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Report IV.

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 IV.

EXPERIMENTAL STUDIES IN THE PHYSIOLOGY OF HEREDITY.

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The present Report deals with the continuation of the experiments with Poultry, Sweet Peas, and Stocks.

Some account is given of our analysis of the various kinds of white plumage in fowls. We have been able to show that, in addition to the white which is dominant to colour, there are two entirely distinct whites which severally behave as recessive to colour, but on crossing give only coloured birds.

In our last Report we gave reasons for regarding the rose-comb as a comb on which an additional element, "roseness," had been superposed, and we suggested that the allelomorphic pair consists in the two states: presence of the factor for rose (R) and absence of that factor (r). The rose-comb is in reality a single comb modified by the presence of a "rose" factor. The omission of this factor enables the single comb to appear. The same considerations apply to the pea-comb, which is single + a pea factor. The true allelomorphic pair in each case is the *presence* of a given factor which is dominant to the *absence* of that factor. This view we have since been able to illustrate by another experiment (p. 18), and recent experience inclines us to regard it as applicable to all Mendelian cases as yet investigated. As the acceptance of the "Presence and Absence" hypothesis seems to demand some general expression for such inter-relation between factors belonging to distinct allelomorphic pairs, we propose the terms *epistatic* and *hypostatic.** For example, the combless, the single-combed, and the rose-combed conditions may, in the light of our present knowledge, be regarded as forming a cumulative series, and we should speak of the factor for single as being dominant to the combless condition but hypostatic to the rose factor; and similarly the rose factor may be referred to as epistatic to the single.

Some experiments with Sweet Peas have led to an extension of our knowledge of the inheritance of stature in this species. A cross was made between the dwarf procumbent "Cupid" and a half-dwarf form known as the "Bush" Sweet Pea. The F_1 plants all "reverted" to the normal tall habit, and subsequent breeding from these demonstrated clearly that the case can be expressed as one of simple dihybridism (see p. 6).

The majority of our Sweet Pea work of the past two seasons was undertaken with a view to further elucidating the phenomenon we have

* Already suggested by one of us in 'Science,' November 15, 1907.

termed gametic coupling. Experiments described in our last Report showed that the offspring of plants heterozygous for the blue factor and for long pollen can be classified (omitting the whites) as purples and reds in the ratio 3 : 1, and as plants with long and round pollen in the same ratio. But the distribution of the pollen among the coloured forms was complex. Instead of there being three long purples to each round one there were actually about twelve; and the deficiency of rounds among the purples was compensated for among the reds, where they were three to four times as numerous as the longs. We pointed out that this peculiar distribution would be brought about if we supposed that the majority of purple-bearing gametes bore also the factor for long pollen, and that the corresponding majority of non-blue gametes were associated with roundness. We suggested that in the present case the choice lay between the following two gametic series from the F_1 plant:—

(*a*) 8 purple long, 1 purple-~~red,~~ round 1 red long, 8 red round.
(*b*) 7 „ 1 „ 1 „ 7 „

The comparative merits of these two systems were discussed in Report III, and we are still unable to decide finally between them. The numbers, hewever, are somewhat more consistent with the scheme based on the 7 : 1 : 1 : 7 ratio.

During the past two years we have come across two cases among Sweet Peas in which the coupling is closer. One of these also relates to the factors for purple and pollen shape (p. 11), but the other has to do with two entirely different pairs of factors, viz., dark and light axil, and fertile as opposed to sterile anthers (p. 16). In both of these instances the distribution of characters in F_2 is in accordance with the view that the gametic series is on a 15 : 1 : 1 : 15 basis.

The undoubted existence of these two grades of gametic coupling in the Sweet Pea suggests that each may find its place in a scheme of increasing intensity of gametic coupling, such as is shown in the accompanying table, where the two allelomorphic pairs are represented by Aa and Bb :—

Gametic series.					Zygotes containing—				
AB.	Ab.	aB.	ab.		A and B.	A only.	B only.	Neither A nor B.	
1	1	1	1	= 4	9	3	3	1	= 16
3	1	1	3	= 8	41	7	7	9	= 64
7	1	1	7	= 16	177	15	15	49	= 256
15	1	1	15	= 32	737	31	31	225	= 1024
$n-1$	1	1	$n-1$	$= 2n$	$3n^2-(2n-1)$	$2n-1$	$2n-1$	$n^2-(2n-1)$	$= 4n^2$

The first term in the series is a simple case of dihybridism in which no coupling exists. The second term we have not yet encountered. But we have an ample series of experimental data which satisfy the third term; and the experimental evidence for the existence of the fourth term rests upon two independent cases.

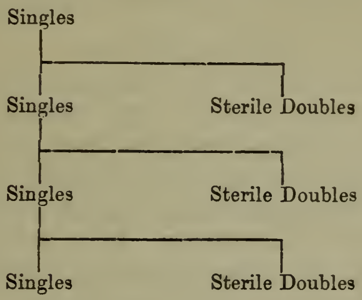
As we have indicated in the table above, there is a general expression for this series of terms. If the number of the gametic series be represented by $2n$, then the number of zygotes formed by such a series is $4n^2$; and this number will be distributed in such a way that there will be $3n^2-(2n-1)$ zygotes with both dominants, two groups of $2n-1$ with one dominant each, and $n^2-(2n-1)$ with neither dominant. It is obvious that, as the value of n increases, the terms containing n become relatively smaller in comparison with those containing n^2. The closer the gametic coupling the rarer become the two middle terms of the series which contain but one dominant apiece. And if n become very large, it is clear that the series

$$3n^2-(2n-1) : 2n-1 : 2n-1 : n^2-(2n-1)$$

will approximate to the series $3n^2 : 0 : 0 : n^2$. In other words, the greater the value of n, the closer we approach to a simple 3 : 1 ratio. When aberrant forms occur in a series which is apparently of the usual 3 : 1 type, it may be worth while examining them with a view to the possibility that they may represent the scarcer terms in a series resulting from close coupling.

During the past two seasons much of our time has been devoted to the inheritance of the hooded character in the Sweet Pea. The hooded standard behaves as a recessive to the erect standard, but in certain strains containing both red and purple flowers the hood is always associated with the latter colour (p. 9). In such cases we must suppose that all the "red" gametes bear the factor for the erect standard, and that this factor is absent from all the gametes which carry purple. We have, in Report III, referred to this phenomenon as one of gametic coupling, but strictly this expression is inapplicable. In the cases of actual gametic coupling discussed in the last paragraph the association is always between the dominant or *present* factors of the different pairs; long pollen is coupled with purpleness, and the dark axil with the fertile anther. The "present" factors would seem to behave in gametogenesis as though they were attracted by one another. But here the phenomenon is of a different order. The two dominant factors, blueness and erect standard, seem to repel one another so that they are not both found in the same gamete; consequently only two kinds of gamete are produced instead of the four characteristic of a normal case of dihybridism, and the result is a simple 1 : 2 : 1 ratio such as we should obtain when dealing with a simple Mendelian pair. For this phenomenon we suggest the term *spurious allelomorphism.*

In Stocks, the work has been chiefly concerned with the inheritance of double flowers. The experiments have brought to light a phenomenon of a new order. Double Stocks being always totally sterile, both as regards male and female organs, are invariably the offspring of single-flowered plants. The succession in these double-throwing strains of singles is thus to be represented as follows:—



Though always the offspring of singles, the doubles are nevertheless the majority, and the genetic mechanism by which this remarkable succession is accomplished remains problematical. The experiments have, however, contributed a first step towards the solution. *Singleness* is an ordinary Mendelian dominant to *doubleness* (Reps. III, p. 44, and II, p. 29), but the singles in the double-throwing strains are of a curious composite nature. The double-throwing singles were crossed reciprocally with a strain of pure singles. The F_1 plants are all alike single; but an examination of F_2 from these plants revealed a remarkable difference between the results of the reciprocals.

For where the pure single was used as mother, F_2 from each F_1 contained doubles, whereas when pure single was the father, some of the F_2 families contained doubles and some were all singles. It follows therefore that the pollen-grains of the double-throwing strains must be all or nearly all* bearers of doubleness; but that the egg-cells are of two kinds, those that bear singleness and those that bear doubleness.

The transmission of the cream-colour in the case of those single whites (known as "sulphur-whites") which throw double creams follows a similar system. The pollen-grains of such plants are all or nearly all* bearers of cream-colour, but the egg-cells are of two kinds, those which bear cream-colour and those which bear whiteness.

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* Pending further inquiry, these statements must not be made in a universal form. Though hitherto no exception has been found in either case, it is still quite possible that a small proportion of the pollen-cells in each case bear the dominant character.

SWEET PEAS.

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

Bush × Cupid Cross.

The Bush Sweet Pea, a form not previously used in these experiments, has a peculiar conformation. After reaching a height of about 8 inches it branches profusely from its lower nodes. Of the stems thus formed about 10—15 grow on, eventually reaching a height of some 3½ feet. The production of branches continues, but those formed later remain short and slender. In an ordinary tall Sweet Pea only about four or five stems attain any considerable extension (without special treatment). The stems of the Bush are thin and rather wiry, especially at the base, and the plants, till they reach a height of about 18 inches, can almost maintain themselves erect without sticks. By that time the stems are mutually entangled by their tendrils, and the compact bush-like form is very pronounced, entirely distinguishing them from any other sort of Sweet Pea.

In both the ordinary tall plants and the ordinary Cupids there appears to be some factor which restrains the production of branches, and thus enables the plant to attain a greater length. The non-branching tall plant attains a height 2 or 3 feet greater than that of the Bush, which must be regarded as a branching "tall." Similarly, the erect or branching Cupid is more stunted in its length than the ordinary or non-branching Cupids. The allelomorphs concerned are evidently:—

Dominant.	Recessive.
1. Tallness (T).	Dwarfness (t).
2. Prostrate: non-branching (P).	Erect: branching (p).

The ordinary tall is TTPP, the prostrate Cupid is ttPP, and the Bush is TTpp. When Bush is crossed with Cupid the two complementary factors, T and P, necessary to the production of the full height, meet each other and the "reversion on crossing" occurs.

In F_2, besides the three forms already mentioned with which we were familiar, there appears also, in consequence of the recombination of the factors, a new type—the erect dwarf (ttpp). These little plants have a very singular appearance, being extremely short and erect, somewhat resembling box-edging.

The numbers in the F_2 generation from six F_1 plants were:—

	Observed.	Calculated.
Tall (= prostrate talls)	219	*217·8*
Bush (= erect talls)............	70	*72·5*
Prostrate Cupids	69	*72·5*
Erect Cupids	29	*24·2*
	387	*387*

The observed numbers approach closely to those calculated on the 9 : 3 : 3 : 1 ratio, and the case is evidently one of dihybridism in which the two pairs of factors concerned are those we have suggested above.

The families resulting from this cross are considered elsewhere (p. 12) in connection with gametic coupling.

Table I.

—		Tall.	Bush.	Cupid prostrate.	Cupid erect.		
Purple erect	long.........	54	18	10	1	83	184 [167]
	round	4	—	1	1	6	
Purple hood	long.........	24	11	5	8	48	
	round	—	—	—	—	—	
Red ...	long.........	3	2	—	—	5	
	round	23	11	6	2	42	
White erect	long.........	43	10	10	3	66	113 [130]
	round	11	2	1	3	17	
White hooded	long.........	20	5	4	1	30	
	round	—	—	—	—		
Colour and pollen unknown*		37	11	32	10		
Total		219	70	69	29		
Expectation ...		217·8	72·6	72·6	24·2		

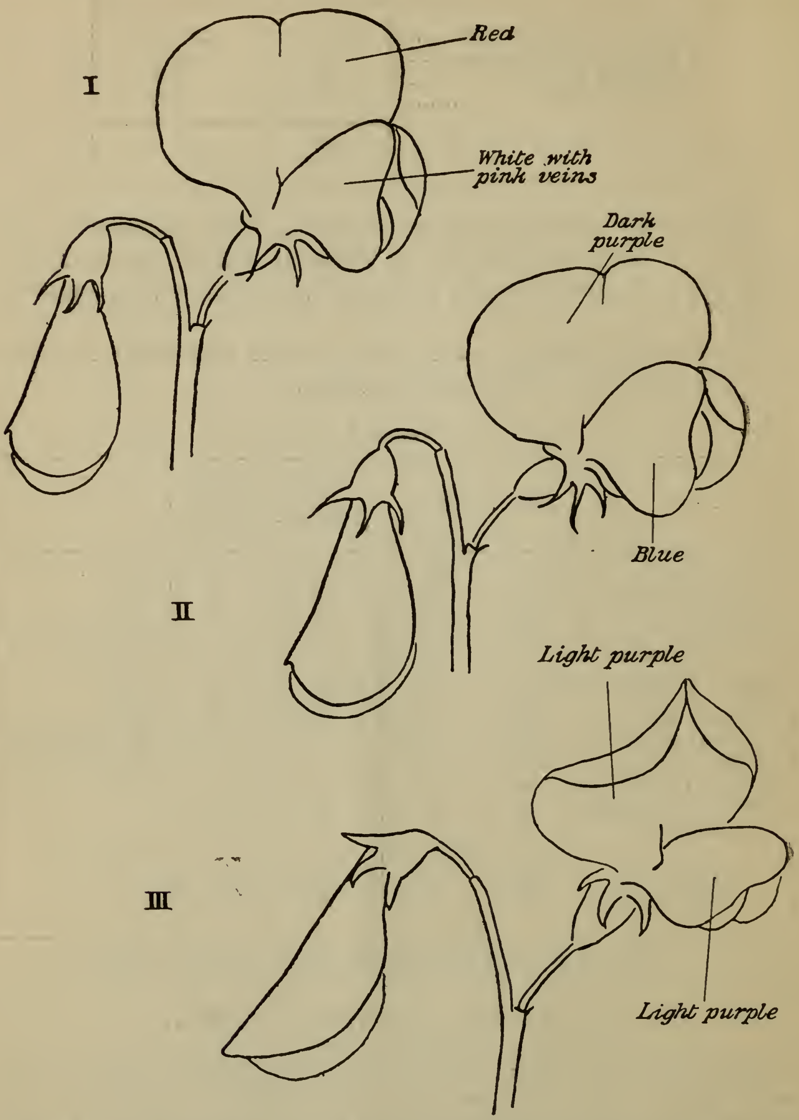
* Owing to late germination and consequent failure to flower.

The Inheritance of the Hooded Character.

The work of the past two seasons has consisted largely in the investigation of the peculiar transmission of the hooded standard. The hood is constituted by a more or less pronounced folding downwards of the top and sides of the standard or vexillum† (*cf.* fig,. p. 8). The hooded varieties may be of almost all the colours known in Sweet

† This shape is associated with, and perhaps caused by, absence of the central notch which is conspicuous in the middle of the erect standard of old-fashioned flowers. The shape of the buds in the two types is consequently very distinct (see figures).

Peas—white, cream, red, pink, mauve, purple—but, so far as we have observed, the hood never occurs in the purple bicolor or Purple Invincible (P. I.), or in the corresponding red bicolor or Painted Lady (P. L.). In all the hooded types standard and wings are more alike in tint; and there is therefore some interdependence between



Diagrammatic representation of the three coloured types which occur in F_2 from Blanche Burpee (hood white) × E. Henderson (erect white), giving F_1 purple erect. I. Painted Lady; II. Purple Invincible; III. Duke of Westminster.

colour and form such that either the bicolor character prevents the development of the hood, or the development of the hood modifies the colour.* The erect type of standard is dominant to the hooded type.

