CHAPTER IX

STATISTICAL STUDY OF INHERITANCE

" L'hybride est une mosaïque vivante."—NAUDIN.

The law of frequency of error " would have been personified by the Greeks, and deified if they had known of it."—FRANCIS GALTON.

§ 1. *Statistical and Physiological Inquiries*

WHEN we study complex phenomena, such as the weather, we usually follow two methods. On the one hand, we may collect a multitude of observations—*e.g.*, as to the rainfall in different localities and at different times of year,—and try from a careful scrutiny of these to make some general induction, which will show the inherent orderliness of sequences, even in such an apparently disorderly complex as the weather. On the other hand, we may give our attention to the actual mechanism of certain occurrences—*e.g.*, heavy rain with westerly winds and low barometric pressure—and seek to show how certain conditions are necessarily followed by certain results. In so doing, we fall back on the general laws of physics, and we may be greatly assisted by crucial experiments—*e.g.*, on the *rôle* of atmospheric dust in connection with the precipitation of water vapour.

Similarly, in regard to the complex facts of inheritance we may pursue the same two methods. We may collect statistics as to the resemblances and differences—*e.g.* as regards stature, colour of eyes, intellectual ability, in successive generations—and try to arrive at some general induction, which will show the inherent orderliness even in a domain where occurrences seem at first sight as capricious as those of weather. On the other hand, we may focus our attention on the detailed course of events in particular cases—we may inquire, for instance, into the behaviour of the germ-cells before, during, and after fertilisation—and try to understand how certain conditions are necessarily followed by certain results. In so doing, we fall back on the general laws of biology, and we are greatly assisted by crucial experiments.

It is the aim of this chapter to *illustrate* what has been done by following the statistical method of inquiry into the facts of inheritance, and to state some of the inductions which have rewarded this mode of procedure. As the subject is not an easy one, and as it has been recently discussed by modern masters like Francis Galton and Karl Pearson, and in expository works such as Dr. H. M. Vernon's *Variation in Plants and Animals* (London, 1903), and Mr. R. H. Lock's *Variation, Heredity, and Evolution* (London, 1906), we shall confine ourselves to a brief sketch.

When we have to study results that depend upon numerous complicated conditions, the statistical method is of special service. Not that it can ever tell us how the conditions lead up to the results, but it will tell us what regularity there is in the occurrence of the results, and by displaying some unexpected correlation between certain antecedents and certain results, it may put us on the track of discovering the mechanism that connects them. Thus, while every one knows that the stature attained by a thousand young men depends upon a multitude of dimensions of different parts of the body, and that these dimensions depend on numerous conditions, of which food is one, climate another, and parentage a third, we owe it to statistical methods that we are able to say definitely what relation the average height of these thousand sons bears to the average height of their fathers, that we are able to say, furthermore, that their stature depends more on the stature of their fathers than on that of their mothers. Thus we get a solid foundation for further inquiries of a deeper sort.

Again, to take another illustration, we know enough in regard to the results of four thousand throws of approximately symmetrical dice, to be able to say dogmatically, in regard to the quite divergent results of four thousand throws of other dice, that the latter must have been loaded. Similarly, as our knowledge of the laws of the random grows, we become able to detect when Nature's dice are loaded.

It should be clearly understood that the generalisation "Like begets like" may be much truer for the race at any given time than for any one relation of parents and offspring. Processes of selection in many forms tend to prune off peculiarities—operating even before birth, operating in very early stages of independent life, and never ceasing to operate—and thus one generation of a race may be very like the preceding generation, although in cases of *individual* heredity there may be marked differences between offspring and their parents. In short, it is very important to realise the distinction between individual heredity and race-heredity. The statistical study of inheritance enables us to do this.

§ 2. *Historical Note*

In order to appreciate the statistical point of view and the general ideas underlying its methods, the reader is advised to read chapter xii. of J. T. Merz's invaluable *History of European Thought in the Nineteenth Century* (vol. ii., 1903, pp. 548–626). He traces the development of methods—*e.g.*: the investigations of Gauss and Laplace on the theory of error; he gives examples of their application—*e.g.* the kinetic theory of gases; and he shows how Quetelet was practically the first to apply statistical methods to human problems in his celebrated work *Sur l'Homme et le Développement de ses Facultés, ou Essai de Physique sociale* (1823).

But "the first who seems to have fully grasped the Darwinian problem from this (statistical) point of view is Mr. Francis Galton, who in a series of papers, and notably in his well-known works on *Hereditary Genius* (1869), and on *Natural Inheritance* (1889), made a beginning in the statistical treatment of the phenomena of Variation." "Mr. Galton's application of the theory of error to the facts of distribution and variation enabled him to bring method and order into such questions raised by the Darwinian theory as natural selection, regression, reversion to ancestral types, extinction of families, effect of bias in marriage, mixture of inheritance, latent elements, and generally to prepare the ground for the combined labours of the naturalist and the statistician" (Merz, p. 618).

Among those who have followed Mr. Galton's lead the most prominent and progressive worker is Prof. Karl Pearson, who has published numerous important mathematical contributions to the theory of evolution in the Transactions and Proceedings of the Royal Society since 1893, and in his journal *Biometrika*. The reader who is not prepared for much mathematics should consult the second edition of Pearson's *Grammar of Science*. See also his *Chances of Death and other Studies in Evolution* (2 vols., 1897).

