THE NUMERICAL RESULTS OF DIVERSE SYSTEMS OF BREEDING, WITH RESPECT TO TWO PAIRS OF CHARACTERS, LINKED OR INDEPENDENT, WITH SPECIAL RELATION TO THE EFFECTS OF LINKAGE[1]

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[Received October 23, 1916]

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I. GENERAL, DEFINITIONS, METHODS

In an earlier paper (JENNINGS 1916) the present author has given formulae for the results of various systems of breeding, with respect to a single pair of characters.[1] When more than one pair are considered, the distribution of characters that Mendelism seemed to give has been greatly modified by the further discovery that characters may be linked. A first and perhaps practically most important step in determining the actual distribution is to deal numerically with two pairs of characters, linked or independent; this is what the present paper undertakes. The problem is to discover formulae which for a given system of breeding will give in later generations the proportions of the different classes of individuals (zygotes) with respect to two pairs of characters, when we know the constitution of the original progenitors. The present paper deals with: random mating; selection with respect to a single character (dominant or recessive); assortative mating with respect to a single character; and self-fertilization. Inbreeding is reserved for separate treatment. Only typical characters, not sex-linked, are dealt with.

(1) DESIGNATION OF FACTORS

The two members of a pair of alternative factors will be designated *A* and *a;* of a second pair, *B* and *b,* the capital letter representing in

[1] Certain points in this earlier paper require mention or correction:

(1) In section (8), page 65, the values given for *AA, aa* and *Aa,* hold for *any* later generation; the constitution of the population does not change with later matings, as stated in the text. This was pointed out to me independently by Dr. C. H. DANFORTH and by Dr. SEWELL WRIGHT. A slip with this correction was enclosed with the reprints distributed. [In the meantime the matter has been fully discussed by WENTWORTH and REMICK (1916).—*Note added in correcting the proof.*]

(2) Essentially the formulae of sections (35) and (36), page 73, had been given by DETLEFSEN (1914, p. 95). DETLEFSEN includes in *n* the first cross, so that his formulae are stated in slightly different terms. I regret that I overlooked DETLEFSEN's work, which contains much of great interest on the theoretical results of continued inbreeding.

(3) In the example under section (28), page 70, the value for *aa* should be 85/144 in place of 91/144.

(4) In table 1, series L, under "How formed," read "$B_n\ F_{n-1}\ G_{n-1}$."

each case the dominant factor. *In giving the constitution of an individual the juxtaposition of the letters will indicate the constitution of the gametes from which the individual was formed, and consequently at the same time the linkage,* if there is linkage. Thus the individual *ABab* is formed from the gametes *AB* and *ab,* and if there is linkage, this is between *A* and *B* on the one hand, between *a* and *b* on the other. The individual *AbaB* was formed from the gametes *Ab* and *aB,* and the linkage, if any, is between *A* and *b* on the one hand, *a* and *B* on the other.

(2) LINKAGE; DESIGNATION OF THE LINKAGE RATIO *r*

When two pairs of factors are dealt with, these may be independent or linked. In the former case any possible combination of the two pairs occurs in the gametes as frequently as any other. But when two factors are linked, the combinations found in the gametes which produced the given parents occur in the gametes produced by those parents more frequently than do other combinations. Thus, if the individual *ABab* was produced by union of the two gametes *AB* and *ab,* then when this individual forms gametes, there will be more gametes of the constitutions *AB* and *ab* than of the constitutions *Ab* and *aB*.

We shall designate the linkage ratio by the letter *r*. This number *r* indicates therefore the number of gametes showing the same combination of factors that occurred in the foregoing generation of gametes, in proportion to 1 showing other combinations. Thus, if in the case just cited, there are produced 3 gametes of the constitution *AB* (or *ab*) to 1 of *Ab* (or *aB*), the value of the linkage ratio *r* is 3. It is practically important to observe that for the working out of numerical proportions, "independence" of factors is merely a special case of linkage,—the particular case in which the value of the linkage ratio *r* is 1. Thus, if we derive general formulae for the results of linkage, these will include also the results when the factors are independent; in the latter case for numerical results it will merely be necessary to give to the letter *r* the value 1. As is well known, the value of *r*, the linkage ratio, may vary in different cases from 1 up to 80 or 100, or more.

In certain known cases, where linkage occurs, it is complete in one sex, the two factors involved acting in that sex like a single one. Thus, from the parent *ABab* there are produced in one sex but two sorts of gametes, *AB* and *ab,* in equal proportions, while the other sex gives *r AB* : 1 *Ab* : 1 *aB* : *r ab*. It is not certain that this completeness of the linkage in one sex holds for all organisms, so that we shall deal both with this case, and the case in which linkage is the same in both sexes.

The relative frequency with which the different gametes are formed of course affects the frequency with which individuals (zygotes) with particular combinations of factors appear in the next generation. Our task is to discover general formulae for the proportions of the different classes of zygotes with respect to two characters, whatever the degree of linkage; formulae from which numerical results are obtainable when the proper values are substituted for r. The solution of this problem is quite independent of the question of the cause of linkage. It merely requires that there shall be in each case some fairly constant average ratio between the number of gametes which show the original combinations and those which show the new combinations; the work of many investigators has shown that this is the case.

When two pairs of factors are dealt with, whether linked or independent, it is not possible from a knowledge of the constitution of the zygotes with respect to each pair taken separately, to tell how the two pairs will be combined; the rules of combination must be worked out for themselves. This principle will receive illustration in the present paper (see section (21)).

(3) METHOD

With respect to two pairs of factors there are 4 diverse sorts of gametes, *AB, Ab, aB* and *ab*. The combinations of these 4 kinds of gametes give 10 diverse kinds of zygotes; these and their origin from the gametes are illustrated in table 6. Owing to this considerable number of diverse kinds of zygotes, direct formulae for the zygotes of a later generation in terms of those of an earlier generation become complex, unless we begin with parents of a single simple type. On this account it is, wherever possible, simpler to break the computation into two steps: (1) to obtain the proportions of the four different kinds of gametes derivable from the given zygotes; (2) from the gametic proportions thus reached, the proportions of the different sorts of zygotes for the next generation are obtained. We shall therefore present formulae for each of these steps, and the computations for any particular case will usually require the use of both these formulae, save in special cases where it is possible to develop single, more comprehensive, formulae.

This method of proceeding by two steps (first finding the gametes, then from these the zygotes) depends upon the principle that *random mating of zygotes gives the same results as random mating of the* *gametes which they produce.* The particular way in which the gametes have been united in the parental zygotes does not affect the results of random mating. This principle is easily demonstrated algebraically.

Where the mating is not at all at random, as in self-fertilization, the principle cannot be employed; we must devise formulae for the direct transformation of one generation of zygotes into a later one.

(4) TWO CLASSES OF FORMULAE; GENERAL AND SPECIAL

Two classes of formulae are obtainable:

General formulae for transforming generation n into generation n + 1. One class is of *general* application, so that whatever the constitution of the parental population, by means of the formulae the constitution of the population in later generations is obtainable. For example, the original population may be composed of diverse individuals in the proportions 3 *ABAB* + 1 *abab* + 1 *AbaB* + 4 *ABaB*, and we may desire to know the constitution of the population in some later generation after breeding by random mating or assortative mating, or the like. Such general formulae can as a rule be given only for determining the constitution of the next following generation; the formulae can then be reapplied for determining the constitution of the next generation, and so on indefinitely. Thus such general formulae may be characterized as formulae for transforming generation *n* into generation *n* + 1.

Special formulae for parents ABab, etc. The second class consists of special formulae, for important particular cases, the main such case being that in which the original parents are all alike and are of the type *ABab* or *AbaB*. For such parents, which represent the case to which the formulae will most commonly be applied, it is possible, for some systems of breeding, to obtain formulae that will give directly the constitution of the population in any later generation, without working out the constitution in the intervening generations. For example, if the original progenitors are *ABab,* we may by a proper formula determine at once what will be the constitution of the population after seven successive random matings, or ten successive self-fertilizations, or the like.

(5) ORDER OF TREATMENT

We shall first set forth the different classes of zygotes and gametes with respect to two pairs of factors, and propose algebraic designations for the proportional numbers in which each occurs in any case.

We shall then take up the derivation of the general and special formulae for each system of breeding, dealing separately with the cases in which linkage is the same in the formation of both sorts of gametes, and that in which linkage is complete in forming one of the sets of gametes. The formulae derived will be grouped in a series of numbered tables, which for convenience of reference will be placed all together at the end of the paper.

(6) CLASSES OF ZYGOTES WITH RESPECT TO TWO PAIRS OF FACTORS, AND THEIR DESIGNATIONS

With respect to two pairs of factors, and having regard to linkage, there are ten diverse types of zygotes, the origin of which is illustrated in table 6. Any or all of these ten types may be included, in various proportions, in any population. The proportional numbers of these various classes of zygotes in any generation will be designated by the letters c to l, with the significations shown in table 1 (page 141). In table 1 we classify as homozygotes those that are homozygotic with respect to both pairs of factors; as heterozygotes those heterozygotic with respect to both pairs of factors; as mixed those homozygotic with respect to one pair, heterozygotic with respect to the other. Any population may be represented by table 1, when proper values are given to the letters c to l.

In the later treatment the letters c to l will be used to designate in brief the proportions of the various types of zygotes to which the given letter is assigned in this table 1; thus, g will be understood to signify always the number of zygotes having the constitution *ABab*; j the number of *ABaB*, etc. In specific cases the values of c to l will be diverse. Thus in the population composed of 3 *ABAB* + 1 *abab* + 1 *AbaB* + 4 *ABaB*, the value of c is 3, $f = 1$, $h = 1$, $j = 4$, while the value of the other letters is 0.

(7) CLASSES OF GAMETES WITH RESPECT TO TWO PAIRS OF FACTORS, AND THEIR DESIGNATIONS

There are four classes of gametes with respect to two pairs of factors. We shall designate their (relative) numbers in any given case by the letters p, q, s and t, with the significations shown in table 2 (page 141).

As in the case of the zygotes, so here, the letter p will at times be used by itself to designate the number of gametes of the type *AB*, q the number of *Ab*, etc.

II. RANDOM MATING

We shall first obtain formulae for the proportional numbers of the different sorts of gametes produced by any population of zygotes (of generation n) ; these will be the gametes for producing generation $n + 1$.

Next we shall get formulae for the zygotes (of generation $n + 1$) resulting from the random mating of this (or of any) set of gametes.

Third, we shall develop formulae by which the proportions of the *gametes* for the next following generation may be obtained when we know the proportions of the gametes for the foregoing generation,—so that the proportions of the zygotes may be omitted from consideration until the generation is reached for which the zygotic proportions are desired.

Finally we shall take up special formulae for particularly important cases, such as that in which the original parents are all *ABab* or *AbaB*.

DERIVATION OF THE PROPORTIONS OF THE DIFFERENT KINDS OF GAMETES PRODUCED BY ANY KNOWN SET OF ZYGOTES

Any population of zygotes may be represented in the way shown in table 1, by giving proper values to $c \ldots l$. Our present question is: What will be the relative numbers of the four different sorts of gametes produced by such a population? Or since the relative proportions of the four sorts of gametes are designated by the letters p, q, s and t (table 2), what we require is to derive the values of p, q, s and t in terms of c to l (of table 1).

In deriving the gametes from the zygotes, it is to be remembered that the original gametic union that produced the zygotes of table 1 (and hence the linkage), is indicated by the juxtaposition of the letters, and that the linkage ratio is r.

(8) LINKAGE RATIO $= r$

Taking first one of the heterozygotes, as *ABab*, the gametes are $r\ AB : 1\ Ab : 1\ aB : r\ ab$. In order to realize these proportions it is evidently necessary that each such zygote should produce $2r + 2$ gametes. To keep the proportions correct throughout, each gamete of table 1, whatever its constitution, must be considered to produce $2r + 2$ gametes, although from a homozygote these will all be alike, and from a mixed zygote there will be but two sorts, in equal numbers. We shall therefore find that the zygotes of table 1 give the gametes shown in the first column of table 3.

Having obtained table 3, we collect from the column "linkage $= r$" the various values for each of the four kinds of gametes *AB, Ab, aB* and *ab*. As in table 2, the total values for the different kinds are to be designated p, q, s and t, respectively. By collecting we obtain table 4.

(9) LINKAGE COMPLETE

In the case that the linkage is complete in forming one of the sets of gametes, the proportions of the gametes of that set will not be those in table 4. Where linkage is complete, each parent zygote produces but two kinds of gametes in equal number,—these being the same two kinds by which this parent was formed. Thus the individual *ABab* produces gametes *AB* and *ab* in equal numbers; the individual *AbaB* produces *Ab* and *aB*, etc. To get the correct proportions throughout we require to assume only that each zygote produces two gametes. The results are given in the second column of table 3. Collecting the values for the four sorts of gametes, and calling their proportions, when linkage is complete, by the capital letters P, Q, S and T, in place of the corresponding small letters, we obtain table 5.

(10) DETERMINATION OF THE PROPORTIONS OF THE DIFFERENT CLASSES OF ZYGOTES PRODUCED BY THE RANDOM MATING OF ANY SET OF GAMETES

The population at the beginning is that shown in table 1 (which of course represents any population whatever, if the correct values are given to the letters c to l). The proportions of the gametes (that is, the values of p, q, s and t) are determined by table 4.

Having thus obtained the values of p, q, s and t, we must next observe the zygotes produced by the random mating of the four sets of gametes, $p \, . \, AB$, $q \, . \, Ab$, $s \, . \, aB$ and $t \, . \, ab$. The mating and results are represented in table 6.

It will be observed that of the resulting zygotes (table 6), the four forming the diagonal from the left upper corner to the right lower corner are homozygotes; the four forming the other diagonal are heterozygotes, and the other eight are mixed. The zygotes resulting from the first random mating ($n = 1$) are therefore those shown in table 7.

Table 7 is the fundamental general table for determining the zygotic proportions resulting from the random mating of any given set of gametes. It will be employed in working out the results of selection and of assortative mating, as well as of random mating.

Example. Tables 4 and 7 furnish the formulae for the two steps necessary to obtain the proportional numbers of the different classes of individuals (zygotes) in the generation $n + 1$, when we know those in generation n,—the mating being at random, and the linkage being the same for both sets of gametes.

For example, suppose that the original population consists of 3 *ABAB* + 1 *abab* + 1 *AbaB* + 4 *ABaB;* that the linkage ratio r is 2, and that breeding is by random mating. What various types of individuals will be present in the next generation, and in what proportions?

Here evidently (referring to table 1),—

$$c = 3, \quad f = 1, \quad h = 1, \quad j = 4$$

while d, e, g, i, k and l are 0. Therefore the gametes produced will be, by table 4 (since $r + 1 = 3$):

$$\begin{aligned} p &= 3 \cdot (6 + 4) + 1 &&= 31 \\ q &= 2.1 &&= 2 \\ s &= 3.4 + 2.1 &&= 14 \\ t &= 3.2 + 1 &&= 7 \\ p + q + s + t & &&= 54 \end{aligned}$$

The gametes will therefore be in the proportions 31 *AB* : 2 *Ab* : 14 *aB* : 7 *ab*.

