

separation of the two groups which I suggested in 1887 is fully justified by the recent work to which I have referred. By putting the two groups on the same level of temperature, but on opposite sides of the temperature curve, as in the evolutionary order forming part of the meteoritic hypothesis, the differences are fully explained.

It will be seen that this work carries us a step beyond that with which I have recently been engaged in connection with the hotter stars.

*General Conclusions.*

(1) The undoubted presence of dark carbon flutings in the solar spectrum, including that near *b*, and of solar lines in the Piscian stars, indicates that the Piscian stars are next in order of development to the Arcturian stars.

(2) The stars observed by Dunér may be divided into seven species, beginning with the hottest and ending with the coolest stars.

(3) The reported presence of bright lines in the Piscian stars must be received with caution, as similar evidence of bright lines might be adduced in the case of other classes of stars in which the spectrum is fully explained by dark lines alone.

(4) The redness of the stars increases as we pass from the earlier to the later species of the group.

(5) The variability in this group is less marked than in the Antarian stars, and may perhaps be accounted for by the revolution of secondary bodies of the nature of comets round the stars themselves.

(6) The place on the temperature curve assigned to these stars on the meteoritic hypothesis is fully confirmed by the more detailed inquiry, and the hypothesis is thereby strengthened.

I am indebted to Mr. Fowler for assistance in the determination of the species and the construction of the map ten years ago, and for additional assistance in discussing the recent work. I have also to express my thanks to Mr. Shackleton for a detailed examination of the recent photographs.

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“Mathematical Contributions to the Theory of Evolution.—On the Law of Reversion.” By KARL PEARSON, F.R.S. (A New Year’s Greeting to Francis Galton.—January 1, 1900.) Received December 28, 1899,—Read January 25, 1900.

(1) *Introductory.*—In a memoir recently presented to the Royal Society, I have endeavoured to emphasise the importance of distin-

guishing between three diverse types of heredity, namely (i), Blended Inheritance, (ii) Exclusive Inheritance, and (iii) Particulate Inheritance.

In a memoir printed in vol. 62, pp. 386—412 of the ‘Proceedings,’ I have dealt at length with the theory of blended inheritance, generalising for this purpose Mr. Galton’s Law of Ancestral Heredity.

Allowing for a certain degree of variation in the constant  $\gamma$ , or “coefficient of heredity,” there discussed, I consider that this theory gives a fairly good first approximation to the facts hitherto observed in this field. But blended inheritance certainly does not cover the whole field of heredity. When a character *blends*, then this law of ancestral heredity tells us the most probable blend for the offspring of given ancestry. It shows us the offspring of exceptional parents regressing towards mediocrity, owing to the fact that without stringent selection the great bulk of their ancestry must be mediocre and not exceptional.\* Thus the main feature of the law of ancestral heredity is regression. Such regression is not what most biologists would understand by *reversion*. In fact, when the inheritance from a variety of ancestry is *blended*, the idea of reversion becomes very obscure; I venture to think meaningless.

Let us suppose stature a blended character, then the array of offspring of a definite *short* statured ancestry will have a mean regressing (here progressing) towards the population mean and a definite variability. Hence the theory of chance enables us at once to determine the frequency of a very tall man born of such short ancestry. The frequency may be small, but sooner or later the tall man will appear. Now let us suppose *one* distant ancestor in the otherwise short ancestry to have been tall. Clearly his existence will hardly affect at all the mean of the array of offspring.

He will not materially influence the chance of a very tall man appearing among the offspring; yet a superficial observer might easily describe the appearance of the very tall man as a case of reversion to the distant tall ancestor. The absurdity of this attribution is manifest when we remember that persons like him would have had sensibly equal frequency with or without the distant tall ancestor. In fact, it seems to me that in the case of characters which continuously vary, and which blend their inheritance, it is hopeless to look for any evidence whatever of reversion. The term is, then, meaningless.

To find reversion we must investigate cases in which characters do not blend, *i.e.*, the individual takes *exclusively* after some one member of the ancestry. In this case the appreciation of reversion becomes possible and its meaning intelligible. Cases of this kind are by no means un-

\* An individual has 1024 10th great parents, and these can hardly be anything else but a fair sample of the population of their generation, if there has not been an excessive amount of in-and-in breeding or much selection.

common. Thus, Mr. Galton writes in his 'Natural Inheritance' (p. 139) : "Parents of different statures usually transmit a blended heritage to their children, but parents of different eye-colours usually transmit an alternative heritage . . . . if one parent has a light eye-colour and the other a dark eye-colour, some of the children will, as a rule, be light and the rest dark ; they will seldom be medium eye-coloured like the children of medium eye-coloured parents."

Again, in his paper on "Basset Hounds,"\* Mr. Galton classifies these hounds as tricolour (T) and non-tricolour (N), remarking, "I am assured that transitional cases between T and N are very rare, and that experts would hardly ever disagree about the class to which any particular hound should be assigned." In other words, Mr. Galton appears to assume exclusive inheritance.† Roughly, in such exclusive inheritance, the offspring takes after one or other parent, or *reverts* to more distant ancestry. It becomes accordingly somewhat difficult to see how the law of ancestral heredity, which applies to blended inheritance, can be transferred to this different field. Yet Mr. Galton in his 'Natural Inheritance' (p. 153) writes: "The broad conclusion to which the present results irresistibly lead, is that the same peculiar hereditary relation that was shown to subsist between a man and each of his ancestors in respect to the quality of stature, also subsists in respect to that of eye-colour." Further, in the paper on Basset Hounds, he actually endeavours to demonstrate the truth of the law on the exclusive colour of these hounds. Now I think we must keep these two matters quite apart. The average stature of an individual is a blend of all his progenitors' characters ; even in a single individual we find contributions from many ancestors ; this is not the case with an exclusive inheritance, and it does not accordingly seem to me possible that "the same peculiar hereditary relation that was shown to subsist between a man and each of his ancestors" for a blended character can also hold for an exclusive character.

It is no longer of the proportions of a character in one individual that we speak, but of the frequency of various types of individuals among the total offspring of a given ancestry. The one statement is a law of blending characters, and the other is a law of distributing the exclusive characters among a group of individuals. In the first case we deal with regression, in the second with reversion. What Mr. Galton really asserts is, that the proportions of reversion in an array of offspring are identical with the proportions of blend in the average

\* 'Roy. Soc. Proc.,' vol. 61, p. 403.

† A remark in the 'Natural Inheritance' (p. 139) that "Stature is due to its being the aggregate of the quasi-independent inheritances of many separate parts, while eye-colour appears to be much less various in its origin," would seem to indicate that Mr. Galton considers that blended inheritance is ultimately based upon exclusive inheritance of parts—a suggestion well worth investigation.

individual. If this be true, then his law, or possibly some generalisation of it, is very comprehensive; it embraces the two distinct types of heritage, blended and exclusive. But I think it most desirable to keep the two ideas quite separate, and speak of the one dealing with blended inheritance as the *Law of Ancestral Heredity*; the second, dealing with exclusive inheritance, as the *Law of Reversion*. If this be done, we shall, I venture to think, keep not only our minds, but our points for observation, clearer; and further, the failure of Mr. Galton's statement in the one case will not in the least affect its validity in the other.

