

II.—Non-Associative Algebra and the Symbolism of Genetics.

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§ 1. INTRODUCTION.

THE statistical material of genetics usually consists of frequency distributions—of genes, zygotes and mating couples—from which new distributions referring to their progeny arise. Combination of distributions by random mating is usually symbolised by the mathematical sign for multiplication; but this sign is not taken literally for the simple reason that the genetical laws connecting the distributions of progenitors and progeny are inconsistent with the laws governing multiplication in ordinary algebra. This is explained more fully in § 2.

However, there is no insuperable reason why the genetical sign of multiplication should not be taken literally; for it is possible with any particular type of inheritance to construct an "algebra"—distinct from ordinary algebra but of a type well known to mathematicians—such that the laws governing multiplication shall represent exactly the underlying genetical situation. These "genetic algebras" are of a kind known as "linear algebras," of which a simple description is given in § 4.

It is not suggested that the use of ordinary algebraic methods in conjunction with the specific principles of genetics will not lead to correct results. It seems, however, that the systematic use of genetic algebras would simplify and shorten the way to their attainment, and perhaps enable much more difficult problems to be tackled with equal ease.

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The construction of genetic algebras has been described in a somewhat abstract way in a previous paper (Etherington, 1939 *b*), to which I shall refer as G.A. Here I propose to consider the symbolism more from the geneticist's point of view, applying it to some simple population problems, without going into the details of the mathematical background. It will be recognised that the current treatment of such problems does in reality make use of genetic algebras without noticing them explicitly. By elaborating the symbolism and adapting it to more complicated genetical premises (*e.g.* in the manner indicated in G.A. § 14), it should be possible to avoid the laborious complexity which other methods in such cases would involve.

Only elementary mathematical knowledge is assumed, and it is hoped that this paper will be found understandable by geneticists whose mathematical knowledge is quite limited.

§ 2. GENETICAL MULTIPLICATION.

Capital letters will be used to represent frequency or probability distributions, referring to either a population, a single individual, or a single gamete; such as (in the case of autosomal allelomorphs)

$P = DD$ = homozygous dominant individual, or population consisting of such;

$P = \alpha DD + \beta DR + \gamma RR$ = population with assigned frequencies $\alpha : \beta : \gamma$ of genotypes, or individual with assigned probabilities α, β, γ of belonging to one or other genotype;

$P = \delta D + \rho R$ = population which produces D and R gametes in given numerical ratio, or gamete which has probability δ of containing D, ρ of containing R.

The *multiplication* of populations—individuals—gametes—means the calculation of progeny distribution resulting from their random mating—mating—fusion. Defining a *population* as a probability distribution of genetic types, we may say in all cases that we are multiplying populations.

Now multiplication in ordinary algebra obeys three laws: (1) the commutative law $PQ = QP$, (2) the associative law $P(QR) = (PQ)R$, (3) the distributive law $P(Q + R) = PQ + PR$.

The validity of the distributive law in the genetic symbolism is sufficiently obvious; it forms the basis of the method of "chess-board diagrams" often used as visual aids in the calculation of progeny distributions.

The associative law is not obeyed in genetical multiplication. This

is seen by comparing the progeny of a mating between the offspring from two individuals or populations, denoted as PQ, and a third individual or population R (*i.e.* the product (PQ)R), with the progeny from P and the hybrid population QR (*i.e.* the product P(QR)). There is clearly no reason why they should be the same, and in fact unless $P=R$ they are found to be different. Thus genetical multiplication is non-associative.

Regarding the commutative law, (i) if we are considering autosomal characters it will be obvious that this law applies, since the results of reciprocal matings are generally speaking identical, although we shall see below that in certain cases non-commutative multiplication can occur.

(ii) One might be tempted to say that with sex-linked characters multiplication is non-commutative, since the results of reciprocal matings are different. But it must be remembered that with sex-linked characters we can only speak of reciprocal matings in connection with the phenotype classification of a population; whereas the calculation of progeny distribution is only possible on the basis of the genotype classification. A given genotype (either involving the Y-chromosome or not) is either female or male, so that a reciprocal mating between genotypes is impossible. Suppose that we are multiplying a male genotype M and a female genotype F: then MF and FM both mean the same thing—the genotype distribution of their offspring; and so multiplication is commutative.

(iii) On the other hand, returning to autosomal inheritance, it is possible for this to be unsymmetrical in the sexes, through either crossing-over values or gametic selection being different in male and female. In such cases it is really optional whether we treat corresponding male and female genotypes as the same type (since their relevant gene content is the same) or as distinct types (since they produce different series of gametes). In the former case, PQ and QP have distinct meanings, referring to reciprocal crosses which do not produce similar distributions of offspring; and multiplication is non-commutative. In the latter case, the situation is as with sex-linkage.

To sum up, genetical multiplication is non-associative, but obeys the commutative and distributive laws; except that in certain cases we have the option of using a varied form of the symbolism in which the multiplication is non-commutative as well as non-associative.

§ 3. NON-ASSOCIATIVE PRODUCTS AND POWERS.

Non-commutative algebra of a special kind (matrix algebra) is widely familiar by reason of its many applications in geometry and physics. (Also in genetics: *cf.* Hogben, 1933; Geppert and Koller, 1938, Chap. 4.)

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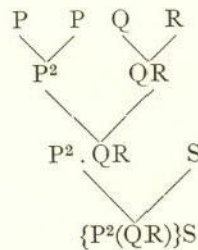
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Hence there is no reason to fear that an algebra which does not obey all the usual laws will necessarily prove unmanageable.

But with non-associative algebra some precautions are required to avoid confusion, especially when dealing with products or powers involving many factors. With such an expression, brackets inserted in different ways would indicate different orders of association of the factors; and the corresponding interpretations of the whole product would refer to the various pedigrees which could be constructed with given ancestors. For example, the product $\{P^2(QR)\}S$ represents the pedigree below. The



separate factors or ancestors P, P, Q, R, S may be thought of as given genotypes or distributions of genotypes. The factor P^2 may arise through self-fertilisation of an individual P, or from the mating of two individuals of the same genetic type, or from random mating within one population P or between two similar populations. The partial products P^2 , QR, $P^2(QR)$, and the final result $\{P^2(QR)\}S$ are probability distributions which, for any particular type of inheritance, can be calculated when P, Q, R, S are known.

