

THE LAW OF ANCESTRAL HEREDITY*.

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(1) To any one who has made a close study of heredity, whether it be in men, mice or plants, there are one or two conclusions which must be accepted at once. The first of these conclusions is:

(a) *That a knowledge of the characters of the parents does not accurately define the character in the offspring.*

Every one is familiar with the fact that given two pairs of parents possessing the like character in the same degree the offspring of one pair will differ from those of the other in respect of this character, and further that all the offspring of the same pair are not alike in the character; and this variation in the offspring of the same pair or of like pairs of parents may be very great indeed.

This point although familiar is frequently neglected. It is so important that it seems worth while to illustrate it by material at my disposal. The pedigrees I give are only samples of many hundreds in my possession, but they are conclusive. I turn first to coat-colour in thoroughbred horses.

(i) The mare *Ally* (bay) covered with *Little John* (bay) gave a roan colt. There are no black coats in the ancestry of either *Ally* or *Little John* back to their great-grandsires and great-grandams. *Jest Ally's* dam has, however, the *Delpini* grey colour, which accounts for the roan. *Ally* again covered, this time by *Interpreter* (bay), gives a *black* filly. There is no black blood in *Ally*, but *Interpreter's* paternal grandsire was the well-known black horse, *Socerer*. Thus two bay horses may give a roan, or two bays may give a black foal. I can cite any number of instances, of course, in which they give bay, brown or chestnut offspring.

* The following paper is put together not as a reply to Mr W. Bateson's rhetorical attack on the Law of Ancestral Heredity (published in his recent book *Mendel's Principles of Heredity*), but simply to indicate to those interested in the matter what are really the fundamental assumptions involved in the Law of Ancestral Heredity, and how far it enables us to describe actually observed experience in man, horse and dog, which I am unable under any hypothesis to bring under Mendel's "Principles." In the course of this year various investigations on heredity in both plant and animal life will I hope be published, and these will tend to throw further light on the laws of heredity.

(ii) *Socerer* was a black horse, son of the black *Trumpator*, out of *Young Giantess*, a bay. But the four grandparents of *Socerer* were two chestnuts, a brown and a bay, and of the eight great-grandparents seven were bays and of one, the *Snap Mare*, I have not been able to ascertain the colour. Where did *Socerer* and *Trumpator* get their blackness from? *Snap* was brown, but his maternal grandsire was the black horse *Gypsy*. In the same way *Rinaldo* black was born of the chestnut *Whiskey Mare* covered by the brown stallion *Milo*, but in the fourth and fifth generation backwards comes in the black *Gypsy* blood through the brown stallion *Snap*.

(iii) A bay filly is the result of crossing the chestnut stallion *General Graham* and the grey *Beningborough Mare*. The chestnut stallion *Prophet* and the grey mare *Virago* give a grey filly. The chestnut stallion *Woodpecker* and the grey *Herod Mare* give a chestnut filly *Chestnut Skin*. Clearly the coat-colour of the parents will not define that of the offspring. The bay filly, however, of the *General Graham* and *Beningborough Mare* cross is elucidated when we know that while it had one chestnut and one grey grandparent, it had two bays for grandparents.

I could multiply these pedigrees indefinitely, but the above will be sufficient to demonstrate the point for horses, i.e. the coat-colour of a horse may be unintelligible unless we examine the ancestry. We may easily find offspring of all shades from grey to black, whose parents had the same colour, say both bays.

I now pass to dogs. Let us first take Basset Hounds. Here the colours are lemon, white and black, and if they all occur the hound is termed tricolour.

(i) In 1885 the tricolour bitch *La Fanfare* put to the tricolour dog *Bourbon* gave the tricolour pup *Bluette*,—melanism appeared in the offspring. In the same year the tricolour bitch *Queen Dido* covered by the tricolour dog *Bourbon* gave the lemon and white pup *Blonde*, or melanism disappeared. In 1887 the lemon and white bitch *Jessie* crossed with the lemon and white dog *K. Bendigo* gave the tricolour hound *Bendigo II*. Thus when melanism is present in the parents it may be absent in the children, or when absent in the parents, it may reappear in the children.

(ii) *His Lordship* was tricolour, but his parents *Scipio* and *Fama* were only lemon and white. His black becomes quite explicable when we note that of his four grandparents two were tricolour.

(iii) Or, in the same litter, the tricolour bitch *Iris* by the tricolour dog *Count* casts five hounds of which three are tricolour and two lemon and white only. It is thus impossible to predict from the character of the parents whether black will or will not appear in the offspring. But here again ancestry throws light on the matter. *Count's* parents *Ugly* and *Rosalind II*. were both lemon and white and *Count* got his black from his paternal grandparents, who were both tricolour. Of *Iris's* parents one showed melanism and the other did not.

What we are dealing with here is not a slight variation in shade, but the presence or total absence of black pigmentation. This point must be borne in mind.

These cases might be enough, perhaps, for dogs, but I cite the following instances out of many for greyhounds*.

I would first state that I have sought in vain for any single colour or combination of colours which breeds true to itself. There is as far as I have been able to ascertain absolutely nothing that can correspond to Mendel's "recessive" character. At first it seemed to me possible that black would be such. *Bessie Hay*, a black bitch covered by *Grinlaw* a black dog, had a litter of entirely black offspring in 1896, and repeated this performance with four instead of five whelps in 1897. But the black bitch *Finest Fury* covered by the black dog *Petronius* in a litter of eight had five black and three red offspring. Black *Middleton* and black *Raven* gave three black, one blue, a red and a fawn offspring, while the black bitch *Mayfly* crossed by the black *Hernas* produced four black and two fawn offspring. In fact almost every possible greyhound colour will be found in the offspring of two black parents,—black, blue, either of these and white, fawn, red, brindled! If we next take such a cross as black and red we find red *Recoil* covered by black *Fortuna Favente* giving six black offspring and we at once consider whether black may be "dominant." But the red bitch *Maid of all Work* threw in a litter to the black dog *Black Marauder* six brindled, one black, one blue offspring and a white bitch with one eye and two ears black. Black *Nebula* crossed by red *Herschel* gave five fawn offspring, one black and one blue and white. Parents of the same colours will be found to give litters of red, and black and white offspring. A blue sire (*Blue Peter VIII.*) and a black dam (*Flotilla*) will produce all the offspring red, while a black bitch covered by a black and white sire will give pure black dogs, pure white dogs, or mixtures of black, red or fawn with white. The black bitch *Queen of the Colonies* covered by the red fawn dog *Dodger* gave beside five black and three red offspring a white bitch. No single colour breeds true to itself, and while all these results are explicable on the basis of ancestry, the Mendelian can only pass them over by asserting that the greyhound is an incorrigible mongrel.

We may next pass to eye-colour in man and I give the following instances†. Father and mother both blue, two out of six children dark brown. Father and mother both blue, one out of six children dark brown (colour of father's maternal grandfather). Father and mother both light grey, four children light grey, and five black or very dark brown (colour of maternal grandmother). Now turn to the opposite end of the scale: Father and mother black or very dark brown,

* Pedigrees taken from data collected by Mr Howard Collins.

† I gave the substance of such pedigrees to Prof. Weldon, who made use of it in his article on Mendel's Law in *Biometrika* (Vol. I. p. 242) in a passage criticised by Mr Bateson in his *Defence of Mendel*, p. 192. I first tested Mendel's theory of dominance on eye-colour in man when I read Mendel's paper in 1900 and then communicated the result to Professor Weldon.

one of eight children light blue (colour of paternal grandfather). Father black and mother dark brown, one child out of three hazel (the colour of paternal grandmother). Father and mother very dark brown or black, two children blue and one black. Father and mother very dark brown or black, two out of four children blue (colour of maternal grandmother). It is clear that neither end of the eye-colour scale gives a recessive character which breeds true to itself. Now note what we get if we attempt to select for several generations *paying attention to ancestry*. Father and mother blue, all four grandparents blue, and the five recorded great-grandparents blue, all four children blue. Parents and grandparents all blue, all eight children blue. Father and mother light grey, and the four grandparents all light grey or blue, all seven children grey. Father and mother grey and all the known ancestry of both grey or blue, all four children grey or blue. Father and mother both dark brown, all known ancestry brown for both, out of nine children seven dark brown, one brown and one light brown. Father and mother hazel, all ancestry to great-grandparents hazel with the exception of a blue-eyed grandfather, all five children hazel.