(2) *The Law of Reversion*.—Let us examine first what I take to be Mr. Galton's view of this law. Out of an array of  $N$  offspring,  $1/4 N$  will follow each parent,  $1/16 N$  follow each of the four grandparents, and  $\frac{1}{2^{2n}} N$  follow each of the  $2^n$   $n$ th great parents. In this manner the total offspring  $N$  is distributed by reversion among the ancestry.

Now I want to draw attention to one or two points here.  $1/4 N$  will not be all the children like, say, their father; for out of the  $1/4 N$  who are like members of his ancestry, those who are like ancestors like him—and these ancestors will occur in certain proportions—will thus also be like him. This holds for each individual ancestor; the number *like* any ancestor will be considerably greater than the number who “follow” that special ancestor. Now let  $\rho_1 N, \rho_2 N, \rho_3 N, \rho_4 N$ , and .....  $\rho_n N$ ... be the number of the offspring like a parent, a grandparent, a great grandparent, and  $n$ th parent, &c.

This brings me to my second point. A special meaning is here given to the word *like*.  $\rho_1 N$  is not in the usual sense of the word *all* the number like the father. If the offspring had the same distribution of character as we find in the general population, then undoubtedly some would have the same quantity or quality of the character as he has—some, for instance, would be blue-eyed if he were blue-eyed—but this is a random likeness and not like in the special sense in which we are using the word.  $\rho_1 N$  are like the father owing to the laws of heredity, the remainder have a random distribution so far as he is concerned, and we exclude any random likeness from our consideration.

How then are we in actual observation to distinguish hereditary from random likeness? \* The answer is simple;  $\rho_1 N$  out of  $N$  pairs of parent and offspring will be absolutely correlated, *i.e.*, have a correlation equal to unity, but the remaining  $(1 - \rho_1) \times N$  pairs will have zero correlation, although there may be random likenesses. Hence, by the theorem given by me in the ‘Phil. Trans.,’ vol. 192, p. 276, the actual correlation will be perfect correlation reduced in the ratio of the

\* I exclude for the present the influence of assortative mating. A likeness to the mother, otherwise random so far as the father is concerned, may thus become a real likeness to the father.

number of correlated pairs to the total number of pairs.\* Thus the correlation of parent and offspring =  $1 \times \rho_1 N/N = \rho_1$ .

It thus follows that  $\rho_1, \rho_2, \rho_3, \dots, \rho_n, \dots$  are the correlation coefficients to be expected between offspring and parent, grandparent, .....*n*th great parent, &c. Here we have assumed equal potency for both sexes and all lines of descent, otherwise these coefficients must be looked upon as mean values of the correlations for different generations of ancestry.

Lastly, it seems to me that reversion may not be the proper word to apply to those who directly follow their parents, and that these may be fairly considered direct inheritors and distinguished from reverts. I shall accordingly assume no *à priori* relation between these two classes, certainly not that direct inheritors and reverts are equally numerous, *i.e.*,  $\frac{1}{2}$  and  $\frac{1}{2}$ , as in Mr. Galton's Law. As for reversion itself I will only suppose it to diminish in geometrical progression as we step backward to more and more distant ancestry. I shall accordingly take  $\beta N$  offspring to follow either parent and  $\gamma \alpha N, \gamma \alpha^2 N, \gamma \alpha^3 N, \&c.$ , to follow grandparent, great grandparent, great great grandparent, &c. With these preliminaries arranged we can now proceed with the analysis.

(3) *The Generalised Law of Reversion.*—The total number of offspring  $N$  is clearly the sum of all those that follow all the successive ancestors, *i.e.*,

$$N = 2\beta N + 4\gamma \alpha N + 8\gamma \alpha^2 N + 16\gamma \alpha^3 N + \dots$$

$$\text{or} \quad 1 = 2\beta + 4\gamma \alpha / (1 - 2\alpha) \dots \dots \dots (i)$$

Now consider how the number of offspring "like" or absolutely correlated with one parent are made up: they are  $\rho_1 N$  in number; they consist first of  $\beta N$ , the number directly inheriting from this parent; also there will be  $\gamma \alpha N$  like each of the parent's parents, and the parent will be like one or other of the parent's parents in  $\rho_1$  proportion of cases; similarly there will be  $\gamma \alpha^2 N$  like each of the parents' grandparents, and the parent is like each of the parents' grandparents in  $\rho_2$  cases; and so on. Thus we have

$$\rho_1 N = \beta N + 2\gamma \alpha \rho_1 N + 4\gamma \alpha^2 \rho_2 N + 8\gamma \alpha^3 \rho_3 N + \dots$$

$$\text{or} \quad \rho_1 = \beta + 2\gamma \alpha (\rho_1 + 2\alpha \rho_2 + 4\alpha^2 \rho_3 + \dots) \dots \dots \dots (ii)$$

Now note how the  $\rho_2 N$  like any one grandparent is made up. We have directly  $\gamma \alpha N$  reverting to this grandparent,  $\gamma \alpha^2 N$  to each of the grandparents' parents, and in each case  $\rho_1 \gamma \alpha^2 N$  like the grandparent; similarly out of those  $\gamma \alpha^3 N$  reverting to any grandparents' grand-

\* In this case there is every reason for supposing  $\sigma_1 = \sigma_2 = \sigma_1' = \sigma_2'$ , and  $m_1 = m_2, m_1' = m_2'$ . Thus  $\Sigma = \sigma_1' \Sigma' = \sigma_1'$ , and since  $r = 1, R = n_1/N$ .

parent, there will be  $\rho_2\gamma\alpha^3N$  like the grandparent, and so on. But beyond these contributions, certain of the  $\beta N$  who follow the parent will be like the grandparent, for the parent is like the grandparent in  $\rho_1$  fraction of cases.

Hence we have finally :

$$\rho_2N = \rho_1\beta N + \gamma\alpha N + 2\rho_1\gamma\alpha^2N + 4\rho_2\gamma\alpha^3N + \dots\dots$$

$$\text{or} \quad \rho_2 = \rho_1\beta + \gamma\alpha + 2\gamma\alpha^2(\rho_1 + 2\alpha\rho_2 + 4\alpha^3\rho_3 + \dots\dots)(iii)$$

Proceeding in the same manner we find

$$\rho_3 = \rho_2\beta + \gamma\alpha\rho_1 + \gamma\alpha^2 + 2\gamma\alpha^3(\rho_1 + 2\alpha\rho_2 + 4\alpha^3\rho_3 + \dots\dots)(iv)$$

$$\rho_4 = \rho_3\beta + \gamma\alpha\rho_2 + \gamma\alpha^2\rho_1 + \gamma\alpha^3 + 2\gamma\alpha^4(\rho_1 + 2\alpha\rho_2 + 4\alpha^3\rho_3 + \dots)(v)$$

and so on.

