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UN SOUND MENDELIAN DEVELOPMENTS,
ESPECIALLY AS REGARDS THE PRESENCE
AND ABSENCE THEORY.

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[*Authors alone are responsible for all opinions expressed in their Communications.*]

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XXVII.

UN SOUND MENDELIAN DEVELOPMENTS, ESPECIALLY AS
REGARDS THE PRESENCE AND ABSENCE THEORY.

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IN this paper it is proposed to show—

- i. That the Presence and Absence theory is unsound.
- ii. That it leads to erroneous conclusions.
- iii. That phenomena to which it has been applied can be analysed by ordinary Mendelian formulæ.

To do this it will be necessary first of all to state some part of the Mendelian position, and to show how formulæ are used in analysis. It is that there are factors or determinants for every character. The characters of similar parents may be represented thus:—

MALE.	FEMALE.
. <i>rqp</i>	<i>pqr</i>

The factors which such parents produce to be handed on to their progeny may be represented thus:—

MALE.	FEMALE.
. <i>ppp</i>	<i>ppp</i>
. <i>ppp</i>	<i>ppp</i>
<hr/>	<hr/>
. <i>qqq</i>	<i>qqq</i>
. <i>qqq</i>	<i>qqq</i>
<hr/>	<hr/>
. <i>rrr</i>	<i>rrr</i>
. <i>rrr</i>	<i>rrr</i>
<hr/>	<hr/>
. &c.	&c.

Being compelled to select similar semi-factors from each parent, the progeny must bear characters similar to those borne by the parents, and must breed true.

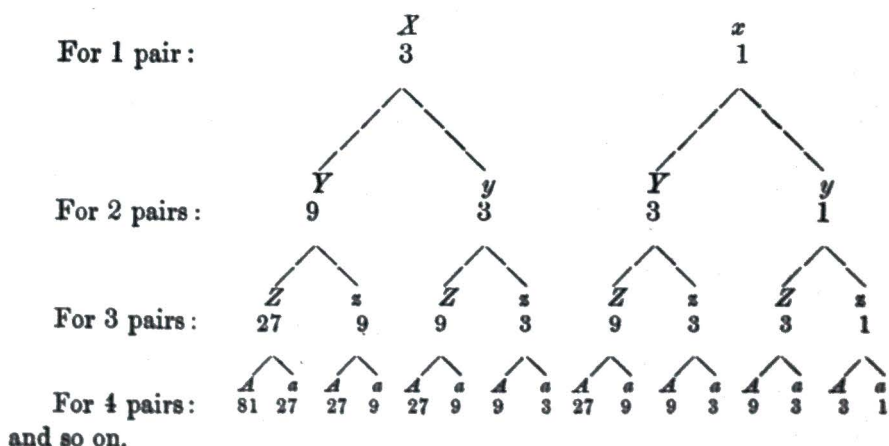
If, however, the parents are not similar, but differ in one or more pairs of alternative characters, the progeny will receive mixed factors from their parents, and will not breed true as regards the differentiating characters, though they will breed true as regards the others.

If the parents differ in one pair of alternative characters, and we represent the dominant by X and the recessive by x , the progeny of their progeny, i.e., their second crosses, split into two groups, one bearing X and the other x , and the number of individuals in the group bearing X is to the number in the group bearing x in the ratio 3 : 1.

If the parents differ in a second pair of alternative characters, say, Y and y , the group bearing X on the one hand and that bearing x on the other split each into two further groups, one bearing Y and the other y ; and the numbers bearing Y are to those bearing y as 3 : 1. Thus there are four groups altogether, one bearing the characters XY , another Xy , another xY , and another xy , and the numbers of individuals in these groups are in the ratio 9 : 3 : 3 : 1.

For every additional pair of alternative characters in which the parents differ, the number of groups into which their second crosses divide is doubled—for one pair there are two groups, for two pairs four groups, for three pairs eight groups, and so on—and the proportional numbers in each group expand in accordance with a well-known mathematical formula.

This can be shown diagrammatically:



If we consider by way of example the case for three pairs of characters, we see that there are eight groups of second crosses; and if we follow the

forking lines from X and x downwards, we see that these eight groups bear the following characters, while the numbers in each are shown by the figures attached, viz., 27 XYZ , 9 XYz , 9 XyZ , 3 Xyz , 9 xYZ , 3 xYz , 3 xyZ , 1 xyz .

The following table shows how the groups and the numbers of individuals in each expand up to the case in which ten pairs of characters are considered:—

NUMBER OF GROUPS.

Number of individuals in each group.	For 1 pair.	For 2 pairs.	For 3 pairs.	For 4 pairs.	For 5 pairs.	For 6 pairs.	For 7 pairs.	For 8 pairs.	For 9 pairs.	For 10 pairs.
1	1	1	1	1	1	1	1	1	1	1
3	1	2	3	4	5	6	7	8	9	10
9		1	3	6	10	15	21	28	36	45
27			1	4	10	20	35	56	84	120
81				1	5	15	35	70	126	210
243					1	6	21	56	126	252
729						1	7	28	84	210
2187							1	8	36	120
6561								1	9	45
19683									1	10
59049										1
Total number of groups =	2	4	8	16	32	64	128	256	512	1024

Reading from the top of the columns of figures downwards, the top groups (always containing one individual) carry every recessive operating in the case; the next groups (of three individuals) carry $n - 1$ of the recessives and one dominant; the next groups (of nine individuals) carry $n - 2$ recessives and two dominants, and so on. Reading from the bottom upwards the same rule holds, if dominants be substituted for recessives and recessives for dominants.

The table will indicate how difficult it is to deal, experimentally or otherwise, with cases in which more than three or four pairs of characters are considered.

