The preliminary articles in the 1936 Yearbook included some discussion of the fundamental nature of genes and chromosomes, but very little about how the chromosomes, the carriers of the genes that are the determiners of hereditary traits, are distributed among the descendants of two parents used as breeding stock. This distribution occurs in certain genetic ratios, which were first discovered by Johann Gregor Mendel and gave the clue to the orderly operation of heredity. Before explaining them, it is necessary to consider what happens when two reproductive cells unite to produce progeny.

WHAT HAPPENS WHEN THE CELLS UNITE

This has been well described by A. H. R. Buller in his account of the discovery of Marquis wheat. Buller not only understood the facts of his science of botany; he had a feeling for its poetry as well. The following description is taken from his book. Telling how all Marquis wheat plants came originally from a single kernel or seed, the offspring of a cross between Red Fife and Hard Red Calcutta selected by the famous Canadian plant breeder, Charles Saunders, Buller wrote: 2

Pollen dust from some stamens removed with forceps from a few flowers of [Red Fife] was placed on the two feathery stigmas of a flower of [Hard Red Calcutta]. The pollen grains germinated, each grain producing a single pollen tube. The pollen tubes, which were exceedingly delicate cylindrical structures, grew down the stigmas and made their way, by elongating at their apices, into the ovary below. This ovary was a tiny chamber containing a single ovule or potential seed attached laterally to its wall. One of the pollen tubes, guided by chemotropic stimuli, directed its course toward the ovule, entered at its mouth or micropyle, and penetrated into its interior as far as the ovum or egg-cell. The egg-cell having been reached, the wall at the tip of the pollen tube liquefied and broke down, and from the opening so produced there were emitted two exceedingly minute dense rounded masses of gelatinous protoplasm known as male nuclei. One of these nuclei, carried by forces as yet not perfectly understood, advanced through the general protoplasm of the egg-cell toward the female nucleus situated in its center. The male and female nuclei, after coming into contact, brought their affinity for one another to a climax by mingling together and forming one whole; and this nuclear fusion, this formation of a single nucleus from two others of opposite sex, marked the completion of the act of fertilization.

1 Many workers in the Department have made contributions to this article. The writer is indebted particularly to George Haines, senior animal husbandman, Office of Experiment Stations, and W. V. Laumbert, senior animal husbandman, Bureau of Animal Industry, who have been very generous with suggestions and help on animal genetics, not only in this article but elsewhere in the Yearbook.

out fertilization, the egg-cell would have * * * withered and died; but, its fertilization having been accomplished, a most extraordinary future was opened to it. Further development became irresistible, with the result that, in the course of a few years, its products became in numbers like the stars on a clear night, or the grains of yellow sand upon a sea beach.

To round out the description, it is necessary to add that when the male and female nuclei fuse, the resulting single nucleus becomes the embryo of a new plant. But this embryo is not the whole seed. It will be noted that there were two male nuclei, only one of which united with the female nucleus. But there was also more than one female nucleus, for this one was attended by two much smaller bodies known as the polar nuclei. During fertilization, these two polar nuclei united with the other male nucleus and from this separate union came the endosperm, the starchy part of the seed, the function of which is to furnish food for the embryonic plant during the initial stages of its growth. This union of a male nucleus with two female polar nuclei is peculiar to plants, and it accounts for the fact that the male parent may immediately impress certain characters on the endosperm and embryo of the seed—a phenomenon known as xenia. Except for xenia and metaxenia, the inheritance from the male parent does not appear until the new plant has grown and produced seed in its turn.

This immediate effect of the two polar nuclei, visible in the endosperm, is commonly seen in corn. When a pollen grain from purple corn pure for this characteristic fertilizes an egg cell of white corn, for example, the resulting seed is purple. In some other seeds, like wheat, the effect of xenia is not evident because the endosperm is covered with female tissue known as the pericarp; but even though it is not always observed, xenia occurs in all seed plants. It might be added here that certain other tissues associated with the seed may sometimes be affected in a similar manner by the male parent. This happens in the case of date fruits, and the phenomenon, which has been called metaxenia, is discussed in the date section of the article on subtropical fruits.

The details of the process of fertilization in animals differs somewhat from that in plants although the end result in each case is a new individual which received half of its heredity from the male parent and half from the female parent. In animals the male reproductive cells, known as spermatozoa, are produced literally by the millions in the testes or sex glands of the male. They are microscopic, motile cells, which are propelled by long hairlike tails. The larger part of the head of the spermatozoon is composed of the nucleus, the part of the cell that carries the hereditary factors. The female reproductive cells, known as ova, are produced in the ovaries or sex glands of the female. They are much larger than the male reproductive cells and are nonmotile. They contain a microscopic nucleus that corresponds in size to the nucleus of the spermatozoon. The remainder of the egg consists largely of food material intended to nourish the young embryo until food connections are established with the tissues of the mother, or in the case of birds and other forms in which development takes

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3 The yolk of the hen’s egg is the true egg; the remainder of the contents within the shell are secreted by the glands of the oviduct or “egg bag.” Most of the yolk consists of food material. The eggs of mammals are much smaller than the eggs of birds. Most mammalian eggs are of a size that makes them barely visible to the naked eye.
place outside of the body of the female, food to nourish the embryo throughout its entire development.

In contrast with plants, the spermatozoon, which corresponds to a pollen grain, and the egg cell, which corresponds to the ovule of the plant, are ready to function in fertilization without further nuclear divisions. The sperm cells are deposited by the millions in the reproductive tract of the female at the time of mating. From the point of deposit they move in a swarm to the innermost part of the reproductive tract (the fallopian tubes) of the female, where they are ready to unite with the egg or eggs as soon as they are freed from the ovary. Normally only one spermatozoon enters the egg and takes part in fertilization although thousands of spermatozoa surround an egg. When the spermatozoon enters the egg its nucleus unites with the nucleus of the egg, and this joining of the two nuclei into a single new nucleus is what is known as fertilization. The new nucleus, which received half of its heredity (genes) from the male parent and half from the female parent, constitutes a new individual. All animals and plants begin their life as such single cells. From that point growth proceeds by a continual process of cell division and as it proceeds the new cells are formed into the tissues and organs of the body of the new animal. The processes of growth are similar in both plants and animals. The embryo observed in the seed of plants is a partially developed plant since it contains many cells that arose by the division of the fertilized ovule.

Now we must consider another aspect of those male and female nuclei whose union was described by Buller for wheat plants.

It is generally recognized that the chromosome number for a given species is constant. For example, every nucleus in each body cell of the Red Fife and Hard Red Calcutta parents contained 21 pairs of chromosomes, or 42 altogether. But the nucleus of each reproductive cell—as distinguished from the body cell—contained only 21 chromosomes, not 21 pairs. (This reduction in number occurs when reproductive cells are formed, as described by Kempton.) These 21 chromosomes in the male Red Fife reproductive nucleus contained a complete set of genes capable of reproducing all the Red Fife characteristics; and the same thing was true for the female Hard Red Calcutta nucleus. The two joined, promptly lost their individual identity, and formed a new nucleus with 42 chromosomes containing all the genes of both parents, and therefore capable of producing their characteristics. From that cell came a new plant, the first-generation or F₁ hybrid between the two.

Under ordinary circumstances, if the two parents are pure, all the F₁ or first-generation plants of the cross are exactly alike, for each individual offspring contains a full set of genes from the mother and a full set from the father and it expresses the dominant characteristics of both of them. Very often also these F₁ hybrid plants are unusually vigorous in size or productiveness or other characteristics, especially if the parents were considerably unlike one another. This is the well known "hybrid vigor" or heterosis, for which several explanations have been suggested.

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4 F₁ is pronounced ef-one. The F stands for filial or filial, depending upon whether it is used as a noun or an adjective, and the subscript numerals indicate which generation is meant—first, second, third, etc.
One of these explanations is that all the dominant genes from both parents have a chance to express themselves in the hybrids. To take an imaginary example, suppose one parent had a dominant gene for height so that it was tall, but it had small leaves because of a recessive gene. Suppose the other parent had large leaves because of a dominant gene, but that a recessive gene for dwarfness made it a short plant. The F₁ hybrid would then be tall because of the dominant gene for height inherited from one parent, and it would have large leaves because of the dominant gene for leaf size inherited from the other parent. A number of such dominant genes might express themselves and in combination make the F₁ hybrid seem unusually vigorous. Or, to consider another characteristic such as disease resistance—each parent might have certain dominant genes that increase resistance. When all of these genes came together in the progeny, it might be more disease-resistant than either of the parents.