Hence we deduce from (iii) and (ii)

$$\rho_2 = \rho_1\beta + \gamma\alpha + \alpha(\rho_1 - \beta)$$

$$\text{or} \quad \rho_2 = (\alpha + \beta)\rho_1 + \alpha(\gamma - \beta) \dots\dots\dots(vi)$$

Similarly from (iv) and (iii)

$$\rho_3 = \rho_2\beta + \gamma\alpha\rho_1 + \alpha(\rho_2 - \rho_1\beta)$$

$$\text{or} \quad \rho_3 = (\alpha + \beta)\rho_2 + \alpha(\gamma - \beta)\rho_1 \dots\dots\dots(vii)$$

Again from (v) and (iv)

$$\rho_4 = \rho_3\beta + \gamma\alpha\rho_2 + \alpha(\rho_3 - \rho_2\beta)$$

$$\text{or} \quad \rho_4 = (\alpha + \beta)\rho_3 + \alpha(\gamma - \beta)\rho_2 \dots\dots\dots(viii)$$

$$\text{Generally} \quad \rho_n = (\alpha + \beta)\rho_{n-1} + \alpha(\gamma - \beta)\rho_{n-2} \dots\dots\dots(ix)$$

with  $\rho_0 = 1$ , by (vi).

To solve equation (ix) assume as usual  $\rho_n = Am^n$ , and we find

$$m^2 - (\alpha + \beta)m + \alpha(\gamma - \beta) = 0.$$

$$\text{Thus} \quad m = \frac{\alpha + \beta \pm \sqrt{(\alpha + \beta)^2 + 4\alpha(\gamma - \beta)}}{2}.$$

$$\text{But by (i)} \quad 1 - 2(\alpha + \beta) = 4\alpha(\gamma - \beta).$$

$$\text{Hence} \quad m = \frac{1}{2} \quad \text{or} \quad m = \alpha + \beta - \frac{1}{2} \dots\dots\dots(x)$$

We have then

$$\rho_n = A_1\left(\frac{1}{2}\right)^n + A_2\left(\alpha + \beta - \frac{1}{2}\right)^n \dots\dots\dots(xi)$$

where  $A_1$  and  $A_2$  are constants.

But  $\rho_0 = 1$ ,  $\therefore A_1 + A_2 = 1$ . Thus we may put

$$\rho_n = (1-c) \left(\frac{1}{2}\right)^n + c(\alpha + \beta - \frac{1}{2})^n \dots\dots\dots (xii)$$

where  $c$  is a constant.

Let us substitute this in equation (ii); we find

$$\begin{aligned} & (1-c)\frac{1}{2} + c\left(\alpha + \beta - \frac{1}{2}\right) \\ &= \beta + 2\gamma\alpha \left\{ (1-c)\frac{1}{2} + 2\alpha(1-c)\frac{1}{2^2} + 4\alpha^2(1-c)\frac{1}{2^3} + \dots\dots \right. \\ & \quad \left. + c\left(\alpha + \beta - \frac{1}{2}\right) + c\left(\alpha + \beta - \frac{1}{2}\right)^2 2\alpha + c\left(\alpha + \beta - \frac{1}{2}\right)^3 4\alpha^2 + \dots\dots \right\} \end{aligned}$$

$$\text{or} \quad = \beta + 2\gamma\alpha \left\{ \frac{\frac{1}{2}(1-c)}{1-\alpha} + \frac{c(\alpha + \beta - \frac{1}{2})}{1-2\alpha(\alpha + \beta - \frac{1}{2})} \right\} \dots\dots\dots (xiii)$$

Write  $\delta = \alpha + \beta - \frac{1}{2}$ , then by (i) we have

$$\alpha\gamma = \frac{1}{2}(\alpha - \delta)(1 - 2\alpha) \dots\dots\dots (xiv)$$

Hence from (xiii)

$$c \left( \delta - \frac{2\gamma\alpha\delta}{1-2\alpha\delta} + \frac{\gamma\alpha}{1-\alpha} - \frac{1}{2} \right) = \delta - \alpha + \frac{\gamma\alpha}{1-\alpha}$$

and by (xiv)

$$c = \frac{(1-2\alpha\delta)(\delta - \alpha)}{(1-2\delta)\{(\alpha - \delta)(1-2\alpha) - (1-\alpha)(1-2\alpha\delta)\}} \dots\dots\dots (xv)$$

Suppose the parental and grandparental correlations observed, then

$$\left. \begin{aligned} \rho_1 &= \frac{1}{2}(1-c) + c\delta \\ \rho_2 &= \frac{1}{4}(1-c) + c\delta^2 \end{aligned} \right\} \dots\dots\dots (xvi)$$

will both be known.

These will give  $c$  and  $\delta$ ; then (xv) will give  $\alpha$  and (xiv)  $\gamma$ , while

$$\beta = \delta - \alpha + \frac{1}{2} \dots\dots\dots (xvii)$$

will determine  $\beta$ , and the whole law of inheritance and reversion will have its constants fully determined.

We have, indeed, from (xvi)

$$\delta = \frac{\rho_1 - 2\rho_2}{1 - 2\rho_1} \dots\dots\dots (xviii)$$

$$c = \frac{(1 - 2\rho_1)^2}{1 - 4\rho_1 + 4\rho_2} \dots\dots\dots (xix)$$

From (xv)

$$\alpha^2 - \frac{2 + e + 4\delta + 2e\delta^2}{2(1 + \delta + e\delta)}\alpha + \frac{1}{2} = 0 \quad \dots\dots\dots (xx)$$

where 
$$e = \frac{1}{1 - 2\rho_1}$$

Lastly from (xiv) 
$$\gamma = \frac{(x - \delta)(1 - 2x)}{2x} \dots\dots\dots (xxi)$$

Thus (xviii) and (xix) give  $\delta$  and  $c$ . (xx) then gives  $\alpha$ , taking the root *less than unity*. Finally (xvii) and (xxi) give  $\beta$  and  $\gamma$ , completing the solution.

(4) *Comparison with Law of Ancestral Heredity*.—Now let us compare these results with those I have obtained from the law of ancestral heredity.\* On p. 390 of the memoir on that subject we have for the  $n$ th midparental correlation with the offspring  $\rho_n = 2^{\frac{1}{2}n}r_n$ , where  $r_n$  is the correlation of the offspring with the individual  $n$ th great grandparent. By p. 394  $\rho_n = c\alpha^n$ . Hence

$$r_n = c(\alpha/\sqrt{2})^n \dots\dots\dots (xxii)$$

or the correlations of the offspring with the ancestry follow a simple geometrical progression.

Comparing this with the result (xii) of this paper, or

$$r_n = (1 - c)(\frac{1}{2})^n + c(\alpha + \beta - \frac{1}{2})^n \dots\dots\dots (xii)$$

where  $c$  is now a different constant, we see that the two cannot possibly be in agreement, unless one of the terms of the latter result vanishes. Thus there is in general a fundamental difference between the law of ancestral heredity and the law of reversion; they give expressions differing in character for the correlations between the offspring and individual ancestors. Let us see when the two laws will agree. There is unfortunately a bad slip in my memoir of 1898. The series at the top of p. 403 leads to

$$\gamma\beta'/(1 - \beta') = 1 \quad \text{and not as there given} \quad \gamma\beta'(1 - \gamma\beta') = 1.$$

Thus we have 
$$\beta'(1 + \gamma) = 1 \quad \text{or} \quad \beta' = 1/(1 + \gamma).$$

Hence 
$$\beta = \frac{1}{\sqrt{2}}\beta' = 1/\{\sqrt{2}(1 + \gamma)\} \dots\dots\dots (xxiii)$$

and therefore by (xii) 
$$\alpha = 1/\sqrt{2}.$$

Thus by (xxii) of this paper

$$r_n = c(\frac{1}{2})^n \dots\dots\dots (xxiv)$$

\* 'Roy. Soc. Proc.' vol. 62, pp. 386—412.



