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SIMPLIFIED SOLUTIONS OF CERTAIN MEN-
DELIAN PROBLEMS IN WHICH FACTORS
HAVE INSEPARABLE EFFECTS.

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XXXVI.

SIMPLIFIED SOLUTIONS OF CERTAIN MENDELIAN PROBLEMS IN WHICH FACTORS HAVE INSEPARABLE EFFECTS.

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IN a paper entitled "Unsound Mendelian Developments, especially as regards the Presence and Absence Theory," published in the Proceedings of this Society in December, 1912, it was shown that, when the effects of different factors are inseparable, the results obtained from two or more crosses in which the same pair of factors is operating can be combined and the relations between factors which are not operating together determined. For the proof then given a simpler can now be substituted. The following are the necessary observations and deductions from Mendel's work, which hold so long as the characters dealt with are related to each other as dominants and recessives and each pair is distributed independently of the others:—

(1) If the original parents differ in n pairs of characters, then 2^n gives the number of groups into which their hybrids' progeny can be divided, and $(3 + 1)^n$ the ratio in which the groups stand to each other numerically.

(2) Conversely, if their hybrids' progeny consist of 2, 4, 8, 16 . . . 2^n groups, the numbers in which are numerically in the ratio $(3 + 1)^n$, then the original parents differed in n pairs of characters.

(3) If the original parents differ in 1, 2, 3 . . . n pairs of characters, then the characters borne by, and the proportionate numbers in, the groups in their hybrids' progeny are:—

When the parents differ

In one pair.	In two pairs.	In three pairs.	
3 X	9 X Y	27 X Y Z	
1 x	3 X y	9 X Y z	
	3 x Y	9 X y Z	
	1 x y	9 x Y Z	
		3 X y z	
		3 x Y z	
		3 x y Z	
		1 x y z	and so on.

(4) The same results follow whether one parent carries all the dominants and the other all the recessives; or the dominants and recessives are carried some by one parent, some by the other. For instance, the same kind of hybrid is produced whether the parents carry the characters XY and xy , or Xy and xY .

(5) The hybrids carry all the dominants of the pairs in which their parents differed.

(6) In the hybrids' progeny the numerically largest group carries all the dominants; the groups next in size carry one dominant less; those next in size again still one less; and so on down to the smallest group which carries all the recessives but no dominants.

(7) In the hybrids' progeny the largest group differs from the smallest in n pairs of characters, each differs from the groups next them in one pair less, and so on. At the same time, the intermediate groups differ among themselves in definite numbers of pairs of characters, which can be ascertained by examining any typical set. For instance, in the two-pair set of four groups

9 $X Y$
 3 $X y$
 3 $x Y$
 1 $x y$

the first and last groups differ from each other in two pairs of characters, and each differs from the two middle groups in one pair. At the same time, the middle groups differ from each other in two pairs.

(8) Each character in which the parents differ appears in half the groups of their hybrids' progeny precisely. In the two-pair set of four groups, X appears in two groups, and, in the three-pair set of eight groups, X appears in four groups. Thus, if any character be carried by more than half the groups in a set, it must be carried by all. If, for instance, the third group in the two-pair set

9 $X Y Z$
 3 $X y Z$
 3 $x Y$
 1 $x y Z$

did not carry Z , it would differ from the first and last groups in more pairs than one and from the other middle group in more pairs than two.

(9) If one or more of the groups in a set of hybrids' progeny carry any character outside those producing the set, that character is common to all the groups in the set. If, for instance, the last group in the following set carried Z and the other three groups did not, then the last group would

differ from the first in more than two pairs of characters and from the two middle groups in more than one:—

9 $X Y$
 3 $X y$
 3 $x Y$
 1 $x y Z$.

The experiments dealt with first in the previous paper were those carried out by Miss Durham on the colours of mice. It will be convenient to consider them first again, and to consider two other important examples after. The details of Miss Durham's experiments are to be found in the fourth "Report to the Evolution Committee of the Royal Society" and in the first volume of the "Journal of Genetics."