§ 3. *A Hint of the Statistical Mode of Procedure*

Some idea of the mode of procedure in dealing statistically with the facts of inheritance may be got from the following statement by an experienced statistician, Mr. G. Udny Yule (1902, p. 196):

"A series of measurements is made of some one variable character, *e.g.* a length, in parents and in their offspring, noting the individual families (the more the better) and not merely measuring the first generation as a whole and then their offspring as a whole. From these measurements an equation is derived, giving, as nearly as may be, the mean character of the offspring in terms of the character of the parent. Supposing X to be the character in the parent, Y the mean character in the offspring, then the simplest form of such equation is:

$$Y = A + B \cdot X,$$

where A is a dimension of the same order as X or Y, and B is a number that will vary from case to case. We have for instance, from the data collected by Mr. Galton for inheritance of stature in man, reduced by Prof. Pearson, the equation relating mean stature of sons and stature of father:

$$Y = 31 \cdot 10 + \cdot 45\, X,$$

i.e. the mean stature of sons is 31·1 inches, together with nine-twentieths of the stature of the father (also in inches, of course). The father's stature is thus some guide to the stature of his offspring; it enables us to form a closer estimate of their stature than we could from a mere knowledge of the mean characters of the race, and we may therefore say that stature is an *inherited* character. The sons do diverge from the race-mean in the same direction as their parent. Quite generally, the statistician speaks of a character as *inherited* whenever the number or "constant" B is greater than zero; if it does not differ sensibly from zero the character is held to be non-heritable, quite apart from the question whether the mean is more or less constant from one generation to the next, a consideration which does not affect the conception of *individual* heredity."

§ 4. *Filial Regression*

It has often been remarked that the children of extraordinarily gifted parents are sometimes very ordinary individuals, and that the children of under-average parents sometimes turn out surprisingly well, both physically and mentally. Every one who has looked into the facts of inheritance in greater detail, and has compared the average of qualities in successive generations, has noticed in a general way that there is a tendency to sustain the same average level from generation to generation. Even the older inquirers, like Lucas, called attention to the fact that extraordinary qualities in families tend to wane away, as if there were some mysterious succession-tax levied on marked deviations from the average, whether in the way of excellence or of defect. But we owe to Mr. Francis Galton's careful statistical work the generalisation known as the Law of Filial Regression, which has replaced a vague impression by a definite formula. He has defined and measured that tendency towards mediocrity —that tendency to approximate to the mean or average of the stock, which is expressed by the term Filial Regression. We may notice at the outset that this has nothing to do with reversion or with degeneration, that it works upwards as well as downwards, forwards as well as backwards.

The data which Galton utilised were chiefly the *Records of Family Faculties*, obtained from about one hundred and fifty families, and dealing especially with stature, eye-colour, temper, artistic faculty, and some forms of disease. These were supplemented by measurements at Galton's anthropometric laboratory, and by observations on sweet peas and to some extent on moths.

Most trustworthy, however, were the data procured in regard to stature, which, as Galton points out, is a quality with many advantages as a subject of investigation. It is nearly constant during mature life, it is readily and frequently measured with accuracy, and it does not seem to be of appreciable moment in sexual selection. Its variability, though small, is normal; that is to say it is expressible in the normal curve of the frequency of error.

As the subject is by no means easy to those unaccustomed to statistical inquiry, and as we cannot within our limits explain the methods which Galton followed, it may be most profitable to give a few illustrative quotations from *Natural Inheritance* (1889).

"If the word 'peculiarity' be used to signify the difference between the amount of any faculty possessed by a man, and the average of that possessed by the population at large, then the law of Regression may be described as follows. Each peculiarity in a man is shared by his kinsmen, but *on the average* in a less degree. It is reduced to a definite fraction of its amount, quite independently of what its amount might be. The fraction differs in different orders of kinship, becoming smaller as they are more remote" (p. 194).

In the population with which Galton dealt the level of mediocrity in height was 68¼ inches (without shoes). The law or fact of regression which the statistics revealed was that the deviation of the sons from the mean of the population (P) is, on the average, equal to one-third of the deviation of the parent from P, and in the same direction. If $P \pm D =$ stature of the parent, then $P \pm \frac{1}{3}D =$ stature of the son. In these inquiries it is convenient to use the fiction of a mid-parent, whose stature is half-way between the stature of the father and the "transmuted stature" of the mother, the last phrase meaning practically the stature that the mother would have if she were not female, *i.e.* an additional inch for every foot.

"However paradoxical it may appear at first sight, it is theoretically a necessary fact, and one that is clearly confirmed by observation, that the stature of the adult offspring must on the whole be more *mediocre* than the stature of their parents, that is to say, more near to the mean or mid of the general population" (p. 95).

While Galton's clearest results were obtained from data as to stature, the general conclusion was confirmed in regard to eye-colour, artistic faculty, and other qualities. There seems no reason to doubt the general occurrence of regression towards mediocrity, though it is doubtless modified in regard to characters which are subject to keen selection, either natural or sexual.

"The law of regression tells heavily against the full hereditary transmission of any gift. Only a few out of many children would be likely to differ from mediocrity so widely as their mid-parent, and still fewer would differ as widely as the more exceptional of the two parents. The more bountifully a parent is gifted by nature, the more rare will be his good fortune if he begets a son who is as richly endowed as himself, and still more so if he has a son who is endowed yet more largely. But the law is even-handed; it levies an equal succession-tax on the transmission of badness as of goodness. If it discourages the extravagant hopes of a gifted parent that his children will inherit all his powers, it no less discountenances extravagant fears that they will inherit all his weakness and disease" (p. 106).