Then the zygotes of the next generation ($n + 1$) will be, by table 7, the following:

ABAB	$= 31^2$	$= 961$	*AbaB*	$= 2.2.14$	$= 56$
AbAb	$= 2^2$	$= 4$	*ABAb*	$= 2.31.2$	$= 124$
ABaB	$= 14^2$	$= 196$	*ABaB*	$= 2.31.14$	$= 868$
abab	$= 7^2$	$= 49$	*abAb*	$= 2.2.7$	$= 28$
ABab	$= 2.31.7$	$= 434$	*abaB*	$= 2.14.7$	$= 196$

By now substituting these values for c to l in table 1, and using anew tables 4 and 7, we may find the zygotic proportions for the third generation, and so on indefinitely. If desired the values for c to l may be reduced to decimal fractions in each case, giving all later proportions in decimals.

(11) DETERMINATION OF THE PROPORTIONS OF THE DIFFERENT CLASSES OF ZYGOTES PRODUCED WHERE ONE SET OF GAMETES FORMED WITH LINKAGE (r) (TABLE 4) MATES WITH ANOTHER SET WITH COMPLETE LINKAGE (TABLE 5)

This represents what appears to be the usual condition, where the gametes from one sex (eggs or sperm) are produced with linkage r, the other set with complete linkage.

In this case, as usual, the population at the beginning is that in table 1.

We determine by table 4 the values for p, q, s and t, and by table 5 the values for P, Q, S and T.

Now to obtain the zygotic proportions in the next generation, in table 6 we substitute in one of the columns of gametes the values P, Q, S and T for p, q, s and t; then we multiply as before to obtain the 16 lots of zygotes. Having performed this operation and classified the results in the same way as was done for table 7, we obtain for the zygotic proportions the table 8.

Example. To transform the zygotes of generation n into those of generation $n+1$, when linkage is complete in one set of the gametes, we therefore use successively the formulae of tables 4, 5 and 8. Suppose that we take the same example given in section (10), page 106, but assume that linkage is complete in one set of gametes.

Then by tables 4 and 5 the two sets of gametes are:

$p = 31$	$P = 10$
$q = 2$	$Q = 1$
$s = 14$	$S = 5$
$t = 7$	$T = 2$

And by table 8 the individuals (zygotes) of the next generation $(n+1)$ are:

$ABAB = 310$	$AbaB = 24$
$AbAb = 2$	$ABAb = 51$
$aBaB = 70$	$ABaB = 295$
$abab = 14$	$abAb = 11$
$ABab = 132$	$abaB = 63$

By substituting these values for c to l in table 1, we may determine the proportions of the different types of individuals in the next later generation, and so on. We may of course, if we prefer, reduce all the proportions to decimal fractions, and employ these decimals in working out results for later generations.

DERIVATION OF THE GAMETES PRODUCED BY THE NEXT GENERATION OF ZYGOTES (GENERATION $n+1$), WHEN THE GAMETES PRODUCED BY THE FOREGOING GENERATION (GENERATION n) ARE KNOWN

If it be desired to determine the zygotic constitution of the population in some later generation (as for example the fifth), it saves much labor to deal for the intervening generations with the gametes alone. That is, by formulae to be set forth, we determine directly from the proportions of the gametes produced by generation 1 the proportions of the gametes produced by generation 2; thence the gametic proportions from generation 3; thence those from generation 4, thence from 5. Only for this final generation do we determine the zygotic proportions.

Our problem is therefore to obtain p_{n+1}, q_{n+1}, s_{n+1} and t_{n+1} from p_n, q_n, s_n and t_n.

(12) *Linkage the same in both sets of gametes*

To derive our formulae, we first obtain the gametes from the original parents (generation n) by table 4; then from these gametes we derive the zygotes (generation $n + 1$) by table 7. From these zygotes, by the method of section (8) and table 3, we find that the gametes produced are the following:

Zygotes of $n + 1$		*Gametes from* $n + 1$
$p^2 . ABAB$	=	$p^2 . (2r + 2)\ AB$
$q^2 . AbAb$	=	$q^2 . (2r + 2)\ Ab$
$s^2 . aBaB$	=	$s^2 . (2r + 2)\ aB$
$t^2 . abab$	=	$t^2 . (2r + 2)\ ab$

$$2pt . ABab = 2pt . r . AB + 2pt . Ab + 2pt . aB + 2pt . r . ab$$
$$2qs . AbaB = 2qs . r . Ab + 2qs . AB + 2qs . ab + 2ps . r . aB$$

$$2pq . ABAb = 2pq . (r+1)\ AB + 2pq . (r+1)\ Ab$$
$$2ps . ABaB = 2ps . (r+1)\ AB + 2ps . (r+1)\ aB$$
$$2qt . abAb = 2qt . (r+1)\ ab + 2qt . (r+1)\ Ab$$
$$2st . abaB = 2st . (r+1)\ ab + 2st . (r+1)\ aB$$

Collecting the values for the gametes AB, Ab, aB, and ab, (from $n + 1$), and removing from each the factor 2, we obtain the formulae given in table 9.

By the continued use of these formulae we may find the proportions of the different gametes produced by any later generation of random mating, without troubling to find the zygotic constitution in any generation save the final one in which we are primarily interested. At any time the zygotic constitution is found by the formulae of table 7.

(13) *Independent factors*

If the factors are independent ($r = 1$), the gametic formulae of table 9 may be simplified through the substitution of 1 for r, giving table 10.

Example. In the example given in section (10), the following values were found for p, q, s and t for the first random mating:

$$p = 31 \qquad q = 2 \qquad s = 14 \qquad t = 7$$

Then by the formulae of the table 9 the values of p, q, s and t for the second random mating will be (when $r = 2$):

$$p = 3.31.47 + 2.31.7 + 2.14 = 4833$$
$$q = 3.2.40 + 2.2.14 + 31.7 = 513$$
$$s = 3.14.52 + 2.2.14 + 31.7 = 2457$$
$$t = 3.7.23 + 2.31.7 + 2.14 = 945$$

$$p + q + s + t = 3.54^2 = 8748$$

Now by the formulae of table 7, we may if we desire, obtain from these results the relative numbers of the different kinds of zygotes resulting from the second random mating.

Or we can by a repeated use of the formulae of the present section obtain the gametic constitution for the third, fourth and later generations; finding in addition the zygotic constitution for any desired generation.

(14) *Linkage complete in one sex, r in the other*

In this case we derive two sets of gametes from the original parents, by means of tables 4 and 5, and these give for generation $n + 1$, the zygotes of table 8. From these zygotes of table 8, we must find two sets of gametes, one with linkage r (by the method illustrated in section (8)), the other with complete linkage (by the method illustrated in section (9)). We must assume that both sexes are represented in each kind of zygote of table 8, so that we must form a first set of gametes from all the kinds of zygotes of table 8 by the method of section (8), then a second set from all by the method of section (9). Performing these operations and collecting the results, we obtain table 11.

In comparing the gametes of set 1 with those of set 2 (in table 11) certain constant relations between the two sets become evident. These are shown in table 12. These relations are of consequence for certain problems, particularly in selection and assortative mating; they are also useful in checking up the correctness of computations.

Example. We will take the example employed in section (10), but now assuming that linkage is complete in one sex. The parent zygotes were $3\,ABAB + 1\,abab + 1\,AbaB + 4\,ABaB$; and $r = 2$.

As shown in section (10), before the first random mating the gametes of the first set, with linkage r, are:

$$p = 31 \qquad q = 2 \qquad s = 14 \qquad t = 7$$

According to section (11), further, the gametes of the second set, with complete linkage, are:

$$P = 10 \qquad Q = 1 \qquad S = 5 \qquad T = 2$$

The zygotes resulting from the first random mating are therefore, by table 8:

$$\begin{array}{llll} ABAB = 31.10 = 310 & & AbaB = 1.14 + 2.5 = 24 \\ AbAb = 2.1 = 2 & & ABAb = 10.2 + 31.1 = 51 \\ aBaB = 14.5 = 70 & & ABaB = 10.14 + 31.5 = 295. \\ abab = 7.2 = 14 & & abAb = 1.7 + 2.2 = 11 \\ ABab = 10.7 + 31.2 = 132 & & abaB = 5.7 + 14.2 = 63 \end{array}$$

The gametes for the second random mating ($n = 2$) are obtained from the values of p_1, q_1, etc., given above, by the formulae of table 11, giving the following:

Set 1: Linkage $r = 2$, in both sexes:

$$\begin{aligned} p_2 &= 3.31.16 + 3.10.47 + 2.(70 + 62) + 14 + 10 = 3186 \\ q_2 &= 3.2.13 + 3.1.40 + 2.(14 + 10) + 70 + 62 = 378 \\ s_2 &= 3.14.17 + 3.5.52 + 2.(14 + 10) + 70 + 62 = 1674 \\ t_2 &= 3.7.8 + 3.2.23 + 2.(70 + 62) + 14 + 10 = 594 \end{aligned}$$

$$p + q + s + t = 5832$$

Set 2: Linkage complete in one sex:

$$\begin{aligned} P_2 &= 10.54 + 31.18 = 1098 \\ Q_2 &= 1.54 + 2.18 = 90 \\ S_2 &= 5.54 + 14.18 = 522 \\ T_2 &= 2.54 + 7.18 = 234 \end{aligned}$$

$$P + Q + S + T = 1944$$

It will be observed that the sum ($p + q + s + t$) is just 3 times the sum of ($P + Q + S + T$), 3 being the value of ($r + 1$).

Now by table 8 we may if we desire find the proportions of the different zygotes resulting from the second random mating; or we may omit this, and find directly the two sets of gametes for the third random mating; and so on.

RANDOM MATING: SPECIAL FORMULAE

(15) *Parents all ABab*

For the specially important case in which the parents are a first cross between *ABAB* and *abab*, (so that they are themselves *ABab*), we may obtain a general formula which shall give us directly the proportions of gametes (and indirectly of zygotes) for producing any generation n, without working out the proportions for intervening generations. For this the following points must be noticed:

Evidently the number of gametes *AB* is the same as the number of *ab*; while the number of *Ab* is the same as of *aB*, and this equivalence will be found to hold throughout random mating. We have therefore, so far as the gametes go, but two unknown quantities to deal with in place of four. In tables 2 and 5, therefore, we can put:

$$p = t \qquad P = T \qquad q = s \qquad Q = S$$

We require therefore but to find p, P, q and Q; these will give us the others.

Now, if at the beginning the parents are all *ABab*, and the linkage ratio is r, then evidently the gametes from these parents are r *AB* : 1 *Ab* : 1 *aB* : r *ab*, so that for producing generation 1 the gametes are:

$$p = r \qquad q = 1 \qquad p + q = r + 1 \qquad p - q = r - 1$$

In the sex (if there is such) in which the linkage is complete, the gametes formed by *ABab* are evidently simply *AB* and *ab* in equal numbers, so that (for producing generation 1):

$$P = 1 \qquad Q = 0 \qquad P + Q = 1 \qquad P - Q = 1$$

(16) Linkage r in both sets of gametes, parents all *ABab*

Now, if we take first the case in which linkage is r in both sexes, we may by table 9 from the above gametic proportions for producing generation 1 determine the gametic proportions for producing generation 2. We shall find these to be as follows:

$$p_2 = 2r^3 + 3r^2 + 2r + 1 = (r + 1)(2r^2 + r + 1)$$
$$q_2 = 3r^2 + 4r + 1 = (r + 1)(3r + 1)$$

Since it is the relative proportions that we desire, we can take out the common factor $(r + 1)$, and we have:

$$p_2 = 2r^2 + r + 1$$
$$q_2 = 3r + 1$$
$$p_2 + q_2 = 2r^2 + 4r + 2 = 2(r + 1)^2$$
$$p_2 - q_2 = 2r^2 - 2r = 2(r^2 - r)$$

If we continue in this way, finding successively the values of p_3, p_4, p_5, q_3, q_4, q_5, etc., certain general relations manifest themselves, particularly with regard to the sums of p and q, and their differences. It turns out that for producing any generation n

$$p_n + q_n = 2(r + 1)^n$$
$$p_n - q_n = 2(r^n - r^{n-1})$$

Solving these two equations for the values of p_n and q_n (and omitting from the result the common factor, 2), we obtain the formulae of table 13.

Having determined the values of p_n, q_n, s_n and t_n by table 13, the proportions of the different classes of individuals (zygotes) in generation n is obtained from table 7.

(17) If there is no linkage ($r = 1$) and the parents are all *ABab* the population will be found to remain constant, in the following proportions:

The four sorts of homozygotes, each	= 1
The two sorts of heterozygotes, each	= 2
The four sorts of mixed, each	= 2

Example. Parents all *ABab,* linkage ratio $r = 3$. What will be the constitution of the population (zygotes) after 4 random matings? By table 13:

$$p_4\ (= t_4) = 4^4 + 3^4 - 3^3 = 310$$
$$q_4\ (= s_4) = 4^4 - 3^4 + 3^3 = 202$$
$$p^2\ (= t^2) = 96{,}100$$
$$q^2\ (= s^2) = 40{,}804$$
$$2pq\ (= 2st) = 125{,}240$$

Total zygotes $= (620 + 404)^2 = 1024^2 = 1{,}048{,}576$.

From which it is evident that by the zygotic formulae of table 7 the proportions of the different sorts of zygotes are:

$$ABAB = \frac{96{,}100}{1{,}048{,}576} = .0916$$

abab = .0916
AbAb = .0389
aBaB = .0389
Total homozygotes = .2611
ABab = .1833
AbaB = .0778
Total heterozygotes = .2611
Each of 4 sorts of mixed = .1194
Total mixed = .4778

(18) Parents all *ABab;* linkage r in one set of gametes, complete in the other

Here, as in section (15), the number of gametes AB is equal to that of ab, while the number of Ab is equal to that of aB, so that:

$$p = t \quad q = s \quad P = T \quad Q = S$$

Also, as we saw in (15), for the first mating ($n = 1$):

$$p = r \quad q = 1 \quad P = 1 \quad Q = 0$$

$$p + q = r + 1; \; p - q = r - 1; \; P + Q = 1; \; P - Q = 1.$$

Now by the use of table 11, we obtain the corresponding values of p, q, P and Q for producing generation 2. We find thus that:

$$p_2 = 2r^2 + 2r + 1 \qquad P_2 = 2r + 1$$
$$q_2 = 2r + 1 \qquad Q_2 = 1$$
$$p_2 + q_2 = 2(r + 1)^2 \qquad P_2 + Q_2 = 2(r + 1)$$
$$p_2 - q_2 = 2r^2 \qquad P_2 - Q_2 = 2r$$

Now if by continued use of table 11, we find the corresponding values for successive generations, we discover that for any number n of generations the gametes which mate to form that generation show the following relations:

$$p_n + q_n = 2^{n-1} (r + 1)^n$$
$$p_n - q_n = 2r^2 \; (2r + 1)^{n-2}$$
$$P_n + Q_n = 2^{n-1} (r + 1)^{n-1}$$
$$P_n - Q_n = 2r \; (2r + 1)^{n-2}$$

Solving these equations for the values of p, q, P and Q, we obtain the formulae of table 14.