Lastly let us look at crosses between blue and dark eyes. Father light blue and mother dark brown, three children blue, four children dark brown. Father dark brown and mother blue, two children blue and four brown-eyed. Father dark brown and mother blue, three brown and six blue-eyed children; here all mother's known ancestry was blue. If blue were "dominant" such results are impossible unless we suppose every dark brown parent above recorded was a hybrid. If blue be "recessive" it ought to breed true, but we have seen that it does not. But as a matter of fact we can pick out cases from the record of one blue and one very dark parent giving almost every conceivable result, e.g. father light blue and mother black, four children blue and one light grey. Father brown and mother blue, eight children ranging from brown to dark brown. In all cases an examination of ancestry throws light, if it does not fully explain in each case what has taken place. It is clear from these cases that parentage will not enable us to predict offspring definitely. But what is also equally clear is that if all the ancestry be the same the offspring may differ among themselves considerably, e.g. by the presence or total absence of black pigmentation. Hence we reach our second conclusion:

(b) *That a knowledge of the whole ancestry while it certainly limits the range of variation does not absolutely define the character of the offspring.*

(2) Before we leave the cases above it is just worth reiterating that nothing corresponding to Mendel's principles appears in these characters for horses, dogs, or men. If black or grey coat-colour in horses were "recessive," when two blacks were mated we should expect only black offspring, but black can disappear for a generation or even two and then reappear. Or, take a case like that of a grey horse *Viscount*, where grey remained dominant for three generations only to disappear before the chestnut of the mare *Blue Stocking* in the *Viscount* and *Blue-Stocking* filly *Miss Johanna*! It is the same with every coat-colour taken, its

relative constancy depends largely on the extent to which it has appeared in the ancestry, and one by one black, bay, chestnut, grey must be dismissed by the Mendelian as neither "recessive" nor "dominant," but as marking "permanent and incorrigible mongrels." The same remark applies to coat-colour in hounds, black must be the mark of incorrigible mongrelism for it is neither recessive nor dominant. It is the same with red and white, no colour in the parents gives for every case consistent offspring.

Nor again do we find that two black-eyed human beings nor two blue-eyed human beings mated together give any sign of the dominance of one or other of these extremes; any more than do intermediate tints to which the description of "incorrigible mongrelism" may by some be applied. It will be clear that for man (and this applies not only to eye-colour, but to hair-colour, and to a whole series of measurable characters * of which we have in each case more than a thousand instances in our Family Records), for horses in coat-colour, and for dogs in coat-colour † nothing approaching Mendelian principles holds. We have therefore to classify large portions of the animal kingdom as exceptions to Mendel's Laws,—and these are cases where the evidence is not based on five or ten individual crosses followed perhaps for two or at most three generations—but on 1000's of crosses, and where the pedigree has been or can be investigated for some of the material for five to ten generations. What may happen in the case of plant hybrids, I am not able from personal observation to assert, but there is enough weight of evidence here to make one pause before one is prepared to admit that Mendel, or his followers, can change each conception of life in which heredity bears a part!

(3) Taking our stand then on the observed fact that a knowledge neither of parents nor of the whole ancestry will enable us to predict with certainty in a variety of important cases the character of the individual offspring we ask: What is the correct method of dealing with the problem of heredity in such cases? The causes A, B, C, D, E, \dots which we have as yet succeeded in isolating and defining are not always followed by the effect X , but by any one of the effects U, V, W, X, Y . We are therefore not dealing with causation but correlation, and there is therefore only one method of procedure possible; we must collect statistics of the frequency with which U, V, W, X, Y, Z respectively follow on A, B, C, D, E, \dots From these statistics we know the most *probable* result of the causes A, B, C, D, E and the frequency of each deviation from this most probable result. The recognition that in the existing state of our knowledge the true method of approaching the problem of heredity is from the statistical side, and that the most that we can hope at present to do is to give the *probable* character of the offspring of a given ancestry, is one of the great services of Francis Galton to biometry.

* Mendelianism fails also for skin-colour in crosses between the black and white races of man.

† Other characters in pedigree stock are being taken into consideration at present.

Yet since the publication of Francis Galton's *Natural Inheritance* in 1889 much progress has been made in the theory of multiple correlation, and also in our treatment of characters not quantitatively measurable, but which we may reasonably suppose to be based on quantitative factors,—as the degree of yellow pigment in the human eye. Further larger series of observations have been collected and reduced, and we are much clearer than we were ten years ago on the nature of regression and 'blend.'

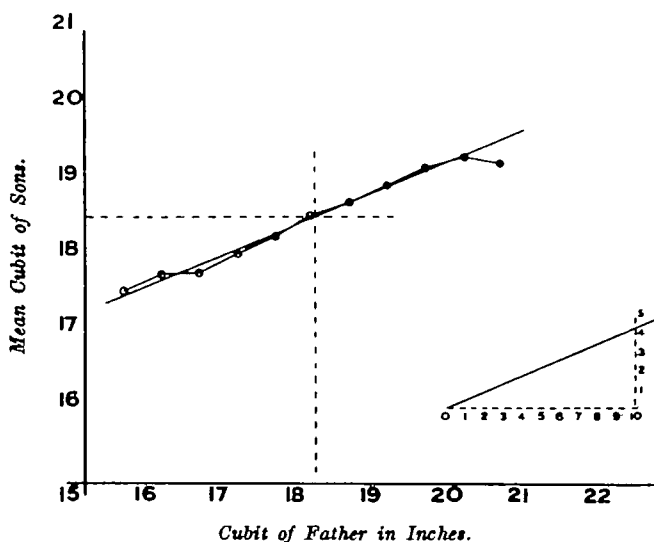
Given two relatives P and Q the general theory of statistics tells us how to dress a table from which we can read off at once the most probable character of P when we know the character of Q . There is no biological theory in this, it is merely an arrangement of statistical information into classes. Such classes may be arranged on an actual quantitative scale, or as in the case of eye or hair colour on a qualitative scale, which with a high degree of probability corresponds to a true quantitative scale in some one or other pigment, whose amount cannot be actually determined. In both cases the methods of statistics allow us to determine:

(a) The variability in character of both P and Q in terms of the range of one of these arbitrary classes.

(b) The average variability in the same terms of an array of P 's corresponding to a given Q , or of an array of Q 's corresponding to a given P .

(c) The first two terms of the closest linear function which expresses the probable character of P or Q in terms of the known character of Q or P .

Inheritance of Cubit.



Probable value of cubit of son Q , for a known cubit in father P . A marked deviation from linearity only occurs in the extreme case of father's cubit, where there were only a few instances to base the son's mean upon.

All this has nothing in it peculiar to heredity, it is simply an application of the higher theory of statistics.

If we ask how closely the above linear function gives the probable Q -value from the known P -value; the answer is: Admirably, for those characters which have been actually tested. I have 21 tables involving three characters for diverse relationships in man and each embracing upwards of 1000 pairs. I choose one, the cubit, perfectly at random and it will be seen at once that, within the limits of random sampling, no function could give the probable character of Q for a given value of P with greater efficiency.

The line here dealt with is the so-called regression line; it is a purely statistical result, and has no relation to any biological theory or hypothesis as to heredity. Its determination depends on the so-called coefficient of correlation of P and Q , which we will write r_{pq} , and their variabilities σ_p and σ_q . In addition we must know the mean, the modal or, what is often sufficient, the median values of P and Q .

Now suppose that instead of one relative P we have any number P_1, P_2, P_3, \dots , and let the corresponding statistical constants be $r_{p_1q}, r_{p_2q}, r_{p_3q} \dots \sigma_{p_1}, \sigma_{p_2}, \sigma_{p_3} \dots$. Then the theory of statistics shows us that, if p_q be the most probable deviation of Q from the type of its generation, and $h_{p_1}, h_{p_2}, h_{p_3} \dots$ be the observed deviations of P_1, P_2, P_3, \dots from the types of their respective generations, then:

$$p_q = J_1 \frac{\sigma_q}{\sigma_{p_1}} h_{p_1} + J_2 \frac{\sigma_q}{\sigma_{p_2}} h_{p_2} + J_3 \frac{\sigma_q}{\sigma_{p_3}} h_{p_3} \dots \dots \dots (i),$$

where $J_1, J_2, J_3 \dots$ are known expressions involving only the r_{pq} 's, and can be calculated as soon as the latter have been found from observation.

Further the variability of Q about its most probable value, when we know the P 's, takes on the average the value $\sigma_q \times \Delta$, where Δ is another well-known and calculable function of the r_{pq} 's.

