all with e. t. on both feet.

SHANK FEATHERING.—*Clear* ♀ × *clear* ♂ gave all clear shanks, with no trace of feathers.

Experiment 5.—*Buff Cochin* ♀ × *Houdan* ♂.

In 1903, late in the season, one Buff Cochin hen was mated with a light Houdan cockerel, and only 5 chicks were hatched, with the following characters :—

COMB.—*Single* ♀ × *Leaf* ♂ gave all with split leaf combs.

DOWN.—*Buff* ♀ × *Black* ♂ gave all blacks marked and shaded with brown and ticked with white.

FEET.—*No-e.t.* ♀ × *e.t.* ♂ gave 4 with e.t. on both feet and 1 with no e.t.

SHANK FEATHERING.—*Feathered* ♀ × *Clear* ♂ gave all with feathered shanks, but the length and number of feathers was reduced to about one-half.

Experiment 6.—*Black Hamburgh* × *Buff Cochin.*

In 1902, two Black Hamburgh pullets were mated with a Buff Cochin cockerel; eggs from this pen produced 84 chicks. At the same time one Buff Cochin pullet was mated with a Black Hamburgh cockerel; eggs from this pen produced 23 chicks. The offspring of these reversed matings had similar characters, so that all may be taken together, *i.e.*, 107, with the following characters :—

COMB.—*Rose* × *Single* gave all rose combs with no trace of single comb.

DOWN.—*Black* × *Buff* gave all blacks marked with brown ; of these, 82 had brown heads only, and 25 had also the body shaded with brown. In the first plumage the two sexes were quite distinct. The cockerels had golden-brown hackles, red-brown saddles, black and brown tails and wings, buff-brown breast regularly spangled with black. The pullets were as dull and sober in colour as the cockerels were brilliant, being black intermixed with light and dark brown, with darker tails and heads and spangled breasts. It seems rather curious that a cross between two breeds, each of which has normally similar plumage in both sexes, should produce offspring in which the two sexes are so distinctly differentiated.

FEET.—*No e.t.* × *No e.t.* gave all with no trace of e.t.

SHANK FEATHERING.—*Clear* × *Feathered* gave all with feathered shanks, but in each the length and number of feathers was reduced to about one-half.

SHANK COLOUR.—*Blue × Yellow* gave all with light blue shanks with no trace of yellow.

CREST.—*Clear × Clear* gave all clear with no trace of crest.

EGG COLOUR.—*White × Brown* gave all with brown eggs of varied hue, none being so brown or so white as the parent breeds.

BROODINESS.—*Non-sitting × Sitting* gave all good sitters; all the pullets wanted to sit after laying about a dozen eggs, and all success-fully hatched two lots of chicks in 1903, making excellent foster-mothers, having the strong incubating instinct of the Cochin combined with lightness of limb of the Hamburgh. The voice of the cross-bred cockerels was a ludicrous compromise between the hoarse prolonged crow of the Cochin and the shrill sharp crow of the Hamburgh. The cross-breds were intermediate in size, carriage and feathering.

In the foregoing first crosses, each of the six possible combinations of the four pure breeds has been effected, and in the one reverse cross tried (Experiment 6), no intrinsic differences could be detected in the offspring through the change of sex. Many different characters are concerned in the six matings, some are like, others are unlike. The matings of like characters in the first crosses (F_1), gave the same result as the like matings in the pure breeds (P_1). The matings of unlike characters in F_1 gave, generally, a definite dominance of one character over the other, *e.g.*, in Experiment 1, white plumage mated with black gave nearly all whites; in Mendelian terms, white was dominant over black, which was recessive. A few exceptions occurred in which the normally recessive black was apparently dominant, *e.g.*, in Experiment 1, a few were black instead of white. Among the hybrid dominants the dominance was clearly of two kinds, *complete* and *incomplete*. Complete dominance resembled the original Mendelian dominance in Peas, where no trace of the recessive character was found in the hybrid dominant, *e.g.*, in Experiment 1, a few were clear white with no trace of black. Incomplete dominance occurred when the influence of the recessive character was manifest in the hybrid dominants in varying degrees, *e.g.*, in Experiment 1, a large proportion were white ticked with black. The following table gives the total results of the first crosses (F_1), showing in (*a*) the names and numbers of the D and R characters that occurred in the unlike matings D × R, together with the respective numbers of the complete and incomplete dominants; and in (*b*) the numbers observed in the like matings R × R.

Total Results of First Crosses (F₁).

(a) Matings of Unlike Characters (D × R).

Expts.	Character.	D.	R.	D.	R.	Com-plete. D.	Incom-plete. D.
1, 5,	Comb	*Leaf*	Single	110	0	9	101
2, 6	,, ...	*Rose*	Single	164	0	164	0
4	,, ...	*Rose*	Leaf	6	0	0	6
1, 2	Down	*White*	Black	143	19	23	120
3	,, ...	*White*	Buff	53	7	2	51
5, 6	,, ...	*Black*	Buff	113	0	0	113
1, 4, 5	Feet	*e.t.*	No e.t. ...	113	3	25	88
3, 5, 6	Shanks	*Feathered* ...	Clear	173	0	0	173
1	,, ...	*White*	Yellow....	105	0	105	0
6	,, ...	*Blue*	Yellow....	107	0	107	0
1	Crest	*Crested*	Clear	105	0	0	105
6	Eggs	*Brown*	White	31	0	0	31
6	Broodiness ..	*Sitting*	Non-sitting	31	0	31	0
			Total ...	1254	29	466	788
			Per cent.	97·7	2·2	36·3	61·4

(b) Matings of Like Characters (R × R).