To avoid clumsiness of notation, it is convenient to use groups of dots in place of brackets, fewness of dots between factors conferring precedence in multiplication. Thus the above product would be written $P^2 \cdot QR : S$. On putting $P=Q=R=S$, it becomes a power of P. (I have discussed elsewhere a notation and nomenclature for non-associative powers (1939 *a*, § 2); *e.g.* the power in question is denoted $P^{2 \cdot 2 + 1}$. We shall be concerned, however, with only two simple types of non-associative powers, namely, the "principal" and "plenary" powers described below.)

Similarly, the product appearing at (10.1) below denotes

$$[\{(ab)(cd)\}(ef)][\{(ab)(cd)\}(gh)].$$

The pedigree for this is easily constructed; but it should be noted that in the context a, b, c, \dots denote gametes, so that ab, cd, \dots are the ancestral zygotes.

We shall find it important to distinguish between, *e.g.*, $P^{2 \cdot 2} = (P^2)^2$ and $P^4 = P\{P(P^2)\} = P : P \cdot PP$. If mating takes place at random in a popula-

tion, initially P , the successive generations, supposed discrete, are represented by the sequence of *plenary powers*

$$P, P^2, P^{2^2}, P^{2^3}, \dots, P^{2^{n-1}}, \dots, \quad (3.1)$$

each the square of the preceding; while the sequence of *principal powers*

$$P, P^2, P^3, \dots, P^n, \dots, \quad (3.2)$$

each obtained from the preceding by multiplication with P , refers similarly to a mating system in which each generation is mated back to one original ancestor or ancestral population.

§ 4. LINEAR ALGEBRAS.

Linear algebras have been studied for some ninety years, and there is an extensive literature of the subject. The following brief description will be sufficient for the present purpose. Attention is confined to algebras "over the field of real numbers"; that is to say, the Greek letters below denote ordinary real numbers, and this convention will be observed throughout the paper.

Beginning with a simple case, a *commutative** *linear algebra of order 2* is determined when two given symbols or *units* A, B are subject to a multiplication table consisting of product rules of the form

$$A^2 = \alpha A + \beta B, \quad AB = \gamma A + \delta B, \quad B^2 = \epsilon A + \zeta B, \quad (4.1)$$

the coefficients being given numerical constants. The algebra then consists of all possible expressions of the form

$$P = \lambda A + \mu B, \quad (4.2)$$

which are called *hypercomplex numbers*.† Addition and multiplication of hypercomplex numbers are carried out as in ordinary algebra, the multiplication table (4.1) being used to reduce a product to the "linear" form (4.2). Thus if

$$P = \lambda A + \mu B, \quad Q = \nu A + \rho B,$$

then

$$P \pm Q = (\lambda \pm \nu)A + (\mu \pm \rho)B, \quad (4.3)$$

$$\left. \begin{aligned} PQ &= \lambda\nu A^2 + (\lambda\rho + \mu\nu)AB + \mu\rho B^2 \\ &= \lambda\nu(\alpha A + \beta B) + (\lambda\rho + \mu\nu)(\gamma A + \delta B) + \mu\rho(\epsilon A + \zeta B) \\ &= (\lambda\nu\alpha + \lambda\rho\gamma + \mu\nu\gamma + \mu\rho\epsilon)A + (\lambda\nu\beta + \lambda\rho\delta + \mu\nu\delta + \mu\rho\zeta)B. \end{aligned} \right\} \quad (4.4)$$

* *Commutative* refers to the nature of multiplication; the *order* is the number of units on which the algebra is based.

† So called because they are a generalisation of the more familiar *complex numbers*. The algebra of complex numbers possesses a *real unit* 1 and an *imaginary unit* i , which are subject to the multiplication table $1^2 = 1, 1i = i, i^2 = -1$.

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A linear algebra based on n units, complex number is throughout) in the table giving a linear product of each n tables (5.3) and (11) respectively.)

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§ 5. THE M

Consider a pair of genotypes

It was implied in (4.1) that $BA=AB$. The linear algebra would be *non-commutative*, however, if different formulæ were prescribed for AB and BA ; and then we should have $PQ \neq QP$. Unless special conditions are satisfied by the coefficients in (4.1), multiplication is non-associative.

A linear algebra of order n is defined in an analogous way. It will be based on n units, and will consist of hypercomplex numbers: a hypercomplex number is an expression which is linear (*i.e.* of the first degree throughout) in the n units; and the algebra will have a multiplication table giving a linear formula for the square of each unit and for the product of each pair of units. (See, for example, the multiplication tables (5.3) and (11.10), which determine linear algebras of orders 3 and 5 respectively.)

The commutative and associative laws of addition,

$$P+Q=Q+P, \quad (P+Q)+R=P+(Q+R),$$

always hold; so do the distributive laws

$$P(Q+R)=PQ+PR, \quad (Q+R)P=QP+RP;$$

but multiplication may be non-commutative, non-associative, or both.

It will be seen that a linear algebra is completely determined when its multiplication table is known.

Given any two linear algebras of orders m and n (*i.e.* given their multiplication tables), it is possible by combining their multiplication tables in a certain way to deduce another linear algebra, of order mn , which is known as their *direct product*. This is of fundamental importance in the general theory of linear algebras, and we shall find (§ 11; *cf.* G.A. § 9) that it is also fundamental in the symbolism of genetics. If the units on which the first algebra is based are A, B, \dots , and those of the second A', B', \dots , then the units of the direct product may be interpreted as $AA', AB', BA', BB', \dots$.