The chief uses of the foregoing formulæ are three, viz., (1) to tell how many groups are formed, with the proportionate numbers of individuals in each, by the second crosses from two individuals differing in one or more pairs of alternative characters; (2) conversely, to tell, from the numbers of groups of second crosses and the proportionate numbers in each, in how many pairs of alternative characters the original parents differed; and (3) to indicate which characters are alternatives and how the two characters in a pair stand to each other as regards dominance and recessiveness.

Let us consider several examples, by way of illustration; and, since they

must be either familiar or readily imagined, we shall take them from domestic animals rather than from plants.

Take first the formula for one pair of characters, viz.,

$$X : x = 3 : 1.$$

A set of second-cross cattle may be divided into two groups by reason of their colours, which are black and red, in the ratio 3 : 1. The formula tells us that, in this case, there is one pair of differentiating characters, namely, black and red, and that these colours are an alternative pair with black dominant and red recessive. It tells us that the grandparents of the second crosses were black on the one side and red on the other. It can be inferred readily that a factor whose function is to produce blackness produces the black character, and another whose function is to produce redness produces the red.

Take next the formula for two pairs of characters, viz.,

$$X : X : x : x$$

$$Y : y : Y : y$$

$$9 : 3 : 3 : 1$$

Another set of second-cross cattle may be divided into four groups by reason of their colour and their horns. The groups are—black and hornless, 9; black and horned, 3; red and hornless, 3; red and horned, 1. The formula tells that there are two pairs of characters concerned, that both dominants are shown by the group of nine, one dominant and the remaining recessive by each group of three, and both recessives by the group of one. Thus the two alternative pairs are blackness and redness on the one hand, and hornlessness and hornedness on the other: the first-named being dominant in each case. The formula cannot tell whether the grandparents were similar to the two end or to the two middle groups, since the same result could come from either mating. As in the previous case, the characters and the factors which produce them are obvious.

Take next the formula for three pairs of characters, viz.,

$$X : X : x : X : X : x : x : x$$

$$Y : Y : Y : y : y : Y : y : y$$

$$Z : z : Z : Z : z : z : Z : z$$

$$27 : 9 : 9 : 9 : 3 : 3 : 3 : 1$$

Still another set of second-cross cattle may be divided into eight groups by reason of their colour, their horns, and their faces. The differentiating characters in the groups and the numbers of individuals in each are—black, hornless, and white-faced, 27; black, hornless, and black-faced, 9; red,

hornless, and white-faced, 9; black, horned, and white-faced, 9; black, horned, and black-faced, 3; red, hornless, and red-faced, 3; red, horned, and white-faced, 3; red, horned, and red-faced, 1. According to the formula there are three pairs of characters concerned in the case. The three dominants are exhibited in the group of twenty-seven, two dominants and the third recessive in each group of nine, one dominant and the two remaining recessives in each group of three, and the three recessives in the group of one. In each group of nine the recessive which is shown is the alternative of the dominant which is not shown. In each group of three the dominant which is shown is the alternative of the recessive which is not shown. Thus the three dominants in this case are blackness, hornlessness, and white-face, while their three corresponding recessives are redness, hornedness, and normal face: normal face being that in which the face colour is the same as that of the body. As in the previous cases, there is no difficulty in identifying the characters and the nature of the factors to which they are due. That being so, we may set down this case, just as the typical one for three pairs of characters was set down, with letters indicating the characters concerned instead of the unknowns, $XxYyZz$.

B = black.

r = red.

P = hornless or polled.

h = horned.

W = white-faced.

n = normal-faced.

To make the descriptions of the groups clearer we shall range them across the page thus:—

27 $B P W$: Black, polled, white-faced.

9 $B P n$: Black, polled, normal-faced.

9 $r P W$: Red, polled, white-faced.

9 $B h W$: Black, horned, white-faced.

3 $B h n$: Black, horned, normal-faced.

3 $r P n$: red, polled, normal-faced.

3 $r h W$: red, horned, white-faced.

1 $r h n$: red, horned, normal-faced.

But many cases have been found since the Mendelian method of analysis came into use in which the interacting characters have been difficult to identify. One of the first was that of fowls' combs. When rose and single combs were mated the first crosses were all roses, and the second crosses roses and singles in the ratio 3 : 1; and, when pea and single combs were mated, the first crosses were all peas, while the second crosses were peas and singles in the ratio 3 : 1. From this it was inferred that the rose and pea combs

were each dominant to the single, and it was expected that either rose or pea would be dominant the one to the other—"that either rose or pea would dominate in the hybrids, and that the F_2 generation" (i.e. the second crosses) "would consist of dominants and recessives in the ratio 3 : 1." But the expectation was not fulfilled, for, when rose and pea were mated, their first crosses were a new kind of comb—walnut—and their second crosses consisted of four kinds, namely, walnut, rose, pea, and single—also new—in the ratio 9 : 3 : 3 : 1. This ratio shows that there are really two pairs of alternative characters concerned in the case. The characters and their factors may be difficult to identify, and, because of this difficulty, they can be represented in the meantime by unknown symbols only. By so representing them, we may be able to trace the connections between some of the determinants and to get some idea of their effects. The formula to meet the case is:—

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

No single character can be identified, nor can the effect of any factor be told. All that can be said is that walnut results with the concurrence of X and Y, rose with X and y, pea with x and Y, and single with x and y. Nor can it be said how far any factor is responsible for the character produced. How far X or how far Y, for instance, is responsible for walnut there is no evidence to show. And no more can it be said, since each is the result of more than one factor, that rose or pea is dominant the one to the other, or that either is dominant to single. What can be said is that a factor in the rose-comb is dominant to a factor in the single, and a factor in the pea is dominant to another factor in the single.