Expts.	R character.	D.	R.
3	Single comb	0	60
4	Black down	0	6
2, 3, 6	No e.t.	0	224
1, 2, 4	Clear shanks ...	2	166
6	No crest	0	107
1	White eggs	0	53
1	Non-sitting	0	53
	Total	2	669
	Per cent. ...	0·2	99·7

The above table shows that out of the 1283 characters observed in the D × R mating of F₁, 1254 (97·7 per cent.) were definitely dominant, the remaining 29 (2·2 per cent.) being apparently recessive. Of the 1254 dominants, 466 were apparently complete, while 788 were obviously incomplete. In Mendel's experiments with Peas, D × R in F₁ gave all complete dominants with no trace of R, but when the hybrid dominants were bred together in F₂, the R character re-appeared, proving that though not patent in F₁, it was nevertheless latent, and that the hybrid dominants raised from D × R, though apparently simple D's were in reality DR's. In these experiments with poultry it is obvious that the incomplete dominants are impure DR's, because they

show the influence of the R character in F_1, in some degree, however slight it may be; but further breeding in F_2 is required to show that the complete dominants are also impure DR's, and the following experiments show clearly that such is the case.

The Mendelian expectation from the mating DR × DR in F_2 is a proportion of 3 dominants to 1 recessive. The two following experiments give the results of two such matings, in several pairs of characters, in two distinct first crosses.

First Crosses Bred Together (F_2).

Experiment 7.—Leghorn-Houdan ♀ × Leghorn-Houdan ♂.

In 1903 12 pullets bred in Experiment 1 were mated with a cockerel bred in the same experiment, and with similar characters; eggs from this pen produced 226 chicks, with the following characters:—

COMB.—DR LEAF (*single*) ♀ × DR LEAF (*single*) ♂ gave 165 leafs and 61 singles, or 2·7 D : 1 R; of these 67 were full leafs, 98 split leafs, 56 ordinary singles, and 5 singles with the hinder end somewhat thickened (*cf.* Experiment 1).

DOWN.—DR WHITE (*black*) ♀ × DR WHITE (*black*) ♂ gave 171 whites and 55 blacks, or 3·1 D : 1 R. Of these, 111 were apparently clear white, 60 white ticked with black, 32 black with white heads, and 23 black ticked with white. A few only were reared, and these developed their first plumage as in the down, except that some of the clear whites developed black ticks, and some of the blacks ticked with white developed into " cuckoos " (*cf.* Experiment 1).

FEET.—DR 5 (*4*) ♀ × DR 5 (*4*) ♂ gave 179 with e.t. and 47 with no e.t. or 3·8 D : 1 R. Of these, 167 had e.t. on both feet, 7 had e.t. on one foot only, 2 had e.t. on one foot and long hallux on the other, 1 had long hallux on both feet, 2 had six toes on each foot, and 47 had no trace of e.t. (*cf.* Experiment 1).

SHANK FEATHERING.—RR Clear ♀ × RR Clear ♂ gave 219 clear, and 7 with feather traces, or 96·9 per cent. R (*cf.* Experiment 1).

Experiment 8.—Hamburgh-Cochin ♀ × Hamburgh-Cochin ♂.

In 1903, 12 pullets bred in Experiment 6 were mated with a cockerel bred in the same experiment. Eggs from this pen produced 119 chicks, with the following characters :—

COMB.—DR ROSE (*single*) ♀ × DR ROSE (*single*) ♂ gave 89 rose combs and 30 singles, or 2·9 D : 1 R. These were respectively indistinguishable from the pure rose and single combs (*cf.* Experiment 6).

DOWN.—DR BLACK (*buff*) ♀ × DR BLACK (*buff*) ♂ gave 88 blacks and 31 buffs, or 2·8 D : 1 R. Of these, 17 were black with whitish throats, 71 black, variably marked and shaded with brown, 9 dark buff, 5 buff ticked with black, 11 light buff, and 6 creamy white. Those that were

reared developed their first plumage, as follows: the blacks with whitish throats became clear black, the blacks marked with brown matured into a medley of nondescript blacks and browns, the variable buffs and creamy whites developed into buffs of various shades, some being more or less mis-marked with brown and black (*cf.* Experiment 6).

FEET.—RR 4 ♀ × RR 4 ♂ gave 119 with no e.t., or all R. Of these, 24 had malformed feet of various kinds (*e.g.*), two toes, united at the base, and bearing a single nail, otherwise they were quite healthy and vigorous (*cf.* Experiment 6).

SHANKS.—DR FEATHERED (*clear*) ♀ × DR FEATHERED (*clear*) ♂ gave 115 feathered and 4 clear, of these, approximately, 17 were fully feathered as in the Cochin grandparent, 20 three-fourths, 57 one-half, as in the parents, 13 one-fourth, 8 with feather traces on upper part of shanks, and 4 were quite clear and free from feathers (*cf.* Experiment 6).

FIRST CROSSES BRED WITH THEIR PARENTS (F_2).

The two following experiments give the results of breeding back the first crosses with one of the parents. The Mendelian expectation for the mating DR × D is all dominants: for DR × R it is equality of dominants and recessives, and for RR × R it is, of course, all recessives.

Experiment 9.—*Leghorn-Houdan* ♀ × *Leghorn* ♂.

In 1903, five pullets bred in Experiment 1 were mated with a White Leghorn cockerel; eggs from this pen produced 135 chicks, with the following characters:—

COMB.—DR LEAF (*single*) ♀ × R Single ♂ gave 74 leafs and 61 singles, or 1·2 D : 1 R. Of these, 8 were full leafs, 66 split leafs, 60 ordinary singles, and 1 single with the hinder end somewhat thickened (*cf.* Experiments 1 and 7).

DOWN.—DR WHITE (*black*) ♀ × D WHITE ♂ gave 135 whites, or all D. Of these, 66 were clear white and 69 white ticked with black (*cf.* Experiments 1 and 7).

FEET.—DR 5 (*4*) ♀ × R 4 ♂ gave 63 e.t. and 72 with no e.t., or 1 D : 1·1 R. Of these, 56 had e.t. on both feet, 4 had e.t. on one foot only, 2 had long hallux on both feet, 1 had six toes on one foot, and no e.t. on the other, and 72 had no trace of e.t. (*cf.* Experiments 1 and 7).

SHANKS.—RR clear ♀ × R clear ♂ gave 135 clear, or all R (*cf.* Experiments 1 and 7).

Experiment 10.—*Hamburgh-Cochin* ♀ × *Hamburgh* ♂.

