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FRANCIS GALTON'S DERIVATION OF MENDELIAN RATIOS IN 1875

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IT is generally believed that before 1900 no one apart from Mendel suspected that the frequencies of the various classes in the F2 generation might approximate to simple ratios. It is, therefore, surprising to find that this is not the case, for in a letter which Francis Galton (1822-1911) wrote to his cousin Charles Darwin he derived the 1 : 2 : 1 ratio deductively reasoning from the premise that inheritance is due to a finite number of persistent particles. This letter, dated 18th December 1875, is preserved in the collection of Darwin Manuscripts at the University Library, Cambridge (Darwin MS. 105 (92, 93)) and a portion of it is reproduced here (plate I). It has already been published by the late Professor Karl Pearson in volume II of his biography of Galton (Pearson, 1914-30, pp. 189-190); but as it does not appear to be generally known it is well worth describing afresh.

The letter forms part of the correspondence between Galton and Darwin over the latter's hypothesis of pangenesis, the central idea of which was that every cell of the body gives off " minute granules or atoms " which he termed " gemmules ". These gemmules congregate in the reproductive organs where they form the hereditary material of the germ cells. Galton did not deny the existence of these gemmules but he refused to believe that " they circulate freely throughout the system " (Darwin, 1868). Consequently he could not see how the hereditary material of the germ cells can possibly be derived from the somatic tissues.

In December 1875 Darwin wrote to Galton asking him how, on his view, it was possible to explain the fact that a hybrid may have every part of the stem, leaf and flower intermediate and will produce millions of buds all of which reproduce exactly this intermediacy. In his very interesting reply Galton deduced Mendelian ratios. It reads as follows:

42 RUTLAND GATE
Dec 19/75

My dear Darwin,

The explanation of what you propose does not seem to me in any way different on my theory, to what it would be in any theory of organic units. It would be this:—

Let us deal with a single quality, for clearness of explanation, and suppose that in some particular plant or animal and in some particular structure, the hybrid

Then a bit of the tinted structure under the microscope would have a form which might be drawn as in a diagram, as follows:— black form
white form

whereas in the hybrid, it would be either that some cells were white and others black, & nearly ~~about~~ the same proportion of each, thus:—

(1)

giving on the whole when less highly magnified, a uniform gray tint;— or else thus:—

(2)

in which __each cell__ had a uniform gray tint.

between white and black forms was exactly intermediate, viz gray,—thenceforward for ever. Then a bit of the tinted structure under the microscope would have a form which might be drawn as in a diagram, as follows:—(see plate I) whereas in the hybrid, it would be either that some cells were white and others black, and nearly the same proportion of each, thus:—(see plate I (1)) giving *on the whole* when less highly magnified a uniform gray tint,—or else thus:—(see plate I (2)) in which *each cell* had a uniform gray tint.

In (1) we see that each cell has been an organic unit (quoad colour). In other words, the structural unit is identical with the organic unit.

In (2) the structural unit would not be an organic unit but it would be an organic *molecule*. It would have been due to the development, not of one gemmule but of a group of gemmules, in which the black and white species would, on statistical grounds, be equally numerous (as by the hypothesis, they were equipotent).

The larger the number of gemmules in each organic molecule, the more *uniform* will the tint of grayish be in the different units of structure. It has been an old idea of mine, not yet discarded and not yet worked out, that the number of units in each molecule may admit of being discovered by noting the relative number of cases of each grade of deviation from the mean grayness. If there were two gemmules only, each of which might be either white or black, then in a large number of cases one-quarter would always be quite white, one-quarter quite black, and one-half would be gray. If there were 3 molecules, we should have 4 grades of colour (1 quite white, 3 light gray, 3 dark gray, 1 quite black and so on according to the successive lines of " Pascal's triangle "). This way of looking at the matter would perhaps show (*a*) whether the number in each given species of molecule was constant and (*b*), if so, what those numbers were.

Ever very faithfully yours,

Francis Galton

Here we find all the elements of the Mendelian explanation with the exception of independent assortment and germinal segregation. Galton's theory of inheritance is particulate. The hereditary units brought together in the hybrid have not fused. There is a definite number of them per cell. For any character-difference the number of determinants can be discovered by finding " the relative number of cases of each grade ", Mendel's ratios. Inheritance may be simple, two units per character-difference, giving the 1 : 2 : 1 ratio, or it may be more complex, depending on more than two units.

Galton pointed out the fact that the successive lines of Pascal's triangle give the ratios for the frequencies of the different grades in more and more complex situations. Thus the fifth line of Pascal's triangle contains the figures 1, 4, 6, 4, 1. These correspond with the ratios which would be obtained if one character-pair were determined by four genes of equal potency. Taking Galton's example of black × white, the relative frequencies for the F2 segregates would approximate to the ratio: 1 black BBBB : 4 dark grey BBBW : 6 grey BBWW : 4 light grey BWWW : 1 white WWWW. Hence Galton had conceived of ratios produced by the interaction of hereditary units as well as the simple Mendelian ratio 1 : 2 : 1. Moreover, he explained his Mendelian theory to Darwin.

At the same time it is important to note that although the first part of Galton's letter refers to a precise situation—the grey offspring from the cross black × white—it is not clear whether the latter part refers to a specific situation or not. Are the " cases ", to which he refers, the individuals resulting from a given cross or the members of an outbreeding and heterogeneous population? The situation is not defined. Galton was thinking in abstract terms, but his identification of the relative frequencies of the different grades with the binomial coefficients as given in Pascal's triangle does constitute a derivation of Mendelian ratios. Clearly this letter should have an important place in the history of genetics. I have therefore discussed its significance in more detail in a book on the subject (Olby, 1966).

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