CHAPTER XXIV

GENETICS

Introduction. A certain strain of wheat is like its parent in hardness, in gluten quality, in early ripening and in resistance to rust. The offspring of domestic cats are domestic cats; we know beforehand that they will be animals, not plants; Chordates, not Mollusks; Mammals, not Amphibians; Carnivora, not Primates; Felidae, not Canidae and domestic cats, not tigers. The phenomenon of inheritance is observed so frequently as to seem a law of nature. The kitten will grow up into a cat possessing many individual peculiarities of its parents and it will also differ from them in other details. The study of the inheritance of parental characteristics by offspring or among forms related by descent and of variations of these parental characteristics with a view of discovering the laws involved constitutes the special field of biological science called Genetics.

We have already studied many examples of asexual and sexual reproduction. In asexual reproduction, the offspring may be half of a single parent as in the fission of an Amoeba. The characteristics of the parent Amoeba are carried over in toto to the daughter cells. In asexual reproduction, the problems of inheritance are not as complicated as those involving sexual reproduction. However, most of the intensive work in heredity has been concerned with inheritance in sexually reproducing forms.

In sexual reproduction the offspring does not develop from the parents' heart or muscles or liver or from any of the organs of metabolism or adjustment. It develops from a fertilized egg which is the result of the union of an egg cell and a sperm cell. The animal, chordate, mammalian, carnivore, cat-like characteristics of the kitten, referred to above, must have been present in some concrete form in the spermatozoan or egg or both. Cytological and other studies indicate that they are present in both sperm and egg.

Not only are the general characteristics thus represented, but

even the peculiar things which mark this animal as a unique individual. There is no other bridge between generations except germ cells. It is evident, therefore, that genetics should include a study of the egg and the sperm.

The organism, from the moment of fertilization onward through life, is subjected to a complex of varying internal and external stimuli, which may modify the course of development. Genetics therefore involves a study of these environmental effects. With the broader questions of the generation of species, *i.e.*, with organic evolution, genetics does not deal directly, but the study throws much light on these problems.

Variations. Differences between individuals of the same species and between offspring of the same parents are well known

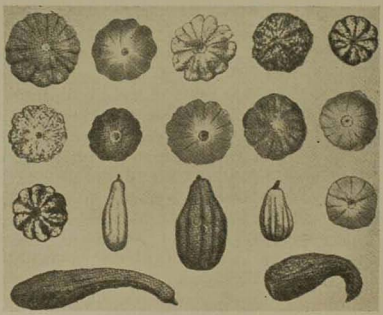


FIG. 350. — Variation in color, shape, size and surface of fruit of summer squash. (From Sinnott, *Botany* — 2nd Edition. McGarw-Hill Book Co. Reprinted by permission.)

(Fig. 350). Professor Walter describes variation as "The most unvarying thing in Nature." Bateson, in 1894, published a great mass of such data in his "Materials for the Study of Variation." Examples of variations are: differences in height and weight of persons; differences in the number of grains in different heads of wheat; the number of seeds in different oranges; immunity to disease; eye color and brachydactylism in man. Some are minute and are revealed only by close study, others are gross and

easily observable. Some are continuous, as the gradual increase in heights of a great body of men ranging by fractional increments from the shortest to the tallest. Some variations are discontinuous; earthworms differ as to the number of complete segments, not by fractions of a segment. Charles Darwin postulated variations as the basis of his theory of evolution. He recorded many examples of variation in many kinds of animals and plants. He did not explain the cause or origin of variations; and in fact little is known even today concerning this fundamental question.

Galton's Laws. Darwin's cousin, Francis Galton, made the first serious studies in inheritance during the later years of the last century. He collected data of human variations of one sort or another and by a method of mathematical analysis deduced what he claimed were laws of human inheritance. He obtained the height of 204 English parents of graduated statures and their 928 mature children. The average height of females is less than that of males by 8%, so Galton multiplied each female height by 1.08 to bring female height to the same standard as male height. He then added the height of the father to the corrected height of mother and divided the result by two. This gave him one number for the height of the two parents. He arranged parental heights in classes. The results in inches were as follows:

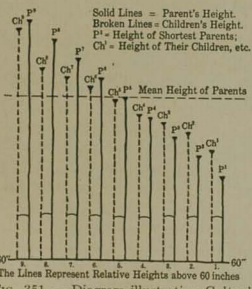


FIG. 351. — Diagram illustrating Galton's Law of Filial Regression.

