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R. A. Emerson

University of Nebraska-Lincoln

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SHORTER ARTICLES AND DISCUSSION

SIMPLIFIED MENDELIAN FORMULÆ

I WAS somewhat surprised by Morgan's and Castle's suggestions for a simplification of Mendelian formulæ.¹ My surprise was not occasioned so much by the forms these suggestions took as by the fact that any pronounced changes were deemed necessary. I had not only employed the usual formulæ in my own work but had found no difficulty worth mentioning in understanding the formulæ used by most other workers in Mendelian fields. My experience with students in elementary courses in genetics had not prepared me for the idea that such formulæ were particularly difficult. Nevertheless I believe in simplifying the formulæ if some system can be found that will be applicable to all sorts of Mendelian inheritance. I believe, however, that I have no right to adopt formulæ for my own cases, no matter how simple they might be, if the same type of formula could not readily be applied to the materials with which other investigators are working. Such procedure on my part would result in no end of confusion if followed by any considerable number of workers each using his own special type of formula. The important question now is not whether I prefer a new style of formula that fits my case but whether it will fit all sorts of cases so that, if it is an improvement on the old style, it can be adopted by others and not necessitate the use of two styles where but one sufficed before.

Let us examine Morgan's and Castle's suggestions in the light of these remarks. Morgan's principal objection to the usual type of formula—that "it is not sufficiently elastic to allow the introduction of a new term in the series, unless a complete revision of the method is made each time that a new mutation in kind occurs"—seems to me to have little merit. Morgan uses eye color in *Drosophila* to illustrate his contention. Four eye colors had been designated as follows: red *PVO*, vermilion *pVO*, pink *PvO*, and orange *pvO*. A fifth color, eosin, arose and was found to produce red when crossed with orange, and hence was assumed to have the formula *PVo*. Morgan regards this as "inconsistent with the scheme already adopted because the small letter *o* stands for a character called eosin," whereas the capital letter *P* had been used for pink, *O* for orange, *V* for vermilion,

¹ AMERICAN NATURALIST, 47: 5-16, and 47: 170-182, 1913.

etc. Morgan's trouble lies in the fact that he is attempting to force a letter to represent a *character* rather than merely one of the *factors* concerned in the development of that character or to represent the character and one of the factors. As a matter of fact, in the formula PVo , the character eosin is not represented by o but by PV when O is *absent* (with the addition, perhaps, of many factors as yet unknown). Similarly P does not stand for pink but for *one* of the factors concerned in the production of pink. One of the other factors concerned in the development of pink Morgan has identified and named O ; there are probably other factors as yet unidentified. For orange he has identified only a single factor and that is this same O . No one has shown more clearly than Morgan that a character is not *determined* by a single factor. Why then should it be thought necessary to designate the first factor identified for any character, say pink, by the initial letter of that word? It is quite likely that P is no more important in the production of pink than is O . And it is equally probable that O is no more concerned in the development of orange than are perhaps a half dozen other factors not yet identified. The logical thing in such cases is to adopt Baur's $A \cdot B \cdot C \cdot$ designations, which fit in readily with current Mendelian usage. True, as Morgan insists, this necessitates the constant use of a key. But what system does not? What is there in Morgan's PVO , or even in his later PVE , to suggest red color?

It is fortunate that Mendelians "have not always taken the pains to state explicitly that the symbols represent both a factor and a residuum," for this, it seems to me, is not true. The residuum left when any factor is lost is usually not represented except by the few factors that have been identified in it. It is careless without doubt to leave so much to be taken for granted, but it would be cumbersome to have to write for pink

$$PvOX_1X_2X_3 \cdots X_n.$$

Perhaps we might use a single X to represent an unknown number of unidentified factors, or perhaps it would be as well to use UR for this unexplored residuum.

I am inclined to agree fully with Castle that Morgan's suggestion for a change in the current Mendelian formulæ is "confusion worse confounded," but here our agreement stops. I can see that it might be possible to do away with the use of small letters, since on the presence-and-absence hypothesis they represent nothing but the absence of factors designated by the corresponding capital letters. The designations of eye colors in

Drosophila (if we adapt Morgan's earlier scheme) would then become *PVO*, *VO*, *PO*, *PV* and *O*, instead of *PVO*, *pVO*, *PvO*, *PVo* and *pvo*, for red, vermilion, pink, eosin and orange respectively. The great difficulty in thus leaving out the small letters comes in distinguishing the heterozygous from the homozygous condition. True we can let *PVO* stand for the heterozygous condition of the three factors and *PPVVOO* for the homozygous condition. Then *PPVO* would indicate what is now commonly expressed by *PPVvOo*. But we now use the single letters when we wish merely to designate *phenotypic* differences or to indicate the factors in gametes, where of course all factors are simplex, and employ duplicate letters only when we desire to indicate *genotypic* differences. If then the small letters are discarded, we shall need to use some arbitrary sign to distinguish phenotypes from genotypes, else *PVO* might as now stand for a group of phenotypically like individuals or for a class having the genotypic constitution now commonly indicated by *PpVvOo*.