But from matings between some of these combs and another kind—the Breda—further information can be gathered. The fowl with this comb "is usually spoken of as combless, for the place of the comb is taken by a covering of short bristle-like feathers. In reality it possesses the vestige of a comb in the form of two minute lateral knobs of comb-tissue."² When this comb is mated with rose on the one hand, or single on the other, the first crosses have two points in common. The progeny of the roses are still roses, but split in two; and the progeny of the singles are still singles, but also split in two. The Breda comb, therefore, carries a factor for splitting or duplicity which is dominant to a factor for non-splitting or simplicity carried by both the rose and single combs. Then, if we represent the duplicity

¹ Punnett's *Mendelism*, 3rd ed., p. 29.

² *Idem*, p. 35.

factor by D , and the simplicity factor by s , the factorial constitutions of pure rose and pure single, so far as we now know them, may be written down in the customary manner as $XXyyss$, and $xyyyss$.

But the matings with the Breda comb show another pair of factors. The rose and single combs are both of some size, while the Breda comb is merely a vestige; and the first crosses of the two former with the Breda are also of some size. Thus, the rose and single combs each carry a factor which allows or causes to be produced a comb of some size, while the Breda carries a factor which is responsible for nothing but the vestige of a comb; and, since the first crosses are of the size of rose and single, the size factor is dominant to the vestige factor. Then, if we represent the former by C , and the latter by v , the constitutions of pure rose and single combs should now be written down $XXyyssCC$, and $xyyyssCC$.

From the same matings the constitution of the Breda comb can also be found. We have seen already that it contains D and v . It can also be shown to contain x and y . Let us go back to the typical examples chosen from cattle. In the third example from cattle differing in three pairs of characters, there were a group black, polled, and white-faced, and another red, horned, and normal-faced. But these two groups had many other characters besides—how many we do not know—in none of which they differed. The characters of these two groups may therefore be written down

$B P W p q r$ in the one case, and
 $r h n p q r$ in the other.

Some of the characters pqr are dominant, some recessive to other characters in other cattle; but most of them are the same as in other cattle. There can be no doubt, however, that pqr are common to both the above groups, else their second crosses would have differed in more than three pairs of characters. Thus it must not be assumed that, when two groups differ in one or more pairs, they have no other characters than those in which they differ. If one group is dominant to another in the way the rose comb is dominant to the single, it must not be assumed that the two groups are each the result of only one factor: that they have no other factors. The real state of affairs is that they may have many others, but, when sufficient crossing brings out no differences, these others (so far as they are mateable) are the same for both groups.

When the Breda comb was mated with the single, the first cross was a split or duplex single comb. The factor for duplicity had effect, but the vestigial factor had no apparent effect. The factors x and y of the single comb also had effect, since the result was still what we call a single comb

though split in two. Thus the Breda comb carried either factors that were recessive to x and y , or the factors x and y themselves. The first crosses of the Breda and single mating were not mated again, and so no second crosses were produced by which this point could be decided.

But from the rose and Breda matings, half the doubt can be decided. There were single combs in the second crosses. Where did they come from? The constitution of the rose parent was $\bar{X}XyyCCss$, and of the Breda, so far as yet known, $rrDD$. From these a single comb, whose constitution we know to be $xyyyCCss$, was bred. The factor xx was not contained by the rose-combed parent, and must therefore have been carried and brought in by the Breda, whose constitution, therefore, must be at least $xrrrDD$. As to whether it also contains yy , there is no direct proof; but the fact that it contains xx , together with the further fact that its progeny when mated with the single comb are apparently different in no way from single, except in duplicity, is very strong presumptive evidence that it does. If a mere opinion were expressed, it would be that the constitution of the Breda comb is $xyyyrrDD$. The matter cannot be settled absolutely until second crosses are bred from Breda with pure pea or walnut, neither of which contains yy .

It may be pointed out, however, that there is further presumptive evidence in support of the above opinion. If it be correct, the constitutions of all the combs discussed should be at least when pure:—

Single	. . .	xx	yy	CC	ss .
Rose	. . .	$\bar{X}\bar{X}$	yy	CC	ss .
Pea	. . .	xx	YY	CC	ss .
Walnut	. . .	$\bar{X}\bar{X}$	YY	CC	ss .
Breda	. . .	xx	yy	rr	DD .

The rose comb and the Breda were crossed. On the assumption that the constitution of the Breda, as given in the above table, is correct, then the rose and Breda differ in three pairs of characters; and, in their second crosses, there should be eight groups with the usual numbers in each, and with the pure individuals showing these constitutions:—

$\bar{X}\bar{X}$	yy	CC	DD	:	Duplex roses,	. . .	27
$\bar{X}\bar{X}$	yy	CC	ss	:	Simplex roses,	. . .	9
$\bar{X}\bar{X}$	yy	cc	DD	:	Combless duplex roses,	. . .	9
xx	yy	CC	DD	:	Duplex singles,	. . .	9
$\bar{X}\bar{X}$	yy	rr	ss	:	Combless simplex singles,	. . .	3
xx	yy	CC	ss	:	Simplex singles,	. . .	3
xx	yy	rr	DD	:	Combless duplex singles,	. . .	3
xx	yy	rr	ss	:	Combless simplex singles,	. . .	1

This result corresponds with the results given in Professor Punnett's "Mendelism,"¹ excepting that there the combless fowl are all lumped together as "Bredas," and the numbers of individuals in each group are not given. Had the Bredas been grouped and counted, the evidence would have been complete. As it is, it is very strongly presumptive that the constitution assumed for the Breda is correct. In any case the foregoing is an example of how the Mendelian formulæ may be applied, and may help us to follow the working of the presence and absence theory.

Unfortunately this theory has not yet been fully explained. It has, however, been used frequently for analytical purposes, and, from statements made in cases in which it has been so used, its general purport can be made out; but, since the underlying logic has not been exhaustively expounded, the principle desired to be established may be difficult to find.

