length divided by the lower leg length) diminishes from 140% during mid fetal months to about 90% at birth. In the adult boy it has diminished to 65%, while it remains at about 80% in the gibbon and about 90% in the adult gorilla and chimpanzee. This relatively shortened foot may be regarded as a more effective adaptation to bipedal locomotion than the longer foot of the gorilla.

We see, then, that even after birth genetic changes occur, which are parallel to the later phylogenetic stages; that is to say, man passes through the same embryological stages that the lower forms do, and even some of the stages in pre-adolescent development are the same in man and the lower primates. But man, as the higher form, goes beyond the point at which the less evolved species stop their development. That is to say, he shows in the proportions of his body special adaptations to the special functions he has to perform as a non-aboreal biped.

---

**THE GENERAL FORMULA OF HEREDITY**

**By Harry H. Laughlin**

Department of Genetics, Carnegie Institution of Washington, Cold Spring Harbor, Long Island, N. Y.

Read before the Academy, Tuesday, April 25, 1933

Modern genetics has thus far worked principally with the theory of the gene. It now needs the aid of additional tools to work out the genetic understanding of the great majority of complex hereditary qualities of plants, animals and man. Practically all of the structural and functional qualities of the many species with which students of evolution work belong to this same category of qualities too complex to be resolved by the theory of the gene. Also, in the same class we must list most of the inborn human qualities with which anatomy, physiology, medicine, psychology, education, the fine arts, athletics and religion are concerned. As anatomical or physiological entities, many of these qualities have been accurately measured or diagnosed, with due allowance for the effects of environment. But only an occasional one has been analyzed into its constituent genes. The fact is that a structural quality like stature in man, or a functional quality like racing capacity in the Thoroughbred horse, far from being based upon a single or a few genes, is the developmental end-product of a great many genes, possibly a score, but more likely a thousand. In the course of development these genes interact, some accelerating their fellows, others cancelling what otherwise would be plus-values in the individual. The result is that the offspring from a given antecedent type often possess the
subject-quality in end-values ranging over a scale from very low to very high.

When we find a quality which is thus definitely measured, and which tends strongly to "run in the family," and which, after continuous effort cannot, without warping the observed facts, be made to fit into previously found rules of heredity, no matter how general such rules may seem, we must not throw away the observed facts; we must throw away our notion that the facts must of necessity fit the previously found rules, and start anew the search for the Formula of Heredity by which Nature has transmitted the particular quality from one generation to the next. It is well to find out how-it-is before we speculate on why-it-is.

Researches in anthropology, physiology, psychology, education and medicine are continuously inventing new and definite yard-sticks for measuring complex traits of the individual. Students of genetics are tracing such measured traits in pedigrees. Thus the situation is being prepared for a new attack upon the genetics of many of these complex qualities. If the quality in question be stature or weight, the yard-stick is already invented. If it be some other more complex quality the yard-stick may have to be invented.

This was the case with racing capacity of the Thoroughbred horse. The yard-stick had first to be invented for measuring quality of performance before a reliable formula for the inheritance of racing capacity could reasonably be sought. This was done by correctly intercompensating sex, age, weight-carried, distance-run and speed. The constituent units of this yard-stick are years for age, pounds for weight-carried, furlongs for distance-run and seconds per furlong for speed. The practical arts, aided by the science of physics, long ago standardized these constituent yard-sticks of racing capacity. This fact made possible the development of a yard-stick for racing capacity as a physiological entity. But there is a constitutional difference between colts, fillies and geldings. To circumvent this difficulty the yard-sticks for racing capacity had to be worked out independently for each sex. When the physiologists give us a mathematical yard-stick for the inherent difference in sex, these three formulas can be made into one, but until then we shall have to put up with the inconvenience of three formulas. To make these three formulas comparable each is reduced to the "par basis," that is, each quality of performance is a ratio in which the individual excellence of performance in a particular race is compared with the highest speed which Thoroughbred "horse flesh" has achieved under the same set of conditions of sex, age, distance-run and weight-carried, other factors being constant.

The General Formula of Heredity was developed in connection with these researches on the genetics of the Thoroughbred horse, which were generously supported by the distinguished horse-breeder, Mr. Walter J. Salmon.
In these researches it required as many years of study to perfect the yardstick for quality of performance, and its corollary individual racing capacity, as it did to find the principles underlying the General Formula of Heredity, and subsequently to find the Pattern Formula of Heredity for the inheritance of racing capacity.