Also (of less importance in the mathematical theory, but equally fundamental in genetics), from any linear algebra of order n a closely related linear algebra called its *duplicate* can be derived, of order $\frac{1}{2}n(n+1)$ if the original algebra is commutative. If the original units are A, B, \dots , those of the duplicate algebra may be interpreted as A^2, B^2, AB, \dots (The process of duplication was described in G.A. § 5; *cf.* also Etherington, 1941; it occurs here in §§ 5-7.)

§ 5. THE MENDELIAN GAMETIC AND ZYGOTIC ALGEBRAS.

Consider a pair of autosomal allelomorphs D, R and the corresponding genotypes

$$A=DD, \quad B=DR, \quad C=RR. \quad (5.1)$$

We shall write optionally DD or D^2 , RR or R^2 . In accordance with mendelian principles and with the notation described at the beginning of § 2, we have the two sets of formulæ:

$$D^2 = D, \quad DR = \frac{1}{2}D + \frac{1}{2}R, \quad R^2 = R; \quad (5.2)$$

$$\left. \begin{aligned} A^2 &= A, & B^2 &= \frac{1}{4}A + \frac{1}{2}B + \frac{1}{4}C, & C^2 &= C, \\ BC &= \frac{1}{2}B + \frac{1}{2}C, & CA &= B, & AB &= \frac{1}{2}A + \frac{1}{2}B. \end{aligned} \right\} \quad (5.3)$$

These give the series of gametes produced by each type of zygote, and the series of zygotes produced by each type of mating couple, with coefficients denoting relative frequencies. *E.g.*, the second of equations (5.2) mean that a heterozygote produces D and R gametes in equal numbers; the second of equations (5.3) means that the offspring of a mating $DR \times DR$ are 25 per cent. DD, 50 per cent. DR, 25 per cent. RR.

A population P can be described by the frequencies either of the gametes which it produces, or of the zygotes which it contains, and accordingly we write:

$$(Gametic\ representation) \quad P = \delta D + \rho R, \quad . \quad . \quad . \quad . \quad . \quad (5.4)$$

$$(Zygotic\ representation) \quad P = \alpha A + \beta B + \gamma C \quad . \quad . \quad . \quad . \quad . \quad (5.5)$$

$$= \alpha DD + \beta DR + \gamma RR, \quad . \quad . \quad . \quad . \quad . \quad (5.6)$$

in which we may assume

$$(Normalising\ conditions) \quad \delta + \rho = 1, \quad \alpha + \beta + \gamma = 1. \quad . \quad . \quad . \quad (5.7, 8)$$

The two representations are connected by (5.2); *i.e.* (5.6) implies (5.4) with

$$\delta = \alpha + \frac{1}{2}\beta, \quad \rho = \frac{1}{2}\beta + \gamma. \quad . \quad . \quad . \quad . \quad (5.9)$$

An examination of the above formulæ in the light of § 4 will show that by using this symbolism we are really dealing with two distinct linear algebras, both having commutative and non-associative multiplication, namely:

(1) The algebra of the symbols D, R with multiplication table (5.2). This will be called the *gametic algebra for simple mendelian inheritance*, and referred to as **G**. A hypercomplex number in this algebra has the form (5.4).

(2) The algebra of the symbols A, B, C with multiplication table (5.3). Call this the *zygotic algebra for simple mendelian inheritance*, and denote it **Z**. A hypercomplex number in **Z** has the form (5.5). Hypercomplex numbers in **G** and **Z** are interpreted as populations only if their coefficients are all positive; and it is generally convenient to require that the coefficients shall satisfy the normalising conditions (5.7, 8).

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R^2 . In accordance with described at the beginning of

$$R^2 = R; \quad (5.2)$$

$$\left. \begin{array}{l} C^2 = C, \\ AB = \frac{1}{2}A + \frac{1}{2}B. \end{array} \right\} \quad (5.3)$$

each type of zygote, and the mating couple, with coefficients of equations (5.2) mean frequencies in equal numbers; the mating of a mating $DR \times DR$ ent. RR .

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$$\cdot \quad \cdot \quad \cdot \quad \cdot \quad (5.4)$$

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$$\cdot \quad \cdot \quad \cdot \quad \cdot \quad (5.6)$$

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multiple mendelian inheritance, in Z has the form (5.5).

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The relation between the two algebras is given by (5.1), which means that a hypercomplex number (or linear form) (5.5) in Z is equivalent to a quadratic form (5.6) in G . The quadratic form is reduced to a hypercomplex number in G by using the multiplication table (5.2). That is to say (cf. 5.9), the zygotic representation determines the gametic; but not *vice versa*, owing to the extra degree of freedom in the zygotic algebra.

Starting from the gametic multiplication table (5.2), the equations (5.3) are built up by the following process: we take the symbols A, B, C defined by (5.1) as units of a new algebra, and then

$$\left. \begin{array}{l} A^2 = DD, DD = D, D = A, \\ B^2 = (\frac{1}{2}D + \frac{1}{2}R)^2 = \frac{1}{4}DD + \frac{1}{2}DR + \frac{1}{4}RR = \frac{1}{4}A + \frac{1}{2}B + \frac{1}{4}C, \\ AB = DD, DR = D(\frac{1}{2}D + \frac{1}{2}R) = \frac{1}{2}A + \frac{1}{2}B, \end{array} \right\} \quad (5.10)$$

and so on. Thus the zygotic multiplication table is constructed from the gametic. This is the process of duplication referred to in § 4, and Z is thus the duplicate of G .

Suppose that we wish to find the progeny distribution of two mating populations P, Q , whose representations, either gametic or zygotic, are given. We have merely to form the product of the two hypercomplex numbers; that is to say (cf. 4.4), we multiply two corresponding representations together as in ordinary algebra, substitute (5.2) or (5.3), and simplify. The validity of the process follows from the fact that it is simply a translation into symbols of the more self-explanatory procedure of chess-board diagrams: in other words, it follows from the fact that genetical multiplication obeys the distributive law.

§ 6. "SHORTCIRCUITED" MULTIPLICATION.