	I	II	III	IV	V	VI	VII	VIII	IX
Parental height . .	64.5	65.5	66.5	67.5	68.5	69.5	70.5	71.5	72.5
Height of children .	65.8	66.7	67.2	67.6	68.3	68.9	69.5	69.9	72.2

One notes that the children of the shortest are taller than their parents and also that the children of the tall parents are shorter than their parents. This indicates a tendency toward the average height, and is known as *Galton's Law of Filial Regression* (Fig. 351), which is stated thus: Average parents produce

average offspring: tall parents produce tall children, short parents produce short children, but the children are not as tall or as short as their parents, that is, there is a tendency toward the average condition; the children inherit the parental characteristics in a less divers degree. Galton would have this law apply to inheritance of all sorts of characters, mental as well as physical. He made a more definite assertion derived from mathematical consideration of the results, namely, that children show only two thirds of the parental deviation from the racial average. By his statistical methods he arrived at another general conclusion known as the *Law of Ancestral Inheritance* (Fig. 352). According to this, he

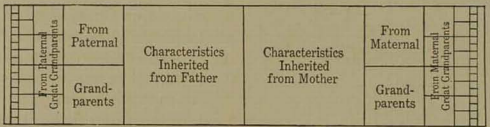


FIG. 352. — Diagram illustrating Galton's Law of Ancestral Inheritance.

asserted that the two parents contributed one half of the total inheritance of the child; the four grandparents, one fourth; the eight great-grandparents, one eighth, etc.

Statistical Methods. Such methods of mathematical analysis have been extended, since Galton's time, by his successor Karl Pearson of England and others. These methods, which constitute the science of biometry, have been applied to the solution of problems of heredity, evolution and other biological questions. The methods are especially applicable to the study of quantitative inheritance which apparently does not lend itself, on account of complexity, to analysis by Mendelian methods to be explained presently. It does not follow, however, that on this account the information gained is necessarily valuable.

Let us study a possible example of how these methods might be applied. Suppose we wish to study, by the statistical method, the inheritance of ray (ridges) numbers of the common scallop, *Pecten*. We must first devise a method by which we can accurately measure that character in parents and offspring, both representative of all scallops. We collect a large number of scallop shells and sort them out into groups of different ray numbers.

The accompanying photograph (Fig. 353) illustrates such a study. Of 135 shells examined, there were 5 shells that had 15 rays; 30 that had 16 rays; 76 that had 17 rays; 20 that had 18 rays and 4 that had 19 rays. We conclude that so far as this character is concerned, the ray number is 17. That is the biological average or mode. We now note that a heavy black line is drawn about the upper ends of the various shell groups. This is the 'variation curve' for this particular experiment. It represents the variation in ray numbers of the scallops studied. The biometrician has devised mathematical formulae which he can apply here to determine how well the specimens taken represent *all scallops*. If his mathematical test proves that our figure is representative of all scallops of this species, then he claims that the biological average for ray numbers in the common scallop is 17. Now we could study the offspring similarly and determine inheritance of ray number. Large numbers of cases are used in statistical studies and the conclusions are generalizations that apply to large numbers. They do not concern individual cases.

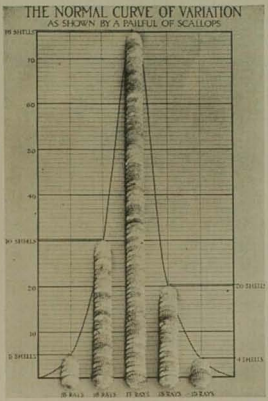


FIG. 353. — Normal curve of variation in rays on scallop shells. (Courtesy of American Museum of Natural History.)

But the practical breeder is not satisfied with generalizations. The farmer is more interested in the milk production of a particular cow or in the performance of his own small herd, but not so much in what that breed does. He may have in *his* herd some of the poorest producers, those down at the lowest end of the variation curve and he would not be inclined to keep those particular cows simply because statistical methods had demonstrated the breed to be a superior milk-producing type. He is not interested in generalizations. He wants something more specific.