"It must be clearly understood that there is nothing in these statements to invalidate the general doctrine that the children of a gifted pair are much more likely to be gifted than the children of a mediocre pair. They merely express the fact that the ablest of all the children of a few gifted pairs is not likely to be as gifted as the ablest of all the children of a very great many mediocre pairs" (p. 106).

Nor must the fact of regression be supposed to affect the general value of a good stock or the general disadvantage of a bad one. Two gifted members of a poor stock may be personally equivalent to two ordinary members of a good stock, but "the children of the former will tend to regress; those of the latter will not" (p. 198).

Let us give a concrete illustration from Prof. Karl Pearson's

Grammar of Science (1900, p. 454). "Fathers of a given height have not sons all of a given height, but an array of sons of a mean height different from that of the father and nearer to the mean height of sons in general. Thus take fathers of stature 72 inches, the mean height of their sons is 70″·8, or we have a *regression* towards the mean of the general population. On the other hand, fathers with a mean height of 66 inches give a group of sons of mean height 68″·3, or they have *progressed* towards the mean of the general population of sons. The father with a great excess of the character contributes sons with an excess, but a less excess of it; the father with a great defect of the character contributes sons with a defect, but less defect of it. The general result is a sensible stability of type and variation from generation to generation."

The quotations which we have given make the general idea of regression quite clear; for the detailed evidence and for further elaboration we must refer to the works of Galton and Pearson.

It is necessary, however, to ask what this statistically established fact of filial regression really means biologically.

Interpretation of Regression.—The facts of regression are expressed as a whole in the striking statistical resemblance between successive generations of a people. There is a continual tendency to sustain the specific average. It can hardly be denied that the similarity is in part the result of similar conditions, *e.g.*, of selection, but this hardly applies to the proportions persisting between tall and short, dark and fair, and so on. That it is not due to completeness of inheritance is obvious, for "the large do not always beget the large, nor the small the small"; the children do not in any precise way repeat the qualities of their parents. (Galton, 1889, pp. 1 and 116.) On what then does this regression depend?

Galton suggests two different reasons for the occurrence of regression (pp. 104, 105). The first is connected with his idea of the stability of type, and may be thus expressed. This word "type" has for its central idea the existence of a limited number of recurrent forms—forms which have attained a considerable degree of organic stability. A deviation from the type may mean the attainment of a new position of organic equilibrium, and many "sports" are said to be very stable; but it may also mean a position of instability from which a regression to the old equilibrium is what might be expected. Just as certain kinds of cells have very definite dimensions, doubtless dependent in part on the optimum adjustment between the volume and the surface, so many animals have a very definite limit of growth, which doubtless represents a condition of constitutional equilibrium. Where this is the case, it is easy to understand that marked deviations in the direction of giants or in the direction of dwarfs would tend to be unstable. Their offspring may tend to regress to the position of stability simply because it is the physiological optimum in given conditions. The regulative phenomena in development would tend to secure the regression, in the same mysterious way as they secure the development of a perfect larva from a mutilated embryo. In the particular case of human stature, a deviation of a few inches may be quite immaterial, but it is easy to think of organisms in which the proportions of the various bodily dimensions are very important.

The other reason which Galton gives for the occurrence of regression is found in what may be called the fact of mosaic inheritance. The child inherits partly from its parents, partly from its ancestry. "In every population that intermarries freely, when the genealogy of any man is traced far backwards, his ancestry will be found to consist of such varied elements that they are indistinguishable from a sample taken at haphazard from the general population. The mid-stature M of the remote ancestry of such a man will become identical with P [the mean of the present population]; in other words, it will be mediocre."

"To put the same conclusion in another form, the most probable value of the deviation from P, of his mid-ancestors in any remote generation, is zero" (p. 105).

Pearson interprets Filial Regression in similar terms. "A man is not only the product of his father, but of all his past ancestry, and unless very careful selection has taken place the mean of that ancestry is probably not far from that of the general population. In the tenth generation a man has [theoretically] 1024 tenth great-grandparents. He is eventually the product of a population of this size, and their mean can hardly differ from that of the general population. It is the heavy weight of this mediocre ancestry which causes the son of an exceptional father to regress towards the general population mean; it is the balance of this sturdy commonplaceness which enables the son of a degenerate father to escape the whole burden of the parental ill. Among mankind we trust largely for our exceptional men to extreme variations occurring among the commonplace, but if we could remove the drag of the mediocre element in ancestry, were it only for a few generations, we should sensibly eliminate regression or create a stock of exceptional men. This is precisely what is done by the breeder in selecting and isolating a stock until it is established." (*Grammar of Science*, 1900, p. 456.)