In 1903, 12 pullets bred in Experiment 6 were mated with a Black Hamburgh cock; eggs from this pen produced 56 chicks, with the following characters:—

COMB.—DR ROSE (*single*) ♀ × D Rose ♂ gave 56 rose combs, or all D. These were indistinguishable from the pure rose comb (*cf.* Experiments 6 and 8).

DOWN.—DR BLACK (*buff*) ♀ × D Black ♂ gave 56 blacks, or all D. Of these, 34 were black with whitish throats, while 22 were slightly marked with brown, chiefly about the head (*cf.* Experiments 6 and 8).

FEET.—RR 4 ♀ × R 4 ♂ gave 56 with no e.t., or all R. All were normal (*cf.* Experiments 6 and 8).

SHANKS.—DR FEATHERED (*clear*) ♀ × R clear ♂ gave 35 feathered and 21 clear, or 1·6 D : 1 R. Of these, approximately 19, were one-half feathered as in the DR parents, 6 were one-fourth, 10 had feather traces on the upper part of the shanks, and 21 were clear and quite free from feathers as in the R parent (*cf.* Experiments 6 and 8).

So far the experiments have been confined to the same kinds of matings used by Mendel and his successors, viz : first crosses bred together (AB × AB) and first crosses bred with the parent breed (AB × A). The three following experiments are, however, rather more complicated, as in some instances three differential characters are concerned rather than the usual Mendelian pair, the matings being AB × C, AB × D, and AB × CD. In these cases it is difficult to apply the Mendelian terminology of D and R without some confusion, because some of the D's are themselves R to other D's, and some of the R's are themselves D over other R's. The omission of the Mendelian terminology in these cases may serve a useful purpose in showing that the Mendelian principles of segregation are independent of the secondary question of dominance. The three following experiments were deliberately designed to put the Mendelian principles to the severest test, and as the sequel shows, the results (though necessarily complicated) as far as segregation is concerned, agree closely with the Mendelian expectation.

FIRST CROSS BRED WITH A DISTINCT PURE BREED (F_2).

Experiment 11.—*Leghorn-Houdan* ♀ × *Black Hamburgh* ♂.

In 1903, five pullets bred in Experiment 1 were mated with a Black Hamburgh cock; eggs from this pen produced 101 chicks, with the following characters :—

COMB.—LEAF (*single*) ♀ × Rose ♂ gave 101 rose combs, or all. Of these, 58 were indistinguishable from the pure rose comb (*cf.* Experiment 2), and 43 were irregular rose combs with a double peak (*cf.* Experiment 4).

DOWN.—WHITE (*black*) ♀ × Black ♂ gave 52 whites and 49 blacks, or 1·0 : 1. Of these, 7 were clear white, 45 white ticked with black

(*cf.* Experiment 2), 24 black with whitish throats, and 25 black with white heads (*cf.* Experiment 4).

FEET.—**5** (*4*) ♀ × 4 ♂ gave 23 with e.t., and 78 with no e.t., or 1 : 3·3. Of these 10 had e.t. on both feet, 13 had e.t. on one foot only (*cf.* Experiment 4), and 78 had no trace of e.t. (*cf.* Experiment 2).

SHANKS.—Clear ♀ × clear ♂ gave 101 clear, or all, with no trace of feathers (*cf.* Experiments 2 and 4, 1 and 7).

<center>*Experiment* 12.—*Leghorn-Houdan* ♀ × *Buff Cochin* ♂.</center>

In 1903, five pullets bred in Experiment 1 were mated with a Buff Cochin cockerel; eggs from this pen produced 106 chicks, with the following characters :—

COMB.—LEAF (*single*) ♀ × Single ♂ gave 60 leafs and 46 singles, or 1·3 : 1. Of these, 5 were full leafs, 55 split leafs (*cf.* Experiment 5), and 46 ordinary singles (*cf.* Experiment 3).

DOWN.—WHITE (*black*) ♀ × Buff ♂ gave 52 whites and 54 blacks, or 1 : 1·0. Of these, 6 were clear white, 46 white patched with buff and brown, and some with odd black ticks also (*cf.* Experiment 3), 54 were black variably marked and shaded with brown, and some with white ticks also (*cf.* Experiment 5).

FEET.—**5** (*4*) ♀ × 4 ♂ gave 45 with e.t., and 61 with no e.t., or 1 : 1·3. Of these 43 had e.t. on both feet, 2 had e.t. on one foot only (*cf.* Experiment 5), and 61 had no trace of e.t. (*cf.* Experiment 3).

SHANKS.—Clear ♀ × Feathered ♂ gave 106 feathered, or all. Of these, approximately, there were 68 half-feathered, 15 three-fourths, and 23 fully feathered (*cf.* Experiments 3 and 5).

<center>FIRST CROSS BRED WITH A DISTINCT FIRST CROSS (F$_2$).</center>

<center>*Experiment* 13.—*Leghorn-Houdan* ♀ × *Hamburgh Cochin* ♂.</center>

In 1903, 12 pullets bred in Experiment 1 were mated with a cockerel bred in Experiment 6; eggs from this pen produced 307 chicks, with the following characters :—

COMB.—LEAF (*single*) ♀ × ROSE (single) ♂ gave 139 rose combs, 77 leafs, and 91 singles. Of these, 83 were regular rose (*cf.* Experiment 2), and 56 were irregular rose combs with double peaks (*cf.* Experiment 4); 6 were full leafs, and 71 were split leafs (*cf.* Experiment 5); all the singles were normal (*cf.* Experiment 3).

DOWN.—WHITE (*black*) ♀ × BLACK (*buff*) ♂ gave 148 whites and 159 blacks, or 1 : 1·1. Of these, 20 were clear white, 87 white ticked with black (*cf.* Experiment 2), 41 white patched with buff and brown (*cf.* Experiment 3), 19 black with whitish throats, 32 black with white heads (*cf.* Experiment 4), and 108 black, variably marked and shaded brown, and some also ticked with white (*cf.* Experiment 5).

FEET.—5 (*4*) ♀ × 4 ♂ gave 127 with e.t. and 180 with no e.t., or 1 : 1·4. Of these, 108 had e.t. on both feet, 19 had e.t. on one foot only (*cf.* Experiments 4 and 5), and 180 had no trace of e.t. (*cf.* Experiments 2 and 3).