Another suggested explanation of hybrid vigor is that it is the result of physiological stimulation, which somehow comes from the mixing of unlike protoplasm from the egg and the sperm.

SEGREGATION OF CHARACTERISTICS IN THE PROGENY

But hybrid vigor is not the immediate point of this discussion. We are not concerned here with what happens in the first hybrid generation, but with what occurs in the second generation, which breeders call the F₂. This is well illustrated in figure 1.

We shall assume that both the original parents have been bred pure, and that the F₁ generation is then inbred or fertilized by its own pollen to produce the F₂ generation—the grandchildren of the original parents. What happens to the chromosomes in the F₂ progeny?

Perhaps this can best be visualized for the present by concentrating on a single pair of genes, let us say a pair governing height. Now genes have alternative forms, called allelomorphs or alleles (allelomorph comes from two Greek words meaning “alternative form”). Suppose that a gene for height in the original male parent was one that made the plant tall. Suppose that the gene in exactly the same place on the corresponding or homologous chromosome in the original female parent was an allel or alternate that made the plant short. The F₁ hybrid would receive both chromosomes, making a pair, with the gene for tallness in one and the gene for shortness in the other. These two genes would be present in every body cell of the F₁. But the time would come when reproductive cells were formed, and this would involve the separation of the two members of a pair of chromosomes, since each reproductive cell receives only one chromosome where there were two in the body cell. Thus whenever an original cell divided to form two male reproductive cells, one of them would be bound to receive the chromosome containing the gene for tallness and the other would be certain to receive the chromosome containing the gene for shortness. If several thousand male reproductive cells were produced by the plant, half of them would have the tallness gene, half the shortness gene. And the same thing would be true of the female reproductive cells.

Next this plant is to be self-fertilized; its own male nuclei are to join with its own eggs to form the primary cells of F₂ plants, the next generation. Obviously there could be four kinds of these new cells.
Seeds of the squash above retain in various combinations characteristics of both parents shown at the top. The pistil that developed into this fruit was fertilized by pollen from a staminate flower of the same plant.

FRUITS OF THE F2 GENERATION

These fruits show how the characteristics of both parents reunite in various combinations to produce new types.

Figure 1.—A cross between two species of cucurbits widely differing in appearance. Typical fruits of the parental types; the first generation, which exhibits dominant characteristics; and the second generation, which exhibits characteristics of both parents in various combinations. This is a typical example of the operation of Mendelism. (Courtesy of New York (State) Agricultural Experiment Station.)

(1) A male nucleus with a tallness gene might join a female cell with a tallness gene, giving "tallness-tallness."

(2) A male nucleus with a tallness gene might join a female cell with a shortness gene, giving "tallness-shortness."
(3) A male nucleus with a shortness gene might join a female cell with a tallness gene, giving "shortness-tallness."

(4) A male nucleus with a shortness gene might join a female cell with a shortness gene, giving "shortness-shortness."

Since there are as many reproductive cells that carry the tallness gene as there are reproductive cells that carry the shortness gene and fertilization of the two kinds of eggs by the two kinds of pollen grains occurs entirely by chance, there would be equal numbers of these four different kinds of new cells if large numbers were produced. But group (2) and group (3) above would be exactly the same in effect, since each is a tall-short combination. Thus the proportions in the total population would be 1 tall-tall to 2 tall-short to 1 short-short. This is a simple Mendelian characteristic, the probable breeding behavior of which is expressed as a 1 to 2 to 1 or 1:2:1 ratio.

Thus the plants in the F₂ generation are not at all like those in the F₁. In the F₁, all are alike; in the F₂, with exactly the same basic characteristics, there are three different kinds of plants, with respect to this pair of genes, and they occur in definite proportions. That is, they occur in definite proportions if the population is large enough and is considered as a whole. If only a few plants were produced, these proportions might not hold; out of any four individuals selected at random, there would obviously be a very small chance that one would be a tall-tall, two tall-short, and one short-short. But for large numbers, the ratios hold well. This might be compared to the fact that any given family may have more boys than girls, or vice versa, but that on the whole the male and female population is about equal.

**Segregation Ratios**

This splitting up into several combinations of characteristics in the second generation is what is technically called segregation, and the generation in which it occurs is often called the segregating generation. Segregation occurs even in pollen grains as is shown in figure 2. It should be noted that segregation may occur in the F₁ if the parents are hybrids rather than bred pure. For example, if the hybrids in this example were the original parents, segregation would begin in the first generation after they were selfed or crossed. But this would be merely a change in names; what was really the F₂ would now be called the F₁. It is important to remember, however, that whenever hybrid material is used to start with—as it often is in practice—segregation is apparent in the first generation. In fact, this is the test that proves whether the parent material is hybrid or pure. If a breeder takes a plant the ancestry of which he does not know, selfs it, and finds the progeny in the next generation segregating into different types, he knows the original plant must have been a hybrid. This is what happens, for example, with ordinary open-pollinated varieties of corn. Upon being selfed, the progeny begins to segregate into types immediately.

Before going on with the discussion of segregation ratios, it might be well to consider what happens on further inbreeding of these F₂ plants. We derived three kinds—the tall-tall, the tall-short, and the short-short. When reproductive cells are formed in the tall-tall plant, obviously every one of them must receive a tallness gene, since there is no other. Thus when such plants are selfed all the descend-
ants of the tall-tall plants will also have the tall-tall combination, and this will go on indefinitely as long as they are selfed. Likewise, the short-short plants will produce only short progeny. Whenever an organism has exactly the same genes for a certain character on both members of a pair of homologous chromosomes, it is said to be homozygous for that character. Ordinarily, it will go on breeding true for that character indefinitely as long as it is selfed. From a genetic standpoint, this is what pure breeding means. Often the effort of the plant breeder is to produce plants that, for practical purposes, are homozygous for all characters. Then he can continue reproducing them indefinitely with the assurance that the progeny will be like the parents. His basic procedure—though there are many necessary modifications and complications—is commonly the one given here.

But what about the third type mentioned above—the plants with the tall-short combination in their cells? Here we have exactly the same combination we had in the F₁. In each cell of this type there is a chromosome containing the gene for tallness and one containing the gene for shortness. One-half of the reproductive cells, then, would get the gene for shortness and one-half the gene for tallness. Thus when the plants with the tall-short combination are inbred, they again segregate in the next generation into 1 tall-tall, 2 tall-short, 1 short-short.

When an organism has two alternative genes for a certain character in its homologous chromosomes, it is said to be heterozygous for that character, as opposed to homozygous.

**Effect of Dominance**

So far, we have dealt only with what are called the genotypes of this tall-short combination in breeding. The segregation in the F₂ really took the form of 1 tall-tall, 2 tall-short, 1 short-short so far as the actual cells of the progeny were concerned. But it happens that with these particular characters of tallness and shortness there is a complication, namely, that tallness is a completely dominant characteristic and shortness a recessive. This means that when a cell contains the gene for tallness in one chromosome of a pair and the gene for shortness in the other, the tallness gene will dominate in the growth of the plant, and the shortness gene will, as it were, recede into the background.
We know that the cell actually contains both genes, but the plant does not show it so far as appearances go; it is a tall plant. In breeding terminology, its phenotype, which literally means its appearance type, is tall; its genotype, which literally means its breeding type, is tall-short. The genotype designates the actual genic constitution regardless of expression. The phenotype is the type that results from the interaction of the genes among themselves, as well as with the environment.

Thus in this case the phenotypic and genotypic ratios are not the same. All the plants with the tall–tall combination in their cells will of course be tall, but so will all the plants with the tall-short combination, because tallness is dominant. So far as the phenotype is concerned, then, the ratio becomes 3 tall plants: 1 short plant (the one with the short–short combination). This also is a simple phenotypic ratio, which is really only a modification of the genotypic 1:2:1 ratio and is produced whenever complete dominance is involved. Where there is no complete dominance, the segregation of the phenotype as well as of the genotype is 1:2:1. This occurs, for example, when the hybrid pink four o’clock, a flower, is selfed. The progeny segregates in the ratio of 1 red : 2 pink : 1 white. Red in this case is partly dominant, but not enough to make plants with the red-white combination red in appearance. They are pink instead.