In Miss Durham's first experiment, agouti-coloured mice were mated with chocolates, and their hybrids' progeny consisted of agoutis, cinnamon agoutis, blacks, and chocolates in the ratio 9 : 3 : 3 : 1. Since there are 2^2 (i.e. 4) groups numerically in the ratio $(3 + 1)^2$, there are two pairs of characters concerned; and, since the effects of the factors producing them are inseparable, the four groups can only be set down with "unknown" symbols, thus:—

Agouti, 9 $X Y$
 Cinnamon agouti, 3 $X y$
 Black, 3 $x Y$
 Chocolate, 1 $x y$

In Miss Durham's second experiment, black was mated with a fifth colour, silver fawn, and their hybrids' progeny consisted of blacks, blues, chocolates, and silver fawns in the ratio 9 : 3 : 3 : 1. By being at the top of a set of four groups black is shown to be carrying two dominants. One may be Y , revealed in the first experiment, but both may be new. Assume that both are new. Then the characters carried by the four groups in the second experiment should be, say—

Black, 9 $Z A$
 Chocolate, 3 $Z a$
 Blue, 3 $z A$
 Silver fawn, 1 $z a$.

In that case the characters carried by black and chocolate, as revealed by the two experiments, should be—

Black, $x Y Z A$
 Chocolate, $x y Z a$.

But this makes black and chocolate differ from each other in two pairs of characters, while the first experiment showed them to differ in one pair only. Thus black carries only one new dominant, say *Z*, which, since it is outside the characters concerned in the first set, must also be carried by the three remaining groups. The characters carried by the four groups are now therefore—

Agouti,	.	.	.	9	<i>X</i>	<i>Y</i>	<i>Z</i>
Cinnamon agouti,	.	.	.	3	<i>X</i>	<i>y</i>	<i>Z</i>
Black,	.	.	.	3	<i>x</i>	<i>Y</i>	<i>Z</i>
Chocolate,	.	.	.	1	<i>x</i>	<i>y</i>	<i>Z</i>

Since *Y* and *Z* are the characters carried by black at the top of the second set, the two pairs concerned are *Y* and *y*, and *Z* and *z*, and, since the characters borne by black and chocolate and the positions in the set of blue and silver fawn are already known, we may write down the set as follows:—

Black,	.	.	.	9	<i>x</i>	<i>Y</i>	<i>Z</i>
Blue,	.	.	.	3		<i>Y</i>	<i>z</i>
Chocolate,	.	.	.	3	<i>x</i>	<i>y</i>	<i>Z</i>
Silver fawn,	.	.	.	1		<i>y</i>	<i>z</i>

But, since it is outside the characters in the set and is carried by both black and chocolate, *x* must also be carried by the two remaining groups, blue and silver fawn.

It is now obvious that there are three pairs of characters and eight different combinations, all of which may now be set down along with the colours of such as have been identified:—

Agouti,	.	.	.	27	<i>X</i>	<i>Y</i>	<i>Z</i>
	.	.	.	9	<i>X</i>	<i>Y</i>	<i>z</i>
Cinnamon agouti,	.	.	.	9	<i>X</i>	<i>y</i>	<i>Z</i>
Black,	.	.	.	9	<i>x</i>	<i>Y</i>	<i>Z</i>
	.	.	.	3	<i>X</i>	<i>y</i>	<i>z</i>
Blue,	.	.	.	3	<i>x</i>	<i>Y</i>	<i>z</i>
Chocolate,	.	.	.	3	<i>x</i>	<i>y</i>	<i>Z</i>
Silver fawn,	.	.	.	1	<i>x</i>	<i>y</i>	<i>z</i>

The two unfound colours could have been found by a cross between the first and the last or between any other two differing in three pairs of characters, but Miss Durham found them by two separate crosses between colours differing from each other in two pairs of characters.