The theory originated at the time the fowls' combs were being studied, and was first used to explain the experimental results in that case, which seemed unusual. Its authors took a different view from that taken in this paper as to the factors concerned in the production of rose, pea, and single combs. Although it seems impossible to think otherwise than that, when a set of second crosses split into four groups standing to each other, as regards the numbers they contain, in the ratio 9 : 3 : 3 : 1, there must be two pairs of differentiating characters concerned, and that each group must bear at least two characters, they took the view that rose, pea, and single comb are each the result of one factor only. Holding this view they saw nothing unusual in the walnut resulting from the mating of rose and pea. It was a compound character, one of a kind "produced by the mutual interaction of factors belonging to distinct allelomorphic systems." The difficulty arose when two first-cross walnut combs mated produced a single comb. How was this to be accounted for? Professor Punnett puts the case thus:—"How are we to express the fact that while single behaves as a simple recessive to either pure rose or to pure pea, it can yet appear in F_2 " (i.e., in the second crosses), "from a cross between those two pure forms, though neither of them should, on Mendel's view, contain the single?"² ("on Mendel's view" ought rather to be on the view that rose and single combs are due to single characters).

The explanation given of the anomaly is that, while walnut is the combined result of the rose and pea factors, and the other combs are each the result of their own individual factors, the single comb emerges from the

¹ p. 37, Diagram

² p. 31.

crossing in the case when the factors for rose and pea are absent. The constitution of the walnut comb is written $RRPP$. That of rose ought to be written RR ; but, in order to indicate that the factor for pea has no hand in the case, i.e., *is absent*, the letter p is added, and the constitution is written $RRpp$. Similarly, to indicate the absence of the factor for rose in its production, the constitution of pea is written $rrPP$. Following these precedents the constitution of single comb ought to be written, say, $SSrrpp$ — SS to denote the factor for single comb, and $rrpp$ the absence of the factors for rose and pea—but it is written $rrpp$. By writing it thus we are not told what does produce the single comb, but what does not; and the danger of rr and pp changing their significance in the course of manipulation is increased by the absence of a positive symbol of some kind to represent the factor for the single comb.

Divided into separate paragraphs to make the reasoning clear, Professor Bateson's statement of the case is as follows:—

1. "A rose comb is not due to an elemental factor which can segregate from the pea comb factor.
2. "The two factors belong to distinct allelomorphic pairs, and each in the gametogenesis of the heterozygote segregates from its own allelomorph, which is simply the absence of the factor in question.
3. "The single comb contains neither R nor P .
4. "The rose comb is a single comb modified by the presence of R , while the pea comb is produced by the presence of P .
5. "We may therefore describe the rose as R no P , and the pea as P no R .
6. "It is convenient to use capital letters for dominants, and small letters for recessives, the rose being written thus, Rp , and the pea rP . The walnut comb is the RP , while rp gives the single."¹

Thus the first two paragraphs affirm rose and pea to be due each to single factors.

The second paragraph states that these factors "segregate" from their own absences. This could be understood if the word "absence" were used metaphorically for real factors alternative to rose and pea; but it is not easy to think of such a thing as a factor segregating from nothing, or, at any rate, from something which is not present.

As already mentioned, the third paragraph tells what the single comb *does not* contain, but not what it *does* contain.

In the fourth paragraph the rose and pea combs become due to something more than R and P , namely, to the effect of the factor for single comb plus

¹ Bateson's "Mendel's Principles of Heredity," p. 66.

that for rose in one case and that for pea in the other. This paragraph is thus inconsistent with the first, and, if it be correct, the descriptions in the next paragraph of rose as " R no P " and pea as " P no R " are incomplete, since they leave out the thing modified by R and P .

One or other of these two statements, viz., that rose is due to a single factor in the first paragraph, or that it is due to more in the fourth, must be wrong.

Consider whether the facts of the case agree with the view that rose and pea combs are each due to single factors. Let RR be the constitution of rose and PP of pea. If RR and PP can be brought in simultaneously to the same comb, they will be brought in either as non-alternative or as alternative factors. In the former case they may have effects that are independent of each other or they may have effects that cannot be separated by the eye the one from the other, but it is difficult to imagine anything being produced in the second crosses but roses and peas and combs the same as the first crosses. On the other hand, if RR and PP are alternatives, their first crosses will be hybrids of the constitution RP , and their second crosses should be of the constitutions RR , RP , and PP in the ratio 1 : 2 : 1. But neither of these results is found in the second crosses from rose and pea. The results do not fit the assumption of hybridization, and, on both assumptions—hybridization and combination—there is a comb produced which has no business to be produced at all. Thus, unless the rose, pea, and walnut second crosses are produced from the first-cross walnuts in some way which allows an extra comb to be produced *ex nihilo*, the assumption that rose and pea combs are each due to single factors must fail.

Consider next whether the assumption holds when the case is dealt with on the presence and absence theory. According to Professor Bateson's sixth paragraph, the constitutions of the four combs, walnut, rose, pea, and single, are $RRPP$, $RRpp$, $rrPP$, and $rrpp$. It must not be forgotten that the small letters merely represent the absence of the factors represented by the large ones. They are merely helps to the memory, and unless as such might as well be absent.

In the case of the single comb, $rrpp$ indicates that it is produced without the assistance of RR or PP . By what, then, is it produced? It must be produced by something, and since RR and PP are both absent, that something must be separate and distinct from both. Causes that are absent can have no hand in producing effects that are present. A cause, by being absent, may allow another cause which it previously obstructed or whose effect it obscured to have effect, but the essential cause of this effect is the one which is present. There being no symbol set down to represent the factor or

factors that produce the single comb, the mnemonics *rr* and *pp* are commandeered instead, and thus are made use of as positive factors. And not only does this happen with the single comb; it happens with other combs also. In the chess-board scheme displaying the presence and absence solution of the problem to be found both in Professor Bateson's and in Professor Punnett's books, the constitutions *Rrpp* (rose) and *rrpP* (pea) are given; and unless the small letters represent positive factors, these two combs are produced by only half a factor—a thing which, so far, has not been found possible, for it would mean that only one parent is necessary. Thus, when the case is dealt with by the presence and absence theory, the assumption that the rose and pea combs are each produced by single factors fails again.

