" Mathematical Contributions to the Theory of Evolution. On the Law of Ancestral Heredity." By KARL PEARSON, M.A., F.R.S., University College, London. Received January 12,—Read January 27, 1898.

(A New Year's Greeting to Francis Galton, January 1, 1898.)

(1) *Introductory.*—In Mr. Galton's ' Natural Inheritance ' we find a theory of regression based upon the " mid-parent." This formed the starting point of my own theory of biparental inheritance.* At the time Mr. Galton published his theory I venture to think that he had not clearly in view some of the laws of multiple correlation with which we are now more familiar. This certainly was my own con-dition when writing my memoir on heredity in 1895, and although in that memoir I pretty fully developed the theory of multiple correlation as applied to heredity, it had not then become such a familiar tool as two years' pretty constant occupation with it has since made it. Accordingly I misinterpreted a second principle of heredity propounded by Mr. Galton, and reached the paradoxical conclusion† that " a knowledge of the ancestry beyond the parents in no way alters our judgment as to the size of organ or degree of characteristic probable in the offspring." I assumed Mr. Galton to mean‡ that the coefficients of correlation between offspring and parent, grand-parent, great-grandparent, &c., were to be taken r, r^2, r^3, &c. The conclusions I drew from this result were, had the result been true, perfectly sound. The recent publication of Mr. Galton's paper on Basset hounds has led me back to the subject, because that paper contains facts in obvious contradiction with the principle above cited from my memoir of 1895. At first, I must confess, I was inclined to lay less stress on Mr. Galton's general law than it deserved, and attributed our divergence to the admitted roughness of colour data. After some correspondence with Mr. Galton and an endeavour on my part to represent his views in my own language, I have come to the conclusion that what I shall in future term *Galton's Law of Ancestral Heredity*, if properly interpreted, reconciles the discrepancies in ' Natural Inheritance ' and between it and my memoir of 1895. It indeed enables us to predict *à priori* the values of all the correlation coefficients of heredity, and forms, I venture to think, the fundamental principle of heredity from which all the numerical data of inheritance can in future be deduced, at any rate, to a first approximation.

* ' Phil. Trans.,' A, vol. 187, pp. 253—318.
† *Ibid.*, p. 306.
‡ I still think that this is the meaning to be extracted from pp. 132–5 of ' Natural Inheritance.'

The confidence I put in the truth of the law is not measured by Mr. Galton's researches on stature or on colour in Basset hounds, however strong evidence these may provide, but rather on the fact that the theory gives *à priori* the correlation between parents and offspring, and that this correlation is practically identical with the value I have myself determined from these and other observations.

With reservations as to how "mid-parent" shall be defined, I would state the law of ancestral heredity as follows:—

If k_s be the deviation of the sth mid-parent* from the mean of the sth ancestral generation, and k_0 be the probable deviation from the mean of the offspring of any individual, σ_s the standard deviation of the sth mid-parental generation, σ_0 of the generation of the offspring, then

$$k_0 = \tfrac{1}{2}\frac{\sigma_0}{\sigma_1}k_1 + \tfrac{1}{4}\frac{\sigma_0}{\sigma_2}k_2 + \tfrac{1}{8}\frac{\sigma_0}{\sigma_3}k_3 + \tfrac{1}{16}\frac{\sigma_0}{\sigma_4}k_4 + \ \ldots \ .$$

This is the somewhat generalised form of the law, which Mr. Galton sums up as "each parent contributes on an average one-quarter, or $(0\cdot5)^2$, each grandparent one-sixteenth, or $(0\cdot5)^4$, and so on, and that generally the occupier of each ancestral place in the nth degree, whatever be the value of n, contributes $(0\cdot5)^{2n}$ of the heritage."[†]

The generalised form above allows for a secular modification of the means and variabilities of the successive generations.

(2) Let $r_1, r_2, r_3, r_4, \ldots$, be the coefficients of correlation between offspring and parent, grandparent, great-grandparent, &c., respectively. Then, if correlation remains constant during the successive generations, $r_{n \sim s}$ would be the correlation between the parent of the nth generation and the parent of the sth generation if they be in the direct line of ascent, for one of these is the $(n \sim s)$th parent of the other. It must be remembered that if r_q be the correlation between an individual qth parent and his offspring, r_q may theoretically have a great variety of values according to the proportion and order of the sexes in the line of descent. If all these r_q's be unequal, then r_q shall be taken to represent their mean value. It will be necessary for our investigations to find the correlation between the nth and sth mid-parents in terms of these r's, which give the correlation between individuals. Let ρ_{ns} be the correlation between the nth and sth mid-parents. Let $_qh_s$ be the deviation of any organ of the qth male sth parent from the mean of that organ for the sth generation of male parents, $_qh'_s$ that of his female mate; let m be any constant not yet

* A father is a first parent, a grandfather a second parent, a great-grandfather a third parent, and so on, in the notation here adopted. The mid sth parent or the sth mid-parent is derived from all 2^s individual sth parents.

† 'Roy. Soc. Proc.,' vol. 61, p. 402.

determined. Then there will be 2^{s-1} male and 2^{s-1} female sth parents, and the "mid-parent" will be defined to be an individual having a deviation from the mean of the sth parental generation

$$= \frac{{}_1h_s + {}_2h_s + {}_3h_s + \dots + m({}_1h'_s + {}_2h'_s + {}_3h'_s + \dots)}{2^s}.$$

This is a somewhat more general definition than Mr. Galton's.

Since $S(h) = 0$, $S(h') = 0$, when the summation extends over all individuals of the sth generation who are parents, it follows that the mean deviation of all possible sth mid-parents is zero.*

Next let us find the standard deviation Σ_s of the sth mid-parents. If their number for the population be N, then

$$N \times \Sigma_s^2 = \frac{1}{2^{2s}} S \{{}_1h_s + {}_2h_s + {}_3h_s + \dots + m ({}_1h'_s + {}_2h'_s + {}_3h'_s + \dots)\}^2.$$

Now, if there be assortative mating, $S({}_qh_s \cdot {}_qh'_s)$ will equal $N\sigma_s\sigma'_se_s$, where e_s is the correlation coefficient for assortative mating in the sth generation and σ_s, σ'_s the standard deviations of male and female mates in that generation. Further, $S({}_qh_s \cdot {}_{q'}h_s)$ and $S({}_qh'_s \cdot {}_{q'}h'_s)$ will not be absolutely zero, because assortative mating would mean a class mating into a like class leading to a correlation between relations in law; but these sums would be of the order e_s^2, and since, at any rate for man, e_s appears to be very small, we may neglect them to a first approximation.†   Hence

$$N \times \Sigma_s^2 = \frac{1}{2^{2s}} \{2^{s-1} S({}_qh_s)^2 + m^2 2^{s-1} S({}_qh'_s)^2 + 2m2^{s-1} S({}_qh_s \cdot {}_qh'_s)\},$$

or $\qquad \Sigma_s^2 = \frac{1}{2^{s+1}} (\sigma_s^2 + m^2\sigma'^2_s + 2m\sigma_s\sigma'_se_s)$ .... (i).

Now let us take m, which is at our choice, equal to σ_s/σ'_s, then

$$\Sigma_s = \frac{1}{2^{\frac12 s}} \sigma_s (1+e_s)^{\frac12} \dots\dots\dots\dots \text{(ii)}.$$

In the next place let us find the coefficient of correlation between two mid-parents, say those of the nth and sth generations. We have

$$N \times \Sigma_s\Sigma_n\rho_{ns} = \frac{1}{2^s2^n} S [\{{}_1h_s + {}_2h_s + {}_3h_s + \dots + m ({}_1h'_s + {}_2h'_s + {}_3h'_s + \dots)\}$$
$$\times \{{}_1h_n + {}_2h_n + {}_3h_n + \dots + m ({}_1h'_n + {}_2h'_n + {}_3h'_n + \dots)\}].$$

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* Reproductive selection, which would weight particular parents, is neglected, or, if not, the h's must be measured from the weighted means of all sth parents.

† Here, as later, I exclude the effects of in-and-in breeding; this case requires special treatment. I hope shortly to publish fuller data for sexual selection in man, based upon a wider system of measurements than are dealt with in my memoir of 1895.