SHANKS.—Clear ♀ × FEATHERED (*clear*) ♂ gave 195 feathered and 112 clear, or 1·7 : 1. Of these, approximately, 92 were one-half feathered, as in the male parent, 31 one-fourth, 72 had feather traces on the upper part of the shanks (*cf.* Experiments 3 and 5), and 112 were clear with no trace of feathers (*cf.* Experiments 2 and 4).

COMBINATION OF TWO OR THREE PAIRS OF CHARACTERS IN F_2.

So far we have dealt simply with the results of mating pairs of single characters separately, and now we have to consider how the Mendelian ratios work out when two or three pairs of single characters are taken together in individual birds. The following tables give, in black figures the Mendelian calculation of the numbers of each type expected, and in plain figures the actual numbers of each type observed in the various experiments of F_2.

The following abbreviations are used to denote the types.—wh. = white, bl. = black, bf. = buff downs ; l.c. = leaf, s.c. = single, r.c. = rose combs ; e.t. = extra toe, no e.t. = no extra toe on feet.

(a) *Combination of Two Characters.*

EXPERIMENT 7.

Down and Comb.

Mendelian calc.	Nos. obs.	Types.
127 ·1	125	wh., l.c.
42 ·3	47	wb., s.c.
42 ·3	40	bl., l.c.
14 ·1	14	bl., s.c.
225 ·8	226	

Down and Feet

Mendelian calc.	Nos. obs.	Types.
127 ·1	138	wh., e.t.
42 ·3	41	bl., e.t.
42 ·3	34	wh., no e.t.
14 ·1	13	bl., no e.t.
225 ·8	226	

Comb and Feet.

Mendelian calc.	Nos. obs.	Types.
127 ·1	135	l.c., e.t.
42 ·3	44	s.c., e.t.
42 ·3	30	l.c., no e.t.
14 ·1	17	s.c., no e.t.
225 ·8	226	

EXPERIMENT 8.

Down and Comb.

Mendelian calc.	Nos. obs.	Types.
66·9	62	bl., r.c.
22·3	26	bl., s.c.
22·3	27	bf., s.c.
7·4	4	bf., s.c.
118·9	119	

EXPERIMENT 9.

Comb and Feet.

Mendelian calc.	Nos. obs.	Types.
33·7	39	l.c., e.t.
33·7	35	l.c., no e.t.
33·7	24	s.c., e.t.
33·7	37	s.c., no e.t.
134·8	135	

EXPERIMENT 12.

Down and Comb.

Mendelian calc.	Nos. obs.	Types.
26·5	35	wh., l.c.
26·5	17	wh., s.c.
26·5	25	bl., l.c.
26·5	29	bl., s.c.
106·0	106	

Down and Feet.

Mendelian calc.	Nos. obs.	Types.
26·5	22	wh., e.t.
26·5	30	wh., no e.t.
26·5	23	bl., e.t.
26·5	31	bl., no e.t.
106·0	106	

Comb and Feet.

Mendelian calc.	Nos. obs.	Types.
26·5	27	l.c., e.t.
26·5	33	l.c., no e.t.
26·5	18	s.c., e.t.
26·5	28	s.c., no e.t.
106·0	106	

EXPERIMENT 13.

Down and Comb.

Mendelian calc.	Nos. obs.	Types.
76·7	63	wh., r.c.
76·7	76	bl., r.c.
38·3	48	wh., s.c.
38·3	43	bl., s.c.
38·3	37	wh., l.c.
38·3	40	bl., l.c.
306·6	307	

Down and Feet.

Mendelian calc.	Nos. obs.	Types.
76·7	62	wh., e.t.
76·7	86	wh., no e.t.
76·7	65	bl., e.t.
76·7	94	bl., no e.t.
306·8	307	

Comb and Feet.

Mendelian calc.	Nos. obs.	Types.
76·7	52	r.c., e.t.
76·7	87	r.c., no e.t.
38·3	41	s.c., e.t.
38·3	50	s.c., no e.t.
38·3	34	l.c., e.t.
38·3	43	l.c., no e.t.
306·6	307	

(b) *Combination of Three Characters.*

EXPERIMENT 7.

Down, Comb, and Feet.

Mendelian calc.	Nos. obs.	Types.
95·3	104	wh., l.c., e.t.
31·7	34	wh., s.c., e.t.
31·7	31	bl., l.c., e.t.
31·7	21	wh., l.c., no e.t.
10·5	13	wh., s.c., no e.t.
10·5	10	bl., s.c., e.t.
10·5	9	bl., l.c., no e.t.
3·5	4	bl., s.c., no e.t.
225·4	226	

EXPERIMENT 12.

Down, Comb, and Feet.

Mendelian calc.	Nos. obs.	Types.
13·2	11	wh. s.c., no e.t.
13·2	6	wh., s.c., e.t.
13·2	19	wh., l.c., no e.t.
13·2	16	wh., l.c., e.t.
13·2	17	bl., s.c., no e.t.
13·2	12	bl., s.c., e.t.
13·2	14	bl., l.c., no e.t.
13·2	11	bl., l.c., e.t.
105·6	106	

EXPERIMENT 13.

Down, Comb, and Feet.

Mendelian calc.	Nos. obs.	Types.
38·3	25	wh., r.c., e.t.
38·3	38	wh., r.c., no e.t.
38·3	27	bl., r.c., e.t.
38·3	49	bl., r.c., no e.t.
19·1	22	wh., s.c., e.t.
19·1	26	wh., s.c., no e.t.
19·1	19	bl., s.c., e.t.
19·1	24	bl., s.c., no e.t.
19·1	15	wh., l.c., e.t.
19·1	22	wh., l.c., no e.t.
19·1	19	bl., l.c., e.t.
19·1	21	bl., l.c., no e.t.
306·0	307	

From the above tables it will be seen that the various experiments give all the possible combination types, and that the actual numbers of these types are, on the whole, in fair agreement with the Mendelian

expectation, calculated by means of the Mendelian ratios. Cases of slight deficiency or excess of certain types will, in most cases, be found to correspond with similar irregularities in the single characters. This leads to the important fact that each single character is inherited independently of the other, the combinations taking place apparently in accordance with the calculus of chance, as Mendel found in Peas. The above experiments with poultry thus confirm Bateson's previous experiments,* and show clearly that there is no correlation between the down, comb, and foot characters observed, but that each is a "unit character" with an independent inheritance.