The essential preliminary tool then for the genetic analysis of the more complex traits is the reliable yardstick for measuring the subject-trait in the individual. With such a tool in hand the next task is to find the formula: \( K = f(M, R) \). That is, \( K \) is the probability that the preindicated or random-selected offspring, with a given \( M \) or prediction-basis, will fall within the selected \( R \) or offspring-class-range. This statement constitutes the mathematical specifications of the task in hand.

The next task is to settle on a prediction-basis—that is, to decide what shall constitute \( M \). We may let the value of the measured subject-quality in the sire alone constitute the prediction-basis; or we may let it be such measure in the dam alone; or we may take the value of the sire, plus the value of the dam, and divide the sum by two; or, as Galton did in the case of human stature, we may make into a prediction-basis the stature of the father, plus the stature of the mother times 1.08, and divide the sum by two. This gives the "mid-parent" of Galton's studies. The mid-parental value is, of course, a prediction-basis or index. It is the \( M \) of the present researches. Similarly, we may take any other group of antecedent near-kin, stress the individuals differentially, and work their measured values into a prediction-basis-index, that is, into an \( M \). Our principal concern here is to stress each such antecedent near-kin in such a manner as to give the most accurate prediction. Theoretically, these relative stresses may begin with the corresponding correlations between the measured values of the trait in the particular antecedent kin-type and in the offspring.

At this point it should be mentioned that both the particular group of antecedent near-kin selected for the prediction-basis-index, and the relative stresses given to individual antecedent kin, are always subject to revision in the direction of a better prediction-basis or \( M \). If, for example, one feels that the sire should be given ten per cent more stress than he actually was given in the working formula, \( M \) should be revised accordingly. If such revised formula gives a better prediction-basis, that is, a steeper and more diagonal Manerkon, then the "feeling," whatever its cause or reason may have been, was in the direction of truth. But if the formula with the new stress placed on the sire proves less true than the original formula, then the "correction" was in the wrong direction. Thus, each Specific Formula of Heredity may be constantly perfected without sacrificing any advantage already found.

The question arises "How can we have two different prediction-bases, that is, two different \( M ' s \), for the same parents, each giving a different
probability-distribution of offspring values, and both of them be true?" This question belongs to the philosophy of probability rather than to the use of probability in such researches as the present one. Philosophers recognize the "difference between truth and probability." The rule "100 per cent true or 100 per cent false" is not the classification of probability studies. Prediction made by probability mathematics may be good or bad; we may have a good prediction-basis or a poor one, both equally true. And in addition we have a criterion for judging decisively whether we are moving in the direction of truth or in the direction of error.

Next it is necessary to decide upon \( R \), the offspring-class-range or "the thing predicted." With a great many data to be used in finding the specific formula for the inheritance of the selected trait, a relatively narrow offspring-class-range can be selected. This is, of course, desirable. In Galton's stature studies he settled upon one inch as the class-range both for mid-parents and for offspring. To illustrate this point, in one trait-study the offspring-class-range might consist in 1.5 centimeters, in another in 0.2 of a gram, and in still another in 1.166 seconds. Thus any arbitrary unit which the particular trait calls for can be used to constitute the offspring-class-range. But when once decided upon, such \( R \), or offspring-class-range, is built into the formula as a unit. This early unit-determination for \( R \) saves a great deal of figuring, and aids to make the later computation of definite probabilities relatively simple.

We now come to \( K \). In all cases the Formula of Heredity makes prediction in terms of \( K \), that is, of the probability that the particular pre-indicated offspring will fall into any offspring-class-range selected from the whole series of such ranges. The mathematical summation of all such probabilities for a given prediction-basis, or \( M \) value, must always equal 1.000. This is one check on the mathematical correctness, but not, of course, on the biological principles underlying the Formula of Heredity.

The next step—the real task—is to find a formula which will manipulate the \( M \) and \( R \) values decided upon, so as to give the correct \( K \) or probability. In practical work one should have at least a thousand data in order to determine a Specific Formula of Heredity for a selected hereditary quality. Indeed five thousand data or more would be much more satisfactory. One datum for such a formula consists in the actual measure of the subject-trait in one individual offspring and the value of the prediction-basis which produced it. In any case the data should be divided into at least ten prediction-basis-classes and into ten offspring-class-ranges. More such classes, depending upon the number of the elementary data, would be desirable.

The method of development of the pattern formula, and its use in finding the Specific Formula of Heredity for any selected trait which "runs in the family," are given in detail in the accompanying tables and diagrams (Charts I, IIA, IIB, III, IV, V) and need not, therefore, be repeated here.
The principal aim of the Formula of Heredity is to provide an accurate mathematical picture of how Nature transmits, from one generation to another, qualities which are designated as inborn, constitutional or hereditary. Such a formula should use the minimum of "straight-jacketing" of the actual observed data. This means that in handling each group of data, for which a constituent curve of the final formula is sought, we must "bend the curve and not the data." It means also that in all preliminary computations the original data-distribution must be preserved as long as possible. That is, whenever possible "use observed data instead of averages and smoothed values."