The original cross with which we started was made in 1904 between the two whites, Blanche Burpee (long pollen, hooded) and Emily Henderson (round pollen, erect standard). The majority of the F_1 plants were P. I. (some being whites, others P. L., according to the factorial composition of the parents), and it is from such plants and their offspring that the data put together in Table II were obtained. From the four F_1 plants 773 plants were raised in F_2, with the following results :—

Erect purples.	Hooded purples.	Erect reds.	Whites (erect and hooded).
232	83	112	346
315 [326]		[109]	[338]
427 [435]			

As was to be expected, the purples are three times as numerous as the reds, and the coloured are to the whites as 9 : 7. From the F_2 generation families were raised in F_3 and F_4, as is recorded in Table II. The striking feature about this series of experiments is that among the *coloured* flowers hoods are only found on the purples. Among some thousands of plants, not a single hooded red has appeared. Nevertheless, the existence of hooded red types is well known in Sweet Peas. We are therefore led to suppose that we are dealing with a strain in which the factor for erect standard is alternative in the gametes to the factor for blue : and, conversely, that every gamete which carries the factor for the erect standard is devoid of the blue factor. Consequently, for these two pairs of factors, only two of the

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* The purple hooded types produced in these experiments are those known as Duke of Westminster and Duke of Sutherland respectively. The former corresponds with P. I., and the latter is represented among the erect types by the purple with purple wings referred to in these Reports as P.p.w.

The colour difference between hooded and flat types is not easy to express, but may readily be perceived when a collection of Sweet Peas is examined. In the erect purple and red bicolors the colour of the standard contains a red quality distinguishing it from that of the wings, which are more blue in the case of purples and more pink in the case of reds. While in a purple bicolor the standard is a chocolate red and the wings are blue or purple, the corresponding hooded type has both parts purple. Similarly in a red bicolor the colour of the standard is a scarlet and that of wings pink or pinkish-white, while in the corresponding hooded type the pigment of both parts is pink. When, as sometimes happens, the standard and wings of a hooded type differ in colour, the difference is rather in the amount of pigment than in its quality, the standard being fuller and the wings lighter, but the pigments of both parts show little difference in tint.

four conceivable classes of gamete exist, viz., blue hooded gametes, and non-blue erect gametes. The spurious allelomorphism (see p. 4), which we must assume to exist between blue and hood on the one hand, and between non-blue and erectness on the other, does not allow of the formation of purple erect, or of red hooded gametes. If this assumption is correct, there should follow certain consequences which may be tested by the data given in Table II.

1. Every hooded purple must be homozygous for the blue factor.	In Experiments 48—53, six hooded purples, although from families in which reds occur, bred true to purple (except in so far as whites might appear).
2. Every red must be homozygous for the erect standard.	In Experiments 54—59, six reds were bred from, and proved to be all homozygous for the erect standard.
3. Every erect purple must be heterozygous for both the erect standard and for blueness, and must therefore give hooded purples, erect purples, and reds, in the ratio 1 : 2 : 1.	The erect purples, whose offspring are recorded in Experiments 1—47, all gave hooded purples and erect reds. Of their 3707 coloured offspring, 902 were hooded purples, 939 were erect reds, and 1920 were erect purples.
4. Every hooded white must be homozygous for the blue factor.	In the only two cases in which the cross between a hooded white and a red has succeeded, the coloured offspring have been purple. We hope to obtain further results in the present year.
5. Since every hooded plant is homozygous for purple, and since long pollen is partially coupled with the blue factor, it follows that round pollen should be much rarer among the hooded than among the erect purples.	So far only two round hooded purples and one round hooded white have been met with in families heterozygous for hood and purple (Experiments 1—47). With this point we shall deal later, in connection with partial coupling (see p. 13).

The phenomenon of association of hood with purple was also witnessed in the F_2 families resulting from the Bush × Cupid cross, with which we have already dealt in another connection (p. 2). Here, again, the hood occurred in F_2, and only on the purples. The numbers—48 hooded purples, 89 erect purples, and 47 erect reds—are very close to the expected ratio, 1 : 2 : 1.

As stated above, in other strains red hooded forms exist. Experiments with these types are in progress, but have not yet been carried far enough to give positive results.

Partial Gametic Coupling.

A. *Between Pollen and Colour.*—In our last Report (p. 9), we showed that the distribution of pollen characters, long grains and round grains, was affected by that of the colour characters, according to a definite system, and we pointed out that the experimental results were explicable on the assumption that in plants, heterozygous for colour and pollen, the gametes were produced in a series of 16, viz., 7 purple long, 1 purple round, 1 red long, and 7 red round. Purple is associated with long pollen and red with round, but in neither case is the coupling complete.

In the four F_1 families from the cross Blanche Burpee × Emily Henderson (Table II, Exps. 1—4), the distribution of the pollen fits in with this scheme, as the following numbers show :—

	Observed.	Expectation on the 7 : 1 : 1 : 7 basis.
Purple long	296	*295*
Purple round	19	*25*
Red long	27	*25*
Red round	85	*82*
	427	*427*

From one of these F_2 families (No. 2), ten erect purples were chosen and grown on in the following year (Nos. 5—14). They produced :—

	Purple long.	Purple round.	Red long.	Red round.
F_3 generation from No. 2................	493	25	25	138
Expectation on 7 : 1 : 1 : 7 basis...	*471*	*40*	*40*	*130*
Expectation on 15 : 1 : 1 : 15 basis...	*490*	*20*	*20*	*151*

The number of round purples and of long reds is in each case decidedly lower than would be looked for on the assumption that the coupling was on a 7 : 1 : 1 : 7 basis, and is much nearer to what would be expected if the coupling were on a 15 : 1 : 1 : 15 basis. In some families, the dearth of these two classes is particularly well marked, and two of them (Nos. 5 and 6) were bred from. From No. 5, five families (Nos. 15—19) were obtained, and these, with the present plant, gave the following result :—

	Purple long.	Purple round.	Red long.	Red round.
No. 5 and its offspring, Nos. 15—19	545	25	40	159
Expectation on 7 : 1 : 1 : 7 basis...	*532*	*45*	*45*	*147*
Expectation on 15 : 1 : 1 : 15 basis...	*554*	*23*	*23*	*169*

The results are irregular. The proportion of red longs to red rounds fits fairly well with the supposition that the coupling is on a 7 : 1 : 1 : 7 basis; but the purple rounds are only half as many as would be expected. The coupling between long and purple seems to be closer, and is in accordance with the supposition that the gametic series is 15 : 1 : 1 : 15. Both in the F_3 generation and in these F_4 plants there is evidently some disturbing process which we cannot at present express, though it is possible that we are dealing with a mixture of families exhibiting the two forms of coupling.

From the other of the two F_3 plants chosen for further experiment (No. 6), we obtained a much more definite result. From it eight families, heterozygous in colour and pollen, were raised (Table II, Nos. 20—27). On adding together the results of these nine families, we obtain the following numbers :—

	Purple long.	Purple round.	Red long.	Red round.
No. 6 and its offspring, Nos. 20—27	583	26	24	170
Expectation on 15 : 1 : 1 : 15 basis...	*578*	*24*	*24*	*177*

It is obvious that the numbers in this group of families accord very closely with the figures expected on a 15 : 1 : 1 : 15 basis; and the view that this is the system actually followed receives confirmation from the distribution of the pollen and colour characters in the F_2 families from the Bush* × Cupid crosses (Table I, p. 7), where the following figures were obtained :—

	Purple long.	Purple round.	Red long.	Red round.
F_2 families ex Bush × Cupid	131	6	5	42
Expectation on 15 : 1 : 1 : 15 basis...	*132·4*	*5·6*	*5·6*	*40·4*

From the closeness with which the recorded results agree with expectation, it is evident that here again we are concerned with a 15 : 1 : 1 : 15 series. And when we come to deal with the inheritance of sterility in the Sweet Pea (p. 16), we shall meet with another case, in which we are undoubtedly concerned with a similar gametic series. We may take it, therefore, that there is good evidence for the existence of gametic coupling in the 15 : 1 : 1 : 15 series, as well as for the derivation of the families exhibiting the higher form from families in

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* The flower of the Bush plants used was a hooded white, exactly like that of Blanche Burpee.

which the lower occurs. We have, then, to recognise that in some families the coupling follows one system and in others another. Each process is, nevertheless, definite. As yet, however, we have not perceived any circumstance to which the distinction can be attributed.

In an earlier paragraph (p. 10), we mentioned that, owing to the partial coupling of long pollen with purple, we should expect hooded purples and hooded whites to be found very rarely with round pollen. When the gametes are produced in series of 16, *i.e.*, 7 purple long, 1 purple round, 1 red long, and 7 red round, it is clear that the chances of two purple round gametes meeting are only 1 in 16^2, *i.e.*, in 256 in families where reds occur. Of these 256 plants, 64 are homozygous for purple. Consequently, the chances of a homozygous purple having round pollen are 1 in 64. In families where hoods occur all the homozygous purples are hooded, and we should, therefore, look for one round hooded purple in 64. In the four F_1 families (Nos. 1—4), 1 round hooded purple occurred among 83 plants. Again, since the hooded whites are homozygous for purple, on our view we should look for one with round pollen out of 64. Actually, one white hooded plant with round pollen occurred among the 18 F_2 families, where the hood was recorded (Nos. 1 and 4). Where expectation demands 1 in 64, experiment gave 2 hooded rounds in 101.

If, however, the coupling is on the 15 : 1 : 1 : 15 basis, the proportion of rounds among the hooded purples and whites should be only 1 in $32^2 \div 4$, *i.e.*, 1 in 256. In No. 6 and its descendants, Nos. 20—27, only one of the 209 hooded purples had round pollen.

These complicated facts may be summarised thus:—From an examination of the families where the hooded standard occurs, it is quite clear that in some of them the coupling of blue factor with long pollen is definitely distributed according to the system 15 : 1, and that in others it follows the system 7 : 1. There are also families which cannot confidently be referred to either class. Since the F_2 derived from Bl. Burpee by E.H. round followed the 7 : 1 system, the heterozygosis between erectness and hood cannot be regarded as the direct cause of the 15 : 1 distribution. The families showing that distribution came in F_3 and later generations from this cross, and the 15 : 1 system seems, therefore, to have been brought into operation by the omission of something which may be supposed to be carried on in those collateral families which follow the 7 : 1 system. Scrutiny of the various groups has, however, failed to discover any consistent difference between those of the 7 : 1 type and those of the 15 : 1 type. In the case of the Bush × Cupid cross the 15 : 1 system appeared at once in F_2.

Table II.

	Exp. number.	Reference number.	Purples, erect.		Purples, hooded.		Reds.		Whites, erect.		Whites, hooded.		Reference number of parent.
			long.	rd.	long.	rd.	long.	rd.	long.	rd.	long.	rd.	
Families from purple parent heterozygous in blue, hood, and pollen.	1	'05, 253	25	2	11	—	3	10	31	15	11	1	
	2	309	50	6	20	—	12	23	(65 long + 15 rd.)				
	3	310	118	8	36	1	8	41	(116 long + 36 rd.)				
	4	312	21	2	15	—	4	11	37	13	6	—	
	5	'06, 302	39	3	26	—	1	20	17	1	1	—	'05, 309
	6	305	55	4	33	—	1	33	—	—	—	—	"
	7	307	25	1	11	—	2	7	11	3	7	—	"
	8	363	9	2	7	—	3	7	4	2	1	—	"
	9	368	5	—	3	—	—	4	5	4	5	—	"
	10	370	4	1	6	—	2	5	2	1	—	—	"
	11	372	76	4	43	—	6	23	20	12	12	—	"
	12	374	69	5	34	—	5	27	25	13	15	—	"
	13	376	11	2	6	—	2	5	13	4	6	—	"
	14	377	23	3	8	—	3	7	8	3	2	—	"
	15	'07, 131	33	1	10	—	5	10	12	3	6	—	'06, 302
	16	132	78	6	44	—	12	30	27	13	13	—	"
	17	133	98	6	57	—	9	51	39	15	21	—	"
	18	134	33	4	15	—	3	13	—	—	—	—	"
	19	136	93	5	45	—	10	35	28	13	22	—	"
	20	137	31	6	23	—	2	23	—	—	—	—	'06, 305
	21	138	65	6	37	1	3	32	—	—	—	—	"
	22	139	24	1	10	—	3	13	—	—	—	—	"
	23	140	43	1	22	—	4	22	—	—	—	—	"
	24	141	73	1	31	—	5	21	—	—	—	—	"
	25	143	18	1	14	—	2	8	—	—	—	—	"
	26	144	37	4	22	—	3	7	—	—	—	—	"
	27	145	29	1	16	—	1	11	—	—	—	—	"

Families from purple parent heterozygous in blue and hood.	28	'06, 303	—	13	—	9	—	13	—	11	—	9	'05, 309
	29	304	65	—	32	—	31	—	45	—	8	—	"
	30	310	—	22	—	8	—	15	—	9	—	3	"
	31	365	29	—	2	—	11	—	20	—	4	—	"
	32	371	35	—	13	—	14	—	—	—	—	—	"
	33	'07, 135	—	17	—	9	—	10	—	6	—	2	'06, 302
	34	142	33	—	17	—	18	—	—	—	—	—	305
	35	146	28	—	12	—	12	—	—	—	—	—	304
	36	147	20	—	8	—	10	—	5	—	3	—	"
	37	148	35	—	12	—	18	—	18	—	4	—	"
	38	149	29	—	21	—	13	—	15	—	5	—	"
	39	150	46	—	28	—	15	—	23	—	16	—	"
	40	152	65	—	20	—	36	—	46	—	2	—	"
	41	153	91	—	46	—	42	—	52	—	11	—	"
	42	154	31	—	17	—	14	—	21	—	8	—	"
	43	155	14	—	8	—	8	—	—	—	—	—	"
	44	156	12	—	6	—	5	—	—	—	—	—	"
	45	157	33	—	15	—	21	—	13	—	8	—	"
	46	158	12	—	5	—	6	—	4	—	2	—	"
	47	159	19	—	7	—	10	—	5	—	7	—	"
Parent a purple hood.	48	'06, 301	—	—	90	—	—	—	—	—	69	—	'05, 309
	49	306	—	—	40	—	—	—	—	—	11	—	"
	50	362	—	—	28	12	—	—	—	—	22	5	"
	51	369	—	—	61	—	—	—	—	—	21	—	"
	52	373	—	—	18	—	—	—	—	—	6	—	"
	53	375	—	—	45	—	—	—	—	—	12	—	"
Parent a red.	54	'06, 308	—	—	—	—	—	41	—	18	—	—	'05, 309
	55	309	—	—	—	—	—	19	—	6	—	—	"
	56	313	—	—	—	—	—	53	—	22	—	—	"
	57	364	—	—	—	—	—	(many)	—	(many)	—	—	"
	58	366	—	—	—	—	—	(")	—	(")	—	—	"
	59	367	—	—	—	—	—	(")	—	(")	—	—	"
Parent a white.	60	'06, 311	—	—	—	—	—	—	—	—	(many)	—	'05, 309
	61	380	—	—	—	—	—	—	—	—	(")	—	"
	62	381	—	—	—	—	—	—	—	—	(")	—	"
	63	382	—	—	—	—	—	—	(many)	—	(")	—	"
	64	386	—	—	—	—	—	—	30	17	10	—	"

B. *Sterility of Anthers and Axil Colour.*—Evidence has been given in a previous Report (II, pp. 83 and 97), for regarding the dark axil of the Sweet Pea as dominant to the light; and in the same Report (p. 91) it was shown that the sterile condition of the anthers is recessive to the fertile.* Further, it was noticed that when light and dark axils, as well as fertile and sterile anthers, occur in the same family, the great majority of the fertile plants have a dark axil, while the light axil is associated more closely with the steriles. The details of the families are shown in Table III. Collecting together the coloured individuals (in which alone the dark axil can appear) of families heterozygous in axil and sterility, and adding in those already recorded in Report II, we obtain the following numbers:—

	From Table.	From Report II.	Total.	
Dark axil fertile	506	121	627	*637*
Dark axil sterile	22	5	27	*27*
Light axil fertile	15	2	17	*27*
Light axil sterile	175	39	214	*194*

As the last column of figures shows, we obtain a fair approximation to the recorded numbers if we suppose the gametes to be produced in series of 32, viz., 15 dark fertile, 1 dark sterile, 1 light fertile, and 15 light sterile. The closeness with which the experimental results accord with the proportions calculated upon this basis leaves little doubt but that we are here concerned with such a series.