SUMMARY OF RESULTS (F_1 and F_2).

In summarising the results of the above experiments, the most natural method will be to deal first with each character separately, *i.e.,* (1) Comb; (2) Down; (3) Feet, etc., tabulating all the results under each, in the four Mendelian expectations, viz. : (*a*) all D's, (*b*) all R's, (*c*) 3 D : 1 R, (*d*) 1 D : 1 R. The details will be briefly reviewed under each character, afterwards the grand totals of all the characters will be also tabulated in the four Mendelian expectations.

The somewhat complicated Experiments 11, 12, and 13 will be brought into line with the others by regarding their results as D's and R's simply, irrespective of their complicated matings.

(1) *Combs.*

(*a*) All D's.

Gen.	Expt.	D.	R.
F_1	1	105	0
F_1	2	57	0
F_1	4	6	0
F_1	5	5	0
F_1	6	107	0
F_2	10	56	0
F_2	11	101	0
Total observations..		437	0
Mendelian calc...		**437**	**0**

(*b*) All R's.

Gen.	Expt.	D.	R.
F_1	3	0	60
Total observations ..		0	60
Mendelian calc. ..		**0**	**60**

(*c*) 3 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	7	165	61	2·7 : 1
F_2	8	89	30	2·9 : 1
F_2	13	216	91	2·3 : 1
Total obs.....		470	182	2·5 : 1
Mendelian calc.		**489**	**163**	**3 : 1**

(*d*) 1 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	9	74	61	1·2 : 1
F_2	12	60	46	1·3 : 1
Total obs. ..		134	107	1·2 : 1
Mendelian calc.......		**120·5**	**120·5**	**1 : 1**

* Bateson and Saunders, Report I (1902), p. 110.

In F_1, the Houdan leaf comb is dominant over both the Leghorn and Cochin singles (Experiments 1 and 5), in a few cases this dominance is complete and the full leaf is reproduced, while, in the majority, it is incomplete, consisting of all kinds of intermediate split leafs.

In F_1, the Hamburgh rose comb is dominant over both the Leghorn and Cochin singles (Experiments 2 and 6), and in all cases the dominance is complete, the hybrid combs being indistinguishable from the pure rose comb.

In F_1 the Hamburgh rose comb is also dominant over the Houdan leaf comb (Experiment 4), and in this we have a case of one dominant being recessive to another dominant. The dominance of rose over leaf is not so complete as that of rose over single, though more complete than that of leaf over single. No exceptions to dominance in F_1, in regard to combs, were observed in any of the experiments.*

In F_2, the hybrid dominant leafs of F_1, mated together, gave dominant leafs and recessive singles in the proportion of $2 \cdot 7 : 1$ (Experiment 7); mated with pure recessive singles they gave dominant leafs and recessive singles in the proportion of $1 \cdot 2 : 1$ (Experiments 9 and 12), and mated with dominant rose they gave all dominant rose combs (Experiment 11).

In F_2, the hybrid dominant rose combs of F_1, mated together, gave dominant rose and recessive singles in the proportion of $2 \cdot 9 : 1$ (Experiment 8), and mated with pure dominant rose they gave all dominant rose combs (Experiment 10).

(2) *Downs.*

(a) All D's.

Gen.	Expt.	D.	R.
F_1	1	94	11
F_1	2	..49	8
F_1	3	53	7
F_1	5	5	0
F_1	6	107	0
F_2	9	135	0
F_2	10	56	0
Total observations..		499	26
Mendelian calc....		525	0

(b) All R's.

Gen.	Expt.	D.	R.
F_1	4	0	6
Total observations..		0	6
Mendelian calc. ...		0	6

(c) 3 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	7	171	55	$3 \cdot 1 : 1$
F_2	8	88	31	$2 \cdot 8 : 1$
Totals obs. ..		259	86	$3 \cdot 0 : 1$
Mendelian calc.		258·7	86·2	3 : 1

(d) 1 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	11	52	49	$1 \cdot 0 : 1$
F_2	12	52	54	$1 : 1 \cdot 0$
F_2	13	148	159	$1 : 1 \cdot 0$
Total obs. ...		252	262	$1 : 1 \cdot 0$
Mendelian calc.		257	257	1 : 1

* *Cf.* Bateson and Saunders, Report I (1902). pp. 94, 97, 98.

In F_2, the hybrid dominant leafs of F_1, mated with the hybrid dominant rose combs of F_1 gave dominant rose and leaf combs and recessive single combs in the proportion of 2·3 : 1 (Experiment 13).

Although the nature of the dominants and recessives raised in F_2 has not yet been tested in F_3, yet judging by the structural details of the incomplete dominants and the recessives of F_2 there can be little doubt that the segregation is on Mendelian lines.

In F_1 the white plumage of the Leghorn is dominant over both the Houdan and Hamburgh black (Experiments 1 and 2) and also over the Cochin buff (Experiment 3). In a few cases this dominance is complete and the clear white is reproduced, while in the majority it is incomplete, the white ground colour being ticked with black (Experiments 1 and 2) or patched with buff and brown (Experiment 3); the black ticking is slight and inextensive compared with the ground colour and the buff and brown patching is chiefly confined to the head, neck, and breast.* A few apparent exceptions to dominance of white occurred in these matings, including blacks, cuckoos, and buffs, but as the sequel shows, caution is necessary before we ascribe these exceptions to failure of dominance.

In F_1 the black plumage, both of the Houdan and the Hamburgh, is dominant over the buff of the Cochin (Experiments 5 and 6), in all cases the dominance is incomplete, the black ground colour being strongly marked and shaded with brown. The dominance of black is more complete in the down than in the adult plumage.

