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The Inheritance of Complex Growth Forms, such as Stature, on Mendel's Theory.

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XI.—The Inheritance of Complex Growth Forms, such as Stature, on Mendel's Theory. By John Brownlee, M.D., D.Sc.

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THE inheritance of complexes is of great interest. The manner in which this arises on a Mendelian basis can be most easily seen by the consideration of a simple case. Let two races of different stature mix in equal numbers. Let for simplicity stature depend on two elements (a, a), (c, c) in one race, and on (b, b), (d, d) corresponding elements in the other. Then the permanent race obtained by free mating without any special selection of one parent or another will consist of the following proportions:—

$$1\begin{vmatrix} a, a \\ c, c \end{vmatrix} + 2\begin{vmatrix} a, a \\ c, a \end{vmatrix} + 1\begin{vmatrix} a, a \\ d, d \end{vmatrix} + 2\begin{vmatrix} a, b \\ c, c \end{vmatrix} + 4\begin{vmatrix} a, b \\ c, d \end{vmatrix} + 2\begin{vmatrix} a, b \\ d, d \end{vmatrix}$$

$$+1\begin{vmatrix} b, b \\ c, c \end{vmatrix} + 2\begin{vmatrix} b, b \\ c, d \end{vmatrix} + 1\begin{vmatrix} b, b \\ d, d \end{vmatrix}$$

Now two factors may come into play: either dominance may not exist and the hybrid be a blend, or, on the other hand, dominance may determine the result of the mating. If dominance does not exist we may rearrange the elements according as they contain one or more element from each original race. On this hypothesis we have the following groups:—

	$1\begin{vmatrix} a, a \\ c, c \end{vmatrix}$	$2\begin{vmatrix} a, a \\ c, d \end{vmatrix}$	$4\begin{vmatrix} a, b \\ c, d \end{vmatrix}$	$2\begin{vmatrix} b, b \\ c, d \end{vmatrix}$	$1\begin{vmatrix} b, b \\ d, d \end{vmatrix}$
		$2\begin{vmatrix} a, b \\ c, c \end{vmatrix}$	$1\begin{vmatrix} a, a \\ d, d \end{vmatrix}$	$2\begin{vmatrix} a, b \\ d, d \end{vmatrix}$	
			$1\begin{vmatrix} b, b \\ c, c \end{vmatrix}$		
Totals,	1	4	6	4	1

That is, stature tends to be graded according to the ordinary point binomial, it being granted probable that each group as above placed has essentially the same stature.

If dominance, however, exist it is a reasonable assumption that each race may supply an equal number of dominant elements (in this case one from each parent). Let a be dominant over b, and d over c, and the grouping becomes—

$$\begin{array}{lccc}
 & 1\begin{vmatrix} a, a \\ c, c \end{vmatrix}, & 2\begin{vmatrix} a, a \\ c, d \end{vmatrix} + 4\begin{vmatrix} a, b \\ c, d \end{vmatrix} + 2\begin{vmatrix} b, b \\ c, d \end{vmatrix}, & 1\begin{vmatrix} b, b \\ a, d \end{vmatrix}, \\
 & 2\begin{vmatrix} a, b \\ c, c \end{vmatrix}, & +\begin{vmatrix} a, a \\ d, d \end{vmatrix} + \begin{vmatrix} b, b \\ c, c \end{vmatrix} & 2\begin{vmatrix} b, b \\ c, d \end{vmatrix} \\
\text{Totals,} & 3 & 10 & 3
\end{array}$$

It can be at once deduced from these results that when there are $2p$ pairs of elements in each parent determining stature, the subsequent grouping of the population is given by

$$(1+4+6+4+1)^p,$$

where there is no dominance,
and

$$(3+10+3)^p$$

where dominance applies to all the pairs and is equally divided between the pairs for each race. The mathematics of the first is easy and has been considered in my previous paper. It leads at once, when mating is random, to a correlation coefficient between parent and offspring of $r = \cdot 5$.

With regard to the second, there are several things to note. For convenience we may write the point binomial as $(1+n+1)^p$.

If we expand by the multinomial theorem, arrange the terms, and then determine the moments, we have:—

the second moment $\mu_2 = \dfrac{2p}{n+2}$,

the third moment $\mu_3 = 0$ as the multinomial is symmetrical,

the fourth moment $\mu_4 = \dfrac{2pn + 4p(3p-2)}{(n+2)^2}$.