This shows us that the correlation with the individual ancestor is halved at each backward step in the pedigree. We see at once that (xii) can only be in agreement with (xxiv)—the letter  $c$  being different in the two, and merely standing for a constant—provided  $\alpha + \beta = \frac{1}{2}$ , or by (i), provided  $\gamma = \beta$ . Thus the condition that blended and exclusive inheritance should lead to the same values for the correlations with the ancestry is: that reversion should form a series starting with the actual parent. If this condition should hold, then, for example, the grandparental correlation must always be one-half the parental either for blended or for exclusive inheritance.

(5) *Correction of an Error in Memoir on Ancestral Heredity.*—It may be of value to insert here the modifications required in my memoir on blended inheritance, owing to the slip just referred to: they apply to the results deduced from (xvii) on p. 403; these are the table on p. 403, and the result immediately under (xviii) on p. 406.

In the first place the law of ancestral heredity may now be written

$$k_0 = \frac{\gamma}{1+\gamma} \frac{\sigma_0}{\sigma_1} k_1 + \frac{\gamma}{(1+\gamma)^2} \frac{\sigma_0}{\sigma_2} k_2 + \frac{\gamma}{(1+\gamma)^3} \frac{\sigma_0}{\sigma_3} k_3 + \dots \dots \dots (\text{xxv})$$

a very simple form.

In the second place we may replace the equation for  $c$  on p. 394 by

$$c = \gamma \frac{2\gamma + 1}{2\gamma^2 + 2\gamma + 1} \dots \dots \dots (\text{xxvi})$$

whence we find for the parental correlation  $ca/\sqrt{2}$  or  $\frac{1}{2}c$

$$r_1 = \frac{1}{2} \gamma \frac{2\gamma + 1}{2\gamma^2 + 2\gamma + 1} \dots \dots \dots (\text{xxvii}).$$

Each succeeding ancestral correlation will be obtained by repeated halving of this value.

Lastly, the result on p. 406 for the fraternal correlation becomes\*—

$$r = \frac{2\gamma^2}{2\gamma^2 + 2\gamma + 1} \dots \dots \dots (\text{xxviii}).$$

The following table indicates the effect of varying  $\gamma$  on the intensity of heredity, and should replace that on p. 403 of the memoir on the ancestral law:—

\* Equation (xviii) on p. 406 of the memoir is correct, but the value of  $r$  in terms of  $\gamma$  below it, since it depends on the erroneous Equation (xvii) of p. 403, as well as the limit given for  $\gamma$  in the foot-note, must be cancelled.

Table of Heredity for divers Values of  $\gamma$ .

Value of $\gamma$ .	0·7.	0·9.	1.	1·2.	2·35.	$\infty$ .
Parental correlation .....	0·2485	0·2851	0·3000	0·3248	0·4000	0·5000
Grandparental correlation ...	0·1243	0·1425	0·1500	0·1624	0·2000	0·2500
Great grandparental correlation .....	0·0621	0·0713	0·0750	0·0812	0·1000	0·1750
Fraternal correlation .....	0·2899	0·3665	0·4000	0·4586	0·6596	1·0000
Regression on $n$ th midparent	0·4970	0·5701	0·6000	0·6497	0·7999	1·0000
Correlation with $n$ th midparent	0·4970(0·7071) <sup>n</sup>	0·5701(0·7071) <sup>n</sup>	0·6000(0·7071) <sup>n</sup>	0·6497(0·7071) <sup>n</sup>	0·7999(0·7071) <sup>n</sup>	(0·7071) <sup>n</sup>

(6) *Difficulties arising when we apply these Results for Blended Inheritance.*

—Now the above table shows us that by varying  $\gamma$  sufficiently we can obtain a considerable range of values for the correlation of characters in kindred. But these values are limited by two serious considerations, namely :—

- (i) The ancestral correlation is halved at each stage.
- (ii) The fraternal correlation appears to become perfect as we approach the upper limit of parental correlation, *i.e.*, 0·5.

Now actual determinations of grandparental correlation in the cases of eye-colour in man, of coat-colour in horses, and of coat-colour in hounds, which I have recently made, do not as a rule seem to justify the statement that the grandparental is half the parental correlation. Further, in two of these cases, the average parental correlation is quite 0·5, but the fraternal correlation is, while larger than 0·4, still a good deal short of perfect. Hence I am bound to conclude that :—

- (i) These characters do not obey the laws of blended inheritance as deduced from the law of ancestral heredity ; or,
- (ii) The laws of blended inheritance, as deduced from the law of ancestral heredity, would be largely modified if we considered the influence of assortative mating, or
- (iii) The fundamental assumption that if all the midparents right away back had the same amount of the character, the average offspring would have also the same amount, is not justified. Thus the result  $\beta = 1/(\sqrt{2}(1 + \gamma))$  in Equation (xxiii), perhaps, is unnecessary, or there may be *two* independent constants of inheritance.

It is quite possible that eye-colour in man and coat-colour in hounds are exclusive and not blended inheritances, so that (i) would cover these cases. On the other hand, I have found parental correlations as high as 0.5 for a new and large series of stature data in man, without fraternal correlation approaching unity. Here (i) can hardly apply, although (ii) may, for the coefficient of assortative mating in this case is remarkably high, nearly 0.3. But I think that, even if (i) or (ii) might help us over our difficulties in certain cases, we ought to carefully reconsider the assumption referred to in (iii). It would surely only be justifiable in the case of an absolutely stable population, each generation of which has existed under an identical environment. In itself it seems to exclude any secular change due to natural selection, or to improved physical or organic environment. In fact, we must proceed with caution when applying the statement that the average of all the offspring of an absolutely same system of midparents would be like those midparents; for a portion of such offspring have very probably been removed by selection, and our average is not really that of *all* the offspring, but of the fitter. In the like manner, we must treat with some caution the principle on which Equation (i) of the present paper is based. It assumes that all the ancestral contributions are to be found in the present progeny; but what if the contributions of certain ancestors by selection, artificial or natural, have been eliminated before reaching the existing generation? What if the coat-colours of certain ancestors were unfashionable, and only their unlike descendants have been put to the stud? Our theory may be quite correct, but it may appear erroneous when tested by facts observed in the case of horse or dog breeding.

Let us investigate whether independent  $\gamma$  and  $\beta$  in our expressions for parental and fraternal correlations would enable us in the case of blended inheritance to reach a value of the former as high as 0.5 without the latter becoming perfect. I find if  $r_1$  be the parental correlation,  $= c\alpha/\sqrt{2}$ , from Equation (xiii) of my memoir on the ancestral law (p. 394), and if  $r$  be the fraternal correlation obtained from Equation (xviii) of the same memoir:

$$r_1 = \frac{\gamma\beta}{\sqrt{2}} \frac{1 - \beta^2(1 + \gamma)}{1 - \beta^2(1 + 2\gamma)} \dots\dots\dots (\text{xxix}).$$

$$r = \frac{2\gamma^2\beta^2}{1 - \beta^2(1 + 2\gamma)} \dots\dots\dots (\text{xxx}).$$

Whence, eliminating  $\gamma\beta$ , we have

$$\left. \begin{aligned} \beta^2 &= \frac{2(r - 4r_1^2)}{r(2 - r)} \\ \gamma &= \frac{\sqrt{2}r_1}{\beta} - \frac{1}{2}r \end{aligned} \right\} \dots\dots\dots (\text{xxx}).$$

and

These give  $\gamma$  and  $\beta$  when the parental and fraternal correlations are known.