The things directly measured by the Formula of Heredity are the amount of regression between parental and offspring generations, and the amount of variation among the offspring with a given prediction-basis. If there were no regression, and no variability among the offspring, then the Formula of Heredity would read: "The value of the offspring equals the value of the parent, or other prediction-basis." But this is rarely the case.

CHART I—THE FORMULA OF HEREDITY

THE GENERAL FORMULA OF HEREDITY \( K = f(M, R) \)

\( K \) is the probability that the pre-indicated or random-selected offspring with a given \( M \) or Prediction-Basis will fall within the selected \( R \) or Class-Range of offspring.

\[
K = \frac{-(FC \sim R)}{2\left[\sigma_1 + 2(\sigma_2 - \sigma_1) \frac{FC - R}{2(FC \sim R)}\right]^2}
\]

I. The Basic Formula \( \rightarrow K = Kf_c \epsilon \)

Each of the Three Structural Units of the Basic Formula fits the General Quadratic Function in relation to \( M \). Type: \( Y = ax^2 + bx + c \).

In more convenient form each such unit:

1. \( FC = f(M) = (fM + gM^2) (C - u) + (hM + iM^2) (C + u) + \epsilon \)
2. \( Kf_c = f(M) = (jM + gM^2) (C - u) + (LM + nM^2) (C + u) + \phi \)
3. \( \sigma_1 = f(M) = (pM + qM^2) (C - u) + (rM + sM^2) (C + u) + t \)

\[
\sigma_e = \frac{1}{2.5066 Kf_c}
\]

\( (C - M) = \frac{M + (M \sim 0)}{2M} \) = "Cancellation ratio" for all \(-M\) values

\( (C + M) = \frac{M - (M \sim 0)}{2M} \) = "Cancellation ratio" for all \(+M\) values

This basic structure is constant for the specific formulas for all measurable hereditary traits, but for each set-up in relation to trait-subject, prediction-basis and class-range of offspring, a specific value must be found for each of the fifteen basic constants, \( f, g, h, i, j, k, l, m, n, o, p, q, r, s \) and \( t \) distributed among the three "Structural Units" of the basic formula.
THE THREE VARIABLES: 

\( M = \) Manton (Gr. \( \mu \alpha \nu \rho \iota \sigma = \) Prophet)

The value of the Prediction-Basis, the antecedent near-kin index.

\( R = \) Ergon (Gr. \( \epsilon \rho \gamma \omicron \nu \omicron = \) Thing Done)

The Thing Predicted—the selected range of offspring-value. \( R = \) always a given value \( \neq 0.5 \) of the offspring class-range.

\( K = \) Eikon (Gr. \( \epsilon \eta \omicron \kappa \omicron \omicron \omega = \) Likelihood)

The Probability that the offspring with a particular \( M \), or prediction-basis, will fall within the selected \( R \), or offspring class-range.

The Three Structural Units of the General Formula.—The part which each plays in the work of the formula.

Each of these Structural Units is a direct function of \( M \), the prediction-basis, and when, in any given Specific Formula of Heredity, the numerical value of each included basic constant is given, the value of each of the several Structural Units and consequently of \( K \), may be found for the selected value of \( M \).

The flexibility of these three Structural Units, by offering a wide choice of "slopes and bends," insures a close mathematical fit for each variation in the inheritance of the subject-trait, which variation has been observed or suspected by previous studies.

Each formula permits, but does not require, symmetry in the particular functional curve for \( +M \) and for \( -M \) values.

I. \( FC = \) Offspring Fluctuation Center for successive values of \( M \).

\[
FC \, = \, f(M) \, = \, (fM \, + \, gM^2 \, (C-M) \, + \, (hM \, + \, iM^2)(C+M) \, + \, 0
\]

II. \( K_{fe} = \) Maximum offspring class-probability for successive values of \( M \).

\[
K_{fe} \, = \, f(M) \, = \, (jM \, + \, kM^2(C-M) \, + \, (lM \, + \, mM^2)(C+M) \, + \, n
\]

III. \( \sigma_1 = \) Standard Deviation for the positive half of the offspring class-probability curve for successive values of \( M \).

\[
\sigma_1 \, = \, f(M) \, = \, (pM \, + \, qM^2(C-M) \, + \, (rM \, + \, sM^2)(C+M) \, + \, t
\]

\( \sigma_1 \) once set in its accompanying conditions determines its companion \( \sigma_2 \)

Let \( R = \) Center of the selected class-range of offspring-value.