Another ratio that is a variation of the 1:2:1 was obtained by Cuénot, crossing yellow and black mice. The dominant gene, designated Y, produces yellow, and its allel, y, produces black. Now it happens that when a cell received the homozygous combination YY, it could not live; that is, this gene was lethal for any cell that received it in both chromosomes of the pair. With only one Y, however, the cell could live. Thus in the segregation 1 YY : 2 Yy : 1 yy, the YY perished, leaving a ratio of 2:1. Since yellow (Y) was dominant, the phenotypic ratio was 2 yellow mice (Yy) to 1 black mouse (yy). There are many lethal genes in animals and plants that would give the same sort of results, but in most cases the lethals are recessives rather than dominants.

Such ratios are useful to the breeder in two ways. If he knows that a certain character is governed by a single pair of genes, he can tell what proportion of each type he will obtain in a large segregating progeny. When he does not know how many genes are involved in a certain character, he can find out, or obtain an estimate, at least, by figuring the ratio in the segregating progeny. If the character segregation is 1:2:1, he concludes he must be dealing with a single pair of genes and that complete dominance is not involved. If it is 3:1, he assumes it is a single pair of genes involving complete dominance. If it is 2:1, he knows it may be a single pair of genes, and that one of the alleles in the double condition is lethal.

6 Knowledge of the 3:1 phenotypic segregation preceded that of the 1:2:1 as a phenotypic ratio. One of the first reports of the latter was made by Correns—German botanist and one of the rediscoverers of Mendel’s original paper—working with the hybrid pink four o’clocks mentioned. There is no gene for pink, but the color is produced by the interaction of the whiteness and the redness genes in the same cell. The same result is obtained in the blue Andalusian fowl, which is produced by crossing a splashed white with a black. The segregation in the F2 is 1 splashed white : 2 blue : 1 black. This ratio also occurs in commercial double carnations, produced by crossing the burster and the single varieties.

7 The genetic formula is somewhat simplified. The designation is in accordance with the practice of designating a recessive gene by a lower-case letter and its dominant allel by the same letter capitalized.
The situation becomes much more complicated when there are two pairs of genes and their alleles to be taken into account instead of one pair. Corn has been a favorite plant for studies of this kind. Figure 3 shows some heritable characters in corn.

Consider a pea plant with a pair of genes for tallness (T—dominant) and a pair of genes for red blossoms (R—dominant) crossed with a plant that has alleles (t and r) of these two genes and is dwarf (recessive) and white-flowered (recessive). The genotypic segregation, including all possible combinations of these two characteristics, would be like this:

Parents: Tall-tall red-red × dwarf-dwarf white-white. The first parent indicated here would produce only gametes (germ cells) carrying genes for tall and red, while the second parent would produce only gametes carrying genes for dwarf and white. The progeny, F₁, of course, would carry both kinds of genes, that is, genotypically they would be tall-dwarf red-white; but in phenotypic appearance they would all be tall and red.

F₁: tall-dwarf red-white × tall-dwarf red-white. The gametes produced by each of the parents here would be of four kinds—tall-red, tall-white, dwarf-red, and dwarf-white.

Figure 3.—Segregation for more than one character is shown on these ears of corn. It will be noted that there is not only a variation in color of the kernels but also a difference in the development of the kernels. Studies of heritable characters of this kind have enabled geneticists to increase their knowledge of heredity greatly beyond the fundamental laws formulated by Mendel.

(Courtesy of Journal of Heredity.)
dwarf-white. These four kinds of gametes would unite by chance to give the various F\textsubscript{2} progeny. Possibly the best way to show the formation of these F\textsubscript{2} genotypes is by what is commonly known as the checkerboard square, presented below. The gametes produced by each parent are shown at the top and side of the checkerboard square. The genotype of each of the progeny formed by the union of all the different kinds of gametes is shown within the squares.

\textbf{F\textsubscript{2}:}

\begin{table}[h]
\centering
\begin{tabular}{|c|c|c|c|}
\hline
\textbf{Parent (gametes)} & \textbf{TR} & \textbf{Tr} & \textbf{tR} & \textbf{tr} \\
\hline
\textbf{TR} & TTRR & TTRr & TtRR & TtRr \\
\hline
\textbf{Tr} & TTTR & TTRr & TtRr & Ttr \\
\hline
\textbf{tR} & TtRR & TtRr & ttRR & ttRr \\
\hline
\textbf{tr} & TtRr & Ttr & ttRr & ttr \\
\hline
\end{tabular}
\end{table}

\textbf{Progeny (zygotes)}

This F\textsubscript{2} checkerboard square adds up to the following genotypes:
1 tall-tall red-red: 2 tall-tall red-white: 2 tall-dwarf red-red: 4 tall-dwarf red-white: 1 tall-tall white-white: 2 tall-dwarf white-white: 1 dwarf-dwarf red-red: 2 dwarf-dwarf red-white: 1 dwarf-dwarf white-white.

But tall is dominant to dwarf and red is dominant to white; that is, every plant with the tall-dwarf combination in its cells would be tall in appearance, and every plant with the red-white combination would have red flowers. Thus in the F\textsubscript{2}, the segregation from the standpoint of phenotype or appearance would be:

\begin{itemize}
\item Tall red — 9 (1 tall-tall red-red + 2 tall-tall red-white + 2 tall-dwarf red-red + 4 tall-dwarf red-white).
\item Tall white — 3 (1 tall-tall white-white + 2 tall-dwarf white-white).
\item Dwarf red — 3 (1 dwarf-dwarf red-red + 2 dwarf-dwarf red-white).
\item Dwarf white — 1 (dwarf-dwarf white-white).
\end{itemize}

This 9:3:3:1 is the basic phenotypic ratio when two independently inherited dominant genes with their two recessive alleles are concerned.

\textbf{Modifications of Basic Ratios}

The basic ratios are modified in various ways. Interaction between the genes accounts for many of the modifications. It will be enough here to analyze five of the most common of these modifications through interaction.

(1) One dominant gene may have no visible effect unless a member of another pair is present. There is an example of this in corn, in which many color genes have been identified by R. A. Emerson and his associates at Cornell University. The dominant gene \( R \) governs red color, and its recessive allele \( r \) produces white. The dominant gene \( Pr \) produces purple, but only if \( R \) is present; otherwise it has no
effect. Suppose we have corn with the genes \( r \) and \( Pr \) (expressed as \( r Pr \)). This is white because, though it contains the gene for purple, \( Pr \), it does not at the same time possess \( R \). Let us cross this with a variety containing the genes \( R \) \( pr \), which is red because it contains the \( R \) without the \( Pr \) that would modify it. Since the \( F_1 \) would have all the genes from both parents, its constitution would be \( R \) \( r \) \( Pr \) \( pr \). It would be purple because it would have both \( R \) and \( Pr \). The genotypes would work out in the 9:3:3:1 ratio already given—that is:

\[
\begin{align*}
9 & \quad R \text{-}Pr \text{---} \quad \text{(purple, because } R \text{ and } Pr \text{ are both present).} \\
3 & \quad R \text{-}pr \text{pr} \quad \text{(red, because } R \text{ is present but not } Pr). \\
3 & \quad rrPr\text{pr} \quad \text{(white, because though } Pr \text{ is present, it has no effect without } R). \\
1 & \quad rrprpr \quad \text{(white—double recessive).}
\end{align*}
\]

Thus the phenotypes add up to 9 purple: 3 red: 4 white, and we get 9:3:4 as the typical ratio for this kind of gene interaction.

(2) Sometimes two dominants have a complementary effect on one another, but neither exerts any visible influence alone. Again we may turn to corn for an example. The dominant gene \( C \) and the dominant gene \( R \) produce colored (red or purple) kernels if they are both present, but neither has any effect alone. The recessive alleles, \( c \) and \( r \), produce white. Suppose we have a variety with the composition \( CCrr \), which is white because only one of the dominant genes is present, and another variety \( ccRR \), white for the same reason. The \( F_1 \) contains the two dominants and the two recessives—\( Cc \) \( Rr \)—and is therefore colored. All the possible combinations would give us the following genotypes in the \( F_2 \):

\[
\begin{align*}
9 & \quad C-R- \quad \text{(colored, because both dominants are present).} \\
3 & \quad C-r r \quad \text{(white, because only one of the dominants is present).} \\
3 & \quad ccR- \quad \text{(white, because only one of the dominants is present).} \\
1 & \quad ccrr \quad \text{(white—double recessive).}
\end{align*}
\]

Here the phenotypes add up to 9 colored: 7 white, and one concludes that 9:7 is the typical ratio for this kind of interaction.