In F_2 the hybrid dominant whites of F_1 mated together gave dominant whites and recessive blacks in the proportion of 3·1 : 1 (Experiment 7), mated with a pure recessive black they gave dominant whites and recessive blacks in the proportion of 1·0 : 1 (Experiment 11), mated with a pure dominant white they gave all dominant whites (Experiment 9), and mated with a pure buff they gave whites and blacks in the proportion of 1 : 1·0 (Experiment 12).

In F_2 the hybrid dominant blacks of F_1 mated together gave dominant blacks and recessive buffs in the proportion of 2·8 : 1 (Experiment 8), and mated with a pure dominant black gave all dominant blacks (Experiment 10).

In F_2 the hybrid dominant whites of F_1 mated with a hybrid dominant black of F_1 gave whites and blacks in the proportion of 1 : 1·0 (Experiment 13). Although the nature of the dominants and recessives raised in F_2 has not yet been been tested in F_3, yet judging by the detailed down markings of the incomplete dominants of white and black parentage, there is little doubt that with these the segregation is on Mendelian lines, at the same time it must be pointed out that wherever the buff element is concerned in the parentage the variation is much more continuous than in F_1 (*cf.* Experiments 8, 12,

* *Cf.* Bateson and Saunders, Report I (1902), pp. 95, 98.

and 13). It may be that white and black are elementary characters, and buff a compound one which in F_2 more than in F_1 is resolved into its component parts, or it may be that black and buff when once united in F_1 do not segregate so sharply as white and black undoubtedly do. In either case it may be significant that in F_1 the dominance of both white and black over buff is much less complete than that of white over black. Experiments are now in progress to test this question.

With regard to the few apparent recessives that occurred in the white matings of F_1. I have only been able to follow up those of Experiment 1, and they have proved an interesting study. These 11 chicks were out of supposed pure white Leghorn hens by a pure recessive black Houdan cockerel (ticked with white), all were born with black down notwithstanding that their 94 birth-mates were dominant whites. These black chicks, though apparently similar in the down, developed into two distinct types in their first plumage, 6 were black and 5 were cuckoo; of the 6 blacks, 5 were practically clear black save for a few inconspicuous white ticks in the crest, these exactly resembled in their plumage the Crève-Cœur breed, the remaining black was mottled all over with white, like a typical light Houdan (this unfortunately died); the 5 cuckoos were grey-white barred with blue-black, with odd black or white feathers; both the blacks and the cuckoos were shaded with brown as in the Houdan parent. Curiously, and unfortunately in some respects, the 6 blacks were all pullets and the 5 cuckoos all cockerels.

With regard to the black birds, the question naturally arose whether they were pure recessives RR or whether the usual dominant white character had receded, leaving them RD. In order to test this, the 5 black pullets were mated with a pure recessive black Houdan cockerel (mottled with white) (Experiment 15); eggs from this pen produced 48 chicks, all of which were black with white heads like the typical Houdan. These results show that the black pullets raised in Experiment 1 were in composition RR, for if they had been RD some dominant white chicks would surely have appeared in this experiment, when they were mated with a pure recessive.

[Note added December, 1904.

After this account was written one of the original white hens was found to have developed distinct colour-ticks in the hackles. To the impurity thus manifesting itself, the appearance of pure recessives in F_1 should, doubtless, be attributed.]

With regard to the nature of the exceptional cuckoo cockerels in Experiment 1, the experiments are not yet completed, though, so far, they have proved interesting, and bid fair to yield useful results. One of the cuckoo cockerels was mated with 2 of the black

pullets; eggs from this pen produced 43 chicks, all of which had black down; 34 were ticked with white, 7 had white heads, and 2 were strongly shaded grey. All were more or less shaded with brown as in the Houdan; 31 of these were reared, and in their first plumage were 17 cuckoos and 14 blacks. Of the cuckoos 7 were cockerels and 10 were pullets, and of the blacks 8 were cockerels and 6 were pullets, so that the correlation of black with ♀ and cuckoo with ♂ in F_1 was not maintained in F_2.

The cuckoos were precisely similar to those of F_1, having a grey-white ground barred with blue-black, with odd black or white feathers. All had a distinct brown shade in the plumage. The blacks were of two types, dark Houdans and Crèves, suggesting that the cuckoo male parent was giving off black gametes. No dominant whites appeared in this mating, suggesting that the cuckoo male parent was *not* giving off dominant white gametes.

Further experiments are now in progress to carry this Mendelian analysis of the cuckoo cock a stage further, although an interesting complication has recently arisen in the fact that this bird has in his second plumage moulted out almost *clear white*, a single feather only, on the back, being slightly tipped with grey.

(3) *Feet.*

(*a*) All D's.

Gen.	Expt.	D.	R.
F_1	1	103	2
F_1	4	6	0
F_1	5	4	1
Total observations..		113	3
Mendelian calc. ...		**116**	**0**

(*b*) All R's.

Gen.	Expt.	D.	R.
F_1	2	0	57
F_1	3	0	60
F_1	6	0	107
F_2	8	0	119
F_2	10	0	56
Total observations ..		0	399
Mendelian calc. ...		**0**	**399**

(*c*) 3 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	7	179	47	3·8 : 1
Total obs.		179	47	3·8 : 1
Mendelian calc.		**169·5**	**56·5**	**3 : 1**

(*d*) 1 D : 1 R.

Gen.	Expt.	D.	R.	Ratio.
F_2	9	63	72	1 : 1·1
F_2	11	23	78	1 : 3·3
F_2	12	45	61	1 : 1·3
F_2	13	127	180	1 : 1·4
Total obs.		258	391	1 : 1·5
Mendelian calc.		**324·5**	**324·5**	**1 : 1**

In F_1 the extra-toe of the Houdan is dominant over the normal foot of the Leghorn, Hamburgh, and Cochin (Experiments 1, 4, and 5).

In some cases the dominance is complete, the extra-toe being repro-
duced in its entirety ; in other cases the dominance is incomplete, all
stages of extra-toe being produced from the almost perfect toe down
to the mere duplication of the nail ; in a few cases the e.t. (in all its
stages) is found on one foot only, the other foot being apparently
normal ; in a few cases there is simply an elongated hallux.*
A few apparent exceptions to dominance of e.t. occurred in Experi-
ments 1 and 5.