For the same \( M \) and \( K_{fe} \) values \( \Sigma K \, = \, 1.0000 \)

\( \sigma_1 \) when \( R < FC; \, \sigma_1 \, = \, \sigma_2 \, + \, (\sigma_2 \, - \, \sigma_1)(\text{Cancellation Ratio} \, = \, 0) \)

Cancellation Ratio \( = \frac{(FC - R) \, + \, (FC \sim R)}{2 \, (FC \sim R)} \)

\( \sigma_2 \) when \( R > FC; \, \sigma_2 \, = \, \sigma_1 \, + \, (\sigma_2 \, - \, \sigma_1)(\text{Cancellation Ratio} \, = \, 1) \)

In \( \sigma_0 \, N \) always \( = \, 1. \, \sigma_0 \, = \, \frac{1}{2.5066K_{fe}} \)

\( \sigma_1 \, + \, \sigma_2 \, = \, 2\sigma_1. \, \text{When} \, \sigma_1 \, = \, 2\sigma_2; \, \sigma_1 \, = \, 2\sigma_2; \, \text{For} \, M \, = \, 0; \, \sigma_1 \, = \, \sigma_2 \)

Usually, but not necessarily, regression causes the following relative values:

For \( +M \) values \( \sigma_1 < \sigma_2; \, \text{for} \, -M \, \text{values} \, \sigma_2 > \sigma_1; \, \text{for} \, M \, = \, 0; \, \sigma_1 \, = \, \sigma_2 \)

THE FIFTEEN BASIC CONSTANTS OF THE GENERAL FORMULA

\( f, g, h, i, j, k, l, m, n, o, p, q, r, s \) and \( t \)

A. The Constants by Structural Units.

The Common Mathematical Basis for the Three Structural Units.
Always each Structural Unit = f(M), and the best present-found curve is always a
cubical, and as here developed, each such parabola is a graph of the General Quadratic
Function.

General Type: \( Y = ax^2 + bx + c \).

In more convenient form: Special Type: \( f(M) = (aM + bM^2)(C - m) + \\
(cM + dM^2)(C + m) + e \)

In the First Structural Unit, \( FC = (fM + gM^2)(C - m) + (hM + iM^2)(C + m) \\
+ o, \) there are five basic constants, \( f, g, h, i \) and \( o. \) Of these, \( f, g \) and \( o \) are in the
\( + M \) region, and \( h, i \) and \( o \) are in the \( - M \) region.

In the Second Structural Unit, \( K_f = (jM + kM^2)(C - m) + (lM + mM^2)(C + m) \\
+ n, \) there are five basic constants, \( j, k, l, m \) and \( n. \) Of these, \( j, k \) and \( n \) are in the
\( + M \) region, and \( l, m \) and \( n \) are in the \( - M \) region.

In the Third Structural Unit, \( \sigma_t = (pM + qM^2)(C - m) + (rM + sM^2)(C - m) \\
+ t, \) there are five basic constants, \( p, q, r, s \) and \( t. \) Of these, \( p, q \) and \( t \) are in the
\( + M \) region, and \( r, s \) and \( t \) are in the \( - M \) region.

B. Work of the Cancellation Ratios.

\[
(C - m) = \frac{M + (M \sim 0)}{2M} = \text{the cancellation ratio for all } - M \text{ values}
\]

\[
(C + m) = \frac{M - (M \sim 0)}{2M} = \text{the cancellation ratio for all } + M \text{ values}
\]

These “cancellation ratios” acting automatically give independence to the particular
function for \( + M \) and for \( - M \) values. The whole curve used whenever a Structural
Unit = \( f(M) \), instead of being a single curve, is in fact a stretch from each of two indepen-
dent curves meeting at \( M = 0 \). There are thus six Structural-Unit curves in all,
and the General Formula automatically puts into use only such stretches of the parabola-
arms as lie in the particular \( + M \) or \( - M \) regions. This independence gives additional
flexibility for actual data-fitting.

C. Analytic Work of the Constants by Groups.

In the formula for each of the six parabolic curves, only three constants are to be found
from the data—two “slope-bend constants” from the \( u \)- and \( v \)-groups, and one “inter-
cept constant” from the \( w \)-group. In every case the used arm of the parabola passes
through the “origin,” i.e., \( M = 0 \), and \( f(M) = \) value of the \( w \)-group constant.

I. The \( U \)-Group. The constants \( u, b, g, k, q \) and \( d, i, m, s \) give scale, sharpness and
direction of bend to the parabola of the particular function for successive values of \( M \).