Prediction.—When we know the heights of a thousand fathers of a given stock, and the heights of their sons, and the mean height of the general population, we have a basis for constructing a "regression equation," which may be used to calculate the *probable* stature of the son of any father. But this prediction may be wide of the mark, since exceptional individual variability often occurs. What will not be wide of the mark, however, is a prediction as to the average height of the sons of a group of, say, fifty fathers. If the formula [stature of son $= 38''\cdot45 + \cdot446 \times$ stature of father] be applied to fifty English middle-class fathers of the same height, it will be found that their sons have an average height differing but little from that indicated by the formula. In regard to all these statistical conclusions, it must be carefully borne in mind that they cannot be applied to individual cases. "Of the individual we can assert nothing as certain, only state the probable. The individual varies owing to the variability of the gametes, and we know nothing of the particular gametes which fused to give the stirp, of which he is the product. All we know in heredity is what degree of resemblance there is on the average. . . . The statistician dealing with heredity is like the physicist dealing with the atom—he can say little or nothing of the individual, his knowledge is of the group containing great numbers." (Pearson, *op. cit.*, p. 457.)

Note on the Term Regression.—As the term *regression*, used by Galton to describe the extent to which an average son is more like the mean of the stock than his father is, has been often misunderstood to imply something in the nature of a "throw-back," it is probably desirable to get rid of it and to substitute for it the technical term *correlation*, which expresses the extent to which a son approximates nearer to his father than to the average of the stock.

The term "regression" which Mr. Galton introduced into biometrics is not really a biological term. As the late Prof. Weldon pointed out in an interesting lecture, there may be regression between two different sets of results of dice-throwing if the second set of results is in some way, but not entirely, dependent upon the first. He protested against regarding regression "as a peculiar property of living things, by virtue of which variations are diminished in intensity during their transmission from parent to child, and the species is kept true to its type (1906, p. 107). This view may seem plausible to those who simply consider that the mean deviation of children is less than that of their fathers; but if such persons would remember the equally obvious fact that there is also a regression of fathers on children, so that the fathers of abnormal children are, on the whole, less abnormal than their children, they would either have to attribute this feature of regression to a vital property by which children are able to reduce the abnormality of their parents, or else to recognise the real nature of the phenomenon they are trying to discuss.

"It seems likely that in cases where the mating of parents is not determined to any serious extent by their likeness or unlikeness in the character discussed, the regression of children on parents has a value very nearly the same, and very nearly equal to $\frac{1}{2}$, for a large series of characters, mental as well as physical, in human beings, and for a large series of characters in the higher animals, at all events, if not in animals generally" (Weldon, 1906, p. 108).

Summary.—Many individual organisms do not differ much from the mean of the race to which they belong. We cannot say "from the species to which they belong," because many systematic or Linnean species include several subspecies or "elementary species" or "varieties," just as there are races and breeds of domesticated animals and cultivated plants. In studying the peculiarities of a whitlow-grass (*Draba verna*), or of a wild heartsease (*Viola tricolor*), or of a pigeon, or of a rabbit, we must, obviously, estimate these peculiarities in reference to the particular stock or race to which they belong.

On the other hand, many individuals differ markedly from the mean of the stock or race to which they belong. In some character or characters they are extraordinary individuals. What is the chief conclusion in regard to the offspring of these individuals? It is that *they are, on an average, more mediocre than their parents.*

As Mr. Yule puts it, "This phenomenon of the relapse of the offspring from the parental type towards mediocrity is termed *regression.* Regression and not constancy of type is, for the statistician, the fundamental phenomenon of heredity and the prime fact to be explained by any physical theory" (1902, p. 197).

It is explained on the general assumption that an inheritance is a mosaic made up of contributions from a complex of ancestors which when traced say to a tenth generation back correspond to an average sample of the stock in question.

NOTE ON REDUCTION OF ANCESTORS.—To appreciate the possible complexity of our mosaic inheritance we must recall the number of our ancestors. We have two parents, four grandparents, eight great-grandparents, about sixteen great-great-grandparents, and so on. "If," as Prof. Milnes Marshall said, "we allow three generations to a century, there will have been twenty-five since the Norman Invasion, and a man may be descended not merely from one ancestor who came over in 1066, but directly and equally from over sixteen million ancestors who lived at or about that date." But on these theoretical lines the existence of one man to-day would involve the existence of nearly seventy thousand millions of millions of ancestors at the commencement of the Christian era. Which is absurd. What the theoretical scheme fails to take account of is the frequent occurrence of close intermarriage—of cousins for instance. When we are dealing with a large group of families, we find individual ancestors figuring in different genealogical trees.

Brooks (*Science*, 1895, p. 121) points out that if the population of a given district had for ten generations married first cousins the total ancestry of each person would be only thirty-eight, instead of the theoretical possible 2046. "An investigation into the ancestry of three persons, not nearly related, living on an island on the Atlantic coast where the records are complete for seven and eight generations, shows that the ancestry of each of the three averages only 382 persons" (Cope, 1896, p. 460).

The problem of reduction in the number of ancestors has been very carefully discussed by genealogists like Prof. Lorenz and Dr. F. T. Richter. We must be content to take one example. Theoretically, Kaiser Wilhelm II. might have had in the direct line the number of ancestors indicated in the upper row on the next page; the second row indicates the number actually known, on to the twelfth generation; the third row gives the number of those possible ancestors of whose existence there is deficient record; and the fourth row gives the probable total.