The Wild Sweet Pea.

Through the assistance of Dr. Harmer we were enabled in 1905 to sow some seed of the wild Sicilian Sweet Pea kindly sent by Dr. Gojacono. The resulting plants were, on the whole, very like the Purple Invincible (P. I.). They were, however, smaller and of less luxuriant habit, and the colour of the wings was of a somewhat brighter blue. As in the P. I., the blue wings were not infrequently flaked with purple. Both light and dark axilled plants occurred.

One of the light axilled plants was fertilised with pollen from the white Emily Henderson (round pollen), a strain which numerous experiments have shown to be homozygous for the factors for uniform colour distribution (D)† and for the light wing (Wl), as well as for the

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* In families where fertiles and steriles come, the total numbers now stand at 1688 fertile and 541 sterile, expectation being 1672 and 557 (*cf.* Table III).

† For nomenclature, see Report III, p. 31.

Table III.

	Purple.				Red.				White.		Reference Number.
	Fertile.		Sterile.		Fertile.		Sterile.		Fertile.	Sterile.	
	dk.	lt.	dk.	lt.	dk.	lt.	dk.	lt.			
Heterozygous for axil.	32	3	—	7	8	—	1	2	10	4	'04 G. 181
	18	—	2	5	7	—	—	4	12	4	'04 F. 141
	19	—	—	7	10	—	—	4	—	—	142
	43	2	—	17	—	—	—	—	—	—	143
	23	2	—	12	—	—	—	—	13	2	144
	53	1	1	14	—	—	—	—	28	5	'05 G. 316
	—	—	—	—	50	—	1	11	41	10	317
	35	2	1	18	6	—	—	2	17	4	'05 F. 120
	—	—	—	—	20	1	1	5	6	4	'06 G. 342
	22	2	1	6	—	—	—	—	11	4	348
	—	—	—	—	57	1	3	21	22	10	349
	28	1	2	6	—	—	—	—	13	—	350
	7	2	—	5	7	2	—	2	5	4	351
	7	—	1	6	—	—	—	—	3	—	352
	—	—	—	—	22	2	1	5	4	3	353
	—	—	—	—	15	1	—	8	9	—	358
	17	—	—	5	—	—	—	3	5	2	354
Homozygous for axil.	—	50	—	19	—	—	—	—	16	5	'05 G. 315
	61	—	19	—	23	—	9	—	25	7	318
	—	81	—	12	—	17	—	7	65	20	'05 T.L. 2
	—	—	—	—	—	55	—	24	54	9	3
	—	84	—	19	—	20	—	7	71	20	5
	—	32	—	20	—	19	—	—	36	9	'06 G. 340
	—	36	—	15	—	14	—	3	40	10	360
	—	175	—	45	—	46	—	23	69	22	'07 G. 90

absence of blueness (b), of one of the colour factors (c), and of the factor for the dark axil. In other words, E. H. rd. is really a light axilled Painted Lady (P. L.) with round pollen, which lacks one of the two factors necessary for the production of colour. All the F_1 plants were of the regular P. I. type with light axils. In the F_2 generation we obtained three colour types, viz., P. I., P. L., and white, together with long and round pollens. The F_2 generation came true to the light axil. The aggregate numbers for the three F_1 plants used were as follows :—

	Observed.	Calculated.
Purple long	81	65
Purple round	1	7
Red long	7	7
Red round	17	17
White long	18	24
White round	4	8

The numbers of the round purples and of the whites are below expectation, but the figures are somewhat scanty.

The chief interest attaching to this cross lies in the light which it throws upon the constitution of the wild purple. The only recessive features which appear in the F_2 generation,* viz., red, white, and round pollen, are those which we know to have been carried into the cross by the E. H. rd. parent. The wild must, therefore, be regarded as homozygous for all the factors dominant to these.

POULTRY.

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

1. *Comb Characters.*

A. *The Relation of the Rose to the Single Comb.*—In our last Report (p. 13) we gave reasons for regarding the phenomena exhibited in the inheritance of the four combs, single, rose, pea, and walnut, as forming a case of dihybridism. We suggested that the allelomorphic pairs concerned are—(1) Rose (R) and absence of rose (r), and (2) Pea (P) and absence of pea (p). On this view the single comb, which makes its appearance in F_2 only in the absence of both R and P, must be looked upon as a common basis upon which these factors may be superposed. Thus every rose is a single to which the factor for roseness (R) has been added. On the removal of this factor by a suitable cross the single is revealed in F_2.

Mr. Hurst suggested that the experiment of crossing Breda × Rose might give an interesting confirmation of these views. For if rose is really single + rose, singles should appear in F_2. The Breda is a breed which has ostensibly no comb. As a matter of fact, in the cocks there are two minute papillæ standing one on each side of the middle line, which are rudiments of a comb structure. As experiment shows, the hens have the duplicity of which these papillæ are the evidence, but in examination of the heads of hens practically no comb tissue can be seen or felt.

When Breda† is crossed with single, F_1 has a large double comb

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* Apart, of course, from the light axil character, in which both parents were homozygous.

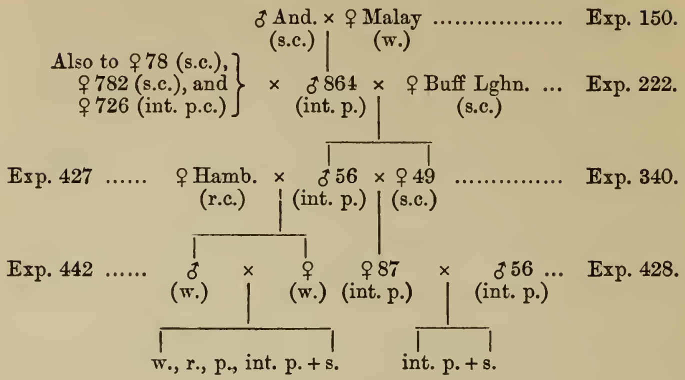
† Madame de Vries, to whom we mentioned our wish to try Bredas, very kindly put us in communication with Dr. Kerbert, of the Zoological Gardens in Amsterdam. He was good enough to interest himself in the matter, and found that Mr. Houwink, of Meppel, was willing to present us with these fowls. For this help, we desire to express our warmest thanks to Mr. Houwink and to others who have assisted us.

formed as two divaricating singles, not unlike that of the Egyptian (Rep. II, p. 113). Evidently, therefore, the Breda has a factor for duplicity which can split the single comb, but it is without the element for the single comb itself. The absence of comb in the Breda cannot be due to any factor which is actively preventing the appearance of a single comb, for if that were so, the Breda condition would be dominant.

The Breda was next crossed with a rose, and the resulting combs were all duplex roses. Two of these were bred together in 1907 and gave duplex and common roses, duplex and common singles, and Bredas. The important point is that singles appear in the F_2 generation from such a cross, and the fact of their appearance is strongly confirmatory of the view expressed above as to the relation subsisting between the rose and the single combs. To express this relation, we propose the terms *epistatic* and *hypostatic*. The factor for rose is epistatic to the factor for single, and the single factor is hypostatic to the rose.

B. *The Malay Comb.*—In Report III (p. 16) we referred to a ♀ Malay which gave all four types of comb when crossed with a single, and was presumably of the constitution RrPp. In 1906 this bird was crossed with a ♂ heterozygous in both R and P (*i.e.*, RrPp), and gave (Experiment 419) 3 singles, 3 roses, 5 peas, and 13 walnuts. We are inclined to believe that she would have given a similar result with a Malay ♂ of the constitution RrPp if we had been able to procure one to breed from, and that the rarity of rose and single combs in this breed is due rather to the rarity of birds which are heterozygous in P than to any other cause. It would appear that the great majority of Malays are homozygous for P, since of the 20 tested by us in our experiments, only four were heterozygous for this factor. The chances of heterozygotes being mated together are therefore not large, and as neither single nor rose can arise except from such a form of mating, we consider it not unlikely that the rarity of these combs results from this cause. Nevertheless we fully recognise that the question cannot be considered settled until two pure Malays, heterozygous for both R and P, have been successfully mated together.

C. *Intermediate Pea-combs.*—In our last Report (p. 16) we referred to certain types of pea-comb in which so little of the pea character was evident that in young chicks they were easily mistaken for singles. For several years we have been carrying on a series of experiments designed to throw light upon the nature of this form of comb, and the pedigree here given will make the account of these experiments less difficult to follow :—



In 1904 a ♂ from a cross between a Malay ♀ and a ♂ Andalusian (Experiment 150), and therefore heterozygous for P, was mated with the following four hens :—

			Pea and int. p.	s.c.
Experiment 223............	♀ 726	int. p.	28	7
„ 222............	♀ 13	s.c.	17	46
„ 225............	♀ 78	„	12	18
„ 224............	♀ 782	„	9	7

In the ♂ (864) and in ♀ 726 the comb was what fanciers call a "floppy" one, hanging over on one side of the head much as in a hen Leghorn. In each case, however, it possessed distinct lateral ridges. Among the offspring of these two birds were a few low pea-combs, but the greater number were of the intermediate type. It was, however, found impossible in many cases to assign the comb of the newly-hatched chicken to either of these two forms of pea-comb with certainty. This mating gave 7 singles out of 35 chicks, a figure not far removed from expectation, which is here 9. And when mated with two s.c. ♀ ♀ in Experiments 224—5, this ♂ gave 21 P. and int. p. to 25 singles—a proportion sufficiently close to the expected equality. So far the story is clear. But when the ♂ was crossed with a Buff Leghorn ♀ (Experiment 222) he is recorded as having given 46 single and only 17 P. and int. p. instead of the equality expected. The great majority of these observations were made on hatching, and we found subsequently that it is often impossible to distinguish between the single and certain forms of intermediate pea-combs at this stage. In this very case one of the few birds reared was ♂ 56, which was registered as a single on hatching. Later he was found to have developed distinct lateral ridges, and the comb, which had started to grow with the erectness of a single, showed a distinct tendency to flop over to one side. On being mated with the single combed ♀ 49 (a sister bird), he is recorded as having given 38 s., 28 pea and intermediate pea, and 3 dubious (the last probably int. p.). These figures support the view that he was heterozygous for P., and that ♀ 49 was a pure single. From this mating (Experiment 340) was saved ♀ 87. The comb of this bird was of the form of an intermediate P. though the lateral ridges were not developed. With ♂ 56 she gave 11 pea and int. p. and 3 singles—a close approach to the expected 3 : 1 ratio (Experiment 428). In the same year (1906) ♂ 56 was tested by crossing him with a pure rose-combed Hamburgh.* The character of the offspring, 13 rose and 14 walnuts, conclusively prove him to have been heterozygous for P. In the following year two of these walnuts were bred together (Experiment 442), and, as expected, gave the usual four types of comb. Of the pea-combs some were recorded as intermediate, while others were of the regular low form of pea-comb characteristic of the pea-combed breeds. We are therefore inclined to regard the intermediate pea-combs, which show so little of the pea character, as differing from the low pea-comb in the nature of the basis upon which the pea character is imposed. That there are many types of single comb is well known, and we are inclined to consider that the nature of the hypostatic element constitutes the difference between what we have termed the intermediate and the low pea-combs.

D. *Irregular Numbers in Walnut Combs.*—In our last Report (p. 14) we drew attention to general instances in which walnut birds mated with singles had given irregular figures. Two such birds, ♂ 549 and ♂ 144, were kept for further study. In 1905 ♂ 549, mated with various s.c. ♀ ♀ (Experiments 373—4), gave 56 s., 47 r., 45 p., and 28 w., where equality is expected. The marked excess of singles and the equally marked deficiency of walnuts led us to mate him with singles in 1906 and 1907. During these two years he gave (Experiments 411, 412, 416, and 449) 31 s., 26 r., 31 p., and 36 w., expectation being 31 of each sort. He was also mated with several walnut ♀ ♀ which had previously been proved to give off equal numbers of the four types of gamete. In these experiments (Experiments 413—5 and 447—8) he gave 6 s., 25 r., 32 p., and 79 w.—expectation being 9 s., 26·5 r., 26·5 p., and 80 w. During 1906—7, therefore, this ♂ gave a regular result, and we are quite at a loss to account for the uneven figures which we obtained from him in 1905.

As already mentioned in Report III (p. 14), the walnut combed ♂ 144 in 1905 gave a normal result with 4 s.c. ♀ ♀ (Experiments 345—6). But with two white Leghorn ♀ ♀ (Experiments 347—8) he gave a very marked deficiency of roses and walnuts.

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* For this bird, we are indebted to the kindness of Mr. Fryer, of Chatteris. It is mentioned in Table IV as G. H., Golden Hamburgh.

Table IV.

For meaning of abbreviations, see Rep. III, p. 22.

1906.