Now, since  $r$  is  $< 1$ ,  $\beta^2$  will be imaginary, if  $r$  be not  $> 4r_1^2$ . Hence we should again need perfect fraternal correlation for  $r_1$  to be as large as 0.5.

Thus with blended inheritance and little or no assortative mating we cannot get a parental correlation as high as the value 0.5, which actually does occur in my data for both men and horses.

We must now consider how the problem will be affected, if we suppose exclusive and not blended inheritance.

(7) *Illustrations of the Law of Reversion in Exclusive Inheritance.*—

(i) Let us first consider what happens if we take the chief feature of Mr. Galton's view, *i.e.*, that the likeness to the parent is the beginning, so to speak, of the reversion series. Then  $\gamma = \beta$  (in the notation of the present memoir). It follows from Equation (i) that:

$$1 - 2(\alpha + \beta) = 0, \text{ or } \delta = 0. \text{ Thus by (xviii)}$$

$$\rho_1 = 2\rho_2,$$

and generally

$$\rho_n = 2\rho_{n-1}.$$

Equation (xx) to find  $\alpha$  now becomes

$$\alpha^2 - (1 + \frac{1}{2}e)\alpha + \frac{1}{2} = 0,$$

while

$$\gamma = \frac{1}{2} - \alpha.$$

Thus as soon as we know  $\rho_1$ , we can find all the ancestral correlations and the whole series of reversions. For example: if  $\rho_1 = 0.4$  we should have  $\rho_2 = 0.2$ ,  $e = 5$ , and  $\alpha^2 - 3.5\alpha + 0.5 = 0$ .  $\therefore \alpha = 0.149$  and  $\gamma = 0.351 = \beta$ . Thus in this case 35 per cent. of the offspring take after each parent, and 30 per cent. revert to higher ancestry. Of this 30 per cent.  $100 \times 0.35 \times 0.149$ , or 5.23 per cent., revert to each of the four grandparents, leaving 9 per cent., about, to revert to great grandparents and higher ancestry still.

(ii) Next suppose Mr. Galton's full view to be correct, and that 1/4 of the offspring follow each parent, 1/16 each grandparent, 1/64 each great grandparent, and so on. Then we have—

$$\alpha = \gamma = \beta = \frac{1}{4}.$$

Hence from  $\alpha^2 - (1 + \frac{1}{2}e)\alpha + \frac{1}{2} = 0$ , we find

$$e = 2.5 \text{ and } \rho_1 = 0.3.$$

Thus we should have:  $\rho_1 = 0.3$ ,  $\rho_2 = 0.15$ ,  $\rho_3 = 0.075$ , &c., or, *precisely the same ancestral correlations in the case of exclusive that we have in the case of blended inheritance by the law of ancestral heredity for the special case of  $\gamma = 1$*  (see table, p. 149).

Thus the law of reversion fits no better than the law of blended inheritance the data to which I have referred (in § 6) when we adopt the  $1/4$ ,  $1/16$ ,  $1/64$  hypothesis, *i.e.*, the original form of Mr. Galton's statement.\*

(iii) Let us suppose the parental correlation to be  $0.5$ , a value not very far from what I have found for eye-colour in man and coat-colour in horses. Then by (xvi)

$$\delta = \frac{1}{2}, \quad \rho_2 = \frac{1}{4}.$$

Putting  $e = \infty$  in (xx) we deduce :

$$\alpha^2 - \frac{1+2\delta^2}{2\delta} \alpha + \frac{1}{2} = 0, \quad \text{or} \quad \alpha^2 - \frac{3}{2}\alpha + \frac{1}{2} = 0,$$

which gives us  $\alpha = 1$  or  $\frac{1}{2}$ .

But remembering the value of  $\delta$  we have, using (xxi),

$$\alpha\gamma = -(\alpha - \frac{1}{2})^2 \quad \text{and} \quad \alpha + \beta = 1.$$

The first equation shows us that  $\alpha = 1$  is impossible, for it gives  $\gamma$  negative. Accordingly we conclude that  $\alpha = \frac{1}{2}$  and  $\beta = \frac{1}{2}$ , while  $\gamma = 0$ . *Thus reversion is totally excluded and one-half the offspring take after each parent.* In this case the grandparental correlation,  $\rho_2$ , is  $0.25$ , the great grandparental  $0.125$ , and so on. The ancestry beyond the parents have no direct influence on the offspring, beyond the fact that they have determined the parents. We are dealing indeed with a case like that investigated in my memoir on "Regression, Heredity, and Panmixia."† So far our theory of exclusive inheritance with parental correlation =  $0.5$  agrees with that of blended inheritance with the same value of the parental correlation. But we have seen that the latter leads to an impossible value for fraternal correlation, *i.e.*, one which does not fit the facts. Does perfect fraternal correlation necessarily flow from exclusive inheritance without reversion? Certainly not, for this would connote that all the offspring of a given set of parents would be alike, or one parent in each family be absolutely prepotent. This is of course not the fact.

Supposing all families to consist of  $n$  members, and that both parents were equipotent in the family, there would be  $2\frac{n}{2}(\frac{n}{2}-1)$  pairs of brethren alike, out of a total of  $\frac{n(n-1)}{2}$  pairs, or the fraternal correlation would be  $(\frac{1}{2}n-1)/(n-1)$ . The average size of a human

\* See 'Natural Inheritance,' chapter viii, p 149, &c. Mr. Galton there uses the correlation coefficients corresponding to blended inheritance for eye-colour, an exclusive inheritance. But, directly investigated, such values are far from holding for eye-colour.

† 'Phil. Trans.,' vol. 187, p. 303.

family is about 4.5; but if we confine ourselves to one sex, we must exclude all sterile marriages and all not leading to two brothers, or two sisters. We might then very well take  $n = 6$ , which gives 0.4 for the fraternal correlation. Thus we might expect in the case of exclusive inheritance that the fraternal correlation would lie between 0.4 and 1, according as to the degree of prepotency of one or other parent in the individual marriage.\*

Thus our theory of exclusive inheritance is not, like that of blended inheritance, incompatible with observed facts, *i.e.*, high values of parental correlation and values substantially less than unity of the fraternal correlation. But for such cases we must deny the existence of any regular and continuous law of reversion. We should have to look upon reversion, if it occurred at all, as merely an irregular and infrequent phenomenon.

On the other hand, if we differentiate the taking after parents from the reversion to ancestry as phenomena of a quite distinct nature, our theory will enable us to surmount, for some cases at least, those difficulties in ancestral correlation, which arise when we take Mr. Galton's Law in its original form to cover both blended and exclusive inheritance. I illustrate this from data for the coat-colour of Basset Hounds in the following section.