Having determined thus the proportions of the gametes, the constitution of generation n in zygotes is obtained by the use of table 8.

Example:—Parents *ABab;* linkage ratio $r = 3$; four generations of random mating ($n = 4$). What is the constitution of the population? By table 14, the gametic proportions preliminary to generation 4 will be:

$$p_4 = 2^2.4^4 + 9.7^2 = 1465$$
$$q_4 = 2^2.4^4 - 9.7^2 = 583$$
$$p_4 + q_4 = 2048$$
$$P_4 = 2^2.4^3 + 3.7^2 = 403$$
$$Q_4 = 2^2.4^3 - 3.7^2 = 109$$
$$P_4 + Q_4 = 512$$

To obtain the zygotes resulting from the mating of these gametes it is well to note the following:

$$Pp = 590,395$$
$$Qq = 63,547$$
$$Pq = 234,949$$
$$pQ = 159,685$$
$$Pp + Qq + Pq + pQ = 1,048,304$$

Then by table 8 (remembering that $p = t$, $q = s$, $P = T$ and $Q = S$), we find that the total number of zygotes $(P + Q + S + T)$ $(p + q + s + t)$ is 4,194,304. Working out, by table 8, the proportions for each of the classes of zygotes, and dividing each by 4,194,304 in order to reduce them to decimals, we find that the population in the fourth generation is:

Homozygotes, *ABAB* and *abab*, each	.141
AbAb and *aBaB*, each	.015
Total	.312
Heterozygotes, *ABab*	.282
AbaB	.030
Total	.312
Mixed, four sorts, each	.094
Total mixed	.376

(19) *Parents AbaB; linkage r in both sets of gametes*

In this case simply interchange the values of p and q in table 13 (of course therefore also the values of t and s), then obtain the zygotic proportions by table 7.

(20) *Parents AbaB; linkage r in one set of gametes, complete in the other*

In this case simply interchange the values of p and q; also of P and Q, in table 14 (of course therefore also the values of t and s, as well as of T and S); then obtain the zygotic constitution by table 8.

(21) *Original parents ABAB and abab in equal numbers, random mating*

In this case if there is linkage the proportions of gametes and zygotes for any generation must be worked out by the general formulae for random mating, given in sections (8) to (14).

When there is no linkage ($r = 1$) it is instructive to compare this case with that in which the parents are all *ABab* (and there is no linkage). If we examine the results with respect to single pairs of characters taken separately, we find them to be identical for the two cases. That is, when the parent population is either *ABab*, or is *ABAB* + *abab*, random mating gives for all later generations with respect to one pair of characters the uniform constitution ¼ *AA* + ½ *Aa* + ¼ *aa;* with respect to the other the constitution ¼ *BB* + ½ *Bb* + ¼ *bb*. But when we consider the two pairs together, we find that the two cases give diverse results; the two pairs of characters are combined diversely in the two cases. This is therefore an example of the fact, mentioned in section (2), that we cannot from a knowledge of the constitution with respect to two pairs of characters taken separately determine what will be the constitution with respect to combinations of the two pairs. In the case of the population derived from the random mating of *ABab*, the proportion of any combination of the two pairs is merely the product of the proportions for the two component pairs taken separately, thus the proportion that are *AABb* is ¼ × ½ = ⅛, etc. But when the original parents are *ABAB* + *abab*, this rule does not hold. The gametes from such parents are in any generation n the following:

$$p_n = t_n = 2^{n-1} + 1$$
$$q_n = s_n = 2^{n-1} - 1$$

The zygotic proportions are then obtainable by table 7. It will be found that these zygotic proportions change from generation to generation, although for each pair of characters taken by itself the proportions are constant. The zygotic proportions in successive generations are:

Random matings	1	2	3	n
ABAB and *abab*, each	4	9	25	D^2_n
AbAb and *aBaB*, each	0	1	9	C^2_{n-1}
ABab	8	18	50	$2D^2_n$
AbaB	0	2	18	$2C^2_{n-1}$
Mixed, 4 sorts, each	0	6	30	$2D_nC_{n-1}$

For the n'th generation the proportions are above given in terms of the series of table 1 in my earlier paper (JENNINGS 1916); thus the value for *ABAB* and *abab* is the square of the n'th term of series D of that paper; the value for *AbaB* is twice the square of the $(n-1)$th term of series C of that paper, etc.

III. Selection with relation to a single character

Suppose that in breeding, selection is exercised with respect to a single character forming one of a pair; for example suppose that of the pair *A* and *a*, individuals showing the character *A* are always selected for further propagation. In our previous contribution (Jennings 1916) we have dealt with the results on the constitution of the population with respect to this pair on which selection is based. But what will be the effect on the constitution with respect to another pair of factors, *B* and *b*, which is linked with the pair on which selection is based? That is, in a population composed of individuals having *A*, *a*, *B* and *b* in the various possible combinations, what will be the resulting constitution due to selecting for the character *A* for a given number *n* of generations?

We shall take up first the case in which the selected character is dominant, next that in which it is recessive. We may proceed upon the same general plan employed for random mating, employing primarily the proportions of gametes in the successive generations as the bases for our work, and deriving the proportions of zygotes secondarily from those for the gametes that produce them.

SELECTION OF DOMINANTS WITH RESPECT TO ONE OF THE PAIRS OF CHARACTERS; GENERAL FORMULAE

(22) *Gametes produced when there is selection of dominants with respect to one pair*

If we have such a population as is shown in table 1, and breed only from those that are dominants with respect to the pair *A* and *a*, this is equivalent to omitting all the zygotes that do not contain *A*; that is, it omits *e*, *f* and *l* of table 1. The gametes produced when there is such selection of dominants are therefore in the proportions shown in table 15 (compare with tables 4 and 5).

(23) *Proportions of the different classes of zygotes produced in the next generation* ($n + 1$)*, when the breeding is by selection for dominant A*

The selection has taken place in the production of the gametes (table 15). These gametes now simply mate at random, so that we can employ directly the tables 7 and 8, for random mating. Therefore when there is selection for dominant *A*, the procedure for finding the proportions of the population in the next generation is as follows:

First give the proper values to the letters *c* to *l*, in table 1, and to *r*.

If linkage is the same $(=r)$ in both sets of gametes, employ first the formulae of table 15, (set 1); then those of table 7; this gives the different classes of individuals in the next generation $n+1$.

If linkage is complete in one set of gametes, employ first table 15 (both sets), then table 8; thus obtaining the proportions of the different classes of individuals in the next generation $(n+1)$.

If it be desired to find the zygotic proportions only for some later generation (as for example the seventh), it is not necessary to find the zygotic proportions for the intervening generations, but one works for these intervening generations with the gametes alone, according to the methods of the following sections (24) and (25).

(24) *Derivation of the gametes produced by the next generation (n+1) of zygotes, when the gametes produced by the preceding generation n are known, (breeding by selection of dominant A)*

If we desire to obtain the zygotic proportions only for some later generation, we may work for the intervening generations only with the gametes, by methods analogous to those set forth for random mating

Linkage the same $(=r)$ in both sexes. We use the method set forth in sections (12), (13) and (14).

in section (12), but exclude from gamete formation the zygotes *aBaB*, *abab*, and *abaB* (since these do not contain *A*). We thus obtain the formulae given in table 16.

Of course the zygotic proportions for generation $n+1$ may now if desired be found from the zygotic formulae of table 7. Or by repeated use of these formulae of table 16 we may find the gametic proportions for any later generation, then by table 7 find the zygotic proportions for that generation.

(25) *Linkage complete in one set, r in the other*

Derivation of the gametes that produce the succeeding generation $(n+1)$, from those that produce the preceding generation (n)

We use the methods set forth in (14), but exclude from gamete formation the zygotes *aBaB*, *abab* and *abaB* (since these do not contain *A*). The formulae we require are indeed obtained directly from those of table 11, by omitting in all cases the factors *Ss*, *Tt*, *St* and *sT*. The results are given in table 17.

By the repeated use of the formulae of this table 17, we may find the gametic proportions for any later generation; then by table 8 find the zygotic proportions for that generation. See the example in section (27).

No formula has been found obtainable for determining the proportions in any given later generation *n*, without working out the values for the intervening generations. Even when the original parents are *ABab* or *AbaB*, the general methods (22) to (25) must be employed. The most important case, in which the original parents are *ABab*, will be found worked out illustratively in section (27).

(26) SELECTION OF DOMINANTS WITH RESPECT TO ONE OF THE PAIRS OF CHARACTERS; SPECIAL FORMULAE FOR THE EFFECT ON THE OTHER PAIR

Possibly the most interesting question in selection with reference to one pair of characters is its effect on another pair of characters, linked with the first pair. We shall take this up here, giving formulae for both the single factor-pairs taken separately.

Proportions of the single factor-pairs taken separately, when there is selection of dominant *A*: From the formulae of table 15, or of tables 16 and 17, taken in connection with those of tables 7 and 8, as set forth in sections (22) to (25), we may readily obtain for the desired generation the proportions of the population with relation to the members of either pair of factors taken separately; that is, with relation to *A* and *a*; or to *B* and *b*. After obtaining for the next generation the gametic proportions of table 16 (if linkage is the same in both sets); or those of table 17 (if linkage is complete in one of the sets of gametes), we observe that the gametic proportions for *A* and *a*, and for *B* and *b*, are those given in table 18.

The zygotic proportions in the next generation $(n + 1)$ are then, with relation to the single factor-pairs taken separately, those given in table 19.

The same proportions for each pair separately would be obtained by deriving the zygotic proportions for the two pairs together according to (24) and (25), then tabulating the constitution with reference to the factors taken separately.

The formulae given in table 19 for *AA, Aa* and *aa* give the same results as are given in sections (19) to (24) of my earlier paper (JENNINGS 1916), in which a single pair of factors was considered by itself. The linkage of course has no effect on the proportions of the pair with reference to which selection is made.

With relation to *BB, Bb* and *bb,* the proportions depend on the amount of linkage; the formulae of the present section enable us to determine precisely how selection with reference to one character (A) affects the proportions with respect to another character linked with it (B and b). If there is no linkage ($r = 1$), the formulae given in table 19 for *BB, Bb* and *bb* give the same results as for those of random mating (sections (1) to (12) in my earlier paper); that is, selection with reference to A and a is random mating with reference to B and b, if the two pairs are not linked.

All these matters are illustrated in the concrete example given in the following sections (27) and (28).

(27) Illustrative example of the results of selecting dominants; parents all *ABab*

To illustrate the use of the formulae for selection of dominants, we will take the most important typical case, in which the parents at the beginning are the dihybrid *ABab*. We will determine the results for several generations of selecting for propagation only those having the dominant factor A. We shall compare the results when there is linkage and when there is none; also the results when linkage is alike in both sexes, and those when linkage is complete in one sex. To keep the numbers relatively small we shall assume the linkage to be 2.

As the original parents (*ABab*) all contain A, none are excluded in the first mating. When there is no linkage the gametes are evidently 1 *AB* : 1 *Ab* : 1 *aB* : 1 *ab*. When the linkage is 2, the gametes are 2 *AB* : 1 *Ab* : 1 *aB* : 2 *ab*.

No linkage ($r = 1$). In this case for the first mating, as we have seen, $p_1 = 1$, $q_1 = 1$, $s_1 = 1$, $t_1 = 1$. We now find the proportions for the succeeding generations, by the formulae of table 16. For the next generation ($n = 2$) they are evidently as follows (since $r + 1 = 2$).

$$p_2 = 2.1.3 + 1.1 + 1 = 8\ (= 2)$$
$$q_2 = 2.1.3 + 1.1 + 1 = 8\ (= 2)$$
$$s_2 = 2.1 + 1 + 1 = 4\ (= 1)$$
$$t_2 = 2.1 + 1 + 1 = 4\ (= 1)$$

As it is only the proportional numbers that we desire, we may divide through by 4, giving the numbers in the last column.

Repeating our use of the formulae of table 16, we find that when there is no linkage the gametic proportions for the first four generations are:

n	=	1	2	3	4
p	=	1	2	3	4
q	=	1	2	3	4
s	=	1	1	1	1
t	=	1	1	1	1
		4	6	8	10

In general, it appears that for any generation n, p and q are each equal to n, while s and t are each 1.

Linkage 2, alike in both sexes ($r = 2$).

For generation 1, as we have seen, $p = 2$; $q = 1$; $s = 1$; $t = 2$. Applying now the formulae of table 16 and noting that $r + 1 = 3$, the proportions for generation 2 are found to be the following:

$$p_2 = 3.2.4 + 2.4 + 1 = 33 = 11$$
$$q_2 = 3.1.5 + 2.1 + 4 = 21 = 7$$
$$s_2 = 3.2 \quad + 2.1 + 4 = 12 = 4$$
$$t_2 = 3.2 \quad + 2.4 + 1 = 15 = 5$$

(We reduce to lowest integral terms by dividing all the proportions by 3.)

In the third generation, by renewed application of table 16, we find the proportions to be:

$$p_3 = 3.11.22 + 2.55 + 28 = 864 = 32$$
$$q_3 = 3.7.23 \quad + 2.28 + 55 = 594 = 22$$
$$s_3 = 3.44 \quad + 2.28 + 55 = 243 = 9$$
$$t_3 = 3.35 \quad + 2.55 + 28 = 243 = 9$$

(We divide through by 27 to reduce to lowest terms.)

