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Report III.

Experimental studies in the Physiology of Heredity

by
W. Bateson and E. R. Saunders

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REPORTS TO THE EVOLUTION COMMITTEE OF THE ROYAL SOCIETY.

REPORT III.

EXPERIMENTAL STUDIES IN THE PHYSIOLOGY OF HEREDITY.

By W. BATESON, M.A., F.R.S., Miss E. R. SAUNDERS, Lecturer, Newnham College, and R. C. PUNNETT, M.A., Fellow of Gonville and Caius College, Cambridge, Balfour Student.

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CORRIGENDA TO REPORT II.

Page 12. In Exp. 18D, for "51" read "54."
„ 16. In Exp. 28B, for "67" read "64."
„ 18. In heading of table, for "20*a* and 20*b*" read "30A and 30B."
„ 33. In left-hand column, for "18B, 19, 18A" read "28B, 29, 28A." and for "31" read "31C."
„ 46. In table, for "K" read "V_1."
„ 85. In I, for "Blanche Burpee × E. H. red," read "× E. H. round."
„ 117, line 8. For "× white" read "× coloured."
„ 121, line 11. For "Abyssian" read "Abyssinian."

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Introduction.

Grants received from the Government Grant Fund, and from the British Association, have been applied in part to the cost of the experiments upon which we now report, and in part to other researches which will be described hereafter. These sums would have been insufficient to enable us to carry on the work, and the scope of the investigation must have been greatly reduced had it not been for the generosity of Mrs. Herringham, who in 1904 placed a fund at our disposal for this purpose. We wish to record our deep sense of obligation to her for this assistance.

The results obtained since the last Report have at length provided expressions which include most of the phenomena witnessed in the case of Sweet Peas and Stocks. These various results can now be treated as parts of a consistent whole, and a great simplification of statement is thus made possible.

Flower-colour in Sweet Peas (LATHYRUS) *and Stocks* (MATTHIOLA).

The phenomena in these two plants are essentially similar in that (1) a purple F_1 results from a cross between certain white* varieties; (2) F_2 consists of purples, reds, and whites. In each case subordinate colour-classes are present among the purples and among the reds. These minor distinctions are for the present disregarded.

The facts show that the appearance of colour is due to the association, in one zygote, of two factors belonging to independent allelomorphic pairs. The presence of either factor alone is insufficient to cause colour in the zygote. One of the two factors was brought in by each original parent.

Speaking of the two factors as C and R, the corresponding allelomorphs are respectively *c* and *r*, the absence of those factors. When all the combinations of two such allelomorphic pairs are represented in F_2, there will, among 16 individuals, be on an average 9 in which both factors are present, and 7 having only one or neither of them, as shown in the accompanying scheme (fig. 1).

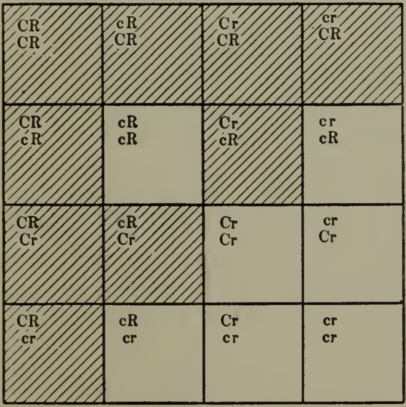

FIG. 1.—Diagram showing the nature of the ratio 9 : 7 in F_2. The character, colour for example, appears only when C and R meet. Each square is a zygote, and the lettering shows its gametic composition. The hatched squares represent coloured plants; the plain are whites.

The 9 will be coloured, the 7 will be white. There will be 4 gametically distinct types among the coloured and 5 among the

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* White here means non-sap-coloured. In the Sweet Peas the two parent forms were white with long pollen, and white with round pollen. In the Stocks the corresponding parent types were white glabrous and cream glabrous. The cream-colour is due to the presence of yellowish plastids, a character recessive to colourless plastids. This feature is quite distinct from sap-colour, and, in that respect, creams are true whites.

whites. Many of these extracted types have already been recognised experimentally.

The ratio of coloured to white is thus 9 : 7. The coloured, however, consist of two main classes, purples and reds, in the ratio 3 purple : 1 red. The ratio of the three classes is therefore 27 purple : 9 red : 28 white. Such a distribution evidently results from the presence of a third allelomorphic pair, B, *b*, the presence or absence of a *blue* factor, which is dominant over the redness; but this only produces a perceptible effect when both C and R are also present. The relation of their distribution to the ordinary tri-hybrid scheme may be shown thus—

$$\underbrace{27 : 9}_{\substack{36\\9}} : \underbrace{9 : 9 : 3 : 3 : 3 : 1}_{\substack{28\\7}}$$

In the Sweet Peas it is clearly the long-pollened white which introduced the factor B; for when crossed with red types it gave purples, whereas the round white gave reds in such crosses. The occurrence on one occasion of red bicolor, the "half-reversion" of Rep. II, p. 84, in F_1 from long white × round white, was due to the circumstance that the particular long white used had no B factor (*cf.* scheme, p. 10).

In Stocks this factor was introduced by the *white* glabrous Stock, not by the cream glabrous; for F_1 from white × red is purple, but F_1 from cream × red is red (see p. 6).

Some outstanding problems are presented by the sub-classes of purples and of reds, which exist in both the Sweet Pea and the Stock F_2 families. Several of these differences depend on the presence of other simple allelomorphs, and are merely superposed on the primary classes, while others are of a more complex nature, which is not yet understood.

The fact is remarkable that in both Stocks and Sweet Peas certain lighter colours are dominant to the darker, in the sense that in families containing both, the darker can be bred from the lighter, while the contrary is impossible.

Thus in the Stocks light purple is to dark purple what in Sweet Peas the reversionary purple with blue wings is to the purple with purple wings; and light red or "flesh"-coloured are to the full red Stocks what the Painted Lady Sweet Pea with light wings is to the Miss Hunt form with magenta wings.

Certain cases in which a *coloured* type was used as an original parent gave results which cannot yet be brought into harmony with this scheme, but the majority now present no difficulty.

The results here summarised agree well with those obtained by Tschermak in Phaseolus, where a somewhat similar case of reversion in

F_1 was studied. The chief difference lies in the fact that in our case the original parents were both white.

Mutatis mutandis, Correns' case in *Mirabilis* presents many points of similarity, but in that plant the pigmentary substances are evidently different.

The phenomena described (Rep. II, pp. 44 to 53) in *Salvia Horminum* are now obviously reducible to the same system, and the figures which we took to represent the ratio 2 : 1 : 1 are in reality* examples of 9 : 3 : 4. It is likely that all plants possessing similar sap-coloured varieties will be found to conform to this scheme. We note, however, that in *Primula Sinensis* (unpublished results of R. P. Gregory) blue has been shown to be recessive, and presumably, therefore, the nature of the pigmentary substances is different.

It is premature to discuss the physiological nature of the two factors which, when they meet, produce colour, but it is not inconceivable that they may yet be isolated.

HOARY LEAVES IN STOCKS.

The character hoariness in Stocks is similarly due to the simultaneous presence of two independent factors which we shall call H and K, allelomorphic to *h* and *k*, the absence of those factors. The F_2 results show that, generally speaking, hoariness, the result of the interaction of H and K, cannot be produced unless C and R, the colour-factors, are also present. The existence of *white*-flowered hoary strains creates a difficulty. As regards "white" *incana*, this difficulty is only apparent, for it is certain that "white" *incana* is in reality a coloured form. Its flowers tinge on fading, and its embryos have the deep green colour characteristic of purple-flowered types. The white hoary Bromptons, however, are a marked exception to the general rule. Their flowers are not in any way coloured, and their seeds have at most a slight green tinge (sometimes none). Bromptons have been little studied in these experiments, and as yet we have no clue to the nature of their peculiarity.†

In a few cases (see *e.g.*, Exp. 28 B) there are rather wide departures from the F_2 numbers indicated by this scheme, and it is no doubt just possible that these figures indicate some further complication. With

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* For instance, Experiments 16 and 17 (Report II, p. 50) give in F_2 respectively 59 purple, 25 pink, 34 white, and 255 purple, 92 pink, 114 white; together, 314, 117, 148, when the expectation is 324, 108, 144. Similarly, Experiment 13 gave F_2 26 purple, 17 white. At that time equality was the supposed expectation, and the excess of purples was remarked on. There can now be no doubt that the true ratio was 9 : 7, which would give 24·2 and 18·8.

† As white Bromptons × cream glabrous give red F_1, it is evident that they do not carry B.

these exceptions, there is now a satisfactory account of all the chief phenomena, many of which were previously quite paradoxical. For example, we had found that

	1.	Cream	glabrous	×	white	glabrous	gave	purple	hoary.
	2.	,,	,,	×	purple	,,	,,	,,	,,
	3.	,,	,,	×	red	,,	,,	red	,,
	4.	White	,,	×	purple	,,	,,	purple	,,
	5.	,,	,,	×	red	,,	,,	,,	,,
but	6.	Any red or purple	,,	×	any red or purple	,,	,,	red or purple	*glabrous.*

These facts were not consistent with the simple supposition that cream, for instance, bore a factor α, which, when it met a factor β borne by, say red, gave hoariness. For since *white* × red also gives hoary F_1, the white must similarly bear α; but though on this reasoning white and cream are alike bearing α, yet when crossed they also give hoary F_1. The explanation is that the types have the following composition :—

White glabrous.........	H and K	C or R
Cream ,, ...	H and K	R or C
Purple ,, ...	H or K	C and R
Red ,, ...	H or K	C and R

Moreover, the whites and purples carry B, while the creams and the reds are without this factor.

That this is the true account appears from the distribution of characters in F_2. From cream glabrous × white glabrous, F_2 consists of coloured *which are all hoary*, and whites and creams *which are all glabrous*. When, however, cream or white glabrous is crossed with a sap-coloured glabrous, all the hoary are coloured in F_2; but of the glabrous some are coloured and some are white.

Again, F_2 from "white" *incana* × sap-coloured glabrous, contains *tinging whites* in both hoary and glabrous classes.

From these considerations it follows that hoary F_2 plants may be of three kinds—(1) those which give all hoary in F_3; (2) those that give 9 hoary to 7 glabrous; (3) those that give 3 hoary to 1 glabrous. All these kinds have been experimentally recognised (see p. 41).

"LATENCY"; RESOLUTION; DETERMINING FACTORS.

Cuénot showed that when in mice a new colour appears in F_1 from colour × albino, this is due to the introduction by the albino of a factor which, when it meets the colour brought in by the coloured parent, modifies it. For instance, when black × white gives grey (*i.e.*, wild colour) F_1, this is due to a grey determining factor, brought in by the albino, meeting the colour brought in by the black. The grey determiner thus dominates over the black determiner to which the original black owes its blackness; and F_2 will be 9 grey, 3 black, 4 albino. Cuénot represents the allelomorphic pairs as—

Colour (C).	No colour (A).
Grey determiner (G).	Black determiner (B).

More strictly, perhaps, we think they may be represented as

Colour (C).	Absence of ditto (c.).
Grey determiner (G).	,, ,, (g.).
Black ,, (B).	,, ,, (b.).

The arithmetical results are, of course, the same.* In the case just mentioned both parents can be regarded as homozygous in B, while the albino is also homozygous in G. But when grey × albino gives in F_2 3 grey : 1 albino, the fact that no new colour appears is due to the circumstance that the albino is homozygous in G. When the same cross gives in F_2 9 grey, 3 black, 4 white, the occurrence of the blacks proves that the albino carried no G, and that both the original parents were homozygous in B.

Albinos extracted from blacks cannot be bearing any determiner dominant to B; and if the blacks give no colours but blacks (and albinos), then the albinos so extracted must be homozygous in B, although they may still carry determiners recessive to B—that of chocolate, for example. If the allelomorphic pairs are expressed in the way indicated, the relation of the plant to the animal cases becomes clear.

Analysis of this kind is applicable to many and perhaps to all of the phenomena which we have hitherto attributed to resolution of a compound allelomorph, though as now appears they are merely expressions of a simple Mendelian process. The polymorphic F_2 of Sweet Peas and Stocks is now almost entirely reducible to terms of the same simple system.

Animal and plant cases differ remarkably in the fact that in animals colour has not yet been shown to be due to the meeting of two complementary factors. For no instance is known of two albino animals giving coloured F_1; and similarly the ratio 9 coloured : 7 albino has not been met with in any F_2 from coloured × albino in animals, though in plants such cases are not now very rare. Consequently, if in animals colour does depend for its appearance on two complementary factors (apart from *determining* factors, which exist in plants and animals alike),

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* The correctness of this representation can be tested by crossing a wild grey mouse with a chocolate. If the view here expressed is right, *blacks* must appear in F_2.

it must be recognised either that they have never separated, or, as is more probable, that one of them is present in all individuals, whether coloured or albino. Animals have probably reached the stage in which one only of the two factors may be absent, whereas in some plants both may be absent from the gamete.

A character such as colour, depending on double factors, or hoariness in Stocks, produced by four factors, may no doubt be properly spoken of as a compound character, and so we may speak of its "resolution," but in a sense different from that we originally intended. The compound is now seen not to be, in its entirety, a unit allelomorphic to another unit-character, but to be made up of several characters, each belonging to an independent allelomorphic pair. Consequently, in these cases, the conception of synthesis becomes superfluous; for the fact that a new type appearing in F_1 may breed true after F_2 is now shown to be an ordinary phenomenon of homozygosis.

Castle and others have spoken of the presence of a determiner, *e.g.*, that for black, in the albino, as a "latency" of black in the albino. It should, however, be realised that it is not "black" as a whole which is latent. One of the factors needed to produce black is present—as a cryptomere, to use Tschermak's term—which cannot be made perceptible unless it meets colour in the zygote.

REVERSION.

The conception of reversion on crossing now takes a definite shape. Such reversion is simply the reappearance of a feature which had disappeared owing to the absence of one of the complementary factors. When 2 white Sweet Peas give a red bicolour F_1 there is reversion to the old "Painted Lady" type, because the two factors necessary for the development of that colour meet again. When the reversion is "total" (see Rep. II, p. 84, etc.) and F_1 is purple, the same two factors meet in the presence of the third element B, the determiner for purple. So for reversion in Stocks: when C meets R, the two whites give red F_1; if B is likewise present, a purple F_1. If both H and K, brought in by 2 glabrous types, meet in the presence of C and R, the further reversion to the hoary structure occurs. Somewhere in the history of the evolution of the modern types, the complementary elements have been split off and eliminated, giving rise to analytical variations.

GAMETIC COUPLING.

Early in the revival of breeding experiments, attention was called, especially by Correns, to the phenomenon of coupling between characters. Complete coupling has so far been most commonly met with among characters of similar physiological nature. Examples of complete coupling between characters apparently quite distinct in nature are less frequent. As an illustration, we may refer to the apparently universal association of procumbent habit with dwarf stature in Cupid Sweet Peas, though in Pisum there is no such association between dwarfness and procumbency.