By a fundamental property of duplicate algebras (Etherington, 1941, Theorem I), multiplication in Z can be "shortcircuited" by working in G : that is to say, to find PQ when P and Q are given zygotically, we first apply (5.2) to obtain the gametic representations, and then multiply *without* applying (5.2). Similarly, to evaluate in Z a complicated non-associative product involving any number of factors, all the operations can be performed in the simpler algebra G , only the final product being left in quadratic form and interpreted as a hypercomplex number in Z .

This corresponds to a well-known fact in genetics (cf. Jennings, 1917, pp. 101-102): in order to obtain the zygotic frequencies of an n th generation, provided that no selection acts on the zygotes, and in the absence of inbreeding, it is sufficient to trace only the gametic frequencies through the $n-1$ intervening generations.

The interpretation is as follows: the coupled symbols (7.1) stand for the types of family into which the population can be sorted, classified according to the parental genotypes: or, we may say, they are the types of *couple* mated in the preceding generation. Hence (7.2) means that if a population of offspring of matings $A \times A$ is mated at random with itself or with a similar population, all the matings are of this type $A \times A$; but if the parental matings were all $B \times B$, then the six couple types occur in numerical proportions $\frac{1}{16} : \frac{1}{4} : \dots$; and so on.

A population for which the relative frequencies of the couple types are

$$\lambda : \mu : \nu : \theta : \phi : \psi \quad (7.3)$$

is represented by a hypercomplex number

$$(Copular representation) \quad P = \lambda AA + \mu BB + \nu CC + \theta BC + \phi CA + \psi AB, \quad (7.4)$$

wherein

$$(Normalising condition) \quad \lambda + \mu + \nu + \theta + \phi + \psi = 1. \quad (7.5)$$

From this we can pass by (5.3) and (5.1, 2) to the zygotic and gametic representations.

As in **G** and **Z**, the product of two hypercomplex numbers in **K** denoting populations gives in the same representation their offspring by random mating. This statement assumes that the couple types are not selected, *i.e.* they are of equal average surviving fertility; just as in **Z** and **G** we supposed no selection on zygotes or gametes. As before, multiplication in **K** can be short-circuited by working in **Z** or **G**.

Corresponding to the Pearson-Hardy law in the zygotic algebra, we have the following facts: a population, as a distribution of copular types, comes into equilibrium after *two* generations of amphimixis; after *one* generation, the equations

$$\theta^2 = 4\mu\nu, \quad \phi^2 = 4\nu\lambda, \quad \psi^2 = 4\lambda\mu \quad (7.6)$$

are satisfied; after two generations the further equation

$$\mu^2 = 16\nu\lambda \quad (7.7)$$

is satisfied; these four are the necessary and sufficient conditions for equilibrium in amphimixis, and imply also other relations such as

$$4\phi^2 = \theta\psi = \mu^2. \quad (7.8)$$

These results are obtained very simply by using short-circuited multiplication, observing that P^2 is necessarily of the form $(\alpha A + \beta B + \gamma C)^2$, and the next generation $P^{2.2}$ of the form $((\delta D + \rho R)^2)$.

§ 8. SYSTEMS OF MATING.

Four systems of mating will be considered. The object in each case is to obtain the distribution of types in a filial generation from the distribution in the preceding generation; also, when it can be done simply, to find the distribution in the n th filial generation, and the equilibrium distribution which this approaches as n increases. For other treatment of these and similar problems, *cf.* Jennings (1916, 1917), Wentworth and Remick (1916), Robbins (1917, 1918), Hogben (1931, Chap. 6; 1933), Geppert and Koller (1938, § 20).

(a) *Self-fertilisation, or Assortative Mating in Absence of Dominance.*

Starting from the zygotic distribution

$$P = \alpha A + \beta B + \gamma C \quad (8a.1)$$

(where $A = DD$, $B = DR$, $C = RR$), if mating proceeds in successive generations by self-fertilisation, or by each individual mating with another of the same type, the first filial generation F_1 will consist of the offspring of $A \times A$, $B \times B$, $C \times C$, occurring in proportions $\alpha : \beta : \gamma$; so that

$$F_1 = \alpha A^2 + \beta B^2 + \gamma C^2. \quad (8a.2)$$

$$= \alpha A + \beta(\frac{1}{4}A + \frac{1}{2}B + \frac{1}{4}C) + \gamma C. \quad (8a.3)$$

$$= (\alpha + \frac{1}{4}\beta)A + \frac{1}{2}\beta B + (\frac{1}{4}\beta + \gamma)C. \quad (8a.4)$$

It will be seen that the frequency of heterozygotes is halved; so if the n th filial generation is denoted

$$F_n = \alpha_n A + \beta_n B + \gamma_n C, \quad (8a.5)$$

we shall have

$$\beta_1 = \frac{1}{2}\beta, \quad \beta_2 = \frac{1}{4}\beta, \quad \beta_3 = \frac{1}{8}\beta, \quad \dots, \quad \beta_n = \frac{1}{2^n}\beta. \quad (8a.6)$$

Also

$$\alpha_1 = \alpha + \frac{1}{4}\beta, \quad \gamma_1 = \frac{1}{4}\beta + \gamma. \quad (8a.7)$$

Let us find the quantities u_1, u_2, u_3, \dots by which the hypercomplex number representing the population increases in the successive generations. We have from (8a.1) and (8a.4):

$$u_1 = F_1 - P = \frac{1}{2}\beta(\frac{1}{2}A - B + \frac{1}{2}C); \quad (8a.8)$$

and similarly we shall have

$$u_2 = \frac{1}{2}\beta_1(\frac{1}{2}A - B + \frac{1}{2}C) = \frac{1}{4}\beta(\frac{1}{2}A - B + \frac{1}{2}C),$$

$$u_3 = \frac{1}{8}\beta(\frac{1}{2}A - B + \frac{1}{2}C), \quad \dots, \quad u_n = \frac{1}{2^n}\beta(\frac{1}{2}A - B + \frac{1}{2}C). \quad (8a.9)$$