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Used also in exp.	Father.	Origin (numbers refer to expts).	Cb.	Used also in exp.	Nature of mating.	Combs.			
											S.	R.	P.	R.P.
1	394	30 31		r.p.		29		p.		R.r.P.p. × r.r.P.p.	8	11	20	19
3	395	659	267	s.	370	585	W. R.	r.	369–70	r.r.p.p. × R.R.p.p.		8		
	396	623	268	r.p.	342	,,	,,	,,		R.r.P.p. × R.R.p.p.		12		8
4	397	390	343	p.		137	342	s.		r.r.P.p. × r.r.p.p.	9		8	
	398	632	268	r.p.	342	,,	,,	,,		R.r.P.p. × r.r.p.p.	3	7	2	5
5	399	2 ♀ s.	W. R.	r.		184	,,	p.		R.R.p.p. × r.r.P.p.		23		23
7	400	215	345	r.		228	345	s.		R.r.p.p. × r.r.p.p.	41	33		
	401	109	180	r.p.	307	,,	,,	,,		R.r.P.p. × r.r.p.p.	3	5	2	6
8	402	3 ♀ s.	Br. L.	s.		345	347	p.		r.r.p.p. × r.r.P.p.	10		19	
10	403	532	285	r.p.	344	6	G. B.	s.	267 268 312 343 344	R.r.P.p. × r.r.p.p.	4	7	6	3
	404	658	267	s.		,,	,,	,,		r.r.p.p. × r.r.p.p.	7			
	405	7	G.B.	,,	267	,,	,,	,,		,,	14			
11	406	285	269	,,	296	365	276	,,	293–7	,,	29			
	407	128	276	,,		,,	,,	,,		,,	31			
12	408	604	211	,,		91	299	,,		,,	23			
	409	150	299	,,		,,	,,	,,		,,	23			
13	410	231	345	r.		183	345	p.		R.r.p.p. × r.r.P.p.	18	16	14	16

14	411	227	269	s.		549	233	r.p.	373–4	r.r.p.p. × R.r.P.p.	11	2	6	6
	412	571	237	,,		,,	,,	,,		,,	10	17	20	18
	413	495	239	r.p.	324	,,	,,	,,		R.r.P.p. × R.r.P.p.	2	6	11	26
	414	578	233	,,	386	,,	,,	,,		,,	1	1	4	7
	415	231	202	,,	302	,,	,,	,,		,,	0	12	11	31
	416	317	W.L.	s.	377	,,	,,	,,		r.r.p.p. × R.r.P.p.	2	4	1	1
15	417	410	276	,,	294	224	339	,,		,,	5	6	4	2
	418	186	339	r.		,,	,,	,,		R.r.p.p. × R.r.P.p.	3	14	5	9
	419	6	Mal.	r.p.	{ 277 334 }	,,	,,	,,		R.r.P.p. × R.r.P.p.	3	3	5	13
16	420	324	236	,,		432	237	s.	326–35	R.r.P.p. × r.r.p.p.	2	1	0	1
	421	465	237	s.		,,	,,	,,		r.r.p.p. × r.r.p.p.	12			
	422	151		,,	{ 211 299 }	,,	,,	,,		,,	16			
	423	299	345	r.p.		,,	,,	,,		R.r.P.p. × r.r.p.p.	13	10	13	6
17	424	339	351	,,		135	299	,,		,,	8	8	6	9
	425	600	215	,,		,,	,,	,,		,,	6	4	3	5
	426	105	299	s.		,,	,,	,,		r.r.p.p. × r.r.p.p.	49			
21	427	167	G. H.	r.		56	222	int.p.	340–1	R.R.p.p. × r.r.P.p.		13		14
	428	87	340	int.p.		,,	,,	,,		r.r.P.p. × r.r.P.p.	3		11	
22	429	515	237	s.		144	253	r.p.	345–8	r.r.p.p. × R.r.P.p.	8	13	8	5
	430	452	276	,,		,,	,,	,,		,,	6	5	6	3
	431	895	W. L.	,,		,,	,,	,,		,,	3	6	5	1
	432	315	W. L.	,,		,,	,,	,,		,,	7	9	9	10
25	433	442	348	p.		435	348	p.		r.r.P.p. × r.r.P.p.	16		51	
26	434	412	377	s.		431	377	s.		r.r.p.p. × r.r.p.p.	15			
30	435	144 279 143	350	r.		323	350	r.		R.R.p.p. × R.R.p.p.		93		
31	436	259	356	,,		496	356	,,		R.r.p.p. × R.r.p.p.	7	25		
32	437	426	370	,,		428	370	,,		,,	7	19		

Table IV—*continued.*

1907.

Pen.	Exp. No.	Mother.	Origin (numbers refer to expts.).	Cb.	Used also in exp.	Father.	Origin (numbers refer to expts.).	Cb.	Used also in exp.	Nature of mating.	Combs. S.	R.	P.	R.P.
1	438	30		r.p.	394	29		p.	394	R.r.P.p. × r.r.P.p.	0	4	7	3
	439	245	345	r.	400	,,		,,		R.r.p.p. × r.r.P.p.	4	1	3	2
	440	151		s.	422	,,		,,		r.r.p.p. × r.r.P.p.	7		13	
	441	W. Wy.		r.		,,		,,		R.R.p.p. × r.r.P.p.		11		9
4	442	398	427	r.p.		377	427	r.p.		R.r.P.p. × R.r.P.p.	2	2	8	10
7	443	442	348	p.	433	432	237	s.	420–3	r.r.P.p. × r.r.p.p.	17		15	
	444	404	237	s.	393	,,	,,	,,		r.r.p.p. × r.r.p.p.	17			
10	445	31		r.p.	394	226	410	,,		R.r.P.p. × r.r.p.p.	5	10	8	7
	446	317	W. L.	s.	416	,,	,,	,,		r.r.p.p. × r.r.p.p.	21			
14	447	578	233	r.p.	414	549	233	r.p.	411–6	R.r.P.p. × R.r.P.p.	2	2	2	4
	448	259	394	,,		,,	,,	,,		,,	1	4	5	11
	449	317	W. L.	s.	446	,,	,,	,,		r.r.p.p. × R.r.P.p.	8	3	4	11
17	450	30		r.p.	438	241	400	s.		R.r.P.p. × r.r.p.p.	1	3	2	0
	451	398	427	,,	442	,,	,,	,,		,,	10	9	3	11
	452	442	348	p.	443	,,	,,	,,		r.r.P.p. × r.r.p.p.	19		12	
25	453	150	299	s.		435	348	p.	433	r.r.p.p. × r.r.P.p.	17		20	
	454	176	410	r.		,,	,,	,,		R.r.p.p. × r.r.P.p.	10	10	15	10
	455	258	394	p.		,,	,,	,,		r.r.P.p. × r.r.P.p.	2		12	

In 1906 he was again mated with these two birds (Experiments 431—2) and gave 10 s., 15 r., 14 p., and 11 w., a fairly regular result. In all we have bred 238 birds from s.c. hens by this ♂, the numbers being 59 s., 61 r., 71 p., and 47 w.

We have noticed that where there is a tendency towards irregularity of numbers the irregularity is nearly always due to a deficiency of walnuts, and that this is frequently associated with some excess of singles. This is brought out in the total numbers for the mating of walnut with single given in Table V. Where expectation is 682 in each case there are actually 716 singles and 644 walnuts. Similarly in the mating together of walnuts of the constitution RrPp, singles are somewhat in excess of expectation (45 to 35), while walnuts are rather below it (279 to 312). These irregularities in the expected distribution of the various types seem to point to the operation in certain cases of some definite disturbance, but we cannot at present venture upon any surmise as to its nature.

E. *Summary of Comb Results.*—Our experiments upon the inheritance of the walnut comb and of its components, the rose, the pea, and the single, are now concluded, and we may briefly recapitulate the explanation which we have already given in our third Report (p. 12). The case is one of simple dihybridism in which both the factors concerned affect the same structure, the comb. These factors are roseness (R) which is allelomorphic to its absence (r), and peaness (P), which is also allelomorphic to its absence (p). A walnut comb is one in which both R and P are present, and such a comb may be either homozygous or heterozygous for one or both of these factors. Judged by the criterion of gametic output, four kinds of walnut comb, and only four, are possible, viz., RRPP, RRPp, RrPP, and RrPp. These four kinds we have met with over and over again, and we have met with no others. So also there are two kinds of rose and two kinds of pea, viz., those homozygous and those heterozygous for the respective dominant factor which they contain. All single combs, whatever their origin, are of the constitution rrpp, and consequently breed true to that character.

As the results which have led us to these conclusions are scattered over four Reports and involve the consideration of over 12,500 birds, we have collected them together in Table V :—

Table V.

Visible nature of mating.	Constitutional nature of mating.	References to Reports and No. of experiment.	Result.			
			S.	R.	P.	R.P.
Rose × Rose	R.R.p.p. × R.R.p.p.	III, 280, 290, 350, 356, 369; IV, 435	—	270 [all]	—	—
	R.R.p.p. × R.r.p.p.	II, 121, 157	—	31 [all]	—	—
	R.r.p.p. × R.r.p.p.	I, 37–40, 85; II, 156; IV, 436–7	235 [*232·5*]	695 [*697·5*]	—	—
Rose × Single	R.R.p.p. × r.r p.p.	I, 24-33; II, 95–7, 103, 113, 122, 136, 151, 184; III, 200, 273, 370; IV, 395	1	484 [all]	—	—
	R.r.p.p. × r.r.p.p.	I, 41, 70–8, 87; II, 100, 102, 112, 113*a*, 114, 115, 118, 139, 147, 149, 192; III, 246, 263-6, 274, 330; IV, 400	703 [*698·5*]	694 [*698·5*]	—	—
Pea × Pea	r.r.P.P. × r.r.P.P.	III, 281	—	—	21 [all]	—
	r.r.P.P. × r.r.P.p.	II, 110, 128	—	—	31 [all]	—
	r.r.P.p. × r.r.P.p.	I, 34-6, 80–1; II, 106, 125; III, 228, 229; IV, 433, 455	210 [*194·25*]	—	567 [*582·75*]	—
Pea × Single	r.r.P.P. × r.r.p.p.	I, 1–23; II, 126, 127; III, 250, 282, 292, 301, 384	5	—	660 [all]	—
	r.r.P.p. × r.r.p.p.	I, 42–62, 82; II, 89, 90, 98, 107–9, 130, 140–1, 145, 148, 154-5, 160; III, 230–1, 368; IV, 397, 402, 443, 452–3	514 [*502*]	—	490 [*502*]	—
Rose × Pea	R.R.p.p. × r.r.P.P.	II, 93, 94, 152, 186	—	—	—	49 [all]
	R.R.p.p. × r.r.P.p.	II, 185, 187; IV, 399, 427, 441	—	47 [*46·5*]	—	46 [*46·5*]

	R.r.p.p. × r.r.P.P.	II, 178, 179, 180	—	—	71 [*77*]	83 [*77*]
	R.r.p.p. × r.r.P.p.	II, 111 ; IV, 410, 439, 454	34 [*32·75*]	32 [*32·75*]	35 [*32·75*]	30 [*32·75*]
Walnut × Walnut	R.r.P.p. × R.r.P.p.	III, p. 15 ; IV, 413–5, 419, 447–8, 442	45 [*35*]	99 [*104*]	132 [*104*]	279 [*312*]
Walnut × Rose	R.r.P.P. × R.r.p.p.	III, 198	—	—	6 [*6·5*]	20 [*19·5*]
	R.r.P.p. × R.r.p.p.	IV, 418	3 [*3·9*]	14 [*11·6*]	5 [*3·9*]	9 [*11·6*]
Walnut × Pea	R.r.P.p. × r.r.P.p.	IV, 394, 438	8 [*9*]	15 [*9*]	27 [*27*]	22 [*27*]
Walnut × Single............	R.R.P.p. × r.r.p.p.	III, p. 14	—	140 [*144·5*]	—	149 [*144·5*]
	R.r.P.P. × r.r.p.p.	III, p. 13 ; II, 150, 161	—	—	309 [*304*]	299 [*304*]
	R.r.P.p. × r.r.p.p.	II, pp. 109–110 ; III, p. 14 ; IV, 398, 401, 403, 411-2, 416, 417, 420, 423, 424-5, 445, 450-1, 429–432	716 [*682·2*]	705 [*682·2*]	664 [*682·2*]	644 [*682·2*]
	R.R.P.P. × r.r.p.p.	III, p. 13.	—	—	—	216 [all]
Single × Single	r.r.p.p. × r.r.p.p.	II, 91, 92, 99, 101, 104, 116–7, 119, 120, 129, 131–3, 138, 146, 149, 157*a*, 158, 183 ; III, 209–211, 237, 247–8, 269, 270, 276, 293–6, 299, 367, 375–7 ; IV, 404–9, 421–2, 426, 434, 444, 446	1937 [all]	—	—	—

The expectations are given in square brackets.

For the various types of mating shown in Table V the expectation based on theory has been added in brackets below the experimental figures in each case. References to the original records used in compiling the table are given throughout.

Dubious and Unconformable Results.—In previous reports 23 birds were recorded at different times as having combs not at once referable to one of the four types studied in these experiments. These birds are not represented in the above summary. The sources of uncertainty were various and in several cases the doubt arose merely through unfamiliarity with the material. These in the light of fuller experience could, without doubt, have been classified easily. The only cases in which genuine doubt arises are those intermediate singles of which a full account is given on p. 19. In the families where these occur the classification is uncertain and mistakes have occurred. Besides these, certain actual unexpected results are recorded as shown in the summary, Table V. Five birds came with single combs in Experiments 13, 21, 22, and 22A where only pea-combs are expected. These may, perhaps, have been of the intermediate pea class. One single comb occurred also in Experiment 26, where roses only are expected.

2. *White Plumage.*

In the last Report (p. 18), it was shown that there are two distinct classes of white fowls: (*a*) those in which white is dominant to colour, and (*b*) those in which the white is recessive to colour. The recessive whites are of at least three kinds, viz.:—

(1) *The White Birds which have arisen in the course of our Experiments* (Rep. III, pp. 19—20).—These birds often have one or more coloured ticks in their plumage, and we formerly regarded these specks of colour as characteristic of the recessive white. This suggestion is, however, incorrect, as we have now had birds of this white strain quite devoid of colour and indistinguishable from dominant whites, except by breeding tests. The down of such birds is also without colour. The recessive whites of this type we shall speak of as R-whites.

(2) *The White of the Silky Fowl.*—Such birds, when adult, are, or may be, perfectly white in plumage. The down of the newly-hatched chicks, however, often contains some buff, especially on the sides of the head, on the body in the position of the lateral *light* stripes of a brown chicken, and on the rump. The amount of buff varies, but we are not sure that the Silkies of our strain ever hatch without any colour; for, at the time they were hatched, this point had not occurred to us.

(3) *The White of the Rose-comb Bantams.*—These always have a few, generally minute, ticks in the adult plumage, though, in other respects, fully white birds. In the down their chicks are *pale bluish.*

Each of these types of white behaves as a simple recessive to colour, but when the R-white is crossed with the Silky white the offspring *are all fully coloured*, with plumage somewhat resembling that of a poor black-red.

This phenomenon is superficially comparable with that seen in Sweet Peas and Stocks where two albinos are crossed with production of a coloured F_1. In the fowls, of course, we are not dealing with albinos at all. The birds all have pigmented eyes, and in the case of the Silky the buff in the down is already an indication of the presence of some pigmentation. As the experiment shows, however, the R-white contains some factor which is complementary to that present in the Silky, and is needed to produce the fully coloured type of plumage. The two complementary factors may be called X and Y. Each of these factors must be regarded as allelomorphic to its absence (*cf.* Rep. III, p. 3); consequently, one parent, say the R-white, may be represented as xxYY, and the Silky as XXyy, and thus the cross of either Silky or R-white with such breeds gives coloured F_1 and 3 coloureds to 1 white in F_2.

The Silky crossed with the white Rose-comb gives whites only in F_1, and hence it is likely that of the two complementary factors, one only is present and common to both these types.

The dominant white we regard as containing an additional factor, D, whose action is to prevent or diminish the production of colour by the factors X and Y.

The details of our experiments are as follows :—

A. *R-Whites.*—In Report III (pp. 19–20), will be found the pedigree of a white ♂ 144 which gave only coloured offspring* when crossed with various coloured birds. Two pairs of his offspring out of a Brown Leghorn ♀ were mated together in 1906. Between them they gave 105 coloured and 33 whites.† The close approximation to the 3 : 1 ratio shows that the white in this case behaves as a simple recessive to colour. Many of these extracted whites were reared, and form the stock of which we have made use in our subsequent experiments.

B. *Silky-White.*—The following evidence collected during the past few years shows that the white plumage of this breed is recessive to colour :—‡

(1) 7 Silkies (4 ♂♂ and 3 ♀♀) crossed with pure coloured birds gave 220 chicks all coloured.