Now, if n be $>s$, any h_s will only (neglecting terms of order e^2) be correlated with its own particular $(n-s)$th parents, male and female, and there will be $\frac{1}{2}(2^{n-s})$ such male parents and $\frac{1}{2}(2^{n-s})$ such female parents. Hence

$$\mathrm{N} \times \Sigma_s \Sigma_n \rho_{ns} = \frac{\mathrm{N}}{2^{s+n}} \big\{ \sigma_s \sigma_n \times 2^{s-1} \mathrm{S}_1(r_{sn}) + m\sigma'_s \sigma_n 2^{s-1} \mathrm{S}_2(r_{sn})$$
$$+ m\sigma_s \sigma'_n 2^{s-1} \mathrm{S}_3(r_{sn}) + m^2 \sigma'_s \sigma'_n 2^{s-1} \mathrm{S}_4(r_{sn}) \big\},$$

$$\rho_{ns} = \frac{\mathrm{N}\sigma_s \sigma_n}{2^s \Sigma_s \Sigma_n} \left\{ \frac{\mathrm{S}_1(r_{sn}) + m\dfrac{\sigma'_s}{\sigma_s} \mathrm{S}_2(r_{sn}) + m\dfrac{\sigma'_n}{\sigma_n} \mathrm{S}_3(r_{sn}) + m^2 \dfrac{\sigma'_s \sigma'_n}{\sigma_s \sigma_n} \mathrm{S}_4(r_{sn})}{2^{n-s+1}} \right\}$$

$$\dots\dots \text{(iii).}$$

Here $\mathrm{S}_1(r_{sn})$ is the sum of all r_{sn} which begin and end with male in the descent, $\mathrm{S}_2(r_{sn})$, of those which begin with female and end with male, $\mathrm{S}_3(r_{sn})$, of those which begin with a male and end with a female, and $\mathrm{S}_4(r_{sn})$ of those which begin and end with a female. Now, as before, put $m = \sigma_s/\sigma'_s = \sigma_n/\sigma'_n$. We thus have, supposing the variability of each generation to be constant,

$$\rho_{sn} = \frac{2^{\frac{1}{2}(n-s)}}{1+e_s} \frac{\mathrm{S}_1(r_{sn}) + \mathrm{S}_2(r_{sn}) + \mathrm{S}_3(r_{sn}) + \mathrm{S}_4(r_{sn})}{2^{n-s+1}}$$

$$= \frac{2^{\frac{1}{2}(n-s)}}{1+e_s} r_{sn}, \quad \dots\dots\dots\dots\dots\dots \text{(iv),}$$

where r_{sn} now stands for the mean value of all the correlation coefficients of an individual and its individual $(n-s)$th parents. It may be written $r_{n \sim s}$, as it depends only on the *difference* of the generations. Hence supposing sexual selection to remain constant, if it exists, for all generations, we see that ρ_{ns} depends only on the difference of generations, and may be written ρ_{n-s}, or :

$$\rho_{n-s} = 2^{\frac{1}{2}(n-s)} r_{n-s} / (1+e).^*$$

Now if there be no selective breeding, e appears, at any rate for man, to be small. Hence we have the important proposition :

The correlation between two mid-parents, p generations apart, is equal to the product of $2^{\frac{1}{2}p}$ and the mean of the coefficients of correlation between an individual and its individual pth parents, when they are taken for all possible combinations of sex.

When no allowance is made for reproductive selection, it has been shown by Miss Alice Lee and myself that the four possible r's

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* The importance of this result is that it reduces the $\dfrac{n(n-1)}{1\cdot2}$ correlation coefficients between n mid-parents of different orders to n coefficients only.

for first parent and offspring are very nearly equal;[*] assuming the equality of all possible r_s's for the sth parent and offspring, and neglecting e we have

$$\left.\begin{array}{l} \Sigma_s = \sigma_s / 2^{\frac{1}{2}s} \\[2mm] \rho_p = 2^{\frac{1}{2}p} r_p \end{array}\right\} \quad \dots\dots\dots\dots\dots \quad \text{(v)}.$$

or, we conclude that very approximately: *The standard deviation of the mid-sth parent may be obtained from the standard deviation of individual sth parents by dividing by* $2^{\frac{1}{2}s}$, *and the correlation between mid-sth parents and mid* ($s + p$)*th parents may be obtained by multiplying the correlation between an individual and any sth parent by* $2^{\frac{1}{2}p}$.

Thus the variability of the sth mid-parent rapidly decreases as we increase s, *i.e.*, as we get back in ancestry the mid-parent comes more and more nearly to represent in all cases the mean of the general population. Whether the correlation tends to decrease or increase will depend on the relative rates of change of $2^{\frac{1}{2}p}$ and r_p.

Since ρ_p must always be less than 1, we obtain at once the interesting limit that the correlation of an individual and a pth parent is always less than $(0\cdot5)^{\frac{1}{2}p}$.

For example the correlation between :

Offspring and parent	must be less than		0·71
,,　and grandparents	,,	,,	0·5
,,　and great-grandparents	,,	,,	0·36
,,　and great-great-grandparents	,,	,,	0·25

Their actual values as deduced from Mr. Galton's law are much smaller, as we shall see later.

(3) The reader will remark that in order to get these results in a simple form we have multiplied the female deviations from the mean by a constant factor m, which has afterwards been taken equal to the ratio of male to female variability. The reason for this was twofold. In the first place σ is certainly not equal to σ', and, consequently, $m = 1$ would not have given

$$\Sigma_s = \frac{1}{2^{\frac{1}{2}s}} \sigma_s, \text{ but } = \frac{1}{2^{\frac{1}{2}(s+1)}} \sqrt{\overline{\sigma_s^2 + \sigma'_s^2}},$$

a more complex form. In the next place we note the fairly close equality of r', r'', r''', r'''', when we neglect reproductive selection; hence $m = \sigma_s / \sigma'_s$ is the only value which appreciably reduces formula (iii) as well as formula (i). I therefore define a mid-parent to be one in which the deviations of the females are reduced to the male standard by first multiplying them by the ratio of male to

female variability. This does not *theoretically* agree with Mr. Galton's definition, for he reduces the female to the male standard by multiplying them by the sexual ratio, or the ratio of the male to the female mean for the organ under consideration. In order, therefore, that my factor of reduction should agree with Mr. Galton's, it is needful that the ratio of the standard deviations should be equal to the ratio of the means, or, in other words, that the coefficient of variation should be the same for the two sexes. Now for the stature of men and women, I find for 1000 cases of each sex the coefficients 4·07 and 4·03 respectively, or the coefficient of variation is sensibly equal for both sexes.* Mr. Galton found from his anthropometric laboratory returns for somewhat fewer numbers, and probably for a lower social class, values of 3·75 and 3·79, again sensibly equal.† Hence the mid-parent, whether defined in my manner or in Mr. Galton's, would have a sensibly equal value in the case of stature, which is the one Mr. Galton dealt with in his 'Natural Inheritance.' The coefficient of variation is, however, not the same for both sexes in the case of all organs,‡ hence for the purpose of simplifying the formulæ, I am inclined to think my modification of Mr. Galton's original definition will prove of service.

(4) I shall now proceed to determine by the law of ancestral heredity the correlation between an individual and any sth parent from a knowledge of the regression between the individual and his mid-sth parent.

By the principles of multiple-correlation if x_0, x_1, x_2, ... x_n be $n+1$ organs, with standard deviations σ_0, σ_1, σ_2 .... σ_n, and correlations r_{01}, r_{02}, r_{03} .... r_{12}, r_{13} .... $r_{n-1, n}$, then the frequency surface is given by

$$z = \text{const} \times e^{-\frac{1}{2R}\left\{ R_{00}\left(\frac{x_0}{\sigma_0}\right)^2 + R_{11}\left(\frac{x_1}{\sigma_1}\right)^2 + \dots + 2R_{01}\left(\frac{x_0 x_1}{\sigma_1 \sigma_2}\right) + \dots \right\}};$$

where
$$R = \begin{vmatrix} 1, & r_{01}, & r_{02}, & r_{03}. & \dots & r_{0n} \\ r_{01}, & 1, & r_{12}, & r_{13}, & \dots & r_{1n} \\ \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ r_{0n}, & r_{1n}, & r_{2n} & \dots & \dots & r_{nn} \end{vmatrix},$$

and R_{pq} is the minor of the constituent of pth row and qth column.

* See 'The Chances of Death,' vol. 1, "Variation in Man and Woman," p. 294.
† *Ibid.*, p. 311. Mr. Galton's family record data gave 1·032 and 1·005 for the ratio of the coefficient of variation of sons to daughters and of fathers to mothers respectively. See 'Phil. Trans.,' A, vol. 187, p. 271.
‡ Many cases are given in the paper on "Variation in Man and Woman," cited above.

Putting $x_1, x_2, \ldots x_n$ constants, say $k_1, k_2, \ldots k_n$, we have for the mean value $\bar{x}_0$ of the corresponding array of x's,

$$\bar{x}_0 = -\left(\frac{R_{01}\sigma_0}{R_{00}\sigma_1}k_1 + \frac{R_{02}\sigma_0}{R_{00}\sigma_2}k_2 + \frac{R_{03}\sigma_0}{R_{00}\sigma_3}k_3 + \ldots + \frac{R_{0n}\sigma_0}{R_{00}\sigma_n}\right)k_n \ldots \quad \text{(vi)}.$$

The standard deviation of x_0 for this array is

$$\Sigma_0 = \sigma_0\sqrt{R/R_{00}} \quad \cdots\cdots\cdots\cdots\cdots \quad \text{(vii)}.$$

These results (vi) and (vii) are the regression formulæ.*

Now let $x_1, x_2 \ldots x_n$ be the mid-parental values of the 1st, 2nd, 3rd, $\ldots$ nth order, and $\bar{x}_0 = k_0$ the mean value of the organ in the offspring.

Then the value of R is given by

$$R = \begin{vmatrix} 1, & \rho_1, & \rho_2, & \rho_3, & \rho_4 \ldots \rho_n \\ \rho_1, & 1, & \rho_1, & \rho_2, & \rho_3 \ldots \rho_{n-1} \\ \rho_2, & \rho_1, & 1, & \rho_1, & \rho_2 \ldots \rho_{n-2} \\ \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots \\ \rho_n, & \rho_{n-1} & \cdots\cdots\cdots\cdots 1 \end{vmatrix} \quad \cdots\cdots \quad \text{(viii)}.$$

and the regression formula is :

$$k_0 = -\left(\frac{R_{01}}{R_{00}}\frac{\sigma_0}{\Sigma_1}k_1 + \frac{R_{02}}{R_{00}}\frac{\sigma_0}{\Sigma_2}k_2 + \ldots + \frac{R_{0n}}{R_{00}}\frac{\sigma_0}{\Sigma_n}k_n\right),$$

if we stop at the nth mid-parent.