Examples of *partial* coupling have not hitherto been adequately studied. A remarkable case occurs in regard to the distribution of the pollen-characters in F_2 from the white long × white round Sweet Pea. There is here a partial coupling between the purple flower-colour and the long pollen. The whole mass of F_2 consists of 3 long : 1 round. The whites taken alone are also 3 long : 1 round. The *purples*, however, show a great preponderance of longs over rounds, about 12 to 1, while among the *reds* the rounds are in excess over the longs, being about 3 to 1. These peculiar distributions only occur in families which contain both red and purple members. Families (in F_3, for example) consisting of purples alone, or of reds alone, or of either associated with whites, have normal compositions. Evidently the abnormal distribution in some way depends on the mode of segregation of the factors B and b from each other. A close approach to the observed F_2 numbers would be given by a system in which each 16 gametes were composed, thus:—

$$7AB + 1aB + 1Ab + 7ab,$$

where A is long pollen and a round pollen.

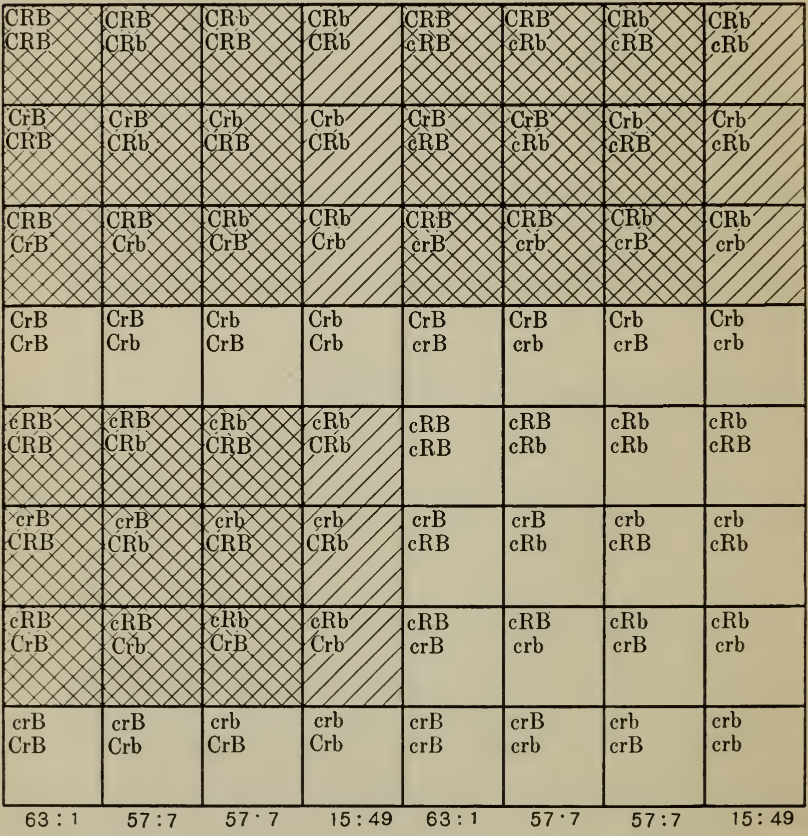
	Purple.		Red.		White.	
	Long.	Round.	Long.	Round.	Long.	Round.
Observed	1528	106	117	381	1199	394
Calculated	1448·5	122·7	122·7	401·5	1220·5	407·4

The distribution of the various characters may then be represented by the accompanying diagram (fig. 2), p. 10.

The significance of such partial coupling is obscure, and it may result from several processes, between which no discrimination can yet be made. Nothing *a priori* limits us to the view that all characters are segregated at one division, but no system of symmetrical dichotomies will give the 7 : 1 system. If, however, the gametes AB and ab belonged to a generation later than aB and Ab, and were produced by three divisions after segregation had taken place, the numbers 8AB + 1aB + 1Ab + 8Ab would result. Our statistics are not large enough to decide positively between 7 : 1 and 8 : 1, though the former ratio fits best. There is no proof that all gametes of one flower are of the same order or generation counting from the fertilised egg, and, for example, we may feel sure that the male and female cells at least belong to different generations. Such a conception would introduce great complexity into these analyses, and in particular we should have to forego the natural view that segregation occurs at the reduction-division. There is another way in which the numbers 7 : 1 might be produced. If it were assumed that two other pairs of unknown factors X, x, Y, y were also present, and that the character A is always coupled with either X, Y, or B, the result would be that the series of 16 gametes would consist of

$$7\mathrm{AB} + 1a\mathrm{B} + 1\mathrm{A}b + 7ab.$$

All the characters would then be distributed in one dichotomy, and the



CRB CRB	CRB CRb	CRb CRB	CRb CRb	CRB cRB	CRB cRb	CRb cRB	CRb cRb
CrB CRB	CrB CRb	Crb CRB	Crb CRb	CrB cRB	CrB cRb	Crb cRB	Crb cRb
CRB CrB	CRB Crb	CRb CrB	CRb Crb	CRB crB	CRB crb	CRb crB	CRb crb
CrB CrB	CrB Crb	Crb CrB	Crb Crb	CrB crB	CrB crb	Crb crB	Crb crb
cRB CRB	cRB CRb	cRb CRB	cRb CRb	cRB cRB	cRB cRb	cRb cRb	cRb cRB
crB CRB	crB CRb	crb CRB	crb CRb	crB cRB	crB cRb	crb cRB	crb cRb
cRB CrB	cRB Crb	cRb CrB	cRb Crb	cRB crB	cRB crb	cRb crB	cRb crb
crB CrB	crB Crb	crb CrB	crb Crb	crB crB	crB crb	crb crB	crb crb
63 : 1	57 : 7	57 · 7	15 : 49	63 : 1	57 · 7	57 : 7	15 : 49

FIG. 2.—Scheme of distribution of colour-factors in F_2. From E. Henderson (Sweet Pea), white, long pollen × white, round.

The table is an expansion of that shown in fig. 1, and exhibits the effect of the blue factor, B. The cross-hatched squares are purple-flowered plants; the single-hatched are red; the plain are whites.

The figures at the foot of each column show the ratio of long-pollened to round-pollened in each square of that column, on the hypothesis given in the text.

apparently partial operation of the coupling would be elucidated. The difficulty in the way of this suggestion is that no characters corresponding with X and Y have yet been identified which fulfil the required conditions.

This discussion cannot now be carried further. It is clear that gametic coupling, however caused, plays a large part in the phenomena of heredity. As another illustration of the coupling of a structural with a pigmentary character, we may mention that in some strains of Sweet Pea (to be described hereafter) the hooded standard is coupled with certain types of flower-colour ; being, so far as we have seen, never found in purple—or red—bicolours. Presumably, the facts related in Rep. II, p. 91, indicate a similar partial coupling between the light axil and the peculiar contabescence of anthers.

Zygotic Coupling must be carefully distinguished from gametic. A character may be developed in those zygotes alone which possess some second character; but in the system of gametic distribution of the allelomorphs there may be no coupling between the two characters. For example, when the peculiar yellow flush is developed in the petals of a plant of *Primula Sinensis* which bears the minute pollen of the long-styled type, the style does not rise above the anthers, constituting the "homostyle" condition.* Such plants are homozygous in respect of yellow flush and long-style pollen, but the two characters are entirely independent in their gametic distributions, as is proved by F_2 from homostyle × short style. Some very important illustrations of zygotic coupling are provided by the characters that are peculiar to one or other sex in sexually dimorphic species.

POULTRY.

(Experiments by W. Bateson and R. C. Punnett.)

Comb Characters.

Relation of Rose-comb to Pea-comb.

In our last Report (p. 112) we showed that, judged by the criterion of gametic output, 4 kinds of r.p. birds exist, viz., r. × p., r.p. × r.p., r.p. × r., and r.p. × p. Birds of the constitution r. × p. gave, on mating with single comb, equal numbers of the 4 types r.p., r., p., and s. Birds of the constitution r.p. r. and r.p. p. gave when crossed with s. equal

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* W. Bateson and R. P. Gregory, 'Roy. Soc. Proc.,' 1905, vol. 76, p. 581.

numbers of r.p. and r., and of r.p. and p. respectively, whilst a pure r.p. bird gave only r.p. when similarly crossed. We suggested that a fifth type of r.p. bird was conceivable, *i.e.*, one giving off equality of r.p. and s. gametes. In order to test this possibility a pure r.p. ♀ was mated with a single comb ♂ (Experiment 268). Three ♀s. resulting from this cross were in the following year mated with their father (Experiments 342 and 343). From these matings all the 4 types of comb resulted. In other words, the gametic output of birds produced by the union of r.p. with s. cannot be distinguished from that of birds produced by mating r. with p. Judged, therefore, by gametic output, only 4 types of comb are known to exist.

Since the publication of the last Report we have been led to alter our views as to the nature of the r.p. comb, and have recently pointed out* that the case may be looked upon as one of simple dihybridism. On this view the allelomorphic pairs are (1) Rose and no-rose; (2) Pea and no-pea—the first member of the pair being in either case dominant to the second. The rose-comb is, therefore, in constitution Rose + no-pea (*R. no P.*) and the pea-comb Pea + no-rose (*P. no R.*). Consequently the zygote formed by the union of r. and p. has the constitution *R. no P. : P. no R.*, and the appearance of the walnut form must be regarded as due to the presence in the zygote of the 2 unit characters *R.* and *P.* which belong to distinct allelomorphic pairs. From such a zygote 4 sorts of gametes must be produced in equal numbers, viz., *R.P.*, *R. no P.*, *P. no R.*, and *no R. no P.* Since the single on this view must be homozygous and producing gametes of the constitution *no R. no P.*, it follows that an *r.p.* bird such as we are considering will, when mated with a single, give rise to 4 zygotic types in equal numbers. Constitutionally these will be (1) *R. no R. : P. no P.*, (2) *R. no R. : no P. no P.*, (3) *P. no P. : no R. no R.*, and (4) *no R. no R. : no P. no P.*, and visibly such birds will be *r.p.*, *r.*, *p.*, and *s.* respectively. Again, when mated together, 2 such *r.p.* birds will produce *r.p.*, *r.*, *p.*, and *s.* birds in the ratio 9 : 3 : 3 : 1. The constitution of such birds is set forth in the accompanying table (p. 13), which shows that the r.p. birds may be of 4 sorts, viz. (1) homozygous for both *R.* and *P.*; (2) homozygous for *R.* and heterozygous for *P.*; (3) homozygous for *P.* and heterozygous for *R.*; and (4) heterozygous for both *R.* and *P.* The relative proportions of birds belonging to the 4 classes (1), (2), (3), and (4) will be 1 : 2 : 2 : 4. As the table shows, one of the 3 roses and one of the peas will be homozygous.

We have already pointed out† that the proportion of the different combs in the various matings affords no criterion for judging between this view and the one previously suggested. The new view, however, explains the identity of the combs produced by the crossing of r. with

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* 'Proc. Camb. Phil. Soc.,' 13, p. 167.

† *Loc. cit.*

p. and of r.p. with s., thus dispensing with the conceptions of compound allelomorphs and synthesis.

RP RP (r.p.)	RP R, no P (r.p.)	RP no R, P (r.p.)	RP no R. no P (r.p.)
R, no P RP (r.p.)	R, no P R, no P (r.)	R, no P no R, P (r.p.)	R, no P no R, no P (r.)
no R, P RP (r.p.)	no R, P R, no P (r.p.)	no R, P no R, P (p.)	no R, P no R, no P (p.)
no R, no P RP (r.p.)	no R, no P R, no P (r.)	no R, no P no R, P (p.)	no R, no P no R, no P (s.)

During the past two years we have tested a considerable number of r.p. combs, with the result that each of the 4 types has been met with over and over again. Speaking generally, this form of comb exhibits much variation in size, shape, and amount of the special feathering on its posterior surface, though hitherto we have been unable to establish any connection between such variations and the gametic output of individuals in which they occur.* We may now consider in rather more detail the matings in which the various types of r.p. combs are concerned.

Pure r.p. (zygotic constitution *R.P.R.P.*).—This type has occurred in 2 Malay bantam hens (Experiments 242, 268, 284) and in a black-red Malay ♂ (Experiment 351) all purchased. It has also occurred in F_2 from an original cross of r. × p. (Experiments 255, 256, 333, 383). Further, we have one case (Experiment 366) where it was formed from 2 r.p. birds which were produced by the mating of r.p./p. with single. Since every bird with an r.p. comb must give off some gametes at any rate containing both *R.* and *P.*, we may, of course, expect some pure r.p. birds to be produced by the mating of any 2 birds with this form of comb. In all the above experiments r.p. combs alone resulted from the union of the pure r.p. bird with a single.

Combs r.p. × *p.* (zygotic constitution *R.P.P. no R.*).—(*Cf.* Experiments 196 to 197, 239, 271, 278, 287, 305, 314, 328, 336, 355, 357 to 358, 385, 387 to 388, 390, 391.)

The birds tested in Experiments 196 to 197, 239, and 287 were Malays with natural r.p. combs. The rest were produced artificially in F_2 from original matings r. × p., r.s. × p.s., or r.p. × s. On mating with singles this type of r.p. comb gave in all 285 r.p. and 296 peas, the expectation, of course, being equality.

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* *Cf.* Report II, p. 112.

Combs r.p. × *r.* (zygotic constitution *R.P.R. no P.*).—(*Cf.* Experiments 233, 283, 297, 316, 338 to 339, 360, 371 to 372.)

The bird tested in Experiment 283 was a ♂ Malay bantam, whilst those in Experiments 233 and 316 were Malay ♀s. The rest were artificially produced. Altogether 289 birds were produced, of which 149 had r.p. and 140 rose-combs, expectation as in the last case being equality.

Combs giving all 4 with Single (zygotic constitution *R. no P. P. no R.*).—(*Cf.* Experiments 208, 212 to 214, 217 to 218, 232, 234, 236, 238, 240 to 241, 243, 249, 251 to 252, 260 to 262, 272, 275, 277, 298, 300, 302 to 303, 306 to 307, 309, 311 to 313, 315, 317 to 320, 323 to 327, 329, 331 to 332, 334, 342 to 343, 345 to 348, 359, 361 to 365, 373 to 374, 382, 386.)

Of the 1,251 birds produced in the above experiments 373 were r.p., 425 pea, 413 rose, and 440 single, expectation in each case being 413. There is a marked deficiency of r.p. and a distinct excess of singles. These disturbances in the expected ratio of equality we are inclined to attribute to the behaviour of the 4 ♂s. used in Experiments 306, 347 to 349, and 373 to 374—cases which must be considered in rather more detail.