Another application of these methods is that of ascertaining the degree of correlation between two different sets of facts. For example, as cited by Shull: "High egg laying in a certain breed of fowl is correlated with the paleness of the yellow color of the exposed parts of the skin." In arriving at an idea as to the degree of correlation, the student determines the *coefficient of correlation.* This ranges between 0.0 and 1.0. A number below 0.5 indicates little correlation, but between 0.5 and 1.0 the number is significant of correlation, and this becomes more probable as the coefficient approaches 1.0. Students interested in biometry are referred to treatises which explain its methods and the application of them.

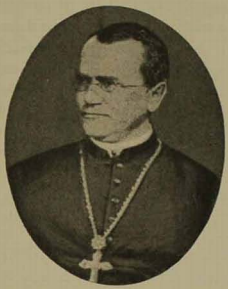


Fig. 354. — Gregor Mendel. (Courtesy of *Genetics.*)

Mendelism. — About the year 1900 a number of investigators became interested in specific breeding experiments in the endeavor to ascertain whether laws of inheritance were operative when particular qualities were kept under observation. Three pioneers were DeVries of Holland, von Tschermak of Austria and Correns of Germany. These men found that this method had been employed nearly forty years before by an earlier worker, Gregor Mendel (Fig. 354), a priest living at Brünn, Austria. Just after the rediscovery, in 1900, of Mendel's paper, other workers at once appeared, such as Bateson in England and Davenport and Castle in America. Mendel had studied science at the University of Vienna. About 1857 he began an experimental inquiry into heredity and worked painstakingly and successfully for eight years. As Castle says, "His keen analytical mind enabled him to plan and execute the most original and fruitful investigations on heredity ever completed." Father Mendel published his epoch-making results in the journal of the local natural history society. He sent an account of his work to the botanist, Professor Nägeli, who was more interested in other things just then and paid no real attention.[1] Charles Darwin had

[1] Nägeli wrote Mendel that the latter's results *were theoretically impossible!*

published the epoch-making " Origin of Species " but a few years before. It is interesting to speculate as to what would have resulted for science had Darwin known Mendel's work.

Mendel worked with varieties of garden peas. There is little variation within each variety because they are self-fertilized. Pollen from the stamens produces sperm cells which fertilize the egg cells in the ovaries of the same flower. Mendel noted that each variety had distinctive characters. One variety was tall, another was dwarf; one variety had smooth-coated seeds, another had wrinkled seeds; one had green-colored seeds, another had yellow seeds. Moreover, there was practically no gradation between green and yellow, between smooth and wrinkled, between tall and dwarf.

The offspring of dwarf peas were dwarfs and those which had green seeds produced green-seeded offspring uniformly and without variation. Mendel worked with seven pairs of contrasting or alternative characters or *allelomorphs*, as they are called. These are:

1. Form of the ripe seeds, *round* or *wrinkled*.
2. Color of the material in the cotyledons, *yellow* or *green*.
3. Color of the seed coat, *white* or *gray*.
4. Form of the ripe pods, *inflated* or *constricted*.
5. Color of the unripe pods, *green* or *yellow*.
6. Position of the flowers, *axial* or *terminal*.
7. Length of the stem, *tall* or *dwarf*.

At first he worked with each pair of allelomorphs separately and kept accurate records.

To cross or hybridize them he had to proceed as follows: For example, to cross a *tall* with a *dwarf* pea, it was necessary to remove all the stamens from *tall* plant flowers and place on their stigmas pollen from *dwarf* plant flowers or vice versa. He found that it made no difference which was taken as female or male, so far as inheritance was concerned. To understand his work a simple typical experiment is described. He crossed *tall* with *dwarf* peas. The resulting seed from this parental generation were all carefully saved and planted the next Spring. They developed into *tall* pea plants exclusively. If there was any dwarfness about them, it was hidden. So Mendel called tallness *dominant* and dwarfness *recessive*. During the second summer, he crossed these *tall hybrid* plants, carefully collecting the seeds as before. He planted them during the third summer, and *tall* and *dwarf* plants appeared.

He counted the two lots. There were about three times as many *talls* as *dwarfs*. The actual numbers were 787 *talls* and 277 *dwarfs*. On intercrossing the *dwarfs*, the resulting plants during the fourth summer were all *dwarfs*. He crossed these again, and the next summer they were all *dwarfs* again and the result continued to be the same. This showed that the first *dwarfs* to reappear were pure recessives like their grandparents.