(2) F_1 birds from Silky × Brown Leghorn crosses bred together have given 156 coloured and 44 light, expectation being 150 and 50.

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* See also p. 34.

† These families are dealt with in connection with colour on p. 34.

‡ Davenport ('Publ. Carnegie Inst. Washington,' No. 52) crossed a Silky ♂ with 4 coloured frizzled ♀♀, and obtained 7 white and 25 dark birds. This result is explicable on the supposition that at least one of the ♀♀ was heterozygous for the factor C.

(3) F_1 birds crossed with pure Silky gave 98 coloured and 79 light birds, expectation being 88·5 of each.

C. *Silky-White* × *R-White.*—We have made this cross in six different cases. All the 113 birds produced were fully coloured. Some of these birds have been kept in order to breed from in 1908. From the analogy of the Sweet Pea case (*cf.* Rep. III, p. 3), we look for coloured and whites in the ratio 9 : 7.

[*Note added July* 19, 1908. From two pens of such F_1 birds mated this year we have had 203 chicks. Of these, 116 were coloured and 87 were light, with or without buff—expectation being 114 coloured and 89 light.]

D. *Dominant White* × *R-White.*—In 1905, our original R-white ♂ was crossed with two White Leghorn hens (Experiments 347, 348) in which white was dominant to colour. The resulting offspring, 38 in number, were all white, as were 50 chicks similarly bred in the following year (Experiments 431, 432). Three of these F_1 birds were kept and their constitution tested by crossing them with: (1) pure coloured birds, (2) recessive whites, and (3) one another, and the three types of experiment may be considered in this order.

(1) The F_1 birds must, on our hypothesis, be heterozygous for D, and should, when crossed with pure coloured birds, give equal numbers of coloured and whites. Actually they gave 43 whites and 56 coloured.

(2) Two of the F_1 birds were further tested by mating them with recessive whites (Experiments 452, 454). On the assumption that the constitution of the dominant white was DDYYXX, and of the recessive white ddYYxx, that of the F_1 bird should be DdYYXx. Such birds would produce equal numbers of gametes of four kinds, viz., DYX, DYx, dYX, and dYx. The gametes of the recessive white are all dYx. The F_1 bird mated with a recessive white should, consequently, give whites and coloured in the proportion 3 : 1. Actually, two F_1 birds so mated gave 62 whites and 15 coloured, expectation demanding 58 of the former and 19 of the latter.

(3) Two F_1 birds mated together (Experiment 433) gave 63 white and 4 coloured. If, as supposed, the constitution of the F_1 bird is DdYYXx, we should get, in F_2, whites and coloureds in the proportion of 13 : 3. The accompanying scheme renders it clear how this is brought about. The proportion of coloured birds found by experiment is distinctly lower than that which is expected. This may be merely the result of chance or it may be due to the fact that the F_1s are heterozygous for Y. That the F_1 birds are heterozygous for D is shown by the result of the cross with a pure-coloured, and the result of mating with an R-white proves them to be heterozygous for X. But neither of these tests can distinguish a bird which is heterozygous for Y from

one which is homozygous. Two birds of the constitution DdYyXx would, when mated together, give whites and coloured in the proportion of 55 : 9—a proportion which is nearer to the result which we have obtained from our only experiment of this nature. Moreover, it is not unlikely that White Leghorns are sometimes heterozygous for Y or even homozygous for its absence; for we know that the breed has been crossed with white Malays for size, and the white Malay is a recessive white.* The point could be tested by crossing with the Silky white, when birds homozygous in Y would give equal numbers of whites and coloureds, while birds heterozygous in Y would give whites and coloured in the ratio 3 : 1. The F_1 birds used in the above experiments are no longer available, but we bred others in 1907, and we hope to test them fully during the present year (1908). For the present we are inclined to consider the dominant white as homozygous for Y and X, and to regard the small number of coloureds which appeared in Experiment 433 as a chance result.

DYX DYX wh.	DYX DYx wh.	DYX dYX wh.	DYX dYx wh.
DYx DYX wh.	DYx DYx wh.	DYx dYX wh.	DYx dYx wh.
dYX DYX wh.	dYX DYx wh.	dYX dYX col.	dYX dYx col.
dYx DYX wh.	dYx DYx wh.	dYx dYX col.	dYx dYx wh.

We may add that the total number of coloureds and whites which have appeared in the various matings into which the F_1 birds entered is very close to expectation. Out of 243 birds, 168 were white and 75 coloured, where 162 white and 81 coloured were expected.† The various experimental results as to the inheritance of white plumage with which we have been dealing are summarised in Table VI. The figures in italics denote the expected figures in each case.

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* For it is known to occur in the breeding of coloured Malays.

† The expectation here, of course, is not a single one, but is arrived at by combining the various expectations concerned.

Table VI.

Cross.	Nature of mating.	Result.		Expectation.	
		white.	colour.	white.	colour.
R-white × colour	ddYYxx × ddYYXX	—	149	—	all
F_1 ex R-white × colour with similar bird	ddYYXx × ddYYXx	33	105	*34·5*	*103·5*
Silky-white × colour	ddyyXX × ddYYXX	—	220	—	all
F_1 ex Silky-white × colour with similar bird	ddYyXX × ddYyXX	44	156	*50*	*150*
F_1 ex Silky-white × colour with pure Silky	ddYyXX × ddyyXX	79	98	*88·5*	*88·5*
Silky-white × R-white	ddyyXX × ddYYxx	—	113	—	all
D-white × R-white	DDYYXX × ddYYxx	88	—	all	—
F_1 ex D-white × R-white with similar bird	DdYYXx × DdYYXx	63	4	*54·5*	*12·5*
[or see p. 30...	DdYyXx × DdYyXx	63	4	*58*	*9*]
F_1 ex D-white × R-white with pure coloured	DdYYXx × ddYYXX	43	56	*49·5*	*49·5*
F_1 ex D-white × R-white with R-white	DdYYXx × ddYYxx	62	15	*58*	*19*

3. *Rose-comb Bantams.*

In our last Report (p. 18) we showed that in the Rose-comb bantam black plumage was dominant over white. During 1906, 3 F_1 ♀ ♀, mated with an F_1 ♂, produced 94 chicks (Experiment 435), of which 70 were black and 24 were light, a close approximation to the expected ratio 3 : 1. The recessive nature of this white was further confirmed by crossing a white Rose-comb ♂ with a brown-breasted Game bantam. Two of the resulting F_1 birds, in colour not very dissimilar to the brown-breasted breed, produced 6 light chicks out of a total of 26 (Experiment 437).

We have also carried out a few experiments with the idea of discovering the relation which the white of the Rose-comb bears to that of the R-white and of the Silky.

The cross Rose-comb white × Silky white was made three times, and gave in all 84 whites. The F_2 generation bred from such birds differed a good deal in their down colour. Some resembled the Silky white, with or without a little buff; others were of the pale smoky blue characteristic of the pure Rose-comb; others, again, were of a darker, smoky tint, and not infrequently developed into adults with a distinct dinginess in hackle and mantle. We have not attempted, however, to follow up these differences. The F_1 birds crossed back with the Silky gave 21 light chicks, and with the Rose-comb gave 26 light chicks. No really coloured bird came in any of the matings from this cross, and we are probably justified in regarding the Silky and the Rose-comb as owing their whiteness to the absence of the same factor.

If this is so, the Rose-comb should give only coloured offspring when crossed with the R-white. Disparity of size offers an insuperable obstacle to the direct cross, and we have only been able to make it indirectly by mating the F_1 ♀ ex Rose-comb × Silky with a ♂ R-white. The mating gave 28 birds, all fully coloured, from which we may infer that the Rose-comb white when crossed with the R-white behaves as the Silky white in giving only coloured birds.

4. *Brown Down Colour.*

In the account of our experiments with Game Bantams we brought forward evidence to show that the pale brown down colour is recessive to the brown striped (Rep. III, p. 21). This conclusion has been confirmed by certain experiments already referred to in connection with the inheritance of recessive white (p. 29). A white ♂ was crossed with a Brown Leghorn ♀; all the offspring were brown striped in the down, and subsequently developed into fully coloured birds. Two pairs of these F_1 birds were bred together, and each gave chicks of three different down colours, viz., brown striped, pale brown, and white. The proportions are shown in the accompanying table :—

	Brown striped.	Pale brown.	White.
Experiment 400	41	15	18
" 410	35	14	15
Total	76	29	33
Expectation......	*77·6* [9]	*25·9* [3]	*34·5* [4]

The ratio is obviously a 9 : 3 : 4 ratio, and the allelomorphic pairs concerned are : (1) presence and absence of colour, and (2) presence and absence of brown stripe. The pale brown is recessive to the brown stripe. An interesting point in connection with this experiment is that both brown striped and pale brown chicks developed into birds practically identical as regards the colour of the plumage.* We are dealing here with a pair of characters which are perfectly distinct in early life but cannot be distinguished later on except by breeding tests.

5. *Andalusians and Bredas.*

A few more chicks were obtained in 1906 from the mating of a black Andalusian ♂ with a blue ♀ (Experiment 407). Of the 33 offspring 16 were blue and 17 were black, expectation being, of course, equality (*cf.* Rep. III, p. 20).

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* Compare the case of Indian Game, Rep. I, p. 88.

In 1906 we obtained from Mr. Houwink, a well-known breeder at Meppel, in Holland, two pairs of Breda fowls, viz., a pair of blacks and a pair of blues. The blacks bred true, giving 33 blacks. The blues, however, gave 8 blacks, 14 blues, and 5 chicks with the very pale blue down characteristic of white splashed Andalusians. Two of these were reared and developed into typical splashed whites. In respect of colour, therefore, the Bredas are to be classed with the Andalusians, and this is confirmed by the fact that we obtained four blues on crossing a splashed white Andalusian ♀ with the black Breda ♂. Further experiments of a similar nature have been carried out by Dr. R. N. Salaman, of Barley, who bred a blue Breda ♂ with blue Andalusian ♀ ♀ and obtained blacks, blues, and splashed whites nearly in the expected ratio 1 : 2 : 1.

6. *Silky Plumage.*

During the past two years this breed has played a large part in our experiments. The work has been concerned primarily with the inheritance of the peculiar pigmentation of the skin and tissues found in these fowls, though we have incidentally been able to confirm Davenport's view* of the recessive nature of the "silky" plumage. From the cross silky × normal plumage we have so far obtained in F_2 77 normal and 22 silky plumaged—expectation being 74 : 25. Again, on crossing the F_1 bird with the Silky (three families) we obtained 25 with normal and 28 with Silky plumage, a close approach to the expected equality.

7. *Mottled Plumage.*

We have already drawn attention to the fact that the white ♂ 144 which formed the starting point of our experiments on the R-white (p. 29) gave only coloured chicks when crossed with coloured hens. A number of his offspring from a Brown Leghorn hen (♀ 465) were reared to maturity. The down colour of all these chicks was brown striped like that of the pure Leghorn, but as they grew up they exhibited two distinct types of plumage. In one type the birds were all fully coloured, while in the other the plumage contained much white. In the latter the individual feathers were barred with colour, though the barring was much blurred and gave the birds their characteristic mottled appearance. We have been unable to carry out any extensive experiments with this mottled character, but for the following reasons we feel little doubt that it behaves as a simple dominant to the fully coloured.

(1) Out of 20 F_1 birds from the Brown Leghorn which were reared

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* Davenport, C. B., "Inheritance in Poultry," 'Publ. Carnegie Inst. Washington,' No. 52, 1906.

to maturity 11 were fully coloured and 9 were mottled. This is close to the equality demanded on the assumption that the ♂ was heterozygous for this character.

(2) Seven fully coloured F_1 birds bred among themselves (Experiments 400, 410, etc.), or with other fully coloured birds, gave no mottled young.

We may add that the ♂ 144, when crossed with a black Andalusian hen (Experiment 346), gave fully coloured blacks and mottled blacks. Dr. Salaman kindly bred from a pair of the fully coloured birds and obtained no mottled birds in the F_2 generation—a result which confirms our own experience of the Brown Leghorn cross.

STOCKS.

(Experiments by E. R. Saunders and H. B. Killby.)

Surface Character and Flower Colour. Summary and Corrigendum.

In the last Report (p. 38), an attempt was made to formulate a scheme which would bring into line the complex, and, in some cases, apparently contradictory results as regards surface character and flower colour, which had been observed in certain unions between Stocks of the following strains:—Glabrous (wallflower-leaved), Ten-week Stocks of various colours, red and white hoary Brompton Stocks, and the purple and white forms of *incana*. It was pointed out that as regards flower colour the results are explicable on the following assumptions: (1) that the sap is coloured red when two factors (denoted by the letters C and R) are both present; (2) that in the absence of either, or both, the sap is uncoloured; (3) that the presence of a third factor (B), in addition to C and R, turns the red sap blue, but that in the absence of C or R, the presence of B cannot be detected merely by inspection. In certain forms other factors in addition to these three may be present, causing either dilution of the sap colour (as, *e.g.*, in pale purple), or the appearance of less pure shades as, *e.g.*, the production of copper and plum instead of full red and purple.

As regards plastid colour (in the sap-coloured forms most easily seen in the centre or "eye" of the flower), the relation of uncoloured (white) to coloured (cream) plastids appears to be that of dominant to recessive, if a certain marked deficiency of creams in F_2, observed in some cases, should prove attributable to accidental irregularity; if, on the other hand, this deficiency should prove real, some less simple relation must evidently exist (see Rep. III, pp. 39 and 50, Table III, cases 24, 29, etc.).

In the case of surface character it was suggested that, similarly as in the case of sap colour, the dominant condition—hoariness—is due to the presence of two factors (H and K), the recessive condition—glabrousness—to the absence of either, or both, but that the flower colour and surface character are so inter-related that the outward manifestation of the presence of H and K only occurs if C and R are present in conjunction with these two factors, *i.e.*, only in sap-coloured individuals. Brompton Stocks might, however, prove an exception to this kind of zygotic coupling.

Since the publication of Report III, it has been pointed out to us by Mr. Doncaster that the assumption of two hoariness factors, H, K, is unnecessary, and that the occurrence of one alone is sufficient to account for the known facts. The double factor hypothesis, which at an earlier stage of the work appeared to offer the simplest solution of the facts, was, by an oversight, unfortunately retained after another explanation of the complications it was invoked to explain rendered it unnecessary.* This simplification is correctly represented if H is omitted from the formulæ and diagrams given in Report III. The composition of the glabrous Ten-week strains can, therefore, be stated thus:—

Glabrous white	CrK
,, cream	cRK
,, sap colours	CRk

Doubling.

During the past two seasons, considerable additional knowledge has been obtained regarding the circumstances under which doubles may be expected to occur, or, on the other hand, to be altogether absent. The evidence obtained from a large number of observations renders it scarcely doubtful that, contrary to the belief still widely held among growers, the double character is inherited in a definite and regular manner, and independently of external conditions.