If the \( u \)-group constant is not equal to zero, each function of \( M \) is a parabola. Its
axis is always parallel to the \( M \) axis, regardless of the values of the other constants.
If the \( u \)-group constant is +, the parabola-arms move toward the right from the
vertex; if − they move toward the left.

If the \( u \)-group constant is equal to zero, the function is a straight line with a slope
equal to the value of its \( u \)-group constant, and an \( M \) axis-intercept equal to the
value of its \( w \)-group constant.

II. The \( V \)-Group. The constants \( v, a, f, j, p \) and \( c, h, l, r \) give the general slope to
and determine the actual vertex of the parabola of the particular function for successive
values of \( M \).

If the \( v \)-group constant is equal to zero, the actual vertex of the parabola is on the
\( M \) axis, at \( M = 0 \), and \( f(M) = \) the value of its \( w \)-group constant.
If the w-group constant is not equal to zero, the actual vertex of the parabola moves to a new "x-selected" coordinate center. Still the used arm of each parabola must always pass through the point \( M = 0 \), and \( f(M) \) = the value of its w-group constant. The availability of a new coordinate center, made possible by developing the parabola from the General Quadratic Function, gives great additional flexibility to the Three Structural Units.

III. The W-Group. The constants \( w, e, o, n, t \) determine the value of the particular function when \( M = 0 \), i.e., the value of the intercept, origin or vertex, as the case may be, along the \( M \)-axis.

The w-group constant thus readjusts the \( y \)-coordinate to any position from its first readjustment which gave only the desired \( x \)-coordinate. Since the section of each \( FC \) curve used must originate at \( M = 0 \), and \( FC = 0 \) the final w-group constant in the \( FC \) formula is always zero. In the \( K_t \) and \( a_1 \) formulas, the final w-group constant is generally +, but it may be zero or −.

NOTES: I. The Basic Formula \( K = f(M,R) \) presents an accurate mathematical picture of Nature's behavior in governing the inheritance of all measurable qualities which in any degree depend upon heredity. The qualities so pictured may be structural or functional, chemical or physiological, mental or spiritual, normal or pathological, good or bad, capacities or defects, tendencies or fruitions, highly hereditary or only slightly so—but each such quality must have some tendency to "run in the family," and it must be measurable in the individual.

II. The three variables \( M, R, K \) are the three coordinates of the geometric framework. The fifteen constants \( f, g, h, i, j, k, l, m, n, o, p, q, r, s \) and \( t \) in their proper relationships as defined by the Basic Formula, and in their correct values as found by accurately curve-fitting the observed inheritance-data, give definite "values, slopes and bends" to the elements of the whole mathematical structure. The General Formula thus defines the basic relationships, and the constants do the actual specific data-fitting.

III. In operation the Formula of Heredity must behave like a machine well designed for its purpose. When we put into it accurate data on antecedent near-kin measurements for a selected trait, the formula must turn out a reliable statement about the possession of a selected trait by the pre-indicated offspring.

USE: I. Immediate—The Formula of Heredity.

This Formula, \( K = f(M,R) \), fits very closely the data for any set of observations on the inheritance of any somatically measurable trait or quality, and it provides the quantitative description of the behavior of heredity as essential to the more accurate genetic analysis of any complex structural or functional quality which tends to "run in the family." Usually such an hereditary quality is based upon the very complex developmental interaction of many genes—far too complex for practical Mendelian analysis.

II. Fundamental—General Prediction Formula.

While the outline of the Basic Formula here given is constructed about the problem of heredity, the Formula \( K = f(M,R) \) might well be called the General Prediction Formula for any measured qualities which are associated to any degree in any manner. The Basic Formula gives a prediction-basis \( M \); it lists a measured range of values of \( R \) in the thing predicted; and it ties up \( M \) and \( R \) by \( K \), which is the correct probability of the particular association—all based upon "experience," i.e., the observed data. \( K = f(M,R) \) is a new general tool capable of high specialization for the analysis and interpretation of measurable phenomena of any kind which are associated to any degree.
If there were complete regression, that is, if all offspring fluctuated in the same manner around the same value, regardless of the values of the parents, then there would be no differential heredity to measure. In such a case the range of value in the quality in question among the offspring

**CHART II A**
would depend entirely upon environment. As a matter of fact, in qualities which "run in the family," there must be some regression, and there is generally a considerable overlapping in offspring-values between a high
The General Formula of Heredity \( K \cdot f(MR) \)

The probability that the pre-indicated or random-selected offspring, with a given \( M \) or Prediction Basis, will fall within the selected \( R \) or Class-range of Offspring.


\[ K \cdot f(MR) = e^{2\pi N \cdot (\rho - 1)} \]

Notes:
1. In the Cartesian geometry of three dimensions, \( K \cdot f(MR) \) is represented by a space-surface, here called a "Manerkon" surface. In its three co-ordinates, i.e., its three variables: \( M \), \( R \), and \( K \). The Manerkon is a sort of "three-dimensional" surface, in the first instance, right and forward. In the second instance, a sort of "three-dimensional" surface, in the first instance, right and forward.