(3) Sometimes one dominant hides the effect of the other when both are present. In oats, the gene \( G \) produces a gray seed coat and the gene \( B \) a black seed coat, but the effect of \( G \) is always hidden if \( B \) is present. The gene \( Y \) produces a yellow seed coat, but only if neither \( B \) nor \( G \) is present. Suppose we cross a variety \( BBGGYY \) (black because \( B \) hides \( G \) and \( Y \)) with a variety \( bbggYY \) (yellow because \( Y \) is present but not \( B \) or \( G \)). The \( F_1 \) is \( BbGgYY \) and is therefore black. All possible combinations would give in the \( F_2 \):

\[
\begin{align*}
9 & \quad B-G-Y- \quad \text{(black because } B \text{ hides } G \text{ and } Y). \\
3 & \quad B-ggY- \quad \text{(black because } B \text{ hides } Y). \\
3 & \quad bbG-Y- \quad \text{(gray because } G \text{ can show its effect without } B). \\
1 & \quad bbggY- \quad \text{(yellow because } Y \text{ is present without } B \text{ or } G). 
\end{align*}
\]

This gives a phenotype ratio of 12 black, 3 gray, and 1 yellow—12:3:1 being the typical segregation for genes interacting in this way.

(4) Sometimes when there are two dominants, one acts as an inhibitor of the other. For example, in corn, \( R \) produces red kernels;
r white kernels; I prevents the action of R; i has no effect. Stated in another way, the recessive (ii) must be present to allow the gene R to be effective. Suppose a variety rri (white, the double recessive) is crossed with RRII (also white because, though R is present, it is inhibited by I). The genotype of the F1 is RrIi and is white. The F2 segregates as:

9 R–I– (white because I inhibits R).
3 R–ii (colored because R can act with i).
3 rri– (white because R is not present and also because I is present).
1 rri (white because R is not present).

The phenotypes here add up to 13 white: 3 colored. This 13:3 phenotypic ratio is commonly called the inhibitor ratio, and the larger number always represents the gene that acts as the inhibitor.

(5) Finally, there may be two dominants, each having the same effect as the other, or as both of them together. In the common shepherds-purse, the seed capsule is triangular in shape if the dominant gene C or the dominant D is present—and also if both are present. If both the recessives of these genes, c and d, are homozygous, the seed capsule is top-shaped. Dr. Shull of Princeton crossed a variety ccdd (top-shaped) with a variety CCDD (triangle-shaped). From the triangular F1 (CcDd) he obtained in the F2:

9 C–D– (triangular—both dominant genes present).
3 C–dd (triangular—one dominant gene present).
3 ccD– (triangular—one dominant gene present).
1 ccdd (top-shaped—double recessive).

This adds up to 15 triangular: 1 top-shaped, giving a 15:1 ratio.


When three genes with their alleles are involved instead of two, the ratios become still more complicated and they will not be illustrated in detail here. The basic phenotypic ratio in the case of three pairs of genes is 27:9:9:3:9:3:3:1. If the genes are considered as ABC and abc, this ratio is 27 ABC: 9 AbC: 9 ABo: 3 AbC: 9 aBo: 3 aBo: 3 abO: 1 abc. Some variations in this basic ratio produced by the interaction of genes are 27:37, 27:9:28, and 63:1.

With more than three pairs of genes, the ratios become even more complicated, especially if there are complex interactions among the genes. It is evident that large numbers of progeny would be needed to furnish a population with proportionate representation of all classes. This need for large numbers of progeny is one of the difficulties in animal genetics, where there is reason to believe that many genes, interacting in a very complex way, are involved in what appears to be a simple characteristic such as high or low milk production.

**Backcrossing and the Backcross Ratio**

The backcross ratio is different from any of those previously explained. The backcrossing technique consists chiefly in crossing an F1 or later progeny back to one of the original parents or to an individual recessive for whatever characteristic is under consideration.
The ratio is now being used to advantage by both the geneticist and the breeder. The genetic make-up of the sow shown in figure 4 is being tested by the backcross method. The geneticist uses it primarily to test for linkage, a phenomenon explained in the next few pages. The breeder uses it chiefly for two purposes—(1) to test whether a given character exists in a pure (homozygous) form or in a hybrid (heterozygous) form in one of the parents used in the backcross and (2) to transfer a valued characteristic such as disease resistance into an otherwise desirable variety that lacks it.

Suppose the breeder is dealing with a gene \( B \), which produces black in Aberdeen Angus cattle and is dominant to its allele \( b \), which produces red. He is not sure whether a given black animal is homozygous or heterozygous, since both \( BB \) and \( Bb \) produce exactly the same appearance. It is necessary for him to know, however, if he wants to go on breeding pure black animals, because if he picks two that are heterozygous the progeny will keep on segregating into blacks and reds. In order to test the composition of an animal by this method, he backcrosses it to a red individual, which, of course, has the double recessive, \( bb \). In the following generations one of two things must happen. (1) All the progeny will be black, in which case he knows that the animal he was testing must have been homozygous, with the composition \( BB \); for \( BB \) crossed with \( bb \) would give every offspring a \( B \) and a \( b \), or \( Bb \), which would make every animal black. (2) He might get an equal number of blacks and reds, in which case he knows that the uncertain animal must be heterozygous, or \( Bb \); for \( Bb \) crossed with \( bb \) would give 1 \( Bb \): 1 \( Bb \): 1 \( bb \), or 1 black: 1 red. In the first case, he can keep on using the animal he has chosen with the assurance that it will breed true. In the
second case he will have to discard the animal and its progeny if he wants a herd pure for black.

Backcrossing, especially with plants naturally selfed, is seldom resorted to for the purpose of determining whether they are homozygous for a given gene. A few progeny from selfed plants are all that are needed for this purpose, and, of course, in self-fertilized plants it is much simpler to self a plant, grow a few progeny, and note whether they segregate.

The 1:1 is a so-called backcross ratio, and it always appears when a recessive is crossed with a heterozygous individual. The backcross method therefore can be used to test the purity of any stock that exhibits a dominant character. Backcross ratios also have been worked out for two and three pairs of genes with their various interactions. For example, in the case of two genes, \( A \) and \( B \), with their alleles, \( a \) and \( b \), a heterozygous plant with the composition \( AaBb \) crossed with the pure recessive \( aabb \) would give 1 \( Aa Bb \): 1 \( Aa bb \): 1 \( aa Bb \): 1 \( aa bb \).

The second use of the backcross is to transfer a certain valued character to an otherwise desirable variety. Suppose the breeder has a plant, \( A \), that has good commercial characteristics but is susceptible to a disease, such as bunt in wheat, and a plant, \( B \), that is worthless commercially but has bunt resistance, a dominant characteristic. He crosses them, determines by suitable tests that the \( F_1 \) is resistant, inbreeds the \( F_1 \), and finds that the \( F_2 \) segregates into disease-resistant and disease-susceptible plants. He may backcross the \( F_1 \) to \( A \), the double recessive for bunt resistance, and obtain the backcross ratio of 1 resistant to 1 susceptible. A second or third backcross may result in successfully retaining bunt resistance and at the same time getting all of the desirable characters of the susceptible parent, \( A \). This backcross method is most successful when only one dominant factor is involved. When the resistant reaction is recessive, the backcross method of breeding is not so successful.

The important thing for the breeder to keep in mind here is that \( B \) contributes worthless commercial characteristics as well as the valuable one of disease resistance, and he must use skill in selecting the particular disease-resistant plants for backcrossing on \( A \). They must have as many \( A \) qualities as possible, but, of course, lack susceptibility to disease. Too much emphasis cannot be placed on the importance of wise selection, especially in view of the fact that usually many genes are involved in even the simplest characters, rather than one dominant gene as in the above example.