The experiments recorded in Reports II and III had already shown that, in most of the glabrous Ten-week strains, *e.g.*, white, Princess May (a cream), flesh, copper, and various purple shades, the singles are of two kinds: (1) those which on self-fertilisation yield only singles; and (2) those which, similarly treated, give a mixture of singles and doubles, the doubles being usually in distinct excess of the singles. This has also been found to hold in the red and white English Brompton Stocks, and is probably true also of the East Lothian (Intermediate) strains. It was found that, in the case of the Ten-week

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* Attention has already been drawn to this correction in the Royal Horticultural Society's 'Report of the Conference on Genetics,' 1906, p. 147; see also Bateson, 'Progressus Rei Bot.,' vol. 1, p. 391.

strains mentioned above, seed obtained commercially and stated to yield a certain proportion of doubles could be relied upon to give the expected mixture, but that the singles so obtained would probably include *both* kinds of individuals, some again throwing doubles and others not. Whether such mixture commonly occurs in similar samples of the Brompton and East Lothian strains the number of plants tested is as yet too small to determine.

The results of the present experiments go to show that once an individual has been identified as belonging to the sporting or to the non-sporting class, it becomes possible to predict the behaviour of its descendants when they in turn are self-fertilised. From a non-sporting individual only non-sporting offspring are obtained; whether self-fertilised or bred *inter se*, such offspring appear incapable of throwing doubles. Conversely, singles derived from an individual belonging to the sporting group have, so far as experiment has yet gone, proved themselves to be also all of the sporting class, giving again both singles and doubles. It is, nevertheless, just possible that a small percentage of singles, offspring of double-throwing singles, may be pure singles, though none have yet been found. Such plants, if they exist, must in any case be rare, but the possibility of their existence must still be borne in mind.

Two of the Ten-week strains, however, differ from those enumerated above in that in each case the race *as a whole* appears to be ever-sporting: 77 individuals were tested in the one case and 33 in the other, and not one was found to breed true to singleness. These two strains are red (crimson) and sulphur-white. The latter race is also remarkable for its behaviour as regards plastid colour. It has been known to growers for at least fifty years, and is usually described as yielding a mixture of singles and doubles, the singles being white and the doubles cream. This statement has been found to be correct so far as the singles are concerned. Among the doubles, however, though the great majority are cream, a small percentage of whites are constantly found to occur. It may well be that in the case of these two races the original seed happened to have been collected exclusively from sporting individuals, and the aim of the gardener to obtain as many doubles as possible has tended to keep the supply, once obtained, from admixture with seed from true-breeding singles. On the other hand, it seems not improbable that the varying percentage of doubles quoted for different strains (from 30 to 80 per cent., but usually about 60 or 70 per cent.) is largely, perhaps wholly, due to the greater or lesser admixture of seed from singles of the non-sporting class, such admixture being very likely to occur where plants are grown on a large scale and harvested in bulk. The same explanation may possibly account for another fact hitherto unexplained. In a treatise advocating a new method for the successful culture of Stocks and Wallflowers, E. Chaté, a French horticulturist, remarks, in passing, that one cause of the decline in the culture of these plants among French gardeners is no doubt disappointment that the 60 or 70 per cent. of doubles obtained in the first year from German grown seed becomes diminished after a few years to 10 or 15 per cent.* If, as in our experience appears frequently to be the case, the seed obtained by Chaté was mixed, having been harvested from pure-breeding singles as well as from sporting singles, and if it be assumed that all the singles are on the average equally productive, then the proportion of the crop represented by pure-breeding singles will tend to increase in successive years, that of the sporting singles to diminish, since a large proportion of the progeny of the latter plants will be double and therefore infertile. Consequently the proportion of doubles in each successive generation must necessarily diminish, unless this effect is in any way counteracted by selection.

In the case of crosses between the various strains mentioned above, the results fully confirm the view expressed in Report III (p. 45), that doubles are only found to occur in the F_1 generation when *both* the parents throw doubles on self-fertilisation. If *only one* of the parents is found to yield doubles when self-fertilised, the F_1 generation will consist entirely of singles.

The further evidence upon which this statement is based is given in Tables I, II, and III. It will there be seen that from 79 matings between various strains, where one parent was known to be throwing doubles and the other not, 1250 F_1 plants were raised, all of which were single (Table I). Whereas the F_1 families obtained from 29 unions, where both individuals were known to be capable of throwing doubles, all showed a mixture of singles and doubles (Table II). In no case were doubles obtained from matings between individuals giving only singles when self-fertilised (Table III).

The consistency of these results, obtained from a considerable number of different strains, and the agreement between them and Mendelian expectation, according as the breeding is with heterozygous or homozygous forms, point strongly to the conclusion that the double character is inherited in accordance with Mendelian principles.

The evidence from the F_2 generation brings out two remarkable features which are not exactly paralleled by any phenomenon of inheritance hitherto observed.

(1) Though F_1 bred between pure singles and double-throwing singles is always single, there is a distinction between reciprocal crosses. For when a pure single is used as ♀ and is pollinated from a plant throwing doubles, *all* the F_1 plants throw doubles in F_2. But when the reciprocal cross is made, *some* of the F_1 plants breed true to singleness while others throw doubles.

(2) A similar difference between reciprocals occurs in regard to the

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* 'Cult. prat. des Giroflées' (N.D.), p. iii.

plastid character in the case of the sulphur-white strain. As stated above (p. 37), this is a strain of white singles throwing doubles which, a small percentage excepted, are cream.* The result in certain crosses, where this race is used as the male parent, indicates that *all* the pollen grains of the sulphur-white carry the cream character; whereas the results obtained when the same form is used as the female show that among the ovules *some* carry the cream character and some the white (see note, p. 5).

There are further complications showing that in some unknown way an interdependence exists between doubleness and the character of the plastids, but these have not yet been studied on a sufficient scale.

These two facts are a clear indication that the composition of the ovules may differ from that of the pollen grains in the same plant.

Table I.—Showing that the F_1 generation from matings where one parent is throwing doubles, and the other not, *is all single.*

A strain which throws doubles on self-fertilisation is described as a "d" strain, one which does not as a "no-d" strain. In Experiments 1—14 the seed parent is throwing doubles and the pollen parent not; in Experiments 15—20 the reverse is the case.

No. of expt.	Parents.		No. of matings.	F_1.	
				Single.	Double.
1	No-d glabrous cream	× d hoary white (East Lothian) ...	3	75	0
2	,,	× d glabrous white	2	35	0
3	,,	× d hoary red (Brompton)............	2	23	0
4	,,	× d glabrous red	3	35	0
5	,,	× d glabrous sulphur-white	7	76	0
6	,,	× d glabrous azure	2	43	0
7	,,	× d glabrous light purple	3	69	0
8	No-d glabrous white	× d hoary white (East Lothian) ...	1	2	0
9	,,	× d glabrous cream (Princess May)	3	35	0
10	,,	× d glabrous red	4	53	0
11	,,	× d glabrous sulphur-white	17	289	0
12	No-d glabrous flesh	× d hoary white (East Lothian) ...	1	19	0
13	,,	× d glabrous sulphur-white	9	151	0
14	,,	× d glabrous light purple	1	9	0
15	d glabrous cream (Princess May)	× no-d glabrous white...................	2	35	0
16	d glabrous red	× ,, ...	2	26	0
17	d glabrous sulphur-white	× no-d hoary red (Brompton)	4	57	0
18	,,	× no-d glabrous flesh	5	102	0
19	,,	× no-d glabrous white..................	3	44	0
20	,,	× no-d hoary white (*incana*).........	5	72	0
			79	1250	0

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* The occasional white double appearing in this strain points to some further complexity which the data at present available are insufficient to explain.

Table II.—Showing that the F_1 generation from matings where both parents are throwing doubles *consists of a mixture of singles and doubles.*

No. of expt.	Parents.	No. of matings.	F_1.	
			Single.	Double.
1	d glabrous cream (Princess May) × d hoary white (East Lothian) ...	1	13	13
2	,, ,, × d glabrous white	2	2	6
3	,, ,, × d glabrous red	2	5	15
4	,, ,, × d glabrous sulphur-white	4	21	35
5	d glabrous red × d glabrous cream (Princess May)	3	14	28
6	d glabrous sulphur-white × d hoary white (East Lothian) ...	7	87	121
7	,, × d glabrous red	4	15	21
8	,, × d glabrous white	1	7	8
9	,, × d glabrous azure	3	35	44
10	,, × d glabrous light purple	2	2	23
		29	201	314

Table III.—Showing *the absence of doubles* in F_1 when both parents are pure-breeding singles.

No. of expt.	Parents.	No. of matings.	F_1.	
			Single.	Double.
1	No-d glabrous cream × no-d glabrous white	7	99	0
2	No-d glabrous white × no-d glabrous cream	1	10	0
3	,, × no-d glabrous white	3	64	0
4	No-d glabrous flesh × no-d glabrous cream	2	55	0
5	No-d glabrous cream × no-d glabrous flesh	1	18	0
		14	246	0

The pollen grains of the ever-sporting race are all, or nearly all, capable of transmitting doubleness, while many of the ovules are carrying singleness. Similarly the pollen grains of the sulphur-white are all, or nearly all, transmitting the cream colour, whereas among the ovules many carry whiteness.

The nature and origin of the distinction between the two classes of ovules cannot be settled without a wide statistical basis of fact, but it is evident that a clue to the solution of the problem presented by these ever-sporting strains is provided by the distinction between reciprocals.

A PRELIMINARY ACCOUNT OF THE INHERITANCE OF COAT-COLOUR IN MICE.

By Florence M. Durham, Lecturer of Newnham College.

(Communicated by W. Bateson, F.R.S.)

During the past five years I have made a series of breeding experiments to determine the heredity of colour in mice.

As regards two important sections of the subject, namely, the nature and genetic behaviour of yellow mice, and the constitution of mice which have coloured coats and pink eyes, the experiments are as yet incomplete. The inquiry into these subjects is being continued, but as in some other respects the work is now complete, I submit a brief statement of the results.

My work has been largely confirmatory of what has been already stated by others. In addition, some new points have been made out. The relation of the dense to the dilute colours has been studied on a considerable scale. In regard to the pied varieties, the existence of a dominant pied condition has been demonstrated. The relation of the pigmentation of the eye to that of the coat has been investigated and in part elucidated.

On inspection, the colours of mice are seen to be very various, and examination shows that the different appearances are due to:—

(1) The nature of the pigment or pigments present.
(2) The density with which the pigment or pigments may occur.
(3) The pattern of their distribution in the hairs.
(4) The development of more or less white.

The allelomorphs to which these appearances are due may be represented thus:—

G. g. Presence and absence of the factor which gives the "agouti" or "grey" pattern in the hairs.

B. b. Presence and absence of the black determiner.

C. c. Presence and absence of colour.

If C is present without G or B, the colour is chocolate. From the analogy of other cases (fowls and various plants) it is possible that this colour is itself the product of two factors, but hitherto it has not been resolved. All albino mice, therefore, are to be represented as those from which C, *i.e.*, the colour chocolate is absent.

The above factors give the following combinations :—

CGB	Grey or agouti
CgB	Black
CGb	Cinnamon agouti
Cgb	Chocolate

D and d represent the presence and absence of a factor which causes the dense deposit of the pigments. CgBD is black; CgBd is blue; CgbD is chocolate; Cgbd is dilute chocolate, or "silver-fawn," as it is called by the fanciers.

When, as will be shown later, the pied condition is dominant, there is evidently another factor P present, which inhibits colour in varying degrees, whereas the recessive pied conditions are due to the absence of S, self-colour.

As described by Bateson (1), though the notation here indicated must be employed in calculating the various expectations, it is possible that the dilution states and the recessive pied states may be caused by subtraction stages of the corresponding dominant factors for dense deposition and self-colour..

Cuénot (2) originally suggested that G should be taken as allelomorphic to B. In the Report to the Evolution Committee, III, p. 7, it was pointed out that this was probably incorrect, and that by crossing agouti with chocolate a test of the correctness of the scheme, here propounded, could be obtained. If G and B were allelomorphic not to each other, but to g and b, their absences respectively, then black should appear in F_2. I have made this experiment, getting in F_2, 22 ag., 6 cinn. ag., 5 black, 3 chocolate, where expectation gives 20·5 ag., 6·75 cinn. ag., 6·75 black, 2·25 chocolate. Cuénot has similarly bred 41 ag., 15 cinn. ag., 15 black, 5 chocolate (expectation being 42·75 ag., 14·25 cinn. ag., 14·25 black, and 4·75 chocolate). The expected black thus appears, and the numbers are thus in close agreement with expectation. Cuénot (2), however, speaks of the appearance of blacks as unexpected. He attempts to account for them on his original scheme by representing black as the dense form of chocolate. This account is, however, inapplicable, for, as I shall show in detail, blue, not chocolate, is the dilute form of black, while chocolate has its own dilute form, silver fawn. This appears at once from the fact that both black × silver fawn and blue × chocolate alike give F_1 black, with 9 black, 3 blue, 3 chocolate, 1 silver fawn in F_2. Chocolate, therefore, equally with black, bears the factor for dense deposition.

The relation of the several colour determiners to each other is inadequately described by use of the terms dominant and recessive; and agouti, black, and chocolate must be regarded as composing a descending series in which black is epistatic* to chocolate, and agouti to both.

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* See Bateson, 'Science,' N.S., vol. 26, p. 653.

The term epistatic is thus applied to denote such a relationship between factors which are not in the same allelomorphic pair. A factor, then, is epistatic to another, when by its presence it conceals the existence of the other factor, although not allelomorphic to it. The terms dominant and recessive should only be applied to express relationship between factors in the same allelomorphic pair.

In dark-eyed mice, the inter-relations of all the colours are now clear, except in so far as yellow and its various combinations are concerned. My results agree with those of Cuénot and others in making it probable that yellows are always heterozygous, but various difficulties are encountered when a more precise statement is attempted. This part of the analysis must be deferred till more experimental data are obtained. The relation of yellow to the factor G is not yet clear. All that can yet be stated is that since G cannot be present in a black or chocolate,* not only the arrangement of the pigment in the agouti hairs, but also the presence of yellow pigment in them must be controlled by this factor.

EYE-COLOUR.

In addition to the factors for coat-colour, the determiners, on which eye-colour depends, have to be considered. It will be shown later that the development of certain coat-colours is also dependent upon these eye-colour determiners.

Mice can be grouped according to the colour of the eyes into two classes, dark-eyed and pink-eyed.

Dark-eyed Mice.—The eyes, viewed *in situ*, are apparently black. But when they are removed differences can be seen at once, and when sections of them are examined microscopically, these differences can be made out more fully. Apparently all mice, which have black pigment present in the coat, have black pigment in their eyes. Thus agouti and its various dilute forms, and black and blue, all have black eyes.

Those mice in which black pigment is absent from the coat, on the other hand, have only chocolate pigment in the eye. Thus, cinnamon agouti, and the dilute forms of cinnamon agouti, and chocolate and silver-fawn, all have chocolate eyes.

The fact that yellow mice have chocolate eyes has already been mentioned by Castle (3). In the clear yellows examined by me, the pigment was chocolate; but, I find, that sooty yellow mice (*i.e.*, yellow mice with some black pigment present in the hairs, giving a sooty appearance) have black pigment in the eyes. Some of these mice appear to have only black pigment present in their eyes, but others have both black and chocolate pigments in their eyes. I do not know

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* Chocolate containing G is cinnamon agouti.

at present how these differences in eye-pigment in sooty yellow mice are related to differences in genetic behaviour.

Ruby Eyes.—The so-called ruby eyes are dark with a red glow in them. They are not common, and three cases of them only have occurred in my breeding experiments. One was a piebald cinnamon agouti and white, one was a white mouse with one small patch of cinnamon agouti behind the right ear, and the third was a piebald chocolate and white. In each case, the iris was heavily pigmented with chocolate, and the choroid was only slightly pigmented with chocolate. No black pigment was found in either tissue.