Comparing this result with the analytical statement of Mr. Galton's law of ancestral heredity given on p. 388, we see that we must have from (v) :

$$\left. \begin{array}{l} R_{01}/R_{00} = -\dfrac{1}{2}\dfrac{\Sigma_1}{\sigma_1} = -\dfrac{1}{2\sqrt{2}} \\[2mm] R_{02}/R_{00} = -\dfrac{1}{4}\dfrac{\Sigma_2}{\sigma_2} = -\left(\dfrac{1}{2\sqrt{2}}\right)^2 \\[1mm] \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots \\ R_{0q}/R_{00} = -\dfrac{1}{2^q}\dfrac{\Sigma_q}{\sigma_q} = -\left(\dfrac{1}{2\sqrt{2}}\right)^q \\ \cdots\cdots\cdots\cdots\cdots\cdots\cdots\cdots \end{array} \right\} \cdots\cdots\cdots \quad \text{(ix)}.$$

There will be n such equations, if we go to the mid-nth parent, and there are n quantities $\rho_1, \rho_2 \ldots \rho_n$ to find. Thus Mr. Galton's statement that the *partial* regression coefficients are $\frac{1}{2}, \frac{1}{4}, \frac{1}{8} \ldots$

* See 'Phil. Trans.,' A, vol. 187, p. 302.

gives us sufficient equations to find the coefficients of *total* correlation between the offspring and the successive mid-parents. Equations (v) will then enable us to find the coefficients of correlation between an individual and any individual ancestor. But these in their turn will suffice to determine all inheritance whether direct or *collateral* (see below). In short if Mr. Galton's law can be firmly established, *it is a complete solution, at any rate to a first approximation, of the whole problem of heredity.* It throws back the question of inheritance upon two constants, which can be once and for all determined; herein lies its fundamental importance. I must confess that this element of simplicity was at first my chief difficulty in accepting the law as laid down in the paper on Basset hounds, and I even yet have a certain hesitation, owing to an apparent difference in collateral heredity in different social classes, and also to the apparent numerical value of the inheritance of fertility in man.

(5) I shall next obtain a solution of equations (ix). Taking the minors of the $n+1$ constituents of the first row, namely, R_{00}, R_{01}, R_{02}, ... R_{0n}, and multiplying them in succession by the constituents of the 2nd, 3rd .... $n+1$th row of R, we have by the ordinary theory of determinants the system :

$$\rho_1 R_{00} + R_{01} + \rho_1 R_{02} + \rho_2 R_{03} + \; .... \; + \rho_{n-1} R_{0n} = 0.$$

$$\rho_2 R_{00} + \rho_1 R_{01} + R_{02} + \rho_1 R_{03} + \; .... \; + \rho_{n-2} R_{0n} = 0.$$

$$\bullet \circ \bullet$$

$$\rho_q R_{00} + \rho_{q-1} R_{01} + \rho_{q-2} R_{02} + \rho_{q-3} R_{03} + \; .... \; + \rho_{n-q} R_{0n} = 0.$$

$$\bullet \bullet$$

$$\rho_n R_{00} + \rho_{n-1} R_{01} + \rho_{n-2} R_{02} + \rho_{n-3} R_{03} + \; .... \; + R_{0n} = 0.$$

Divide each of these equations by R_{00} and let us use instead of (ix) the somewhat more general system which will allow us to consider one or two limiting cases, and rather more generally than Mr. Galton has done "to tax the bequests of each generation," as he expresses it :[*]

$$\frac{R_{01}}{R_{00}} = -\gamma\beta, \qquad \frac{R_{02}}{R_{00}} = -\gamma\beta^2, \qquad \frac{R_{03}}{R_{00}} = -\gamma\beta^3, \quad \&c. \; .. \quad (x),$$

where γ and β are two constants ; we then find :

$$-\rho_1 + \gamma\beta + \gamma\beta^2\rho_1 + \gamma\beta^3\rho_2 + \;\ldots\ldots + \gamma\beta^n\rho_{n-1} = 0.$$

$$-\rho_2 + \gamma\beta\rho_1 + \gamma\beta^2 + \gamma\beta^3\rho_1 + \;\ldots\ldots + \gamma\beta^n\rho_{n-2} = 0.$$

$$\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

$$-\rho_q + \gamma\beta\rho_{q-1} + \gamma\beta^2\rho_{q-2} + \gamma\beta^3\rho_{q-3} + \;\ldots\ldots + \gamma\beta^n\rho_{n-q} = 0.$$

$$-\rho_{q+1} + \gamma\beta\rho_q + \gamma\beta^2\rho_{q-1} + \gamma\beta^3\rho_{q-2} + \;\ldots\ldots + \gamma\beta^n\rho_{n-q-1} = 0.$$

$$\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

$$-\rho_n + \gamma\beta\rho_{n-1} + \gamma\beta^2\rho_{n-2} + \gamma\beta^3\rho_{n-3} + \;\ldots\ldots + \gamma\beta^n = 0.$$

Multiply the $\overline{q+1}$th equation by $1/\beta$, and subtract from the qth; we have

$$\frac{1}{\beta}\rho_{q+1} - \rho_q(1+\gamma) + \gamma\beta^n\rho_{n-q} = 0 \;\ldots\ldots\ldots \quad \text{(xi)}.$$

Assume $\rho_q = c\alpha^q$, hence :

$$\frac{\alpha}{\beta} - (1+\gamma) + \gamma\beta^n\alpha^{n-2q} = 0.$$

But since α and β are both less than unity, the last term will be vanishingly small when n is indefinitely large, thus :

$$\alpha = \beta(1+\gamma) \;\ldots\ldots\ldots\ldots\ldots \quad \text{(xii)}.$$

Substituting $\rho_q = c\alpha^q$ in the first of the equations for the ρ's above, we have :

$$c\left(-\alpha + \gamma\beta\frac{\beta\alpha - \beta^n\alpha^n}{1-\beta\alpha}\right) = -\gamma\beta.$$

Or, taking as before $(\alpha\beta)^n = 0$ for n very large :

$$c = \frac{1-\beta\alpha}{\alpha\left(\dfrac{1}{\gamma\beta} - \beta - \dfrac{\alpha}{\gamma}\right)},$$

$$c\alpha = \frac{1-\beta^2(1+\gamma)}{\dfrac{1}{\gamma\beta} - \beta\dfrac{(1+2\gamma)}{\gamma}}, \;\ldots\ldots\ldots\ldots \quad \text{(xiii)}.$$

(xii) and (xiii) contain a complete solution of the fundamental equations for the ρ's given above, so long as we go only to a finite number of mid-parents, *i.e.*, q may be very large, but not comparable with $n = \infty$.

(6) *Special Cases.*

(*a*) Put $\gamma = 1$, $\beta = \frac{1}{2}$. It follows that $\alpha = 1$, and $c = 1$. Hence if

$$\frac{\mathrm{R}_{0q}}{\mathrm{R}_{00}} = -\frac{1}{2^q},$$

all the total mid-parental correlations would be perfect, and, there-fore, any one mid-parent would suffice to fully determine any other and the offspring. The individual parental correlations would then be

$$\frac{1}{\sqrt{2}}, \quad \frac{1}{2}, \quad \frac{1}{2\sqrt{2}}, \quad \frac{1}{4}, \quad \ldots$$

for parent, grandparent, great-grandparent, &c., with offspring.*

(*b*) More generally, suppose any values of γ and β which lead to $c = 1$, then

$$c = 1 = \frac{1 - \beta^2(1+\gamma)}{\dfrac{\gamma+1}{\gamma}[1 - \beta^2(1+2\gamma)]},$$

whence we find $\beta(\gamma+1) = 1$, that is, $\alpha = 1$; or again, all mid-parental correlations are perfect. Thus, as in case (i), the individual parental correlations could be represented by

$$r, \quad r^2, \quad r^3, \quad \ldots$$

These are the values I took in my memoir of 1895.† I took these values then because they seemed to express Mr. Galton's method of passing from individual parental to individual grand-parental total regression.‡ I had not perceived that there was any antinomy between Mr. Galton's theory of regression and his law of ancestral heredity. Had I done so I should certainly, at that date, have given the preference to the former, and rejected his law of partial coeffi-cients of regression in favour of the values, based on numerical observation, of his total regression coefficients.

(*c*) Put $\gamma = 1$, $\beta = \dfrac{1}{2\sqrt{2}}$; this is Mr. Galton's form of the law. We find at once

$$\alpha = \frac{1}{\sqrt{2}}, \qquad c = \frac{3}{5} = 0\cdot6.$$

Hence we have for the successive mid-parental correlations ρ_1, ρ_2, ρ_3, &c.,

$$\frac{0\cdot6}{\sqrt{2}}, \quad 0\cdot3, \quad \frac{0\cdot3}{\sqrt{2}}, \quad \&c.$$

and for the individual *mean* parental correlations, r_1, r_2, r_3, &c.

$$0\cdot3, \quad 0\cdot15, \quad 0\cdot075, \quad \&c.$$

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* This is what, I think, must follow from any theory of the "continuity of the germ plasma," and of its exact quantitative addition and bisection on sexual repro-duction.

† 'Phil. Trans.,' A, vol. 187, pp. 303–5.

‡ See 'Natural Inheritance,' p. 133. Mr. Galton puts $r = \frac{1}{3}$ for a parent, $r^2 = \frac{1}{9}$ for a grandparent, and so on.