Thus when r is 2 in both sexes, the gametic proportions for the first four generations are:

n	=	1	2	3	4
p	=	2	11	32	379
q	=	1	7	22	269
s	=	1	4	9	86
t	=	2	5	9	76
		6	27	72	810

Linkage complete in one sex; $r=2$. In the sex in which the linkage is r, the parents $ABab$ of course produce gametes in the proportions 2 AB : 1 Ab : 1 aB : 2 ab; these form the gametes of set 1. In the sex in which linkage is complete, the gametes formed are evidently 1 AB : 0 Ab : 0 aB : 1 ab (set 2). Using the letters p, q, s and t for the set 1 and P, Q, S and T for set 2, the gametes for the first generation ($n=1$) are therefore:

Set 1	*Set 2*
$p=2$	$P=1$
$q=1$	$Q=0$
$s=1$	$S=0$
$t=2$	$T=1$

To obtain the gametic proportions in preparation for the next generation, we begin with the values just given, and employ the formulae of table 17. We thus find that for $n=2$:

Set 1	*Set 2*
$p_2=3.2.1+3.1.4+2.4+0+0=26$	$P_2=1.6+2.2=10$
$q_2=3.1.2+3.0.5+2.0+2+2=10$	$Q_2=1.2=2$
$s_2=3.1+2.0+2+2=7$	$S_2=1.1=1$
$t_2=3.1+2.4+0+0=11$	$T_2=1.3+2.1=5$
54	18

Repeating the use of the formulae of table 17, but now beginning with the values for $n=2$, and so on, we find that for the first four generations the gametic proportions are as follows (under each value of n is given in the first set the value of p, q, etc., in the second the value of P, Q, etc.):

n	1		2		3		4	
	Set 1	Set 2	Set 1	Set 2	Set 1	Set 2	Set 1	Set 2
p and P ($=AB$) =	2	1	26	10	117	42	310	108
q and Q ($=Ab$) =	1	0	10	2	45	12	122	36
s and S ($=aB$) =	1	0	7	1	24	5	53	13
t and T ($=ab$) =	2	1	11	5	30	13	55	23
Totals	6	2	54	18	216	72	540	180

Having now obtained the gametic proportions for each of the three diverse cases, it is a simple matter to compute for any generation the proportions of the ten different sorts of zygotes. For the cases where the linkage relations are the same in both sexes we use the formulae of table 7; for the case where linkage is complete in one sex we employ the formulae of table 8. The results for the four generations are given in table 20. In each generation the results are given for the three diverse linkage relations; where r is given as 1 there is of course no linkage; where $r = 2$ the linkage ratio is 2 to 1 in both sexes; the third case, where the linkage is 2 to 1 in one sex and complete in the other, is indicated by putting $r = 2+$.

The results for each case are given twice; first as whole numbers, as they will be obtained from the formulae; then as decimal fractions, for comparison with the other cases. For example, in the first place of the first column we find $1 = .0625$. This means that out of the total 16 zygotes, one will be $ABAB$, and that this is equal to .0625 of the total.

(28) *The proportions for single factor-pairs taken separately; example:* In our example (27) we select entirely with reference to the pair A and a. The most interesting question doubtless is: What effect has this on the proportions of the various combinations of B and b, when the two pairs are linked?

This question may be answered from the formulae of table 19, employing the gametic proportions already given in table 20. We give the results for both the pairs, A and a, and B and b.

From table 19, the values are in the first generation:

When there is no linkage ($r = 1$):

$AA = 4$	$Aa = 8$	$aa = 4$
$BB = 4$	$Bb = 8$	$bb = 4$

When $r = 2$:

$AA = 9$	$Aa = 18$	$aa = 9$
$BB = 9$	$Bb = 18$	$aa = 9$

When $r = 2+$ (linkage complete in one sex):

$AA = 1$	$Aa = 2$	$aa = 1$
$BB = 1$	$Bb = 2$	$bb = 1$

Thus for this first generation all values of r give the same result for each of the combinations.

In later generations the results differ for the different values of r. Table 21 gives the proportions of the different combinations for the first four generations.

As table 21 shows, when there is linkage there is a steady increase in the proportion of BB over bb, as also of BB over Bb, as a result of selection for the character A.

SELECTION OF RECESSIVES

Only individuals *not* containing the factor A are selected for propagation. That is, selection is of individuals aa only.

We may deal at the same time with the two cases (1) where linkage is the same in both sexes, and (2) where linkage is complete in one sex, for the two give here the same results.

(29) *Gametes produced when there is selection of recessives with respect to one pair of factors*

Suppose that of the zygotes of table 1, only those that are recessive with respect to the pair A and a are bred, that is, only those that contain aa. In this case all zygotes are omitted except e, f and l. These give only gametes aB and ab, so that for the gametes we have only the proportions s and t to deal with. If we determine the gametic proportions in accordance with the principles in section (22), we find that

$$s = (r+1)(2e+1)$$
$$t = (r+1)(2f+1)$$

But as it is only the relative proportions that are important, we may divide both these by $(r+1)$, giving table 22.

Furthermore, if we determine the proportions for the two sorts of gametes when linkage is complete, we find them to be identical with those in table 22. This table therefore serves for the gametic proportions whether linkage is or is not complete.

(30) *Proportions of the different sorts of zygotes produced in the next generation ($n+1$), when the breeding is by selection of recessives aa*

Here, as in (23), the selection has occurred in the production of the gametes, and the gametes now mate at random. We can therefore employ directly the table for random mating. Since however in the case of selection of recessives the gametes are the same whether linkage is complete or not, we need to employ only table 7. But as only a few of the classes of zygotes of table 7 are formed, it will simplify matters to make a new table, including only those classes. This gives us table 23. Thus the total procedure in the case of selection of recessives aa is as follows:

Give the proper values to the letters c to l in table 1.

Employ first the formulae of table 22.

With the results from table 22 employ the formulae of table 23. These give the proportions of the different classes of individuals in the next generation $n + 1$.

(31) *Derivation of the gametes produced by the next generation $n+1$ when the gametic proportions from generation n are known*

In the very first selection the factor A was entirely excluded and can never reappear, so that no farther selection occurs, and all future breeding is by random mating. The gametes p and q thus never appear. We may therefore apply directly the gametic formulae for random mating, as given in table 9, but including only those parts based on s and t alone. This gives us:

$$s_{n+1} = (r+1)s(s+t)$$
$$t_{n+1} = (r+1)t(s+t)$$

But both the right hand members can be divided by $(r+1)(s+t)$, giving merely

$$s_{n+1} = s_n$$
$$t_{n+1} = t_n$$

that is, the proportions of s and t are constant from generation to generation; it follows that the proportions of the three possible types of gametes given in table 23 are likewise constant from generation to generation.

Thus, in the case of selection of recessives with respect to the pair A and a, we require only to obtain for the first generation the values of s and t by the formulae of table 22; these values hold for all generations. We then obtain the proportions of the zygotes by the formulae of table 23, and these values likewise hold for all generations. If we carry through in detail an analysis in the case where linkage is complete in one sex, we come to the same result.

Put in another way, selection of recessives with respect to A and a gives random mating with respect to B and b, no matter what the linkage is, and no matter whether linkage is alike in both sexes, or is complete in one sex.

IV. Assortative mating with respect to one of the pairs of characters: dominant with dominant, recessive with recessive

(32) *General.* In assortative mating with respect to a single pair of characters (as A and a), all individuals containing A mate together at random; likewise all individuals not containing the factor A. The

most interesting question involved is: What is the effect of this on a second pair of factors (B and b), that are linked with the first pair? The proportions of all possible combinations of the two pairs must of course be determined.

Assortative mating is in some sense a combination of selection for dominants on the one hand, of recessives on the other, with of course continual subtraction of the recessive products from the dominant group, and their addition to the recessive group. The chief difficulty to be met is the necessity of keeping the proportions of the two groups correct with reference to each other; they cannot be dealt with separately. This adds some complications, and to meet the difficulty certain additional designations and classifications will be introduced.

The population at the beginning is that shown in table 1. We observe that in this population the classes c, d, g, h, i, j and k contain the dominant factor A; it will be convenient to designate their sum by the letter D. The classes e, f, and l contain only the recessive factors aa; the sum of these three classes will be called R. The sum of all $(D+R)$ will be denominated N. For ease of reference we incorporate these in the numbered table 24.

PRODUCTION OF THE GAMETES IN ASSORTATIVE MATING

(33) For the production of gametes from the dominant zygotes (of table 1) we employ directly the formulae of table 15.

(34) For the production of gametes from the recessives we might use the formulae of table 22. It is needful, however, as will appear later, to use certain other designations for the gametic proportions in place of s and t (or S and T), in order to distinguish the gametes obtained from the recessives from those obtained from the dominants. We will therefore employ the Greek equivalents for those letters, using the lower case letters, as heretofore, for gametes formed with linkage r, the capital letters for those formed with complete linkage. This transforms table 22 into table 25. It will be observed that σ and Σ have the same values, as do also τ and T, but it is needful to distinguish them for the following reason. When we obtain the complete set of gametes from both dominants and recessives, one set formed with linkage r, the other set with complete linkage, either set may be reduced to lower terms or to decimals, independently of the other. Since the ratio of gametes derived from the dominants to those derived from the recessives is diverse in the two sets, after reduction Σ and σ may have diverse values, as may also T and τ.

(35) *Proportions of the different types of zygotes obtained from the dominants; linkage alike in both sets of gametes*

To obtain the proportions of the different classes of zygotes of generation $n + 1$, given by the mating of the gametes from the dominants of generation n, we employ directly the formulae of table 7, using of course the values of p, q, s, t obtained from table 15. To obtain correctly the final values for assortative mating it is necessary to first obtain these zygotic proportions in the forms of fractions. For this, we must divide the number in each class of zygotes by the total number of zygotes produced. This total number produced is, according to table 7, $(p+q+s+t)^2$. Furthermore, by table 15,

$$p+q+s+t = (2r+2)(c+d+g+h+i+j+k)$$

(When the letters c, d, etc., are the proportions for generation n). Now, from this, according to table 24,

$$p+q+s+t = 2(r+1)D$$

Whence

$$(p+q+s+t)^2 = 4(r+1)^2D^2$$

So, to obtain the zygotic proportions in the form of fractions, we must divide each value of table 7 by this expression $4(r+1)^2D^2$. Thus, for example:

$$ABAB = \frac{p^2}{4(r+1)^2D^2}$$

and similarly for all the 10 classes of zygotes of table 7.

Having obtained thus the relative proportions of the different types of zygotes derived from the dominant parents, we desire to know what proportions these are of the total resulting population (derived from *both* dominant and recessive parents). Now according to table 24, the dominant parents formed the fraction D/N of all parents; their progeny will therefore form D/N of all progeny, and to obtain the proportions of the entire population formed by the various classes of these progeny, we must multiply each of these proportions by D/N. The result of this will be clear from an example. As we saw in the last paragraph, the proportion for $ABAB$ before this operation is $p^2/4(r+1)^2D^2$; multiplying this by D/N we obtain:

$$ABAB = \frac{p^2}{4(r+1)^2DN}$$

Similarly, the proportions of the total population for all the ten types of zygotes derived from the dominants will be the values given in table 7, each divided by $4(r+1)^2DN$.

(36) *Proportions of the progeny (generation $n+1$) derived from the recessives (linkage either the same in both sets or complete in one set)*

To obtain the proportions of the various types of zygotes of the next generation ($n+1$) derived from the recessives of generation n, we proceed in a manner parallel to that employed for the dominants (35). We first obtain the gametic proportion σ and τ and if needed, Σ and T from table 25. Then the proportions of the different classes of zygotes may be obtained from table 23, if we use σ and τ or Σ and T in place of s and t.

To obtain the proportions in the form of fractions, we must divide the numbers representing each class of zygotes by the total number of zygotes. By table 23 the total number of zygotes produced is $(\sigma+\tau)^2$, or $(\sigma+\tau)(\Sigma+\mathrm{T})$ if linkage is complete in one set, the two expressions being equivalent. By table 25,

$$\sigma+\tau=\Sigma+\mathrm{T}=2(e+f+l),$$

and by table 24, $2(e+f+l)$ is equivalent to $2\,R$. Therefore the total number of zygotes produced, $(\sigma+\tau)^2$ or $(\sigma+\tau)(\Sigma+\mathrm{T})$ is equal to $4\,R^2$.

We must therefore divide each of the zygotic values in table 23 by $4\,R^2$. This gives the proportions that each of the classes of zygotes are of the total zygotes produced by the recessives.

To obtain in fractional form the proportions that these are of the population as a whole (derived from both dominants and recessives), we must multiply these fractions thus far obtained by the fraction that their recessive parents are of all parents; that is, by R/N. This gives the following:

	Linkage r in both sexes	Linkage complete in one sex
$e(=aBaB)$	$=\dfrac{\sigma^2}{4\,RN}$	$\dfrac{\Sigma\sigma}{4\,RN}$
$f(=abab)$	$=\dfrac{\tau^2}{4\,RN}$	$\dfrac{\mathrm{T}\tau}{4\,RN}$
$l(=abaB)$	$=\dfrac{2\sigma\tau}{4\,RN}$	$\dfrac{\Sigma\tau+\sigma\mathrm{T}}{4\,RN}$

Thus from the recessive parents of generation n we obtain only three sorts of zygotes of generation $n+1$, in the proportions just given.

(37) To obtain now the proportions of the population in generation $n+1$ that are formed by each of the ten possible sorts of zygotes, we must simply add the proportions derived from the dominants to those from the recessives. But only the three classes of zygotes last dealt with (e, f and l) require an addition from the recessives, the others being derived entirely from the dominants. Thus the proportion of $c(=ABAB)$ is $\frac{p^2}{4(r+1)^2DN}$, while that of $f(=abab)$ is $\frac{t^2}{4(r+1)^2DN} + \frac{\tau^2}{4RN}$.

Now to free our proportions from the fractional form, we must reduce them all to a common denominator. This common denominator will evidently be $4(r+1)^2RDN$. We therefore reduce all the fractions to this denominator, and conserve merely the numerators as our proportions. This gives the results shown in table 26 (column 1). These proportions can of course be at once reduced to the fractional form by dividing each by $4(r+1)^2RDN$.

(It will be observed that the only reason for the appearance of R in the values is the occurrence of R in the denominators of the table given in section (36). If we began with a population in which there were no recessives (if for example the parents were all $ABab$), then for that generation the fractions shown in the table of section (36) would not occur, and as a result no R would appear in the values of table 26. Thus if there are no recessives in generation $n(R=0)$, we do not give R the value 0 in table 26, but merely omit it entirely. If R be given the value 0 correct results will not be obtained.)

For R, D, and N only proportional values are required; thus if the values are $R=217$, $D=434$, $N=651$, we may employ simply $R=1$, $D=2$, $N=3$, since these are the proportional values.

(38) *Assortative mating; linkage complete in one sex; general formula*

When linkage is complete in one of the sets of gametes the results are to be worked out on the same principles as in the last case (32) to (37), save that for the proportions of the population produced by the dominants, we employ for the gametes both columns of table 15, followed for the zygotes by table 8. Then to obtain in fractional form the proportions from the dominants, we divide by the total number of zygotes produced from the dominants, which by table 8 is $(P+Q+S+T)(p+q+s+t)$. But by table 15

$$p+q+s+t = (2r+2)(c+d+g+h+i+j+k) = (2r+2)D \quad \text{(table 24)}$$
$$P+Q+S+T = 2(c+d+g+h+i+j+k) = 2D \quad \text{(table 24)}$$

Hence $(P+Q+S+T)(p+q+s+t) = 4(r+1)D^2$, which is the total number of zygotes produced by the dominants. We therefore divide each value in table 8 by $4(r+1)D^2$, obtaining thus the fractional proportions for the different zygotes obtained from the dominants. To determine what proportions these are of the entire population, we must, as in section (35), multiply each of these proportions by D/N. The general upshot of this division by $4(r+1)D^2$ and multiplication by D/N will be to divide each value in table 8 by $4(r+1)DN$. The proportions from the recessives will be as set forth in (36).