Pink-eyed Mice are of many kinds.

(a) *The Albino.*—This type has apparently no dark colouring matter present, either in its eye or in its coat. I believe, however, that the whiteness of the coat is not due alone to the air in the spaces of the hair, but that a white substance of the nature of a pigment is present in the hairs (4).

(b) *Pink-eyed Mice with Coloured Coats.*—The eyes of these mice are only apparently unpigmented. Sections of them examined under the microscope show that both iris and choroid are pigmented, though very slightly.

The further description and the genetic behaviour of these mice will be dealt with later in another paper. Experiment has, however, already proved that their composition is very various. Several types of colour can be distinguished among the so-called pink-eyed "lilac" mice. They may, or may not, possess the factors B and D, and, consequently, when bred with chocolates, they may give blacks, blues, chocolates, or silver-fawns. So far as my experience goes, however, this mating never produces agouti.

Dense and Dilute Colorations.

The dense colour form is dominant over the dilute form. Thus black is dominant over blue, and chocolate is dominant over silver-fawn. Black is epistatic to chocolate, and it follows, therefore, that blue is epistatic to silver-fawn. All colours are dominant to albino. The offspring of a mating between a homozygous coloured mouse and an albino will be coloured, but the colour of the offspring will depend upon the epistatic determiner which may be carried by either parent.

Thus the offspring of a black mouse by an albino with chocolate determiner will be black, but the offspring of a chocolate mouse by an albino with black determiner will be black, because black is epistatic to chocolate.

Black.—Black when mated with albino with black determiner gives black in F_1. In the second generation F_2 there should be blacks and albinos in the ratio of 3 : 1.

The experimental numbers are—

Black.	Albino.
54	11

The calculated numbers are—

Black.	Albino.
48·75	16·25

Black when mated with chocolate gives black in F_1.

In F_2 there should be 3 blacks to 1 chocolate.

The experimental numbers are—

Black.	Chocolate.
42	17

The calculated numbers are—

Black.	Chocolate.
44·25	14·75

Black mated with albino carrying the chocolate determiner gives all black in F_1.

In F_2, according to calculation, there should be a ratio of—

9 black : 3 chocolate : 4 albino.

The experimental numbers are—

Black.	Chocolate.	Albino.
76	24	27

The calculated numbers are—

Black.	Chocolate.	Albino.
71·44	23·81	31·75

If these heterozygous blacks carrying both chocolate and albino are mated with albino with chocolate determiner, the results should follow a ratio of—

9 black : 3 chocolate : 12 albino.

The experimental numbers are—

Black.	Chocolate.	Albino.
18	5	27

The calculated numbers are—

Black.	Chocolate.	Albino.
18·75	6·25	25

Black is dominant over blue, because the concentrated colour is dominant over the weak.

Black × blue = black F_1.

In F_2 there should be a proportion of 3 blacks : 1 blue.

The experimental numbers are—

Black.	Blue.
50	13

The calculated numbers are—

Black.	Blue.
47·25	15·75

If the heterozygous black carrying blue be mated with an albino bearing dense and black determiners, the first generation will all be black. In the second generation there should result black, blue, and albino in the ratio of 9 : 3 : 4.

The experimental numbers are—

Black.	Blue.	Albino.
21	4	6

The calculated numbers are—

Black.	Blue.	Albino.
17·44	5·81	7·75

When black is mated with silver-fawn, the resulting offspring are black, because black is epistatic to chocolate, and the dense colour is dominant over the dilute. In dealing with the second generation, there are four factors to be taken into account—the two pigments, black and chocolate, and the concentration and dilution.

There should result in F_2, blacks, blues, chocolates, and silver-fawns, and the proportions should be in the ratio of—

9 black : 3 blue : 3 chocolate : 1 silver-fawn.

The experimental numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.
67	21	20	5

The calculated numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.
63·56	21·19	21·19	7·06

It is obvious, if the factors concerned in the mating be considered, that exactly the same result will be arrived at if a chocolate mouse be mated with a blue mouse. Here the chocolate mouse carries the factor of concentration, while the blue mouse is responsible for blackness.

From such matings, black mice must result in the first generation, since black is epistatic to chocolate and density is dominant over dilution. In the second generation there should be the same proportion, viz. :—

9 black : 3 blue : 3 chocolate : 1 silver-fawn.

The experimental numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.
44	17	17	8

The calculated numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.
48·375	16·125	16·125	5·375

The matings in which albinos are introduced as black × albino with silver-fawn determiner, or blue × albino with chocolate determiner, or silver-fawn × albino with black determiner, or chocolate × albino with blue determiner, should in the same way yield like results in F_2. There should be 27 blacks, 9 blue, 9 chocolate, and 3 silver-fawn, and 16 albino in the second generation. I have only worked out one of these matings fully. Blue was mated with albino with chocolate determiner.

The experimental numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.	Albino.
33	10	8	2	12

The calculated numbers are—

Black.	Blue.	Chocolate.	Silver-fawn.	Albino.
27·42	9·14	9·14	3·05	16·25

Blue.—When blue is mated with silver-fawn, the resulting offspring are blue, and in the second generation there should be a proportion of 3 blue to 1 silver-fawn.

The experimental numbers are—

Blue.	Silver-fawn.
46	17

The calculated numbers are—

Blue.	Silver-fawn.
47·25	15·75

When the heterozygous blues from this mating are mated with silver-fawns there should be an equal number of blues and silver-fawns.

The experimental numbers are—

Blue.	Silver-fawn.
37	36

The calculated numbers are—

Blue.	Silver-fawn.
36·5	36·5

When blue is mated with albino with silver-fawn determiner the resulting offspring are blue.

In the second generation there should be a ratio of—

9 blue : 3 silver-fawn : 4 albino.

The experimental numbers are—

Blue.	Silver-fawn.	Albino.
55	26	36

The calculated numbers are—

Blue.	Silver-fawn.	Albino.
65·81	21·94	29·25

Chocolate.—Chocolate is dominant over silver-fawn. I have made this mating very often, always with the same result, chocolate offspring in F_1, but the matings were not carried into the second generation.

Chocolate mated with albino with chocolate determiner gives chocolate in the first generation.

In F_2 there should be 3 chocolate : 1 albino.

The experimental numbers are—

Chocolate.	Albino.
99	27

The calculated numbers are—

Chocolate.	Albino.
94·5	31·5

Heterozygous chocolate carrying albino mated with albino with chocolate determiner should give equal numbers of chocolate and albino.

The experimental numbers are—

Chocolate.	Albino.
14	15

The calculated numbers are—

Chocolate.	Albino.
14·5	14·5

Chocolate carrying albino mated with albino with silver-fawn determiner should give an equal number of albinos to coloured mice and a proportion of three chocolates to one silver-fawn.

The experimental numbers are—

Chocolate.	Silver-fawn.	Albino.
13	4	18

The calculated numbers are—

Chocolate.	Silver-fawn.	Albino.
12·75	4·25	18

Silver-fawn mated with albino carrying chocolate determiner gives all chocolate in F_1.

In F_2 there should be 9 chocolate : 3 silver-fawn : 4 albino.

The experimental numbers are—

Chocolate.	Silver-fawn.	Albino.
19	4	6

The calculated numbers are—

Chocolate.	Silver-fawn.	Albino.
16·31	5·44	7·25

Silver-fawn carrying albino mated with silver-fawn carrying albino should give 3 silver-fawn : 1 albino.

The experimental numbers are—

Silver-fawn.	Albino.
30	8

The calculated numbers are—

Silver-fawn.	Albino.
31·5	9·5

Piebald Mice.

Both Cuénot (2) and Allen (5) state that in mice the piebald condition behaves in accordance with Mendelian principles as a recessive character in relation to total pigmentation.

Cuénot also suggests that the forms which are only slightly piebald, that is, in which the patches of white are small and few, will dominate over those which, on the contrary, exhibit large and many patches of white; and also that when two of these latter are mated together their young will also be of the same character, bearing large and many patches of white.

In this connection the case of black-eyed whites may be given. These mice, which show no trace of colour in the fur, may be taken as representing the extreme case of piebald marking. I have not succeeded in obtaining a race of them which breeds true. The young are very various in appearance, ranging from black-eyed whites, through all grades of piebald marking to heavily pigmented forms, although, so far, no selfs have appeared.

In my experiments I have dealt with piebald mice of two kinds. One kind belongs to the class described already by Cuénot and Allen, and behaves as recessive to self-colour. That is, mated with self-coloured mice, these piebalds give only self-coloured young. In the second generation the piebald returns again in the proportion of one piebald to three selfs.

The experimental numbers are—

Self.	Piebald.
330	124

The calculated numbers are—

Self.	Piebald.
340·5	113·5

These piebalds mated with albinos with self determiner give only self-colours in the first generation. In the second generation there are selfs, piebalds, and albinos.

The experimental numbers are—

Self.	Piebald.	Albino.
259	90	125

The calculated numbers are—

Self.	Piebald.	Albino.
266·625	88·875	118·5

Albino mice can likewise carry piebald, viz., absence of the self-determiner. Mice of this kind mated with self-coloured mice homozygous as to self-character, give only selfs in the first generation. In the second generation selfs, piebalds, and albinos are obtained.

The experimental numbers are—

Self.	Piebald.	Albino.
163	53	69

The calculated numbers are—

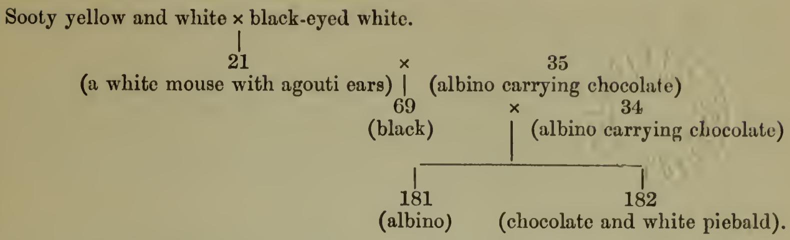
Self.	Piebald.	Albino.
160·31	53·44	71·25

Dominant Piebald.—But the second kind of piebald mouse behaves differently, and the piebald character, which it carries, behaves as a dominant. The mice of this class have all been derived from the union of a sooty yellow-and-white mouse, of unknown origin, with a black-eyed white mouse from Atlee, the well-known fancier. There is not enough evidence to show whether both, or if only one, which of the parents is responsible for the transmission of the dominant piebald character. Four of the descendants of these mice were mated with homozygous self mice, and threw 8 selfs and 13 piebalds. This suggests that they are DR in character, the piebald character being dominant. The piebalds of this class were inter-mated eight times, and gave 12 selfs and 44 piebalds.

The calculated numbers on the supposition of the mice being DR in character would be 14 selfs and 42 piebalds.

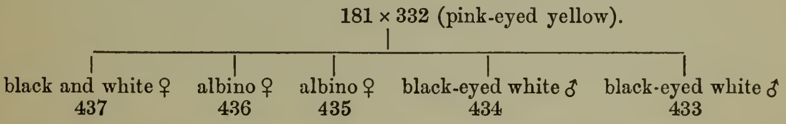
Intermatings between piebalds descended from the same union, which have been derived from matings with albinos, show likewise that the piebalds were able to produce self-coloured mice. From matings of this kind I have obtained 30 piebalds, 12 selfs, 27 albinos. The expected ratio is 9 : 3 : 4, which would give 38·25 piebalds, 12·75 selfs, 17 albinos, so the albinos are in distinct excess.

The inheritance of the black-eyed white character has been transmitted through these mice, and I will quote from the tables to show the descent in some detail.



181 × 182 gave 4 albinos, 2 chocolate and white piebalds. These latter piebalds have given 10 chocolate and whites and 1 albino, but no selfs.

181, the albino, was mated with a pink-eyed, yellow mouse, which had been given to me by Mr. Darbishire. The resulting young were 2 black-eyed whites, 1 black and white piebald, and 4 albinos.



The piebald doe 437 was mated both with 434 and with 433, the black-eyed white bucks, and gave 4 piebalds, 2 selfs, and 8 albinos.

One of these albinos was mated with one of the piebalds, and gave 3 albinos and 3 piebalds. These latter piebalds gave 1 albino, 3 piebalds, and 1 self-coloured mouse.

435 (albino) was mated with a homozygous pink-eyed lilac mouse, and gave 2 piebald lilac and white pink-eyed mice, and from these lilac and white mice I obtained 4 piebalds, 2 selfs, and 4 albinos. 435 (albino) was also mated with a silver-fawn mouse, and gave 2 chocolate and white piebalds. From them I obtained 5 chocolate and white piebald, 2 silver-fawn and white piebald, 2 chocolate selfs, 1 silver-fawn self, 3 black-eyed whites, and 6 albinos.

A piebald from the union of 437 and 434, mated with a chocolate mouse, gave 3 chocolate and white piebalds, and from them I have obtained 15 chocolate and white piebalds, 4 chocolate selfs, and 4 black-eyed whites. From two of these black-eyed whites, I have obtained 4 black-eyed whites and 2 chocolate and white piebalds.

There are thus, genetically, two entirely distinct types of piebalds, which to the eye are indistinguishable. The genetic relations of these two types are as yet unknown.

Unconformable Case.

Finally, I must mention one case, which I am unable to account for. I bred a black doe, by mating a blue with a black. The parents were both homozygous. They never threw any albinos or chocolates in any of their litters. Nor did any of their offspring show any signs of being heterozygous.

The black doe, so obtained, was mated with five different albinos. She was taken from albino to albino. One of these albinos was descended from the dominant piebald race, and the result of this union was 3 albinos, 4 chocolates, and 1 chocolate and white piebald. Her other matings resulted in 21 blacks.

The albino was mated with two other homozygous blacks, and 6 blacks resulted; and mated with a homozygous chocolate, 6 chocolates resulted. Apart from the unconformable result, there was no reason to suspect any error in this case.

In conclusion, I offer my thanks to Mr. Bateson, for his kindness in giving both help and advice while I have been carrying on the experiments recorded.

The expenses of these experiments have been partly defrayed by grants from the Government Grant Fund of the Royal Society.

List of Mice.

Chocolate.—Only chocolate pigment present in the hair; the hairs are heavily loaded with pigment.

Silver-fawn.—Only chocolate pigment present, but in less amount than in the case of the chocolate mouse. This is the dilute form.

Black.—Both black and chocolate pigments are present; the hairs are heavily loaded with pigment.

Blue.—This is the dilute variety of the black.

Agouti.—This is also called golden agouti, and is the colour of the wild mouse. There are three pigments present in the hairs—yellow, black, and chocolate. The bases of the hairs are black, and the hairs are barred with yellow. Some hairs have no yellow in them and some are tipped with yellow.

There are several dilute forms of agouti known, according to whether all or only one of the pigments is diluted in amount.*

Cinnamon Agouti.—Both chocolate and yellow pigments are present, but no black, and the hairs are ticked as in the case of the agouti.

Dilute forms of the cinnamon agouti are also known.

Yellow.—The clear yellow appears to have only yellow pigment in its hairs. In the sooty yellow, black is always discoverable in the hairs with the aid of the microscope.

Cream is the dilute variety of yellow.

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* The terms golden agouti and cinnamon agouti are wrongly applied in the account given in "The Present State of Knowledge of Colour Heredity in Mice and Rats," W. Bateson, 'Zool. Soc. Proc.,' 1903, and should be as given above.