Since the facts of the case which the presence and absence theory was first set up to explain are not as they were taken to be, the theory itself comes under suspicion, and the suspicion is deepened when symbols are used mnemonically at one time and positively at another. A little further consideration will show the theory to be unsound on its own merits, and will bring out the nature of the fallacy.

Doubt has already been raised as to whether a factor could segregate from its own absence. It was raised upon the statement that "the two factors" (i.e. for rose and pea) "belong to distinct allelomorphic pairs, and each in the gametogenesis of the heterozygote segregates from its own allelomorph, which is simply the *absence* of the factor in question." There is no question about a factor "segregating" from its own allelomorph, that is, vacating a position which its allelomorph is about to occupy. The question is, Can a factor's allelomorph be its own absence, and can the factor segregate from its absence?—that is, Can a factor segregate from no factor at all? Unless the word be used figuratively for what has taken the place of the absent factor, the action suggested is impossible. For, when a factor is removed from any position, its place must be taken by something else—and as yet we know of nothing that can do so but another factor—and the only "segregation" possible must take place with that something else. If a book be taken from its shelf, we may say that its absence is left—that the book has "segregated" from its absence—but we can only say so figuratively, for what is really left is air and dust; and, when the book is put back again, we may say that it takes the place of its absence, but we can only say so figuratively.

In dealing with the application of the presence and absence theory to Mendel's peas, Professor Punnett writes¹:—"On this theory the dominant character of an alternative pair owes its dominance to the presence of a factor

¹ Punnett, p. 31.

which is absent in the recessive. The tall pea is tall owing to the presence in it of a factor for tallness, but in the absence of this factor the pea remains a dwarf. All peas are dwarf, but the tall is a dwarf plus the factor which turns it into a tall. Instead of the characters of an alternative pair being due to two separate factors, we now regard them as the expression of the only two possible states of a single factor, viz., its presence or its absence."

Dealing with the general question, Professor Bateson writes that "All observations point to a conclusion of great importance, namely, that a dominant character is the condition due to the *presence* of a definite factor, while the corresponding recessive owes its condition to the *absence* of the same factor."¹

Without doing more than remark that the latter part of Professor Punnett's statement virtually makes the presence and absence theory turn two factors into one, only to be obliged immediately to turn the one factor into two again, it may be said that these two statements are ambiguous. They are open to two interpretations, and unfortunately the worse one is frequently taken. If these statements mean that the long factor turns a short pea's progeny tall, and that on its removal the tall pea's progeny become short again, *but that the short pea is still due to the same cause or causes that made it short before the introduction of the long factor*, there is no ground for quarrel with the statements further than that *they do not state the whole case*. But this is not the usual interpretation put upon them; and the other interpretation, which is probably taken because of the above incomplete statement, is that, while a factor itself is the cause of a dominant character, its absence is the cause of the corresponding recessive. This credits a thing which is absent with the work done by another thing which is present *but overlooked*. The real state of affairs is that the ABSENCE OF THE LONG FACTOR MAY BE THE CAUSE OF THE ABSENCE OF THE LONG CHARACTER, BUT IT IS NOT THE CAUSE OF THE PRESENCE OF THE SHORT.

If long and short peas were crossed and re-crossed again and again so as to produce alternate generations of long and short peas, the view might be taken that the absence of the long factor allowed the effect of the short to become visible, but that would not deprive the short character of its own essential cause. Under such circumstances the absence of the long factor might be regarded as a "condition" necessary to the emergence of the short character; but this does not justify us in preferring this condition as the cause of the production of the short character over a still more essential condition. If a pedestal supporting a bust be knocked away, we are not justified in

¹ Mendel's "Principles," p. 54.

preferring the absence of the pedestal as the cause which brings the bust to the ground and overlooking the action of gravity.

As might be expected, the presence and absence theory, when used for analytical purposes, falls into the error of overlooking real recessives. Being frequently hidden, they are not always readily identified and connected with their proper dominant. Then, when the dominants in a case under analysis are already allotted their own *absences* as their only possible recessives and one or more recessives turn up without their connexion with their dominants being identified, so many more factors are introduced beyond the number which the case can hold. One such case will be sufficient by way of example.

Mr. C. C. Hurst made a long series of experiments with rabbits.¹ He started with what seemed to be only three kinds, namely, grey, black, and albino. But the albinos were found to be of two kinds, and thus he really started with four pure kinds. When greys and blacks were mated, the first crosses were all grey, and the second crosses greys and blacks in the ratio 3 : 1. Thus grey seemed dominant to black. When greys were mated with one albino, the first crosses were all grey, and the second crosses greys and albinos in the ratio 3 : 1. Thus, grey seemed dominant to albino also. But when grey was mated with the other albino, while the first crosses were grey, the second crosses were greys, blacks, and albinos in the ratio 9 : 3 : 4. Thus, while the first two cases indicated that there was only a pair of determinants concerned in each, the last case showed that there were more. In this last case there are presumably two pairs of determinants concerned; but one of the second-cross groups of three is indistinguishable from the group of one. Three of the albinos form one of the two groups of three, and the fourth albino forms the group of one. If this assumption results in a disagreement with the facts, it can be abandoned. Let us find what each determinant stands for. Write down the four groups by name, with the non-committal formula and unknown symbols below :—

9 Grey.	3 Black.	3 Albino.	1 Albino.
<i>X</i>	<i>X</i>	<i>x</i>	<i>x</i>
<i>Y</i>	<i>y</i>	<i>Y</i>	<i>y</i>

At first sight it would appear as if the two dominants were albino and black; but, since albino is carried by the last group, it must be recessive, and, since the same character is carried by the third group, it must be

¹ See Journal of the Linnæan Society, Zoology, vol. xxix, p. 283.

represented by x , which is common to both groups. Its dominant must therefore be X .