Next, as in (37), we reduce all the fractions to a common denominator, which in this case will be $4(r+1)RDN$. This enables us to discard the denominator, employing as the proportions of the different kinds of zygotes only their numerators. The results are given in the last column of table 26.

(39) Thus in assortative mating, to determine the proportions of the different classes of zygotes of the next generation $n+1$, when those of generation n are known, the order of procedure is as follows:

Give the proper values for the parents (generation n), to the letters c to l in table 1, and classify these parents into dominant D and recessive R, in accordance with table 24; find the proportional values of D, R, and N (of that table). These proportional values of R, D and N may be reduced or altered in any way that is convenient, provided the proportionality is maintained.

Obtain from the dominants the proportions of the different sets of gametes produced, by table 15. Thus the values of p, q, s and t are obtained; also (if required) of P, Q, S and T.

Obtain by table 25 the corresponding gametic proportions from the recessives, thus getting the values of σ and τ (and if required, of Σ and T).

Then, employing these gametic values, the proportions of the different classes of zygotes in generation $n+1$ are those shown in table 26.

By repetition of the procedure, the proportions for succeeding generations are obtainable.

See the example, section (42).

(40) *Derivation of the gametic proportions for the gametes produced by generation $n+1$, when those produced by n are known; assortative mating*

When we desire to obtain the zygotic proportions only for some later generation, we may shorten the procedure by working for the intervening generations only with the gametic proportions, by methods analogous to those for random mating, (12), (13) and (14), and selection of dominants (24) and (25). For this purpose we employ the values given in table 26 for the different sorts of zygotes; then determine the proportions of the different sorts of gametes produced by each,—employing in general the methods of (12), but remembering that the gametes from zygotes e, f and l are to be classified as σ and τ (or Σ and T).

The results are given in tables 27 and 28. In the repeated use of these tables, the values for D and R of the next generation $(n+1)$ are to be found by the following equations (given in those tables):

$$p+q+s+t = (r+1)D, \text{ of generation } n+1$$
$$P+Q+S+T = D, \text{ of generation } n+1$$
$$\sigma+\tau \text{ (or } \Sigma+\mathrm{T}) = R, \text{ of generation } n+1$$

Then these values of R and D are of course to be employed in the equations for finding the gametic proportions of the next generation (see the example, section 42). Only the relative values of R and D are required; if $D=99$ and $R=33$, we may use $D=3$, $R=1$.

To find for any generation the zygotic proportions, we of course employ the results of tables 27 and 28 in table 26.

(41) *The proportions for the single factor-pairs taken separately*

One of the chief points of interest is the effect of assortative mating with respect to one pair, on the proportions of another pair linked with the former. If we mate assortatively with respect to A and a, what are the results on the proportions of the pair B and b, which are linked with A and a?

The formulae already given include all that is required for answering this question; we require merely to add together the proportions of the different zygotes that show a common constitution with respect to one of the factor pairs. For example, it is clear that $ABAB$, $AbAb$, and $ABAb$ are all to be classified as AA, when only the pair A and a is considered. It will be well to give the formulae obtained in this way from table 26, for each pair taken separately. In table 26 it will be observed that with respect to the pair *A* and *a,* the zygotes *c, d* and *i* are *AA; g, h, j* and *k* are *Aa,* while *e, f* and *l* are *aa.* With respect to *B* and *b* the zygotes *c, e* and *j* are *BB; g, h, i* and *l* are *Bb,* while *d, f* and *k* are *bb.* Adding the proportions accordingly, we obtain for the proportions of the single factor-pairs taken separately the values given in table 29.

For the pair *A, a,* table 29 will be found to give the same values as the formulae of section (15) of my former paper (JENNINGS 1916).

(42) *Example to illustrate the use of the tables for assortative mating*

Suppose that a population consists in generation 1 of 2 *ABAB* + 1 *AbAb* + 2 *aBaB* + 1 *abab* + 4 *ABab* + 3 *AbaB* + 1 *ABAb* + 2 *ABaB* + 3 *abaB.* The linkage ratio is 2($r=2$), and there is assortative mating with respect to *A* and *a.*

Here, from tables 1 and 24, dominants *D* are:

$$c=2;\ d=1;\ g=4;\ h=3;\ i=1;\ j=2;\ k=0;\ \text{so that } D=13$$

The recessives *R* are:

$$e=2;\ f=1;\ l=3;\ \text{so that } R=6$$

Then from the dominants *D,* by table 15:

$$\begin{aligned} p &= 3(4+1+2)+4.2+3 = 32 & P &= 11 \\ q &= 3(2+1+0)+3.2+4 = 19 & Q &= 6 \\ s &= 3.2+3.2+4 = 16 & S &= 5 \\ t &= 3.0+4.2+3 = 11 & T &= 4 \\ p+q+s+t &= (2r+2)D = 78 & P+Q+S+T &= 2D = 26 \end{aligned}$$

From the recessives *R,* by table 25:

$$\begin{aligned} \sigma &= 2.2+3 = 7 & \Sigma &= 7 \\ \tau &= 2.1+3 = 5 & \mathrm{T} &= 5 \\ \sigma+\tau &= 2R = 12 & \Sigma+\mathrm{T} &= 2R = 12 \end{aligned}$$

Having thus the gametes from generation 1, we may from them find either the gametes from the next generation (2), by tables 27 and 28; or we may find at once the zygotic constitution of generation 2, by table 26. Both will be illustrated.

Gametic proportions for succeeding generations.—We shall first find the gametic proportions for the gametes derived from generation 2. Assume first that the linkage is the same ($r=2$) in both sets of gametes. Then by table 27 (remembering that *R* is 6 and *D* is 13).

$$p = 6.3.32.67 + 6(2.32.11 + 19.16) = 44640 = .3796$$
$$q = 6.3.19.62 + 6(2.19.16 + 32.11) = 26964 = .2772$$
$$s = 6(3.32.16 + 2.19.16 + 32.11) = 14976 = .1273$$
$$t = 6(3.19.11 + 2.32.11 + 19.16) = 9810 = .0834$$
$$p+q+s+t = 96390 = .8675$$

Therefore $D = \frac{96390}{3} = 32130$

$$\sigma = 6.16.27 + 13.3^2.7.12 = 12420 = .1056$$
$$\tau = 6.11.27 + 13.3^2.5.12 = 8802 = .0748$$
$$\sigma+\tau = 21222 = .1804$$

Therefore $R = 21222$

Total gametes $= 117612 = 1.0000$

If we desire we may reduce R and D in such a way as to make $R = 1$; that is, if we divide both by the value of R, we obtain: $R = 1$; $D = 1.513$.

Having found the proportions of the different sorts of gametes derived from generation 2, as well as R and D, for generation 2, we may now employ these values (either the entire numbers or the decimals) in finding anew the gametic proportions from generation 3, and the proportions of recessives and dominants in that generation. These may then be employed anew to find the proportions for generation 4, etc., until we reach the generation for which we wish to find the zygotic proportions.

If we assume that linkage is complete in one sex, we shall, for determining the proportions of the gametes derived from generation 2, employ table 28 in place of table 27 (used above). It is not necessary to represent the operations in detail; they will give us the following values for the proportions from the second generation:

Set 1	*Set 2*
$p = 30072$	$P = 10140$
$q = 17664$	$Q = 5772$
$s = 9834$	$S = 3162$
$t = 6690$	$T = 2346$
$p+q+s+t = 64260 = 3D \therefore D = 21420$	$P+Q+S+T = 21420 = D$
$\sigma = 8226$	$\Sigma = 8226$
$\tau = 5922$	$\mathrm{T} = 5922$
$\sigma+\tau = 14148 = R$	$\Sigma+\mathrm{T} = 14148 = R$
Total in set 1 = 7840	Total in set 2 = 35568

If $R = 1$, $D = 1.513$ (in generation 2).

The proportions in either or both sets may be reduced to smaller numbers by dividing all of the set by any number. It is not necessary that both sets should be divided by the same number. Thus set 1 may be reduced to decimals by dividing by the sum of the total for its set; set 2 by the total for that set.

Using these values (reduced or not), we may now find the proportions of the gametes from generation 3, and so on.

Zygotic proportions in any generation. By table 26 we may find the proportions of the different kinds of zygotes in generation 2 or 3, employing the gametic proportions already determined. As an illustration we will find these for generation 2 (employing the gametic values from generation 1 as given on page 131).

Linkage the same in both sets	Linkage complete in one set
c (=*ABAB*) $= 6.32^2 = 6144 = .1151$	$6.32.11 = 2112 = .1187$
d (=*AbAb*) $= 6.19^2 = 2166 = .0406$	$6.19.6 = 684 = .0384$
e (=*aBaB*) $= 6.16^2+13.3^2.7^2 = 7269 = .1362$	$6.5.16 + 13.3.7.7 = 2391 = .1344$
f (=*abab*) $= 6.11^2+13.3^2.5^2 = 3651 = .0684$	$6.4.11 + 13.3.5.5 = 1239 = .0697$
g (=*ABab*) $= 6.2.32.11 = 4224 = .0792$	$6\,(11.11+32.4) = 1494 = .0840$
h (=*AbaB*) $= 6.2.19.16 = 3648 = .0684$	$6\,(6.16+19.5) = 1146 = .0707$
i(=*ABAb*) $= 6.2.32.16 = 7296 = .1367$	$6\,(11.19+32.6) = 2406 = .1353$
j (=*ABaB*) $= 6.2.32.16 = 6144 = .1151$	$6\,(11.16+32.5) = 2016 = .1133$
k (=*abAb*) $= 6.2.19.11 = 2508 = .0470$	$6\,(6.11+19.4) = 852 = .0479$
l (=*abaB*) $= 6.2.16.11 + 13.3^2.2.7.5 = 10302 = .1931$	$6\,(5.11+16.4) + 13.3.(7.5+7.5) = 3444 = .1931$
Total $= 4.3^2.6.13.19 = 53352 = 1.000$	Total $= 4.3.6.13.9 = 17784 = 1.000$

Effect on the single factor-pairs taken separately. In generation 2, by table 29:

Linkage r in both sets	Linkage complete in one set
$AA = 6.51^2 = 15606 = .2925$	$6.17.51 = 5202 = .2925$
$Aa = 2.6.51.27 = 16524 = .3097$	$6.17.27 + 6.51.9 = 5508 = .3097$
$aa = 6.27^2 + 3^2.13.12^2 = 21222 = .3977$	$6.9.27 + 3.13.12.12 = 7074 = .3977$
Total $= 6.78^2 + 3^2.13.12^2 = 53352 = 1.000$	Total $= 17784 = 1.000$
$BB = 6.48^2+3^2.13.7^2 = 19557 = .3666$	$6.16.48+3.13.49 = 6519 = .3664$
$Bb = 2.6.48.30+2.3^2.13.7.5 = 25470 = .4774$	$6.16.30+6.48.10+3.13.70 = 8490 = .4774$
$bb = 6.30^2+3^2.13.5^2 = 8325 = .1560$	$6.10.30+3.13.25 = 2775 = .1560$
Total $= 53352 = 1.000$	Total $= 17784 = 1.000$

It will be observed that after this single assortative mating the proportions of *BB, Bb* and *bb* are the same whether the linkage is alike in both sets or is complete in one set; they would likewise be the same whatever the linkage, or if there were no linkage. But in later generations the proportions are diverse for different linkages, and depending on whether linkage is the same in both sets or complete in one set.

V. Self-fertilization

Thus far we have mainly used the proportions of the different types of gametes as our units, determining from these the proportions of the different sorts of zygotes, in accordance with the principle that the random mating of any set of zygotes gives the same results as the random mating of the gametes they produce. Self-fertilization differs so greatly from random mating that it is no longer convenient to base the work on this principle; we therefore deal directly with the zygotes, obtaining formulae by means of which from the zygotic proportions in earlier generations we can determine those in later generations.

In self-fertilization the linkage ratio r would perhaps be the same for both the sets of gametes produced by the single self-fertilizing individual. It is conceivable however that linkage might be found complete in the formation of one of the two sorts of gametes. We shall therefore deal, as usual, with both cases.

(43) General formula for determining the zygotic proportions in generation $n+1$, when those for generation n are known

The population at the beginning is that shown in table 1 (proper values being given to the letters c to l). These produce the gametes shown in table 3. Next the gametes produced by any single zygote mate together at random; those of column 1, table 3, in the case where linkage is the same in both sets of gametes; those of column 1 with those of column 2 (table 3), where linkage is complete in one set of gametes.

By making these matings; determining the zygotes produced (for generation $n + 1$), then collecting the proportions of each kind of zygote of generation $n + 1$, we obtain the formulae of table 30, giving directly the proportions of the zygotes of generation $n + 1$ in terms of those of generation n. Column 1 gives the results when linkage is the same in both sets of gametes; column 2 the results when linkage is complete in one set.

Example. Let us take the example given in section (10), supposing however that breeding is by self-fertilization. That is, we begin with a population consisting of 3 *ABAB* + 1 *abab* + 1 *AbaB* + 4 *ABaB;* the linkage ratio r being 2. Then by table 1:

$$c = 3 \qquad f = 1 \qquad h = 1 \qquad j = 4$$

By table 30 the population in the next generation will be the following:

If linkage is the same in both sets				If linkage is complete in one set of gametes		
ABAB	$= 3^2.(12+4)+1$	= 145	= .448	3 (12+4)	= 48	= .444
AbAb	$= 2^2.1$	= 4	= .012	2.1	= 2	= .019
aBaB	$= 3^2.4+2^2.1$	= 40	= .123	3.4+2	= 14	= .130
abab	$= 3^2.4+1$	= 37	= .114	3.4	= 12	= .111
Homozygotes		= 226	= .698		= 76	= .704
ABab	= 2.1	= 2	= .006		= 0	= .000
AbaB	= 2.4	= 8	= .025	4.1	= 4	= .037
Heterozygotes		= 10	= .031		= 4	= .037
ABAb	= 4.1	= 4	= .012		= 1	= .009
ABaB	$= 2.3^2 4+4.1$	= 76	= .235	2.3.4+1	= 25	= .231
abAb	= 4.1	= 4	= .012		= 1	= .009
abaB	= 4.1	= 4	= .012		= 1	= .009
Mixed		= 88	= .272		= 28	= .259
Totals		= 324	= 1.000		= 108	= 1.000

By substituting anew the values here found for the letters c to l in table 1, and reapplying the formulae of table 30, we can find if desired the proportions in generation $n + 2$, and so on for later generations. Either the actual numbers, or the proportions as reduced to decimals (the last column in each case, above) may be used for the further computations.

(44) *Special formulae for the case in which the original parents are ABab*

In this specially important case, where at the beginning of self-fertilization the parents are the result of a cross between two individuals (*ABAB* and *abab*) differing in two pairs of characters, we shall develop formulae for obtaining at once the proportions of the different sorts of zygotes after any number n of self-fertilizations.