But what about the *hybrid talls?* Mendel inbred them. In the third summer the population contained some *dwarfs* again. The first *hybrid talls* could not have been all pure *talls* or pure dominants because on inbreeding they produced some recessives. But, nevertheless, they might have contained some pure dominants like the *original talls* and also some *hybrids* like the parents. This proved to be the case, because Mendel was able to show that the *talls* in the second filial generation consisted of one third pure dominants and two thirds hybrids or impure dominants. Of the whole population of the second filial generation, this meant that, $\frac{1}{4}$ were pure dominant, *tall;* $\frac{1}{2}$ *hybrid tall* or impure dominant and $\frac{1}{4}$ *dwarf* or pure recessive.

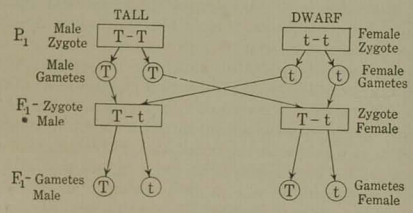
Similar proportions obtained when Mendel interbred the other pairs of characters. On crossing yellow-seeded peas with green-seeded he obtained, in the second filial generation, 6022 yellow peas to 2001 green peas, and in another experiment, 5474 round seeds to 1850 wrinkled seeds or about a proportion of 3 to 1 in each case, as before when hybrids were crossed. The first group proved to be $\frac{1}{4}$ pure yellow, $\frac{1}{2}$ hybrid yellow, $\frac{1}{4}$ pure green and in the latter experiment, $\frac{1}{4}$ pure round; $\frac{1}{2}$ hybrid round and $\frac{1}{4}$ pure wrinkled. A dominant character may be labeled by the capitalized first letter of the word denoting that character and the recessive allelomorph by the small letter form of the *same* letter, *i.e.*, Tall — T and dwarf — t.[1]

Mendel's Laws. As a result of these experiments, Mendel was able to explain the phenomena and came to the conclusion that laws or principles of inheritance were involved. These are now called the Mendelian Laws.

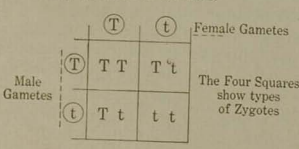
1. *Unit Characters.* Mendel thought of the organism as an aggregate of distinct and separate *unit characters*, such as tallness,

[1] Some workers prefer the reverse of this, *i.e.*, to use the *small* initial letter of the recessive for the recessive and the capital form of the same letter for the dominant, *i.e.*, in this case "d" = dwarf and "D" = tall.

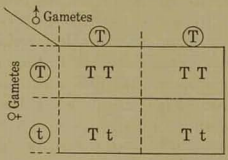
green cotyledons and smooth seed coat. Since a hybrid tall-dwarf pea, on being interbred, produced both tall and dwarf offspring, he believed that these *hybrids* contained both tall and dwarf unit characters although they *looked* tall. Then he conceived that each body cell of all individuals contained a double set of every type of unit character, but that gametes contained only single unit characters. That is, in modern terminology the body cells of the tall pea contained a double set of *tall* unit characters or, TT; and their gametes would all be merely T. Cells of dwarf plants would contain a double set of dwarf unit characters, *i.e.*, tt, but their gametes, only one, *i.e.*, t. When a "T" gamete and a "t" gamete united, the zygote would be "Tt" or the hybrid *tall-dwarf*. Their male gametes would be equal numbers (50% each) of "T" and "t" and the female gametes also 50% "T" and 50% "t." We can represent the breeding experiment in diagram form as shown below:



Now interbreed the F_1 hybrids which have equal numbers of T and t gametes. What would happen? According to the "laws" of probability, the union of these, in fertilization, would be 25% "TT"; 25% "Tt"; 25% "tT" and 25% "tt," or what is the same thing: 25% "TT"; 50% "Tt" and 25% "tt." The hypothesis can be diagrammed as follows.



Mendel's actual breeding experiment agreed with this hypothetical result. Now if the hypothesis is correct, it can be tested by crossing a *pure* tall with a *hybrid* tall. The experiment would be figured as follows.



Let us suppose that the male gametes come from a pure tall and female gametes come from a hybrid tall.[1] Accordingly, 50% of the offspring should be TT and 50%, Tt. But mere inspection of the progeny would not reveal this since all talls look alike. Since all are, at any rate, tall, the experiment gives that much information for theoretically that is what they should be.