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$$u_1 + u_2 + u_3 + \dots + u_n = \left(\frac{1}{2} + \frac{1}{4} + \frac{1}{8} + \dots + \frac{1}{2^n} \right) \beta \left(\frac{1}{2}A - B + \frac{1}{2}C \right). \quad (8a.10)$$

The sum of the geometrical progression in brackets is $1 - (\frac{1}{2})^n$. Hence the n th filial generation is

$$F_n = aA + \beta B + \gamma C + \left(1 - \frac{1}{2^n} \right) \beta \left(\frac{1}{2}A - B + \frac{1}{2}C \right) \quad (8a.11)$$

$$= \left(a + \frac{1}{2}\beta - \frac{1}{2^{n+1}}\beta \right) A + \frac{1}{2^n}\beta B + \left(\frac{1}{2}\beta + \gamma - \frac{1}{2^{n+1}}\beta \right) C. \quad (8a.12)$$

As the number of generations increases, this quickly approaches the limiting stable distribution

$$(a + \frac{1}{2}\beta)A + (\gamma + \frac{1}{2}\beta)C. \quad (8a.13)$$

(b) *Assortative Mating* (*Dominants* \times *Dominants*, *Recessives* \times *Recessives*).

The initial zygotic distribution

$$P = aA + \beta B + \gamma C \quad (8b.1)$$

may be written phenotypically

$$P = (a + \beta)\mathfrak{D} + \gamma C, \quad (8b.2)$$

Here

$$\mathfrak{D} = \frac{a}{a + \beta}A + \frac{\beta}{a + \beta}B = \frac{aA + \beta B}{a + \beta}, \quad (8b.3)$$

representing the genotype distribution of the dominants in P .

With the system of mating under consideration, the first filial generation is

$$F_1 = (a + \beta)\mathfrak{D}^2 + \gamma C^2 \quad (8b.4)$$

$$= \frac{(aA + \beta B)^2}{a + \beta} + \gamma C^2. \quad (8b.5)$$

Therefore

$$\begin{aligned} (a + \beta)F_1 &= (a^2A^2 + 2a\beta AB + \beta^2B^2) + (a + \beta)\gamma C^2 \\ &= a^2A + 2a\beta(\frac{1}{2}A + \frac{1}{2}B) + \beta^2(\frac{1}{4}A + \frac{1}{2}B + \frac{1}{4}C) + (a + \beta)\gamma C \\ &= (a^2 + a\beta + \frac{1}{4}\beta^2)A + (a\beta + \frac{1}{2}\beta^2)B + (\frac{1}{4}\beta^2 + a\gamma + \beta\gamma)C. \end{aligned} \quad (8b.6)$$

It will be found that $F_1 - P$ is a multiple of $\frac{1}{2}A - B + \frac{1}{2}C$, and hence that F_n can be found by summation of a series, just as in Case (a). The series in this case is not a geometrical progression, but it is of a type whose sum is easily obtained. Following the procedure of Case (a), it will be found that the total increase in n generations can be expressed as

$$\begin{aligned}
& \left\{ \frac{\frac{1}{2}\beta}{(a+\frac{1}{2}\beta)(a+\beta)} + \frac{\frac{1}{2}\beta}{(a+\beta)(a+\frac{3}{2}\beta)} + \dots + \frac{\frac{1}{2}\beta}{(a+\frac{1}{2}n\beta)(a+\frac{1}{2}(n+1)\beta)} \right\} \beta(a+\frac{1}{2}\beta)(\frac{1}{2}A-B+\frac{1}{2}C) \\
&= \left\{ \left(\frac{1}{a+\frac{1}{2}\beta} - \frac{1}{a+\beta} \right) + \left(\frac{1}{a+\beta} - \frac{1}{a+\frac{3}{2}\beta} \right) + \dots + \left(\frac{1}{a+\frac{1}{2}n\beta} - \frac{1}{a+\frac{1}{2}(n+1)\beta} \right) \right\} \beta(a+\frac{1}{2}\beta)(\frac{1}{2}A-B+\frac{1}{2}C) \\
&= \left\{ \frac{1}{a+\frac{1}{2}\beta} - \frac{1}{a+\frac{1}{2}(n+1)\beta} \right\} \beta(a+\frac{1}{2}\beta)(\frac{1}{2}A-B+\frac{1}{2}C) \\
&= \left\{ \beta - \frac{\beta(a+\frac{1}{2}\beta)}{a+\frac{1}{2}(n+1)\beta} \right\} (\frac{1}{2}A-B+\frac{1}{2}C). \quad (8b.7)
\end{aligned}$$

The n th filial generation is obtained by adding (8b.7) to (8b.1). We obtain

$$\begin{aligned}
F_n &= aA + \beta B + \gamma C + \beta(\frac{1}{2}A - B + \frac{1}{2}C) - \frac{\beta(a+\frac{1}{2}\beta)}{a+\frac{1}{2}(n+1)\beta}(\frac{1}{2}A - B + \frac{1}{2}C) \\
&= (a+\frac{1}{2}\beta)A + (\frac{1}{2}\beta + \gamma)C - \frac{\beta(a+\frac{1}{2}\beta)}{a+\frac{1}{2}(n+1)\beta}(\frac{1}{2}A - B + \frac{1}{2}C). \quad (8b.8)
\end{aligned}$$

As n increases, the fraction with $a+\frac{1}{2}(n+1)\beta$ in the denominator approaches zero. Hence F_n approaches a stable distribution, namely, $(a+\frac{1}{2}\beta)A + (\frac{1}{2}\beta + \gamma)C$, the same as in Case (a). (Cf. 8a.13.)

(c) Fraternal Mating.

In this and the following case it is necessary to use the copular representation (7.4), from which of course the zygotic representation can be deduced. The determination of F_n is much more difficult than in Cases (a) and (b). It is best obtained with the aid of matrix algebra; and as this is beyond the scope of this paper, I content myself with showing only in each case how the copular representation of any generation is deduced from the preceding.