2. For the same values of \( M \), \( R \), and \( K \), the established class-range steps along the entire applicable \( K \)-range, will always equal \( f(MR) \) or certainty. For greater accuracy, each class should begin at \( f(MR) \) in class-range, though they may, with fair accuracy, begin at any point. But such one-class-range steps must always proceed in both directions until the maximum proportional value of \( K \) is reached.

3. On the same values of \( M \), \( R \), and \( K \), the "manerkon" surface, the "Manerkon" surface, with the "faster and broader" the Manerkon, and the greater the tendency of its axis to parallel the \( K \)-axis, the narrower the prediction.

4. In any specific formula of Heredity, a specific value must be found for each of the known constants, of the Basic Formula. Such constants, if correct, give a considerable flexibility in the Manerkon, so that it will fit very closely any of the original-case results.

5. The actual Manerkon, if carefully constructed, may be used directly for selecting the particular problem in hand, as for finding graphically a value of \( K \) in \( K \cdot f(MR) \).
prediction-basis and a low prediction-basis. This is better illustrated by
the accompanying table and diagram (Charts IV and V) than can be ex-
pressed in words.

\[ \frac{1}{K_{fe}} \cdot \left( \frac{(FC-R)}{2} + \frac{(FC-\bar{R})}{2} \right) \]

Example I.

\[
\begin{align*}
M & = -1.35 \\
FC & = 0.05 \\
K_{fe} & = 0.151 \\
\sigma_1 & = 3.79 \\
\sigma_2 & = 3.03
\end{align*}
\]

Example II.

\[
\begin{align*}
M & = +2 \\
FC & = 1.7 \\
K_{fe} & = 0.14 \\
\sigma_1 & = 3.2 \\
\sigma_2 & = 2.85
\end{align*}
\]

<table>
<thead>
<tr>
<th>OFFSPRING-CLASS- RANGE</th>
<th>PROBABILITY THAT THE OFFSPRING WILL FALL WITHIN THE PARTICULAR OFFSPRING-CLASS- RANGE</th>
</tr>
</thead>
<tbody>
<tr>
<td>-10 ± 0.5</td>
<td>( K = 0.1315e^{-2.602} ) = 0.0001</td>
</tr>
<tr>
<td>-9 ± 0.5</td>
<td>( K = 0.1315e^{-4.347} ) = 0.0005</td>
</tr>
<tr>
<td>-8 ± 0.5</td>
<td>( K = 0.0135e^{-5.951} ) = 0.0018</td>
</tr>
<tr>
<td>-7 ± 0.5</td>
<td>( K = 0.1315e^{-2.057} ) = 0.0060</td>
</tr>
<tr>
<td>-6 ± 0.5</td>
<td>( K = 0.1315e^{-3.696} ) = 0.0162</td>
</tr>
<tr>
<td>-5 ± 0.5</td>
<td>( K = 0.1315e^{-1.927} ) = 0.0361</td>
</tr>
<tr>
<td>-4 ± 0.5</td>
<td>( K = 0.1315e^{-0.541} ) = 0.0665</td>
</tr>
<tr>
<td>-3 ± 0.5</td>
<td>( K = 0.1315e^{-0.342} ) = 0.1010</td>
</tr>
<tr>
<td>-2 ± 0.5</td>
<td>( K = 0.1315e^{-0.041} ) = 0.1262</td>
</tr>
<tr>
<td>-1 ± 0.5</td>
<td>( K = 0.1315e^{-0.004} ) = 0.1310</td>
</tr>
<tr>
<td>0 ± 0.5</td>
<td>( K = 0.1315e^{-0.004} ) = 0.1234</td>
</tr>
<tr>
<td>+1 ± 0.5</td>
<td>( K = 0.1315e^{-0.012} ) = 0.1085</td>
</tr>
<tr>
<td>+2 ± 0.5</td>
<td>( K = 0.1315e^{-0.090} ) = 0.0890</td>
</tr>
<tr>
<td>+3 ± 0.5</td>
<td>( K = 0.1315e^{-0.447} ) = 0.0881</td>
</tr>
<tr>
<td>+4 ± 0.5</td>
<td>( K = 0.1315e^{-0.964} ) = 0.0486</td>
</tr>
<tr>
<td>+5 ± 0.5</td>
<td>( K = 0.1315e^{-1.636} ) = 0.0323</td>
</tr>
<tr>
<td>+6 ± 0.5</td>
<td>( K = 0.1315e^{-1.006} ) = 0.0201</td>
</tr>
<tr>
<td>+7 ± 0.5</td>
<td>( K = 0.1315e^{-2.922} ) = 0.0120</td>
</tr>
<tr>
<td>+8 ± 0.5</td>
<td>( K = 0.1315e^{-5.041} ) = 0.0063</td>
</tr>
<tr>
<td>+9 ± 0.5</td>
<td>( K = 0.1315e^{-7.390} ) = 0.0032</td>
</tr>
<tr>
<td>+10 ± 0.5</td>
<td>( K = 0.1315e^{-4.643} ) = 0.0015</td>
</tr>
<tr>
<td>+11 ± 0.5</td>
<td>( K = 0.1315e^{-5.302} ) = 0.0007</td>
</tr>
<tr>
<td>+12 ± 0.5</td>
<td>( K = 0.1315e^{-4.507} ) = 0.0003</td>
</tr>
<tr>
<td>+13 ± 0.5</td>
<td>( K = 0.1315e^{-7.160} ) = 0.0001</td>
</tr>
<tr>
<td>+14 ± 0.5</td>
<td>( \Sigma K = 0.9995 )</td>
</tr>
</tbody>
</table>