Here

$$r_1 = \tfrac{1}{4}\,(r_1' + r_1'' + r_1''' + r_1''''), \qquad r_2 = \tfrac{1}{8}\,S(r_2'), \quad \&c.$$

Further, for the regressions on the mid-parents (not partial but total), or $\rho_1\dfrac{\sigma_0}{\Sigma_1}$, $\rho_2\dfrac{\sigma_0}{\Sigma_2}$, $\rho_3\dfrac{\sigma_0}{\Sigma_3}$, &c., we have, on the assumption that all generations are equally variable,

$$0\text{·}6, \quad 0\text{·}6, \quad 0\text{·}6, \quad \&c.$$

Or we may express the law of ancestral heredity in Mr. Galton's form in the following simple statement:—*The total regression of the progeny on the mid-parent of any generation is constant and equal to* 0·6.

Let us see how these results agree with observations. Mr. Galton[*] tells us that his first estimate of mid-parental regression was $3/5 = 0\text{·}6$. This estimate exactly agrees with theory. He afterwards[†] changed the value to $2/3 = 0\text{·}67$, which is less in agreement. My own calculations,[‡] on Mr. Galton's data, give $r_1' = 0\text{·}3959$, $r_1'' = 0\text{·}3603$, $r_1''' = 0\text{·}2841$, $r_1'''' = 0\text{·}3018$, or $r_1 = 0\text{·}3355$ instead of 0·3. The probable error is, however, 0·026. If we do not weight fertility the parental correlation[§] $= 0\text{·}41 \pm 0\text{·}03$, a value which is distinctly too high for Galton's law. It must be remembered, however, that our deductions from that law are based on equality of variation in each generation, and that this equality is by no means the fact. I hope shortly to get final values for parental heredity from my family measurements, which have now reached a total of nearly 1,100 families, and thus settle how far Galton's law needs to be modified. On the whole the confirmation obtained from stature data for the law of ancestral heredity is very striking;[||] I am inclined to think even more convincing than that obtainable from the Basset hounds, and this for a reason to be considered later. It suffices here to observe that we do not need to know the characters of parents, grand-parents, great grand-parents to test Mr. Galton's law ; any single relationship, near or far, direct or collateral (see below), will bring its quota of evidence for or against the law.

It will be seen that the table (p. 397) differs in principle from Mr. Galton's on p. 133 of his 'Natural Inheritance.' In particular, supposing equal variability for all generations, the individual grand-parental regression is not the square of the parental regression, but the *half* of it. Mr. Galton's law of ancestral heredity contradicts

* 'Natural Inheritance,' p. 97.

† *Ibid.*, p. 97.

‡ 'Phil. Trans.,' A, vol. 187, p. 270.

§ 'Roy. Soc. Proc.,' vol. 60, p. 279.

|| Good evidence in its favour is also to be deduced from the inheritance of the cephalic index. See paper by Fawcett and Pearson, *infrà*, p. 413.

Table of Heredity according to Galton's Law.

Order.	Individual parent.	Mid-parent.	
	Correlation and regression.	Correlation.	Regression.
1	0·3000	0·4243	0·6
2	0·1500	0·3000	0·6
3	0·0750	0·2121	0·6
4	0·0375	0·1500	0·6
5	0·01875	0·1061	0·6
6	0·009375	0·0750	0·6
....	....	....	....
qth	$0 \cdot 6 \left(\dfrac{1}{2}\right)^q$	$0 \cdot 6 \left(\dfrac{1}{\sqrt{2}}\right)^q$	0·6

Remarks.—The correlation of the individual first parent is to be taken as the mean of the four possible parental correlations due to differences of sex, if these are not sensibly equal, and a like rule holds for the individual sth parent. The individual parental regression is based on the assumption that the variability of offspring and parent are the same. In dealing with the mid-parent, female deviations must first be reduced to male by multiplying them by the ratio of male to female variability.

his views on regression, and it is the latter which, judging from both theory and observation, I now hold must be discarded.*

(7) Mr. Galton's law gives us the partial regression coefficients when *all* the mid-parents are known. It is desirable to deduce from the theory of multiple correlation the values of the partial regression coefficients when we take 1, 2, 3, 4,.... mid-parents only. When q mid-parents are taken let the partial regression coefficients be ϵ_{1q}, ϵ_{2q}, ϵ_{3q}, ϵ_{4q}, ... ϵ_{qq}; then again we have for the mean of the offspring k_0:

$$k_0 = \epsilon_{1q} \frac{\sigma_0}{\sigma_1} k_1 + \epsilon_{2q} \frac{\sigma_0}{\sigma_2} k_2 + \ldots + \epsilon_{qq} \frac{\sigma_0}{\sigma_q} k_q \ldots \ldots \quad \text{(xiv)},$$

where σ_0 is the standard deviation of the offspring and σ_p of the pth parental generation. Comparing this with the regression formula immediately under (viii) we have

$$\epsilon_{pq} = -\frac{\mathrm{R}_{0p}}{\mathrm{R}_{00}} \frac{\sigma_p}{\Sigma_p} = -2^{\frac{1}{2}p} \frac{\mathrm{R}_{0p}}{\mathrm{R}_{00}}, \quad \text{by (v)}.$$

* I do not agree with the last column of Mr. Galton's table giving the variability of arrays. For single correlation the variability (standard deviation) of an array $= \sigma \sqrt{1 - r^2}$, where r is the correlation and *not* the regression. With equal variability of all generations, r in the case of the individual parent may be replaced by the regression. But the correlation is not equal to the regression in the case of mid-parents, because the variability of the mid-parent by (v) is increasingly less than that of the offspring.

Now make use of the general equations for the ρ's given just below equation (x), substituting for the R's in terms of the ϵ's, and remembering that we are to stop at $n = q$, that $\rho_p = c\alpha^p$, and that $1/\sqrt{2} = \alpha$. We have after some reductions the system:

$$1 = \frac{1}{c}\epsilon_{1q} + \alpha^2\epsilon_{2q} + \alpha^4\epsilon_{3q} + \alpha^6\epsilon_{4q} + \ldots + \alpha^{2q-2}\epsilon_{qq},$$

$$1 = \epsilon_{1q} + \frac{1}{c}\epsilon_{2q} + \alpha^2\epsilon_{3q} + \alpha^4\epsilon_{4q} + \ldots + \alpha^{2q-4}\epsilon_{qq},$$

$$1 = \epsilon_{1q} + \epsilon_{2q} + \frac{1}{c}\epsilon_{3q} + \alpha^2\epsilon_{4q} + \ldots + \alpha^{2q-6}\epsilon_{qq},$$

$$\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

$$\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots$$

$$1 = \epsilon_{1q} + \epsilon_{2q} + \epsilon_{3q} + \ldots + \frac{1}{c}\epsilon_{q-1\,q} + \alpha^2\epsilon_{qq},$$

$$1 = \epsilon_{1q} + \epsilon_{2q} + \epsilon_{3q} + \ldots + \epsilon_{q-1\,q} + \frac{1}{c}\epsilon_{qq}.$$

Subtracting the $(q-1)$th of these equations from the qth, the $(q-2)$th from the $(q-1)$th, &c., and introducing the values of $\alpha^2 = \frac{1}{2}$ and of $c = 0\cdot6$, we find

$$0\cdot4\,\epsilon_{q-1\,q} - 0\cdot7\,\epsilon_{qq} = 0.$$

$$0\cdot4\,\epsilon_{q-2\,q} - 0\cdot7\,\epsilon_{q-1\,q} - 0\cdot15\,\epsilon_{qq} = 0 \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\quad \text{(xv)}.$$

$$0\cdot4\,\epsilon_{q-3\,q} - 0\cdot7\,\epsilon_{q-2\,q} - 0\cdot15\,\epsilon_{q-1\,q} - 0\cdot075\,\epsilon_{qq} = 0.$$

$$0\cdot4\,\epsilon_{q-4\,q} - 0\cdot7\,\epsilon_{q-3\,q} - 0\cdot15\,\epsilon_{q-2\,q} - 0\cdot075\,\epsilon_{q-1\,q} - 0\cdot375\,\epsilon_{qq} = 0.$$

and so on, each new coefficient being now half the last. These equations give successively the ratios of $\epsilon_{q-1\,q}$, $\epsilon_{q-2\,q}$, $\epsilon_{q-3\,q}$, &c., to ϵ_{qq}. Hence the last of the previous set of equations will then give ϵ_{qq}. Thus the partial regression coefficients for any limited number of mid-parents can be found. This last equation also gives us

$$S(\epsilon) = 1 - \frac{1-c}{c}\epsilon_{qq} = 1 - \frac{2}{3}\epsilon_{qq},$$

a convenient formula for measuring how nearly the mean offspring of q mid-parents, all selected with a peculiar character, $k_1 = k_2 = k_3 = \ldots = k_q = K$ has attained that character. For in this case

$$k_0 = S(\epsilon k) = K \times S(\epsilon),$$

and $$k_0/K = 1 - \frac{2}{3}\epsilon_{qq} \ldots\ldots\ldots\ldots\ldots\ldots\quad \text{(xvi)}.$$

Hence the more nearly $1 - \frac{2}{3}\epsilon_{qq} =$ unity the more nearly the offspring has the full character of its selected parentage. I venture to call this expression the *stability of the stock*. It is a measure of the stock breeding true.