The ♂s. in Experiments 306 and 349 gave only 10 r.p. birds out of a total of 93, *i.e.*, only half the number expected, although the total number of chicks hatched was fairly large. These cases were not followed up, but when the same phenomenon reappeared in Experiment 373, the ♂ bird was mated also to 4 pure Br. L. ♀s. (Experiment 374). Again, there was a marked deficiency of r.p. chicks, pointing to something unusual happening among the gametes of this ♂. The bird has been kept in order that further experiments may be made next year.

Experiments 347 to 348 seem to point to a disturbance of a somewhat different nature. The ♂ (No. 144 of 1904) was originally mated with 3 single combed ♀s. to test the nature of his comb. Later on a black Andalusian ♀ and 2 Wh. L. ♀s. were introduced. The ♂ turned out to be giving off all 4 kinds of gametes, giving with the 3 original ♀s. and the black Andalusian 18 s., 26 r., 26 p., and 25 r.p. With the 2 White Leghorn hens, however, he gave an extraordinary deficiency of r. and r.p., the numbers being 17 s., 2 r., 17 p., and 3 r.p.

In the case of each of these 4 birds the numbers are so aberrant that we can for the present hardly avoid regarding them as due to some disturbing circumstances. The number of chickens involved is 309, viz., 107 s., 75 r., 86 p., and 41 r.p. Subtracting these numbers from the sum totals given above, we are left with 333 s., 338 r., 329 p., and 332 r.p., which is a very close approach to the expected ratio of equality.

Rose Pea-combs Mated Together.

Zygote *R. no P. P. no R.* × zygote *R. no P. P. no R.* In the last Report (p. 110) were mentioned four experiments of this nature in which the figures obtained were not far removed from the expected ratio of 9 : 3 : 3 : 1.

Further experiments of the result of this type of mating were made in 1904, and are set out in the table below:—

	s.	r.	p.	r.p.
Experiment 201	2	5	7	16
" 202	2	5	9	8
" 204	10	5	4	15
" 205	2	9	8	22
" 206	2	4	5	9
" 215	4	19	19	33
" 216	2	4	5	11
" 244	—	—	2	2
" 245	1	5	4	13
" 253	6	8	14	36
" 254	3	5	9	12
	34	69	86	177
Expectation	22·9	68·7	68·7	206·1

The result discloses a distinct excess of singles and peas, together with a deficiency of r.p.s. Examination of the table shows that whilst the result in certain cases (*e.g.*, Experiments 201, 205, 216, 245) fits closely with expectation, it is in other cases far removed from it. Thus in Experiment 204 we should have expected not more than 2 singles, whereas the actual number is 10. Yet the subsequent Experiments 212 and 300 prove that the ♀ was then giving off all four sorts of gamete in equal numbers, whilst Experiments 208 and 303 show that the same was also true of the ♂. It is conceivable, of course, that the numbers in Experiment 204 may be the result of chance, but, having regard to the fact that wherever any serious disturbance of the ratio 9 : 3 : 3 : 1 occurs it is generally accompanied by both excess of singles and deficiency of r.p.s., we are more inclined to attribute such aberrations to the presence of some disturbing circumstance hitherto undetermined.

"*Extracted*" *Combs from mating r.p.* × *r.p.*

Singles "extracted" from the cross r.p. × r.p. were mated together in Experiments 209, 210, 247, and 248. Of the 144 chicks resulting, all were single.

Seven extracted roses were tested, with the result that one turned out to be homozygous (Experiment 273) and the rest heterozygous (Experiments 246, 263 to 6, and 274). With single combed ♂s. these 6 birds produced 176 chicks, of which 92 were single and 84 rose. Extraction has clearly no influence upon the behaviour of rose and single combs.

An extracted ♂ pea-combed bird produced (in Experiment 230) 2 singles and 3 peas with a Br. L. ♀. In Experiment 231 an extracted pea-combed ♀ gave, with an s.c. ♂, 5 singles and 8 peas. In Experiment 228 an extracted p.c. ♂ was bred with 3 extracted p.c. ♀s., and gave 20 singles to 34 peas, the expectation being 13·5 : 40·5. Such an aberration from the expected ratio may easily be the result of chance, though it is possible that it may be due to the prevalence of intermediate pea-combs.

Intermediate Pea-combs.—In certain families where the pea-comb was concerned, heterozygote (p.s.) birds occurred with some frequency showing so little of the pea character that as young chicks they could easily be taken for singles. The median ridge is very high, approaching the single comb, whilst the lateral ridges are much reduced. Such a comb requires very close scrutiny in the newly hatched chick to distinguish it from a single. In one case such a bird, recorded as a single when a chick, eventually grew up with one of these intermediate pea-combs. Experiments with reference to the nature of this comb are still in progress, and until they are complete we propose to defer our detailed account. We have alluded to the case here because it may have some bearing on the excess of singles in Experiments 231 and 357. At the time of that experiment we had not fully grasped the distinction between the intermediate pea and the single comb, and it may very well be that some of the combs then recorded in certain families as single were in reality of the intermediate type.

The Malay Comb.

In the last Report (p. 111) we drew attention to the paradox that real rose and single combs are not known to occur among Malays when bred pure, and we suggested as a possible explanation that the ♂s. only are capable of producing all four forms of gamete. In a subsequent note (p. 112) we alluded to a ♀ Malay which was recorded to have given (with a single combed ♂) 2 s.c., 1 r., 1 p. and 1 r.p. This ♀ was again tested in 1905 (Experiment 334) and gave with a Br. L. ♂ 7 s., 2 r., 2 p., and 3 r.p. There is, therefore, no doubt that ♀ Malays as well as ♂s. can give off all four kinds of gamete. Unfortunately we were unable to procure a ♂ Malay of this nature in 1905, and the absence of roses and singles in pure Malays must, for the present, remain unexplained.

Colour.

White × *Colour.*—The experiments described in the last two Reports have already shown that white behaves as a dominant to colour, and the evidence obtained in the past two seasons confirms this. Four extracted whites, viz., ♀ 463 (Experiment 196), ♀ 425 (Experiments 214, 238, and 251), ♂ 375 (Experiments 273, 274), and ♂ 415 (Experiments 338 and 339) were shown to be homozygous. Matings of the nature DR × DR are shown in the following table:—

	Light.	Coloured.
Experiment 204	31	3
,, 205	35	6
,, 206	17	3
,, 211	209	57
,, 212 ,, 300	21	7
,, 220	11	3
,, 299	186	58
,, 307	56	24
	566	161
Expectation	545	182

There is a slight deficiency of coloured birds due in part to the small number produced in Experiments 204 to 206 where 3 ♀s. resulting from a cross between Wh. Dork. and I. G. were mated with their brother. In part also the excess of lights arises from the occasional difficulty of distinguishing at the hatching stage between a chick which will grow into a pile (viz., orange-red and white) from one which will develop into a white. Usually the pile is slightly marked with buff on the head or elsewhere, but in cases where the eggs were opened a day or two before hatching, or where the chick died in the shell, this buff might easily be overlooked, and the chick in consequence registered as uncoloured. Indeed, such a case actually happened, a bird recorded as uncoloured in down on being reared turning out to be a pile. We believe that the deficiency of coloured birds in Experiment 211 is due to this cause, for on repeating the experiment in 1905, and paying particular attention to this point, the expected proportion of coloured birds appeared.

The matings of DR birds with RR gave on the whole a fairly close approach to the expected ratio of equality. As the table shows (see p. 20), irregularities occur here and there, but whether these are merely fortuitous we cannot at present say:—

	Light.	Coloured.		Light.	Coloured.
Experiment 203 ...	3	4	Experiment 310 ...	9	12
" 207 ...	8	4	" 311 ...	13	15
" 213 ...	10	14	" 312 ...	6	7
" 221 ...	9	7	" 315 ...	3	4
" 223 ...	27	36	" 316 ...	5	5
" 232 ...	11	20	" 317 ...	8	7
" 233 ...	2	9	" 318 ...	11	6
" 240 ...	8	11	" 319 ...	1	—
" 247 ...	19	13	" 320 ...	15	13
" 249 ...	5	4	" 324 ...	18	31
" 259 ...	25	15	" 325 ...	4	4
" 301 ...	5	19	" 383 ...	7	4
" 302 ...	5	7	" 384 ...	2	8
" 304 ...	2	2	" 385 ...	7	8
" 308 ...	5	4	" 386 ...	4	3
" 309 ...	14	14	" 390 ...	10	13
	158	183		123 158	140 183
			Total	281	323
			Expectation	302	302

Recessive Whites.—One of the most interesting features of the past two years' work has been the demonstration of the existence of two sorts of white birds. To the first class belong the whites which we have just been considering. These behave as dominants to colour, and may for convenience be termed D-whites. The second class behave as recessives to colour, and may be spoken of as R-whites. Such R-whites we have already found in several breeds of fowls, viz., in Rosecomb bantams, Wyandottes, Dorkings, and Silkies. It is possible that a White Leghorn ♀ used by Hurst in one of his experiments (Rep. II, p. 134, Experiment 2) was also of this nature. These R-whites *are characterised by the possession of a few minute ticks in their otherwise pure white plumage*, a feature which we have already mentioned in the case of the white Rosecomb bantam (*cf.* Rep. II, p. 117, note). These minute ticks we have also found in white Wyandottes and in Silkies. Such evidence on the nature of the R-white as we have up till now collected may be conveniently considered under the headings of the different breeds which we have used.

(α) *Rosecomb Bantams.*—Two pens of whites (Experiments 280 and 290) bred in 1904 were proved to come true to colour. The down colour of the chicks was very pale bluish white, not unlike that of the white-splashed Andalusians. In Experiment 279 a few chicks were produced from a pen of blacks. The down colour of these was similar to that found in other black breeds, viz., black with white ventral surface. In

1905 crosses were made between black and white (Experiments 350, 356, 369), and all the resulting 88 chicks were black in the down. Certain of these have been reared, and in their adult plumage are either pure black or black with some white spangling. The spangling is probably a separate character with an independent inheritance. White Rosecomb ♂s. were also crossed with a coloured ♀ bantam* of unknown origin (Experiment 291), and an F_2 game bantam produced in Experiment 267. In both cases all the chicks were coloured. The R-white character of the Rosecomb bantam is therefore recessive to colour. The F_1 birds we hope to breed from in 1906.

(β) *Silkies.*—During the past summer a trio of Silkies was procured from Mr. Frank Rice, a well-known fancier. The ♂ and one of the ♀s. were each crossed with a Br. L. (Experiments 335 and 393). All the 10 offspring hatched out were coloured much like Br. L.'s, and there seems no doubt but that these Silkies resemble the R-white type. Here again birds have been reared in order to continue the experiments next year.

(γ) *Extracted R-Whites.*—We have among our records a set of experiments which were made with reference to comb characters, but which at the same time demonstrate indirectly the recessive nature of this type of white. In Experiment 93 (Rep. II, p. 100) a White Dorking of Creswell's strain was mated with an Indian game ♂. The occurrence of coloured birds from such a mating was at the time looked on with surprise, and they were considered as unexplained exceptions to the ordinary dominance of white (Rep. I, p. 141, note). Reasons have since been given for regarding this Wh. D. ♀ as a heterozygote of the two forms of white (Rep. II, p. 118 and p. 117 note). One of the coloured birds (♂ 904) resulting from this experiment was mated with a Br. L. ♀ (Experiment 164). From his breeding he must have been a heterozygote formed by a colour-bearing and an R-white gamete. Two of the coloured offspring resulting from this union were bred together (Experiment 253). Assuming they were each formed by the union of an R-white gamete from ♂ 904 and a colour-bearing gamete from the Br. L. ♀, we should look from such a mating for coloured and white offspring in the proportion of 3 : 1. Actually there were produced 46 coloured and 18 light chicks. One of these light birds (♂ 253) was reared, and in its adult plumage was pure white except for traces of pigment at the base of some of the tail feathers. In 1905 this bird was mated with 4 coloured hens (Experiments 345, 346). All the 95 chicks produced were without exception coloured. Many of these have been reared, and next year will form the basis of future experiments to elucidate the nature of the R-white.

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* Kindly given us by Mr. F. Slade.

1902. Experiment 93 .... ♂ I. G. × Wh. D. ♀
1903. Experiment 164 .... ♂ 904 (coloured) × Br. L. ♀
1904. Experiment 253 .... ♂ 834 (coloured) × 679 ♀
1905. Experiments 345 and 346... ♂ 253 (R—white) × 4 ♀s. (all coloured)
95 coloured chicks.

Andalusians.—In Report I it was suggested that the blue colour of the Andalusian is probably* heterozygous, and in Report II (p. 118) figures were given in support of this view. During the past two years additional evidence has been acquired, and every form of mating has now been tested with the following results:—

No. of Experiment.	Nature of Mating.	Result.		
		Black.	Blue.	Wh. spl.
Rep. II, p. 118 ...	Blue ♀ s. × blue ♂	22	36	17
Exp. 276............	Blue ♀ s. × blue ♂	19	42	22
(Total numbers for blue and blue		41	78	39)
Rep. II, p. 118 ...	Wh. spl. ♀ × Blue ♂	—	34	20
,, ,, ...	Black ♀ × Blue ♂	19	27	—
Exp. 269............	Wh. spl. ♀ s. × wh. spl. ♂ ...	—	—	40
,, 270............	Black ♀ × wh. spl. ♂	—	20	—
,, 294............	Black ♀ × black ♂	25	—	—

The colour of most of the chickens was determined in the down. In the blacks the down is black with the exception of the ventral surface, the tips of the wings, and sometimes parts of the head, which are white. The down in the blues is slaty-blue, similarly marked with white, whilst in the white splashed it is of an exceedingly pale blue tint as a rule, though sometimes practically colourless.

The above figures bear out the view we previously expressed as to the heterozygous nature of the blues, though before leaving this subject reference must be made to an apparently exceptional case. Among the young birds reared in Experiment 269 was one white ticked ♀. This bird behaved as if she were white × colour, whilst all Andalusians and their pure-bred offspring of all three sorts behave as coloured when

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* This is true for other breeds also. Thus, we have found brown-striped down of Brown Leghorn dominant to the pale brown down of Malays (Experiments 339, 334, 361) and of Malay Bantams (Experiments 242, 283).

crossed with coloured birds. The carriage and appearance of this bird was quite unlike that of the Andalusians. Moreover, her shanks were yellow. We have little hesitation in regarding her as the result of some accident.

Brown-breasted Bantams.—We mentioned (Rep. II, p. 121) that we had received from Mrs. Staples-Browne a trio of bantams, F_1 from Brown-breasted × Black-red game. These birds were bred together in 1904, and the ♂ was bred with other hens in 1904 and 1905. The breeds concerned in these experiments are characterised by three forms of *down*-colour:—

	Down-colour.
Brown-breasted Game	Very dark brownish black.
Blk.-red Game	Brown striped.
Blk.-red Malay Bantam ...	Pale brown with some brownish buff on rump: quills showing dark.