Since we begin with *ABab,* the population is represented merely by $g = 1$ (of table 1, while all the other proportions c to l of table 1 are 0). Employing table 30 we find that after one self-fertilization ($n = 1$), the different classes of zygotes are represented as follows:

Zygotes of $n = 1$	Column 1, linkage the same $(= r)$ in both sets of gametes	Column 2, linkage complete in one of the sets of gametes
c $(= ABAB)$ d $(= AbAb)$ e $(= aBaB)$ f $(= abab)$	r^2 1 1 r^2	r 0 0 r
Total homozygotes	$2r^2 + 2$	$2r$
g $(= ABab)$ h $(= AbaB)$	$2r^2$ 2	$2r$ 0
Total heterozygotes	$2r^2 + 2$	$2r$
i $(= ABAb)$ j $(= ABaB)$ k $(= abAb)$ l $(= abaB)$	$2r$ $2r$ $2r$ $2r$	1 1 1 1
Total mixed	$8r$	4
Grand total	$4(r + 1)^2$	$4(r + 1)$

Now, as we work out the proportions in later generations, we find that certain relations of equality shown in the above list hold for all generations. The four kinds of homozygotes are divisible into two pairs, those retaining the linkage of the parents (that is, c and f, or $ABAB$ and $abab$); and those not retaining the original linkage (that is d and e, or $AbAb$ and $aBaB$). The two former are always equal, and so are the two latter; that is, $c = f$, and $d = e$. Furthermore, the four kinds of mixed are always present in equal proportions. The two sorts of heterozygotes, g and h, differ in their proportional values. These relations simplify the problem, since they enable us to reduce our number of unknown quantities. Thus, instead of dealing separately with the four classes of mixed, we may find merely the total proportion of mixed (which we may call M), and we can then know that the proportion for any particular sort (as $ABaB$) will be ¼ that of M. Similar relations hold for the two sorts of homozygotes in each of the pairs. The result is that there are just five diverse quantities to deal with; the two sorts of homozygotes; the corresponding two sorts of heterozygotes, and the mixed.

In our list of the proportions of the different kinds of zygotes of generation 1 just given, each proportion is of course essentially a fraction, and its actual value is obtained by dividing the value given by the total for all; that is, by $4(r+1)^2$ in column 1, or by $4(r+1)$ in column 2. Thus in column 1 the actual fractional proportion for $g(=ABab)$ is $2r^2/4(r+1)^2$, for h it is $2/4(r+1)^2$, etc. Now, it turns out to be most convenient to deal with certain of these proportions explicitly as fractions. The same fractions found in generation 1 occur in later generations, and it is best to designate certain of the important fractions by single letters. The fractions given by the heterozygotes turn out to be of special importance, and in particular a designation is required for the fraction given by the sum of the two sorts of heterozygotes ($g+h$) and that given by their difference ($g-h$). Where linkage is complete in one set, however (column 2) $g+h$ and $g-h$ are the same, since h is zero; in this case therefore we require but one designation. In column 1 (linkage $= r$ in both sets) we shall call the sum of $g+h$ by the letter v, the difference ($g-h$) by the letter w. In column 2 (linkage complete in one set) we shall call the sum $g+h$ by the letter u; the difference $g-h$ is likewise u. That is, from the table on page 136.

Linkage $= r$ in both sets	Linkage complete in one set
$v = \dfrac{r^2+1}{2(r+1)^2}$ $w = \dfrac{r^2-1}{2(r+1)^2}$	$u = \dfrac{r}{2(r+1)}$

It is important to bear in mind the facts (1) that v, w and u are *fractions;* (2) that their values do not change from generation to generation, but are always those just given. It will be observed that the values for the different sorts of zygotes after one self-fertilization, as given on page 136, can be given in terms of these fractions, thus:

	Column 1	Column 2
$c = f =$	$\dfrac{v+w}{4}$	$\dfrac{u}{2}$
$d = e =$	$\dfrac{v-w}{4}$	0
Homozygotes $=$	v	u
$g =$	$\dfrac{v+w}{2}$	u
$h =$	$\dfrac{v-w}{2}$	0
Heterozygotes $=$	v	u
$i = j = k = l =$	$\dfrac{1-2v}{4}$	$\dfrac{1-2u}{4}$
Mixed $=$	$1-2v$	$1-2u$

(The values for the mixed result merely from the fact that they are equal to the total, minus the sum of the heterozygotes and homozygotes.)

If now we work out by table 30 the proportions of the different sorts of zygotes in later generations, and express our results in terms of the fractions v, w, and u, we discover for any generation n the following general relations:

	Linkage $= r$ in both sets	Linkage complete in one set
Sum of the two classes of homozygotes, $(c+f)+(d+e)$	$=\frac{2^{n-2}}{2^n}+v^n$	$\frac{2^{n-2}}{2^n}+u^n$
Difference of the two classes of homozygotes, $(c+f)-(d+e)$	$=w^1+w^2+w^3\ldots w^n$	$u^1+u^2+u^3\ldots u^n$
Sum of the two classes of heterozygotes, $g+h$	$=v^n$	u^n
Difference of the two classes of heterozygotes, $g-h$	$=w^n$	u^n

These equations may readily be solved for the values of $c+f$ and of $d+e$; also for the values of g and h. Since we know that $c=f$ and $d=e$, this will give us at once the values of c, d, e, f, g and h. We can, of course, then readily obtain the value of the total mixed (since these constitute merely the remainder) and of any particular class of mixed (since the four classes of mixed are equal). Carrying out these solutions, we obtain the final formulae set forth in table 31.

Example. Let us suppose that, beginning with the parent $ABab$, there have been three self-fertilizations; that the linkage ratio is 2; and that linkage is the same in both sets of gametes.

Here we have:

$$r=2 \qquad v=\tfrac{5}{18} \qquad u=\tfrac{3}{18} \qquad n=3$$

Hence:

$$\text{Total homozygotes} = \frac{2^2-1}{2^2}+\left(\tfrac{5}{18}\right)^3 = \tfrac{3}{4}+\tfrac{125}{5832} = \tfrac{4499}{5832} = .7714$$

$$c(=ABAB) = \frac{2^2-1}{2^4}+\tfrac{1}{4}\left[\left(\tfrac{5}{18}\right)^3+\left(\tfrac{3}{18}\right)^3+\left(\tfrac{3}{18}\right)^2+\tfrac{3}{18}\right]=\tfrac{1415}{5832}=.2427$$

$$d(=AbAb) = \frac{2^2-1}{2^4}+\tfrac{1}{4}\left[\left(\tfrac{5}{18}\right)^3-\left(\tfrac{3}{18}\right)^3-\left(\tfrac{3}{18}\right)^2-\tfrac{3}{18}\right]=\tfrac{1669}{11664}=.1431$$

$e(=aBaB)=.1431$

$f(=abab)=.2427$

Total heterozygotes $=\left(\tfrac{5}{18}\right)^3=\tfrac{125}{5832}=.0214$

$g(=ABab)=\tfrac{1}{2}\left[\left(\tfrac{5}{18}\right)^3+\left(\tfrac{3}{18}\right)^3\right]=\tfrac{76}{5832}=.0130$

$h(=AbaB)=\tfrac{1}{2}\left[\left(\tfrac{5}{18}\right)^3-\left(\tfrac{3}{18}\right)^3\right]=\tfrac{49}{5832}=.0084$

Total mixed $=\tfrac{1}{4}-2\left(\tfrac{5}{18}\right)^3=\tfrac{1208}{5832}=.2071$

Any single class of mixed (as $ABAb$) $=\tfrac{1}{4}\times\tfrac{1208}{5832}=.0518$

If we assume that linkage is complete in one of the sets of gametes, we have $u = 1/3$; the results are then obtained in a similar manner; they are as follows:

$$\text{Total homozygotes} = .7870$$
$$d = e = .0764$$
$$c = f = .3171$$
$$\text{Total heterozygotes} = (1/3)^3 = 1/27 = .0370$$
$$g(=ABab) = (1/3)^3 = .0370$$
$$c = f = .3171$$

Total mixed $= 1/2^2 - 2(1/3)^3 = 38/216 = .1759$

Any single class of mixed, as $ABaB = (1/2)^4 - 1/2(1/3)^3 = .0439$

If we classify the results with respect to either of the single pairs of factors (as A and a), we of course obtain the same results given in section (25) of my previous paper (JENNINGS 1916), that is:

$$AA \text{ (or } BB) = \frac{2^n - 1}{2^{n+1}}$$

$$aa \text{ (or } bb) = \frac{2^n - 1}{2^{n+1}}$$

$$Aa \text{ (or } Bb) = \frac{1}{2^n}$$

(45) *Parents AbaB (derived from a cross of AbAb with aBaB)*

In this case, the results are as given in table 31, but with the following alterations in the formulae:

The values for c and d are to be interchanged.

The values for e and f are to be interchanged.

The values for g and h are to be interchanged.

The values remain unchanged for the total homozygotes; for the total heterozygotes; for the total mixed; and for any particular class of mixed.

REMARKS ON INBREEDING. To obtain a general formula for inbreeding with brother by sister mating, when two linked pairs of characters are considered, one begins with a family composed as in table 1, proper values being given to the letters c to l. When such a family is inbred, the linkage ratio being r for both sexes, it gives 55 diverse types of families (the number of families being $\frac{n(n+1)}{2}$ where n is the number of differing individuals in the original family). By determining the types of families produced from each of these 55 families, and collecting the results for each of the possible 55 kinds of newly formed families, one obtains formulae giving the constitution in families in the generation $n + 1$, when that in generation n is known. Such formulae are complex, some of the 55 equations being made up of as many as 24 terms. It hardly seems worth while to publish the complex table of formulae thus obtained; possibly it may be employed later to obtain the actual gametic constitution of the population in later generations for the more important special cases, as when the original parents are all *ABab*, and the like. The entire subject of inbreeding with relation to two pairs of linked factors is therefore reserved for further treatment. The paper of DETLEFSEN (1914) contains discussions and formulae for certain special cases of inbreeding when two pairs of independent factors are dealt with. The present writer would find it a relief if some one else would deal thoroughly with the laborious problem of the effects of inbreeding on two pairs of linked factors.

SUMMARY

This paper derives formulae for finding in later generations the results of continued breeding by a given system, when two pairs of characters, linked or independent, are considered. Its primary purpose is to render it possible to determine the effects of linkage on the distribution of the factors. The systems of breeding considered are: random mating; selection with respect to a given single character; assortative mating with respect to a single character; and self-fertilization. In each system two cases are dealt with; that in which linkage is the same in both sets of gametes; and that in which linkage is complete in one set. In each system general formulae are derived for transforming generation n into generation $n + 1$. In several systems special formulae are given for finding directly in any later generation n the proportions of the population, when one begins with parents that are a cross between *ABAB* and *abab*; or between *AbAb* and *aBaB*. With regard to selection and assortative mating with respect to a single character, formulae are given for the effect on the single pairs taken separately; thus for the effect of selection or assortative mating with respect to one character on the distribution of another character linked with that one.

The formulae are collected for convenience in 31 tables, which are placed in order at the end of the paper.

LITERATURE CITED

DETLEFSEN, J. A., 1914 Genetic studies on a cavy species cross. Carnegie Institution of Washington, Publication No. 205, 134 pp.

JENNINGS, H. S., 1916 The numerical results of diverse systems of breeding. Genetics **1**: 53-89.

WENTWORTH, E. N., and REMICK, B. L., 1916 Some breeding properties of the generalized Mendelian population. Genetics **1**: 608-616.

TABLES FOR USE IN COMPUTING THE NUMERICAL RESULTS OF DIVERSE SYSTEMS OF BREEDING, WITH RESPECT TO TWO PAIRS OF FACTORS

Table 1. The ten diverse possible classes of zygotes with respect to two pairs of factors (*A*, *a* and *B*, *b*), with the algebraic designations (*c* to *l*) that will be employed to represent their respective proportions. By giving the proper values to the letters *c* to *l*, any population may be represented by this table.

Homozygotes	*Heterozygotes*	*Mixed*
c.ABAB	*g.ABab*	*i.ABAb*
d.AbAb	*h.AbaB*	*j.ABaB*
e.aBaB		*k.abAb*
f.abab		*l.abaB*

With respect to the single pairs taken separately:

$$AA = c+d+i \qquad aa = e+f+l \qquad Aa = g+h+j+k$$
$$BB = c+e+j \qquad bb = d+f+k \qquad Bb = g+h+i+l$$

Table 2. The four possible classes of gametes with respect to two pairs of factors, with the algebraic designations (*p*, *q*, *s*, *t*) for their relative proportions.

p.AB *q.Ab* *s.aB* *t.ab*

(To distinguish certain classes of gametes, in some cases the capital letters, *P, Q, S, T,* will be used in place of the lower case letters; and in assortative mating, for special purposes the corresponding Greek letters σ and τ will be used for *s* and *t*. See tables 5, 8, 25, 26, etc.)

Table 3. Gametes given by the ten sorts of zygotes of table 1, when the linkage is r; and when linkage is complete.

Zygotes	Gametes produced	
	1. Linkage $= r$	2. Linkage complete
$c.ABAB$	$c.(2r+2)AB$	$2c.AB$
$d.AbAb$	$d.(2r+2)Ab$	$2d.Ab$
$e.aBaB$	$e.(2r+2)aB$	$2e.aB$
$f.abab$	$f.(2r+2)ab$	$2f.ab$
$g.ABab$	$g.(r\,AB+1\,Ab+1\,aB+r\,ab)$	$g.AB+g.ab$
$h.AbaB$	$h.(r\,Ab+1\,AB+1\,ab+r\,aB)$	$h.Ab+h.aB$
$i.ABAb$	$i.(r+1)AB+i.(r+1)Ab$	$i.AB+i.Ab$
$j.ABaB$	$j.(r+1)AB+j.(r+1)aB$	$j.AB+j.aB$
$k.abAb$	$k.(r+1)ab+k.(r+1)Ab$	$k.ab+k.Ab$
$l.abaB$	$l.(r+1)ab+l.(r+1)aB$	$l.ab+l.aB$

Table 4. Linkage r. Proportions of the different kinds of gametes produced by a population of zygotes (of table 1) in terms of the proportions of the zygotes.

$$p(=AB) = (r+1)(2c+i+j)+rg+h$$
$$q(=Ab) = (r+1)(2d+i+k)+rh+g$$
$$s(=aB) = (r+1)(2e+j+l)+rh+g$$
$$t(=ab) = (r+1)(2f+k+l)+rg+h$$
$$p+q+s+t = (2r+2)(c+d+e+f+g+h+i+j+k+l)$$

Table 5. Linkage complete. Proportions of the different kinds of gametes produced by a population of zygotes (table 1), in terms of the proportions of the parent zygotes.

$$P(=AB) = 2c+g+i+j$$
$$Q(=Ab) = 2d+h+i+k$$
$$S(=aB) = 2e+h+j+l$$
$$T(=ab) = 2f+g+k+l$$
$$P+Q+S+T = 2(c+d+e+f+g+h+i+j+k+l)$$
$$p+q+s+t \text{ (of table 4)} = (r+1)(P+Q+S+T)$$

Table 6. Random mating of the four types of gametes (of table 2), with the zygotes produced.