In F_2 the hybrid dominant e.t.'s of F_1 mated together gave dominant
e.t.'s and apparently recessive no e.t.'s in the proportion of 3·8 : 1
(Experiment 7) ; mated with pure recessive no e.t.'s they gave dominant
e.t.'s and apparently recessive no e.t.'s in the varying proportions of
1 : 1·1 (Experiment 9), 1 : 1·3 (Experiment 12), 1 : 1·4 (Experiment 13),
and 1 : 3·3 (Experiment 11).

The two exceptions to dominance in Experiment 1 of F_1 were
fortunately of two sexes, and when mated together gave 22 chicks, of
which 14 had e.t. and 8 with normal feet. The same cockerel was
also mated with 4 Hamburgh-Cochin hens raised in Experiment 6, all,
of course, with pure R normal feet, 24 chicks were raised, of which
11 had e.t. and 13 no e.t. The same pullet (Experiment 1) also gave
some chicks with e.t. when mated with a pure Leghorn cockerel with
R normal feet. These results prove that the apparently recessive feet
with no trace of e.t. in Experiment 1 are in reality RD's, as both birds
gave chicks with e.t. when bred together and with pure recessives.
This is apparently a case where the usual dominant character has
receded in F_1 to re-appear in F_2, and may safely be described as a true
instance of the failure of dominance.† The fact of a recessive character,
like normal foot, dominating occasionally in F_1 and proving in F_2 to
be in reality RD is unfortunate, because it may lead to serious com-
plications, e.g., in Experiments 7, 9, 11, 12, and 13, noted above, we
have no certainty that all the apparent recessives are RR's, as a few
of them may be RD's, and if each bird with normal foot has to be
tested individually in F_3 before it can be counted in F_2, it will be
impossible to test the foot character on a statistical basis without great
labour and expense, and it is quite possible that on account of this
complication the foot character will have to be abandoned in future
experiments, notwithstanding that in reality its inheritance may be
in accordance with the Mendelian principles. Judging broadly from
the above experiments in F_2, it is evident that the segregation is on
Mendelian lines, the only notable exception being Experiment 11
where the ratio is 1 : 3·3 instead of the equality expected.

In this experiment, there is not only a large excess of recessives, but
even the dominants are abnormal, tending towards the recessive

* *Cf.* Bateson and Saunders, Report I (1902), p. 97.
† *Cf.* Bateson and Saunders, Report I (1902), pp. 102, 113, 115.

character, for the majority of those with e.t. have it on one foot only, which is quite different from the normal result in all the other experiments, where the one-sided e.t.'s are in a small minority. These facts point to some abnormal disturbance in this experiment.

(4) *Shank-feathering.*

<table>
<tr><td colspan="4" align="center">(a) All D's.</td><td colspan="4" align="center">(b) All R's.</td></tr>
<tr><td>Gen.</td><td>Expt.</td><td>D.</td><td>R.</td><td>Gen.</td><td>Expt.</td><td>D.</td><td>R.</td></tr>
<tr><td>F_1</td><td>3</td><td>60</td><td>0</td><td>F_1</td><td>1</td><td>2</td><td>108</td></tr>
<tr><td>F_1</td><td>5</td><td>5</td><td>0</td><td>F_1</td><td>2</td><td>0</td><td>57</td></tr>
<tr><td>F_1</td><td>6</td><td>107</td><td>0</td><td>F_1</td><td>4</td><td>0</td><td>6</td></tr>
<tr><td>F_2</td><td>12</td><td>106</td><td>0</td><td>F_2</td><td>7</td><td>7</td><td>219</td></tr>
<tr><td></td><td></td><td></td><td></td><td>F_2</td><td>9</td><td>0</td><td>135</td></tr>
<tr><td>Total observations..</td><td></td><td>278</td><td>0</td><td>F_2</td><td>11</td><td>0</td><td>101</td></tr>
<tr><td>Mendelian calc. ...</td><td></td><td>278</td><td>0</td><td>Total observations ..</td><td></td><td>9</td><td>621</td></tr>
<tr><td></td><td></td><td></td><td></td><td>Mendelian calc. ..</td><td></td><td>0</td><td>630</td></tr>
</table>

<table>
<tr><td colspan="5" align="center">(c) 3 D : 1 R.</td><td colspan="5" align="center">(d) 1 D : 1 R.</td></tr>
<tr><td>Gen.</td><td>Expt.</td><td>D.</td><td>R.</td><td>Ratio.</td><td>Gen</td><td>Expt.</td><td>D.</td><td>R.</td><td>Ratio.</td></tr>
<tr><td>F_2</td><td>8</td><td>115</td><td>4</td><td>28·7 : 1</td><td>F_2</td><td>10</td><td>35</td><td>21</td><td>1·6 : 1</td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td>F_2</td><td>13</td><td>195</td><td>112</td><td>1·7 : 1</td></tr>
<tr><td>Total obs. ..</td><td></td><td>115</td><td>4</td><td>28·7 : 1</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td></td><td></td><td></td><td></td><td></td><td>Total obs. ..</td><td></td><td>230</td><td>133</td><td>1·7 : 1</td></tr>
<tr><td>Mendelian calc. ....</td><td></td><td>89·2</td><td>29·7</td><td>3 : 1</td><td>Mendelian calc. ....</td><td></td><td>181·5</td><td>181·5</td><td>1 : 1</td></tr>
</table>

In F_1 the shank-feathering of the Cochin is dominant over the clear shanks of the Leghorn, Houdan, and Hamburgh (Experiments 3, 5, and 6). In all cases the dominance is incomplete, the length and number of the feathers being reduced to a fairly uniform one-half. No exceptions to this incomplete dominance were observed.

In F_2, the hybrid dominant feathered shanks of F_1, mated together, gave a large number of dominant feathered shanks, with a few recessive clear shanks (Experiment 8); mated with pure recessive clear shanks, they gave dominants and recessives in the proportion of 1·6 : 1 (Experiment 10) and 1·7 : 1 (Experiment 13). The Mendelian expectation for Experiment 8 was 3 D : 1 R, while the actual result was most exceptional, being, in fact, nearer 30 : 1 than 3 : 1.