Of these three forms of down-colour, brownish-black is dominant to both brown stripe and pale brown; heterozygous birds showing rather more brown, especially on the head. Brown stripe is dominant to pale brown.* The evidence for these statements appears in the following table:—

Composition of ♀.		Composition of ♂.	Result.		Expectation.	
			Br. blk.	Br. str.	Br. blk.	Br. str
Exp. 267.	Br. blk. × br. str.	Br. blk. × br. str.	58	18	57	19
„ 268.	Pale br. × pale br.	„	7	6	6·5	6·5
„ 342.	Br. blk. × pale br.	„	16	7	17·25	5·75
„ 343.	Br. str. × pale br.	„	20	11	15·5	15·5

In Experiment 268, in addition, one exception occurred, viz., a pale brown chick. The origin of this exception was unexplained. We incline to regard it as due to some mistake.

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* This is true for other breeds also. Thus, we have found brown-striped down of Brown Leghorn dominant to the pale brown down of Malays (Experiments 339, 334, 361) and of Malay Bantams (Experiments 242, 283).

Explanation of Abbreviations used in Table.

W. L.	White Leghorn.	W. And.	White splashed Andalusian.
Br. L.	Brown Leghorn.	B. And.	Blue Andalusian.
Buff L. ...	Buff Leghorn.	Bk. And.	Black Andalusian.
I. G.	Indian game.	Mal. ...	Malay.
G. B.	Game bantam.	Mal. b.	Malay bantam.
Eg.	Egyptian.	Sil.	Silky.
O. E. G. ...	Old English game.	W. R. ...	White Rosecomb.
Wy.	Wyandotte.	B. R. ...	Black Rosecomb.

s.	single comb.	int. p.	intermediate pea comb.
r.	rose comb.	doub.	double comb.
p.	pea comb.	slk.	" silky " comb.
r.p.	rose-pea (= " walnut ") comb.	e.	with extra toe.
r.s.	rose containing single.	n.e.	without extra toe.
p.s.	pea " "		

The presence or absence of an extra toe has always been recorded, but in view of the irregularity of dominance mentioned in the last Report we have not attempted any further analysis of the behaviour of this character. All showing any indication of extra toe on both feet or on one only are recorded as e.t.

In the column giving the nature of the mating it has not been thought necessary to retain the complicated system of notation indicating ancestry which was used in the last Report. The breeding of any bird can, in each case, be ascertained from the pedigrees.

Table giving Details of Poultry Experiments (Combs and Feet).

1904.

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Nature of mating.	**Combs.** Offspring. s.	r.	p.	r.p.	Dubious.	**Feet.** Offspring. e.	No e.
1	196	463	W. L.	s.	no e.		Mal.		r.p.	n.e.		s. × r.p.			9	9			18
	197	839	90	,,	n.e.	200	,,		,,	,,		,,			8	6			14
	198	191	139	r.	,,		,,		,,	,,		r.s. × r.p.			6	20			26
	199	52	Mal.	r.p.	,,	389	,,		,,	,,		r.p. × r.p.				7			5
2	200	1 839	W. L. 90	s.	,,	197	256	172	r.	,,		r.s. × r.r.		27					27
3	201	843	190	r.p.	,,	232	806	190	r.p.	,,		r.p. × r.p.	2	5	7	16			31
	202	858	,,	,,	,,		,,	,,	,,	,,		,,	2	5	9	8			24
4	203	15	Mal.	,,	,,	288	689	152	,,	e.	303	,,			2	5		4	3
	204	682	152	,,	e.	212, 300	,,	,,	,,	,,	,,	,,	10	5	4	15		18	16
	205	530	,,	,,	,,		,,	,,	,,	,,	,,	,,	2	9	8	22		24	16
	206	701	,,	,,	,,		,,	,,	,,	,,	,,	,,	2	4	5	9		16	4
	207	664	I. G.	p.	n.e.		,,	,,	,,	,,	,,	p. × r.p.			5	7		3	8
	208	5 ♀ s.		s.	,,		,,	,,	,,	,,	,,	s. × r.p.	19	18	11	13		23	35
5	209	759	164	,,	,,		987	189	s.	n.e.		s. × s.	32						32
	210	323	166	,,	,,		,,	,,	,,	,,		,,	42						42
6	211	3 ♀ s.		,,	,,		457		,,	,,		,,	266						266
	212	682	152	r.p.	e.	204, 300	,,		,,	,,		r.p. × s.	4	5	2	4		3	13
	213	851	150	,,	n.e.	218	,,		,,	,,		,,	8	4	9	2			24
	214	425	167	,,	,,	238, 251	,,		,,	,,		,,	5	1		1			7

1904—*continued.*

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Nature of mating.	Combs. Offspring. s.	r.	p.	r.p.	Dubious.	Feet. Offspring. e.	No e.
7	215	765	150	r.p.	n.e.		909	189	r.p.	n.e.		r.p. × r.p.	4	19	19	33			75
	216	851	”	”	”	213	”	”	”	”		”	2	4	5	11			22
	217	546	W. L.	s.	”		”	”	”	”		s. × r.p.	10	9	7	8			34
	218	312, 363		”	”		”	”	”	”		”	21	27	24	21			93
8	219	446	143	doub.	”		309		doub.	”		doub. × doub.	6 *double.*					3	3
	220	342	”	”	”		”		”			”	14 ”					4	9
	221	335	Eg.	”	e.		”		”			”	15 ”					9	7
9	222	13	Buff L.	s.	n.e.		864	150	int. p.	n.e.		s. × int. p.	17 *int. p.* 46 *s.*						62
	223	726	172	int. p.	”		”	”	”	”		int. p. × int. p.	28 *p. and int. p.* 7 *s.*						35
	224	782	Br. L.	s.	”		”	”	”	”		s. × int. p.	9 *int. p.* 7 *s.*						16
	225	78	O. E. G.	”	”		”	”	”	”		”	12 *int. p.* 18 *s.*						30
10	226	364		”	”		256	172	r.p.	”		s. × r.p.	2		1	3			6
	227	895	W. L.	”	”	231	”	”	”	”		”	3	4	5	5			17
11	228	912 690 921	190	p.	”		919	190	p	”		p.s. × p.s.	20		34				54
	229	79	111	”	e.		”	”	”	”		”	2		9			8	3
	230		Br. L.	s.	n.e.		”	”	”	”		s. × p.s.	2		3				5
	231	912	190	p.	”	228	257		s.	”		p.s. × s.	5		8				13
	232	843	190	r.p.	”	201	”		”	”		r.p. × s.	7	11	5	9			32
	233	13	Mal.	”	”	316	”		”	”		”		1		9			10
	234	701	152	”	e.		”		”	”		”	1	1	4	6		6	6
12	235	146	157, *a*	s.	”		116	157, *a*	”	e.		s. × s.	31					30	1
	236	163	180	r.p.	n.e.	244	”	”	”	”		r.p. × s.	1	1		1		2	1

13	237	987	Br. L.	s.	n.e.		799	Br. L.	s.	n.e.	s. × s.	52					52
	238	425	167	r.p.	"	214, 251	"	"	"	"	r.p. × s.	3	2	2			7
	239	12	Mal.	"	"		"	"	"	"	"			16	12		28
	240	887	172	"	c.	255	"	"	"	"	"	7	5	4	3	9	10
	241	269	180	"	n.e.	254	"	"	"	"	"	8	3	6	4		21
	242	54	Mal., *b*	"	"		"	"	"	"	"				18		18
	243	386	185	"	c.		"	"	"	"	"	1	3	1	1	2	4
14	244	163	180	"	n.e.	236	713	180	r.p.	"	"			2	2		4
	245	269	"	"	"	241	"	"	"	"	"	1	5	4	13		23
15	246	873	190	r.	"		955	190	s.	"	r.s. × s.	12	11				23
	247	326	174	s.	"		"	"	"	"	s. × s.	33					33
	248	934	176	"	"		"	"	"	"	"	37					37
	249	742	179	r.p.	"		"	"	"	"	r.p. × s.	2	1	5	1		9
	250	26	Mal.	p.	"		"	"	"	"	p. × s.			8			8
	251	425	167	r.p.	"	214, 238	"	"	"	"	r.p. × s.		3	2			5
16	252	11	Buff L.	s.	"		834	164	r.p.	"	"	18	13	15	14	19	40
	253	679	164	r.p.	"		"	"	"	"	r.p. × r.p.	6	8	14	36	12	52
	254	269	180	"	"	241	"	"	"	"	"	3	5	9	12	11	18
17	255	740	172	"	c.	271	283	172	"	c.	"				97	57	40
		680	"			278											
		887	"			240											
		9	162			272											
	256	2 ♀ s.		s.c.	n.e.		"	"	"	"	s. × r.p.				6	4	2
18	257	798	185	r.p.	"	260	814		p.	n.e.	r.p. × p.			10	4		12
	258	743	"	"	"	261	"		"	"	"			16	22		38
	259	386	"	"	c.	262	"		"	"	"			9	19	16	12
	260	798	"	"	n.e.	257	733		s.	"	r.p. × s.	3	4	5	2		14
	261	743	"	"	"	258	"		"	"	"	3	3	5	3		14
	262	386	"	"	c.	259	"		"	"	"	2	1	7	2	2	10
20	263	371	175	r.	n.e.		231		"	"	r.s. × s.	14	11				25
	264	674	167	"	c.		"		"	"	"	16	21			17	20
	265	736		"	n.e.		"		"	"	,	21	22				43
	266	367	174	"	"		"		"	"	"	26	28				54
21	267	2 ♀ s.	G. B.	s.	"		6	G. B.	"	"	s. × s.	76					76

1904—*continued.*

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Nature of mating.	Combs. Offspring. s.	r.	p.	r.p.	Dubious.	Feet. Offspring. e.	No e.
	268	55	Mal. B.	r.p.	n.e.		6	G. B.	s.	n.e.		r.p × s.				14			14
22	269	3 ♀ s.	W. And.	s.	,,		535	W. And.	,,	,,		s. × s.	40						40
	270	737	Bk. And.	,,	,,		,,	,,	,,	,,		,,	20						20
	271	740	172	r.p.	e.	255	,,	,,	,,	,,		r.p. × s.			8	3		3	8
	272	9	162	,,	,,	,,	,,	,,	,,	,,		,,	7	9	6	13		21	14
23	273	343	172	r.	e.		375	167	s.	,,		r. × s.		10				3	7
	274	319	,,	,,	,,		,,	,,	,,	,,		r.s. × s.	3	1				3	1
24	275	4 ♀ s.		s.	n e.		456	185	r.p.	,,		s. × r.p.	10	10	16	17			53
25	276	3 ♀ s.	B. And.	,,	,,		969	B. And.	s.	,,		s. × s.	86						86
	277	6	Mal.	r.p.	,,	334	,,	,,	,,	,,		r.p. × s.	2	1	1	1			5
	278	680	172	,,	e.	255	,,	,,	,,	,,		,,			10	11		7	12
26	279	2 ♀ s.	B. R.	r.	n.e.			B. R.	r.	,,		r. × r.		6					6
27	280	2 ♀ s.	W R.	,,	,,			W. R.	,,	,,		,,		65					65
28	281	3 ♀ s.	I. G.	p.	,,			I. G.	p.	,,		p. × p.			21				21
	282	264		s.	,,			,,	,,	,,		s. × p.			7				7
29	283	3 ♀ s.	Br. L.	,,	,,		53	Mal. B.	r.p.	,,		s. × r.p.		66		79			145
	284	54 55	Mal. B.	r.p.	,,	242, 268	,,	,,	,,	,,		r.p. × r.p.				19			18
	285	163	Eg.	doub.	,,		,,	,,	,,	,,		doub. × r.p.		4		13			17
	286	56		r.	e.	291	,,	,,	,,	,,		r. × r.p.		5		2		2	5
30	287	4 ♀ s.		s.	n.e.		9	Mal.	r.p.	,,		s. × r.p.			44	48			92
	288	15	Mal.	r.p.	,,	203	,,	,,	,,	,,		r.p. × r.p.			3	1			4
	289	11	,,	,,	,,		,,	,,	,,	,,		,,			3	5		1	7
31	290		W. R.	r.	,,			W. R.	r.	,,		r. × r.		26					26
	291	56		,,	e.	286		,,	,,	,,		,,		12				5	3
32	292	5 ♀ s.		s.	mixed		5	Mal.	p.	,,		s. × p.			76				

1905.

3	293	25	211	s.	n.c.		365	276	s.	n.c.		s. × s.	9						9
	294	410	276	,,	,,		,,	,,	,,	,,		,,	25						25
	295	316	W.L.	,,	,,		,,	,,	,,	,,		,,	17						17
	296	285	269	,,	,,		,,	,,	,,	,,		,,	8						8
	297	370	216	r.p.	,,		,,	,,	,,	,,		r.p. × s.		11		10			21
4	298	2 ♀ s.		s.	,,		593	239	r.p.	,,		s. × r.p.	13	10	17	10			50
6	299	3 ♀ s.		,,	,,		457		s.	n.c.		s. × s.	244						244
	300	682	152	r.p.	c.	204, 212	,,		,,	,,		r.p. × s.	3	4	2	3		3	8
	301	765	Mal.	p.	n.c.		,,		,,	,,		p. × s.			23				23
	302	231	202	r.p.	,,		,,		,,	,,		r.p. × s.	4	4	2	2			12
8	303	3 ♀ s.	W. L.	s.	,,		689	152	r.p.	c.	203–8	s. × r.p.	2	5	4	3		5	10
	304	665	Mal.	p.	,,		,,	,,	,,	,,	,,	p. × r.p.			3	1		2	2
10	305	3 ♀ s.		s.	,,		389	203	,,	,,		s. × r.p.			14	22	3	17	21
11	306	3 ♀ s.		,,	,,		23	218	,,	n.c.		,,	17	17	10	6			50
12	307	109	180	r.p.	,,		26	211	s.	,,		r.p. × s.	14	23	22	21			80
	308	58	259	,,	c.		,,	,,	,,	,,		,,	2		3	4		2	7
	309	539	239	,,	n.c.	319	,,	,,	,,	,,		,,	6	7	9	6			28
	310	466	197	,,	,,		,,	,,	,,	,,		,,	5	6	3	7			21
	311	486	283	,,	,,		,,	,,	,,	,,		,,	5	8	6	7			27
	312	601	252	,,	c.		,,	,,	,,	,,		,,		5	3	5		6	7
13	313	2 ♀ s.		s.	n.c.		559	283	r.p.	,,		s. × r.p.	11	7	8	9			35
14	314	3 ♀ s.		,,	,,		360	216	,,	,,		,,			18	19	5		43
15	315	12	253	r.p.	,,		37	211	s.	,,		r.p. × s.		3	1	3			7
	316	13	Mal.	,,	,,	233	,,	,,	,,	,,		,,		8		2			10
	317	53	259	,,	c.		,,	,,	,,	,,		,,	3	6	2	4		7	8
	318	36	218	,,	n.c.		,,	,,	,,	,,		,,	4	2	6	5			17
	319	539	239	,,	,,	309	,,	,,	,,	,,		,,				1			1
	320	474	283	,,	,,	326	,,	,,	,,	,,		,,	11	8	7	2			28
	321	767	Mal.	p.	,,		,,	,,	,,	,,		p. × s.			3				3
	322	766	,,	r.p.	,,		,,	,,	,,	,,		r.p. × s.			2				2
	323	414	217	,,	,,	361, 364	,,	,,	,,	,,		,,		2	2				4
	324	495	239	,,	,,		,,	,,	,,	,,		,,	9	10	15	14			49