It will be noticed that, when X has a chance of showing itself, the rabbits are coloured, while, when x has a similar chance, they are albinos. The difference between X and x is that X is concurrent with colour-production, and x with albinism. It is no unfair assumption, therefore, that, in some way not disclosed, X allows or causes colour to be made, while x does not. Thus, the factor which allows colour to be produced as in the grey is dominant to that which does not allow it to be produced as in the albino.

The factors left over to have effect in the production of some particular colour are Y and y ; and, since grey occurs in the group of nine, and black in the group of three, Y must be the factor connected with grey, and y with black.

Substituting now the initial letters of the words 'colour,' 'grey,' 'black,' and 'albino' for the symbols previously used, we can write down the whole case thus:—

Grey.	Black.	Grey albino.	Black albino.
C	C	a	a
G	b	G	b

And this solution agrees with the facts of the case. The constitutions of the pure individuals in each group are grey $CCGG$, black $CCbb$, grey albino $aaGG$, and black albino $aabb$. One albino contains the factor for greyness, while the other contains that for blackness, just as Mr. Hurst found; and in the first crosses the greys will behave as dominants to all, just as Mr. Hurst found, while the second crosses from all possible pairs will come out in agreement with experimental and other observations, thus:—

1. Grey \times black will give 3 grey : 1 black.
2. Grey \times grey albino will give 3 grey : 1 albino.
3. Grey \times black albino will give 9 grey : 3 black : 3 grey albino : 1 black albino.
4. Black \times grey albino will give the same result.
5. Black \times black albino will give 3 black : 1 albino.
6. Grey albino \times black albino will give albinos only.

The presence and absence theory arrives at a different result. It introduces an extra factor which pushes the factor for blackness out into a new position. The factors employed are—grey (G), absence of grey (g); presence of colour (C), absence of colour (c); and black (B). The factor g

is extra ; and *B*, which was formerly a recessive, is now something common to all. The reason for this divergence is that, since, on the presence and absence theory, the only possible alternative to *G* is its own absence, *g*, there is no alternative left for black but to be pushed out of its place. But this solution is not consistent with the facts of the case, for the factor for blackness was not carried by the original grey parent, nor was it common to all Mr. Hurst's crosses. He showed clearly that it was introduced by one of the albinos. Let us see how the problem is solved on the presence and absence theory. "Applying the presence and absence system to the case of the colours of rabbits, the first pair of allelomorphs can obviously be represented as—

Dominant	Recessive
1. Presence of colour (<i>C</i>).	Absence of colour (<i>c</i>).

The second pair we have so far spoken of as the *grey* determiner and the *black* determiner, regarding the two as allelomorphic to each other. But it is equally possible to describe them thus

2. Grey determiner (<i>G</i>).	Absence of ditto (<i>g</i>).
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Then in the case where grey \times albino gives in *F*² 9 grey : 3 black : 4 albino, we simply have to regard *B*, the black determiner, as common to both parents, and the same numerical result is produced."¹ The error arises through failing to realize that *g* and *B* are the same.

Another solution of the same problem on the presence and absence theory might also be quoted :—"Agouti," i.e. grey, "was previously known to be a simple dominant to black, i.e., an agouti is a black rabbit plus an additional greying factor which modifies the black rabbit into agouti. This factor we will denote by *G*, and we will use *B* for the black factor. Our original agouti and albino parents we may therefore regard as in constitution *GGCCBB* and *ggccBB*." With regard to this statement it might be asked : if agouti, since it is dominant to black, is a "black rabbit plus an additional greying factor," might it not be regarded equally as an albino plus an additional greying factor, since it also "behaves as a dominant to the albino variety?" With regard to the above case, it might be pointed out that in a parallel case, viz., that of colour in pigeons, in which the second crosses were 9 black, 3 blue, 4 white, just as the rabbits were 9 agouti, 3 black, 4 albino, a parallel² solution was not found as it ought to have been.

¹ Bateson, p. 76.

² Punnett, pp. 48 and 60.

While the presence and absence theory, being unsound, must lead to erroneous conclusions, some of the work it has helped to produce is workably sound. This happens in cases where no real recessive is identified to raise confusion with the unidentified "absence." The theory originated in the error of taking characters due to several causes to be due to one; and it fails in assuming a factor's absence to be its own recessive, with the result that, when a real recessive is identified as active, a factor just one too many for the case to hold has to be introduced, as we saw in the case of the rabbit colours. We shall see this if we analyse by the Mendelian method a case which has been brought to a correct conclusion by the presence and absence method, and incidentally we shall see the power of the Mendelian formulæ in analysis. We shall take the case of mouse-colours dealt with by Cuénot and Miss Durham.

Miss Durham's first experiment, in which two pairs of characters are concerned, was with agouti and chocolate mice. The second crosses were 9 agouti : 3 cinnamon agouti : 3 black : 1 chocolate.¹ Write down these groups with the non-committal scheme below:—

Agouti.	Cinnamon agouti.	Black.	Chocolate.
P	P	p	p
Q	q	Q	q

In Miss Durham's second experiment, the second crosses from black and silver-fawn were 9 black : 3 blue : 3 chocolate : 1 silver-fawn.² From the first experiment we know black to consist of pQ and chocolate of pq . As to the other characters in the case, we can only write down non-committal symbols. Thus the provisional scheme becomes

Black.	Blue.	Chocolate.	Silver-fawn.
p		p	
Q		q	
S	S	s	s
R	r	R	r

The new characters may or may not be the same as the previous ones. Ss is obviously the same as Qq , or a new pair in which S concurs with Q and s with q . In that case the two pairs could not be separated, and we therefore take Qq as representing both Qq and Ss , which are either the same or two inseparable pairs. The pair Rr is obviously new, since it can concur with no other pair already present. It is just possible for R to be the same as p ,

¹ Evolution Committee Report, iv, p. 42.