Agouti was mated with blue, and their hybrids' progeny consisted of agoutis, dilute agoutis, blacks, and blues in the ratio 9 : 3 : 3 : 1. The

characters carried by three of these colours are already known, and, if we set down the set of four with the three known combinations, we shall readily infer the characters carried by the fourth group:—

Agouti,	9	$X Y Z$
Dilute agouti,	3	
Black,	3	$x Y Z$
Blue,	1	$x Y z$

Since it is carried by more than half the groups in the set, Y must be carried by all. The differentiating characters are therefore X and x and Z and z , and, since three of the combinations they can form, namely XYZ , xYZ , and xYz , are already appropriated, the remaining combination must belong to dilute agouti, whose three characters are therefore XYz .

In Miss Durham's final experiment cinnamon agouti and silver fawn were mated, and their hybrids' progeny consisted of cinnamon agoutis, dilute cinnamon agoutis, chocolates, and silver fawns in the ratio 9 : 3 : 3 : 1. If we again arrange these four groups in the usual order with the characters of the three which are already known set down against them, we shall be able to infer the characters carried by the fourth:—

Cinnamon agouti,	9	$X y Z$
Dilute cinnamon agouti,	3	
Chocolate,	3	$x y Z$
Silver fawn,	1	$x y z$

Since it is common to three groups, y must also be carried by the fourth. The differentiating characters in the set are therefore X and x and Z and z , and, since three of the four possible combinations are already appropriated, the remaining combination Xyz must belong to dilute cinnamon agouti.

Thus the complete set of eight groups consists of—

Agouti,	27	$X Y Z$
Dilute agouti,	9	$X Y z$
Cinnamon agouti,	9	$X y Z$
Black,	9	$x Y Z$
Dilute cinnamon agouti,	3	$X y z$
Blue,	3	$x Y z$
Chocolate,	3	$x y Z$
Silver fawn,	1	$x y z$

In parts of the country where tame rabbits have become feral, black young are sometimes found in the nests of wild grey parents. Thus grey

seems dominant to black. In the course of his experiments recorded in the "Journal of the Linnean Society" for 1904, Mr. C. C. Hurst bred both black and grey rabbits which bred true, and, when they were mated, their hybrids were grey, while their hybrids' progeny were greys and blacks in the ratio 3 : 1 (actually 38 and 10). Thus the previous inference is confirmed, and black and grey seem each the result of single factors.

But later experiments by Professor Castle of Harvard—a statement of whose work is to be found in "Science" for 1907, new series, vol. xxvi—show this conclusion to be erroneous. He dealt with six colours which he divided in two groups according as they were judged to be produced by or without certain pigments. Two different pigments and a factor which affected their localization were judged to be producing the following six colours (*B* stands for black pigment, *Y* for yellow, and *A* for the localization factor) :—

Series I.			Series II.		
Grey,	<i>B</i>	<i>Y A</i>	Black,	<i>B</i>	<i>Y</i>
Blue-grey,	<i>B</i> (dilute)	<i>Y A</i>	Blue,	<i>B</i> (dilute)	<i>Y</i>
Yellow, ¹	<i>B</i> (traces)	<i>Y A</i>	Tortoiseshell, ²	<i>B</i> (traces)	<i>Y</i> .

Among the six colours Professor Castle found the following Mendelian relations :—

- (1) Grey is dominant to blue-grey, black, and yellow.
- (2) Blue-grey is dominant to blue.
- (3) Black is dominant to blue and tortoiseshell.
- (4) Yellow is dominant to tortoiseshell.
- (5) Grey is produced by mating black with either yellow or blue-grey.

Since it is dominant to three different colours, grey must be the result of three different factors at least, and since they are intermatable, so also must the other five colours. There should therefore be three pairs of factors in operation, and eight different colours in all. Since blue-grey, black, and yellow differ each from grey in one pair of characters, the first four groups in the set are determined at once, namely—

Grey,	.	.	.	.	27	<i>X Y Z</i>
Blue-grey,	.	.	.	.	9	<i>X Y z</i>
Black,	.	.	.	.	9	<i>X y Z</i>
Yellow,	.	.	.	.	9	<i>x Y Z</i> .

¹ and ²; these are the English equivalents of white-bellied yellow and sooty yellow.