1905—*continued.*

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Nature of mating.	Combs. Offspring. s.	r.	p.	r.p.	Dubious.	Feet. Offspring. c.	No c.
	325	209	258	r.p.	n.c.		37	211	s.	n.c.		r.p. × s.	2	3		3			8
16	326	474	239	,,	,,	320	432	Br. L.	,,	,,		,,	1	2	3	3			9
	327	488	,,	,,	,,		,,	,,	,,	,,		,,	10	12	11	11			44
	328	162	258	,,	,,		,,	,,	,,	,,		,,			15	8			23
	329	577	239	,,	,,		,,	,,	,,	,,		,,	2	2	4	4			12
	330	582	232	r.	,,		,,	,,	,,	,,		r.s. × s.	9	7					16
	331	151	258	r.p.	,,		,,	,,	,,	,,		r.p. × s.	4	2	6	2			14
	332	324	236	,,	c.		,,	,,	,,	,,		,,		2	1	1		1	3
	333	208	206	,,	n.c.		,,	,,	,,	,,		,,				14			14
	334	6	Mal.	,,	,,	277	,,	,,	,,	,,		,,	7	2	2	3			15
	335	349	Sil.	slk.	c.		,,	,,	,,	,,		slk. × s.		8 *silk.*				5	2
17	336	3 ♀ s.		s.	n.c.		421	216	r.p.	,,		s. × r.p.			58	52			108
	337	600	215	r.p.	,,		,,	,,	,,	,,		r.p. × r.p.			20	44			64
18	338	264		s.	,,		415	204	,,	,,		s. × r.p.		21		20			41
	339	452	276	,,	,,	346	,,	,,	,,	,,		,,		6		10			16
20	340	49	222	,,	,,		56	222	int.p.	,,		s. × int.p.	38 + 28 *int. p.*				3		69
	341	2 ♀ s.	Wy.	r.	,,		,,	,,	,,	,,		r. × int.p.		4					4
21	342	623, 632	268	r.p.	,,		6	G. B.	s.	,,		r.p. × s.	8	7	3	5			23
	343	649	268	,,	,,		,,	,,	,,	,,		,,	4	11	5	10			30
	344	532	285	,,	,,		,,	,,	,,	,,		,,	4	2	4	3			13
22	345	3 ♀ s.		s.	,,		144	253	r.p.	,,		s. × r.p.	14	24	19	17			74
	346	452	276	,,	,,	339	,,	,,	,,	,,		,,	4	2	7	8			21
	347	895	W. L.	,,	,,		,,	,,	,,	,,		,,	6	1	8	1			15
	348	315	,,	,,	,,		,,	,,	,,	,,		,,	11	1	9	2			23

25	349	3 ♀ s.	211	s.	n.e.		116	258	r.p.	n.e.		s. × r.p.	16	9	14	4			43
26	350	4 ♀ s.	W. R.	r.	,,		760	B. R.	r.	,,	356	r. × r.		55					58
30	351	357	Br. L.	s.	,,			Mal.	r.p.	,,		s. × r.p.				28			28
	352	667	Mal.	r.p.	,,			,,	,,	,,		r.p. × r.p.				4			4
	353	682	,,	,,	,,	385		,,	,,	,,		,,				9			9
	354	681	,,	,,	,,			,,	,,	,,		,,				5			5
32	355	2 ♀ s.		s.	,,		192	258	,,	,,		s. × r.p.			26	33	2		61
33	356	,,	W. R.	r.	,,		760	B. R.	r.	,,	350	r. × r.		24					24
34	357	424	230	s.	,,		184	258	r.p.	,,		s. × r.p.			3	13			16
	358	603	211	,,	,,		,,	,,	,,	,,		,,			16	11			27
35	359	537	239	r.p.	,,		384	Br. L.	s.	,,		r.p. × s.	6	3	5	4			18
	360	379	215	,,	,,		,,	,,	,,	,,		,,		9		4			13
	361	414	217	,,	,,	323, 364	,,	,,	,,	,,		,,	7	3	1	2			13
36	362	2 ♀ s.		s.	,,		292	216	r.p.	,,		s. × r.p.	8	6	8	10			32
37	363	502	283	r.p.	,,		482	Br. L.	s.	,,		r.p. × s.	10	4	3	6			24
	364	414	217	,,	,,	323, 361	,,	,,	,,	,,		,,	2	1		5			8
	365	643	242	,,	,,		,,	,,	,,	,,		,,	5	4	5	3			16
	366	418	215	,,	,,		,,	,,	,,	,,		,,				9			7
	367	404	Br. L.	s.	,,	393	,,	,,	,,	,,		s. × s.	32						32
38	368	505	224	,,	,,	387		I. G.	p.	,,		s. × p.	6		5				11
39	369	2 ♀ s.	B. R.	r.	,,		585	W. R.	r.	,,		r. × r.		7					7
	370	659	267	s.	,,		,,	,,	,,	,,		s. × r.		6					6
40	371	289	269	,,	,,		257	202	r.p.	,,		s. × r.p.		8		6			14
	372	515	Br. L.	,,	,,		,,	,,	,,	,,		,,		10		9			18
41	373	2 ♀ s.	211	,,	,,		549	233	,,	,,		,,	39	27	36	16			118
	374	4 ♀ s.	Br. L.	,,	,,		,,	,,	,,	,,		,,	17	20	19	12			68
42	375	285	269	,,	,,		W. And.	269	s.	,,		s. × s.	16						16
	376	227	,,	,,	,,		,,	,,	,,	,,		,,	16						16
	377	317	W. L.	,,	,,		,,	,,	,,	,,		,,	36						36
43	378	2 ♀ s.	211	,,	,,			Mal.	p.	,,		s. × p.	31						31
44	379	435	Eg.	doub.	,,		431	Eg.	doub.	e.		doub. × doub.		*11 doub.*				6	5
	380	2 ♀ s.		s.	,,		,,	,,	,,	,,		s. × doub.		*7 doub.*				7	
	381		Wy.	r.	,,		,,	,,	,,	,,		r. × doub.		9				8	1
45	382	2 ♀ s.	211	s.	,,		467	283	r.p.	n.e.		s. × r.p.	13	10	15	10			48

1905—*continued.*

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Ft.	Used in exp.	Nature of mating.	Combs. Offspring. s.	r.	p.	r.p.	Dubious.	Feet. Offspring. e.	No e.
46	383	295	206	r.p.	e.		133	211	s.	n.c.		s. × r.p.				11		10	1
	384	665	Mal.	p.	n.c.		,,	,,	,,	,,		s. × p.			10				10
	385	682	,,	r.p.	,,	353	,,	,,	,,	,,		s. × r.p.			10	5			15
	386	578	233	,,	,,		,,	,,	,,	,,		,,		1	2	4			7
47	387	505	224	s.	,,	368	183	258	r.p.	,,		s. × r.p.			5	2			7
	388	1		,,	,,		,,	,,	,,	,,		,,			4	6			10
	389	52	Mal.	r.p.	,,	199	,,	,,	,,	,,		r.p. × r.p.				3			3
48	390	2 ♀ s.	Br. L.	s.	,,		198	260	,,	,,		s. × r.p.			11	12			23
49	391	2 ♀ s.	211	,,	,,		57	258	,,	,,		,,			18	10			28
51	392	350	Sil.	silk	e.		348	Sil.	silk	e.		silk. × silk		8 *silk.*				7	1
	393	404	Br. L.	s.	n.c.	367	,,	,,	,,	,,		s. × silk.		2 *silk.*				2	

SWEET PEAS (*Lathyrus odoratus*).

(Experiments by W. Bateson, E. R. Saunders, and R. C. Punnett.)

Sweet Peas.

Among the various crosses mentioned in our last report as having reached the F_2 stage was that of Emily Henderson with long pollen (E. H. l.) × Emily Henderson with round pollen (E. H. rd). The F_1 plant resulting from these 2 strains of whites is always coloured and is almost always purple. In the F_2 generation from the purple F_1 appear 3 main colour classes, viz.,[*] blues, reds, and whites. The blues may be subdivided into (1) purples with blue wings, *i.e.*, "Purple Invincible" (P. I.); (2) purples with purple wings (P.p.w.); and (3) Picotees (Pic.). Similarly the reds may be classed as (1) reds with pale pink wings, *i.e.*, "Painted Lady" (P. L.); (2) reds with red wings, *i.e.*, "Miss Hunt" (M. H.); and (3) tinged whites (T. W.). Further, any plant may have long or round pollen, and any coloured plant may exhibit either a dark or a light axil. The work of the past two years has been chiefly concerned with the results of this original cross, and it is now apparent that we are dealing with 7 pairs of allelomorphic characters. These are—

Dominant.		Recessive.	
†1st colour factor	(C).	Absence of 1st colour factor	(c).
2nd ,, ,,	(R).	,, 2nd ,,	(r).
Blueness	(B).	,, blueness	(b).
Light wing	(wl).	Dark wing	(wd).
Uniform colour distribution	(D).	Colour on edge only	(E).
Long pollen	(L.).	Round pollen	(rd.).
Dark axil.		Light axil.	

Blues, Reds, and Whites.—For the present we may confine our attention to the first three of these allelomorphic pairs. As the scheme shows, the manifestation of colour depends upon the simultaneous presence of C and R in the zygote. Any plant homozygous for either c or r, or for both, must be white. Whether a coloured plant belongs to the blue or to the red class depends upon the presence or

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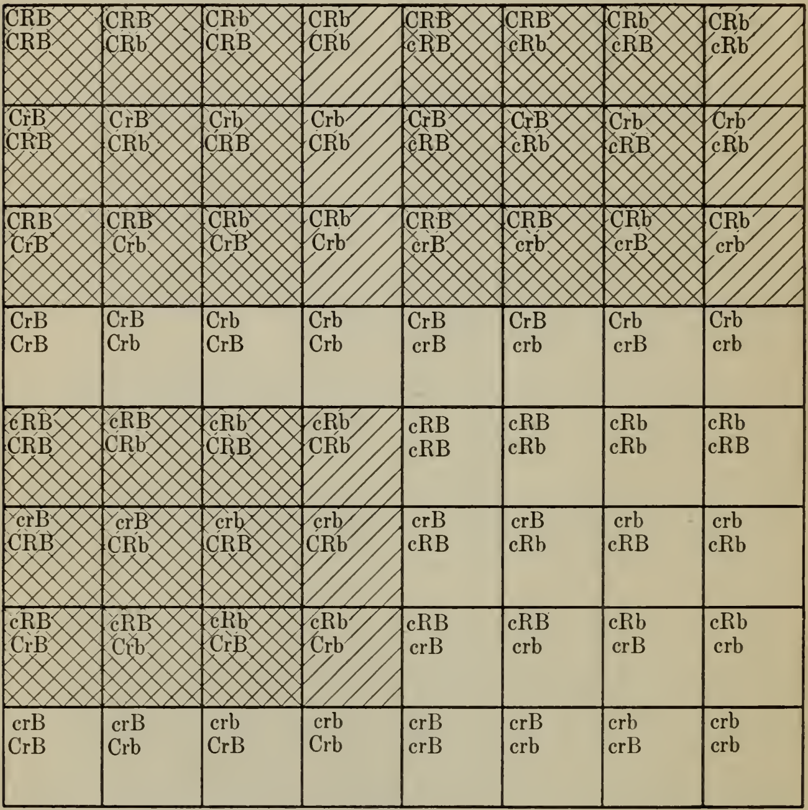
[*] There are apparently but two classes of sap-coloured Sweet Peas, viz., blues and reds. The blues resulting from the E. H. cross are all purple in shade, but, bearing in mind the existence of various tints in other strains, we prefer to make use here of the more comprehensive term.

[†] The behaviour of these two factors strongly suggests that one of them (C) may be a colour-forming stuff which gives rise to colour when acted upon by the other factor (R). We should then have to regard this latter as of the nature of an enzyme, but, in the absence of direct chemical evidence, we consider it advisable to use non-committal terms for the present.

absence of B in the zygote, but the blue character can only show itself in such zygotes as contain both C and R.

We consider the pure E. H. long strain used to be homozygous for C, r, and B, and the pure E. H. rd. strain to be homozygous for c, R, and b. Consequently the zygote formed by the cross E. H. l × E. H. rd. must be of the constitution Cc.Rr.Bb. And such an F_1 zygote gives rise in gametogenesis to equal numbers of 8 kinds of gametes, viz., CRB, CRb, CrB, Crb, cRB, cRb, crB, crb. The various zygotes formed by these gametes when the F_1 plant is selfed are shown in the accompanying figure (fig. 2).



CRB CRB	CRB CRb	CRb CRB	CRb CRb	CRB cRB	CRB cRb	CRb cRB	CRb cRb
CrB CRB	CrB CRb	Crb CRB	Crb CRb	CrB cRB	CrB cRb	Crb cRB	Crb cRb
CRB CrB	CRB Crb	CRb CrB	CRb Crb	CRB crB	CRB crb	CRb crB	CRb crb
CrB CrB	CrB Crb	Crb CrB	Crb Crb	CrB crB	CrB crb	Crb crB	Crb crb
cRB CRB	cRB CRb	cRb CRB	cRb CRb	cRB cRB	cRB cRb	cRb cRb	cRb cRB
crB CRB	crB CRb	crb CRB	crb CRb	crB cRB	crB cRb	crb cRB	crb cRb
cRB CrB	cRB Crb	cRb CrB	cRb Crb	cRB crB	cRB crb	cRb crB	cRb crb
crB CrB	crB Crb	crb CrB	crb Crb	crB crB	crB crb	crb crB	crb crb
63 : 1	57 : 7	57 · 7	15 : 49	63 : 1	57 · 7	57 : 7	15 : 49

FIG. 2.—Scheme of distribution of colour-factors in F_2. From E. Henderson (Sweet Pea), white, long pollen × white, round.

The table is an expansion of that shown in fig. 1, and exhibits the effect of the blue factor, B. The cross-hatched squares are purple-flowered plants; the single-hatched are red; the plain are whites.

The figures at the foot of each column show the ratio of long-pollened to round-pollened in each square of that column, on the hypothesis given in the text.