The relationship of these moments is such that for all values of $n > 4$, $\dfrac{\mu_4}{\mu_2}$ is > 3, or the resulting curve partakes of the qualities of Type IV. rather than of the normal curve. But $n = 4$ is not the dividing point. When $n = 2$ the point binomial obviously is the square of $(1+1)$ and therefore is of the type which gives rise to the normal curve. In this case $\mu_2 = \dfrac{p}{2}$ and $\mu_4 = \dfrac{3p^2 - p}{4}$. We may therefore take it that this curve represents the dividing line, and that when n is greater than 2, a curve with moment relationships more nearly those of the symmetrical form of Type IV.

should describe the result and not the normal curve. In the same way if $n < 2$ we have a curve with the moment relationships of Type II. In the case considered $n = 3{\cdot}3$, or the point binomial is represented by $(3+10+3)^p$. To illustrate the manner in which this curve approximates to the normal we may take $p=4$, *i.e.* there are eight pairs of allomorphs originally present in each parent. The distribution of this and the corresponding normal distribution are then :—

Point binomial—81, 1080, 5724, 15240, 21286, 15240, 5724, 1080, 81.
Normal curve—115·2, 1136, 5764, 15226, 21042, 15226, 5764, 1136, 115·2.

It is to be noticed that the point binomial gives a "leptokurtic" distribution, that is, one in which the radius of curvature at the apex is less than that of the normal curve; in other words, one corresponding to that of Type IV., but not identical with it. On the numbers given by the total, namely, 66536, the difference between the two is most marked; but on one-tenth of the numbers, namely, 6654, a number much in excess of that obtained in ordinary observations, the normal curve is an exceedingly good fit, giving by the test $\chi^2 = 3{\cdot}1$ or $P = {\cdot}91$. It is interesting to observe that with only eight pairs of allomorphs a normal distribution of stature within the limits of error of observation is at once derived.

Such a condition of dominance is, however, hardly likely to occur; it is much more probable that there will be some blended inheritance as well, so that the resulting curve should be something between

$$(1+4+6+4+1)^p$$

and

$$(3+10+3)^p.$$

With free mating and equal fertility the proportion of the mixed population is $(3+10+3)^p$. The meaning of the value of n in the point binomial $(1+n+1)^p$ is therefore as follows:—If n is equal to $3{\cdot}3$ all matings are equally fertile, if n is $>3{\cdot}3$ then the matings of hybrid with hybrid are most fertile and if n is $<3{\cdot}3$, the matings of the purer races.

The manner in which asymmetry arises may be seen by going back to the simple case.

Let $\quad x \left| \begin{matrix} a,\ a \\ c,\ c \end{matrix} \right| \quad \text{and} \quad y \left| \begin{matrix} b,\ b \\ d,\ d \end{matrix} \right| \quad$ mate at random ;

after one generation we have a stable population composed of

$$x^4 \left| \begin{matrix} a,\ a \\ c,\ c \end{matrix} \right| \; 2x^2y \left| \begin{matrix} a,\ b \\ c,\ c \end{matrix} \right| + \ldots .$$

Arranging these as before, we find for blended inheritance the following groups:—

$$x^4, \quad 4x^3y, \quad 6x^2y^2, \quad 4xy^3, \quad y^4,$$

and for mixed dominant inheritance,

$$x^4+2x^3y, \quad 2x^3y+6x^2y^2+2xy^3, \quad 2xy^3+y^4.$$

If $y=2x$ the latter reduce to

$$5, \qquad 44, \qquad 32,$$

so that the ultimate population is given by

$$(5+44+32)^p$$

where p is the number of double pairs originally present in either parent. This case is obviously asymmetric, but with p large quickly approaches symmetry. It is not, however, necessary to assume that two races mix. In each race diverse pairs must necessarily exist. It is possible that these may appear in proportions sensibly obeying the normal law. This, however, makes no difference in the preceding theory. Variation of individuals will but tend to smooth the curve (see note). Asymmetry also arises if the number of dominant elements from each race is unequal.

If the hypotheses above discussed are granted, two points emerge demanding consideration:—

(1) How far does this grouping accord with the observed statistics?

(2) How far does the grouping permit of the correlation coefficients found by observation?

(1) Every large series of statistics of a population give groups to which Type IV. corresponds better than the normal curve. Those of Pearson,* Powys,† etc., may be taken as types. In the case of the diagrams given by the former, it is very noticeable that at the apex the statistics give a value in excess of that shown by the normal curve fitted to the statistics, and at the limits there is a defect on the part of the statistics resembling that just found theoretically. With the curves of the Scottish insane given by Tocher ‡ the same is also found.