**LINKAGE AND CROSSING OVER**

Although the discussion of ratios has dealt with genes, it should be kept in mind that the genes are located in chromosomes. Just what genes or chromosomes are, or by what means they exert their fateful control over the characteristics of organisms, remains an unsolved mystery of science. A chromosome may be thought of as merely an aggregation of genes that stick together, like a chain composed of a series of links, each somewhat different from the others; or as a spiral of protoplasm inclosed in a matrix and divided into sections, each section being a gene; or as a package containing
genes, like a druggist's vial containing pills. The point is that genes occur in groups; and since they do, all of the genes on one chromosome and the characters controlled by these genes tend to be inherited together in what is known as linked-inheritance or linkage.

This is quite different from the idea held by Mendel, the father of modern genetics. One of Mendel's laws was that all characteristics assort independently of each other in inheritance—the theory of independent assortment. As a matter of fact, apparently all the characteristics Mendel studied in peas were so located that they did assort independently. This was one of the most lucky of scientific accidents. If Mendel had happened to deal with linked characteristics or those involving the interaction of genes, the results might have been so complicated that he could not have worked out his clear-cut laws with the knowledge then available.

It was about 1905 when Bateson and Punnett in England discovered characteristics that did not assort independently but remained together in inheritance. As more evidence of this kind accumulated, various theories were proposed to account for it. The one finally accepted was that genes for certain characteristics tend to be linked together in what were called linkage groups. When Sutton in 1902 showed that chromosomes, the existence of which was known through microscopic studies of the cell, play the dynamic role in inheritance, it took only one more step to demonstrate that the genes in a linkage group are carried on a specific chromosome and the number of linkage groups and chromosomes is the same. Corn, for example, has 10 chromosomes and 10 linkage groups. However, it is not possible by looking at a chromosome to tell what genes it contains. The breeder must first discover by actual test what characteristics tend to be linked together in inheritance; then he assumes that the genes determining these characteristics are located in the same chromosome. In some cases, notably the pomace fly and the corn plant, it has been possible by such breeding tests to assign a large number of genes to definite chromosomes.

But the situation is not so simple as this account might indicate. A given gene does not always stay in the same chromosome. Kemp-pton's article in the 1936 Yearbook described how a pair of homologous chromosomes become twisted together during the formation of reproductive cells, and how they may exchange equal portions during this process. This is called crossing over, and it is equivalent to saying that genes are exchanged between the two chromosomes. Thus the original linkage group is changed and a new combination within the linkage group is formed.

Suppose, to take an imaginary example, that on one chromosome there is a gene $A$ determining resistance to a certain disease and not far from it a gene $B$ determining broad leaves. In the corresponding places on the homologous chromosome of the pair, there is a gene $a$ determining susceptibility to the disease and a gene $b$ determining narrow leaves. When these chromosomes segregate in inheritance, every plant that is disease-resistant will have broad leaves and every one that is not resistant will have narrow leaves, since $AB$ are located in one chromosome and $ab$ in one chromosome. But suppose that in the reproductive cells of one plant, $A$ and $a$ are exchanged by crossing over. Now $Ab$ will be in one chromosome and $aB$ in the
Figure 5.—Models of chromosomes (A) broken into "chromatids" (longitudinal sections), showing two ways (B, C) in which the sections might wrap around one another to produce the cross-overs shown in D. These chromosome models were prepared by H. B. Newcombe and G. B. Wilson, of the Department of Genetics, McGill University, Montreal, Canada. (Courtesy of Journal of Heredity.)
other, and there will be an opportunity to obtain new true-breeding strains as a result of these recombinations. Figure 5 illustrates two ways in which linkage groups are broken up by crossing-overs.

If the genes were very close together, the break would obviously have to occur within a very narrow range to bring about an exchange, and if they were next to each other it would have to occur exactly between them. In other words, the closer the genes are on a chromosome the less likelihood there is that a break will occur in the right place to make an exchange possible. Geneticists have taken advantage of this fact to locate the position of genes on chromosomes without actually seeing the genes. For example, if in a case of linkage 20 recombinations are obtained out of every 100 progeny, the two genes are said to be located about 20 units apart on the chromosome, for the number of new combinations that are obtained when linkage is involved depends upon the amount of crossing over, and this in turn depends on the distance of the genes apart. In this case the genes would be said to have 20 percent linkage, since the degree of linkage is designated by the amount of crossing over. Cross-overs are extremely frequent and they may make breeding operations either more difficult or easier, depending upon a breeder’s desire for new combinations.

It is this physical fact that enables the geneticist to draw maps showing the locations of genes on chromosomes. First, by appropriate tests he determines that two genes, A and B, are located on the same chromosome. Then, by breeding many progeny, he determines the percentage of cases in which there is crossing over. By getting a whole series of percentages for other genes—C, D, E, F, G, H, etc.—in relation to both A or B, he can determine how close these are to the genes already located. Without ever seeing or identifying any of the genes, he can determine mathematically their relative position on the chromosome, and knowing the percentages of crossing over between them, he can make a genetic map of a chromosome showing the approximate locations of the genes. Other techniques are available for aiding in chromosome mapping.

**Effect of Linkage on Segregation**

The effect of linkage on segregation ratios may be illustrated with the fowl. Landauer and other investigators have demonstrated a linkage between the creeper characteristic, which causes a marked shortening of the long bones of the wings and legs (the fowl seems to creep), and single comb. Rose comb (R) is dominant, and single comb (r) is recessive. Creeper (Cr) is dominant, and normal or non-creeper (cr) is recessive. To show how this linkage affects ratios an example of an actual cross is given. One parent is normal and rose-combed (cr cr RR), the other is creeper and single-combed (Cr cr rr). The “creeper” parent is heterozygous for this condition because when homozygous it is lethal, the embryos dying at about the seventy-second hour of incubation. When these parents are crossed, one-half of the F1 progeny have all four genes and are of the genotype $\text{Cr} \, R \, r$. They are creeper and rose-combed because of the effects of the two

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14 This form is used in linkage studies to designate which genes are linked. In this case cr and R are on one chromosome and Cr and r on its homologue.
dominants. Now the F₁'s of this type are backcrossed on double recessives, that is, fowls with single comb and normal wings and legs, \( cr\, r \). If the creeper and single-combed condition were assorted independently, we would get the normal backcross ratio—1 creeper rose comb: 1 creeper single comb: 1 normal rose comb: 1 normal single comb.

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<th>Normal, rose comb</th>
<th>Creeper, single comb</th>
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\frac{cr\, R}{cr\, R} \times \frac{Cr\, r}{cr\, r} = \frac{Cr\, R}{cr\, r} \]

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\frac{cr\, R}{Cr\, r} \times \frac{cr\, r}{cr\, r} = \frac{cr\, R}{cr\, r} \]

<table>
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<th>Double heterozygote, creeper, rose comb</th>
<th>Normal, rose comb</th>
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\frac{cr\, R}{Cr\, r} \times \frac{cr\, r}{cr\, r} = \frac{cr\, R}{cr\, r} \]

**Figure 6.**—Test for linkage between rose-comb and creeper genes.

But this does not occur. Instead the following proportions, as shown by Landauer, are obtained—normal rose comb 3,219: creeper single comb 3,383: creeper rose comb 15: normal single comb 9. In other words, the normal rose comb and creeper single-comb birds (parental types) are enormously in excess of the number expected. The conclusion therefore is that the genes for normal wings and legs and rose comb are on the same chromosome, and those for the creeper condition and single comb are on its mate or homologue. When the chromosomes segregate, the original combination of genes stays together, and the few cases of the opposite combination are due to crossing over. Without crossing over there could not be a creeper bird with rose comb, or a normal one with single comb. Since 0.36 percent of the progeny were of these types, there must have been crossing over between the genes on the chromosome carrying the creeper rose comb characters and their alleles in 0.36 percent of the gametes produced by the parent heterozygous for both characteristics. This is referred to as 0.36 percent crossing over. The matings and segregations are shown in figure 6. The proportions were obtained by Landauer.¹⁴

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Figure 7.—A Plymouth Rock × Bantam cross, showing the barring gene, which is sex-linked: A, Barred Plymouth Rock male parent; B, Rose Comb Black Bantam female parent; C, D, first generation; E, F, G, H, second generation. Note that barring is dominant (no black birds in the first generation) and a 3:1 ratio is obtained in the second generation. There are, however, no black males in this generation.
A special case of linkage of particular importance is the linkage associated with sex. Maleness and femaleness may be considered to be characteristics just as truly as any others. If they were determined exactly like other characteristics, however, the world would be very different than it is. Suppose, to take a hypothetical case, that in animals there was a gene $M$ for maleness and an allele $m$ for femaleness. Whenever a male and a female——$MM$ and $mm$——crossed, all the progeny would be $Mm$. If $M$ were dominant, they would all be males, and no further reproduction would be possible. If neither gene were dominant, all the progeny would be male-female, that is, hermaphrodite. Neither of these conditions occurs; instead, in the population at large, males and females are born in approximately equal numbers. If sex is determined by a gene, then, it does not operate like other genes.