Suppose that initially

$$P = \lambda AA + \mu BB + \nu CC + \theta BC + \phi CA + \psi AB, \quad (8c.1)$$

and that brothers and sisters are mated at random. Then the filial generation is

$$F_1 = \lambda(AA)^2 + \mu(BB)^2 + \nu(CC)^2 + \theta(BC)^2 + \phi(CA)^2 + \psi(AB)^2. \quad (8c.2)$$

Using short-circuited multiplication (*i.e.* (5.3) instead of (7.2)),

$$\begin{aligned}
F_1 &= \lambda(A)^2 + \mu(\frac{1}{4}A + \frac{1}{2}B + \frac{1}{4}C)^2 + \nu(C)^2 + \theta(\frac{1}{2}B + \frac{1}{2}C)^2 + \phi(B)^2 + \psi(\frac{1}{2}A + \frac{1}{2}B)^2 \\
&= \lambda AA + \mu(\frac{1}{16}AA + \frac{1}{4}BB + \frac{1}{16}CC + \frac{1}{4}BC + \frac{1}{8}CA + \frac{1}{4}AB) + \nu CC \\
&\quad + \theta(\frac{1}{4}BB + \frac{1}{2}BC + \frac{1}{4}CC) + \phi BB + \psi(\frac{1}{4}AA + \frac{1}{2}AB + \frac{1}{4}BB) \\
&= (\lambda + \frac{1}{16}\mu + \frac{1}{4}\psi)AA + (\frac{1}{4}\mu + \frac{1}{4}\theta + \phi + \frac{1}{4}\psi)BB + (\frac{1}{16}\mu + \nu + \frac{1}{4}\theta)CC \\
&\quad + (\frac{1}{4}\mu + \frac{1}{2}\theta)BC + \frac{1}{8}\mu CA + (\frac{1}{4}\mu + \frac{1}{2}\psi)AB. \quad (8c.3)
\end{aligned}$$

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$$= \lambda AA + \mu$$

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(d) Filial Mating.

Starting from an arbitrary copular distribution as in (c), suppose that each individual (or each individual of one sex) is mated with the parent of opposite sex. Then

$$\begin{aligned} F_1 &= \lambda AA.A + \mu BB.B + \nu CC.C + \theta BC.(\frac{1}{2}B + \frac{1}{2}C) + \phi CA.(\frac{1}{2}C + \frac{1}{2}A) \\ &\quad + \psi AB.(\frac{1}{2}A + \frac{1}{2}B) \quad (8d.1) \\ &= \lambda A.A + \mu(\frac{1}{4}A + \frac{1}{2}B + \frac{1}{4}C)B + \nu C.C + \theta(\frac{1}{2}B + \frac{1}{2}C)^2 + \phi B(\frac{1}{2}C + \frac{1}{2}A) + \psi(\frac{1}{2}A + \frac{1}{2}B)^2 \\ &= \lambda AA + \mu(\frac{1}{4}AB + \frac{1}{2}BB + \frac{1}{4}BC) + \nu CC + \theta(\frac{1}{4}BB + \frac{1}{2}BC + \frac{1}{4}CC) \\ &\quad + \phi(\frac{1}{2}BC + \frac{1}{2}AB) + \psi(\frac{1}{4}AA + \frac{1}{2}AB + \frac{1}{4}BB) \\ &= (\lambda + \frac{1}{4}\psi)AA + (\frac{1}{2}\mu + \frac{1}{4}\theta + \frac{1}{4}\psi)BB + (\nu + \frac{1}{4}\theta)CC + (\frac{1}{4}\mu + \frac{1}{2}\theta + \frac{1}{2}\phi)BC \\ &\quad + \phi.CA + (\frac{1}{4}\mu + \frac{1}{2}\phi + \frac{1}{2}\psi)AB. \quad (8d.2) \end{aligned}$$

§ 9. COMPACT MULTIPLICATION TABLES.

If P and Q are any two normalised hypercomplex numbers in \mathbf{G} (say $\delta D + \rho R$, $\delta'D + \rho'R$, where $\delta + \rho = \delta' + \rho' = 1$), then

$$PQ = \frac{1}{2}P + \frac{1}{2}Q. \quad (9.1)$$

This may be shown directly by multiplying and applying (5.2); or more briefly by observing that $\frac{1}{2}P + \frac{1}{2}Q$ is also normalised, so that by (6.5)

$$\begin{aligned} P^2 &= P, \quad Q^2 = Q, \\ \frac{1}{2}P + \frac{1}{2}Q &= (\frac{1}{2}P + \frac{1}{2}Q)^2 = \frac{1}{4}P^2 + \frac{1}{2}PQ + \frac{1}{4}Q^2 = \frac{1}{4}P + \frac{1}{2}PQ + \frac{1}{4}Q, \end{aligned}$$

from which (9.1) follows.

The result (9.1) may be regarded as a compact form of the gametic multiplication table, since it includes the three equations (5.2) as special cases. (It must be noted that (9.1) only applies if P, Q are normalised. The more general result is: $PQ = \frac{1}{2}(\delta' + \rho')P + \frac{1}{2}(\delta + \rho)Q$.)

It will be convenient to use the letters a, b, c, \dots to denote each either D or R, and then the compact multiplication table may be written

$$ab = \frac{1}{2}a + \frac{1}{2}b. \quad (9.2)$$

Applying to this the process of duplication, we obtain

$$ab.cd = (\frac{1}{2}a + \frac{1}{2}b)(\frac{1}{2}c + \frac{1}{2}d),$$

i.e.

$$ab.cd = \frac{1}{4}ac + \frac{1}{4}ad + \frac{1}{4}bc + \frac{1}{4}bd, \quad (9.3)$$

which gives a compact form of the zygotic multiplication table: for it includes all the six equations (5.3) as special cases. *E.g.* on putting $a=c=D$, $b=d=R$, we get from (9.3) the formula for B^2 .