The above is in no sense a biological theory, it is based on no data whatever except the actual statistics; it is merely a convenient statistical method of expressing the observed facts. If the facts are there it expresses them up to a certain point,—the most probable or most frequent value of the individual given his relatives. It cannot possibly within this range be upset by any hypothesis of heredity, Mendelian or otherwise, for it is based on no biological assumptions whatever. It is merely a convenient description of statistical tabulations.

I now proceed to limitations based on actual experience.

(i) The correlation coefficients between relatives are positive.

There is overwhelming evidence in favour of this in insects, animals and plants, for direct relationship back to great-great-grandparents and in a considerable range of collateral relationships—fraternal and avuncular.

But it may be shewn that if the r 's are positive, increasing the number of relatives used as a basis of prediction reduces the value of Δ . The rate of reduction decreases considerably as we increase the number of correlations, but for the first increase from one on to two, three ... six, etc. it is very sensible.

We therefore conclude that :

There will be less average deviation from the probable character of an individual when we increase the number of relatives on which the prediction is based.

As a special case we say that :

Prediction will be closer when we use the ancestry as well as the parents in forming it, than when we use the parents alone.

As soon as we accept the positive character of the correlation coefficients between offspring and ancestry this is an absolutely certain result. It could only be invalidated if the parents defined the offspring absolutely, i.e. if Δ for two parents was zero, or the correlation with parentage perfect. But this is completely negated by the fact * that the same pair of parents will produce offspring with very different characters,—e.g. two bay horses may give a black horse and not only a bay. Thus it seems to me that any hypothesis of inheritance which neglects ancestry is foredoomed to failure in the wide range of vital types for which we have shewn already that parentage does not define offspring uniquely. The variation in offspring of the same parents is not merely confined to slight differences in size of organs, but in many covers differences in colour, for example, as great as those upon which the Mendelians have based their discrimination between dominant and recessive characters.

(ii) In actual measurement on many series the J 's come out less than unity and there are theoretical reasons for holding that this must always be the case.

Hence if the variability of the offspring generation be not much larger than that of the generation of any relative, the probable deviation from type of any individual will only receive from any relative a fraction of his observed deviation from his type.

This is Mr Galton's principle of regression, the exceptionality of P_1 is on the average only exhibited in part by his relative Q . This purely statistical and legitimate conclusion was seized upon as a biological law, and all life, but for constant selection, was assumed to be in a state of regression to some distant ancestry. The expression (i) does not warrant this assertion at all. To begin with there is no reason to suppose :

(a) That $\sigma_q = \sigma_{p_1} = \sigma_{p_2} = \sigma_{p_3} = \dots$ or that the variability of all generations is the same. In numerous and large series I have not found it so †.

* For all the characters yet dealt with whether quantitative or qualitative in insects, animals and plants, there is no approach to $\Delta=0$.

† The offspring generation tends almost universally to be more variable than that of any ancestral generation—parents are a selected portion of the community.

(b) $h_p, h_{p_1}, h_{p_2}, \dots$ are deviations from the type of each generation. I have never found the types of each generation identical. They often differ very sensibly.

(c) Each individual ancestor contributes only a fraction of his deviation from type to the probable deviation in type of the offspring. But if the ancestry be maintained for two or three generations at a given deviation from type the contributions of the different terms of (i) provide a probable deviation in type of offspring which may be equal to or may even exceed that of the ancestry.

This point is over and over again forgotten when biologists talk of regression as if it were a persistent retrogressive factor.

As a matter of fact with the numbers we already have for man, breeding true for three or four generations gives a value of p_q within a small percentage of the selected h_p , and this is only slowly modified, if the stock continues to breed true to itself. There is no such thing in statistical theory as a *necessary* regression if the selected stock pair with selected stock. The rapid establishment of breeds is not evidence therefore against the present view of heredity. On the contrary it flows at once from it.

(4) So far there is practically no assumption in our treatment of heredity, which has not been justified by ample experience, e.g. the close linearity in distribution of the probable value of a character in one relative for a known value of a character in a second. Further it enables us to predict probable values from any group of known relatives. When however we predict from direct ancestors only we state more particularly the law of ancestral heredity. If we are content with parents, or possibly in some cases with grandparents also, we have material for making a fairly close prediction, but if we want to deal with whole lines of ancestry, we are met at once by the difficulty of collecting statistical material for the correlation of the offspring's character with that of the higher antecedents. In man few observations or measurements have been made on a higher than the grandparental generation, and even in pedigree animals, where we can go much further back, the characters recorded are never quantitative, but concern colour or markings. To get over this absence of material Mr Galton originally proposed that we should correlate not with each individual ancestor but with the mean of each ancestral generation, females being reduced to a male standard. There is no assumption in this because, of course, correlation can statistically be worked for any such group of ancestry. But as we do not know the values of the correlation coefficients of the higher groups, Mr Galton suggested that we should take the J_1, J_2, J_3, \dots of equation (i) on p. 217 equal to $\frac{1}{2}, \frac{1}{4}, \frac{1}{8} \dots$ respectively. This was undoubtedly an assumption, although not an unreasonable one *à priori*. That the intensity of ancestral heredity diminishes as we go backwards is demonstrated by both experiment and observation; and a geometrical series naturally first arises as a measure of such diminishing influence. But the law could only be demonstrated on the base of the first few terms of the J -series, and

Mr Galton's evidence from stature only gave a rough test of the series $\frac{1}{2}, \frac{1}{4}, \frac{1}{8}, \dots$ having the right trend. He did not himself claim more for it than this; thus after suggesting that $J_1 = \frac{1}{2}$ and $J_2 = \frac{1}{4}$, he writes: "It would, however, be hazardous to extend this sequence with confidence to more distant generations*."

Referring again to this point, Mr Galton says in 1897: "I stated it briefly and with hesitation in my book on *Natural Inheritance*†."

When I personally first came to investigate the matter from the more purely mathematical side, it seemed to me better to start with the coefficients of correlation and make no assumption as to the values of the regression coefficients in the J -series of p. 217‡. Each coefficient found would serve as the basis of a limited amount of prediction, and we must plod away finding coefficients for as many generations for as many characters in as many races as we possibly could. When these were known, we should possibly be able to predict the relationship between the correlation coefficients of successive generations even beyond the limits of observation and experiment. If we had to make an hypothesis at all, it seemed to me most reasonable to suppose the correlation not the regression coefficients of each generation of ancestry to diminish in a geometrical series. This view I kept steadily before me, but it was very difficult to find material going sufficiently far back to test it. Theoretically I shewed that if these correlations formed a geometrical series then the regression coefficients, or J 's, would also form a geometrical series, if we neglected the effects of assortative mating§, but the data I had collected did not as far as they went justify Mr Galton's proposed $\frac{1}{2}, \frac{1}{4}, \frac{1}{8}, \dots$ series.

Taking the matter broadly we may say that the Law of Ancestral Heredity implied two ideas:

(a) That the proper method to proceed in heredity within the race is by the statistical theory of multiple correlation—this does not exclude the truth of any physiological theory, although it may serve to confirm or refute such a theory. The correlation between parent and offspring in man will remain about .45 to .5, whatever theory of gametes may eventually be accepted, and the prediction of probable character in son from actual character in father remains equally valid.

(b) That a knowledge of the nearer coefficients of correlation, i.e. those between offspring, and parents, grandparents, and possibly great-grandparents, will suggest the more distant ones, and that probably these, and consequently the multiple regression coefficients, are expressible as a geometrically decreasing series.

This is the hypothesis involved in my own expression of the Law of Ancestral

* *Natural Inheritance*, p. 186.

† *R. S. Proc.* Vol. xli. p. 401. I have elsewhere shewn that the evidence from Basset Hounds admits of other interpretations. *R. S. Proc.* Vol. 66, p. 140 *et seq.*

‡ "Regression, Panmixia and Heredity." *Phil. Trans.* Vol. 187, p. 253 *et seq.*

§ "On the Law of Ancestral Heredity." *R. S. Proc.* Vol. 62, p. 394.

Heredity, and I believe it is a generalisation, which Mr Galton might, perhaps, be willing to accept in place of his much more definite series of $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, etc.