(2) With regard to the values of the correlation coefficients we are on firm ground. As we have seen, the hypothesis of blended inheritance leads to correlation coefficients as follows:—

Parent and offspring	·5
,, ,, grand-offspring	·25
,, ,, great-grand-offspring . . .	·125
,, ,, great-great-grand-offspring . .	·0625

* Pearson, "On the Laws of Inheritance in Men," *Biometrika*, vol. ii. p. 357.

† Powys, "Data for the Problem of Evolution in Man," *Ibid.*, vol. i. p. 30.

‡ Tocher, "Anthropometry of the Scottish Insane," *Ibid.*, vol. v. p. 298.

These, however, are not what are found. The progression derived by Pearson from direct observation for the same relationship, is*

$$\cdot 5, \quad \cdot 33, \quad \cdot 22, \quad \cdot 15.$$

As before observed, these values arise on a Mendelian basis with dominance if a coefficient of assortive mating of $r = \cdot 25$ be assumed. In the case of stature in man this is even exceeded. Professor Pearson finds that for this quality $r = \cdot 28$, so that although for purposes of calculation it is assumed that $r = \cdot 25$, this value is in defect. With the grouping assumed in this paper, the coefficient of correlation between parent and child without assortive mating is found to be $r = \dot{3}$, exactly as in the case considered by Professor Pearson.† In this case, however, the increase produced by the degree of assortive mating considered is not so large as in that where dominance is assumed to come exclusively from one side. The coefficient of correlation between parent and offspring is raised from $r = \dot{3}$ to $r = \cdot 46$, somewhat in defect of the value $r = \cdot 5$ found from observation. It is, however, in the highest degree improbable that pure dominance regulates inheritance. Blending, as already remarked, must also occur, and as a like coefficient of assortive mating must be held to apply in this case, the increase in the value of the coefficient to the neighbourhood of $r = \cdot 5$ is almost a necessity, since for pure blended inheritance the correlation of parent and offspring is in the neighbourhood of $r = \cdot 6$ when the coefficient of assortive mating is given by $r = \cdot 25$.

To settle this question, inquiries into the constitution of races will require to be made, but I think that I have shown that there is nothing necessarily antagonistic between the evidence advanced by the biometricians and the Mendelian theory.

Conclusions.

(1) If the inheritance of stature depends upon a Mendelian mechanism, then the distribution of the population as regards height will be that which is actually found, namely, a distribution closely represented by the normal curve.

(2) There is nothing in the values of the coefficients of inheritance found by Sir Francis Galton and Professor Pearson which cannot be explained on the basis of Mendelian inheritance.

Note I.

Let $\phi(x)$, assumed symmetrical, represent the crude distribution of x as indicated above, and let each portion of the population vary according to

* *Biometrika*, vol. ii. p. 373. † *Trans. Roy. Soc.*, 1903, p. 53.

the normal curve $y = ae^{\frac{-x^2}{2\sigma^2}}$. Let in addition the second and fourth moments of ϕx be denoted by μ_2 and μ_4. Then for any point x the final distribution of the population will be given by

$$y = a\int_{-\infty}^{\infty}\phi(x')e^{\frac{-(x-x')}{2\sigma^2}}dx'.$$

Let the moments of this be denoted by ν_2 and ν_4: then

$$\nu_2\int_{-\infty}^{\infty}ydx = a\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}x^2\phi(x')e^{\frac{-(x-x')^2}{2\sigma^2}}dxdx'$$

$$= a\sqrt{2\pi\sigma^3}\int_{-\infty}^{\infty}\phi x'dx' + a\sqrt{2\pi}\sigma\int_{-\infty}^{\infty}x'^2\phi(x')dx',$$

or

$$\nu_2 = \sigma^2 + \mu_2;$$

likewise

$$\nu_4 = 3\sigma^4 + 6\sigma^2\mu_2 + \mu_4,$$

so that

$$\frac{\nu_4}{3\nu_2^2} = \frac{3\sigma^4 + 6\sigma^2\mu_2 + \mu_4}{3\sigma^4 + 6\sigma^2\mu_2 + 3\mu_2^2},$$

and is $>$ or <1 according as $\mu_4 >$ or $<3\mu_2$.

This curve then tends to approach the normal curve of error in its moment relationships, but it is to be remembered that σ^2 must be small compared with μ_2, and also that if dominance exist perfect normality is impossible.

Note II.

In case of misunderstanding, it may be well to state that I have used the word *blend* in the sense that the quality resulting from the combination of two different elements lies between that of the separate elements, and not in the sense that either of the elements is modified by the combination, as is sometimes done.

(*Issued separately January* 13, 1911.)