But a more satisfactory experiment than the last can be made. We can back cross a hybrid "Tt" with a pure dwarf, "tt." (See Fig. 359.) The student can construct the diagram of such an experiment and can see that the results should be 50% "Tt" and 50% "tt." Actual experiment confirmed this. Mendel's explanation as to the dual or *diploid* nature of the body in unit character representation and the simple or *haploid* condition in the gametes has been accepted by geneticists. If the student refers back to the description of the behavior of the chromosomes in gamete formation (Fig. 298 *A*), he will see that the reduction divisions confirm the theoretical explanation given by Mendel. According to the Mendelian theory, if the somatic cells contain a duplex set of the same unit character, for example "TT," the organism is *homozygous* with regard to that character. If the somatic cells contain both of the alternative characters, for example "Tt," then the organism is *heterozygous* as to that character.

It should be noted that if contrasting characters which had been inbred in the first filial generation (F_1) reappear unchanged

[1] It makes no difference which sex is pure or hybrid. The important thing is that one parent is *pure* tall (TT) and the other *hybrid* tall (Tt).

♂ = male; ♀ = female.

in the second filial generation (F_2), such results indicate the *unit character* quality of such traits in heredity. The organism is an aggregation of its unit characters.

2. *Segregation.* A second principle or law developed by Mendel is that of segregation. If two forms having contrasting unit characters, *i.e.*, allelomorphs, are hybridized, the hybrid may resemble one of these characters, but two classes of offspring will reappear in the F_2 generation, *i.e.*, when the hybrids (F_1) are inbred. We have studied an explanation as to how this takes place. Body cells and primordial germ cells contain pairs of unit characters. When gametes are formed, each receives *one member* of each *pair* of unit characters which are thus *segregated* when sex cells are formed. If both members of a factor pair are alike, *i.e.*, if the zygote is homozygous, then there will be but one type of gamete; but a hybrid, whose cells are heterozygous, will produce gametes of two kinds. Individual unit characters are *segregated* when gametes are formed.

3. *Dominance.* A third law of Mendel is that of dominance. For example, hybrids of tall and dwarf peas appear tall; hybrid round-seeded by wrinkled-seeded peas are round-seeded; yellow peas by green peas hybrids appear yellow. Tall, round, yellow are respectively dominant over dwarf, wrinkled, green. When the hybrids are interbred, the character which was latent in the F_1 generation reappears, and such characters are termed recessive, *i.e.*, dwarf, wrinkled and green.

In order to understand Mendel's theory better, it will be worth while to work out a simple problem somewhat more completely. Let us work with another pair of characters chosen by Mendel. In the following diagrams, oblongs represent zygotes and circles outside of oblongs represent gametes; the letters inside the circles are abbreviations for unit characters being tested; the capital letter "R" represents a dominant character and the small letter "r" represents the recessive character allelomorphic to "R." The following experiments have to do with hybridizing peas that have *round* (*R*), *i.e.*, smooth, ripe seeds with a variety whose seeds are *wrinkled* (*r*). Let us divide the problem into several steps.

(*A*) In Fig. 355, we have a diagrammatic representation of a preliminary but necessary experiment. The purpose of this is to prove the purity of the strain. Both parents have round seeds and the seeds of the offspring are round also. If we interbred the

latter, we would find the same results. The diagram represents Mendel's idea of the disposition of the unit characters in parents; in gametes and in offspring — namely, diploid in parents; haploid in gametes and diploid again in offspring. Moreover, parents and

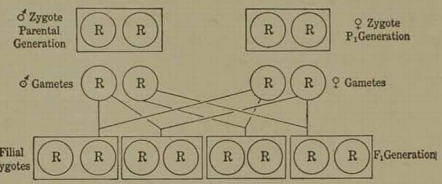


FIG. 355. — Breeding round-seed peas with round-seed peas.

offspring are homozygous. Repeated inbreeding should give the same results.

(*B*) Let us now establish proof of the purity of the other allelomorph, namely, the wrinkled peas. The experiment as explained by Mendel is represented by Fig. 356. If both parents are homozygous for "wrinkled," it is evident that the offspring must also be like them. Repeated interbreeding gives no other results, provided the strain is as represented here.

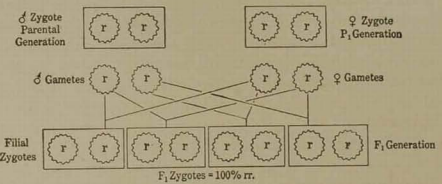


FIG. 356. — Breeding wrinkled-seed peas with wrinkled-seed peas.