(5) Assuming we had the data for quantitatively measurable characters one would prefer to deal with such, but failing this I have asked myself how far the successive correlation coefficients for ancestry in qualitative characters (which we may reasonably suppose to have a quantitative scale behind them) fall into a geometrical progression. In eye-colour for man I have previously given* the four parental and the eight grandparental correlations. Mr F. Lutz has completed† the series, as far as it is possible to do on Mr Galton's material, by investigating the correlation of offspring with the great-grandparents, arranged in four groups. Mr L. Bramley-Moore and I had given the four parental and two of the grandparental coat-colour correlations for horses in 1899‡. Mr N. Blanchard published two further grandparental correlations recently§, and he has now completed the whole series of eight, and they will be found in a note attached to this paper. Dr Alice Lee worked out the great-grandparental and the great-great-grandparental correlation from the data provided by Mr Blanchard's MS. pedigree books; these are given in a second note below.

We have reached the following results:

| Mean Correlation | Eye-colour in Man | Coat-colour in Horse |
|---------------------------|-------------------|----------------------|
| Parental | ·4947 | ·5216 |
| Grandparental | ·3166 | ·2976 |
| Great-grandparental | ·1879 | ·1922 |
| Great-great-grandparental | — | ·1469 |

When we note that the probable error of these coefficients is about the order ·03, one is at once struck with their substantial agreement. We are forced to the conclusions:

- (i) That eye-colour in man and coat-colour in horses are inherited in sensibly the same manner.
- (ii) That the original series proposed by Mr Galton $\frac{1}{2}$, $\frac{1}{4}$... for these correlations|| will not fit them at all.

It might be supposed that pigmentation followed some other rule than measurable characters. But in recent work on measurable characters for 12 series, each numbering upwards of 1000 cases, I have found for man the mean parental value ·46. This is the largest inheritance series for man yet worked out, being based on measurements of upwards of 1100 families, so I am pretty

* *Phil. Trans. A*, Vol. 195, p. 106.

† See Note on the Influence of Change in Sex on Inheritance. *Biometrika*, Vol. II. p. 287.

‡ *Phil. Trans. A*, Vol. 195, p. 93.

§ *Biometrika*, Vol. I. p. 361.

|| *Natural Inheritance*, p. 133.

confident that parental inheritance for man lies between $\cdot45$ and $\cdot5$, and is quite incompatible with a value of $\frac{1}{3}$ *

I now turn to the problem of how far the data can be represented by a geometrical series. I fitted the best geometrical series first to the horse only, then to man, and finally to both with the following results.

| A. Horse, observed | Best Geometrical Series | Man, observed |
|--------------------|-------------------------|-----------------|
| $\cdot52$ | $\cdot48$ | $\cdot49$ |
| $\cdot30$ | $\cdot32$ | $\cdot32$ |
| $\cdot19$ | $\cdot21$ | $\cdot19$ |
| $\cdot15$ | $\cdot14$ | — |
| B. Man, observed | Best Geometrical Series | Horse, observed |
| $\cdot49$ | $\cdot50$ | $\cdot52$ |
| $\cdot32$ | $\cdot31$ | $\cdot30$ |
| $\cdot19$ | $\cdot19$ | $\cdot19$ |
| — | $\cdot12$ | $\cdot15$ |

In the first case, the series being a, ar, ar^2, \dots we have :

$$a = \cdot4809 \text{ and } r = \cdot6602.$$

In the second case :

$$a = \cdot5007 \text{ and } r = \cdot6167.$$

If we take the best geometrical series embracing the data for both races we have :

| C. Horse, observed | Man, observed | Best Geometrical Series |
|--------------------|---------------|-------------------------|
| $\cdot52$ | $\cdot49$ | $\cdot49$ |
| $\cdot30$ | $\cdot32$ | $\cdot32$ |
| $\cdot19$ | $\cdot19$ | $\cdot20$ |
| $\cdot15$ | — | $\cdot13$ |

Here we have :

$$a = \cdot4921 \text{ and } r = \cdot6428.$$

Lastly, if we take $a = \cdot5$, $r = \frac{2}{3}$ as close round numbers, we have :

| D. Horse, observed | Man, observed | Close Series |
|--------------------|---------------|--------------|
| $\cdot52$ | $\cdot49$ | $\cdot50$ |
| $\cdot30$ | $\cdot32$ | $\cdot33$ |
| $\cdot19$ | $\cdot19$ | $\cdot22$ |
| $\cdot15$ | — | $\cdot15$ |

Within the errors of observation this close series represents excellently the observed results for either eye-colour in man or coat-colour in the horse. In other words :

* As long as the only data for a measurable character in man—Mr Galton's stature data—gave a parental correlation of about $\frac{1}{3}$ it seemed needful to emphasise the distinction between the results for eye-colour and stature. In the light of my present knowledge, the distinction between the two classes of characters seems not so clear or needful. A large series of pedigree dogs at present in hand gives a parental correlation almost identical with that of horse and man.

As far as the available data at present go inheritance coefficients for ascending ancestry are within the limits of observational error represented by a geometrical series and by the same series.

From this it follows that*: *The contributions of the ancestry also follow a geometrical series, although not that originally proposed by Mr Galton.*

(6) Mr Galton has assumed, that if the relatives include all the ancestry, and if all these ancestry had the same deviation h , the offspring will have a probable deviation of h . This is really the introduction of a biological hypothesis, the truth of which can only be tested by observation. Mr Galton deduces this result in the following manner: he supposes a stable population, i.e. one in which the mean and variability of each generation remain the same, and the parents in each generation are the whole or at any rate a random sample of that generation; there must also be no reproductive selection, or fertility must not be correlated with the character of which the inheritance is under consideration. Further there must be no assortative mating. Under these circumstances we have the following form of (i) p. 217:

$$p_q = (J_1 + J_2 + J_3 + \dots) h,$$

and since Mr Galton holds that p_q will then equal h , we have

$$J_1 + J_2 + J_3 + \dots = 1 \dots\dots\dots(2).$$

Any geometrical series $\epsilon(1 + \rho + \rho^2 + \dots)$ for the J 's will satisfy this condition if $\epsilon = 1 - \rho$; the series $\frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \frac{1}{16} + \dots$ is not the only one satisfying (2)†.

But it is doubtful‡ how far this conclusion is justifiable. Statistically it is of course unnecessary. (i) is a relation between the probable deviation of Q from its mean and the actual deviations of each P from their individual means. There is no reason why the means of Q and of all the P 's should be the same. They may be different owing to environment or to selection. Further there is no reason why the variabilities should be the same; parents may be a selection out of the general community in each generation. As soon as we realise that the h 's are deviations from the generation means, and these are not all the same, and that the variability in each generation differs, the need for the relation

$$J_1 + J_2 + J_3 + \dots = 1$$

ceases to be apparent.

In data like eye-colour in man and coat-colour in thoroughbred horses there has been undoubtedly a secular change going on; the proportion of blue eyes in the latest offspring is considerably less than in the great-great-grandparents, while the early grey horses have largely disappeared from the stud-book. Further we find each ancestral generation is roughly speaking less variable than

* R. S. Proc. Vol. 62, p. 394.

† R. S. Proc. Vol. 62, p. 402, and Vol. 66, p. 147.

‡ It is hardly consonant, for example, with what we know of eye-colour, where there is an assortative mating coefficient of .1002: see *Phil. Trans. A*, Vol. 195, p. 113.

the one below it. Men who live to be parents are a more select group than their offspring and this is still more true of grandparents and higher ancestry. To be a great-great-grandparent means to have a healthy stock, and such men form a selection only of the community in each generation. Hence neither for man nor the thoroughbred horse need we *a priori* expect to find, for the correlation coefficients as actually determined, the relation $J_1 + J_2 + J_3 + \dots = 1$ or $\epsilon = 1 - \rho$ satisfied. The actual statistics for man and the horse conclusively prove that it is not satisfied. If we had a population in which all members were randomly mated and were parents of equal fertility; further if every generation had the same mean and variability, then we might have $\epsilon = 1 - \rho$, but then the correlations of ancestry and offspring would probably take very different values from what we find them to have in the cases of man and horse under existing circumstances.