The nature of the dominants, too, was different, for, while the Mendelian expectation was approximately 30 full-feathered and 60 half-feathered, the actual result was 17 full-feathered, 20 three-fourths, 57 half-feathered, 13 one-fourth, and 8 with feather traces. In fact, the dominants in F_2 represented a continuous series of feathering, ranging from full to clear, while in F_1 they were uniformly half-feathered. In Experiments 10 and 13 there was also continuous

variation among the dominants, but the series only extended from one-half-feathered to clear, and the number of recessives was not far from the Mendelian expectation. From this it would appear that the Mendelian principles are at work in these aberrant phenomena, but are masked by something not yet perceived. It will be best, therefore, to reserve any attempt at explanation of them until the Mendelian analysis is completed in F_3.

Both in F_1 and F_2, among the recessive matings, a few slight traces of dominant feathering appear; these are apparently confined to Experiments 1 and 7, and, as similar traces appeared in the Houdan P_1, it is evident that the impurity came from that side, especially as it was never observed in the Leghorn.

One curious feature in this impure inheritance, is that in both experiments, where it showed itself, the actual parents did not show it, and, in the case of Experiment 7, neither the two parents nor the grandparents showed it, though the collaterals did ("uncles") (cf. Experiments 1 and 7). The impurity, therefore, seems to have remained latent for two generations in the direct line, though appearing in the collaterals.

Grand Totals (F_1 and F_2).

(a) All D's.

Characters.	D.	R.
Combs	437	0
Downs	499	26
Feet	113	3
Shanks	278	0
Total obs.	1327	29
Mendelian calc.	1356	0

(b) All R's.

Characters.	D.	R.
Combs	0	60
Downs	0	6
Feet	0	399
Shanks	9	621
Total obs.......	9	1086
Mendelian calc.	0	1095

(c) 3 D : 1 R.

Characters.	D.	R.	Ratio.
Combs....	470	182	2·5 : 1
Downs ...	259	86	3·0 : 1
Feet	179	47	3·8 : 1
Shanks ...	115	4	28·7 : 1
Total obs.	1023	319	3·2 : 1
Mendelian calc....	1006·5	335·5	3 : 1

(d) 1 D : 1 R.

Characters.	D.	R.	Ratio.
Combs....	134	107	1·2 : 1·0
Downs....	252	262	1·0 : 1·0
Feet	258	391	1·0 : 1·5
Shanks ...	230	133	1·7 : 1·0
Total obs.	874	893	1·0 : 1·0
Mendelian calc. ..	883·5	883·5	1 : 1

The adding together of the results of different characters in different experiments may not be strictly legitimate, but, as each character in each experiment has been first dealt with separately, and all the details which go to make up the totals have been given, the objections

to this method are reduced to a minimum, and are far outweighed by the advantages of the large numbers thus made available.

In regarding the 5560 observations as a whole, one cannot but be impressed by the close approximation to the Mendelian expectation ; at the same time, it must not be forgotten that, although most of the characters have appeared to segregate, in accordance with the Mendelian principles, we do not yet know that the extracted recessives are pure, nor do we know that the complete dominants consist of pure and impure in the Mendelian proportions; several generations will have to be bred before these questions can be definitely determined.

If, however, the experiments be taken as they stand, the close agreement with the Mendelian expectation cannot be without significance.

Summary of Conclusions from Experiments with Poultry.

(1) When certain pure breeds are mated with their own kind, certain structural and colour characters breed true to type ; in some of these characters there is little or no variation, while in others the variation about the type is considerable.

(2) When these pure breeds are crossed with one another, certain of these characters are usually dominant over the corresponding character, which is recessive. Dominant characters are rose comb, white plumage, extra toe, feathered shanks, white and blue shanks, crested head, brown egg-colour and broodiness, while leaf and single comb, black and buff plumage, normal foot, clear shanks, yellow shanks, uncrested head, white egg-colour and non-broodiness are all recessive to the above corresponding dominants. In their turn, some of these recessives are themselves dominant over others, *e.g.*, leaf comb and black plumage are dominant over single comb and buff plumage, which remain recessive.

Dominance appears to be of two kinds, *Complete* and *Incomplete*. Complete dominants are practically indistinguishable from the pure dominants ; incomplete dominants are variable, showing the influence of the recessive character in different degrees, the intensity of the dominant character being correspondingly diminished. In some character matings the dominance is apparently always complete, in some it is always incomplete, and in others it is sometimes complete, but more often incomplete. On the whole, the incomplete dominants appear to be about twice as numerous as the complete dominants. The pure recessive is always quite distinct from both kinds of dominants.

(3) When the offspring of the dominant first crosses are bred together, and with various dominants and recessives, some of their progeny exhibit the dominant, and others the recessive, character, the proportions of each being, as a rule, in close agreement with Mendel's

law. In these crosses the dominants are again complete and incomplete, the former being indistinguishable from the pure dominants, and the latter corresponding to the incomplete dominants in the first crosses with fair consistency. The recessives are, as a rule, similar to the original ones, but their purity has not yet been tested.

(4) No correlation was found between the comb, down, and foot characters, each, apparently, being a unit-character with an independent inheritance. When any two or three of these characters were considered together in individual birds, the numbers of each type in the second crosses approximated closely to the numbers calculated by means of Mendel's law.

(5) A few exceptions to the general results stated in (2) and (3) may be briefly noted : (*a*) a few recessives appeared in some of the first crosses instead of the usual dominants ; these proved to be of two kinds, impure and pure, the former giving some dominants when mated with a pure recessive (p. 80), while the latter did not (p. 79). The appearance of a few impure recessives in the first cross indicates that the normally recessive character (normal foot) may sometimes dominate, which fact may lead to future complications. The pure colour recessives in F_1 are, without doubt, to be ascribed to impurity in a white parent, signs of which subsequently revealed themselves. (*b*) In all the second crosses, where buff plumage and shank-feathering were concerned, the variation of the offspring appeared to be much more continuous than in the corresponding matings of the first crosses. Experiments are in progress to test the nature of these exceptions by Mendelian analysis.