Lastly, to find the standard deviation of the array $= \sigma_0\sqrt{\overline{R/R_{00}}}$ we have only to express R in terms of the minors of its first row, or,

$$R = R_{00} + \rho_1 R_{01} + \rho_2 R_{02} \ldots + \rho_q R_{0q}.$$

$$R/R_{00} = 1 - c\left(\epsilon_{1q}z^2 + \epsilon_{2q}z^4 + \epsilon_{3q}z^6 + \ldots + \epsilon_{qq}z^{2q}\right)$$

$$= 1 - 0\cdot 3\left(\epsilon_{1q} + \frac{1}{2}\epsilon_{2q} + \frac{1}{4}\epsilon_{3q} + \ldots + \frac{1}{2^{q-1}}\epsilon_{qq}\right)\ldots\ldots\ldots \quad (xvii).$$

In the limit when $q = \infty$

$$R/R_{00} = 1 - 0\cdot 3 \times \tfrac{1}{2}\left(1 + \tfrac{1}{4} + \tfrac{1}{16} + \ldots\right) = 1 - 0\cdot 2 = 0\cdot 8,$$

and $$\sqrt{\overline{R/R_{00}}} = 0\cdot 8944.$$

The following table has been calculated from these formulæ:—

Table of Pedigree Stock according to Galton's Law.*

Number of generations.	Ratio of variability of offspring to that of whole population.	Partial regression coefficients.						Stability. S(ϵ).
		ϵ_1.	ϵ_2.	ϵ_3.	ϵ_4	ϵ_5.	ι_6.	
1	0·9055	0·6	—	—	—	—	—	0·6000
2	0·8946	0·5122	0·2927	—	—	—	—	(0·5) 0·8049
3	0·8945	0·5015	0·2553	0·1459	—	—	—	(0·75) 0·9027
4	0·89445	0·5002	0·2507	0·1276	0·0729	—	—	(0·875) 0·9514
5	0·8944	0·5000	0·2501	0·1253	0·0638	0·0365	—	(0·9375) 0·9717
6	0·8944	0·5000	0·2500	0·1250	0·0627	0·0319	0·0182	(0·9687) 0·9879
∞	0·8944	0·5000	0·2500	0·1250	0·0625	0·03125	0·015625	(0·9844) 1

* To save possible labour, in case it should ever be needed to investigate the partial regression coefficients for more generations, I place here the ratios of the first six ϵ's:

$\epsilon_{q-1\,q}/\epsilon_{qq} = 1\cdot 75$; $\epsilon_{q-2\,q}/\epsilon_{qq} = 3\cdot 4375$; $\epsilon_{q-3\,q}/\epsilon_{qq} = 6\cdot 859,375.$
$\epsilon_{q-5\,q}/\epsilon_{qq} = 13\cdot 714,843$; $\epsilon_{q-6\,q}/\epsilon_{qq} = 27\cdot 428,709.$

(8) I venture to think this table of considerable suggestiveness, and will now point out some of the conclusions that may be drawn from it.

(i) With a view of reducing the *absolute* variability of a species it is idle to select beyond the grandparents, and hardly profitable to select beyond parents. The ratio of the variability of pedigree stock to the general population decreases 10 per cent. on the selection of parents, and only 11 per cent. on the additional selection of grand-parents. Beyond this no sensible change is made. We cannot then reduce variability beyond 11 per cent. by the creation of a pedigree stock, *i.e.*, by breeding from selected parents for 2, 3, 4, ... n generations. In some cases of course we appear to decrease variability—for example, if we *increase* the average size of an organ—for the *absolute* variability is then a smaller proportion of the actual size, and the relative variability, or coefficient of variation, may thus be steadily decreased. If Mr. Galton's law be true, then pedigree stock would retain only a slightly diminished capacity for variation about the new type. For example, the absolute variability of men of average height, 69·2 inches, being 2·6 inches, the absolute variability of men of 72 inches, obtained by selecting any number of 6-foot ancestors, would hardly fall short of 2·3 inches.*

(ii) Two different classes of pedigree stock exist. In the one we start with the general population, and select special characters for 1, 2, 3, ... n generations. In the other we know the pedigree for 1, 2, 3, ... n generations, but have no reason for supposing that before these generations the stock was absolutely identical with the general population.

In the former case we put for the mid-parents

$$k_1 = k_2 = k_3 = \ldots = k_n = K, \quad k_{n+1} = k_{n+2} = \ldots = k_\infty = 0.$$

Hence the regression formula is

$$k_0 = \left(\tfrac{1}{2} + \tfrac{1}{4} + \tfrac{1}{8} + \ldots + \frac{1}{2^n} \right) K = \left(1 - \frac{1}{2^n} \right) K.$$

The values of k_0/K are tabulated in the last column of the table above in brackets. They give the ratio of character in offspring to character in ancestors, if ancestors of equal full character have been selected for n generations. We see that in six generations the offspring will have been raised to within 1·6 per cent. of the selected ancestral character.

In the latter case we must use the partial regression coefficients

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* The probability of an individual of selected stock differing widely from the type is of course much less than in the general population, because the stock is, as a rule, far less numerous.

ϵ_1, ϵ_2 .... of the table. For example, in the case of Mr. Galton's Basset hounds, $0\cdot5015$, $0\cdot2553$, and $0\cdot1459$ were the coefficients to be used, rather than $0\cdot5$, $0\cdot25$, and $0\cdot125$, when he proceeded to apply the law to three generations. These give the proper allowance for the ancestry beyond the pedigree. Thus the great-grandparents ought to have been given about a fifth more weight. If we proceed to six generations in pedigree stock of the latter type then the offspring will be within $1\cdot2$ per cent. of the selected ancestry, *i.e.*, their stability as given by the last column $= 0\cdot9879$.

(iii) Now let us apply these results to the all-important problem of panmixia and degeneration. Suppose a selection made of a particular character for n generations, starting from the general population. Then the offspring in the $(n+1)$th generation will have $1-\dfrac{1}{2^n}$ of the character on the average. Now, stopping selection, let us breed with a first generation of mid-parents with $1-\dfrac{1}{2^n}$ of the character. The offspring will have:

$$\frac{1}{2}\left(1-\frac{1}{2^n}\right)+\frac{1}{4}+\frac{1}{8}+\frac{1}{16}+\ldots+\frac{1}{2^{n+1}}$$

$$=\frac{1}{2}\left(1-\frac{1}{2^n}\right)+\frac{1}{2}\left(1-\frac{1}{2^n}\right)-1-\frac{1}{2^n} \text{ of the character.}$$

The $\overline{n+2}$th generation will have:

$$\frac{1}{2}\left(1-\frac{1}{2^n}\right)+\frac{1}{4}\left(1-\frac{1}{2^n}\right)+\frac{1}{8}+\frac{1}{16}+\ldots+\frac{1}{2^{2n+2}}$$

$$=\frac{1}{2}\left(1-\frac{1}{2^n}\right)+\frac{1}{4}\left(1-\frac{1}{2^n}\right)+\frac{1}{4}\left(1-\frac{1}{2^n}\right)=1-\frac{1}{2^n}$$

of the character, and so on. The law is obvious; the offspring will always have the same amount of the character as had the generation after selection ceased. If we start with pedigree stock with *unknown* ancestry beyond the nth generation, we reach the same conclusion. Thus, after three generations the offspring will have $0\cdot9027$ of the selected parents' character. Now stop selection and the fourth generation will have:

$$0\cdot9027\ \epsilon_1+\epsilon_2+\epsilon_3+\epsilon_4$$

$$=0\cdot4515+0\cdot2507+0\cdot1276+0\cdot0729=0\cdot9027,$$

the fifth generation will have

$$0\cdot9027\ (\epsilon_1+\epsilon_2)+\epsilon_3+\epsilon_4+\epsilon_5=0\cdot9027,$$

again, and so on. The general law is obvious.

2 G

Thus, on the basis of the law of ancestral heredity the case against panmixia is even stronger than it appeared in my memoir on heredity.*   Assuming Mr. Galton's law of regression, I there showed that panmixia was possible with a stable focus of regression, but that the supporters of the consistent theory of panmixia must place that focus of regression, in order that degeneration should be continuous, in a position inconsistent with observed facts (p. 314).   We now see that with the law of ancestral heredity even this is not possible, a race with six generations of selection will breed within 1·2 per cent. of truth ever afterwards, unless the focus of regression instead of being steady actually regredes.   Of course there are many ways in which this law may be modified.   For example, fertility may be a maximum with the average, say, of the unselected original population, and after a selection it may remain correlated, having the lesser values of the selected character more fertile than others.†   Then, of course, the stock would degenerate with panmixia.‡   This would, however, be reproductive selection, not panmixia in the ordinary significance, reversing natural selection.   We are far too ignorant at present of the correlation of fertility with other characters to base any sweeping principle like that of degeneration by panmixia upon it.   Our attitude at present can only be that there are no facts, and that there is no workable theory of heredity yet discovered which favours in any way degeneration by panmixia.

(9) *Taxation of Inheritance.*—If we assume Mr. Galton's law of ancestral heredity to be a limiting statement, we can at once from our general formulæ ascertain the influence of "taxing the inheritance" in any other than Mr. Galton's form.   He has, in fact, taxed the inheritance (where by "inheritance" I understand deviation from the mean of the general population, not actual size of the character), 50 per cent. in each transmission.   There may, however, be two types of taxation, a general taxation on the individual receipts and a special tax on each transmission—corresponding, so to speak, to a duty paid by an individual on coming into receipt of the entire ancestral property, and a stamp duty on each conveyance of an individual ancestor's contribution.   The first is represented by the γ of our equation (x), and the second by the $\sqrt{2\beta}$.