(7) Supposing all mating to be random* we can find ϵ and ρ and all the J 's by the method of my first paper on the "Law of Ancestral Heredity†." In the notation of the present paper, if a^n be the correlation coefficient of "the $n+1$ th mid-parent" with the offspring, and if $J_q = \epsilon' \rho'^{q-1}$, we find:

$$r = \rho' + \epsilon' \dots \dots \dots (3),$$

$$-a + \epsilon' \rho' a / (1 - \rho' r) = -\epsilon' \dots \dots \dots (4);$$

whence:

$$\rho'^2 - \rho' \frac{1 + r^2 - 2ar}{r - a} + 1 = 0 \dots \dots \dots (5).$$

Hence taking $a = .5$ and $r = .3$ as close enough to the observed values we have:

$$\rho' = .2251, \quad \epsilon' = .4415.$$

Formula (i) of p. 217 using "mid-parents" now becomes:

$$p_q = .4415 \left\{ \frac{\sigma_0}{\Sigma_1} h_{p_1} + .2251 \frac{\sigma_0}{\Sigma_2} h_{p_2} + (.2251)^2 \frac{\sigma_0}{\Sigma_3} h_{p_3} + \dots \right\}.$$

Here $\Sigma_1, \Sigma_2, \Sigma_3 \dots$ are the standard deviations of the mid-parental groups, and $\Sigma_s = \sigma_s / (\sqrt{2})^s$, if σ_s be the standard deviation of the s th generation of ancestors. Thus:

$$\begin{aligned} p_q &= .4415 \times \sqrt{2} \left\{ \frac{\sigma_0}{\Sigma_1} h_{p_1} + .2251 \sqrt{2} \frac{\sigma_0}{\Sigma_2} h_{p_2} + (.2251 \sqrt{2})^2 \frac{\sigma_0}{\Sigma_3} h_{p_3} + \dots \right\} \\ &= .6244 \left\{ \frac{\sigma_0}{\Sigma_1} h_{p_1} + .3184 \frac{\sigma_0}{\Sigma_2} h_{p_2} + (.3184)^2 \frac{\sigma_0}{\Sigma_3} h_{p_3} + \dots \right\} \\ &= \epsilon \left\{ \frac{\sigma_0}{\Sigma_1} h_{p_1} + \rho \frac{\sigma_0}{\Sigma_2} h_{p_2} + \rho^2 \frac{\sigma_0}{\Sigma_3} h_{p_3} + \dots \right\}. \end{aligned}$$

Clearly $\epsilon = .6244$ is not equal to $1 - \rho$ or .6816, or Mr Galton's hypothesis is certainly not satisfied either for man or horse. But since we know in these cases

* R. S. Proc. Vol. 66, p. 149.

† R. S. Proc. Vol. 62, p. 894.

that $\sigma_1 = \sigma_2 = \sigma_3 = \dots = \sigma_0$ is not true, and further that $h_{p_1}, h_{p_2}, h_{p_3} \dots$ are measured from different means, we have no *a priori* right to suppose it ought to be satisfied.

(8) It is not without interest to follow up what would happen in man and horse if, with our present numbers, we supposed the conditions for a stable population to be really satisfied. Let us select about the deviation h from the common mean for s generations, then the offspring would have a probable deviation from that mean of

$$\epsilon \frac{(1 - \rho^s)}{1 - \rho} h.$$

If we then ceased to select, but bred the offspring among themselves for t generations, the offspring of the t th generation would have a probable deviation from the mean of

$$\epsilon \cdot \frac{1 - \rho^t}{1 - \rho} \cdot (\sqrt{2r})^t h.$$

Let us turn these results into numbers, remembering that $\epsilon = \cdot 6244$ and $\rho = \cdot 3184$.

| | | |
|---|---|-------------|
| Result of selecting all ancestry for one generation | = | $\cdot 62h$ |
| " " " two generations | = | $\cdot 82h$ |
| " " " three " | = | $\cdot 89h$ |
| " " " innumerable " | = | $\cdot 92h$ |

In other words indefinitely long selection would only raise us to $\cdot 92$ of the desired character. We should therefore not get the whole of the desired character *without selecting beyond it*. But on the other hand by merely selecting for two generations we should get within ten, and for three generations within four per cent. of the possible maximum of indefinitely protracted selection. Hence selection for a very few generations would raise the selection rapidly to within a small percentage of the maximum result.

Generations after which selection is stopped and simple breeding-in of selected stock follows.

| | First | Second | Third | Innumerable |
|-----------------------------------|-------------|-------------|-------------|-------------|
| Last offspring of selection ... | $\cdot 62h$ | $\cdot 82h$ | $\cdot 89h$ | $\cdot 92h$ |
| First generation of in-bred stock | $\cdot 59h$ | $\cdot 78h$ | $\cdot 84h$ | $\cdot 86h$ |
| Second " " " | $\cdot 56h$ | $\cdot 73h$ | $\cdot 79h$ | $\cdot 81h$ |
| Third " " " | $\cdot 52h$ | $\cdot 67h$ | $\cdot 74h$ | $\cdot 77h$ |
| Tenth " " " | $\cdot 35h$ | $\cdot 46h$ | $\cdot 49h$ | $\cdot 51h$ |

Next let us suppose selection stopped and the stock to breed-in or mate with its likes. The above table shows how it would slowly degenerate. The essential

point to be noted is that while two or three generations of selection would carry us up to 80 or 90 per cent. of the desired character, ten generations following this of merely in-breeding without any selection would not have cost us 50 per cent. of the character so acquired. Quick influence of selection, slow effect of regression would be the result of combining the actually observed values with Mr Galton's theory as to what should hold for a stable population.

The reader must not forget that the illustration here given is absolutely hypothetical; the statistical constants obtained are deduced from material to which Mr Galton's conditions hardly apply even as a rough approximation. Yet it is possible that something of the kind here indicated may occur in special cases. But if so, we ought to be very cautious of using vague categories in problems of heredity. If the mean tint of a seed, say, be yellow, and h would carry us well into the green end of the scale, $4h$ might still be green, and certainly for three and possibly for a good many more generations we might consider the stock arising from a *single* selection to be breeding true to itself, although actually it might be slowly regressing to the original tint of the early ancestry. It seems absolutely necessary in all such cases to have some colour standard and determine quantitatively whether successive generations do or do not tend to slowly approach or depart from it. The statement that ancestry has no influence might well be deduced by the use of a rough category, which would still class $.62h$ with $.52h$.

(9) Conclusions.

(a) In all cases as those of man, horse and dog, where parents of identical character do not produce identical offspring, the theory of statistics shows us that closer prediction may be obtained when we predict from many instead of few relatives. This follows from the consideration that all the heredity coefficients are *positive*.

Attention is therefore properly paid to ancestry in such cases, and it is very misleading to suggest that any law of heredity can be universal which neglects ancestry.

(b) The law of ancestral heredity in its most general form is not a biological hypothesis at all, it is simply the statement of a fundamental theorem in the statistical theory of multiple correlation applied to a particular type of statistics. If statistics of heredity are themselves sound the results deduced from this theorem will remain true whatever biological theory of heredity be propounded.

(c) The law of ancestral heredity as founded on the theory of multiple correlation involves no *biological* theory of regression. The term regression has unfortunately been taken from statistical theory and interpreted in a biological sense. In statistics the regression is always to the mean of the forecasted character, but no assumption is made that this mean is identical with that of the foreknown character*. Further, if there be a number of cognates, we can *a priori*,

* There is a "regression" for example if we predict breadth of skull from its length. I think it might be useful to adopt the word "predicate" for the forecasted and "cognate" for the foreknown character.

i.e. before quantitative analysis, not state whether the total amounts they will contribute to the predicate will or will not indicate a biological regression*.

(d) The law of ancestral heredity as a pure statistical statement has been supplemented by hypotheses which need verification and are semi-biological. These may (i) either be hypotheses as to the multiple regression coefficients, or (ii) as to the individual coefficients of correlation.

Mr Galton has assumed that the former are the geometrical series $\frac{1}{2}, \frac{1}{4}, \frac{1}{8} \dots$. I have assumed that the *mean* correlation coefficients for each ancestral generation form some geometrical series. It follows from my assumption that the regression coefficients would also form a geometrical series, but not necessarily Mr Galton's.

(e) In eye-colour in man and coat-colour in horses the mean ancestral coefficients of regression form within the limits of errors of random sampling a geometrical series, but it is not Mr Galton's series:

·5000, ·2500, ·1250, ·0625 ...,

but more nearly:

·6244, ·1988, ·0630, ·0202

In other words actual statistics show that in man and horse the parents are much more and the grandparents and higher ancestry less influential than on Mr Galton's hypothesis.

Thus the law of ancestral heredity (by which we are to understand the theory of multiple correlation together with the hypothesis that the mean ancestral correlations or the regression coefficients form a geometrical series) fits the data for horse and man remarkably well.