Generations	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX.	X.	XI.	XII.
(1) Theoretical number	2	4	8	16	32	64	128	256	512	1024	2048	4096
(2) Actual number known.	2	4	8	14	24	44	74	111	162	200	225	275
(3) Inadequately known.								5	15	56	117	258
(4) Probable total.								116	177	256	342	533

§ 5. *Law of Ancestral Inheritance*

In all ordinary cases of reproduction the offspring has a strictly dual or bi-parental inheritance. Whether the inheritance be blended, particulate, or exclusive in its expression, it is made up, to begin with, of equal contributions from the two parents. Obviously, however, if the concept of the continuity of the germ-plasm be correct, the contribution from the father is made up of contributions from his two parents, and the contribution from the mother is made up of contributions from her two parents. And so on backwards. Thus we reach the idea, so often referred to in this volume, that an individual inheritance is a mosaic of ancestral contributions. Incidental corroborations of this fruitful idea are familiar to all—*e.g.* in the re-expression of trivial details which were characteristic features of, say, the grandfather or the great-grandmother. To Mr. Galton's careful statistical work, however, we owe a generalisation which formulates the share which the various ancestors have on an average in the inheritance of any individual organism. This is the Law of Ancestral Inheritance.

Galton's Statement of his Law.—Mr. Galton based his generalisation on data as to stature and other qualities in man and as to coat-colour in Basset hounds. His law is as follows: "The two parents between them contribute *on the average* one-half of each inherited faculty, each of them contributing one-quarter of it. The four grandparents contribute between them one-quarter, or each of them one-sixteenth; and so on, the sum of the series $\frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \frac{1}{16} + \ldots$, being equal to 1, as it should be. It is a property of this infinite series that each term is equal to the sum of all those that follow: thus $\frac{1}{2} = \frac{1}{4} + \frac{1}{8} + \frac{1}{16} + \ldots$, $\frac{1}{4} = \frac{1}{8} + \frac{1}{16} + \ldots$, and so on. The prepotencies or sub-potencies of particular ancestors, in any given pedigree, are eliminated by a law that deals only with *average* contributions, and the varying prepotencies of sex in respect to different qualities are also presumably eliminated." Thus an inheritance is not merely dual, but through the parents it is multiple, and the *average* contributions made by grandparents, great-grandparents, etc., are definite, and diminish in a precise ratio according to the remoteness of the ancestors.

Diagrammatic Expression.—The proportions contributed on an average by the parents, grandparents, great-grandparents, etc., may be seen at a glance from a diagram (on the opposite page) which we have borrowed from one of Mr. Galton's papers.

Pearson's Statement of Galton's Law.—Prof. Karl Pearson states Galton's law in the following form: "Each parent contributes on an average one-quarter or $(0{\cdot}5)^2$, each grandparent one-sixteenth or $(0{\cdot}5)^4$, and so on; the occupier of each ancestral place in the nth degree, whatever be the value of n, contributes $(0{\cdot}5)^{2n}$ of the heritage." He calls attention to the extreme importance of the law, for "if Darwinism be the true view of evolution—*i.e.* if we are to describe evolution by natural selection combined with heredity—then the law which gives us definitely and concisely the type of the offspring in terms of the ancestral peculiarities is at once the foundation-stone of biology and the basis upon which heredity becomes an exact branch of science" (*Grammar of Science*, 1900, p. 479). Elsewhere he says: "The law of ancestral heredity is likely to prove one of the most brilliant of Mr. Galton's discoveries; it is highly probable that it is the simple descriptive statement which brings into a single focus all the complex lines of hereditary influence. If Darwinian evolution

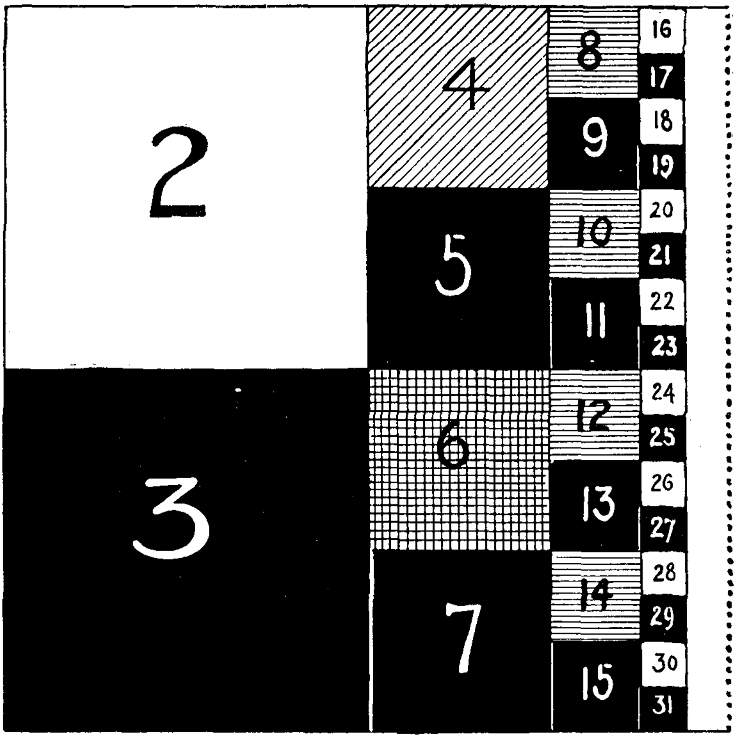

FIG. 29.—Diagram illustrating Galton's Law of Ancestral Inheritance. (After Galton.) The figure was originally due to Mr. A. J. Meston (*The Horseman*, Chicago, Dec. 28, 1897).