Mr. Galton, in his memoir on Basset hounds, has stated certain conditions of the law of ancestral heredity, and he concludes (p. 403) that his conditions are only fulfilled by the series

$$\tfrac{1}{2} + (\tfrac{1}{2})^2 + (\tfrac{1}{3})^2 + \ldots$$

* 'Phil. Trans.,' A, vol. 187, p. 308 *et seq.*

† This is how I should at present account for the degeneration of pedigree wheat.

‡ Some influence of this kind is possibly sensible in highly civilised communities. See "Reproductive Selection," in my 'Chances of Death,' vol. 1, pp. 98 *et seq.*

It seems to me that they are equally well fulfilled by the series

$$\gamma\beta' + \gamma\beta'^2 + \gamma\beta'^3 + \ldots,$$

provided the sum of this series is equal to unity,

or $\qquad \gamma\beta'/(1-\gamma\beta') = 1$, that is $\gamma\beta' = \frac{1}{2}$.

But $\qquad \gamma\beta'^q = -\dfrac{R_{0q}}{R_{00}}\dfrac{\sigma_q}{\Sigma_q} = \gamma\beta^q \times (\sqrt{2})^q$ by (x),

or $\beta' = \sqrt{2}\beta$ of our previous notation.

Hence the conditions laid down are fulfilled by our general solution (x) provided

$$\gamma\beta = \frac{1}{2\sqrt{2}} \ldots\ldots\ldots\ldots\ldots\ldots (\text{xvii}).$$

I do not assert that such a law is more probable than Mr. Galton's, or indeed as simple. But it throws back the theory of inheritance on at least one arbitrary constant γ, and therefore while covering Mr. Galton's law of ancestral heredity ($\gamma = 1$), allows a greater scope for variety of inheritance in different species.

It seems worth while to notice the changes that result in ancestral correlation when we put on a total " tax " γ. As a numerical illustration, take this tax at 10 per cent., then $\gamma = \frac{9}{10}$. We find

$$\beta = 0\cdot39284, \text{ and by (xii) and (xiii)}:$$

$$\alpha = 0\cdot74639. \quad c = 0\cdot58953.$$

From these values we can form a table exactly like that on p. 397. On examination of it, we see that the effect of a " general tax " is to increase sensibly all the correlations. In particular the more distant ancestry play a relatively greater part than they would do under Mr.

Table of Heredity. Tax 10 per cent.

Order.	Individual parent.	Mid-parent.	
	Correlation and regression.	Correlation.	Regression.
1	0·3111	0·4400	0·6223
2	0·1642	0·3284	0·6569
3	0·0867	0·2451	0·6933
4	0·0457	0·1830	0·7319
5	0·0241	0·1366	0·7725
6	0·0127	0·1019	0·8154
qth	$0\cdot5895(0\cdot5278)^q$	$0\cdot5895(0\cdot7464)^q$	$0\cdot5895(1\cdot0556)^q$

Galton's unmodified law. Now the direct correlations as given by that law certainly appear somewhat small for both stature and cephalic index in man. Hence it is quite possible that when more extensive data are forthcoming, it will be found necessary to modify Mr. Galton's form and take γ less than unity. The above table will suffice to indicate the general direction of the correlation changes which result when γ is varied. One point should be noticed, the *total* regression on an individual mid-parent (note, not the *partial* regression) continually increases as we go further back, and will ultimately be greater than unity; in our case this will happen at the 10th generation. Now in such a generation an individual has 1024 10th great-grandparents, and, were they independent, the mean of these could hardly differ widely from the population mean. Hence the total regression coefficient being greater than unity is not so significant as it might at first sight seem. What it amounts to is this : that if we only knew of an individual that his mid-parent in a very distant generation had more of a character than the then population mean, and knew nothing about his other mid-parents, then the individual would probably have more of that character than the mid-parent. The apparent paradox arises from the very small variability of a distant mid-parent, and hence the extreme improbablility of a mid-parent differing very widely from the population mean. Of course with close in-and-in breeding the modification introduced by assortative mating could not be neglected, and our whole investigation would need modification.* Until, however, we have more measurements to deal with, it is idle to develop at length all the consequences which flow from the generalised form of Galton's law.

(10) *Collateral Heredity.*—There is another point on which the law of ancestral heredity gives us full information, namely, the correlation between brothers, cousins, and all other collateral relatives. In my memoir of 1895, I felt bound to reject Mr. Galton's regression coefficient for brothers, because its value seemed to me in contradiction with experience. I wrote (p. 285) :—

" There is not, I think, sufficient ground at present for forming any definite conclusion as to the manner in which lineal is related to collateral heredity. It does not seem to me necessary that the coefficient for the former should be half that for the latter, as supposed by Mr. Galton."

And again :—

* I hope to return to this point again. We have neglected e in equations (ii) and (iv). In endeavouring to follow back my own family to its fourth, and even sixth great-grandparents, I was surprised to find only one first and one second cousin marriage among the ascertainable ancestors. According, however, to O. Lorenz (' Lehrbuch der Genealogie,' s. 305), the present German Emperor has only 44 instead of 64 sixth parents, and 275 instead of 4096 twelfth parents !

" I doubt whether the correlation coefficients for collateral hered-ity—at any rate in the middle classes—can be greater than 0.5."

Strangely enough Mr. Galton's law of ancestral heredity which I then rejected, while accepting a part of what I now consider his erroneous theory of regression, gives just the link between linear and collateral heredity which I was then seeking!

Let x_1 and x_2 be the deviation of two brothers forming part of the array having

$$k_0 = \gamma\beta' k_1 + \gamma\beta'^2 k_2 + \gamma\beta'^3 k_3 + \ldots.$$

for its mean, x_1 and x_2 being measured from the general population mean. Let x_1 and x_2 differ from the mean of the array by x' and x'', then

$$x_1 x_2 = (k_0 + x')(k_0 + x'').$$

Now let us sum $x_1 x_2$ for all pairs of brothers in a given array, then since x' and x'' correspond to any pair of chance deviations within the array $S(x'x'') = 0$, $S(x') = S(x'') = 0$. Hence for the array $S(x_1 x_2) = S(k_0^2) = 2n k_0^2$,[*] where n is the number of pairs of brothers in the population with the series of mid-parents k_1, k_2, k_3, &c. Now write

$$k_0 = \gamma\beta \frac{\sigma_0}{\Sigma_1} k_1 + \gamma\beta^2 \frac{\sigma_0}{\Sigma_2} k_2 + \gamma\beta^3 \frac{\sigma_0}{\Sigma_3} k_3 + \ldots.$$

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[*] The appearance of the 2 here requires notice. Let there be ν brothers to the array of any single series of mid-parents; then if s be the standard-deviation of the array, the distribution of brothers corresponding to a given k_0

$$= \frac{\nu}{\sqrt{2\pi s}} e^{-\frac{1}{2}(x'/s)^2}.$$

Hence the frequency of a brother between x' and $x' + \delta x'$ occurring with a brother between x'' and $x'' + \delta x''$

$$= \frac{\nu^2}{\sqrt{2\pi s^2}} e^{-\frac{1}{2}(x'/s)^2} dx' \, e^{-\frac{1}{2}(x''/s)^2} dx''.$$

If we take as limits x' and x'', both $= +\infty$ to $-\infty$, we shall clearly take each brother *twice* over with each other brother. Hence—

$$S(x_1 x_2) = \frac{1}{2} \int_{-\infty}^{+\infty} \int_{-\infty}^{+\infty} \frac{\nu^2}{2\pi s^2} (k_0 + x')(k_0 + x'') e^{-\frac{1}{2}\left\{ (x'/s)^2 + (x''/s)^2 \right\}} dx' \, dx'' = \frac{1}{2}\nu^2 k_0^2.$$

Now allow one pair of brothers to each system of mid-parents, and

$$S(x_1 x_2) = 2 k_0^2$$

for one mid-parental system, or if there be n such mid-parental systems,

$$S(x_1 x_2) = 2n k_0^2.$$

Actually the same mid-parental system may be repeated many times, only in this case the possible correlation of fertility with the character under discussion must be guarded against.

and note that

$$S(nk_q^2) = N\Sigma_q^2, \quad S(nk_qk_{q'}) = N\Sigma_q\Sigma_{q'}\,\rho_{nq},$$

where σ_0 is the standard deviation of the offspring, N is the total number of pairs of brothers or mid-parents of each order, and Σq is as before the standard deviation of the group of qth mid-parents. Noticing that $\rho_{q'\sim q} = c\alpha^{(q'\sim q)}$, we have if r be the correlation between brothers

$$N\sigma_0^2 r = S[S(x_1x_2)] = 2S(nk_0^2)$$
$$= 2N\sigma_0^2\,S(\gamma^2\beta^{2q} + 2\gamma^2\beta^{q+q'}c\alpha^{(q'-q)}),$$

the sum now referring to all values of q and q' from 1 to ∞, q being unequal to q', and $q' \sim q$ taken positive.

