SPECIAL ARTICLES

A POSSIBLE MENDELIAN EXPLANATION FOR A TYPE OF INHERITANCE APPARENTLY NON-MENDELIAN IN NATURE

As research in genetic problems proceeds, the work of many investigators shows that in all probability certain characters of the organism depend for their visible manifestation in the zygote upon the simultaneous presence of more than one mendelizing factor.

One of the classic examples of this condition is that of the inheritance of the walnut comb in fowls reported by Bateson[1] (1909,

[1] Bateson, W. (1909), "Mendel's Principles of Heredity," Camb. (Eng.) University Press.

p. 60). The chief point of interest in this investigation was the fact that the simultaneous presence in the zygote of R, the factor for rose comb, and P, the factor for pea comb produce an entirely new character, namely, the *walnut comb*. Two walnut-combed birds produced by a cross of pea comb $\times$ rose comb gave, when crossed together, an F_2 progeny consisting of walnut, rose, pea and single comb, in a ratio of 9, 3, 3, 1.

A similar result would be obtained if the parents used in the original cross were walnut comb of the formula RRPP and single comb rrpp.

In this last case if we focus our attention on the walnut comb we should see that it recurred in approximately 9 out of 16 of the F_2 progeny.

A *character* dependent solely upon *one* mendelizing factor is present in three fourths of the F_2 progeny. The ratio of those lacking it to those having it being as 1:3. When, however, two factors are needed for the manifestation of a character, as in the case of the walnut comb, the character is lacking in a far greater number of F_2, namely, in 7 out of 16. The ratio of those lacking the character in question to those having it becomes 1:1.3 instead 1:3, as in the case involving only one factor.

If *three factors* are necessary for the manifestation of a given character, the F_2 ratio shows a still greater proportionate increase of animals lacking the character. If the simultaneous presence of factors A, B and C is necessary for the manifestation of a given character, the number showing the character in F_2 may be calculated as follows: F_2 will be made up of 27ABC, 9ABc, 9AbC, 9aBC, 3abC, 3aBc, 3Abc, 1abc. Only the 27 ABC animals will show the character question, and the ratio of those lacking the character to those having it will be as 1.3:1.

An actual cross of this sort is the following: a wild black agouti mouse having the factors B for black, A for agouti and D for intensity was crossed with a dilute brown mouse having the factors b for brown, a for non-agouti and dil for dilution.

F_1 animals were all Aa Bb Ddil, all of them having the character in question, namely, *intense black agouti pigmentation.*

When these F_1 animals are crossed together they should give a ratio of 27 intense black and 140 other colors, while the expected numbers obtained were 107 intense black agouti and 140 other colors, while the expected numbers are 105.3 intense black agouti and 141.7 other colors, respectively.

Another cross with mice recorded by Phillips and the writer[2] (1913) will serve to illustrate the case of four factors. Here the ratio expected is one animal having the character in question, to 2.16 lacking it.

From Table I.[3] it will be seen that there are in F_2 436 animals possessing the character in question (intense black agouti) to 744 lacking it, the expected numbers being 373 to 807.

As the number of factors increases, the ratio of animals which *do not* show the character to those that do increases rapidly.

With 10 factors it becomes 16.7:1, with 15 factors, 73.8:1, and with 20 factors 314.3:1.

It will be convenient to present this in tabular form as follows:

Number of Factors	Ratio of Animals Lacking Character to Those Having It
1	1:3
2	1:1.3
3	1.3:1
4	2.1:1
5	3.2:1
10	16.7:1
15	73.8:1
20	314.3:1

The general principle involved is that, with the addition of each factor involved, the number of F_2 animals possessing the character in question is multiplied by three, while the *total* number of F_2 zygotes is multiplied by four. It will be seen, therefore that the difference between the number of animals *with* the char-

[2] Little, C. C. (1913) and Phillips, J. C., "A Cross Involving Four Pairs of Mendelizing Characters in Mice," *Am. Nat.*, Vol. 47, pp. 760–762.

[3] *Loc. cit.*, p. 761.

acter and those *lacking* it grows progressively greater with each factor added.

The practical value of the principle may prove to be considerable as it serves to explain cases in which a character dominant in F_1 almost completely disappears in F_2, and in which an apparently non-mendelian result is obtained involving a reversal of dominance.

For supposing that a certain character, x, depended for its visible manifestation upon the simultaneous presence in the zygote of 20 factors which we may designate as A, B, C . . . T. Then if an animal possessing this character and the above mentioned factors is crossed with one from a race lacking all these factors, F_1 *would all be of the formula Aa Bb Cc . . . Tt. All would develop the character in question since all had a single representation of the twenty factors. If, however, these* F_1 *animals were bred inter se* F_2 *would give approximately only one animal in 314 which had the character in question.* If only a small number of F_2 were raised the character might well be thought lost and perhaps not truly inherited by F_1.

An entirely different result would, of course, be obtained if the factors in question needed to be present in *all* the gametes of the zygote in order for the character to be visibly manifested. In such a case as this none of F_1 would show the character, and its reappearance in F_2 would follow the ordinary rules of mendelian segregation and recombination.

This note is merely offered in the hope that it may be of use in the explanation, on a Mendelian basis, of certain results which might otherwise be offered as examples of non-mendelian inheritance.

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