What actually does determine sex is another of the unsolved problems. It is known, however, that in many animals, sex is associated with a chromosome peculiarity. In the dog, the cat, the pig, the cow, the horse, and some other animals it is believed that the female has one more chromosome than the male. In these cases the male contains all the chromosomes contained in the body cell of the female, and in addition one so-called $X$ chromosome—not a pair. The female, who has a pair of these $X$ chromosomes, therefore always has one more chromosome than the male with $X$. In some species of *Drosophila*, each sex has a pair of sex chromosomes, but they are different in males and females. The odd chromosome found in the male is designated as $Y$, so that the female has the composition $XX$ and the male the composition $XY$. In moths and birds, this situation is reversed; the male has a pair of sex chromosomes called $ZZ$ and the female a single $Z$ chromosome and a $W$ chromosome. The effect of a typical sex-linked gene-barring is shown in figures 7 and 8.

If sex is determined by a gene (or even a number of genes in combination) on a sex chromosome, this arrangement would bring about a segregation that accords with the facts. Let us say the female is the one homozygous for sex, with the combination $XX$. The male is heterozygous, with the combination $XY$. When the chromosomes are reduced to form reproductive cells, every reproductive cell produced by the female has an $X$ chromosome. Out of every two reproductive cells produced by the male, however, one has an $X$ chromosome and one has a $Y$. When a female cell met an $X$ male cell, the union would give the combination $XX$, which would become a female organism. The female cell that met a male $Y$ would have the combination $XY$, which would become a male organism. In the $WZ$ type of sex determination males are homozygous, $ZZ$, and females heterozygous, $WZ$. In both cases, males and females would be produced in approximately equal numbers in the population as a whole.

On the other hand, it is possible that sex is not determined by a gene or genes. One theory is that it is determined by a certain balance between all the chromosomes. There might well be a different
Figure 8.—The reciprocal of the cross shown in figure 7: A, Rose Comb Black Bantam male parent; B, Barred Plymouth Rock female parent; C, D, first generation; E, F, G, H, second generation. Note that in this cross the Black Bantam is a male and the Plymouth Rock a female. The color factors show typical sex-linked inheritance—also what is known as "criss-cross inheritance." The latter is common in cases of sex-linked inheritance. In this cross it is readily seen when the parental and first generation types are compared. The black color of the male parent is shown only in the female of the first generation and the barred characteristic of the parental female is shown only in the male. In the second generation there is an equal number of barred and black males and females, respectively.
balance between an organism with one $X$ or one $Z$ chromosome and an organism with two.

The sex chromosomes do more than determine sex (granted that they do that). They also carry genes determining other less unique characteristics such as barring, mentioned above. All the genes on a sex chromosome, naturally, are in a single linkage group, and they are associated with sex in inheritance. How does this work out?

As an example, we might take the type of color blindness in man that renders a person unable to distinguish between red and green. This is a sex-linked characteristic; it is recessive and its determining gene is located on the $X$ chromosome. Now it has been shown that when an $X$ chromosome from a female cell combines with a $Y$ in the male cell, the result is a male organism, a son. On the other hand, when an $X$ from a male cell combines with an $X$ from a female, the result is a female, a daughter. This is another way of saying that a son can receive the $X$ chromosome only from his mother. The father's $X$ chromosome, on the other hand, can go only to the daughter. Thus if the father's $X$ chromosome contains the gene for color blindness, it will go to his daughter but will be expressed only if both father and mother transmit color blindness, since the two recessives must come together. A son who is color blind could have inherited the trait only from his mother, from whom alone he receives the $X$ chromosome.

A sex-linked characteristic, it should be noted, is quite different from a sex-limited characteristic. A sex-limited characteristic is one that can be expressed by one sex only; genes for it may be contained in the other sex, but there is something that inhibits its expression. Thus milk production may conceivably be inherited by both males and females, but its actual expression is limited to females. Horns in Rambouillet sheep are limited to males; presumably there is something in the glands of the females that inhibits the expression of horns, or perhaps something in the glands of the male that compels the expression.

**MUTATION OF GENES AND CHROMOSOMES**

Other phenomena in addition to linkage and crossing over affect the orderly transmission of a given set of genes to offspring. In a broad sense these phenomena may be classed as mutations. Gene mutations involve a change in one or more genes, and they are now understood to be caused in any one of a number of ways, as by heat reaching the cell at a certain stage of its development, or by radiations of certain wave lengths. In the latter case, it has been suggested that a gene may be altered by a direct hit from an electric particle. In any case, once a gene in a reproductive cell has mutated, it is thereafter inherited in the new form, unless there is another mutation. It is now commonly believed that many, perhaps most mutations, are harmful to the organism.

Polyploidy brings about similar results. This is an increase in the number of chromosomes in the cell, beyond the number that is normal for the particular organism. Polyploidy frequently occurs when organisms only distantly related are crossed. Presumably some or all of the chromosomes from the two parents are so unlike that they are
unable to join in pairs, with the result that the number cannot be
reduced in the regular way when reproductive cells are formed. The
unpaired chromosomes are then left over to increase the regular num-er in the reproductive cell. Sometimes there is only one extra
chromosome, sometimes several, sometimes a whole extra set, or more
than one extra set. The phenomenon is treated at greater length in
Dr. Blakeslee's article, which appears in a separate of this Yearbook.

Naturally geneticists deal with other concepts besides Mendelian
ratios, linkage, sex-linked factors, lethal factors, multiple allelomorphs,
and other phenomena discussed in this article. They are paying con-
siderable attention to such things as chromosomal aberrations, trans-
locations, gene frequency, epistasis, and genetic tensions. As yet the
real importance of some of these newer concepts is not known. Some
may have a profound effect upon our knowledge of heredity, others
may be of little importance or may prove to be another way of stating
something that is already known.

The influence of environment on the expression of genes cannot be
ignored. For instance, in the case of animals it is only under certain
specific conditions of feeding, care, and management that genes for
rapidity and economy of gain, or for high milk production, can be
fully expressed. Taking production as an example, it is conceivable
that one strain of dairy cattle might have genes that would enable it
to produce at a high level on a diet that would reduce the production
of another strain to a very low level. In other words, there is no
universally optimum environment but an optimum for a specific gene
or genes. Temperature and nutrition have been found to produce
important effects even on such characters as coat color in rabbits and
rats. In certain kinds of rabbits low temperatures cause new hair to
come in black, whereas at higher temperatures the hair developing on
the same parts of the body is white. Thus it is evident that the
geneticist must consider the interaction of the genes with the environ-
ment in accurately describing their expression.

GENETIC ANALYSIS—PLANTS AND ANIMALS COMPARED

Intensive study of one animal form, the small pomace fly of the
genus Drosophila, principally by Thomas Hunt Morgan and his
students, has contributed very largely to the understanding of the
mechanism of heredity. Because of its short life span (it lives only
13 days on the average), its minute size, which permits hundreds
of flies to be grown in small vials, its small number of chromosomes,
and the presence in the species of a large number of different char-
acters, it has proved to be remarkably good material for genetic
study. But even with Drosophila, progress has been made at the
cost of much painstaking labor, and probably over 25,000,000 flies
have been raised and examined with meticulous care by students of
this species.

With the laboratory rodents and the fowl progress has also been
relatively rapid. The manner of inheritance of many traits, such as
color and various defects of structure and function, has been clearly
determined and it has been shown that the types of inheritance (inde-
dependent, linked, and sex-linked) are the same for these forms as for
Drosophila and many plants. And the masterful analysis by Wright
of the results of many years of inbreeding of guinea pigs by the Department of Agriculture has contributed much to what is known of the consequences of inbreeding, cross-breeding, and various other systems of mating, in both plants and animals.