"The area of the square diagram represents the total heritage of any particular form or faculty that is bequeathed to any particular individual. It is divided into subsidiary squares, each bearing distinctive numbers, which severally refer to different ancestors. The size of these subsidiary squares shows the average proportion of the total heritage derived from the corresponding ancestors. . . . The subject of the pedigree may be called 1. Thenceforward whatever be the distinctive number of an ancestor, which we will call n, the number of its sire is $2n$, and that of its dam is $2n+1$. All male numbers in the pedigree are therefore even and all female numbers are odd. To take an example—2 is the sire of 1, and 3 is the dam of 1; 6 is the sire of 3 and 7 is the dam of 3. Or, working backwards, 14 is a male who is mated to 15; their offspring is 7, a female, who is mated to 6; their offspring is 3, a female, who is mated to 2, and their offspring is 1, the subject. . . . The numbered squares could be continued indefinitely; in this small diagram they cease with the fourth generation, which contributes a 16th part of the total heritage, therefore the whole of the more distant ancestry, comprised in the blank column, contributes one-sixteenth also" (Galton, 1898).

be natural selection combined with heredity, then the single statement which embraces the whole field of heredity must prove almost as epoch-making to the biologist as the law of gravitation to the astronomer."

Criticisms.—Since the importance of the law is so great, we must devote some attention to certain criticisms which have been made. It goes without saying that those who wish to criticise the basis on which the generalisation is founded must first consult the original documents, referred to in the bibliography.

It must be borne in mind that the Law of Ancestral Inheritance is a statistical conclusion dealing with what is true on an average for a large number of cases. To say that we know of particular cases where it certainly does not hold—where, for instance, the amount of resemblance between an individual and his paternal grandfather is far greater than is represented by the fraction $\frac{1}{16}$ —is no argument against the induction. It is like saying that the statistics showing the percentage of deaths in cases of scarlet fever must be wrong because we know of large families which were visited by the disease without a single fatal result!

It may be urged against the crispness of Galton's Law, (1) that the hereditary relation is a complex affair; (2) that most organic qualities, and the amounts of resemblance in successive generations, can seldom be measured with the accuracy possible in the case of a quality like stature; and (3) that the actual quota of any character which forms part of a heritage is something different from the expression which that quota finds in development—for the expression depends in part on the conditions of nurture. For these and similar reasons it may seem suspicious that the fractions indicating the average contributions of parents, grandparents, great-grandparents, etc., should be representable in such a simple series as $\frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \ldots$.

The general answer is, of course, that when the data are large enough, the irregularities of result due to particular peculiarities, such as a highly prepotent great-grandfather or a very inadequate nurture, are smoothed out. It is noteworthy that in the case of Mendelian phenomena, which some regard as fatal to Galton's Law, there is frequently a very precise proportion in the numbers of offspring favouring the two original parental types which were crossed at the beginning of the observed lineage.

But the general worth of Galton's Law is not invalidated, though it be found with further inquiry that the series $\frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \frac{1}{16} + \ldots$, should be replaced by some other series. In point of fact, Pearson's studies led him to conclude that the series 0·6244, 0·1988, 0·0630, etc., was more accurate than the series 0·5, 0·25, 0·125, etc.

Pearson's Statement of the Law of Ancestral Inheritance.—Galton's Law states that in a given generation the average heritage is made up of ancestral contributions—$\frac{1}{2}$ parental, $\frac{1}{4}$ grandparental, $\frac{1}{8}$ great-grandparental, and so on.

This is a statistical conclusion, not a physiological interpretation. It deals with average heritages and applies to masses rather than to the component individuals considered separately. Thus he says, "The neglect of individual prepotencies is justified in a law that avowedly relates to average results" (1897, p. 402).

But while Galton did not mean his Law to apply to individual cases, it must be *approximately* true of a large number of individual cases in any generation. If it is true as an average formula, it must find approximate illustration in a large number of individual cases, though the precise fractions $\frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \ldots$, will not apply.

Prof. Karl Pearson has given a statement of the law of ancestral inheritance somewhat different from Galton's, but his methods and general results are practically the same. The following quotation (1903a, p. 215) is useful:

"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, . . . 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. . . . 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."

Summary.—Galton formulated his Law of Ancestral Inheritance as follows : "The two parents contribute between them on the average one-half or (0·5) of the total heritage of the offspring ; the four grandparents, one-quarter, or $(0{\cdot}5)^2$; the eight great-grandparents, one-eighth, or $(0{\cdot}5)^3$, and so on. Thus the sum of the ancestral contributions is expressed by the series $[(0{\cdot}5) + (0{\cdot}5)^2 + (0{\cdot}5)^3$, etc.], which, being equal to 1, accounts for the whole heritage" (1897, p. 402).

But it is quite legitimate to accept the general idea of this Law without accepting the fixity of the fractions of partial inheritance which it expresses.

Mr. G. Udny Yule states the law of ancestral heredity in the most general way possible when he says : "This law, that *the mean character of the offspring can be calculated with the more exactness, the more extensive our knowledge of the corresponding characters of the ancestry*, may be termed the Law of Ancestral Heredity" (1902, p. 202).

Prof. Weldon (1902) states the law of ancestral inheritance in the following terms: "*The degree to which a parental character affects offspring depends not only upon its development in the individual parent, but on its degree of development in the ancestors of that parent.*" Mr. Yule suggests that, instead of the word "affects," which to some extent implies a direct physical influence, it would be more accurate to read "serves as a basis for estimating the character of."