In 36 of the 64 zygotes so formed both R and C are present, and these zygotes consequently develop into coloured plants. The remaining 28 give rise to whites, and the ratio of coloured to white is therefore 9 : 7. Of the 36 coloured 27 are either homozygous or heterozygous for B and consequently are blue, the remaining 9 being reds. Hence we expect in F_2 blues, reds, and whites in the proportion 27 : 9 : 28. Actually experiment* has so far given 1,634 blues, 498 reds, and 1,593 whites out of a total of 3,725 F_2 plants (*cf.* Table, p. 37) where theory would demand 1,571 blues, 524 reds, and 1,630 whites. Bearing in mind the fact that all these plants were left to nature and that *Megachile* was often at work (*cf.* Rep. II, p. 95), a slight excess of blues is what we should expect, for vicinism (de Vries) might result in the production of a blue plant from a non-blue ♀ gamete, but would never prevent a blue ♀ gamete from giving rise to a blue plant.

Picotees and Tinged Whites.—In families where picotees and tinged whites occur these types behave as recessives to the corresponding fully coloured purples and reds. The tinged whites bear to the reds the same relation that the picotees do to the purples. The 4 classes pur., pic., red, and T. W. appear in F_2 in the ratio 9 : 3 : 3 : 1. The actual numbers (Table, p. 37) are 819 pur., 259 pic., 252 red, and 68 T. W., where expectation is 780, 260, 260, and 86 respectively. The slight deficiency of T. W., the ultimate recessive among the colours, and the small excess of the dominant purple is to be expected when the vicinism due to *Megachile* is borne in mind. It may be added that the recessive nature of Pic. and T. W. to purple and red respectively has been confirmed by the behaviour of the F_3 generation.

Light Wings and Dark Wings.—In some F_2 families 2 sorts of

DD wl.wl. (P.I.)	DD wl.wd. (P.I.)	DE wl.wl. (P.I.)	DE wl.wd. (P.I.)
DD wl.wd. (P.I.)	DD wd.wd. (P.p.w.)	DE wl.wd. (P.I.)	DE wd.wd. (P.p.w.)
DE wl.wl. (P.I.)	DE wl.wd. (P.I.)	EE wl.wl (Pic.)	EE wl.wd. (Pic.)
DE wl.wd. (P.I.)	DE wd.wd. (P.p.w)	EE wl.wd. (Pic.)	EE wd.wd. (Pic.)

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* These figures include families where Blanche Burpee (white) was used as the long parent in place of E. H. long. In such cases there appears to be no difference in the distribution of the characters under consideration as compared with the cross E. H. long × E. H. rd.

purples and reds can be distinguished. The purples may have purple standards and blue wings (Purple Invincible), or they may have deep purple wings (P.p.w.). Similarly among the reds the wings may be pale as in Painted Lady, or red as in Miss Hunt. These differences were not always regarded in F_2 plants, but subsequent breeding of F_3 plants from F_2 individuals showed that* dark wings (P.p.w. or M. H.) are recessive to light wings (P. I. or P. L.). Thus from the seed of an F_2 pur. lt. ax. long were grown F_3 plants in 1904, of which 24 were P. I., 12 were P.p.w., and 11 were Pic., a fairly close approximation to the expected ratio 9 : 3 : 4. We regard the F_2 plant as having been heterozygous for both D and wl, and therefore of the constitution DE.wl.wd. Consequently its gametes were Dwl, Dwd, Ewl, and Ewd, and the number and constitution of the zygotes produced by such gametes is shown in the accompanying table. In 1905 a further generation was raised from many of these F_3 plants. The results obtained are set forth below—

F_3 parent.	Constitution of F_3 parent.	F_4 generation.			Expectation.		
		P.I.	Ppw.	Pic.	P.I.	Ppw.	Pic.
P.I. (1 plant) ...	Dwl. Dwl.	all	—	—	all	—	—
P.I. (3 plants)...	Dwl. Ewl.	70	—	31	76	—	25
P.I.	Dwl. Dwd.	(not met with)					
P.I. (4 plants)...	Dwl. Ewd.	103	32	42	100	33	44
Ppw. (4 plants)	Dwd. Dwd.	—	all	—	—	all	—
Ppw. (3 ,,	Dwd. Ewd.	—	86	36	—	92	30
Pic. (5 ,,	Ewl. Ewl. or Ewl. Ewd. or Ewd. Ewd.	—	—	all	—	—	all

A number of crosses made between various F_4 individuals gave results which further illustrate the working of the scheme. Certain of these crosses also demonstrated the existence of different kinds of Pics. Thus 1 Pic. on being crossed with a homozygous p.p.w. gave 5 P.p.w. only, and was, therefore, in all probability of the constitution Ewd.Ewd. Another Pic. similarly crossed gave 2 P. I.s, thus proving that the light wing factor (wl) must have been present in this instance.

Pollen.—The character round pollen we have shown to be recessive to long pollen. Of the 3,725 F_2 plants (Table, p. 37), 2,844 were long and 881 were round, a ratio of 3·23 : 1. Here, again, vicinism would account for the slight excess of longs. In our last Report (p. 89) we pointed out that whilst the ratio 3 : 1 appears to hold good for the

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* We have not regarded these distinctions in the case of the picotees and tinged whites.

whites, the blues show a great excess of longs and the reds of rounds. The more recent results are in accordance with the earlier ones, and the total numbers now available are as follows :—

	Long.	Round.	*Ratio.*
Blue	1528	106	*14·41 : 1*
Red	117	381	*1 : 3·25*
White	1199	394	*3·04 : 1*
	2844	881	*3·23 : 1*

These proportions are quite definite throughout the different families, and indicate some form of gametic coupling between the blue and long and between the red and round factors (*cf.* p. 9). We hope to give a full account of this phenomenon when the experiments now in progress are completed.

In families where picotees and tinged whites are present, the proportion of rounds is lower among the purples but higher among the picotees, though, as the table below shows, the proportion of longs is not very different in the reds and tinged whites :—

	Long.	Round.	*Ratio.*
Purple...............	777	42	*18·5 : 1*
Picotee	235	24	*9·8 : 1*
Red	60	192	*1 : 3·2*
Tinged white	18	50	*1 : 2·8*

The system most nearly fitting the observed figures is that mentioned in the Introduction (p. 9). On that hypothesis, of 16 gametes 7 bear B (blue factor) with long pollen ; 1 bears B with round pollen ; 7 bear *b* (absence of blue) with round pollen ; 1 bears *b* with long pollen. The ratio of long to round would then be

In the blue	11·8 : 1
,, red	1 : 3·26
,, white	3 : 1
,, whole F_2 generation	3 : 1

The following figures show the closeness with which this system corresponds with observation :—

	Purple.		Red.		White.	
	Long.	Round.	Long.	Round.	Long.	Round
Observed	1528	106	117	381	1199	394
Calculated	1448·5	122·7	122·7	401·5	1220·5	407·4

There are, however, reasons for anticipating that other specific complications in the system of coupling will be disclosed when a further analysis is made, based upon the other characters.

Axil.—Of the 2132 coloured plants 1587 had dark and 545 had light axils, giving a ratio of 2·92 : 1. One would have expected vicinism to have led to a slight excess of dark axils. That the balance is a trifle the other way is probably due to the fact that the axils are sometimes difficult to distingish when the plants are not recorded before they are somewhat past their prime. In such cases the axils fade, and some dk. ax. plants might be recorded as lt. ax., though the reverse could not occur. On the other hand, one must not overlook the possibility that there may be some coupling of dk. ax. with absence of C and R. That the axil character may be concerned in the phenomenon of gametic coupling is shown by its behaviour in families where picotees and tinged whites occur. The following figures, which have been brought together from such families, point to a distinct coupling of lt. ax. with red :—

	Dk. ax.	Lt. ax.	*Ratio.*
Blues	818	260	*3·15 : 1*
Reds	204	116	*1·76 : 1*

We hope that the experiments now in progress will throw further light on this interesting phenomenon.

Details of F_2 from white, long pollen × ditto round pollen and reciprocal, F_1 being purple.

	Reference number.	Pur.				Pic.				Red.				T.W.				White.	
		dk.		lt.		dk.		lt.		dk.		lt.		dk.		lt.			
		l.	r.	l.	r.	l.	r.	l.	r.	l.	r.	l.	r.	l.	r.	l.	r.	l.	r.
With Pic. and T.W.	Report II, p. 89	176	11	45	2	39	7	15	1	10	23	6	17	2	5	3	7	195	73
	1904, No. 81	81	3	29	0	29	0	3	0	7	16	6	6	2	7	1	2	104	32
	1905 ,, 250	87	7	30	1	25	1	12	3	10	20	3	16	2	4	1	4	125	40
	,, ,, 251	15	1	4	1	7	0	0	0	0	8	1	0	0	0	0	0	19	6
	,, ,, 252	102	3	44	1	44	5	9	1	4	24	4	13	4	7	1	1	182	69
	,, ,, 254	23	1	6	1	7	1	1	0	1	3	1	1	0	1	0	1	30	4
	,, ,, 308	97	8	38	2	33	5	11	0	6	31	1	14	0	7	2	4	141	46
		819 [*780*]				259 [*260*]				252 [*260*]				68 [*86*]				1066 [*1078*]	
Without Pic. and T.W.	1904, No. 71	23	6	10	0					0	6	0	4					39	9
	,, ,, 72	36	3	9	0					4	11	0	1					27	7
	,, ,, 73	60	6	18	2					5	18	0	4					44	19
	,, ,, 74	39	1	18	1					2	9	3	2					38	15
	1905 ,, 253*	32	2	5	0					3	6	0	4					42	16
	,, ,, 309*	59	2	11	4					8	17	4	4					63	15
	,, ,, 310*	125	6	29	3					5	29	3	12					116	36
	,, ,, 311*	30	3	12	1					2	7	0	5					34	7
		556 [*532*]								178 [*177*]								527 [*552*]	
	Total	Blue ... 1634 [*1571*]								Red ... 498 [*524*]								White... 1593 [*1630*]	

* Original cross E. H., round × Blanche Burpee, long : hoods appear in F_2.

STOCKS.

(Experiments by E. R. SAUNDERS.)

Flower-Colour and Hoariness.

The general scheme underlying the complications witnessed in the case of Stocks is now clear, and an outline of it is given in the Introduction. As stated (Rep. II, p. 8), though any two sap-coloured glabrous strains of Ten-Week Stocks give glabrous F_1, yet the mating of white with cream or of either with a sap-coloured variety, results in hoary F_1. The distribution of the characters, sap-colour and hoariness, in F_2 shows (1) that the colour is due to the combination of two independent factors which we shall call C and R, each of which is allelomorphic to *c* and *r* respectively—absence of the same factors.

(2) That the hoariness is similarly due to the combination of another pair of factors H and K allelomorphic to *h* and *k*—absence of each respectively.

(3) That the hoariness due to presence of H and K is not manifested unless C and R are also both present.

In F_2 from *cream glabrous* × *white glabrous* all the hoary are sap-coloured and all the glabrous are white or cream (*i.e.*, non-sap-coloured), though in F_2 from white or cream × sap-coloured, there are coloured glabrous as well as uncoloured glabrous and coloured hoary plants. The two classes, sap-coloured hoary and non-sap-coloured glabrous, are in the ratio 9 : 7. Therefore the cream and the white parents both carry H and K, though, being without sap-colour, they are glabrous.*

In F_2 from *white* (*or cream*) *glabrous* × *sap-coloured glabrous* there are 3 coloured : 1 white, but again the hoary to glabrous are 9 : 7. Therefore the sap-coloured type contains one of the components of hoariness, say H. The allelomorphic composition of the three kinds of glabrous plants may be represented thus :—

White	CrHK.
Cream	cRHK.
Sap-colours	CRHk.

The assignment of C and R is of course arbitrary, for all that can be declared is that one is present in cream and one in white. Similarly it may be either H or K which is absent in the sap-coloured types.

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* Otherwise, if cream contained one factor (H) and white the other (K), or if one type (say cream) contained both factors, and the other (white) neither, some of the F_2 plants should be glabrous and sap-coloured, since some gametic unions would yield zygotes containing CRHk or CRhK. But this, as stated above, is not the case.

The combinations of characters exhibited in F_2 is graphically shown in the diagrams. The squares represent zygotes. The hoary are indicated with shading (partial or complete), the coloured similarly with blue. Each undivided square represents a homozygote yielding an unmixed F_3 similar in character to itself. In a subdivided square the several combinations of colour and shading indicate the (qualitatively, not quantitatively) different F_3 forms derivable from that particular zygote.

In this discussion the sap-coloured plants have been dealt with as a whole. As a matter of fact they consist (as stated in the Introduction) of two main classes, purples due to the presence of a factor B, and reds in which the same factor is absent (*b*). Each of these two classes may be again divided into subordinate groups, purple and plum on the one hand, red and copper on the other; and the evidence clearly shows that the subdivision of each class is simply due to the superposed distribution of another factor which may be present or absent, determining the quality of the colour in the respective classes.* The factor which determines the appearance of the subordinate colour forms is evidently introduced by the white, for these modified colours occurred in F_2 from white × red, but not in F_2 from cream × red (Rep. II, p. 27).

These four sap-colours are all that appear in F_2 from white × cream, but the *pale* colours, flesh and pale purple, for example, characteristic of other strains, would need a separate analysis to exhibit their interrelations.

In the diagrams no account is taken of the distinction between white and cream. As previously stated, cream, that is, yellow plastid colour, is recessive to white or uncoloured plastids, and it might be expected that this plastid-character was merely superposed on the others; but a large and unexplained deficiency of creams noticed in several cases indicates a distinct complication. How far this deficiency is attributable to the late-flowering habit of the cream forms is at present undetermined.

The factors determining colour and surface-character being thus interrelated, it is evident that the nature of only a small proportion of the numerous types of individuals composing F_2 will be recognisable by inspection alone. In the case of white glabrous × cream glabrous only 10 distinct forms can be distinguished in this generation without further breeding, viz., 2 (white and cream) among the glabrous, and 8 (4 self sap-colours and the corresponding bicolours) among the hoary

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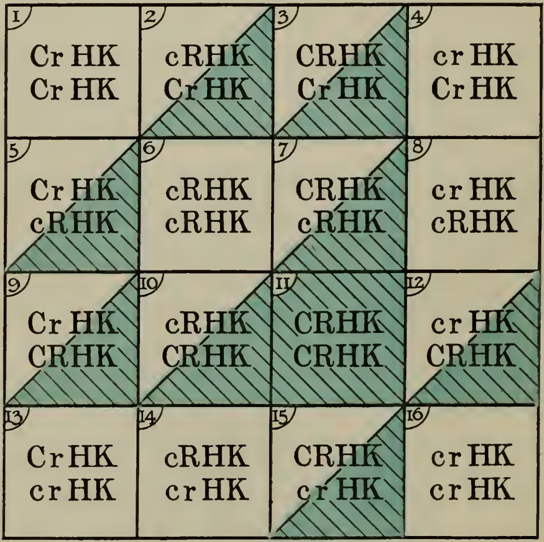
* The relations existing between the four sap-colours, purple, plum, red, and copper, appear to be similar to those observed by Tschermak in the case of the *reinviolett*, *aschviolett*, *reinrosa*, and *aschrosa*, resulting in F_2, from a cross between a blood-red hoary and a white glabrous, if, indeed, the two series of colours are not identical. 'Beihefte z. Bot. Centralb.,' Bd. 16, Heft 1, 1903.

plants. But the recombinations of the several factors discussed above yield 243 distinct types in F_2, requiring 1024 (4^5) individuals to exhibit them all in their relative proportions. On setting out the possible combinations, 108 of these types will be found to occur among hoary, 135 among glabrous individuals. In the case of the hoary plants much can be learnt from the results of *self*-fertilisation; thus 54 F_2 types can be distinguished if the analysis of the F_3 families, thus produced, is merely qualitative, 81 if the quantitative composition is also known. The whole 108, however, can only be identified if the self-fertilisation is supplemented by suitable cross-breeding, since by this method only, as yet, are we able to distinguish between two otherwise similar individuals, one being homozygous as regards C and heterozygous as regards R and the other heterozygous as to C and homozygous as to R (*cf.* sqs. 3 and 9 with sqs. 7 and 10, fig. 3). In the glabrous plants, on the other hand, constitutional differences other than those affecting plastid colour can only be detected by *cross*-breeding. Table II shows

FIG. 3.—F_2 from White glabrous × Cream glabrous.