Thus:
$$r = 2\gamma^2(\beta^2 + \beta^3c\alpha + \beta^4c\alpha^2 + \beta^5c\alpha^3 + \ldots$$
$$+ \beta^3c\alpha + \beta^4 + \beta^5c\alpha + \beta^6c\alpha^2 + \ldots$$
$$+ \beta^4c\alpha^2 + \beta^5c\alpha + \beta^6 + \beta^7c\alpha + \ldots$$
$$+ \beta^5c\alpha^3 + \beta^6c\alpha^2 + \beta^7c\alpha + \beta^8 + \ldots$$
$$+ \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots)$$

Hence summing parallel to the diagonal:

$$r = 2\gamma^2\left\{\frac{\beta^2}{1-\beta^2}\left(1+\frac{2c\alpha\beta}{1-\alpha\beta}\right)\right\}\ldots\ldots\ldots \quad \text{(xviii)}.$$
$$= \frac{2\gamma^2}{8\gamma^2-1-2\gamma} \text{ by (xii), (xiii), and (xvii).}$$

Let us evaluate this on Mr. Galton's law and on the hypothesis of a 10 per cent. tax.*   On the first hypothesis $\beta = \dfrac{1}{2\sqrt{2}}$, $\alpha = \dfrac{1}{\sqrt{2}}$, and $\gamma = 1$, hence $r = 0.4$.   On the second hypothesis (p. 403) $\beta = 0.39284$, $\alpha = 0.74639$, and $\gamma = 0.9$; hence $r = 0.4402$.

We can also obtain less accurate values of fraternal correlation in other ways. Suppose two brothers to be considered as sons of one mid-parent k_1 only. In this case we must take 0.6 for the regression (see the table, p. 403), or

$$x_1 = 0.6k_1 + x', \qquad x_2 = 0.6k_1 + x'',$$

and as before :

$$S(x_1x_2) = 2 \times (0.6)^2 \times S(nk_i^2),$$
$$N\sigma_0^2 r = 2 \times 0.36 \times N\Sigma_1^2,$$
$$r = 0.36.$$

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* [The above value for fraternal correlation shows that γ must be > 0.6076; that α must be < 1, only gives $\gamma > 0.5469$.]

If we suppose two individual parents with no assortative mating, we have

$$r = 2(r_1{}^2 + r_2{}^2) \quad \ldots\ldots\ldots\ldots\ldots\ldots \quad \text{(xix)},$$

where r_1 and r_2 are the male and female parental correlations. With Galton's law $r_1 = r_2 = 0\cdot3$, and r again $= 0\cdot36$. Assuming the value $r_1 = r_2 = \frac{1}{3}$ adopted by Mr. Galton in his 'Natural Inheritance' (p. 133) for parental regression, the fraternal regression deduced from this ought to have been $\frac{4}{9} = 0\cdot44$, and not $0\cdot67$ as obtained by Mr. Galton.* The mean of the sister-sister, brother-brother, brother-sister correlations that I found in 1895,† duly weighted for the number of pairs in each case, is exactly $0\cdot4000$. The value as it might have been *à priori* predicted from Galton's law $= 0\cdot4000$, with a rise to $0\cdot4402$, if we " tax " up to 10 per cent.

I conclude therefore that this law of ancestral heredity is at least to a first approximation in agreement as complete as could possibly be expected with the facts we as yet know as to collateral heredity. It confirms the view I took in 1895, that fraternal heredity cannot be taken greater than $0\cdot5$. I think the high value (about $0\cdot6$) obtained from Mr. Galton's " special data " must be explained by my suggested cause‡ (*a*) *i.e.*, unconscious selection of approximately equal heights in brothers who join Volunteer regiments; for the explanation (*b*) is taken away if we accept Galton's law without a modified γ.

(11) Turning now to the inheritance of cousins, we notice that their regression may be represented by

$$x_1 = \tfrac{1}{4}h_1 + \tfrac{1}{4}k_0 \ldots + \tfrac{1}{4}h_1{}' + \tfrac{1}{4}k_0{}' + x',$$
$$x_2 = \tfrac{1}{4}h_1{}'' + \tfrac{1}{4}k_0 \ldots + \tfrac{1}{4}h_1{}''' + \tfrac{1}{4}k_0{}'' + x''.$$

Here h_1 and $h_1{}''$ are children of the same parents and have fraternal correlation; $h_1{}'$ and $h_1{}'''$ are their other parents, and without a double cousin marriage have no correlation with each other, or neglecting sexual selection with h_1 or $h_1{}''$; k_0 is the mid-parental system§ of h_1, and therefore of $h_1{}''$; $k_0{}'$ and $k_0{}''$ the mid-parental systems of $h_1{}'$ and $h_1{}'''$, and accordingly, if there be no in-and-in breeding, uncorrelated with each other or with k_0.

Summing first for the array corresponding to h_1, $h_1{}''$,

$$\mathrm{S}(x_1 x_2) = n\{\tfrac{1}{16} h_1 h_1{}'' + \tfrac{1}{16} k_0(h_1 + h_1{}'') + \tfrac{1}{16} k_0{}^2\},$$

---

* Mr. Galton took $r = 2r_1$; this is part of what, I think, the erroneous theory of regression developed in 'Natural Inheritance,' a theory which is inconsistent with the law of ancestral heredity given in the same work.

† 'Phil. Trans.' A, vol. 187, p. 281.

‡ 'Phil. Trans.,' A, vol. 187, p. 284.

§ This means that $k_0 = \tfrac{1}{2}k_2 + \tfrac{1}{4}k_3 + \tfrac{1}{8}k_4 + \ldots$ where k_q is the common mid-qth parent of the two cousins.

where n is the number of pairs of cousins corresponding to h_1, h_1''. The factor 2 (see footnote, p. 404) does not occur here, as the cousins form parts of separate, and not identical, arrays. Now let us sum for all possible mid-parental systems, then if r' be the correlation of cousins and N the total number of cousin pairs :

$$N\sigma_0{}^2 r' = S[S(x_1 x_2)]$$
$$= \tfrac{1}{16}\{S(nh_1h_1'') + S[nk_0(h_1 + h_1'')] + S(nk_0{}^2)\}.$$

But $S(nh_1h_1'') = $ product moment for pairs of brothers $= N\sigma_0{}^2 r$.

$S(nk_0{}^2) = N\sigma_0{}^2 r$, by what precedes.

$S[nk_0(h_1 + h_1'')]$ is exactly the same as the sum of *all* offspring with the mid-parental system of ancestry beyond, since h_1 is not to be equal to h_1'',

$$= 2S[nh_1(\tfrac{1}{2}k_2 + \tfrac{1}{4}k_3 + \tfrac{1}{8}k_4 + \ldots)] \text{ for all values of } h_1.$$

$$= 2N(\tfrac{1}{2}\rho_1\sigma_0\Sigma_1 + \tfrac{1}{4}\rho_2\sigma_0\Sigma_2 + \tfrac{1}{8}\rho_3\sigma_0\Sigma_3 + \ldots),$$

$$= 2N\sigma_0{}^2(\tfrac{1}{2}c\alpha^2 + \tfrac{1}{4}c\alpha^4 + \tfrac{1}{8}c\alpha^6 + \ldots),$$

$$= 2N\sigma_0{}^2\frac{\tfrac{1}{2}c\alpha^2}{1 - \tfrac{1}{2}\alpha^2} = 0\cdot4 \times N\sigma_0{}^2.$$

Thus $N\sigma_0{}^2 r' = \tfrac{1}{16}N\sigma_0{}^2(2r + 0\cdot4)$,

and $\qquad\qquad r' = 0\cdot075.$

Mr. Galton's value is $\tfrac{2}{27} = 0\cdot074$ ('Natural Inheritance,' p. 133). Had we, however, applied his method correctly, considering cousins as the offspring of brothers, and adopted the value $0\cdot3$ given by his law of ancestral heredity for parent and offspring, we should have found $0\cdot0360$, instead of our present $0\cdot075$. Considering cousins as having two grandparents the same, we should have found $0\cdot0450$.

Second Cousins.—The correlated parts of their mid-parental systems are

$$\tfrac{1}{4}h_1 + \tfrac{1}{16}h_2 + \tfrac{1}{16}k_0,$$
$$\tfrac{1}{4}h_1' + \tfrac{1}{16}h_2' + \tfrac{1}{16}k_0,$$

where h_1 and h_1' are cousins, h_2 and h_2' brethren, and

$$k_0 = \tfrac{1}{2}k_3 + \tfrac{1}{4}k_4 + \tfrac{1}{8}k_5 + \ldots.$$

is the mid-parental system of h_2 and h_2'.

In order to work out the correlation, we shall clearly want that of h_1 and h_2', or of nephew and uncle.

Here $\qquad\qquad x_1 = \tfrac{1}{4}h_2 + \tfrac{1}{4}k_0 + x' + \ldots$

$$x_2' = k_0 + x'',$$

give the correlated parts of the mid-parental systems.

Hence if r'' be the uncle-nephew correlation and N the total number of pairs

$$N\sigma_0^2 r'' = \tfrac{1}{4}S(nk_0h_2) + \tfrac{1}{4}S(nk_0^2)$$

$$= \tfrac{1}{4}(0\cdot2 + r)N\sigma_0^2,$$

since

$$S(nh_2k_0) = \sigma_0 N(\tfrac{1}{2}\rho_1\Sigma_1 + \tfrac{1}{4}\rho_2\Sigma_2 + \ldots)$$

$$= \sigma_0^2 N(\tfrac{1}{2}c\alpha^2 + \tfrac{1}{4}c\alpha^4 + \ldots)$$

$$= \sigma_0^2 N\frac{\tfrac{1}{2}c\alpha^2}{1 - \tfrac{1}{2}c\alpha^2} = 0\cdot2 \times \sigma_0^2 N.$$

Thus $r'' = 0\cdot15$, or is double the correlation of first cousins. Here, as throughout, the variations of all generations, in this case those of uncles and nephews, have been treated as equal.