In a later paper Prof. Weldon discussed the validity of Galton's Law, and wrote as follows.—

. . . "The results so far achieved make it probable that Mr. Galton's original prediction will be verified for the large class of cases to which he intended it to apply, and that the influence of the different generations of ancestors, as measured by the regression coefficients between these and existing individuals, will be found to diminish with the remoteness of the ancestors, according to the terms of a simple geometric series, which is sensibly the same at least for all those characters among the higher animals which have been properly examined" (Weldon, 1906, p. 108).

§ 6. *Illustration of Results reached by Statistical Study*

While we can neither explain the methods nor summarise the arguments, it may be permissible to cite some of the results reached by the statistical study of inheritance, always bearing in mind the caution that the validity of a statistical result depends on the value of the data. The world of organisms is very large and heterogeneous, and results that hold good for certain forms of life may not be true of others.

It has been shown statistically that in the human race the father is prepotent in the matter of stature, and this for offspring of both sexes (Pearson).

It has been shown statistically that a subtle quality like fertility is a heritable quality, and more detailed statements can be made—*e.g.* that the woman inherits fertility equally through the male and female lines.

The immediate practical bearing of some of these researches is evident. Thus Messrs. Rommel & Philipps (1906) have shown in regard to Poland China hogs: (1) that there has been an increase of ·48 in the size of litter in the twenty years between 1882 and 1902, and (2) that the size of litter is a character transmitted from mother to daughter. "It would appear proved that, by judicious selection for breeding purposes of sows from large litters, the average for the breed may be increased."

Prof. Karl Pearson has been led by rigorous statistical methods to statements like the following:—

"If selection were to act upon our 5′ 9″ Englishmen, and the 6′ among them were the type best fitted to survive, then with fairly stringent selection it would not take more than six generations to produce a type sensibly 6′ high, and this type would be permanently established even if selection ceased. . . . Our determination of the quantitative strength of heredity is thus seen to give values quite intense enough to produce rapid and permanent changes of type, when selection is stringent."

Prof. Pearson has worked out the following case. Suppose the mean height of a population be 5 ft. 8 in., that a start is made with individuals 6 ft. 2 in., and that for successive generations individuals of this height are selected as parents. It is calculated that in the first generation the offspring would show 0·62 of the particular quality selected (h), viz. 6 in. of deviation above the general mean height. It is calculated that after two generations the offspring will show 0·82h, after three generations 0·89h, and so on up to 0·92h. Thus by persistent selection an array of individuals would result, almost all of whom were over six feet in height.

But if at a given generation the artificial selection of tall parents stops, and the tall array is left to inbreed, there will be a gradual sinking back towards the mean height of the population. This general conclusion is in accordance with the experience of breeders (in non-Mendelian cases), who, having temporarily secured a high-class breed by persistent artificial selection, find that there is a gradual deterioration during a period of inbreeding without selection.

The importance of definite conclusions of this kind can hardly be overestimated.

"Looked at from the social standpoint, we see how exceptional families, by careful marriages, can within even a few generations obtain an exceptional stock, and how directly this suggests assortative mating as a moral duty for the highly endowed. On the other hand, the exceptionally degenerate isolated in the slums of our modern cities can easily produce permanent stock also: a stock which no change of environment will permanently elevate, and which nothing but mixture with better blood will improve. But this is an improvement of the bad by a social waste of the better. We do not want to eliminate bad stock by watering it with good, but by placing it under conditions where it is relatively or absolutely infertile" (Pearson, *Grammar of Science*, p. 486).

By statistical methods Pearson has reached the interesting conclusion that while blended inheritance illustrates *regression*, it is to cases of exclusive inheritance that we should look for *reversion* (*i.e.* the reappearance of a character which occurred in a definite ancestor). In exclusive inheritance, in which the offspring inherits the full character of either parent, and does not blend the two, the law of ancestral inheritance in the strict sense ceases to hold, for it presupposes a blend. Thus eye-colour in man rarely, if ever, blends, and it is in regard to such characters that we should look for reversion.

As a matter of fact, Pearson notes that of exclusive inheritance with reversion he has as yet (1900) discovered no case, except possibly coat-colour in dogs. He gives a list of various phenomena which are often misinterpreted as reversions, and Mendelian experiments (*q.v.*) have still further reduced the number of alleged cases.

By statistical methods Pearson has sought to ascertain how far the inheritance of *the duration of life* extends, and has reached the important conclusion that in a large percentage of cases there is evidence in the death-rate that discriminate selection is at work. It is no longer possible to say of natural selection, as Lord Salisbury did in 1894, that "no man, so far as we know, has seen it at work." "It is at work, and at work among civilised men, where intra-group struggle—*i.e.* autogeneric selection—is largely suspended, with an intensity of a most substantial kind. Of the existence of natural selection there can be no doubt; we require careful experiments and observation to indicate the rapidity of its action. In a few years we may hope no longer to hear natural selection spoken of as hypothetical, but rather to listen to a statement of its quantitative measure for various organisms under divers environments" (*Grammar of Science*, p. 500).