² *Ibid.*

that is recessive to P and dominant to r , but this is unlikely. It would mean a series like that of the horse colours. Assume Rr to be a new pair for the present. The assumption can be dropped later if found inconsistent with the facts. Then the provisional scheme for these four colours and the two left behind in the first experiment becomes

Agouti.	Cinnamon agouti.	Black.	Blue.	Chocolate.	Silver-fawn.
P	P	p		p	
Q	q	Q	Q	q	q
		R	r	R	r

But we can go farther. The first experiment showed that agouti and chocolate differ in only two characters. Therefore agouti contains R . The same experiment showed also that cinnamon agouti and agouti differ in only one character. Cinnamon agouti, therefore, also contains R . The second experiment showed that blue differs from black and from silver-fawn each in one character. Therefore blue and silver-fawn both contain p . We can now write these six colours more fully:—

Agouti.	Cinnamon agouti.	Black.	Blue.	Chocolate.	Silver-fawn.
P	P	p	p	p	p
Q	q	Q	Q	q	q
R	R	R	r	R	r

At this stage IT CAN BE PREDICTED that, when the complete set of colours is worked out, there will be eight groups in all, viz., one for every combination of six characters in groups of three.

In Miss Durham's third experiment, agouti and blue gave 9 agoutis: 3 dilute agoutis (a new colour): 3 blacks: 1 blue.¹ Thus dilute agouti differs from agouti, black, and blue, each in one factor. Its composition might be found in several ways. The simplest is to write down the possible combinations in groups of three of the six factors $PQRpqr$, and select that which fits the case. There are eight groups, viz., PQR , pQR , PqR , PQr , Pqr , pQr , pqR , and pqr . Since dilute agouti differs from agouti in one factor, it must contain two dominants and one recessive, and it must be found therefore in the second, third, or fourth group. It cannot be pQR , since that represents black. It cannot be PqR , since then it would differ from blue in three characters. It can only be PQr .

In Miss Durham's fourth experiment, the last of the eight groups was

¹ "Journal of Genetics," vol. i, No. 2, p. 177.

found. Cinnamon agouti and silver-fawn gave cinnamon agouti, dilute cinnamon agouti (the new colour), chocolate, and silver-fawn in the ratio 9 : 3 : 3 : 1.¹ Thus dilute cinnamon agouti differs from each of the others in one factor, and it can only be *Pqr*. If we now write down the eight groups, we see that they are really such a set as might be produced in the second crosses from two parents differing from each other in three pairs of characters. We may therefore set down in addition the numbers for each group.

Agouti.	Cinnamon agouti.	Dilute agouti.	Black.	Blue.	Chocolate.	Dilute cinnamon agouti.	Silver-fawn.
<i>P</i>	<i>P</i>	<i>P</i>	<i>p</i>	<i>p</i>	<i>p</i>	<i>P</i>	<i>p</i>
<i>Q</i>	<i>q</i>	<i>Q</i>	<i>Q</i>	<i>Q</i>	<i>q</i>	<i>q</i>	<i>q</i>
<i>R</i>	<i>R</i>	<i>r</i>	<i>R</i>	<i>r</i>	<i>R</i>	<i>r</i>	<i>r</i>
27	9	9	9	3	3	3	1

In this case the two methods of analysis arrive at the same result; but the presence and absence method arrived at this result because no effective recessive was disclosed to raise confusion among the absences, and there was therefore no need to introduce a factor more than the case could contain. Had such been disclosed, the presence and absence theory would have had to give it a name; its dominant would then have had two recessives—its absence and the disclosed character—and confusion would have resulted. So long as the presence and absence theory introduces no superfluous factor it works like the Mendelian theory itself, although those who use it may imagine they are working with the other.

Since the presence and absence theory is unsound, it follows that any theory depending upon it is also unsound, and that work done upon the presence and absence or upon any dependent theory will have to be revised. In this connection it may be suggested that the first essential is that more attention be given to the logical consequences of the Mendelian formulæ.

It is not necessary to give less attention to micrographic and internal aspects, but it is necessary to give more to macrographic and external.

By way of illustration, several tentative solutions of cases suggested by the data given in Professors Bateson's and Punnett's volumes might be put forward. It must be understood clearly, however, that these solutions are only *tentative* because the complete data have not been available.

¹ "Journal of Genetics," vol. i, No. 2, p. 177.

(i) Whole-coloured yellow rabbits were mated with Himalayan rabbits which are white with black "points."¹ The first crosses were whole-coloured agoutis. Thus, whole colour is dominant to the Himalayan pattern.

The second crosses were agouti (27), yellow (9), black (9), tortoiseshell (3), and Himalayan (16). The whole-coloured rabbits are thus—agouti (9) : yellow (3) : black (3) : tortoiseshell (1). Black and yellow are thus dominants: together they produce agouti, and their recessives together produce tortoiseshell.

The three pairs of factors concerned in the case are thus:—

Y, which produces Yellow when concurrent with *b*, and its recessive *y*.

B, which produces Black when concurrent with *y*, and its recessive *b*.

W, Whole colour, and its recessive *h*, Himalayan pattern.