(f) In man and horse we find the means of each generation differ, and further the variabilities of each generation differ. It is an assumption to suppose under these circumstances that the sum of the regression coefficients (or rather that part of them which we have represented by J_1, J_2, J_3, \dots) is unity.

Any geometrical series for the regression coefficients which satisfies the condition $\epsilon = 1 - \rho$ (like Mr Galton's does) would give on the supposition of equal means and variabilities for each generation *no regression whatever* after a stock began to in-breed.

If we may apply (which is very doubtful) our values for the J 's in man and horse to cases in which the means and variabilities of each generation remained the same, there would result the following principle:

Two or three generations of selection would produce a stock of upwards of 90 per cent. of the selected character, but no amount of selection, unless of a greater

* It is curious that the original numbers selected by Mr Galton for the regression coefficients $\frac{1}{2}, \frac{1}{4}, \frac{1}{8}$, etc. indicate no regression whatever towards the predicate mean, after the first generation, if the stock in-breeds or breeds with its likes. It is characteristic of how conceptions are misunderstood, that this point of "regression" is what the majority of biologists have seized as the one easily comprehended principle out of the whole of Mr Galton's work!

than the desired amount of character, would give us more than 92 per cent. of it. After selection ceases a very slow regression sets in, which would be hardly perceptible without very definite quantitative measurement for the first three or four generations of in-breeding.

No rough classification like a Mendelian category would enable us to test whether such slow regression is really taking place, i.e. whether "recessives" are really breeding true to their stock*. And above all no Mendelian theory can (a) replace the statistical treatment unless it shows that offspring are absolutely determined by their parents, for if the correlation be not perfect, a better prediction must be obtainable by using the positively correlated ancestry, or (b) be proved without careful quantitative analysis of the variations falling within the wide categories adopted.

Appendix I. Note on a paper by G. U. Yule.

This paper was written before I was aware that Mr G. U. Yule was writing some account of the law of ancestral heredity, and was sent to press before I had seen his paper (*The New Phytologist*, November and December, 1902). With much of his paper, I agree, for example, with his insistence on the point that the laws of intra-racial heredity are not incompatible with Mendelian principles holding for hybridisation. I should lay, however, far less stress than he does on the value of the existing evidence in favour of those principles. That evidence certainly justifies the making of new and crucial experiments, but these will have to be made with much greater caution and closer quantitative definition of the categories employed before we can say with certainty how far either of the two principles of dominance and segregation actually applies even to the cases of hybridisation already dealt with by the Mendelians. I shall be surprised if the laws which govern intra-racial and inter-racial heredity are not more closely related than appears to me possible under the recent formulation of Mendelian Principles by Mr Bateson. Further Mr Yule does not seem to me to have clearly expressed my personal position with regard to the law of ancestral heredity. I believe that my memoir of 1896 was the first in which the equations of multiple regression were worked out and applied to the problem of heredity. Such equations are, I presume, what Mr Yule refers to and says may be termed the law of ancestral heredity. But the objection to such form of the law is simply the impossibility of working it out for all the ancestry, and for all characters of all races. The problems that arise at once in our minds are: Is there any relationship between the correlations of offspring and successive ancestors? Are these correlations in cases, where direct selection of the characters is small or can be allowed for, the same or approximately the same for different characters of the same race, or for divers characters of different races? Is there any relation between the correlations, which appears fairly in accordance with observation and yet will simplify the otherwise appalling complexity of the multiple regression equations? The memoir of 1896 gave the general regression equations, and indicated what results would flow supposing one or other of a variety of hypotheses due to Galton, Weismann and others were true. The memoir of 1898 adopted the simpler hypothesis that the correlation coefficients decrease in geometrical progression, *it did not involve the fixity of the numerical constants of heredity* which Mr Yule tells us has not

* For example, if we selected extreme chestnut (towards roan-chestnuts) for two generations only in the horse, yet if the progeny in-bred for 10 generations, the offspring would still be well in the chestnut range of coat-colour, and no category like chestnut would tell us whether the horses were breeding true or regressing.

stood the test of time. This simpler hypothesis, discussed in the present paper, still seems to me to stand the test of time. Lastly, I think, the reader of Mr Yule's paper would believe from the words: "Selective mating, natural selection, reproductive selection, the effect of circumstance, had all in turn to be recognised as causes affecting the values of the constants of heredity," that these factors were introduced *post hoc*, i.e. after observation had failed to give fixity of constants, whereas almost the reverse is the true case. The definition of selective mating was given in my first paper to the Royal Society on biparental inheritance in 1895* before I had applied the formulæ to actual data at all. Reproductive selection was considered in 1896†, and the influence of natural selection on correlation (including the coefficients of heredity) was given in College Lectures of the session 1896-7, and put into a form identical with that of the memoir just issued‡ in August 1897. The memoir of 1898 on the law of ancestral heredity was written with a knowledge of the influence of the three factors of selective mating, natural selection and reproductive selection on the constants of heredity. As a matter of fact they had been biometrically defined in or before the memoir of 1896, and were not "all in turn recognised as causes affecting the values of the constants of heredity," or used to bolster up some theory which had not stood the test of time.

What I felt in 1896, I still feel, namely: that the problem of heredity from the purely statistical standpoint is an extremely difficult one, that the factors of selective mating, natural selection, reproductive selection, environmental influence are extremely complex, especially when we place plants or insects in very artificial surroundings for the purpose of experimenting on their laws of reproduction. Still these factors do not invariably tend in one direction, and when we take long series, as free from their influence as is practically possible, we shall be able to judge from the clustering of the heredity coefficients round certain values—a phenomenon which I think is obvious in existing results—what in broad lines is the quantitative intensity of heredity for different relationships, and for different characters in different species. Mr Yule indicates that he has a theory which allows him to determine the influence of the environmental, reproductive, selective and mating factors; I can only say that I, as well as most biometricians, will heartily welcome its publication, if it not only allows, in the case of any heredity statistics which it is feasible to collect, for the correcting of the heredity constants for all these influences, but achieves this by some hypothesis which is *a priori* as reasonable, and *a posteriori* as justified as the simple one that ancestral correlations diminish in a geometrical progression.

Appendix II. On Inheritance (Grandparent and Offspring) in Thoroughbred Racehorses.

BY NORMAN BLANCHARD, B.A.

(1) At the suggestion of Professor Karl Pearson I have recently worked out the remaining four cases for the inheritance of coat-colour in thoroughbred horses, viz. those between foals—colts or fillies—and their paternal and maternal grandams. The work was done in a somewhat different manner to that on the four earlier tables. In order to consider the bearing of coat-colour inheritance on Mendel's theory, actual colour pedigrees were formed going back to the great-great-grandparents and in some cases to the fifth and eighth generation of ancestry. Further, in order to get more striking colour contrasts than are now-a-days possible, the first three volumes of the stud-book were dealt with, I thus went back to the earliest records of coat colour in thoroughbreds. Here we find 2 to 3 per cent. of black horses and 9 to 10 per cent. of

* "On Regression and Inheritance in the case of two Parents," *R. S. Proc.* Vol. 58, 1895.

† "On Reproductive Selection," *R. S. Proc.* Vol. 59, p. 801, 1896.

‡ *Phil. Trans.* Vol. 200, pp. 1-66, 1902.

greys, while in the recent studbooks these percentages are hardly 2 per cent. and '5 to 1 per cent. respectively. In the early colour records the finer distinctions, e.g. "black or brown," "bay or chestnut," etc., of the modern terminology rarely appear, but this is not of importance. A thousand cases were taken for each series, and the correlation Tables I. to IV. were constructed as in Pearson and Bramley-Moore's memoir on *Inheritance of Coat-Colour in Horses**, in fact the method there used was followed identically, the fourfold division between chestnut and bay being used for the short tables. The following results were obtained, the notation being that of Professor Pearson's memoir: *On the Correlation of Characters not quantitatively measurable*†.