Returning to the correlation r''' of second cousins we have

$$N\sigma_0^2 r''' = \tfrac{1}{16}\{S(nh_1h_1') + \tfrac{1}{16}S(nh_2h_2') + \tfrac{1}{16}S(nk_0^2) + \tfrac{1}{4}S(nh_1h_2')$$
$$+ \tfrac{1}{4}S(nh_1'h_2) + \tfrac{1}{2}S\left(nk_0\frac{h_1 + h_1'}{2}\right) + \tfrac{1}{8}S\left(nk_0\frac{h_2 + h_2'}{2}\right)\}.$$

Evaluating each of these terms we have—

$$S(nh_1h_1') = Nr'\sigma_0^2; \quad S(nh_2h_2') = Nr\sigma_0^2; \quad S(nk_0^2) = Nr\sigma_0^2.$$

$$S[n(h_1h_2' + h_1'h_2)] = \text{product moment of } \textit{all} \text{ uncles and nephews}$$
$$= 2Nr''\sigma_0^2.$$

$$S[nk_0(h_1 + h_1')] = \text{product moment of } \textit{all} \text{ offspring and the mid-}$$
parental system of their grandfathers $= 2S(nk_0h_1)$ for all values of h_1

$$= 2S\left[nh_1\left(\tfrac{1}{2}\frac{h_3 + h_3'm}{2} + \tfrac{1}{4}\frac{h_4 + h_4' + m(h_4'' + h_4''')}{4} + \ldots\right)\right]$$

$$= 2(\tfrac{1}{2}r_2\sigma_0^2 N + \tfrac{1}{4}r_3\sigma_0^2 N + \tfrac{1}{8}r_4\sigma_0^2 N + \ldots)$$

$$= 2N\sigma_0^2(\tfrac{1}{2}c\alpha^4 + \tfrac{1}{4}c\alpha^6 + \tfrac{1}{8}c\alpha^8 + \ldots) = 2N\sigma_0^2\frac{\tfrac{1}{2}c\alpha^4}{1 - \tfrac{1}{2}\alpha^2},$$

$$= 2N\sigma_0^4 \times 0\cdot1.$$

Similarly, $S[nk_0(h_2 + h_2')] = 2N\sigma_0^2 \times 0\cdot2$ as before (p. 408).

Thus finally: $r''' = \tfrac{1}{16}(r' + \tfrac{1}{16}r + \tfrac{1}{16}r + \tfrac{1}{2}r'' + \tfrac{1}{4} \times 0\cdot2 + \tfrac{1}{16} \times 0\cdot4)$

or

$$r''' = 0\cdot0171875.$$

More distant collateral relationships, which can be found in like manner, and may be needed for the case of in-and-in breeding, say

from single pairs, are given in the table below. This case, which offers some striking applications of Galton's law, I postpone for the present.

Collateral Heredity according to Galton's Law.

Relationship.	Correlation.
Brethren.....................	0·4000
Uncle and nephew	0·1500
Great uncle and nephew	0·0625
First cousins	0·0750
First cousins once removed	0·0344
Second cousins................	0·0172
Second cousins once removed....	0·0082
Third cousins................	0·0041

Had we regarded second cousins as grandchildren of brethren, we should have found 0·0090 instead of 0·0172 for example, showing the degree of approximation of the incomplete theory.

(12) *On Cross Heredity.*—In my memoir on heredity of 1895, I have defined *cross heredity* as the correlation between different organs in any two relations.[*] If we consider Galton's law of ancestral heredity to be applicable to the inheritance of any character or quality whatsoever, then we can obtain from it a solution of the whole problem of cross heredity. This solution seems so simple and plausible that it deserves careful consideration, and I hope shortly to be able to test it by the measurements in my possession.

Let A and B be any two relatives; 1 and 3 represent any two organs in A, 2 and 4 the same organs in B.

Now suppose we investigate the manner in which the index 1 to 3 is inherited by B, *i.e.*, let us find the correlation between the indices 1 to 3 and 2 to 4. Let ρ be the coefficient of heredity between the degrees of blood A and B, and suppose it by Galton's law to take the same value for all qualities and characters, then r will be the correlation not only between 1 and 2, and 3 and 4, but also between the indices 1 to 3 and 2 to 4. The value of this correlation was given by me in ' Roy. Soc. Proc.,' vol. 60, p. 493, Equation iv, and is

$$\rho = \frac{r_{12}v_1v_2 - r_{14}v_1v_4 - r_{23}v_2v_3 + r_{34}v_3v_4}{\sqrt{v_1^2 + v_3^2 - 2r_{13}v_1v_3} \ \sqrt{v_2^2 + v_4^2 - 2r_{24}v_2v_4}}$$

where v_1, v_2, v_3, v_4 are the coefficients of variation of the four organs, and the r's are their coefficients of correlation.

Now if there be no secular selection $v_1 = v_2$, $v_3 = v_4$, and $r_{13} = r_{24}$;

[*] ' Phil. Trans.,' A, vol. 187, p. 259.

further, by Galton's law, $r_{12} = r_{34} = \rho$, for both are coefficients of direct heredity.

Hence

$$\rho = \frac{(v_1{}^2 + v_3{}^2)\rho - 2v_1 v_3 \dfrac{r_{14} + r_{23}}{2}}{v_1{}^2 + v_3{}^2 - 2v_1 v_3 \mathrm{R}}, $$

where R is the organic correlation between the two organs in the same individual. Thus it follows at once that

$$\tfrac{1}{2}(r_{14} + r_{23}) = \rho \times \mathrm{R}.$$

Or the mean of the two coefficients of cross heredity is the product of the coefficient of direct heredity into the correlation of the two organs in the same individual. Now in all cases of interchangeable relationship, *i.e.*, brother and brother, or cousin and cousin, $r_{14} = r_{23}$, and it is highly probable that this is also true where the relationship is not interchangeable, *e.g.*, parent and offspring.* Thus we reach the exceedingly simple rule for cross heredity. *Multiply the coefficient of direct heredity by the coefficient of organic correlation, and we have the coefficient of cross heredity.*

For example, the organic correlation between femur and humerus is about 0·85 for Aino or French males. Hence we should expect to find the cross heredity between femur of parent and humerus of offspring to be about $0\cdot3 \times 0\cdot85 = 0\cdot25$. Thus Galton's law, even if it be not absolutely correct, will still serve as a useful standard to test the problems of cross heredity.

(13) *Conclusion.*—The above illustrations of Galton's law will suffice to prove the wide extent of its applications. If either that law, or its suggested modification, be substantially correct, they embrace the whole theory of heredity. They bring into one simple statement an immense range of facts, thus fulfilling the fundamental purpose of a great law of nature. It is true that there are difficulties which will have to be met, among which I would note two in particular :

(i) Galton's law makes the amount of inheritance an absolute constant for each pair of relatives. It would thus appear not to be a character of race or species, or one capable of modification by natural selection. This seems to me *a priori* to be improbable. I should imagine that greater or less inheritance of ancestral qualities might be a distinct advantage or disadvantage, and we should expect inheritance to be subject to the principle of evolution. This diffi-

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* For example, the correlation between the arm length of one brother and the stature of a second, must be equal to the correlation between the arm length of the second and the stature of the first. It is probable, but requires statistical confirmation, that the correlation between stature of parent and arm length of offspring is equal to the correlation between arm length of parent and stature of offspring.

culty would be to some extent met by introducing the coefficient γ, which I would propose to call the coefficient of heredity, and consider as capable of being modified with regard to both character and race. As such a law would cover Mr. Galton's case, there does not seem any objection to using the more general formula, until it is found that the strength of heredity is the same for all characters and races. Of course it may well be argued that heredity is something prior to evolution, itself determining evolution, and not determined by it. If this be so, its absolute fixity for all organs and races ought to be capable of observational proof.

(ii) For the inheritance of fertility in man from parent to offspring, Miss Alice Lee has recently worked out 6,000 male, and 4,000 female cases. The result shows that fertility is probably a heritable character, but the correlation between parent and offspring is scarcely one-tenth of that given by Galton's law. The difficulties of any fairly exact determination of the amount of fertility inherited in man under the present artificial conditions are very great, but even allowing for these, I think we must assert that fertility is inherited in man, but in a degree very much less than Galton's law would require.

I hold, then, that, as far as our knowledge goes at present, we must be cautious about treating γ as exactly equal to unity. That is a limiting value which certainly gives strikingly good results for a great deal of what is yet known, but we must wait at present for further determinations of hereditary influence, before the actual degree of approximation between law and nature can be appreciated. Even with regard to such determinations, there must be no haste to assert that they actually do contradict Galton's law. That law states the value of certain *partial* regression coefficients, the total regression coefficients that we have deduced from them are only correct on certain limiting hypotheses, the most important of which are the absence of reproductive selection, *i.e.*, the negligible correlation of fertility with the inherited character, and the absence of sexual selection. I propose to deal with the results of Galton's law, when assortative mating is taken into account, especially in the case of in-and-in breeding, in another paper. At present I would merely state my opinion that, with all due reservations, it seems to me that the law of ancestral heredity is likely to prove one of the most brilliant of Mr. Galton's discoveries; it is highly probable that it is the simple descriptive statement which brings into a single focus all the complex lines of hereditary influence. If Darwinian evolution be natural selection combined with *heredity*, then the single statement which embraces the whole field of heredity must prove almost as epoch-making to the biologist as the law of gravitation to the astronomer.