Notes:

1. As a check, \( \Sigma [K_{fe}e^{-x}] = 1.000 \) .

\[ \sum e^{-x} = \frac{1}{K_{fe}} \]
2. For any given prediction-basis value (i.e., for any $M$) the summation of probability for the several offspring-class-values must equal 1.000 or certainty. That is, the particular offspring must have some sort of value, and this formula simply computes the probability that the particular offspring-value will fall within any selected offspring-value-range.

3. The basic things directly measured for building a Specific Formula of Heredity are Regression between the parental and the offspring generations, and Variation among the offspring, each in reference to a given Prediction-basis (i.e., $M$).

4. The Formula of Heredity handles correctly each possible combination of Parent-offspring Regression and Offspring Variation. For example, with no regression and no offspring-variation, the Formula of Heredity becomes simply: Measure of parent (or other prediction-basis) = Measure of offspring.

The mathematical procedure in finding a Specific Formula of Heredity, from the observed data as herein outlined, is given the name "manerkon analysis." Manerkon is an abbreviation of the names given to each of the three Cartesian coördinates used in plotting the formula geometrically. (See Chart III.) In each Formula of Heredity, one coördinate represents the prediction-basis which is the Manton, or $M$. Another stands for the thing predicted, that is, the Ergon, or $R$, while the third stands for probability, that is, the Eikon, or $K$.

In most cases the geometric shape of the model of any Specific Formula of Heredity, that is, of "the manerkon," will be found to be a "skewed saddle." If, however, we find a case in which mediocre values depend upon relatively more recessive aspects of the trait's constituent genes than either very low or very high values, then instead of a "skewed saddle" the shape of the geometric model of the Specific Formula of Heredity will be a "skewed camel's hump."

In the geometric analysis of the Formula of Heredity it is noted that there are only three "structural units." Let us make an analogy to ship building. Although the thing we are building is not a ship, it is a manerkon, "a sort of ship turned wrong side out," still its structural units are closely analogous. The first structural unit of the manerkon is the curve of Offspring-fluctuation-centers plotted as $FC = f (M)$. This ground-curve is comparable to the keel of a ship. The next structural unit is the $K_{fc}$, plotted as $K_{fc} = f (M)$. This is the "stanchion height" of the manerkon. $K_{fc}$ stands for the offspring-class of greatest frequency which is produced by the particular $M$, or prediction-basis. A series of $K_{fc}$'s, or "stanchions," are erected vertically above the "keel"—that is, above the curve of Offspring-fluctuation-centers. The third structural unit of the manerkon is $\sigma_1$—the standard deviation in the plus direction. This corresponds to "the spring of the ribs" or the beam of the ship. In order to give greater flexibility in fitting the actual data, the standard deviation to the right and to the left of the "stanchion height," that is, of the $K_{fc}$ are made independent of each other. Geometrically the model of
the Specific Formula of Heredity is the manerkon which results from assembling these three structural units in accordance with the operative instructions of the Formula of Heredity. (See Chart II.B.)