§ 7. *Application to Individual Cases.*

Galton suggested in a cautious way, when he formulated his Law, that it might be applicable to the individual, and many have run away with the idea that Galton's Law means that an individual inheritance is made up of contributions $\frac{1}{2}$ parental, $\frac{1}{4}$ grandparental, $\frac{1}{8}$ great-grandparental, and so on. But this application to the individual is very rarely justified, and, in any case, it is a distinct idea. Darbishire (1906) proposes to distinguish from Galton's Law what he calls the *Law of Diminishing Individual Contribution*, which may be stated thus: "The germ plasm of an individual contains contributions from all of its progenitors; the amount of the contributions being large in proportion as the progenitor is near—*i.e.*, large in the case of the parents, smaller in the case of the grandparents, and so forth." This, Darbishire somewhat sarcastically says, "is a very good type of biological Law: it has the advantage of simplicity; it is also, except in a few cases, untrue." He is undoubtedly right in distinguishing this physiological theory (in which there is widespread belief) from Galton's statistical conclusion, "which does not pretend to account for anything," but we are not prepared to follow him in dismissing it as invalid. It appears to us that there are not a few cases where Mendelian interpretations do not work, and where a theory of ancestral contributions, more numerous and more conspicuous in proportion to the nearness of the ancestors, is at present justifiable. Galton's statistical conclusion may "not pretend to account for anything," but there must be something in individual heredity to account for it. And when Darbishire says, "Galton's Law definitely states that on the average a half of the filial generation are like the parental, a quarter like the grandparental, and an eighth like the great-grandparental, and so on," we venture to think he is taking considerable liberties with Galton's own statement of his Law.

§ 8. *Statistical and Physiological Laws*

Darbishire has tried by means of a diagram to clear up the prevalent confusion which opposes statistical and physiological formulæ. In the figure there is a diagrammatic representation of four successive generations; a^1, b^1, x^1; a^2, b^2, x^2, etc., represent adult individuals of these generations; α^1, β^1, ω^1; α^2, β^2, ω^2; etc., represent the germ-cells produced by those individuals. Now the statistical formulation contents itself with keeping above the line A—B, and deals with the successive generations as generations, stating the relation of hereditary resemblance which subsists between them. But the physiological interpretation seeks to penetrate below the line A—B, and seeks to show by a theory of germinal contributions how it is that a^1

gives rise to a^2, which may be more or less different, how a^2 gives rise to a^3, which again may be more or less different.

To bring out the contrast between statistical and physiological conclusions, Darbishire refers to the familiar riddle "*Why do white sheep eat more than black ones?*" with its answer "*Because there are more of them.*" "When you ask the riddle you do not say that you are not referring to individual white and black sheep, but the man of whom the riddle is asked *invariably* thinks you are" —with interesting consequences. "If he is a biologist he may be trying to think of some physiological explanation of the fact,

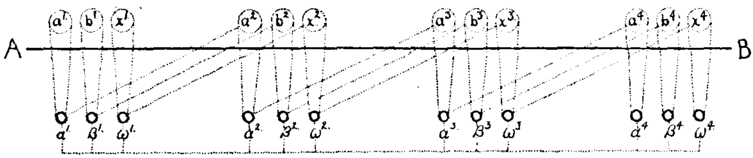

FIG. 30.—Diagram to illustrate the difference between statistical and physiological formulation. (After Darbishire.)

in connection possibly with the well-established relation between pigmentation and the getting rid of waste products." "In the answer he is told that the amount eaten by the sum-total of white sheep as compared with that eaten by the sum-total of black sheep is the subject under discussion."

"If the antithesis between truths about masses, and truths about individuals, which constitutes the point in this riddle, were more widely and more clearly perceived than it is to-day, there would no longer be that confusion in the minds of most biologists which prevents them seeing the profound difference that exists between a physiological law like Mendel's, which is true of units, and a statistical one like the Law of Ancestral Inheritance, which is true of masses. All intending students of heredity should be asked this riddle; and if they cannot detect the fallacy in it they should be declared unfit for their intended task."

While it is a confusion of thought to oppose a statistical conclusion and a physiological interpretation, it cannot be denied that the Galtonian and the Mendelian views of heredity are not yet in harmony.

In a certain number of cases a knowledge gained by experiment enables us to say that from two parents D and R a certain kind of offspring will result—D(R)—and that the progeny of D (R) × D(R) will be in the proportions 1DD + 2D(R) + 1RR; and we can interpret the result by a theory of the segregation of the gametes of D(R) into two sets of pure gametes which bear *in potentia* the contrasted characters embodied in the original parents D and R.

In other cases, however, a knowledge of the characters of the parents does *not* enable us to predict the results of an individual pairing, and we fall back on the law of ancestral inheritance which states the average result—the most probable result.

As it appears to us, Mendelian phenomena are illustrated when the parents differ in sharply defined contrasted characters which cannot blend or compromise, and the extension of experiment will doubtless go on increasing our knowledge of these unit characters and their behaviour. The formulation will remain whether the theory of the segregation of pure gametes be confirmed or not. In other cases, however, the Galtonian formulation seems the only one applicable, and here the need is to work out—perhaps along the lines of Weismann's germinal selection of determinants—a conceivable physiological interpretation.

Unless we misunderstand the situation, there is this clear difference between Mendelian and Galtonian formulæ—that Mendelian formulæ apply to the progeny of known crosses or hybrids, while Galtonian formulæ apply to intra-racial heredity.

We must refer the reader to Mr. Yule's discussion (1902) of the supposed antagonism between Mendelian and Galtonian conceptions—a discussion which leads this expert to conclude "that Mendel's Laws and the Law of Ancestral Heredity are not necessarily contradictory statements, one or other of which must be mythical in character, but are perfectly consistent the one with the other, and may quite well form parts of one homogeneous theory of heredity."