But the characters carried by blue and tortoiseshell can also be determined. Blue is recessive to both blue-grey and black, and therefore differs from each in one pair of characters. Thus it carries one dominant less. This dominant cannot be Z , for then blue would differ from blue-grey in three pairs of characters. Nor can it be Y , for then blue would differ from black in three pairs of characters. It can only be X , and the characters carried by blue are therefore Xyz . For similar reasons the characters carried by tortoiseshell must be xyZ . Thus the complete set of eight with the colours so far identified as belonging to six of the possible combinations is

Grey,	.	.	.	.	27	X	Y	Z
Blue-grey,	.	.	.	.	9	X	Y	z
Black,	.	.	.	.	9	X	y	Z
Yellow,	.	.	.	.	9	x	Y	Z
Blue,	.	.	.	.	3	X	y	z
	.	.	.	.	3	x	Y	z
Tortoiseshell,	.	.	.	.	3	x	y	Z
	.	.	.	.	1	x	y	z .

The two unfound colours could be found by mating blue-grey with tortoiseshell or yellow with blue.¹

The same conclusion is arrived at by the same line of argument as that previously taken with the mice. The six colours found can be arranged in two sets of four groups each. In a set of four groups the largest is dominant to both the intermediate groups, and each of these is dominant to the smallest. By this method of identification the two sets become, with provisional symbols,

	1		2	
Grey, . .	9	X Y	Grey, . . . 9	A B
Black, . .	3	X y	Blue-grey, . . . 3	A b
Yellow, . .	3	x Y	Black, . . . 3	a B
Tortoiseshell, . .	1	x y	Blue, . . . 1	a b .

By being at the top of two sets, grey must carry three dominants at least, and perhaps four. But, since black appears in both sets, grey can carry only three, for if it carried four the characters of grey and black would be $XYAB$ and $XyaB$, and then the two colours would differ from each other in more

¹ It is probable that blue-grey and blue are merely different names for the first two colours in a set of four found by Professor Punnett and called by him cinnamon, chocolate, dilute cinnamon and orange. (*Journal of Genetics*, Nov. 1912.) In that case dilute cinnamon and orange would bear the characters xYz and xyz .

than one pair of characters. If we call the third dominant Z , then the characters carried by the first set of four groups are

Grey,	.	.	.	.	9	X	Y	Z
Black,	.	.	.	.	3	X	y	Z
Yellow,	.	.	.	.	3	x	Y	Z
Tortoiseshell,	.	.	.	.	1	x	y	Z

Blue-grey differs from grey in one pair of characters. There are only three possible combinations which fulfil this condition, namely, XYz , XyZ , and xYZ , but, as the last two are already appropriated by black and yellow, the remaining one, XYz , must belong to blue-grey.

The characters belonging to three of the groups in the second set are now known, and, if we write down the four groups with the characters of the three already known, we shall be able to infer the characters belonging to the fourth:—

Grey,	.	.	.	.	9	X	Y	Z
Blue-grey,	.	.	.	.	3	X	Y	z
Black,	.	.	.	.	3	X	y	Z
Blue,	.	.	.	.	1			

By being common to three groups, X must be common to all four, and the differentiating characters in the set are therefore Y and y , and Z and z . The only combination left for blue to carry is Xyz . This is precisely the same result as before, and again the two unfound colours belong to the combinations xYz and xyz .

Still another example might be considered—more especially as it has received a different interpretation—in which the distribution of the characters is obscured by some of the factors having inseparable effects and also by the effects of certain factors being suppressed by those of others. This is the well-known example of the fowls' combs. Rose-combed fowl were mated with pea-combed, and, while their hybrids had walnut-shaped combs, their hybrids' progeny had four different kinds: walnuts, roses, peas, and singles in the ratio 9 : 3 : 3 : 1. Since there are four groups in the usual proportion, there are two pairs of characters, but since the effects of the factors are inseparable, the set must be set down with "unknown" symbols, thus:—

Walnut,	.	.	.	.	9	X	Y
Rose,	.	.	.	.	3	X	y
Pea,	.	.	.	.	3	x	Y
Single,	.	.	.	.	1	x	y

There is another kind of comb carried by a Dutch breed of fowl, called the Breda, which is described as having "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." Yet these combless fowl carry a factor which suppresses the effects of other factors and another which has the effect of splitting real combs in two.

