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SHORTER ARTICLES AND DISCUSSION

SIMPLICITY VERSUS ADEQUACY IN MENDELIAN FORMULAE

T. H. MORGAN

In this journal for March, 1913, Professor William E. Castle discusses and criticizes in a friendly spirit certain suggestions concerning Mendelian nomenclature that I brought forward in the January number of the same journal. There are so many essential points on which we agree and so few on which we disagree that I should like to make clear the necessity of having for our work on *Drosophila* a dual set of symbols. Castle finds, on the other hand, that for mice and for guinea - pigs a single set of letters, *abc*, suffices to make clear his results and to cover his theoretical ideas.

There are three reasons why in certain cases it seems necessary to use more than a single system of lettering for factors.

1. Castle's scheme gives us no way of adequately representing heterozygous forms. In dealing with such combinations it is an essential both to the author and to the reader to have the heterozygote represented with its constituent allelomorphs. Instead of making the system more cumbersome the dual set of symbols is helpful.

2. We are dealing in *Drosophila* with about one hundred mutations of which forty-five have been sufficiently studied to show that they fall into three groups. Within these groups the factors concerned show linkage to each other, but no factor of one group shows linkage with any factor of any other group. Linkage means some sort of relation

which we interpret in terms of a linear series. We further interpret this series in terms of chromosomes, but even if the series is taken merely as an abstract principle the need of a dual system of letters to express the order of the factors in a paired linear series is imperative, so that we may represent interchanges between the pairs. To take the sex-linked group of factors, for example. In a heterozygous female there are two linear series present, corresponding to her duplex condition, or, as we think, to the two homologous sex chromosomes. Any factor in the one series has a correlative factor in the other series (in the other chromosome) in a corresponding position, and in order to treat the linkage of the factors we must have some method of representing and of distinguishing them. If from the mother the factors *aBcdE* enter the combination and from the father *AbCDe*, the heterozygous female is represented by the two groups:

aBcdE
AbCDe

In all problems relating to crossing-over of the factors from the one series to the other the location of each factor (and its allelomorph) is expressed by the formula just given, whereas one in which even the *duplex* condition is represented by small letters in a single line *(abcde)* fails to indicate the order of the factors in their mutual relations in the two series.

3. In cases in which sex-linked factors are involved the half formula of the female will sometimes suffice (if thought of in duplex), but in the male the half formula will not suffice when some of the factors are sex-linked and others not. If *a* and *b* are sex-linked, then the formula *abcde* fails to represent the condition in the male, for only *cde* are present in duplex.

In contrasting his scheme with mine Castle (page 176) uses the full formulae for my cases and the abbreviated formulae for his own, to the apparent advantage of the latter. If he tried to express in his formulae what I have expressed in mine, and had omitted from my formulae what he omits from his own, the advantage would have appeared differently. For shorthand purposes the most abbreviated form of any system will be employed in each particular case, except where for special reasons the comparative formula, in spite of its length, gives a clearer idea of the relations involved. When representing eye colors, for instance, we put into the formulae only the symbols for the particular eye colors under consideration, but not, of course, the symbols for other eye colors that are not being used. Castle gives the impression that I would use all the known symbols for eye color each time I wrote out the formula for the eyes, but obviously nothing of the sort is intended, for we have other eye colors that do not appear in papers that are not concerned with them.

Castle uses small letters for the recessive mutants, as I also propose to do in exactly the same sense. He scores a point — admittedly — when he says that in my formulae the factor *B* which he reads as black is the only factor that is not present in the black fly. There is just one unfortunate line on page 13 that gives Castle the opportunity to make this jibe, while the whole spirit of the paper goes to show that the small letter stands for the factor carried by the recessive mutant. In order that no misunderstanding of this sort may again arise let me state that small *p* is the factor for pink; small *b* the factor for black; small *v* the factor for vermilion; small *m* the factor for miniature. The allelomorphs of these factors in the normal flies are dominant and are represented by the capital letters *P*, *B*, *V*, *M*. These are the allelomorphs that I assume to have changed in some way to give the factors for the mutations in question.

I do not understand, after the very explicit statement in my paper, why I failed to make clear what I meant by "residuum" and as I can not hope to make the matter any clearer I shall not attempt here to discuss it further.

In writing my original paper I had considered the question as to the manner of representing the dominant mutant, but since that paper dealt mainly with the presence and absence theory, in which absence meant the recessive condition, I decided not to complicate the discussion with the treatment of the dominant and did not mention dominant except in a footnote on page 13. Castle has called attention to the necessity for considering this matter and has pointed out a distinct weakness in my scheme, if the aforesaid footnote be made the basis for the case of dominants. I gladly avail myself, therefore, of this occasion to further develop this topic. Agreeing that at times it is important to distinguish in the same formula between the dominant mutant factors and the dominant normal allelomorphs of recessive mutant factors, I would suggest that in such cases the letter standing for dominant mutant factor be primed:* *D'E'F'*. The allelomorphs of these factors that occur in the normal type can be most conveniently represented by *d'e'f'*. The entire scheme will be:

Recessive mutants . . . . *abc*
Their allelomorphs . . . . *ABC*

* Or in more general terms; if the factor is named after the dominant character, prime the allelomorphs. Since in the case of Drosophila we always take the symbol from the name of the mutant the above statement is equivalent to saying, if the mutant is dominant, prime the allelomorphs.

Dominant mutants . . . . *D'E'F'*
Their allelomorphs . . . . *d'e'f'*

In many cases it may not be necessary to distinguish whether the dominant is the normal or the mutant form. In this, as in all cases, abbreviated formulae that readily suggest themselves as occasion arises will be employed, and in general, of course, only as much of the scheme will be used as is essential for the matter in hand. But when more complicated questions arise than can be discussed on Castle's curtailed formula, the plan here suggested may, I hope, be found both simple and convenient.