(8) *Application to Basset Hounds.*—Understanding that I was desirous of testing my theory on a character which was definitely exclusive, Mr. Galton, with his invariable kindness, at once placed at my disposal his material on Basset Hounds. The reader will remember from the statements in Mr. Galton's own memoir ('*Roy. Soc. Proc.*,' vol. 61, p. 403) that these dwarf bloodhounds are either lemon and white, or black, lemon, and white; and here, as in Mr. Galton's work, they will be classified as non-tricolour and tricolour, or by the symbols N and T. In dealing with the offspring I was in many cases unable to determine the sex of the dog, as that information is not in the stud book,† and all individuals are not again recorded as sires or dams, nor do they possess obviously male or female names. Thus in my principal tables all the offspring of both sexes are clubbed together. To measure the legitimacy of this, I have formed separate tables of the two sexes in the case of sires and dams. Further, in dealing with great grandparents there were so few of each of the eight individual types alone, that I have formed merely one table, that of great grandparent and offspring, disregarding the line of descent.

\* The mother and father may be equipotent on the average, but in the individual family one or other be markedly prepotent. It is to this prepotency of the individual, regardless of sex, that the increase of fraternal correlation beyond 0.4 is very probably due.

† Sir Everett Millais, '*The Basset Hounds Club Rules and Stud Book*,' 1874—1896.

## Tables of Inheritance of Coat-colour in Basset Hounds.

## Sire and Offspring.

(1) All Offspring.

	T.	N.T.	Totals.
T.	477	236	713
N.T.	63	53	116
Totals	540	289	829

Sires.

(2) ♂ Offspring.

	T.	N.T.	Totals.
T.	248	113	361
N.T.	31	28	59
Totals	279	141	420

Sires.

(3) ♀ Offspring.

	T.	N.T.	Totals.
T.	192	103	295
N.T.	24	18	42
Totals	216	121	337

Dams.

## Dam and Offspring.

(4) All Offspring.

	T.	N.T.	Totals.
T.	369	94	463
N.T.	169	191	360
Totals	538	285	823

Dams.

(5) ♂ Offspring.

	T.	N.T.	Totals.
T.	195	45	241
N.T.	93	92	185
Totals	288	137	426

Dams.

(6) ♀ Offspring.

	T.	N.T.	Totals.
T.	146	41	187
N.T.	64	85	149
Totals	210	126	336

Dams.

Sire's Sire and Offspring.

(7) All Offspring.

	T.	N.T.	Totals.
T.	335	157	522
N.T.	28	24	52
Totals	393	181	574

Sire's Sires.

Sire's Dam and Offspring.

(8) All Offspring.

	T.	N.T.	Totals.
T.	266	112	378
N.T.	128	70	198
Totals	394	182	576

Sire's Dams.

Dam's Sire and Offspring.

(9) All Offspring.

	T.	N.T.	Totals.
T.	344	156	500
N.T.	49	22	71
Totals	393	178	571

Dam's Sires.

Dam's Dam and Offspring.

(10) All Offspring.

	T.	N.T.	Totals.
T.	233	81	314
N.T.	161	101	262
Totals	394	182	576

Dam's Dams.

Great grandparent and Offspring.

(11) All Offspring.

	T.	N.T.	Totals.
T.	1220	404	1624
N.T.	461	171	632
Totals	1681	575	2256

Great grandparent.



## Whole Siblings (same litter).

(12) First Sibling.

	T.	N.T.	Totals.
T.	942	317	1259
N.T.	317	448	765
Totals	1259	765	2024

Second Sibling.

## Whole Siblings (different litters).

(13) First Sibling.

	T.	N.T.	Totals.
T.	324	108	432
N.T.	108	160	268
Totals	432	268	700

Second Sibling.

## Half Siblings (Dam's side).

(14) First Sibling.

	T.	N.T.	Totals.
T.	1766	842	2608
N.T.	842	722	1564
Totals	2608	1564	4172

Second Sibling.

## Half Siblings (Sire's side).

(15) First Sibling.

	T.	N.T.	Totals.
T.	8898	4828	13726
N.T.	4828	8466	8294
Totals	13726	8294	22020

Second Sibling.

The extraction of eleven tables from Mr. Galton's data papers I owe to Miss Alice Lee, D.Sc.. A twelfth is due to Mr. K. Tressler. For the other three I am responsible. Of the determinations of the correlation coefficients, I owe five to Miss Alice Lee, no less than six to Mr. L. N. G. Filon, M.A., and the remaining four only are my own work. The method by which the correlation coefficients have been calculated will be explained and justified in another memoir; it is a novel process, which we believe to be of considerable importance, and which we have already applied to a variety of attributes not capable of exact quantitative measurement. The probable error of this method of determining the correlation has also been ascertained, and may be taken in the present cases to range from 0.01 to 0.04, so that differences which are significant can be appreciated.

### Coefficients of Correlation.

#### Sire and offspring :—

Sire and all offspring.....	0.1775
Sire and ♂ offspring .....	0.2280
Sire and ♀ offspring .....	0.1104

#### Dam and offspring :—

Dam and all offspring .....	0.5239
Dam and ♂ offspring.....	0.5077
Dam and ♀ offspring.....	0.5445

Mean parental correlation .....  $\rho_1 = 0.3507$

#### Grandparent and offspring :—

Sire's sire and all offspring.....	0.2144
Sire's dam and all offspring .....	0.0976
Dam's sire and all offspring .....	-0.0032
Dam's dam and all offspring .....	0.2215

Mean grandparental correlation...  $\rho_2 = 0.1326$

#### Great grandparent and offspring :—

All great grandparents and all offspring	0.0404	$\rho_3 = 0.0404$
------------------------------------------	--------	-------------------

#### Siblings\* :—

Whole siblings from same litter .....	0.5084
Whole siblings from different litters ...	0.5257
Half siblings, dam's side .....	0.2222
Half siblings, sire's side .....	0.1070

\* Every writer on heredity must have felt the inconvenience of our language having preserved no word for either member of a pair of offspring of either or both sexes from the same parent. After some hesitation, I have ventured to reintroduce a good Anglo-Saxon word with this sense.

Now several noteworthy conclusions follow at once from these numbers :—

(1) *Direct Inheritance.*

(a) The dam has a great prepotency in the matter of coat-colour. Mr. Galton has already remarked on this.\* We here see that, quantitatively, the dam is, on the average of both sexes, thrice as highly correlated with the offspring as the sire. While she has reached the high value 0·5, he has fallen below 0·2, and the theoretical value 0·3 of the unmodified law of ancestral heredity is neither satisfactory for the individual cases nor for their average.

(b) Offspring take more after the dam than the sire, but ♂ offspring more than ♀ after the sire, and ♀ offspring more than ♂ after the dam. In other words, the parent hands down its characteristics more strongly to its own than to the opposite sex.

(c) Curiously enough, the sire's parents seem to have more influence than the dam's. In particular the dam's sire has, within the probable error of our determinations, no influence at all. In the unchanging line of descent, the dam's dam has more influence than the sire's sire, which is what we should expect from (a); but (a) also makes the male element of much less importance than the female, and so the dam's sire insignificant as compared with the sire's dam. The final result is thus to give a slight preponderance to the sire's over the dam's parents.

(2) *Collateral Inheritance.*

(a) The degree of resemblance between puppies of the same parents is not greater when they are of the same than when they are of different litters.

It is clear, however, that we have only been able to find comparatively few pairs of whole siblings from different litters, and the difference between 0·5084 and 0·5257 is of the order of the probable error of the differences. With greater numbers, possibly a more sensible difference might be found for the correlation of siblings from the same and different litters. At present there seems nothing to warrant the idea that puppies from the same litter have the high degree of resemblance which we find between twins in the case of mankind.