Gametes — *Zygotes*

$$\left.\begin{array}{l} p.AB \\ q.Ab \\ s.aB \\ t.ab \end{array}\right\} \times \left\{\begin{array}{l} p.AB \\ q.Ab \\ s.aB \\ t.ab \end{array}\right. =$$

$p.^2$ *AB* *AB*	$pq.$ *AB* *Ab*	$ps.$ *AB* *aB*	$pt.$ *AB* *ab*
$qp.$ *Ab* *AB*	$q.^2$ *Ab* *Ab*	$qs.$ *Ab* *aB*	$qt.$ *Ab* *ab*
$sp.$ *aB* *AB*	$sq.$ *aB* *Ab*	$s.^2$ *aB* *aB*	$st.$ *aB* *ab*
$tp.$ *ab* *AB*	$tq.$ *ab* *Ab*	$ts.$ *ab* *aB*	$t.^2$ *ab* *ab*

Table 7. Proportions of the various types of zygotes resulting from the random mating of the four types of gametes (of tables 2 and 6), in terms of the proportions of the gametes.

Homozygotes		*Mixed*	
$c(=ABAB)$	$=p^2$	$i(=ABAb)$	$=2pq$
$d(=AbAb)$	$=q^2$	$j(=ABaB)$	$=2ps$
$e(=aBaB)$	$=s^2$	$k(=abAb)$	$=2qt$
$f(=abab)$	$=t^2$	$l(=abaB)$	$=2st$

Total homozygotes $=p^2+q^2+s^2+t^2$. Total mixed $=2(pq+ps+qt+st)$

Heterozygotes

$g(=ABab)=2pt$
$h(=AbaB)=2qs$

Total heterozygotes $=2(pt+qs)$

Total zygotes $=(p+q+s+t)^2$

Table 8. Proportions of the various types of zygotes resulting from the random mating of the four types of gametes produced with linkage r (table 4), with the four types produced with complete linkage (table 5).

Homozygotes	*Mixed*
$c(=ABAB) = Pp$	$i(=ABAb) = Pq+pQ$
$d(=AbAb) = Qq$	$j(=ABaB) = Ps+pS$
$e(=aBaB) = Ss$	$k(=abAb) = Qt+qT$
$f(=abab) = Tt$	$l(=abaB) = St+sT$
Total homozygotes $= Pp+Qq+Ss+Tt$	Total mixed $= Pq+pQ+Ps+pS+Qt+qT+St+sT$

Heterozygotes

$g(=ABab) = Pt+pT$

$h(=AbaB) = Qs+qS$

Total heterozygotes $= Pt+pT+Qs+qS$

Total zygotes $= (P+Q+S+T)(p+q+s+t)$

Table 9. Random mating, linkage the same $(=r)$ in both sets of gametes. Formulae for the proportions of the gametes derived from generation $n + 1$ (therefore *producing* generation $n + 2$), in terms of the gametes derived from generation n (and therefore producing generation $n + 1$). That is, formulae for p_{n+1}, q_{n+1}, s_{n+1}, t_{n+1}, in terms of p_n, q_n, s_n, t_n.

Gametes from generation $n+1$		In terms of gametes from generation n
$p(=AB)$	$=$	$(r+1)p(p+q+s)+rpt+qs$
$q(=Ab)$	$=$	$(r+1)q(p+q+t)+rqs+pt$
$s(=aB)$	$=$	$(r+1)s(p+s+t)+rqs+pt$
$t(=ab)$	$=$	$(r+1)t(q+s+t)+rpt+qs$
$p+q+s+t$	$=$	$(r+1)(p+q+s+t)^2$

Table 10. Random mating; independent factors (no linkage). Proportions of the different kinds of gametes derived from generation $n + 1$, in terms of those derived from generation n. This is table 9, simplified for the case of no linkage $(r = 1)$.

Gametes from $n + 1$		In terms of gametes from n
$p(=A\mathrm{B})$	$=$	$2p(p+q+s)+pt+qs$
$q(=Ab)$	$=$	$2p(p+q+t)+qs+pt$
$t(=ab)$	$=$	$2t(q+s+t)+pt+qs$
$s(=aB)$	$=$	$2s(p+s+t)+qs+pt$
$p+q+s+t$	$=$	$2(p+q+s+t)^2$

Table 11. Random mating; linkage complete in one set of gametes, r in the other. Formulae for the proportions of the two sets of gametes derived from generation $n+1$, in terms of the gametic proportions of the two sets derived from generation n.

Gametes from $n+1$ — In terms of gametes from n

Set 1. Gametes with linkage r.

$$p(=AB) = (r+1)p(P+Q+S)+(r+1)P(p+q+s)+r(Pt+pT)+Qs+qS$$

$$q(=Ab) = (r+1)q(P+Q+T)+(r+1)Q(p+q+t)+r(Qs+qS)+Pt+pT$$

$$s(=aB) = (r+1)s(P+S+T) + (r+1)S(p+s+t)+r(Qs+qS)+Pt+pT$$

$$t(=ab) = (r+1)t(Q+S+T) + (r+1)T(q+s+t)+r(Pt+pT)+Qs+qS$$

$$p+q+s+t = 2(r+1)(P+Q+S+T)(p+q+s+t)$$

Set 2. Gametes with complete linkage

$$P(=AB) = P(p+q+s+t)+p(P+Q+S+T)$$

$$Q(=Ab) = Q(p+q+s+t)+q(P+Q+S+T)$$

$$S(=aB) = S(p+q+s+t)+s(P+Q+S+T)$$

$$T(=ab) = T(p+q+s+t)+t(P+Q+S+T)$$

$$P+Q+S+T = 2(P+Q+S+T)(p+q+s+t)$$

Table 12. Random mating, linkage complete in one set of gametes, r in the other set. Certain relations between the proportions of the gametes of the two sets, in any given generation. Derived from table 11.

(The same relations hold for the two sets of table 15, in selection for dominants.)

Set 1		*Set 2*
$p+q$	=	$(r+1)(P+Q)$
$p+s$	=	$(r+1)(P+S)$
$q+t$	=	$(r+1)(Q+T)$
$s+t$	=	$(r+1)(S+T)$
$p+q+s+t$	=	$(r+1)(P+Q+S+T)$

Table 13. Random mating, original parents all *ABab;* linkage r in both sets of gametes. Proportions of the different classes of gametes for producing any required generation n.

Gametes for producing generation n

$$p(=t) = (r+1)^n+r^n-r^{n-1}$$

$$q(=s) = (r+1)^n-r^n+r^{n-1}$$

If the original parents are *AbaB*, interchange the values of $p(=t)$ and $q(=s)$.

Table 14. Random mating, original parents all *ABab;* linkage r in one set of gametes, complete in the other. Proportions of the different classes of gametes for producing any required generation n.

Gametes for producing generation n		
$p(=t)$	=	$2^{n-2}(r+1)^n+r^2(2r+1)^{n-2}$
$q(=s)$	=	$2^{n-2}(r+1)^n-r^2(2r+1)^{n-2}$
$P(=T)$	=	$2^{n-2}(r+1)^{n-1}+r(2r+1)^{n-2}$
$Q(=S)$	=	$2^{n-2}(r+1)^{n-1}-r(2r+1)^{n-2}$

If the original parents are *AbaB*, interchange the values of $p(=t)$ and $q(=s)$; also interchange the values of $P(=T)$ and $Q(=S)$.

Table 15. Selection for dominant A. Proportions of the different kinds of gametes produced by a population of zygotes (of table 1), in terms of the proportions of the zygotes; when linkage is r; and when it is complete.

Set 1. Linkage r	Set 2. Linkage complete
$p(=AB) = (r+1)(2c+i+j)+rg+h$	$P(=AB) = 2c+g+i+j$
$q(=Ab) = (r+1)(2d+i+k)+rh+g$	$Q(=Ab) = 2d+h+i+k$
$s(=aB) = (r+1)j+rh+g$	$S(=aB) = h+j$
$t(=ab) = (r+1)k+rg+h$	$T(=ab) = g+k$
$p+q+s+t = (2r+2)(c+d+g+h+i+j+k)$	$P+Q+S+T = 2(c+d+g+h+i+j+k)$

The relations shown in table 12 hold for the two sets of table 15, as well as for those of table 11.

Table 16. Selection for dominant A; linkage the same $(=r)$ in both sets of gametes. Proportions of the different sorts of gametes derived from generation $n+1$, in terms of those derived from generation n.

Gametes produced by generation $n+1$		In terms of gametes produced by generation n
$p(=AB)$	=	$(r+1)p(p+q+s)+rpt+qs$
$q(=Ab)$	=	$(r+1)q(p+q+t)+rqs+pt$
$s(=aB)$	=	$(r+1)ps+rqs+pt$
$t(=ab)$	=	$(r+1)qt+rpt+qs$
$p+q+s+t$	=	$(r+1)(p+q)(p+q+s+t)$

Table 17. Selection of dominant A; linkage complete in one set of gametes; r in the other. Proportions of the two sets of gametes derived from generation $n+1$, in terms of the gametic proportions of the two sets derived from generation n.

Set 1. Gametes with linkage r

Gametes from $n+1$ — In terms of gametes from n

$$p(=AB) = (r+1)p(P+Q+S)+(r+1)P(p+q+s)+r(Pt+pT)+Qs+qS$$
$$q(=Ab) = (r+1)q(P+Q+T)+(r+1)Q(p+q+t)+r(Qs+qS)+Pt+pT$$
$$s(=aB) = (r+1)(Sp+sP)+r(Qs+qS)+Pt+pT$$
$$t(=ab) = (r+1)(Qt+qT)+r(Pt+pT)+Qs+qS$$
$$p+q+s+t = 2(r+1)[(p+q)(P+Q+S+T)+(P+Q)(s+t)]$$

Set 2. Gametes with complete linkage

$$P(=AB) = P(p+q+s+t)+p(P+Q+S+T)$$
$$Q(=Ab) = Q(p+q+s+t)+q(P+Q+S+T)$$
$$S(=aB) = S(p+q)+s(P+Q)$$
$$T(=ab) = T(p+q)+t(P+Q)$$
$$P+Q+S+T = 2[(p+q)(P+Q+S+T)+(P+Q)(s+t)]$$

Table 18. Proportions of the gametes containing A or a; and of those containing B or b. (In terms of tables 9 to 11, or of tables 15 to 17; these relations of course hold equally of random mating and of selection of dominants.)

Set 1. Gametes with linkage r	Set 2. Gametes with complete linkage
$A = p + q$	$A = P + Q$
$a = s + t$	$a = S + T$
$B = p + s$	$B = P + S$
$b = q + t$	$b = Q + T$

Table 19. Proportions of the different classes of zygotes in generation $n+1$, with reference to the single factor-pairs taken separately, in terms of the gametes of tables 9 to 11 or of tables 15 to 17.

Set 1. Linkage (r) the same in both sets of gametes	Set 2. Linkage complete in one set of gametes; r in the other
$AA = (p+q)^2$	$AA = (p+q)(P+Q)$
$Aa = 2(p+q)(s+t)$	$Aa = (p+q)(S+T)+(P+Q)(s+t)$
$aa = (s+t)^2$	$aa = (s+t)(S+T)$
$BB = (p+s)^2$	$BB = (p+s)(P+S)$
$Bb = 2(p+s)(q+t)$	$Bb = (p+s)(Q+T)+(P+S)(q+t)$
$bb = (q+t)^2$	$bb = (q+t)(Q+T)$

Table 20. Selection of parents containing dominant *A*. Original parents all *ABab*. Proportions of the 10 possible sorts of individuals (zygotes) produced for the first 4 generations (n) when there is no linkage ($r=1$), when the linkage ratio is 2 in both sexes ($r=2$), and when the linkage is 2 in one sex, but complete in the other ($r=2+$).

$n=$	1			2		
	$r=1$	2	2+	1	2	2+
ABAB	=1=.0625	4=.1111	2=.1667	4=.1111	121=.1670	260=.2675
AbAb	=1=.0625	1=.0278	0=.0	4=.1111	49=.0672	20=.2058
aBaB	=1=.0625	1=.0278	0=.0	1=.0278	16=.0219	7=.0072
abab	=1=.0625	4=.1111	2=.1667	1=.0278	25=.0343	55=.0566
Homo.	=4=.2500	10=.2778	4=.3333	10=.2778	211=.2894	342=.3519
ABab	=2=.1250	8=.2222	4=.3333	4=.1111	110=.1509	240=.2469
AbaB	=2=.1250	2=.0555	0=.0	4=.1111	56=.0768	24=.0247
Hetero.	=4=.2500	10=.2778	4=.3333	8=.2222	166=.2277	264=.2716
ABAb	=2=.1250	4=.1111	1=.0833	8=.2222	154=.2112	152=.1564
ABaB	=2=.1250	4=.1111	1=.0833	4=.1111	88=.1207	96=.0988
abAb	=2=.1250	4=.1111	1=.0833	4=.1111	70=.0960	72=.0741
abaB	=2=.1250	4=.1111	1=.0833	2=.0555	40=.0549	46=.0473
Mixed	=8=.5000	16=.4444	4=.3333	18=.5000	352=.4829	366=.3765
Total	=16=1.	36=1.	12=1.	36=1.	729=1.	972=1.

$n=$	3			4		
	$r=1$	2	2+	1	2	2+
ABAB	=9=.1406	1024=.1975	1638=.3160	16=.1600	143,641=.2189	33,480=.3444
AbAb	=9=.1406	484=.0934	180=.0347	16=.1600	72,361=.1103	4.392=.0452
aBaB	=1=.0156	81=.0156	40=.0077	1=.0100	7,396=.0113	689=.0071
abab	=1=.0156	81=.0156	130=.0251	1=.0100	5,776=.0088	1,265=.0130
Homo.	=20=.3125	1670=.3221	1938=.3738	34=.3400	229,174=.3493	39,826=.4097
ABab	=6=.0937	576=.1111	927=.1788	8=.0800	57,608=.0878	13,070=.1345
AbaB	=6=.0937	396=.0764	171=.0330	8=.0800	46,268=.0705	3,494=.0359
Hetero.	=12=.1875	972=.1875	1098=.2118	16=.1600	103,876=.1583	16,564=.1704
ABAb	=18=.2813	1408=.2716	1098=.2118	32=.3200	203,902=.3107	24,336=.2504
ABaB	=6=.0937	576=.1111	531=.1024	8=.0800	65,188=.0993	9,754=.1003
abAb	=6=.0937	396=.0764	315=.0608	8=.0800	40,888=.0623	4,786=.0492
abaB	=2=.0313	162=.0312	154=.0297	2=.0200	13,072=.0199	1,934=.0199
Mixed	=32=.5000	2542=.4904	2098=.4049	50=.5000	323,050=.4923	40,810=.4199
Total	=64=1.	5184=1.	5184=1.	100=1.	656,100=1.	97,200=1.