With the larger animals progress has not been so great and the criticism is frequently made that genetics has contributed little of importance to animal breeding. Much of this criticism is unjustified. While the direct contribution to breeding practice has not yet been great, genetics has contributed in a large way to an understanding of the basic principles of breeding, and many concepts and superstitions, such as telegony (an alleged effect of a sire on later progeny of the same dam by another sire) and maternal impressions, have been discarded as a result. It is now possible more readily to eliminate undesirable hereditary traits from breeding stock. Application of this knowledge has been employed especially in the elimination of such abnormalities as lethal conditions, which have been found to be inherited to some extent in most classes of animals.

The way in which the breeder of dairy cattle, for example, is today shaping some of his breeding methods on the basis of genetic principles is greater than is ordinarily realized. Within a period of 10 years breed associations have adopted herd tests for the purpose of securing records on all animals in a herd instead of the best ones only—a recognition of the fallacy of selective testing. They are publishing daughter-dam records for sires in recognition of the need of determining the genetic make-up of outstanding sires. Great emphasis is being placed on the sire that has proved through the progeny test that he possesses a superior inheritance. Finally, many courses for the study of the principles of Mendelian inheritance as applied to dairy cattle are now held regularly.

In a negative way also genetics has contributed to practical breeding. A knowledge of Mendelian laws has brought an understanding of the consequences of the various systems of mating that have shown the limitations of selection and certain other breeding practices.

In plant production it is usually possible to obtain large numbers of progeny in a relatively short time and at little expense. The segregation by classes permits a determination of the ratios between them, and this makes it possible to formulate a hypothesis to explain the mode of inheritance and the genotype of the parents in a rather conclusive manner for most qualitative and some quantitative characteristics. By the application of the principles of Mendelism it has also been possible to work out the genetic basis for the more simply inherited unit characters in animals, explain the occurrence of unexpected progeny, and predict the frequency with which they may be expected in the future. With a background of such information the breeder can decide whether he wishes to continue to breed a dam that produces progeny meritorious in some such character as conformation even though a certain percentage of her progeny have a very undesirable characteristic and must be culled.

An understanding of the mechanism of sex determination was also largely dependent upon genetic discoveries. Cytologists had postulated the sex chromosomes as the basic sex-determining mechanism, but it remained for the discovery of sex-linked characters and the genetic
analysis of such characters to furnish final proof of the correctness of this hypothesis. In poultry a large number of sex-linked genes have been studied and the facts obtained from some of these studies have been put to practical use in certain crosses to determine the sex of chicks at the time of hatching. There is also some evidence that certain genes affecting such characters as maturity and rate of winter egg production are sex-linked, and, if these observations are substantiated, the information should eventually enable the poultryman to incorporate these genes more easily into his flock.

Aside from such rapid-breeding forms as *Drosophila*, Mendelian analysis with animals in the sense of locating individual genes or finding the number of genes that determine a given character will always be more difficult than with plants, and a complete analysis with the larger animals will probably never be made.

**Why Progress in Animal Genetics Is Slow**

There are numerous reasons why animal genetics has not made and cannot hope to make as rapid progress in working out a complete genetic analysis as has been possible with plants. Some of these reasons will be discussed below.

1. The male and the female are different individuals. Thus self-fertilization, an important method used extensively in plant breeding, is not possible in the breeding of livestock. The progeny always has genes contributed by both parents, and since each parent has a different set of genes this greatly retards the rate of production of genetically pure forms. Progress in plant genetics has been aided by the ability to determine the genotype through the segregation of progeny produced by self-fertilization. The mating of brother and sister or of a parent to his or her offspring is an approach to the self-fertilization method used by the plant breeder, but the progeny test, as shown in figure 9, is being more and more widely used as a method of determining the genotype in animal breeding.

2. The rate of maturity and breeding is relatively slow. In most plants with which genetic progress has been made, it is possible to obtain at least one generation a year. An animal—for example, a calf—must often be kept 2 years before it produces any progeny. In turn, the female progeny must be kept 2 years before it produces milk, in case this is the character to be measured. Another year is required to get the complete lactation. If the first calf happens to be a female, at least 5 years are required to get the first record of production on dam and daughter. Further records on other progeny will be needed to determine the genotype of the dam.

3. The number of progeny of any pair of individuals is usually too small to be sure of the genotype of the parents. Earlier in this article, it was pointed out that the genotype of the individual is determined by the type of progeny it produces. Backcrossing to the homozygous recessive strain was found to be the easiest way to determine the genotype. Applying this to a dairy animal, let us assume that dominance is involved in inheritance of milk yield. If the animal in question were a cow and if a bull carrying the recessive factors were available, so many years would be required to get sufficient milk records on the female progeny of this cow in order to have data on which
sound conclusions might be based regarding the genotype of the dam that the procedure would be impracticable. Moreover, only half of the calves would be females, and not all of these would be raised so that milk records could be obtained for them.

A case of polled condition in cattle involving a single pair of genes will help to explain this, although it should be kept clearly in mind that milk production is probably due to several pairs of genetic factors.

In cattle the polled condition \((P)\) is dominant and horns \((p)\) recessive. Suppose a polled cow produces a polled heifer calf, but in later matings produces a horned bull calf (simple recessive). It is desired to know if the genotype of the polled heifer calf is \(PP\) or \(Pp\). In the former case, the heifer might advantageously be kept for breeding purposes, but in the latter case, it might be undesirable to do this in view of the fact that she would transmit the gene for horns to one-half her progeny. Of course, she could be used for breeding purposes and produce no horned calves if mated to a \(PP\) sire even though the gene for horns would be transmitted to one-half her progeny.

Figure 9.—Brother and sister matings are the closest approach that the livestock breeder can make to the self-fertilization method used by the plant breeder. Here is shown a cross-bred Berkshire-Yorkshire sow with pigs by a Yorkshire-Berkshire sire. The ratio is 7 white pigs: 2 black with some white. Both of the latter type died. (Courtesy of Journal of Heredity.)

After reaching sexual maturity, the polled heifer ($P^-$) is mated to a horned bull ($pp$). If she carries horns, one-half of the calves should be horned. If all the calves are polled, it will be necessary to produce four to six calves to obtain a reasonable degree of assurance that the polled heifer does not carry the gene for horns. Here, it has taken several years to determine the genotype of the polled heifer for one pair of genes, which may be expressed in calves of either sex. Consider how much more complex the problem becomes when the characteristic concerned is due to the action of several pairs of genetic factors, expressed only by females and not by them until they have reached sexual maturity, as in the case of milk production or egg production. Further, a cow that has produced four to six calves will not be available very much longer for breeding purposes.

The case of horns involving the action of only one pair of genes is the simplest kind that will be encountered. Suppose we are concerned with the inheritance of characters behaving like comb type in fowls. Here, two pairs of genes are involved. The double recessive for both pairs of genes results in a single-combed bird. The dominant gene of one of the pairs produces pea comb and the dominant gene of the other, rose comb. When the dominant genes are present in both pairs, a walnut comb results. The ratios to be expected in cases where two pairs of factors are involved have been pointed out in the previous discussion. At least 16 individuals would be necessary to represent the segregating groups in the proportion in which they occur in the $F_2$ generation.

Warwick has suggested that inguinal hernia in swine is due to the operation of at least two pairs of recessive genes. This characteristic does not ordinarily appear in sows, although sows transmit the genes for it. To determine whether a sow transmits hernia, it would be desirable to mate her with a herniated boar (backcross) and ascertain if any of her male pigs were herniated. The ratios expected would depend somewhat on the genotype of the sow. If she did not transmit both recessive factors, none of the pigs would be herniated. Still we would not know whether she transmitted the recessive gene of one of the allelic pairs. If she were heterozygous for one pair of factors and homozygous recessive for the other pair—that is, with the constitution $Aa \, bb$—one-half of her male progeny from the herniated boar would have hernias. If she were heterozygous for both pairs of factors, with the constitution $Aa \, Bb$, one-fourth of the male progeny would be expected to have hernias. Modifying factors may still further complicate the situation. Therefore, it is usually considered advisable, instead of testing the individual concerned in a definitely planned experiment, to go ahead with the usual breeding operations, and if the parents produce herniated pigs, to assume that both parents transmit the undesirable characteristics, and discard them so as to eliminate the possibility that their progeny will carry an undesirable recessive to still more descendants.