(b) A comparison of the correlations for half siblings on the dam's side and on the sire's side again emphasises, if the breeding be straightforward, the great prepotency of the dam in the matter of coat-colour. The fact that we have upwards of five times as many pairs of half siblings on the sire's side as on the dam's side shows how large a fashion there is in selecting sires. It is possible that largely used and

\* 'Roy. Soc. Proc.,' vol. 61, p. 404. The Table II, p. 410, requires interchange of headings, as already pointed out by Mr. Galton.

possibly overworked sires lose some of their hereditary influence, while not losing their power of fertilising the dam.\*

(c) The great reduction in the degree of fraternal correlation when we turn from whole to half siblings is very remarkable, and is, at any rate for half siblings on the dam's side, not very explicable.

Had we assumed the parental correlation to be 0.3507, and found  $\gamma$  from (xxvii), *i.e.* = 1.4722, we should have deduced from (xxviii) for the fraternal correlation the value 0.5236, which is in fair accordance with the observed result for whole siblings. But, as we have seen, (xxvii) and (xxviii) belong to a theory which gives very poor values for the grandparental and great-grandparental correlations, *i.e.*, 0.1753 and 0.0877, instead of 0.1326 and 0.0402. Further, we should on that theory have expected the average correlation for half siblings to be half the value above, since one-half of the common ancestry is cut off, *i.e.*, 0.2618, and not 0.1646, as it actually is. Thus the fraternal correlation does not appear to be in accord with the theory of blended inheritance. Its determination in the general case of exclusive inheritance *with reversion* seems a problem of considerable difficulty, which in this case is rendered much greater by the immense prepotency of the dam, so that it would seem very desirable to differentiate the sexes when dealing with the resemblance of siblings reverting to ancestral types.

(9) *Application of the Theory of Reversion to Basset Hounds.*—We have for mean values  $\rho_1 = 0.3507$ ,  $\rho_2 = 0.1326$ ,  $\rho_3 = 0.0404$ . Now these correlations certainly do not obey the relation  $\rho_1 = 2\rho_2$ ,  $\rho_2 = 2\rho_3$  required, when we take (xxiii) to govern the law of ancestral heredity (*cf.* § 6 (iii)). A glance at the table on p. 149 will show that such a series of  $\rho$ 's as the above cannot fit into it. Still less do they appear consonant (except to the first roughest approximation) with Mr. Galton's form of that law, *i.e.*,  $\gamma = 1$ . Nor do they satisfy for the same reasons the law of reversion when we start the reversion series from the parents, *i.e.*, put  $\beta = \gamma$  as in § 7 (ii).

Accordingly, I have tried to find what would be the value of  $\rho_3$ , if  $\rho_1$  and  $\rho_2$  had the values given above, and our generalised law of reversion were correct. Turning to § 3, and substituting in (xviii) and (xix) for  $\rho_1$  and  $\rho_2$  we have :

$$\delta = 0.286336, \quad c = 0.698761,$$

\* There is also to be considered the possibility of error of the record in the sire's case. Given a large stud of hounds and servants of average carelessness, and a bitch may easily go astray even after she is lined by the dog required. Sir Everett Millais, in a lecture on Telegony, delivered at St. Thomas' Hospital, in 1895, stated that he knew of "quite two dozen such examples resulting in supposed telegony." "The master is the last person to whom such little lapses of duty are confided." But if two dozen *mésalliances* can be palmed off as telegony, how many alliances within the blood may be conveniently overlooked?

Equation (xx) becomes

$$x^2 - 1.56851x + 0.5 = 0$$

or,

$$x = 0.445057.$$

Hence  $\gamma = 0.019594,$   $\beta = 0.341279.$

This effectually shows us that for this case  $\gamma$  cannot be taken equal to  $\beta$ , or the reversion series started from the parents.

Further, we reach from Equation (xi):

$$\rho_n = 0.30124\left(\frac{1}{2}\right)^n + 0.698761(0.286336)^n.$$

Such a value again demonstrates that in this case the ancestral correlation differs totally in form from what might be deduced from the theory of blended inheritance, *i.e.*, it shows us how we must distinguish between a law of regression and a law of reversion.

Putting  $n = 3$ , we have  $\rho_3 = 0.0541$  for the calculated value of the great grandparental correlation. This may be, I think, considered in satisfactory agreement with the observed value 0.0404. Had we determined our  $\delta$  and  $c$  by the method of least squares, so as to satisfy the three relations

$$\rho_1 = \frac{1}{2}(1 - c) + c\delta, \quad \rho_2 = \frac{1}{4}(1 - c) + c\delta^2, \quad \rho_3 = \frac{1}{8}(1 - c) + c\delta^3$$

as closely as possible, we should have got, of course, still more accordant results.

We can now put down our general conclusions:

63.256 per cent. of Basset Hounds take after their parents .....	(50)
3.488    "                "                revert to grandparents .....	(25)
3.105    "                "                "       great grandparents .....	(12.25)
2.764    "                "                "       great <sup>2</sup> "       .....	(6.25)
2.460    "                "                "       great <sup>3</sup> "       .....	(3.125)
2.190    "                "                "       great <sup>4</sup> "       .....	(1.5625)
1.949    "                "                "       great <sup>5</sup> "       .....	(0.78125)
1.735    "                "                "       great <sup>6</sup> "       .....	(0.390625)

14.053 per cent. of Basset Hounds revert to still higher ancestry (0.390625). Now the divergence here from Mr. Galton's original statement of the law is most significant; I have put in brackets the percentages deduced from that statement. In our case we have a comparatively small reversion to each generation of ancestry, but the percentage, 1.7, is still sensible in the case of the 8th ascending generation. In Mr. Galton's case we have very substantial reversions to grandparents and great grandparents, but the rate of diminution instead of being the loss of about 1/9 at each stage is 1/2! As a result, the reversion to the 8th ascending generation is less than 0.4. It can-

not be denied that the difference is of extreme biological interest. In the former case we have a comparatively small total reversion widely spread; in the latter a much larger total reversion concentrated on the first stages of ancestry. Which system is more accordant with facts? It needs far wider observation and experiment than are yet available to settle this. So far we can only say that the former case covers Mr. Galton's as a special sub-case, and that the data for Basset Hounds appear capable of treatment under the wider rule, but can only be fitted with some straining to the special case. Are there or are there not physiological reasons for supposing that resemblance to a parent arises from a different source from reversion to an ancestor? Here reversion to an ancestor must not be measured by cases of resemblance to an ancestor, for a portion of this resemblance is due to common likeness to the parent; we must approach the matter from the standpoint of cases in which the offspring inherits a character like that of the grandparent or higher ancestor, and *unlike* that of the parent.\* Current use of the term "reversion" at least justifies us for the time being in not speaking of all inheritance, including likeness to parents as reversion, and in our theory we may be permitted to differentiate parental and reversional inheritance of exclusive characters, if we find it needed by our numerical data. Here, as elsewhere, we sadly need a widely extended range of observation and experiment.