Sable.—All three pigments are found in the hairs of the sable mouse. The back is dark and ticked like agouti, but the flanks and belly are yellow.

Albino.—Apparently no coloured pigment in the coat or eyes.

The pink-eyed coloured mice will be described in another paper.

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ON SEX-INHERITANCE IN THE MOTH *ABRAXAS GROSSULARIATA* AND ITS VAR. *LACTICOLOR.*

By L. DONCASTER, M.A., Lecturer on Zoology, Birmingham University.

(Communicated by W. Bateson, F.R.S.)

In the 'Proc. Zoo. Soc.,' 1906, vol. 1, p. 125 (with Plate VIII), a preliminary account was given by Doncaster and Raynor of the inheritance of the variety *lacticolor* of *Abraxas grossulariata.* This variety is a Mendelian recessive, differing from the type chiefly in the great reduction and somewhat different shape of the black markings. In the wild state it is exceedingly rare, and is found almost exclusively in the female.

Breeding experiments gave the following results:—

Lact. ♀ × *gross.* ♂ gave *gross.* ♂, *gross.* ♀.
Heterozygous *gross.* ♀ × heterozygous *gross.* ♂ gave *gross.* ♂, *gross.* ♀, *lact.* ♀.
Lact. ♀ × heterozygous *gross.* ♂ gave *gross.* ♂, *lact.* ♂, *gross.* ♀, *lact.* ♀.
Heterozygous *gross.* ♀ × *lact.* ♂ gave *gross.* ♂, *lact.* ♀.
Lact. ♀ × *lact.* ♂ gave *lact.* ♂, *lact.* ♀.

The important points about these results are: (1) that *lacticolor* males can be obtained by pairing a *lacticolor* female with a heterozygous male, in which case *lact.* ♂. *gross.* ♂, *lact.* ♀, *gross.* ♀, are obtained in roughly equal numbers (Table III below). (2) The converse cross, heterozygous female × *lacticolor* male gives all the males *gross.* (heterozygous), all the females *lact.* (Table IV).

In explanation of these facts it was suggested that the sex-determinants behave as Mendelian allelomorphs, segregating in gametogenesis, and that the *lacticolor* character was coupled with the female determinant. But it was assumed that both male and female individuals were heterozygous in respect of sex, and this resulted in making the whole hypothesis rather complicated.

A simpler explanation has been offered by Bateson and Punnett,* viz.: (1) that the sex-determinants behave as Mendelian allelomorphs, femaleness being dominant; (2) that female individuals are heterozygous in respect of sex, having the constitution ♀ ♂ and producing male-bearing and female-bearing eggs in equal numbers; males are homozygous, of constitution ♂ ♂ producing only male-bearing spermatozoa; (3) that there is repulsion between the determinant for femaleness and the *grossulariata* determinant in oogenesis, so that male-bearing eggs bear *grossulariata*, female-bearing eggs the *lacticolor* character.

We then get the following results from the various matings: ♂, ♀ representing the sex determinants; G, L the *gross.* and *lact.* characters respectively.

Parents.	Constitution.	Gametes.	Offspring.
Lact. female *Gross.* ♂	LL ♀ ♂ GG ♂ ♂	L ♀, L ♂ G ♂, G ♂	LG ♀ ♂ = *gross.* female LG ♂ ♂ = *gross.* male
Heterozygous female Heterozygous male	GL ♀ ♂ GL ♂ ♂	L ♀, G ♂ G ♂, L ♂	LG ♀ ♂ = *gross.* female LL ♀ ♂ = *lact.* female GL ♂ ♂ = *gross.* male GG ♂ ♂ = *gross.* male
Lact. female Heterozygous male	LL ♀ ♂ GL ♂ ♂	L ♀, L ♂ G ♂, L ♂	LG ♀ ♂ = *gross.* female LL ♀ ♂ = *lact.* female LG ♂ ♂ = *gross.* male LL ♂ ♂ = *lact.* male
Heterozygous female *Lact.* male	GL ♀ ♂ LL ♂ ♂	L ♀, G ♂ L ♂, L ♂	LL ♀ ♂ = *lact.* female GL ♂ ♂ = *gross.* male

This explanation was thus in accordance with all the facts, and this year it has received important confirmation. For it now appears that when a wild *grossulariata* female is paired with a *lacticolor* male, all the male offspring are *grossulariata* and all the females *lacticolor*, *i.e.*, the same result is obtained with wild females which have never been

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* 'Science,' 1908, N.S., vol. 27, p. 785.

crossed with the rare *lacticolor* variety, as is produced by pairing a first-cross *grossulariata* female with a *lacticolor* male.*

The wild females used in these experiments were derived from different parts of the country, some from districts in which *lacticolor* is unknown. It may, therefore, be regarded as certain that in the moth *Abraxas grossulariata* males are normally homozygous in respect of the *grossulariata* character, but all females are heterozygotes carrying recessive *lacticolor*. But since in oogenesis there is repulsion or incompatibility between the dominant *grossulariata* and the dominant female determinant, the male-bearing eggs all bear *grossulariata*, the female-bearing *lacticolor*.

Both kinds of eggs are fertilised by spermatozoa bearing determinants for maleness and the *grossulariata* character, and so homozygous males and heterozygous females are produced indefinitely. The exceptional and very rare production of a wild *lacticolor* must be due to some accidental disturbance of the association of the *grossulariata* determinant with the male-bearing egg.

The following tables give the detailed results of my experiments. Mr. Raynor's results subsequent to those already published are in agreement, with a small percentage of exceptions which are possibly due to accident. The exceptions are as follows: Among nine families, comprising 680 individuals, from the mating *gross.* ♀ × *lact.* ♂, three *grossulariata* ♀s were recorded, and one *lacticolor* ♂. Two *grossulariata* ♂s appeared in families from *lact.* ♀ × *lact.* ♂ (among 280 *lacticolor* individuals), and one *grossulariata* ♀ from wild ♀ × *lact.* ♂, among 54 *lacticolor* ♀s. Two *lacticolor* ♀s also appeared in a family from *lact.* ♀ × wild ♂.

Table I.—Lacticolor ♀ × grossulariata ♂ (wild).

Pairing.	Gross. ♂.	Gross. ♀.
'05.3..................	15	16
'07.3..................	30	34
Total	45	50

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* In some families of this type of mating there was a very large excess of females, and in one (No. 1907.19) no males were produced

Table II.—Heterozygous ♀ × heterozygous ♂.

Pairing.	Gross. ♂.	Gross. ♀.	Lact. ♂.	Lact. ♀.
'04. 2	7	1	—	4
'07. 8	5	3	—	1
'07.13	2	—	—	2
Total	14	4	—	7

Table III.—Lacticolor ♀ × heterozygous ♂.

Pairing.	Gross. ♂.	Gross. ♀.	Lact. ♂.	Lact. ♀.
'06. 7	31	34	33	36
'06. 2	1	2	—	—
'06. 6	5	4	1	—
'07. 1	1	—	1	1
'07. 4	8	8	12	11
'07.15	—	2	3	2
'07.16	3	6	5	7
'07.22	4	—	1	2
'07.23	10	6	9	11
Total	63	62	65	70

Table IV.—Heterozygous ♀ × lacticolor ♂.

Pairing.	Gross. ♂.	Lact. ♀.
'06. 4	25	30
'06. 8	74	54
'06.18	13	10
'06.19	12	14
'06.21	17	16
'06.27	4	6
Total	145	130

Table V.—Wild ♀ × lacticolor ♂.

Pairing.	Gross. ♂.	Lact. ♀.
'07. 6	2	15
'07. 7	7	7
'07.12	10	11
'07.19	—	19
Total	19	52

NOTE ON THE INHERITANCE OF SEX IN CANARIES.

By Florence M. Durham, Lecturer of Newnham College, Cambridge, and Dorothea C. E. Marryat.

(Communicated by W. Bateson, F.R.S. Received September 26, 1908.)

It has long been known to fanciers of canaries that certain curious results occur when cinnamons are mated with other varieties. The cinnamon canary is so called on account of the colour of its plumage, which is of a brownish tint, due to the presence of a chocolate melanin and the absence of black melanin. The green canary has both pigments present in its feathers. The most definite feature of the cinnamon is, however, the colour of the eye in the newly-hatched bird. In ordinary canaries the eyes on hatching look black, but in cinnamons they look pink. The eyes become dark in appearance as the bird grows older, so that in the adult cinnamon it is extremely difficult, if not quite impossible, to distinguish the colour of its eye from that of a common canary by simple inspection. Microscopical examination, however, shows that the pigment of the cinnamon eye is different from that of the normal eye, being chocolate only, and not black. All birds with black in their feathers have black in their eyes.

All birds with cinnamon feathers are, of course, cinnamons, and have had pink eyes on hatching; but it should be premised that birds may be in plumage pure yellow, owing to the absence of melanins, and it is not possible by examination of a yellow bird during life to tell whether it was originally pink-eyed or black-eyed.

To avoid ambiguity, the cinnamons will be referred to as pink-eyed and the other varieties as black-eyed.

The pink-eyed character is a Mendelian recessive, and the offspring of two pink-eyed birds is always pink-eyed.

When pink-eyed and black-eyed varieties are bred together, the fanciers are agreed that the results are as follows :—

1. Pink-eyed hen and black-eyed cock gives all young of both sexes black-eyed.

2. Black-eyed hen and pink-eyed cock will give all *male* offspring black-eyed. The female offspring are most commonly pink-eyed; black-eyed hens may occur, but all the *pink-eyed offspring are hens* without exception, so far as is known.

Statements to this effect are made in most of the books on canary breeding. A particularly full account is given by Mr. C. L. W. Noorduijn,* who has also been good enough to answer several questions on this subject.

We commenced our experiments three years ago, for the purpose of investigating the problem constituted by this peculiar inheritance. These experiments are still in progress, but as the phenomena are so closely parallel to those discovered by Doncaster in the case of *Abraxas grossulariata* and its variety *lacticolor*, it seems desirable to publish a preliminary account of the work at the present time.

The results obtained have been as follows :—

Mating.	Offspring.			
	♀.		♂.	
	B.	P.	B.	P.
1. P♀ × B♂	7		19	
2. B♀ × P♂	4	33	30	
3. B♀ × F_1 B♂ ...	18	13	24	
4. F_1 B♀ × F_1 B♂ ...	1	2	2	
5. P♀ × F_1 B♂ ...	24	21	5	19
6. F_1 B♀ × P♂		6	4	

B, black-eyed. P, pink-eyed.

On comparing these results with Doncaster's for *Abraxas grossulariata*, it is evident that there is a close agreement between the two sets of phenomena, except in so far that whereas the mating No. 2, dominant ♀ × recessive ♂, has in the canaries sometimes given dominant ♀s, these were not proved to occur in the corresponding families of *grossulariata*. With this exception, therefore, the interpretation suggested for that case by Bateson and Punnett† can

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* 'Album der Natuur,' 1903, p. 71.

† 'Science,' vol. 27, N.S., 1908, p. 785.

be applied to the results in the canaries. The female is taken as being heterozygous in sex, femaleness being a dominant, and the male is regarded as homozygous in the absence of femaleness. The black-eyed character B is a dominant and the pink-eyed character b (absence of B) is recessive.

In the ordinary case in which black-eyed ♀ × pink-eyed ♂ gives black-eyed cocks and pink-eyed hens, the assumption that there is spurious allelomorphism or repulsion between femaleness and B gives a consistent representation of the facts. The ordinary black-eyed hen is thus ♀ ♂ Bb, and her ova are respectively ♀ b and ♂ B. The black-eyed cock is ♂ ♂ BB. The pink-eyed cock is ♂ ♂ bb, and the pink-eyed hen is ♀ ♂ bb. The matings 1, 2, 3, and 5 of the previous table can thus be represented as follows :—

1.	Pink-eyed ♀	×	black-eyed ♂.
Composition......	bb ♀ ♂		BB ♂ ♂
F_1	black-eyed hens ♀ ♂ Bb		black-eyed cocks ♂ ♂ Bb

2.	Black-eyed ♀	×	pink-eyed ♂.
Composition......	Bb ♀ ♂		bb ♂ ♂
Gametes	B ♂ b ♀		all b ♂
F_1	pink-eyed hens bb ♀ ♂		black-eyed cocks Bb ♂ ♂

3.	Black-eyed ♀	×	black-eyed F_1 ♂.
Composition......	Bb ♀ ♂		Bb ♂ ♂
Gametes	B ♂ b ♀		B ♂ b ♂
Result	black-eyed hens Bb ♀ ♂ pink-eyed hens bb ♀ ♂		black-eyed cocks BB ♂ ♂ and also Bb ♂ ♂

5.	Pink-eyed ♀	×	black-eyed F_1 ♂.
Composition......	bb ♀ ♂		Bb ♂ ♂
Result	black-eyed hens Bb ♀ ♂ pink-eyed hens bb ♀ ♂		black-eyed cocks Bb ♂ ♂ pink-eyed cocks bb ♂ ♂

Matings 4 and 6 in the previous table need not be represented here, because they are in reality identical with No. 3 and No. 2 respectively, for the black-eyed hens, whether they come from a pink-eyed mother or not, are, in fact, heterozygous in the black-eye and pink-eye characters.

Whatever be the truth regarding the transmission of sex, there is thus no escape from the remarkable conclusion that just as the normal females of the moth *Abraxas grossulariata* are in reality hybrids in the *lacticolor* character, so the ordinary black-eyed hen canaries are hybrids in the pink-eye character.

Though the general course of the phenomena can be thus represented, two difficulties remain. The first is that mentioned above, that black-eyed hens have been produced by the mating black-eyed hen × pink-eyed cock. Only two of our hens have behaved in this way, and unfortunately we know nothing of the origin of these birds. No suggestion can be offered yet as to the causation of these departures from the usual rule.

Lastly, though but for the exceptional results, the scheme suggested successfully represents the qualitative features of the inheritance, the quantitative results are not according to expectation. It may be observed, however, that the departures affect the relative numbers of the two sexes as much as those of the varieties, and of course the scheme presupposes numerical equality between the output of males and females in each case. Curiously enough in the first series of the *Grossulariata* experiments, similarly wide departures from this equality were observed,[*] though in the later series the numbers showed fair simplicity and steadiness. We have as yet no clue to the meaning of these larger fluctuations, which are repeatedly encountered, when the output of the sexes is observed under experimental conditions.

We have to thank Professor Bateson for his help and advice. The expenses are in part defrayed by a grant from the Government Grant Fund.

CORRIGENDA TO REPORT III.

Page 20. In pedigree at top, for ♂ 253 read ♂ 144.
,, 20. Delete note at bottom of page.
,, 23. In Exp. 200, for "r.s. × r.r." read "s. × r.r."
,, 29. In Exp. 378 the figure 31 should come under the column headed p. instead of under that headed s.

By an unfortunate mistake it is stated in Report III that *two separate factors* are concerned in producing hoariness besides those which produce colour. The error arose through a misinterpretation made in earlier stages of the analysis, which was carelessly retained after each of the results on which it was based had been otherwise elucidated. The diagrams of tables there given are correct otherwise, and show clearly that *one* hoariness-factor is required in addition to the two colour-factors.

We are indebted to Mr. Doncaster for this important correction.

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[*] Doncaster and Raynor, 'P.Z.S.,' 1906, vol. 1, pp. 130—131.

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