(2) Table I. reduces to

Paternal Grandams.

| Colts. | | Bay and darker | Chestnut and lighter | Totals |
|--------|----------------------|----------------|----------------------|--------|
| | Bay and darker ... | 486 | 188 | 674 |
| | Chestnut and lighter | 172 | 154 | 326 |
| | Totals | 658 | 342 | 1000 |

This gives:

$$h = \cdot 4070105, \quad H = \cdot 3672283,$$

$$k = \cdot 4509851, \quad K = \cdot 3603667,$$

and the equation:

$$\begin{aligned} \cdot 3212093 = r + \cdot 0917778r^2 + \cdot 1107746r^3 + \cdot 0606283r^4 \\ + \cdot 0308582r^5 + \cdot 0443421r^6 + \cdot 0101909r^7 + \cdot 0339243r^8 + \text{etc.} \end{aligned}$$

the root of which is

$$r = \cdot 3085.$$

From Table II. we have

Maternal Grandams.

| Colts. | | Bay and darker | Chestnut and lighter | Totals |
|--------|----------------------|----------------|----------------------|--------|
| | Bay and darker ... | 539 | 149 | 688 |
| | Chestnut and lighter | 198 | 114 | 312 |
| | Totals | 737 | 263 | 1000 |

giving:

$$h = \cdot 6341100, \quad H = \cdot 3300624,$$

$$k = \cdot 4901880, \quad K = \cdot 3537792,$$

* *Phil. Trans. A*, Vol. 195, pp. 92 *et seq.*

† *Phil. Trans. A*, Vol. 195, pp. 1—47.

and the equation :

$$\begin{aligned} \cdot 2735648 = r + \cdot 1554165r^2 + \cdot 0631895r^3 + \cdot 0928545r^4 \\ + \cdot 0100882r^5 + \cdot 0608670r^6 - \cdot 0007343r^7 + \cdot 0412678r^8 + \text{etc.} \end{aligned}$$

the root of which is

$$r = \cdot 2614.$$

From Table III.

Paternal Grandams.

| Fillies. | | Bay and darker | Chestnut and lighter | Totals |
|----------|----------------------|----------------|----------------------|--------|
| | Bay and darker ... | 525 | 189 | 714 |
| | Chestnut and lighter | 175 | 111 | 286 |
| | Totals | 700 | 300 | 1000 |

giving :

$$h = \cdot 5243986, \quad H = \cdot 3517190,$$

$$k = \cdot 5689150, \quad K = \cdot 3393338,$$

and the equation :

$$\begin{aligned} \cdot 2111434 = r + \cdot 1491612r^2 + \cdot 0817246r^3 + \cdot 0906581r^4 \\ + \cdot 0138143r^5 + \cdot 0606133r^6 + \cdot 0014633r^7 + \cdot 0420798r^8 + \text{etc.} \end{aligned}$$

the root of which is

$$r = \cdot 2041.$$

From Table IV.

Maternal Grandams.

| Fillies. | | Bay and darker | Chestnut and lighter | Totals |
|----------|----------------------|----------------|----------------------|--------|
| | Bay and darker ... | 542 | 163 | 705 |
| | Chestnut and lighter | 187 | 108 | 295 |
| | Totals | 729 | 271 | 1000 |

giving :

$$h = \cdot 6097900, \quad H = \cdot 3312572,$$

$$k = \cdot 5388334, \quad K = \cdot 3380886,$$

and the equation :

$$\begin{aligned} \cdot 2505039 = r + \cdot 1750152r^2 + \cdot 0701968r^3 + \cdot 0976633r^4 \\ + \cdot 0088602r^5 + \cdot 0630885r^6 + \cdot 0001216r^7 + \cdot 0419921r^8 + \text{etc.} \end{aligned}$$

the root of which is

$$r = \cdot 2392.$$

(3) The eight grandparental correlations for the horse are given below together with the corresponding ones for eye-colour in man for the sake of comparison. The whole series has now been determined by Pearson and Bramley-Moore* or myself†.

* *Loc. cit.* p. 93.

† *Biometrika*, Vol. 1. p. 361.

| | | Horse. Coat-colour | Man. Eye-colour |
|---|-------------------------------|-----------------------|--------------------|
| 1 | Pat. Grandfather and Son ... | 3238 | 4213 |
| 2 | Pat. Grandfather and Daughter | 3609 | 3802 |
| 3 | Mat. Grandfather and Son ... | 3590 | 3717 |
| 4 | Mat. Grandfather and Daughter | 3116 | 2969 |
| 5 | Pat. Grandmother and Son ... | 3085 | 2722 |
| 6 | Pat. Grandmother and Daughter | 2041 | 2205 |
| 7 | Mat. Grandmother and Son ... | 2614 | 2623 |
| 8 | Mat. Grandmother and Daughter | 2392 | 3180 |
| | Mean | 2961 | 3179 |

It will be seen at once that the *mean* result for men is substantially in agreement with that for horses. We can hardly suppose grandparental correlation for the characters in man and horse dealt with to differ much from .3. The mean value of grandparental correlation in the horse for cases 1 to 4 drawn from the modern studbooks is .3388 and for cases 5 to 8 drawn from the older records .2533. I believe this is due to the close relationship of so many of the horses in the earliest period of breeding. The difference may also to some extent depend on the somewhat rougher appreciation and description of colour. If there be any influence of change of sex in the intensity of heredity for coat-colour in the horse, it is not manifested in the above statistics, which thus differ widely from those of eye-colour in man.

TABLE I.

Colts and Paternal Grandams.

Paternal Grandams.

| | bl. | bl./br. | br./bl. | br. | br./b. | b./br. | b. | b./ch. | ch./b. | ch. | ch./ro. | ro./ch. | ro. | ro./gr. | gr./ro. | gr. | Totals |
|---------|-----|---------|---------|-----|--------|--------|-----|--------|--------|-----|---------|---------|-----|---------|---------|-----|--------|
| bl. | 8 | — | — | 6 | — | — | 11 | — | — | 12 | — | — | — | — | — | 3 | 40 |
| bl./br. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| br./bl. | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — | — | 1 | 2 |
| br. | 8 | — | — | 39 | — | — | 75 | — | — | 20 | — | 2 | — | — | — | 7 | 151 |
| br./b. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| b./br. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| b. | 13 | — | — | 95 | — | — | 230 | — | — | 101 | — | 2 | 1 | — | — | 39 | 481 |
| b./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ch./b. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ch. | 2 | — | — | 27 | — | — | 113 | — | — | 82 | — | 1 | — | — | — | 16 | 241 |
| ch./ro. | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | 1 |
| ro./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ro. | — | — | — | 2 | — | — | 2 | — | — | 1 | — | — | — | — | — | 2 | 7 |
| ro./gr. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| gr./ro. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 |
| gr. | — | — | — | 10 | — | — | 16 | — | — | 13 | — | — | — | — | — | 37 | 76 |
| Totals | 31 | — | — | 180 | — | — | 447 | — | — | 230 | — | 5 | 1 | — | — | 106 | 1000 |

TABLE II.

Colts and Maternal Grandams.

Maternal Grandams.

| | bl. | bl./br. | br./bl. | br. | br./b. | b./br. | b. | b./ch. | ch./b. | ch. | ch./ro. | ro./ch. | ro. | ro./gr. | gr./ro. | gr. | Totals |
|---------|-----|---------|---------|-----|--------|--------|-----|--------|--------|-----|---------|---------|-----|---------|---------|-----|--------|
| bl. | — | — | — | 6 | — | — | 13 | — | — | 4 | — | — | — | — | — | 3 | 31 |
| bl./br. | — | — | — | — | — | — | 1 | — | — | 1 | — | — | — | — | — | — | 2 |
| br./bl. | — | — | — | — | — | — | 89 | — | — | 17 | — | 1 | 1 | — | — | 10 | 155 |
| br. | 3 | — | — | 34 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| br./b. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| b./br. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| b. | 6 | — | — | 73 | — | — | 309 | — | — | 76 | — | 1 | — | — | — | 35 | 500 |
| b./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ch./b. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ch. | 3 | — | — | 29 | — | — | 132 | — | — | 58 | — | — | 2 | — | — | 14 | 238 |
| ch./ro. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ro./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ro. | — | — | — | 1 | — | — | 1 | — | — | 1 | — | — | 1 | — | — | 1 | 5 |
| ro./gr. | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | — |
| gr./ro. | — | — | — | — | — | — | 22 | — | — | 7 | — | — | — | — | — | 30 | 68 |
| gr. | 2 | — | — | 7 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Totals | 14 | — | — | 150 | — | — | 573 | — | — | 164 | — | 2 | 4 | — | — | 93 | 1000 |

TABLE III.

Fillies and Paternal Grandams.