Their second crosses will be represented by the following scheme:—

<i>Y B W</i> = whole-coloured agoutis,	.	.	27
<i>Y B h</i> = Himalayan agoutis,	.	.	9
<i>Y b W</i> = whole-coloured yellow,	.	.	9
<i>y B W</i> = whole-coloured blacks,	.	.	9
<i>y b W</i> = whole-coloured tortoiseshells,	.	.	3
<i>y B h</i> = Himalayan blacks,	.	.	3
<i>Y b h</i> = Himalayan yellows,	.	.	3
<i>y b h</i> = Himalayan tortoiseshells,	.	.	1

(ii) Black barb pigeons were mated with white fantails.² The first crosses were black with white splashes. Thus splashing was dominant to the plain colour, and had been carried, though obscured, by the white fantails. Thus, also, black *seemed* dominant to white, but the second crosses revealed the white fantails to be carrying another obscured character, namely, blue which is black's recessive. There were 9 blacks : 3 blues : 4 whites. It is a case similar to Hurst's rabbits, and may be represented thus:—

Black (9) Blue (3) Black albino (3) Blue albino (1)

<i>C</i>	<i>C</i>	<i>a</i>	<i>a</i>
<i>B</i>	<i>bl</i>	<i>B</i>	<i>bl</i>

The three pairs of factors are—

C, colour and its recessive *a*, albino.

B, black and its recessive *bl*, blue.

S, splashed and its recessive *p*, plain.

¹ Punnett, p. 56.

² Punnett, p. 60.

Their second crosses will be represented as follows:—

$C B S$	= Black, splashed	27
$C B p$	= Black, plain	9
$C bl S$	= Blue, splashed	9
$a B S$	= Black albino, splashed	9*
$a bl S$	= Blue albino, splashed	3*
$a B p$	= Black albino, plain	3*
$C bl p$	= Blue, plain	3
$a bl p$	= Blue albino, plain	1*

The different albinos (*) cannot, of course, be distinguished from each other by the eye.

(iii) From two white kinds of sweet pea, Professors Bateson and Punnett were able to extract six kinds of coloured sweet peas whose colour-factors the whites had been carrying without their effects being apparent.¹ From these six coloured kinds the white factors were eliminated and the coloured kinds bred and observed separately. The point to be noticed is that there are six groups: an unusual number. Is there something wrong with the Mendelian formulæ, or are there really more than six groups or less?

The first crosses from the two whites were a purple flower with blue wings. The second crosses were purples and reds in the ratio 3 : 1. Thus purple is dominant to red. But the purples on the one hand, and the reds on the other were subject to a set of parallel variations. The first-cross purple had bluish wings; and this same kind appeared in the second crosses with two others, of which one had its wings darkened from bluish to purple, while the third was a dilute form of the first. Corresponding to these were a red with lighter wings, a red with red wings, and a dilute form of the first.

Taking the purples as the example, the ratios in which the three kinds appear are purple with bluish wings, 9; purple with purple wings, 3; dilute purple, 4. If the Mendelian formulæ be correct, we have here a set of four groups in which the two last are not separated. The formula to meet the case is

Purple with bluish wings.	Purple with purple wings.	Dilute purple.	Dilute purple.
9	3	3	1
X	X	x	x
Y	y	Y	y

Where X is carried the colour is dense; where x is carried it is dilute, and the densing factor is dominant to the diluting. Where Y appears the colour

¹ Punnett, pp. 74, &c., and Bateson, pp. 93, &c.

is partially eliminated from the wings, and they are light; where *y* appears it is not: only in the case of the third group, which is dilute, this elimination is not clearly visible.

In the whole case there are thus three pairs of factors concerned, viz.:

P, Purple and its recessive *r*, red.

D, Densifying and its recessive *d*, diluting.

E, Eliminating colour from the wings, and its recessive *e*, non-eliminating.

Their second crosses will be as follows:—

<i>PDE</i> = Dense purple with light wings	27
<i>PD e</i> = Dense purple with dark wings	9
<i>P d E</i> = Dilute purple with light wings	9
<i>r DE</i> = Dense red with light wings	9
<i>r d E</i> = Dilute red with light wings	3
<i>r D e</i> = Dense red with dark wings	3
<i>P d e</i> = Dilute purple with dark wings	3
<i>r d e</i> = Dilute red with dark wings	1

Thus there ought to be eight groups; and it is very probable that only six were found because the dilute purples and reds with dark wings were not distinguishable by the eye from those with light wings.

Several minor suggestions might be made: first, that factors may not drop out and leave none in their place, or—which is the same thing—come in without displacing others. In connection with sweet peas it has been suggested that the numerous cultivated varieties have arisen from the wild “by a process of continuous loss.” In the table above, the variety at the top (*PDE*) is the same in colour as the wild Sicilian form. It is suggested that one or more of the factors *PD* and *E* have dropped out and given us our cultivated varieties: for instance, that *E* dropped out of the wild Sicilian variety and gave us a purple variety with dark wings. That may be in part: it may be that *E* dropped out, but when it did so, another factor, in this case its recessive, *e*, took its place.

A tendency has been manifested on the part of some workers, particularly in America, to take it for granted that every observable character must have an “absence.” It may be suggested now that there may be danger even in the narrower assumption that every character has an alternative. It is certainly wrong to assume that every dominant character can have only one recessive and every recessive only one dominant.

It might also be suggested that the use of the words *epistatic* and *hypostatic* might be revised. They are used to indicate the relative positions of the

factors for groups in a set: factors which prevent others from manifesting their effects being regarded as higher or *epistatic*, and the concealed factors being regarded as lower or *hypostatic*. In the case of mice "the determiner for grey" is spoken of as epistatic to that for black, and that for black as epistatic to the determiner for chocolate. There are, however, several determinants concerned in the production of each of these colours; and we can only express the relative positions of the alternative pairs of these determinants, for which purpose the words *dominant* and *recessive* are equally appropriate.

If, on the other hand, the words are used to indicate the relative positions of groups in a set, they can do so only partially. In the set $9XY : 3Xy : 3xY : 1xy$, the first group might be called epistatic to the other three, and the second and third groups each to the fourth; but how is the relationship of the two middle groups to each other to be indicated?

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