The difference between high and low milk production certainly is due to the operation of several pairs of genetic factors. Estimates of different investigators have ranged from 3 to nearly 20 pairs of genes. This increases the number of animals necessary to give a complete segregating population beyond any possibility of a single pair of par-
ents producing sufficient progeny to determine the genotype accurately. With 10 pairs of genes, which has been suggested by Turner as the minimum number controlling milk production, 1,048,546 animals would be required to give a complete F₂ population and 1,024 progeny to give a complete backcross generation. Obviously, it is impossible to get enough progeny from matings between the same two individuals, yet genotypes of a pair cannot be ascertained otherwise. Moreover, to allow for chance variations, it is usually considered necessary to have at least three times as many individuals as are needed for the complete segregating population.

(4) Animal-breeding research is very costly. It is much more expensive to produce a single individual than would be required in the case of a single plant. Special care, feeding, management, and adequate space are required. The progeny of any single mating is small as contrasted with the large number of seeds produced by most plants. The cost of keeping the numbers of animals needed to work out a rather complex ratio involving several pairs of genetic factors is almost prohibitive.

(5) Many of the characteristics of economic importance do not readily group by classes. Color, horns, and many of the more obvious characteristics are inherited in a relatively simple manner, but the genetic basis for characteristics concerned with the production of milk, meat, eggs, wool, etc., is more complex. The genes determining milk-producing capacity may act in a cumulative manner, or dominance may govern their expression to a greater or lesser extent. It is probable that if several pairs of genes are involved, various kinds of gene interactions occur, which adds to the complexity of determining the mode of inheritance of such characters.

In cases where a large number of genes are operative in determining a quantitative characteristic such as yearly butterfat production, different genotypes may give rise to the same phenotype. For example, with genes A, B, and C, assuming that A was responsible for 150 pounds; a, 25 pounds; B, 75 pounds; b, 25 pounds; C, 100 pounds; and c, 25 pounds, one might have an individual producing 350 pounds of butterfat with the genotype Aa bb Cc, or aa Bb CC. Such conditions make the identification of the effect of the different genes very difficult, if not impossible. When a large population is needed in order to have representatives of the different types, the difficulties encountered in studying quantitative characters, which includes so many of those of economic importance, are apparent.

(6) Modifying factors, which play an important part in the inheritance of many characters, tend to spread the classes so that one grades into another. The mode of inheritance of these factors is similar to that of the other genes concerned, yet their presence may completely change the results obtained. For example, in some poultry there is an inhibiting gene preventing the appearance of any color. The presence of this gene results in the white of the White Leghorn. Yet the White Leghorn may carry many color genes, expression of which is inhibited until suitable crosses with other breeds permit their expression in the absence of the inhibitor. In quantitative characters, such genes may increase or reduce the expression of another gene, as in the case of the relative amounts of color and of white in spotted animals.
Environmental effects may prevent the expression of certain genes. The characters of economic importance in livestock are influenced to a considerable extent by environment. For example, it is well known that a dairy cow may not produce up to her inherent capacity if she receives an insufficient food supply. To be sure, the plant is subject to environmental influences also, but ordinarily plants are placed under more adequate control, or at least the effect of environment can be evaluated more easily and at less expense. The identification of the role of the individual gene becomes practically impossible unless the environmental effects are known and kept constant.

Breeding Programs and the Future of Animal Genetics

Fortunately there is a brighter side to this picture. It is not necessary to know how many genes affect each character nor the effect of each individual gene entering into the final expression of a given quantitative character in order to make progress in animal breeding. Again we may use the inheritance of milk yield as an example. We now know that the cow that produces 350 pounds of butterfat cannot be depended on to transmit the inheritance for that level of production to all her offspring. But if a herd of such cows are mated to a certain sire and all or most of the daughters produce 400 to 450 pounds of butterfat under the same environmental conditions, then we know that the sire possesses a genotype for a higher level of production than did the dams to which he was mated. Furthermore, the continuous use of sires that have demonstrated through the progeny test that they possess a genotype for higher levels of production will result in concentrating the factors determining the higher levels of production in the germ plasm of the herd. (The genotype of the dam as well as that of the sire can be determined by the progeny test, but the time required is so much greater and the inheritance of the individual dam is transmitted to so few progeny that it is much more feasible to work through the sire.) Thus progress is made in animal breeding by working with the end result of numerous genes, even though the number of genes involved is not known, nor the part that an individual gene plays in bringing about the end result.

Research work is gradually bringing about a knowledge of the extent to which some of the more common environmental variations may influence the expression of a character. In dairy cattle, for instance, knowledge is being accumulated concerning the effect on production of a number of factors, including age; the use of box stalls as compared to stanchions; the number of milkings per day; different ratios of grain or the all-roughage ration. Such information helps in evaluating a sire when, as frequently happens, the dams and daughters did not make their records under entirely comparable conditions, since suitable corrections can be made. However, more knowledge is needed to solve many of the problems that confront such a system of breeding as that outlined above. For example, when a sire is mated to dams with a very high level of production and the daughters of that mating have a somewhat lower level of production than the dams, it is difficult to determine what the genotype of the sire is, unless he has also been mated to cows possessing a lower level of production to see whether
he raised it or not. Likewise, when a sire is mated to dams with a level of, say, 350 pounds of butterfat and his daughters prove to be considerably above that level, it is impossible to know whether he has a genotype that will enable him to improve the germ plasm of a herd of cows with an average level of, say, 600 pounds, perhaps made under different environmental conditions than the record of the first herd.

The so-called proved-sire system of breeding progresses most rapidly where (1) the sire is mated at an early age to a large group of females, so that there is a sufficient number of female progeny to make possible the evaluation of his genotype before he reaches too advanced an age; (2) there is no selection of the daughters and their dams on the basis of high records; (3) records are made under environmental conditions that are comparable for both daughters and dams; and (4) environmental conditions are sufficiently good to enable the animals to express levels of production approaching their inherent capacity.

The difficulties encountered with the breeding of larger animals as contrasted with the progress made with insects, plants, and laboratory animals lend support to the idea that it never will be practicable, or perhaps possible, to identify the action of each gene in animal breeding. Genetic principles may be worked out with laboratory animals or insects that may be kept at much less cost and will reproduce rapidly. In experiments with larger animals, the genes will not necessarily have to be identified, but evaluations may be made by methods analogous to those employed in proving dairy sires in order to determine transmitting ability. It makes little difference to the dairyman whether 350 pounds of butterfat is produced because the animal was of the genotype $Aa \, bb \, Cc$, $aa \, Bb \, CC$, or what not, except that crosses of strains of certain genotypes would be expected to produce animals superior to either parent. In practice, it probably would be more satisfactory to test the complementary action of the genes from different animals by trial crossing rather than to attempt to discover the specific genes carried by each animal and the part they play in determining and transmitting characteristics.

The complementary action of unidentified genes has been successfully used with corn. Strains have been inbred to insure that they were homozygous, and by trial and error it has been found that the progeny from certain crosses are superior to ordinary varieties. The practice of similar methods would appear to offer promise in animal breeding, though experimental evidence will be needed in order to determine whether the results would be superior to, or more reliable than, those obtained by the proved-sire system. Then too, when close inbreeding in animals results in a loss of efficiency in characteristics of economic value, as is often the case, the cost of maintaining these closely inbred strains for crossing will be much greater than is the case with inbred strains of corn. Not all inbred strains of corn respond with marked hybrid vigor when crossed, and many strains have to be crossed in order to find those that result in increased yields. If this same amount of work is necessary with livestock, the expense of this method of breeding appears quite formidable, particularly in the case of cattle and horses. With smaller animals, like swine, the limitation is somewhat reduced and in fact experimental work of this kind is rapidly getting under way.
With the larger animals it is apparent that breeding progress will come about largely through what might be called a mass determination of the genotype. By the application of the progeny test and the use of sires proved in that manner, it will probably be possible to produce strains of animals in the various species containing combinations of genes that will give better average production than any strains now in existence. This method, combined, perhaps, with some inbreeding to produce greater homozygosity of the desired characters, holds great promise for the improvement of all forms of livestock. Progress obviously will be slow, however, owing to the difficulties that have been enumerated.

That genetics has not contributed more to livestock-breeding practice is not surprising. As a science it is less than 40 years old, and many of the basic discoveries have been made in the last 20 years. But the principles underlying breed improvement have been determined, and progress in the future should be more rapid. While Mendelian analysis has taken first place in some forms of life, it is certain that with the larger animals such an analysis will remain secondary to the testing of various breeding systems with the aim of synthesizing better and better strains.