But Castle's suggestion is far from what is outlined above. He would use no letter to represent red eye color in *Drosophila* but merely write *normal*. For vermilion he would use *v*, for pink *p*, for pink-vermilion *pv*, etc. My first notion on reading the list of designations for eye color in fruit flies was that Castle used them only as abbreviations for the names of the colors, and *v* is really a better abbreviation for vermilion than is say Verm. or V'r'm'l'n. Now why, I thought, should one suggest such *character* abbreviations as a revised *Mendelian* terminology when Mendelism is concerned fundamentally with *gametic* factors and only incidentally with the *zygotic* characters that happen to develop through the interaction of particular combinations of gametic factors in a particular environment. But Castle's terminology is not concerned with mere abbreviations for characters, as witness:

The revised terminology is more convenient than Morgan's in calculating the expected result of any mating, and is equally reliable. The results of every possible mating within the series can be readily computed without the confusing presence of the large letters.

Here I must frankly admit that I have experienced great difficulty in using Castle's terminology in calculating the expected results of matings in case of the eye colors in *Drosophila*, though this is probably due to some misunderstanding of just how Castle's formulæ are to be used. For instance, a cross of *v* (vermilion) with *p* (pink) should, if ordinary usage were fol-

lowed, produce *vp* (vermilion-pink) whereas it actually produces red.

The use of capital letters for dominant factors and small letters for recessive ones, while it may work well in some cases, would be difficult of application in others. Brown color in beans is dominant² to yellow but recessive to black. Shall we then use *B* or *b*? True, Castle limits the use of the capital letter to the "factor responsible for a variation which is dominant in crosses with the *normal*" (italics mine), but who is to say what is the normal color of beans? The use of capital letters for some characters and small letters for others is, however, a minor matter and would not alone disqualify the proposed terminology.

When one is considering any new scheme, it is natural that he should try it out on material with which he is familiar. I have, therefore, attempted to apply Castle's suggestions to aleurone colors in maize. To make the matter as simple as possible, I will leave out of consideration color patterns and also the various dilutions or intensities of color and limit myself to the statement that aleurone may be purple, red, or white. In an account of certain crosses published last year³ I made use of the symbols suggested by East and Hayes: *C* a general color factor, *R* concerned with *C* in the production of red, *P* resulting in purple when both *C* and *R* are present, and *I* an inhibitor of color development. I listed 14 kinds of white aleurone.⁴ Now if we were to adapt Castle's formulæ for albino mice to these white maize types, we might use *wP* for whites transmitting purple in crosses, *wr* for whites transmitting red, and *wPr* for those transmitting both purple and red. But there are seven kinds of whites, all of which might yield purples in appropriate crosses with non-purples. How shall we distinguish between them? Of course we could add to *w* the letters *C*, *R*, *P*, *I* or such ones of these as might be necessary to indicate the factors latent in a particular white, but *wCRPI* is no improvement over *CRPI* from the standpoint of simplicity. Students in elementary courses in genetics who have used maize for laboratory material have had little trouble in calculating that when a white maize *CCrrPpIi* is crossed with another white maize *ccRRPpIi* there

² On the presence-and-absence hypothesis it is hardly allowable to speak of the relation of two non-allelomorphic characters in terms of dominance. Brown is epistatic to yellow and hypostatic to black. Each is dominant to its own absence.

³ AMERICAN NATURALIST, 46: 612-615, 1912.

⁴ I now have much additional evidence for my assumption as to the different sorts of white aleurone.

should result, on the average out of every 16 grains in the first generation, 3 purple, 1 red and 12 white grains. I do not doubt that the calculation could be made with equal rapidity and accuracy if the small letters were omitted and the capital letters used in the same significance. The cross would then be: *CCPI* \times *RRPI*. The greatest difficulty with this plan would come in designating the white now known as *crpi*, unless we employ a mere dash, —. It is possible that there is some simple way of applying Castle's scheme to such a case as this, a way which I have stupidly overlooked or perhaps I have not understood the scheme at all. If there is some simple terminology that is workable, I shall be glad to use it, but I must confess to being suspicious of very simple formulæ for the complex phenomena of inheritance.

R. A. EMERSON

UNIVERSITY OF NEBRASKA