Paternal Grandams.

| | bl. | bl./br. | br./bl. | br. | br./b. | b./br. | b. | b./ch. | ch./b. | ch. | ch./ro. | ro./ch. | ro. | ro./gr. | gr./ro. | gr. | Totals |
|---------|-----|---------|---------|-----|--------|--------|-----|--------|--------|-----|---------|---------|-----|---------|---------|-----|--------|
| bl. | — | — | — | 5 | — | — | 13 | — | — | 9 | — | — | — | — | — | 1 | 28 |
| bl./br. | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | 1 | 1 |
| br./bl. | — | — | — | — | — | — | 83 | — | — | 31 | — | — | — | — | — | 6 | 166 |
| br. | 8 | — | — | 38 | — | — | 1 | — | — | — | — | — | — | — | — | — | 1 |
| br./b. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| b./br. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| b. | 15 | — | — | 91 | — | — | 270 | — | — | 109 | — | — | — | — | — | 32 | 517 |
| b./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ch./b. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ch. | 2 | — | — | 25 | — | — | 113 | — | — | 60 | — | — | — | — | — | 14 | 214 |
| ch./ro. | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | 1 |
| ro./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ro. | — | — | — | 1 | — | — | 4 | — | — | — | — | — | — | — | — | — | 5 |
| ro./gr. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| gr./ro. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| gr. | 1 | — | — | 12 | — | — | 17 | — | — | 11 | — | — | — | — | — | 25 | 66 |
| Totals | 28 | — | — | 172 | — | — | 502 | — | — | 221 | — | — | — | — | — | 79 | 1000 |

TABLE IV.

Fillies and Maternal Grandams.

Maternal Grandams.

| | bl. | bl./br. | br./bl. | br. | br./b. | b./br. | b. | b./ch. | ch./b. | ch. | ch./ro. | ro./ch. | ro. | ro./gr. | gr./ro. | gr. | Totals |
|---------|-----|---------|---------|-----|--------|--------|-----|--------|--------|-----|---------|---------|-----|---------|---------|-----|--------|
| bl. | 1 | — | — | 4 | — | — | 9 | — | — | 5 | — | — | — | — | — | 6 | 25 |
| bl./br. | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | 1 |
| br./bl. | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | 1 |
| br. | 1 | — | — | 33 | 1 | — | 84 | — | — | 29 | — | — | 1 | — | — | 7 | 156 |
| br./b. | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | 1 |
| b./br. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| b. | 6 | — | — | 80 | — | — | 322 | — | — | 73 | — | — | — | — | — | 40 | 521 |
| b./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ch./b. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ch. | 2 | — | — | 17 | — | — | 138 | — | — | 60 | — | — | — | — | — | 15 | 232 |
| ch./ro. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ro./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| ro. | — | — | — | 1 | — | — | 2 | — | — | — | — | — | — | — | — | — | 3 |
| ro./gr. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| gr./ro. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| gr. | 1 | — | — | 9 | — | — | 17 | — | — | 8 | — | — | — | — | — | 25 | 60 |
| Totals | 11 | — | — | 144 | 1 | — | 573 | — | — | 177 | — | — | 1 | — | — | 93 | 1000 |

Appendix III. On Inheritance (Great-grandparents and Great-grandparents and Offspring) in Thoroughbred Racehorses.

By ALICE LEE, D.Sc.

FROM Mr Blanchard's racehorse coat-colour pedigrees, I have, paying no attention to sex, been able to extract 1155 cases of great-grandparent and offspring and 978 cases of great-great-grandparent and offspring. When it is noted that there are 16 types of great-grandparental and 32 types of great-great-grandparental relationship, so that 48 correlation tables would be required for the full working out of these cases, it will be noted why in this preliminary study, I have not differentiated between the sexes.

Tables I. and II. reproduce my data.

From Table I. I find in the fourfold division hitherto adopted :

Great-Grandparents.

| Offspring. | | Bay and darker | Chestnut and lighter | Totals |
|------------|----------------------|----------------|----------------------|--------|
| | Bay and darker ... | 601 | 264 | 865 |
| | Chestnut and lighter | 166 | 124 | 290 |
| | Totals | 767 | 388 | 1155 |

Hence

$$h = \cdot 671,102, \quad k = \cdot 423,602,$$

and the equation is :

$$\cdot 198,115 = r + \cdot 141,813r^2 + \cdot 075,166r^3 + \cdot 085,182r^4 + \text{etc.}$$

giving as root

$$r = \cdot 1922.$$

From Table II. we have :

Great-great-Grandparents.

| Offspring. | | Bay and darker | Chestnut and lighter | Totals |
|------------|----------------------|----------------|----------------------|--------|
| | Bay and darker ... | 497 | 252 | 749 |
| | Chestnut and lighter | 130 | 99 | 229 |
| | Totals | 627 | 351 | 978 |

I find

$$h = \cdot 725,258, \quad k = \cdot 361,420,$$

and the equation

$$\cdot 149,092 = r + \cdot 131,061r^2 + \cdot 068,681r^3 + \cdot 077,532r^4 + \text{etc.}$$

which gives

$$r = \cdot 1469.$$

We see from these results that the ancestral relationships in coat-colour for the horse are far more intense than was originally supposed for the like grades of relationship. We have in round numbers :

Parental correlation = $\cdot 50$.

Grandparental correlation = $\cdot 30$.

Great-grandparental correlation ... = $\cdot 20$.

Great-great-grandparental correlation = $\cdot 15$.

As far as this series goes, not the coefficient itself, but the difference appears halved at each ascent, and it is clear that the $\frac{1}{2}, \frac{1}{4}, \frac{1}{8}, \frac{1}{16}, \dots$ series cannot possibly hold for the regression coefficients of the multiple correlation series.

TABLE I.

Great-Grandparents and Offspring.

Great-Grandparents.

| Offspring. | | bl. | bl./br. | br./bl. | br. | br./b. | b./br. | b. | b./ch. | ch./b. | ch. | ch./ro. | ro./ch. | ro. | ro./gr. | gr./ro. | gr. | Totals |
|------------|---------|-----|---------|---------|-----|--------|--------|-----|--------|--------|-----|---------|---------|-----|---------|---------|-----|--------|
| | bl. | 4 | — | — | 17 | — | — | 46 | — | — | 27 | — | — | — | — | — | 2 | 96 |
| | bl./br. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | br./bl. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | br. | 6 | — | — | 35 | — | — | 97 | — | — | 49 | — | — | — | — | — | 9 | 196 |
| | br./b. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | b./br. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | b. | 17 | — | — | 82 | — | — | 297 | — | — | 149 | — | — | — | — | — | 28 | 573 |
| | b./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | ch./b. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | ch. | 1 | — | — | 34 | — | — | 103 | — | — | 75 | — | — | — | — | — | 22 | 235 |
| | ch./ro. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | ro./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | ro. | — | — | — | 2 | — | — | 8 | — | — | 4 | — | — | — | — | — | 2 | 16 |
| | ro./gr. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | gr./ro. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | gr. | — | — | — | 5 | — | — | 13 | — | — | 13 | — | — | — | — | — | 8 | 39 |
| Totals | | 28 | — | — | 175 | — | — | 564 | — | — | 317 | — | — | — | — | — | 71 | 1155 |

TABLE II.

Great-great-Grandparents and Offspring.

Great-great-Grandparents.

| Offspring. | | bl. | bl./br. | br./bl. | br. | br./b. | b./br. | b. | b./ch. | ch./b. | ch. | ch./ro. | ro./ch. | ro. | ro./gr. | gr./ro. | gr. | Totals |
|------------|---------|-----|---------|---------|-----|--------|--------|-----|--------|--------|-----|---------|---------|-----|---------|---------|-----|--------|
| | bl. | 2 | — | — | 14 | — | — | 40 | — | — | 24 | — | — | — | — | — | 7 | 87 |
| | bl./br. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | br./bl. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | br. | 3 | — | — | 21 | — | — | 69 | — | — | 43 | — | — | — | — | — | 6 | 142 |
| | br./b. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | b./br. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | b. | 5 | — | — | 70 | — | — | 273 | — | — | 143 | — | — | — | — | — | 29 | 520 |
| | b./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | ch./b. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | ch. | 1 | — | — | 17 | — | — | 89 | — | — | 61 | — | — | — | — | — | 19 | 187 |
| | ch./ro. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | ro./ch. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | ro. | — | — | — | 2 | — | — | 7 | — | — | 5 | — | — | — | — | — | 1 | 15 |
| | ro./gr. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | gr./ro. | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| | gr. | — | — | — | 6 | — | — | 8 | — | — | 10 | — | — | — | — | — | 3 | 27 |
| Totals | | 11 | — | — | 130 | — | — | 486 | — | — | 286 | — | — | — | — | — | 65 | 978 |