Ratio of hoary to glabrous ...... 9 : 7.
,, coloured to white ...... 9 : 7.



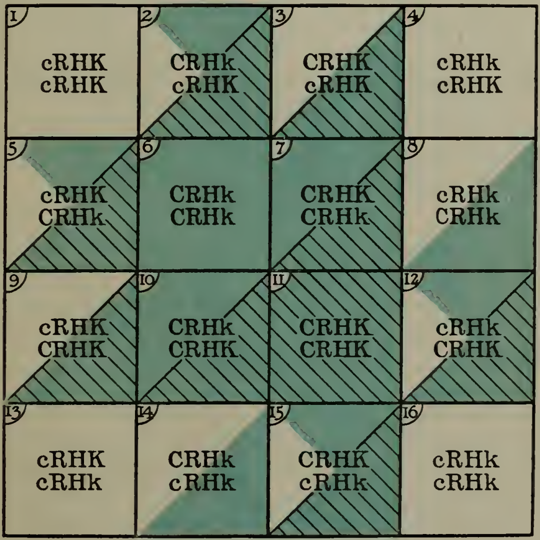
1 Cr HK Cr HK	2 cRHK CrHK	3 CRHK CrHK	4 cr HK Cr HK
5 Cr HK cRHK	6 cRHK cRHK	7 CRHK cRHK	8 cr HK cRHK
9 Cr HK CRHK	10 cRHK CRHK	11 CRHK CRHK	12 cr HK CRHK
13 Cr HK cr HK	14 cRHK cr HK	15 CRHK cr HK	16 cr HK cr HK

Each square is a zygote. When C meets R there is sap-colour in the flower (indicated by blue), and though H and K are present in all, the coloured alone are hoary (indicated by hatching). The undivided squares represent homozygotes with uniform offspring. The subdivision of a square shows that the zygote it represents will give a mixed offspring, but no attempt is made to show the *proportions* in which the various forms will occur in F_3.

the 54 qualitatively different types of hoary individuals which will occur in F_2, and their distribution among the 8 recognisably distinct forms appearing in that generation. The evidence already available plainly indicates that if the experiment were carried out upon a sufficiently large scale the full number of types would be obtained. Briefly summarised the facts were as follows: Fifty-seven hoary F_2 plants were tested by self-fertilisation. In the case of 15 the results were inconclusive owing to the small number of offspring obtained; the remaining 42 were found to correspond with 18 of the 54 qualitatively different types shown in Table II. [These types are marked in the table with an asterisk.] A full analysis of the F_3 families is given in Table III.

FIG. 4.—F_2 from Cream Glabrous × Sap-coloured Glabrous.

Ratio of hoary to glabrous .... 9 : 7
,, coloured to white .... 3 : 1



Hatching indicates hoariness. Blue shows sap-colour in the flower. Homozygous plants with uniform offspring are indicated by undivided squares. Squares representing heterozygotes are subdivided, and the distribution of colour and hatching in them shows the nature of the mixture to be found in their progeny (F_3), but no attempt is made to show the *proportions* in which the various forms will occur.

Certain other corollaries which follow from this account of the gametic composition of the F_2 plants can be tested by the F_3 generation, and these also may be considered in the particular case of white glabrous × cream glabrous (CrBHK × cRbHK).

EXPECTATION (see Argument p. 38 and fig. 3, p. 40).	RESULTS OBSERVED (see Detailed Analysis, Table III, p. 49, and Table IV, p. 52).
1. That some of the hoary F_2 plants will be *heterozygous* in regard to *both* C and R, giving a mixed offspring in the proportion of 9H : 7G.	Fourteen hoary F_2 plants gave a mixture of hoary and glabrous in proportions varying between 9 : 7·9 and 9 : 5·9, *the average ratio being exactly 9H : 7G.*
2. That others will be *heterozygous* only as regards *either* C *or* R, and will yield a mixture in the ratio of 3H : 1G.	Twenty-two hoary F_2 plants gave a mixture of hoary and glabrous in proportions varying between 3 : 1·3 and 3 : 0·7; *the average ratio being exactly 3H : 1G.*
3. That others will be *homozygous* as regards C and R, and will yield only hoary offspring.	Five hoary F_2 plants yielded together 704 offspring, *all hoary.*
4. That the numbers of these three kinds of individuals will be in the ratio of 4 : 4 : 1.	The numbers of the three kinds of individuals obtained from 41 plants taken at random were 14, 22, and 5 respectively, where the expectation is 18·2 : 18·2 : 4·6.
5. That all the F_2 glabrous plants will breed true to glabrousness. [All presumably contain H and K, and in respect of surface character are of one kind in composition as well as in appearance, and in character of offspring by self-fertilisation.]	Thirty-five glabrous F_2 plants were self-fertilised, and yielded *all* (750) *glabrous* offspring.
6. That the F_2 glabrous plants, which occur under two forms (whites and creams) will consist as regards the plastid character of the three Mendelian categories DD, DR (whites), and RR (creams).	Creams have already been shown to breed true. Of 33 F_2 glabrous whites, 24 when self-fertilised gave a mixture of white and cream, nine gave whites only.
7. That the group of non-sap-coloured plants (in this case identical with the glabrous group) will be composed in respect of the sap colour character of five kinds of individuals: those containing C, of which some will be homozygous, some heterozygous: others containing R, similarly of two kinds homozygous and heterozygous: and, lastly, others containing neither C nor R. Further, that these five classes of individuals will occur among whites and creams alike.	Thirty-one F_2 whites were tested against seven F_2 creams in 35 different combinations. Two cases in which the number of offspring did not exceed three may be disregarded. Of the rest, one mating gave all sap-coloured hoary, 20 gave all non-sap-coloured glabrous, and 12 gave a mixture of the two (see Table IV).
If this be so, it follows that though *any* F_2 white or cream will breed true as regards the sap and surface characters when *self*-fertilised, some, when crossed together, will yield all hoary sap-coloured; others will yield all	

EXPECTATION (see Argument, p. 38, and fig. 3, p. 40)—*contd.*	RESULTS OBSERVED (see Detailed Analysis, Table III, p. 49, and Table IV, p. 52)—*contd.*
glabrous non-sap-coloured; others, again, will yield a mixture of the two. The relative frequency of the three kinds of matings will be 2, 31, and 16 respectively (see fig. 3, p. 40).	Observed frequency of matings 1, 20, and 12 respectively.
8. That in such matings *some* glabrous individuals (whether white or cream) will sometimes give one result, sometimes another, according to the constitution of the particular individual with which they are bred; whereas *others* will invariably give the same result (*cf.* type of sq. 16, fig. 3, p. 40).	Of the seven creams employed, one gave a total offspring of only eight, and may therefore be disregarded. Of the remaining six, four when bred with some whites gave *a mixture* of hoary and glabrous, but with others gave *all glabrous;* one sometimes gave *a mixture* and sometimes *all hoary;* one *always* gave glabrous only (10 matings) (see Table IV).
9. That when the F_2 glabrous plants are crossed with either of the original pure glabrous types the offspring will be *all hoary, all glabrous, or a mixture of the two,* according to the constitution of the particular F_2 individual.	Two matings with pure-bred whites gave *all hoary;* eight matings with pure-bred creams gave *all glabrous*, and one gave *a mixture.* It happened that one of the two bred with pure white was one of the eight bred with pure cream; it must therefore have been a homozygous type containing R but not C (*cf.* sq. 6, fig. 3, p. 40). (For details of experiment, see Table IV.)

The gametic composition of the glabrous strains, white, cream, red, being thus made clear, it remains to consider the hoary types, purple and white *incana* and white Bromptons. The mating purple *incana* and cream glabrous we may represent as CRBHK × cRbHK. Redistribution of these factors should give the following result: A mixed F_2 composed of hoary and glabrous, sap-coloured and non-sap-coloured, selfs and bicolours, purples and reds, whites and creams. In these all the hoary are sap-coloured and all the glabrous non-sap-coloured, and the ratio between the two contrary characters constituting a pair is in each case 3 : 1. The facts were as follows: From 4 fruits gathered from an F_1 cross-bred, 46 brown, 47 intermediate and 126 green seeds were obtained. Of the plants raised from green seeds 92 flowered and gave 79 purple selfs and 13 bicolours; 34 red selfs and 7 bicolours, 32 whites and 11 creams were obtained from the intermediate and the brown seeds respectively. We thus get the following results:—

173 hoary	46 glabrous	= 3 : 0·8
173 sap-coloured.........	46 non-sap-coloured ...	
126 purple	47 reds	= 3 : 1·1
113 self sap-colours ...	20 bicolours	= 3 : 0·5
32 white	11 creams	= 3 : 1·0

We again notice a distinct deficiency of cream forms (bicolours), otherwise the results accord with expectation. It may be that a further complication, apart from the late flowering habit of the cream forms, is here indicated, but owing to the fact that a certain proportion of the hoary plants failed to flower before the end of the season this point must, at present, remain undecided.

From "white" *incana* × cream glabrous we get the same series in F_2 as from purple *incana* × cream glabrous, with white and cream hoary in addition (see Rep. II, p. 18). But, as stated in the Introduction, "white" *incana* is undoubtedly a coloured form in reality, and the tinging which may be seen in fading flowers reappears in both hoary and glabrous F_2 whites from white *incana* × sap colours. On the other hand, in F_2 from white *incana* × cream (a genuine non-sap-coloured form) the hoary whites and creams tinge, but the glabrous plants give no sign of coloration on fading, and are evidently truly colourless in regard to sap. The case of white Bromptons, which give no visible indication of colour on fading, needs further investigation.

In the matings between hoary and glabrous forms, as with unions between two glabrous strains, the constitution of the F_2 plants is revealed by further breeding, and several types, otherwise indistinguishable, have been experimentally recognised in this way.

We can now comprehend more clearly the significance of the results in an earlier experiment (Rep. II, p. 9, Experiments 17A and 17B). Two F_2 glabrous whites from cream glabrous × white *incana* gave *all hoary* when crossed with pure-bred glabrous white. Of these two individuals one gave *all glabrous* when crossed with pure-bred glabrous cream. Both F_2 plants carried RHK (for both parent types contain these factors) but not C (otherwise they themselves would have given evidence of colour).

But pure-bred glabrous white carries CHK, hence when mated with *any* such glabrous F_2 white (or cream) or its descendants, the offspring will be *all hoary*. Conversely, any such F_2 glabrous plant or any of its descendants × a pure-bred cream similar to the parent cream will give *all glabrous*, for neither carry C. Further, *any* two such F_2 glabrous plants (whether white or cream) when mated together will give *all glabrous*. In fact, the results of Experiments 17A and 17B are to be regarded as holding not merely for particular individuals but for all the glabrous members of the F_2 family. Evidence fully bearing out this statement is furnished by the following experiments: 16 F_3 whites from 5 F_2 white parents of parentage similar to those employed in the above experiments, mated with a pure-bred cream gave 128 glabrous: 12 of these same F_3 whites descended from 4 of the 5 F_2 plants, crossed with an F_3 cream, gave 101 plants all glabrous.

Double Flowers.—The occurrence and distribution of double flowers has already been recorded in detail (Rep. II, p. 29). In the case of unions between glabrous strains the results were such as to suggest that no white, cream (excluding Princess May), or flesh-coloured plant used in these matings was throwing doubles, but that individuals belonging to other sap-coloured strains, notably the red, were undoubtedly giving off doubles. These strains have now been further tested, and the results are in accordance with the above supposition. No doubles were obtained from the white, cream or flesh-coloured strains in either of the two succeeding generations; on the other hand, the red race yielded doubles in abundance. From one red plant, 13 singles and 9 doubles were obtained in the first generation; 11 of these singles gave 134 singles and 200 doubles in the next generation; the doubles occurred in *every* family, and in most cases were in excess of the singles.

Taken all together the facts point to the following conclusions:—

(1) Doubles only occur in F_1 when both parents are throwing doubles, viz., are heterozygous. In F_2 they may not only occur when this is the case, but also when only one parent is heterozygous. When both parents are homozygous they are absent altogether. On this view the results of Experiments 15, 16, 19D, and 19E (Rep. II, pp. 8, 13, 35, 37) fall into line; red glabrous × dark purple glabrous gave doubles in F_1—both were, therefore, heterozygous. Since the same dark purple glabrous × light purple glabrous gave no doubles in F_1, the light purple was, therefore, presumably homozygous; doubles should, however, appear in F_2, and this was the case.

(2) Purple and white *incana* and all the white and cream glabrous plants hitherto used, Princess May excepted, have been homozygous.

(3) The sap-coloured glabrous strains employed probably comprised both homozygous and heterozygous individuals. The reds examined have so far proved to be all heterozygous, but in the case of the flesh-coloured race heterozygous individuals were evidently used in some unions with *incana* (Rep. II, Experiment 29, Table II, p. 33, also Experiment 31C),* homozygous plants in other matings with *incana* (*loc. cit.*, Experiment 1 (1)), and in all matings with glabrous races (Rep. II, pp. 37, 38).

As yet, however, we are without explanation of the remarkable fact that heterozygotes frequently yield a large excess of the latent form.

Experiments with M. sinuata.—From a mating between *sinuata* var. *glabra* and the type-form 12 hoary cross-breds were obtained in F_1 (see Rep. II, p. 39). Self-fertilisation of one of these cross-breds gave the expected mixture of hoary and glabrous plants in F_2, showing that in this species hoariness and glabrousness are related to one another precisely as in *incana*.