The Breda comb was mated with both rose and single combs. When mated with the single comb their hybrid had "a large double comb formed as two divaricating singles." From this result four factors can be assigned to the single comb and four to the Breda. The single comb is already known to carry the characters x and y ; but, since it produces a real comb when mated with the rudimentary Breda, it must carry a factor for the production of a real comb which is dominant to a factor for the rudiment of a comb in the Breda; and, since it produces a split comb when mated with the Breda, it must also carry a factor for an unsplit comb which is recessive to a factor for producing a split comb in the Breda. If we designate these new pairs of characters R = real comb, r = rudimentary, S = split, and s = unsplit, then the characters carried by the single comb are now, $xyRs$. The Breda comb carries the characters r and S , and it must also carry x and y , for, did it not do so, its hybrid with a single comb would have been something else than a single.

Thus there are now four pairs of characters connected with fowls' combs, and the full set of sixteen groups of hybrids' progeny might be set out with the kind of comb belonging to each combination predicted.

When the Breda comb was mated with the rose comb, "the resulting combs were all duplex roses." Here again the two previously unknown dominants are brought to light, namely, that for a real comb carried by the rose comb, and that for splitting which must have been carried by the Breda comb. When the hybrids were bred from, their progeny were counted into six groups only, but, as there were more than four groups, there must have been at least eight real groups, some of which were inseparable through the action of the suppressing rudimentary factor brought in by the Breda. The rose comb carries the factors $XyRs$, the Breda comb the factors $xyrS$. Thus the two differ in three pairs of characters, and their hybrids' progeny should have consisted of the eight groups which can be formed by combining the three pairs of characters X and x , R and r , and S and s , in all the ways

possible consistent with the action of dominance. The eight real groups and the six which were found are as follows:—

ACTUAL.		FOUND.
27	Split rose comb,	Split rose comb.
9	Split single comb,	Split single comb.
9	Unsplit rose comb,	Unsplit rose comb.
9	Unsplit single comb,	Unsplit single comb.
3	Split Breda comb with rose suppressed,	Split Breda comb.
3	Split Breda comb with single suppressed,	
3	Unsplit Breda comb with rose suppressed,	Unsplit Breda comb.
1	Unsplit Breda comb with single suppressed,	

The ordinary single comb was mated with still another comb which was brought from Cairo. This comb was itself a single comb, excepting that it was split in two, and, by its progeny with the ordinary unsplit comb, it "proved to be a distinct dominant over single comb." It therefore carried the characters $xyRS$.

Thus there are at least four pairs of characters distributable among fowls' combs; and the complete set of sixteen groups may now be set down with the kinds of combs producible and the ordinary names of such as have been found indicated:—

- 81 $X Y R S$ Walnut comb, split
- 27 $X Y R s$ Walnut comb, unsplit (*ordinary walnut*)
- 27 $X Y r S$ Walnut rudiment, split
- 27 $X y R S$ Rose comb, split
- 27 $x Y R S$ Pea comb, split
- 9 $X Y r s$ Walnut rudiment, unsplit
- 9 $X y R s$ Rose comb, unsplit (*ordinary rose*)
- 9 $X y r S$ Rose rudiment, split
- 9 $x Y R s$ Pea comb, unsplit (*ordinary pea*)
- 9 $x Y r S$ Pea rudiment, split
- 9 $x y R S$ Single comb, split (*the Cairo comb*)
- 3 $X y r s$ Rose rudiment, unsplit
- 3 $x Y r s$ Pea rudiment, unsplit
- 3 $x y R s$ Single comb, unsplit (*ordinary single*)
- 3 $x y r S$ Single rudiment, split (*the Breda comb*)
- 1 $x y r s$ Single rudiment, unsplit.

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