Similarly, the compact copular multiplication table is

$$ab.cd : ef.gh = \frac{1}{16}(a+b)(c+d)(e+f)(g+h),$$

i.e.

$$ab.cd : ef.gh = \frac{1}{16}ac.eg + \frac{1}{16}ac.eh + \dots \quad (16 \text{ terms}), \quad (9.4)$$

which includes the 21 equations (7.2).

§ 10. OFFSPRING OF CONSANGUINEOUS MARRIAGES.

Formulae for the probability of RR offspring of various kinds of consanguineous marriages were given by Dahlberg (1929), and his verbal arguments may be translated into non-associative algebra. As an example, consider the distribution of genotypes DD, DR, RR in the offspring of a marriage between first cousins. This distribution will be found from a non-associative product of the form

$$ab.cd : ef : ab.cd : gh. \quad (10.1)$$

Here each of the letters stands for either D or R; ab and cd denote the genetic constitutions of the common grandparents of the cousins; the two sibs, parents of cousins, are both represented by $ab.cd$; and the cousins themselves by $ab.cd : ef$ and $ab.cd : gh$ respectively.

Simplifying (10.1) by repeated use of (9.1), we have

$$\begin{aligned} ab.cd : ef &= \left\{ \frac{1}{2} \left(\frac{a+b}{2} + \frac{c+d}{2} \right) \right\} \frac{e+f}{2} = \left(\frac{a+b+c+d}{4} \right) \left(\frac{e+f}{2} \right) \\ &= \frac{1}{2} \left(\frac{a+b+c+d}{4} + \frac{e+f}{2} \right) = \frac{1}{8}(a+b+c+d+2e+2f). \end{aligned}$$

Similarly,

$$ab.cd : gh = \frac{1}{8}(a+b+c+d+2g+2h).$$

Therefore

$$ab.cd : ef : ab.cd : gh = \frac{1}{84}(a^2+b^2+c^2+d^2+60 \text{ product terms}). \quad (10.2)$$

We must now take into account whatever information is given about the genetic constitution of the four grandparents. We might, for example, be given the genotype of one of them. Assuming, however, that they are merely random members of a stable population,

$$P = \delta^2 DD + 2\delta\rho DR + \rho^2 RR = \delta D + \rho R, \quad (\delta + \rho = 1)$$

then the probability of a being D or R is δ or ρ , and so for each of the ancestral gametes. Hence (10.2) yields for the offspring of first cousins the probability distribution

$$\begin{aligned} \frac{1}{84} \{ (4\delta + 60\delta^2) DD + 60\delta\rho DR + (4\rho + 60\rho^2) RR \} \\ = \left(\frac{1}{18}\delta + \frac{1}{18}\delta^2 \right) DD + \frac{1}{8}\delta\rho DR + \left(\frac{1}{18}\rho + \frac{1}{18}\rho^2 \right) RR, \quad (10.3) \end{aligned}$$

agreeing with Dahlberg's result.

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§ 11. FURTHER GENETIC ALGEBRAS.

Consider inheritance depending on two pairs of autosomal allelomorphs, say D, R and D', R' . The corresponding gametic algebras \mathbf{G}, \mathbf{G}' have multiplication tables:

$$\left. \begin{array}{lll} D^2 = D, & DR = \frac{1}{2}D + \frac{1}{2}R, & R^2 = R; \\ D'^2 = D', & D'R' = \frac{1}{2}D' + \frac{1}{2}R', & R'^2 = R'. \end{array} \right\} \quad (11.1)$$

Taking both pairs into account, there are four gametic types:

$$DD', \quad DR', \quad RD', \quad RR', \quad (11.2)$$

whose multiplication table is constructed as follows:—

$$\left. \begin{array}{l} DD'.DD' = D^2, D'^2 = DD', \\ DD'.DR' = D^2, D'R' = D(\frac{1}{2}D' + \frac{1}{2}R') = \frac{1}{2}DD' + \frac{1}{2}DR', \\ DR'.RD' = DR, D'R' = (\frac{1}{2}D + \frac{1}{2}R)(\frac{1}{2}D' + \frac{1}{2}R') = \frac{1}{4}DD' + \frac{1}{4}DR' + \frac{1}{4}RD' + \frac{1}{4}RR', \end{array} \right\} \quad (11.3)$$

and so on. (10 equations.)

(It will be seen that although multiplication is non-associative we assume, *e.g.*, $DD'.DR' = D^2.D'R'$. This is justified because the combination of dashed and undashed symbols is mere juxtaposition, not genetical multiplication.) This is precisely the process referred to in § 4 of forming the direct product of the two algebras \mathbf{G}, \mathbf{G}' , which is well known in the theory of linear algebras.

Alternatively, let us use a, b to denote each either D or R , and a', b' similarly for D' or R' , so that, for example, aa' can denote any of the four gametic types. Then we can write the joint multiplication table in the compact form:

$$aa'.bb' = ab.a'b' = (\frac{1}{2}a + \frac{1}{2}b)(\frac{1}{2}a' + \frac{1}{2}b'), \quad (11.4)$$

i.e.

$$aa'.bb' = \frac{1}{4}aa' + \frac{1}{4}ab' + \frac{1}{4}ba' + \frac{1}{4}bb'. \quad (11.5)$$