**Constituent Equations for the Three Structural Units in K=f(M,R)**

When the values of the constants are those stated above.

\[
\text{FC} = (M - 0.075 M^2)(C_m) + (0.35 M + 0.15 M^2)(C_m) + 0 \\
\text{Kr} = (0.001 M + 0.002 M^2)(C_m) + (-0.001 M + 0.0005 M^2)(C_m) + 0.13 \\
\text{O}_1 = (-2 M^2)(C_m) + (2 M - 0.1 M^2)(C_m) + 0.366 \\
\text{O}_2 = 2.50065 K_f
\]

The "Probability Overlap" Between Examples I and II.

---

**Chart V**

The shape of the manerkon—the geometric model of the Specific Formula of Heredity—aids substantially in the genetic analysis which seeks the constituent genes of the complex subject-trait, particularly the number and
potency of such genes. The highest point of the manerkon suggests that for those particular values the subject-trait or quality depends upon a relatively greater number of recessive aspects of its constituent genes than do the values of the subject-quality at the lower points of the manerkon. In the case of human stature it seems clear that tallness, which breeds truer than shortness, is such a case. On the other hand, racing capacity in the Thoroughbred horse, in a plus-direction, seems to depend upon a relatively greater number of dominant aspects of the constituent genes than does low capacity. Thus the determination of the genic constitution of the more complex hereditary traits would seem to be more possible of attainment by bringing to bear upon each particular problem not only the theory of the gene, but also probability mathematics in reference to the somatic aspects of the quality as a whole. Manerkonic analysis as herein outlined furnishes a suitable instrument for this latter work.

While both manerkonic and Mendelian analyses can be used successfully as tools on the same problem, still each type of analysis is essentially suited to the study of some special type of trait which definitely "runs in the family." Mendelian genetics is particularly suited to the analysis of qualities which can be attributed to definite genes which are traced in their development from the chromosomes to the somatic adult, and which genes can be traced genetically in their segregation and recombination. Manerkonic analysis is essentially suited to those very complex somatic traits, whether functional or structural units, with which we are primarily concerned in the evolution of species, in the improvement of domestic plants and animals, and in race-betterment in man, but which traits have thus far proven vastly too complex for Mendelian analysis alone.

In scientific study accuracy of prediction is one of the best proofs of soundness of interpretation. In most Mendelian studies the best prediction does not state with certainty what a particular pre-indicated offspring will be like, but, from a mating of a given genetic type, it computes the probability that the offspring will possess a certain trait, or a certain complex of segregable qualities. The actual trait-distribution among a large number of offspring, produced by the same genetic type of parents, tests the soundness of the particular prediction. So, in manerkonic analysis of the genetics of qualities which are variable but not definitely segregable as entities, such as racing capacity in the Thoroughbred horse, and stature in man, we must devise a mathematical formula which, based upon the particular trait actually developed by the nearest antecedent blood-kin of the prospective offspring, will give the probability that the particular pre-indicated offspring will, if it is actually produced and lives under standard conditions, develop the measured subject-quality within a definitely selected range of value.

Besides finding the Specific Formula for the inheritance of racing capacity
in the Thoroughbred horse, a few other uses have already been made of the General Formula. By following the General Formula as a pattern a Specific Formula has been worked out for the inheritance of stature in man, based upon Galton's 928 cases.

A still different type of use has been made of the General Formula of Heredity. One of its constituent formulas, namely, \( FC = f(M) \), has supplied the set-up for determining the direction and measuring the rate of evolution. This analysis brings out clearly that in evolution the thing to measure is not the difference between the somatic mean of the parents and the somatic mean of the offspring, but rather the difference between the somatic mean of the parents and the "point of no biological regression," which might properly be called the "genetic mean." By the use of \( FC = f(M) \) these "two means" can be plotted geometrically. In such plotting the coordinates are time and the yard-stick which measures the subject-quality. The more "short-time," accurate and intimate measures of genetics are counted on to collaborate with the "long-time" giant-scale measures of paleontology. Thus the General Formula offers an instrument for coördinating evolution and genetics.

For example, the monumental work of Professor Henry Fairfield Osborn on "Titanotheres of Ancient Wyoming, Dakota and Nebraska" contains records of progressive change in many exactly measured anatomical structures of these forms, traced through fairly-well-measured successive geologic time-epochs. Thus, in definitive change in skull-length, the Titanotheres research presents the two coordinates—successive measures of the subject-quality and a measured time-sequence—necessary for common study by evolution and genetics.

All studies in heredity look primarily to the development of a prediction formula. The present researches compose an accurate mathematical picture of how Nature transmits a measured hereditary quality from one generation to another. It seems probable that many other definite uses may be found for the General Formula of Heredity as a tool or instrument for research in both genetics and evolution.