In another experiment a cross was made between the glabrous variety of *sinuata* and white *incana*; only 3 plants were obtained,

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* *Cf.* Corrigenda, Report III.

and of these only 2 were raised to maturity. These plants (as stated in Rep. II, p. 40) were at first destitute of the stalked glands characteristic of *sinuata*, but examination of the plants in the second season showed a few scattered glands on the stem, pedicels, calyx, and ovary; on the leaves they were absent or very rare, whereas in pure *sinuata* they are abundant on all these parts. It, therefore, appears that gland formation in such cross-breds, though comparatively slight and of late occurrence, is not wholly absent as is the case with a strictly recessive character. The flowers and fruits were of the *sinuata* type, the corolla being small and with narrow petals, the pods slightly contracted between the seeds.

Another family of *sinuata-incana* cross-breds was obtained by mating extracted cream glabrous (an F_3 plant from cream glabrous × white *incana*) with a *sinuata* cross-bred (an F_1 plant from *sinuata* var. *glabra* × *sinuata* type). Five plants were obtained, of which 2 flowered. Glands were very numerous on the stem, pedicels, and calyx, less abundant on the ovary, and very scarce on the leaves. As in the cross-breds of the preceding experiment, the leaves were intermediate as regards outline and character of tomentum between the parent species, but in this case the corolla resembled *incana* both in size and shape of petals. Though the cross in the earlier experiment was between the pure-bred types, and in the present case between an extracted individual and a cross-bred, the one parent was in each case wholly of *sinuata*, the other of *incana* descent. The structural differences between the two F_1 families require further investigation.

Table I.—F_2 from Matings between Glabrous Strains.

Mating.	Numbers observed.		Expectation.		
	Hoary.	Glabrous.	Hoary.	Glabrous.	Ratio.
White × cream ……	128	95	126	98	9 : 7
White × sap-colours	169	103	153	119	9 : 7
Cream × sap-colours	284	188	265	206	9 : 7
	Sap-coloured glabrous.	Non-sap-coloured glabrous.	Sap-coloured glabrous.	Non-sap-coloured glabrous.	
White × cream ……	0	75	0	75	0 : all
White × sap-colours	37	41	33	44	3 : 4
Cream × sap-colours	82	95	76	101	3 : 4
	Non-cream.	Cream.	Non-cream.	Cream.	
White × cream ……	59	16	56	19	3 : 1
Cream × sap-colours	82	13	71	24	3 : 1

Table II.—Showing various kinds of *Qualitatively* different Individuals existing among Hoary F_2 Plants from the Cross White Glabrous × Cream Glabrous, and Relative Number of each.

* An asterisk indicates that the form thus marked has been experimentally recognised.

Relative numbers of F_2 types.	Colours of F_2 types.	Colours yielded in F_3 by the several F_2 types.									
		Purple self.	Purple bicolour.	Plum self.	Plum bicolour.	Red self.	Red bicolour.	Copper self.	Copper bicolour.	White.	Cream.
*64	Purple self	+	+	+	+	+	+	+	+	+	+
*32	,,	+		+		+		+		+	
*32	,,	+	+	+	+					+	+
32	,,	+	+			+	+			+	+
*16	,,	+		+						+	
16	,,	+				+				+	
*16	,,	+	+							+	+
8	,,	+	+	+	+	+	+	+	+		
8	,,	+								+	
4	,,	+	+	+	+						
4	,,	+	+			+	+				
*4	,,	+		+		+		+			
2	,,	+		+							
2	,,	+				+					
2	,,	+	+								
1	,,	+									
*32	Purple bicolour		+		+		+		+		+
*16	,,		+		+						+
16	,,		+				+				+
8	,,		+								+
4	,,		+		+		+		+		
2	,,		+		+						
2	,,		+				+				
1	,,		+								
*32	Plum self			+	+			+	+	+	+
*16	,,			+	+					+	+
16	,,			+				+		+	
8	,,			+						+	

Table II—*continued.*

* An asterisk indicates that the form thus marked has been experimentally recognised.

Relative numbers of F_2 types.	Colours of F_2 types.	Colours yielded in F_3 by the several F_2 types.									
		Purple self.	Purple bicolour.	Plum self.	Plum bicolour.	Red self.	Red bicolour.	Copper self.	Copper bicolour.	White.	Cream.
4	Plum self			+	+			+	+		
*2	,,			+				+			
2	,,			+	+						
1	,,			+							
*16	Plum bicolour				+				+		+
8	,,				+						+
2	,,				+				+		
1	,,				+						
*32	Red self					+	+	+	+	+	+
16	,,					+	+			+	+
*16	,,					+		+		+	
8	,,					+				+	
4	,,					+	+	+	+		
2	,,					+		+			
2	,,					+	+				
1	,,					+					
*16	Red bicolour						+		+		+
8	,,						+				+
2	,,						+		+		
1	,,						+				
*16	Copper self							+	+	+	+
8	,,							+		+	
*2	,,							+	+		
1	,,							+			
8	Copper bicolour								+		+
*1	,,								+		

Number of types, 54. Number of individuals, 576.

Table III.—Analysis of F_3 Generation derived from Sap-coloured F_2 Plants in the Operation [(Cream Glabrous × White Glabrous) × Self] × Self.

Colour of F_2 plants.	Reference No. of F_2 plant.	Analysis of F_3 families.												
		Surface character.			Colour of hoary plants.								Colour of glabrous plants.	
		Hoary.	Glabrous.	Ratio of H : G.	Purple self.	Purple bicolour.	Plum self.	Plum bicolour.	Red self.	Red bicolour.	Copper self.	Copper bicolour.	White.	Cream.
Purple self	1	91	75	9 : 7·4	32	8	23	3	15	4	1	2	59	16
	2	138	120	9 : 7·8	44	14	26	10	24	3	13	2	87	31
	3	127	100	9 : 7·1	52	7	31	2	16	3	4	0†	90	8
	4	209	73	3 : 1·0	80	6	42	18	30	5	12	1	59	10
	5	74	53	9 : 6·4	25	9	14	1	14	3	6	0	40	12
	6	164*	108*	9 : 5·9	72	26	35	10	—	—	—	—	75	25
	7	173*	124*	9 : 6·4	64	19	31	3	—	—	—	—	86	24
	8	108*	32*	3 : 0·9	49	18	25	5	—	—	—	—	22	9
	9	81*	71*	9 : 7·9	24	5	6	0	—	—	—	—	21	5
	10	120*	95*	9 : 7·1	76	15	—	—	—	—	—	—	75	21
	11	152	107	9 : 6·3	79	—	32	—	26	—	10	—	106	—
	12	234	58	3 : 0·7	109	—	45	—	40	—	24	—	55	—
	13	164	—	all : 0	100	—	16	—	33	—	11	—	—	—
	14	178*	54*	3 : 0·9	97	—	53	—	—	—	—	—	46	—
Purple bicolour	15	76	40	?		29	—	11	—	7	—	5	—	—
	16	176*	54*	3 : 0·9		33	—	21	—	—	—	—	—	26
	17	208*	57*	3 : 0·8		41	—	16	—	—	—	—	—	12

* In the case of purples which do not yield the red classes, the proportion of hoary and glabrous can be calculated from the seed colour; all numbers thus obtained are marked with an asterisk.

† Absence of a form, due presumably to the small total, is indicated by 0, in other cases by a —.

Table III—*continued.*

Colour of F_2 plants.	Reference No. of F_2 plant.	Analysis of F_3 families.												
		Surface character.			Colour of hoary plants.								Colour of glabrous plants.	
		Hoary.	Glabrous.	Ratio of H : G.	Purple self.	Purple bicolour.	Plum self.	Plum bicolour.	Red self.	Red bicolour.	Copper self.	Copper bicolour.	White.	Cream.
Plum self	18	170	61	3 : 1·1			108	19	—	—	35	0	49	8
	19	172	47	3 : 1·0			98	26	—	—	25	10	37	8
	20	176	70	3 : 1·2			79	22	—	—	47	6	49	7
	21	119	42	3 : 1·0			55	17	—	—	18	3	28	9
	22	45	12	3 : 0·8			35	10	—	—	—	—	10	2
	23	138	46	3 : 0·9			106	24	—	—	—	—	28	6
	24	112	37	3 : 1·0			86	24	—	—	—	—	33	2
	25	219	—	all : 0			140	—	—	—	47	—	—	—
	26	144	—	all : 0			100	—	—	—	35	—	—	—
Plum bicolour	27	134	53	3 : 1·2				94	—	—	—	—	—	24
Red self	28	101	36	3 : 1·1					58	12	23	4	26	8
	29	152	116	9 : 6·9					77	17	35	14	96	12
	30	66	50	9 : 6·8					42	4	13	8	42	8
	31	53	20	3 : 1·1					21	11	12	3	14	5
	32	80	36	3 : 1·3					54	—	24	—	36	—
	33	33	10	3 : 0·9					20	—	10	—	9	—
Red bicolour	34	48	41	9 : 7·7						28	—	15	—	41
	35	50	40	9 : 7·2						31	—	17	—	39
	36	13	4	3 : 0·9						7	—	3	—	4
	37	66	57	9 : 7·8						31	—	21	—	47

Copper self...........	38	60	16	3 : 0·8							44	8	11	1
	39	54	23	3 : 1·3							42	8	18	2
	40	22	6	3 : 0·8							14	4	4	0
	41	62	—	all : 0							51	4	—	—
Copper bicolour......	42	115	—	all : 0								100	—	—

Conclusions in regard to F_2 Plants analysed in Table III.

Reference No. of plant.	Factors and characters as to which the plant is heterozygous.	Factors and characters as to which the plant is homozygous.
1, 2, 3, 5	C, R, B, plastid colour, quality of sap-colour	H, K
4	C (or R), B ,, ,, ,, ,,	R (or C) H, K
6, 7, 9	C, R ,, ,, ,, ,,	B, H, K
8	C (or R) ,, ,, ,, ,,	R (or C), B, H, K
10	C, R, plastid colour	B, H, K, quality of sap-colour (full)
11	C, R, B, quality of sap-colour	H, K, plastid colour (white)
12	C (or R), B, quality of sap-colour	R (or C), H, K, plastid colour (white)
13	B, quality of sap-colour	C, R, H, K, plastid colour (white)
14	C (or R), quality of sap-colour	R (or C), B, H, K, plastid colour (white)
15	B, quality of sap-colour. ? C, R	H, K, plastid colour (cream)
16, 17	C (or R), quality of sap-colour	R (or C), B, H, K, plastid colour (cream)
18—21	C (or R), B, plastid colour	R (or C), H, K, quality of sap-colour (modified)
22—24	C (or R), plastid colour	R (or C), B, H, K, quality of sap-colour (modified)
25, 26	B	C, R, H, K, plastid colour (white), quality of sap-colour (modified)
27	C (or R)	R (or C), B, H, K, plastid colour (cream), quality of sap-colour (modified)
28, 31	C (or R), plastid colour, quality of sap-colour	R (or C), b, H, K
29, 30	C, R, plastid colour, quality of sap-colour	b, H, K.
32, 33	C (or R), quality of sap-colour	R (or C), b, H, K, plastid colour (white)
34, 35, 37	C, R, quality of sap-colour	b, H, K, plastid colour (cream)
36	C (or R), quality of sap-colour	R (or C), b, H, K, plastid colour (cream)
38—40	C (or R), plastid colour	R (or C), b, H, K, quality of sap-colour (modified)
41	Plastid colour	C, R, b, H, K, quality of sap-colour (modified)
42		C, R, b, H, K, plastid colour (cream), quality of sap-colour (modified)

Table IV.—Showing Different Results obtained from the *same* Glabrous F_2 Individual in Different Matings with other Glabrous Plants, both Extracted and Pure-bred.

	Analysis of F_3 families.	
	Surface character.	Plastid colour.
Matings between F_2 whites and F_2 creams.		
$W_1 \times C_1$	19 hoary	
$W_{10} \times C_2$	2 glabrous	Wh.
$W_{11} \times C_2$	6 ,,	Wh. and cr.
$W_{13} \times C_3$	38 ,,	Wh. and cr.
$W_{14} \times C_4$	46 ,,	Wh. and cr.
$W_6 \times C_5$	26 ,,	Wh.
$W_7 \times C_5$	6 ,,	Wh. and cr.
$W_8 \times C_5$	26 ,,	Wh. and cr.
$W_9 \times C_5$	16 ,,	Wh.
$W_{19} \times C_5$	13 ,,	Wh. and cr.
$W_{20} \times C_6$	21 ,,	Wh. and cr.
$W_{21} \times C_6$	28 ,,	Wh. and cr.
$W_2 \times C_7$	34 ,,	Wh. and cr.
$W_3 \times C_7$	3 ,,	Wh. and cr.
$W_4 \times C_7$	35 ,,	Wh.
$W_5 \times C_7$	18 ,,	Wh. and cr.
$W_{12} \times C_7$	33 ,,	Wh. and cr.
$W_{15} \times C_7$	9 ,,	Wh.
$W_{16} \times C_7$	21 ,,	Wh.
$W_{17} \times C_7$	34 ,,	Wh.
$W_{18} \times C_7$	26 ,,	Wh.
$W_{22} \times C_7$	41 ,,	Wh. and cr.
$W_{23} \times C_7$	33 ,,	
$W_4 \times C_1$	Hoary and glabrous	Wh.
$W_{22} \times C_1$	,, ,,	Wh. and cr.
$W_{24} \times C_1$	,, ,,	Wh.
$W_{14} \times C_3$	,, ,,	Wh. and cr.
$W_{19} \times C_4$	,, ,,	Wh. and cr.
$W_{25} \times C_5$	,, ,,	Wh. and cr.
$W_{26} \times C_5$	,, ,,	Wh. and cr.
$W_{27} \times C_5$	,, ,,	Wh. and cr.
$W_{28} \times C_5$	,, ,,	Wh.
$W_{29} \times C_6$	,, ,,	Wh. and cr.
$W_{30} \times C_6$	,, ,,	Wh. and cr.
$W_{31} \times C_6$	,, ,,	Wh. and cr.
Matings between F_2 whites and pure-bred creams.		
W_{12} × pure-bred cream	29 glabrous	Wh. and cr.
W_{13} × ,, ,,	9 ,,	Wh. and cr.

Table IV—*continued.*

	Analysis of F_3 families.	
	Surface character.	Plastid colour.
Matings between F_2 whites and pure-bred creams—*continued.*		
W_{17} × pure-bred cream ...	35 glabrous	Wh.
W_{21} × ,, ,, ...	28 ,, ...	Wh. and cr.
W_{29} × ,, ,, ...	17 ,, ...	Wh. and cr.
W_{30} × ,, ,, ...	34 ,, ...	Wh. and cr.
W_{31} × ,, ,, ...	48 ,, ...	Wh. and cr.
W_{32} × ,, ,, ...	6 ,, ...	Wh. and cr.
W_{18} × ,, ,, ...	Hoary and glabrous	
Matings between F_2 whites and pure-bred whites.		
W_{31} × pure-bred white ...	16 hoary	
W_{33} × ,, ,, ...	16 ,,	

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