The zygotic algebra is obtained by duplicating the gametic, and is the direct product \mathbf{ZZ}' . That is to say, it is immaterial whether the process of duplication is carried out before or after that of forming the direct product (Etherington, 1941, Theorem V). There is one point, in this connection, which requires elucidation. It has been pointed out that by pairing the four gametic types (11.2) we obtain the ten types of zygote, namely:

$$\begin{array}{llll} DD'.DD', & DD'.DR', & DD'.RD', & DD'.RR', \\ & DR'.DR', & DR'.RD', & DR'.RR', \\ & RD'.RD', & RD'.RR', & RR'.RR', \end{array} \quad (11.6)$$

which figure in (11.3). There are, however, only nine genotypes, namely:

$$\begin{array}{llll} DDD'D', & DDD'R', & DDR'R', & DRD'D', \\ & DRD'R', & DRR'R', & RRD'D', \\ & & RRD'R', & RRR'R', \end{array} \quad (11.7)$$

there being no distinction between the double heterozygotes $DD' \cdot RR'$ and $DR' \cdot RD'$, which both give rise to the genotype $DRD'R'$. The fact is that for calculating progeny distributions it is really optional whether we use the *zygotic algebra* based on the ten zygotic types (11.6), or the *genotypic algebra* based on the nine genotypes (11.7). The latter is obtained from the former simply by suppressing the distinction between $DD' \cdot RR'$ and $DR' \cdot RD'$. To geneticists the genotypic algebra would seem to be the obvious one to use; but the zygotic algebra is mathematically much simpler—firstly, because it is a direct product of simpler algebras; secondly, because it is a duplicate algebra; thirdly, because its multiplication table can be written in the compact form (11.5). In the final interpretation of any results obtained by use of the zygotic algebra, the distinction between the equivalent double heterozygotic types can be suppressed; just as with any zygotic or genotypic algebra, in the final interpretation of any calculation, the distinction between genotypes which are the same phenotype may be dropped in order to obtain a result true for phenotypes.

Some genetic algebras representing more complicated types of symmetrical inheritance were considered in G.A., including (§ 14) a group of three linked series of multiple allelomorphs, and (§ 15) inheritance in tetraploids. These algebras can all be manipulated on the lines illustrated for simple mendelian inheritance, the extra complication being to some extent offset by the consistent use of compact multiplication tables. As long as only symmetrical inheritance is considered, and zygotic types (differing in their gametic formation) are used rather than genotypes (differing in their relevant gene content), the corresponding gametic, zygotic and copular algebras are related by duplication; and two or more independent genetic algebras of the same kind (**G**, **Z** or **K**) can be combined by forming their direct product.

Let us finally consider briefly an *unsymmetrical* genetic algebra, *i.e.* representing inheritance which is not symmetrical in the sexes.

Consider a single gene difference D , R on the X-chromosome in a species where the male is heterogametic. The gametic types are

$$\text{Ova, } D, R; \quad \text{Sperm, } D, R, Y; \dots \quad (11.8)$$

and the zygotic types with the gametes which they produce give the multiplication rules:

$$\left. \begin{array}{l} \text{Female, } a \equiv DD = D, \quad b \equiv DR = \frac{1}{2}D + \frac{1}{2}R, \quad c \equiv RR = R; \\ \text{Male, } d \equiv DY = \frac{1}{2}D + \frac{1}{2}Y, \quad e \equiv RY = \frac{1}{2}R + \frac{1}{2}Y. \end{array} \right\} \quad (11.9)$$

Hence $ad = D(\frac{1}{2}D + \frac{1}{2}Y)$, $bd = (\frac{1}{2}D + \frac{1}{2}R)(\frac{1}{2}D + \frac{1}{2}Y)$, and so on; whence we have the zygotic multiplication table:

heterozygotes $DD' \cdot RR'$
 genotype $DRD'R'$. The fact
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ch they produce give the

$$\left. \begin{array}{l} R, \quad c \equiv RR = R; \\ \frac{1}{2}R + \frac{1}{2}Y. \end{array} \right\} \quad (11.9)$$

$\frac{1}{2}Y$), and so on; whence

$$\left. \begin{array}{lll} ad = \frac{1}{2}a + \frac{1}{2}d, & bd = \frac{1}{4}a + \frac{1}{4}b + \frac{1}{4}d + \frac{1}{4}e, & cd = \frac{1}{2}b + \frac{1}{2}e, \\ ae = \frac{1}{2}b + \frac{1}{2}d, & be = \frac{1}{4}b + \frac{1}{4}c + \frac{1}{4}d + \frac{1}{4}e, & ce = \frac{1}{2}c + \frac{1}{2}e. \end{array} \right\} \quad (11.10)$$

Since two males or two females produce no offspring, we must write also

$$a^2 = b^2 = c^2 = d^2 = e^2 = ab = bc = ca = de = 0.$$

It will be seen that the zygotic algebra is not obtained entirely by the process of duplication, since this would give, *e.g.*, $a^2 = a$. If a population is denoted

$$P = aa + \beta b + \gamma c + \delta d + \epsilon e, \quad (11.11)$$

and the male and female components are normalised separately:

$$a + \beta + \gamma = \delta + \epsilon = 1, \quad (11.12)$$

and if Q is another population represented in the same manner, then the product PQ describes the population of offspring, and will be automatically normalised.

An equally satisfactory scheme is to write instead of (11.9)

$$\left. \begin{array}{lll} a \equiv DD = D, & b \equiv DR = \frac{1}{2}D + \frac{1}{2}R, & c \equiv RR = R, \\ d \equiv DY = D + Y, & e \equiv RY = R + Y, \end{array} \right\} \quad (11.13)$$

giving

$$ad = a + d, \quad bd = \frac{1}{2}a + \frac{1}{2}b + \frac{1}{2}d + \frac{1}{2}e, \quad \text{etc.} \quad (11.14)$$

We deal in this case with the female and male components of a population separately:

$$F = aA + \beta b + \gamma c, \quad M = \delta d + \epsilon e. \quad (a + \beta + \gamma = \delta + \epsilon = 1.) \quad (11.15)$$

The offspring by random mating is given by their product, separated similarly into two components.

The numerical coefficients which appear on the right sides of (11.14) correspond to the asymmetrical extensors of Hogben's matrix notation (1933), just as the coefficients in (5.3) correspond to the symmetrical extensors.

SUMMARY.

The sign \times is used by geneticists to indicate crossing of types. Literal interpretation of this as a symbol of multiplication leads to a type of algebra in which the associative law $P \times (Q \times R) = (P \times Q) \times R$ is not obeyed. The different "algebras" which in this way correspond to the various possible modes of inheritance known in genetics are therefore necessarily different from the algebra of ordinary numbers. They are of a kind known as "linear algebras," and it is shown that various genetical problems can be conveniently treated by means of a symbolism based on this fact.

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