Table 21. Selection of parents containing dominant *A*. Original parents all *ABab*. Proportions of the different sorts of individuals for the single factor pairs taken separately, for the first four generations of selection, when there is no linkage ($r=1$); when the linkage ratio is 2 in both sexes ($r=2$), and when the linkage is 2 in one sex but complete in the other ($r=2+$). Primarily to illustrate the effect of selection with respect to one factor-pair (A, a) on another factor-pair (B, b), linked with the former, or independent of it.

$n =$	1			2	
r = 1	2	2+	1	2	2+
AA = 1	1	1	4	4	4
Aa = 2	2	2	4	4	4
aa = 1	1	1	1	1	1
Totals 4	4	4	9	9	9
BB = 1	1	1	1	25	121
Bb = 2	2	2	2	40	154
bb = 1	1	1	1	16	49
Totals 4	4	4	4	81	324
$n =$	3			4	
r = 1	2	2+	1	2	2+
AA = 9	9	9	16	16	16
Aa = 6	6	6	8	8	8
aa = 1	1	1	1	1	1
Totals 16	16	16	25	25	25
BB = 1	1681	2209	1	961	14641
Ab = 2	2542	2350	2	1426	14278
bb = 1	961	625	1	529	3481
Totals 4	5184	5184	4	2916	32400

Table 22. Selection of recessive *aa*; linkage either *r*, or complete. Proportions of the different kinds of gametes produced by a population (table 1), in terms of the proportions of the zygotes given in table 1.

$$s \text{ or } S(=aB) = 2e+l$$
$$t \text{ or } T(=ab) = 2f+l$$
$$s+t \text{ (or } S+T) = 2(e+f+l)$$

Table 23. Selection of recessive aa; linkage either r in both sets of gametes, or complete in one set. Proportions of the different classes of zygotes, in any generation n, in terms of the gametes (table 22) from generation 1.

$$e(=aBaB) = s^2 \quad (\text{or } sS)$$
$$f(=abab) = t^2 \quad (\text{or } tT)$$
$$l(=abaB) = 2st \quad (\text{or } sT+St)$$
$$\text{Total zygotes } (e+f+l) = (s+t)^2, \ (\text{or } (s+t)(S+T))$$

Table 24. Assortative mating. Designations to be employed for the sums of the classes of zygotes of table 1 that are dominant (D) with respect to the character A; that are recessive (R) with respect to that character; and for the sum of all (N). In terms of the proportions given in table 1.

$$D = c+d+g+h+i+j+k$$
$$R = e+f+l$$
$$N = D+R$$

Table 25. Assortative mating. Proportions of the different kinds of gametes produced by the recessives (aa) of a population (table 1), in terms of the zygotes producing them. (This table is the same as table 22, but with substitution of Greek letters for the corresponding English ones, for the exigencies of work with assortative mating.)

Set 1. Gametes formed with linkage r

$$\sigma(=aB) = 2e+l$$
$$\tau(=ab) = 2f+l$$
$$\sigma+\tau = 2(e+f+l)$$

Set 2. Gametes formed with complete linkage

$$\Sigma(=aB) = 2e+l$$
$$\mathrm{T}(=ab) = 2f+l$$
$$\Sigma+\mathrm{T} = 2(e+f+l)$$

Table 26. Assortative mating. Proportions of the different classes of zygotes in the next generation $n+1$, in terms of the gametes producing them (of tables 15 and 25), and of the proportions of D, R, and N of table 24.

N.B. Where R is 0, simply omit R from the values; do *not* give R the value of 0 (see note in section (37)). For R, D and N any values that conserve their correct relative proportions may be employed.

Zygotes of $n+1$	Column 1. Proportions when the linkage (r) is the same in both sets of gametes	Column 2. Proportions when the linkage is complete in one set of gametes, r in the other
$c(=ABAB)$	Rp^2	$R\,Pp$
$d(=AbAb)$	Rq^2	$R\,Qq$
$e(=aBaB)$	$Rs^2+D(r+1)^2\sigma^2$	$R\,Ss+D(r+1)\Sigma\sigma$
$f(=abab)$	$Rt^2+D(r+1)^2\tau^2$	$R\,Tt+D(r+1)\mathrm{T}\tau$
$g(=ABab)$	$2Rpt$	$R(Pt+pT)$
$h(=AbaB)$	$2Rqs$	$R(Qs+qS)$
$i(=ABAb)$	$2Rpq$	$R(Pq+pQ)$
$j(=ABaB)$	$2Rps$	$R(Ps+pS)$
$k(=abAb)$	$2Rqt$	$R(Qt+qT)$
$l(=abaB)$	$2Rst+2(r+1)^2D\sigma\tau$	$R(St+sT)+D(r+1)(\Sigma\tau+\sigma\mathrm{T})$

Table 27. Assortative mating. Linkage (r) the same in both sets of gametes. Formulae for deriving the proportions of the different kinds of gametes produced by generation $n+1$, when the gametes produced by generation n are known.

N. B. Where R is 0 it is to be omitted from the equations; *not* given the value 0.

(1) From the dominants

Gametes from $n+1$		In terms of gametes from n, and of R and D of generation n
$p(=AB)$	=	$R(r+1)p(p+q+s)+R(rpt+qs)$
$q(=Ab)$	=	$R(r+1)q(p+q+t)+R(rqs+pt)$
$s(=aB)$	=	$R[(r+1)ps+rqs+pt]$
$t(=ab)$	=	$R[(r+1)qt+rpt+qs]$

(2) From the recessives

$$\sigma(=aB) = Rs(s+t)+D(r+1)^2\sigma(\sigma+\tau)$$
$$\tau(=ab) = Rt(s+t)+D(r+1)^2\tau(\sigma+\tau)$$
$$D_{n+1} = \frac{p+q+s+t}{r+1} \text{ of generation n+1}$$
$$R_{n+1} = \sigma+\tau \text{ of generation } n+1$$

Table 28. Assortative mating; linkage complete in one set of gametes, r in the other. Formulae for the gametes produced by generation $n+1$, in terms of those produced by generation n.

N.B. Where R is 0, the factor R is to be omitted from the equations. It must *not* be given the value 0.

Set 1. From the sex in which linkage is r.

(1) From the dominants

Gametes from $n+1$ — In terms of gametes from n, and of R and D of n

$p(=AB) =$
$$R(r+1)P(p+q+s)+R(r+1)p(P+Q+S)+R(rPt+rpT+Qs+qS)$$
$q(=Ab) =$
$$R(r+1)Q(p+q+t)+R(r+1)q(P+Q+T)+R(rQs+rqS+Pt+pT)$$
$$s(=aB) = R(r+1)(Ps+pS)+R(rQs+rqS+Pt+pT)$$
$$t(=ab) = R(r+1)(Qt+qT)+R(rPt+rpT+Qs+qS)$$

(2) From the recessives

$$\sigma(=aB) = R(2Ss+St+sT)+D(r+1)(2\Sigma\sigma+\Sigma\tau+\sigma\mathrm{T})$$
$$\tau(=ab) = R(2Tt+St+sT)+D(r+1)(2\mathrm{T}\tau+\Sigma\tau+\sigma\mathrm{T})$$

Set 2. From the sex with linkage complete.

(1) From the dominants

$$P(=AB) = RP(p+q+s+t)+Rp(P+Q+S+T)$$
$$Q(=Ab) = RQ(p+q+s+t)+Rq(P+Q+S+T)$$
$$S(=aB) = RS(p+q) \quad +Rs(P+Q)$$
$$T(=ab) = RT(p+q) \quad +Rt(P+Q)$$

(2) From the recessives

$$\Sigma(=aB) = R(2Ss+St+sT)+D(r+1)(2\Sigma\sigma+\Sigma\tau+\sigma\mathrm{T})$$
$$\mathrm{T}(=ab) = R(2Tt+St+sT)+D(r+1)(2\mathrm{T}\tau+\Sigma\tau+\sigma\mathrm{T})$$
$$D_{n+1} = P+Q+S+T = \frac{p+q+s+t}{r+1} \text{ (of generation } n+1)$$
$$R_{n+1} = \sigma+\tau = \Sigma+\mathrm{T} \text{ (of generation } n+1)$$

Table 29. Assortative mating. Proportions of the different classes of zygotes in generation $n+1$, with respect to the two pairs of factors taken separately, in terms of the gametes from generation n, and of R and D of generation n. Derived from table 26.

Zygotes	Column 1. Proportions when the linkage is the same (r) in both sets of gametes.	Column 2. Proportions when the linkage is complete in one set, r in the other set of gametes.
$AA(=c+d+i)$	$R(p+q)^2$	$R(P+Q)(p+q)$
$Aa(=g+h+j+k)$	$2R(p+q)(s+t)$	$R(P+Q)(s+t)+R(p+q)(S+T)$
$aa(=e+f+l)$	$R(s+t)^2+(r+1)^2D(\sigma+\tau)^2$	$R(S+T)(s+t)+$ $(r+1)D(\Sigma+\mathrm{T})(\sigma+\tau)$
Total	$R(p+q+s+t)^2+(r+1)^2D(\sigma+\tau)^2$	$R(P+Q+S+T)(p+q+s+t)$ $+(r+1)D(\Sigma+\mathrm{T})(\sigma+\tau)$
$BB(=c+e+j)$	$R(p+s)^2+(r+1)^2D\sigma^2$	$R(P+S)(p+s)+(r+1)D\Sigma\sigma$
$Bb(=g+h+i+l)$	$2R(p+s)(q+t)+2(r+1)^2D\sigma\tau$	$R(P+S)(q+t)+R(p+s)$ $(Q+T)+(r+1)D(\Sigma\tau+\sigma\mathrm{T})$
$bb(=d+f+k)$	$R(q+t)^2+(r+1)^2D\tau^2$	$R(Q+T)(q+t)+(r+1)D\tau\mathrm{T}$
Total	$R(p+q+s+t)^2+(r+1)^2D(\sigma+\tau)^2$	$R(P+Q+S+T)(p+q+s+t)$ $+(r+1)D(\Sigma+\mathrm{T})(\sigma+\tau)$

Table 30. Self-fertilization; proportions of the different kinds of zygotes in generation $n+1$, in terms of their proportions in generation n (the proportions in generation n are those given in table 1). Column 1, results when linkage is the same in both sets of gametes; column 2, when linkage is complete in one set.

Zygotes of $n+1$	In terms of proportions of zygotes of generation n	
	1. Linkage the same in both sets	2. Linkage complete in one set
$c(=ABAB)$	$(r+1)^2(4c+i+j)+r^2g+h$	$(r+1)(4c+i+j)+rg$
$d(=AbAb)$	$(r+1)^2(4d+i+k)+r^2h+g$	$(r+1)(4d+i+k)+rh$
$e(=aBaB)$	$(r+1)^2(4e+j+l)+r^2h+g$	$(r+1)(4e+j+l)+rh$
$f(=abab)$	$(r+1)^2(4f+k+l)+r^2g+h$	$(r+1)(4f+k+l)+rg$
Total homozygotes	$2(r+1)^2(2c+2d+2e+2f+i+j+k+l)+2(r^2+1)(g+h)$	$2(r+1)(2c+2d+2e+2f+i+j+k+l)+2r(g+h)$
$g(=ABab)$	$2(r^2g+h)$	$2rg$
$h(=AbaB)$	$2(r^2h+g)$	$2rh$
Total heterozygotes	$2(r^2+1)(g+h)$	$2r(g+h)$
$i(=ABAb)$	$2(r+1)^2i+2r(g+h)$	$2(r+1)i+g+h$
$j(=ABaB)$	$2(r+1)^2j+2r(g+h)$	$2(r+1)j+g+h$
$k(=abAb)$	$2(r+1)^2k+2r(g+h)$	$2(r+1)k+g+h$
$l(=abaB)$	$2(r+1)^2l+2r(g+h)$	$2(r+1)l+g+h$
Total mixed	$2(r+1)^2(i+j+k+l)+8r(g+h)$	$2(r+1)(i+j+k+l)+4(g+h)$
Total	$4(r+1)^2(c+d+e+f+g+h+i+j+k+l)$	$4(r+1)(c+d+e+f+g+h+i+j+k+l)$

Table 31. Self-fertilization. Formulae for the zygotic constitution of the population derived from original parents *ABab* by any number n of successive self-fertilizations.

Let r = the linkage ratio

n = the number of successive self-fertilizations.

$$u = \frac{r}{2(r+1)}$$

$$v = \frac{r^2+1}{2(r+1)^2}$$

$$w = \frac{r^2-1}{2(r+1)^2}$$

The proportions of the 10 diverse classes of zygotes are designated by the letters c to l, as in table 1. Then after n successive generations of self-fertilization:

	Column 1. Linkage = r in both sets of gametes	Column 2. Linkage complete in one of the sets of gametes
Total homozygotes	$\frac{2^{n-1}+1}{2^{n-1}} + v^n$	$\frac{2^{n-1}-1}{2^{n-1}} + u^n$
$c(=ABAB)$	$\frac{2^{n-1}-1}{2^{n+1}} + \frac{v^n+w^n+w^{n-1}+w^{n-2}+\ldots w}{4}$	$\frac{2^{n-1}-1}{2^{n+1}} + \frac{u^n}{2} + \frac{u^{n-1}+u^{n-2}+\ldots u}{4}$
$d(=AbAb)$	$\frac{2^{n-1}-1}{2^{n+1}} + \frac{v^n-w^n-w^{n-1}-w^{n-2}-\ldots w}{4}$	$\frac{2^{n-1}-1}{2^{n+1}} - \frac{u^{n-1}+u^{n-2}+\ldots u}{4}$
$e(=aBaB)$	$=d$	$=d$
$f(=abab)$	$=c$	$=c$
Total heterozygotes	v^n	u^n
$g(=ABab)$	$\frac{v^n+w^n}{2}$	u^n
$h(=AbaB)$	$\frac{v^n-w^n}{2}$	0
Total mixed	$\frac{1}{2^{n-1}} - 2v^n$	$\frac{1}{2^{n-1}} - 2u^n$
$i(=ABAb)$	$\frac{1}{2^{n+1}} - \frac{v^n}{2}$	$\frac{1}{2^{n+1}} - \frac{u^n}{2}$
$j=k=l=i$		

If the original parents are *AbaB:*

The values for c and d are to be interchanged.

" " " e " f " " " "

" " " g " h " " " "

The values for the mixed (i, j, k, l) remain unchanged, also the values for total homozygotes; total heterozygotes; and total mixed.