(10) *On the Variability of Basset Hounds having regard to Sex and Pedigree.*—We have already indicated that our justification in applying the methods of normal correlation to coat-colour is considered in another memoir. We merely suppose at present that there is some variable, following approximately the law of normal variation, on which the coat-colour can be thrown back. This being so, let  $h$  in terms of this variable be the distance of its mean value from the division line between tricolour and non-tricolour, and let  $\sigma$  be the standard deviation of this variable for the same group. Then if  $\chi = h/\sigma$ , we easily deduce by aid of tables of the probability integral from the correlation tables in § 8 the following results :—

\* Of C and D brown-eyed parents, A and B, the offspring, have respectively brown and blue eyes. Is the process by which B gets the blue eyes of his grandfather or great grandfather qualitatively different from that by which A gets the brown eyes of his parents? The problem can hardly be answered at present, but I see no *à priori* reason for a negative.

Table of Values of  $\chi$ .

	$\chi$ .		$\chi$ .
Sire .....	1.0806	with all his offspring.....	0.3891
„ .....	1.0782	„ his ♂ „ .....	0.4242
„ .....	1.1522	„ „ ♀ „ .....	0.3611
Dam .....	0.1575	„ all her offspring.....	0.3954
„ .....	0.1315	„ her ♂ „ .....	0.3521
„ .....	0.1422	„ „ ♀ „ .....	0.3186
Sire's sire .....	1.3372	„ all his offspring.....	0.4808
„ dam .....	0.4023	„ „ her „ .....	0.4790
Dam's sire .....	1.1536	„ „ his „ .....	0.4909
Dam's dam .....	0.1134	„ „ her „ .....	0.4790
Great grandparents ..	0.5824	„ all their offspring...	0.6592
Whole siblings, same litters .....			0.3108
„ „ different litters.....			0.2980
Half siblings, sire's side .....			0.3143
„ „ dam's side.....			0.3190

Now, if there were no secular change due to artificial or other selection,  $h$  would remain the same in each generation, and therefore  $\sigma = h/\chi$  would give a proper measure of the variability due to sex or to relative position in ancestry. The table at once suggests a number of interesting points, which I proceed to note.

(a) Turning first to the offspring, as given in the second column, we observe that the dogs with the longest pedigree have the largest  $\chi$ . We have, in fact, the values of  $1/\chi$  for pedigrees stretching to great grandparents, grandparents, parents, and merely to brethren, respectively, as

$$1.517 : 2.064 : 2.550 : 3.221,$$

or, roughly, we have a geometrical series with the ratio of about 1.3.

Now this result may be reached in more than one way, either (i) decreasing  $h$ , or (ii) increasing  $\sigma$ . Increase of  $h$  would signify that, for the longer pedigree, the mean of the quantity on which the coat-colour depends is being thrust further into the tricolour section; decrease of  $\sigma$  would signify greater concentration in the tricolour section within which the mean lies. Whether the longer pedigree signifies the more modern hounds, or the more careful preservation of ancestors' names in the more fashionable hounds, we reach practically the same conclusion: the process of breeding is emphasising melanism. Further, by comparing the ♂ and ♀ offspring in the case of both sire and dam, we conclude that this process is sensibly more significant for the male than the female offspring. As very often only one or two puppies out of a litter are recorded in the 'Stud Book,' this apparently artificial selec-

tion, which is more stringent for the males than the females, appears to be, theoretically at least, a mistake when we remember that the potency of the female is thrice that of the male in coat-colour.

Within the groups of grandoffspring and siblings the differences are hardly significant enough for special conclusions to be drawn.

(b) Turning next to the parental groups, we see that (i) the sires and dams, neither of which can be considered to form a more modern group than the other, have yet remarkably different values of  $\chi$ , that for the sire being about seven times as great as that for the dam. The sires are thus far more stringently selected than the dams, and a great deal of this difference must undoubtedly be due to the lesser variability of the sires. Here again the breeders, if they are selecting at all for coat-colour, would appear, at least theoretically, to be in error. (ii) Grandsires, ♂ and ♀, appear to be less variable than the sires, and granddams, ♂ and ♀, less variable than the dams. This may be due to the original paucity of the breed, or be an instance of the general rule to which I have elsewhere referred, *i.e.*, that parents are a selection out of the general population, and so less variable than their offspring.

(c) But this rule meets with a remarkable exception in the case of ♀ parentage; both granddams and dams are more variable than their offspring, and very significantly so. An examination of dam and female offspring shows that the ♀ offspring have a value of  $\chi$  double as great as that of their dams. With few original dams, it is difficult to understand how they could be more variable than their offspring. Considering the great prepotency of the dam, it is difficult to attribute this increase of  $\chi$  entirely to the action of the less variable sire; one is more or less forced to believe that there is a process of stringent selection of the offspring which are entered on the record going on, and that thus a group of dams possibly fairly variable, and with a not very marked tendency to melanism, is represented in the next generation by offspring of a more stringently selected character; the stringent selection of sires may have contributed, but can hardly be the sole source of this change.

A further conclusion is worth noting: Parents, whether male or female, when they have male are apparently more variable than when they have female offspring.

#### (10) *General Results.*

(a) The laws hitherto propounded for blended inheritance do not appear to cover the cases of exclusive inheritance, *e.g.*, such cases as eye-colour in man, coat-colour in horses or hounds, &c.

(b) The law of ancestral heredity must be distinguished from a law of reversion. Neither seem to fit the facts if we adopt the amounts of heritage,  $\frac{1}{2}$ ,  $\frac{1}{16}$ ,  $\frac{1}{32}$ , &c., from parent, grandparent, great grandparent, &c., originally taken as a first approximation by Mr. Galton.



(c) That the mean correlation of an  $n$ th parent with the offspring is one-half that of an  $(n-1)$ th parent also appears doubtful. (This would follow if reversion were started from the parent.)

(d) Testing theory by the case of Basset Hounds, we find much difficulty, owing partly to the great prepotency of the dam, and partly to the large amount of artificial selection which is evidenced at every turn, and obscures what may be termed the *natural* laws of inheritance.

(e) There is an urgent need to widely extend our knowledge of heredity by new experiments and observations on other organs in different races. Facts are of the first necessity at the present time, and facts collected on a large scale for a wide range.\*

\* It may be of service to indicate to would-be investigators what has already been done or is now in hand :—

In man :—

- (a) Stature (direct to first degree and collateral, fraternal).
- (b) Head index ( " " " " ).
- (c) Span and forearm (direct to first degree and collateral, fraternal).
- (d) Eye-colour (direct to second degree, collateral, fraternal and avuncular).
- (e) Shape of head, physique, intellectual capacities, tastes (collateral only).
- (f) Fertility (direct to second degree).
- (g) Longevity (direct and collateral, fraternal).

In horses :—

- (h) Coat-colour (direct to second degree and collateral).  
 (i) Fecundity (direct to second degree and collateral, fraternal and avuncular).

In hounds :—

- (j) Coat-colour (direct to third degree and collateral).

In moths :—

- (k) Wing-markings (direct and collateral).

In daphnia :—

- (*l*) Shape of spine (direct and collateral).

In all these cases the coefficients of correlation have already been worked out, or material is being collected to determine them, by Mr. Francis Galton, Professor W. F. R. Weldon, Dr. Warren, or by my collaborators and myself at University College. Hence I would impress upon others to take as far as possible widely different characters in widely different races. Above all, cases in which artificial selection plays a great part, *i.e.*, dogs, fancy pigeons, &c., ought to be avoided.