(*C*) Now let us cross *round* seeds with *wrinkled* seeds, using for one parent, material tested as in experiment *A*, and for the other parent material tested as in experiment *B*. We can use round seed male and wrinkled seed female or vice versa. Fig. 357 represents the experiment as Mendel explained it. The gametes of the round

parent are all round and those of the other parent are all *wrinkled*. When fertilization takes place, in every filial zygote there is a combination of a round and a wrinkled unit character. But since all the seeds appear to be round, we conclude that round is dominant

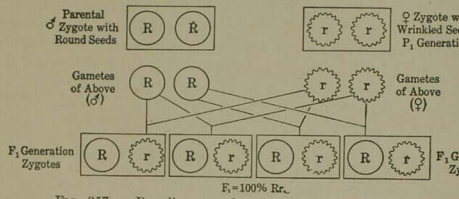


FIG. 357. — Breeding round-seed peas with wrinkled-seed peas.

and wrinkled is recessive. Moreover, all the filial zygotes are heterozygous because each now carries a pair of allelomorph characters.

(*D*) We will now interbreed these hybrids. The theoretical representation of such an experiment is shown in Fig. 358. Each parent produces two kinds of gametes and in equal numbers. The chances are, that in fertilization four combinations will be made as shown in the diagram. One (*a*) out of every four zygotes will be homozygous round; two (*b* + *c*) will be heterozygous

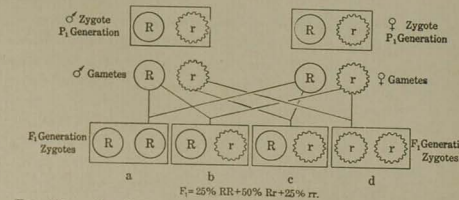


FIG. 358. — Breeding hybrid round-wrinkled seed peas with hybrid round-wrinkled seed peas.

round-wrinkled and one (*d*) will be homozygous wrinkled. Actual experimentation gives results as figured. Continued inbreeding of the homozygous round would produce only homozygous round, as indicated in Fig. 355. Also continued inbreeding of the

recessive homozygous wrinkled would produce only homozygous wrinkled, as shown in Fig. 356. Experiment confirms this. But suppose we interbred heterozygous round-wrinkled with heterozygous round-wrinkled, then what? Our results should be as indicated by this same Fig. 358, and they prove to be so.

(*E*) Now we can test this hypothesis further. Suppose we interbreed a homozygous wrinkled with a heterozygous round-wrinkled. Since one (homozygous) parent is like the original, as

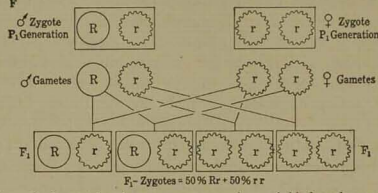


FIG. 359. — Back crossing homozygous recessive wrinkled-seed peas with hybrid (heterozygous) round-wrinkled seed peas.

shown in Fig. 356, and the other parent a hybrid, such an experiment would be called "back crossing." Fig. 359 represents this test. Here the hybrid is crossed with a recessive homozygous wrinkled. The results should be as presented and they prove to be so.

(*F*) Or we can cross a heterozygous round-wrinkled with a homozygous dominant round. The results should be as shown in Fig. 360, and they are. The student may find it useful to conduct similar breeding experiments *on paper*, using the other allelomorphs

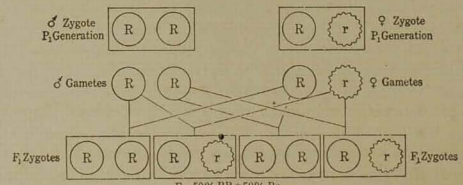


FIG. 360. — Back crossing homozygous dominant round peas with hybrid (heterozygous) round-wrinkled seed peas. All *appear* round.

that Mendel worked with. Experiment *F* does not give such analytical information as experiment *E* and a study of the results corroborates this.

Factor Hypothesis: the Gene. The expression "unit character" was somewhat indefinite. As work along these lines progressed, after 1900, this indefiniteness gave way to a clearly defined conception of the so-called *unit character*. The term has been succeeded by the word *gene*. A gene, according to present ideas, is an ultramicroscopic, multi-molecular protoplasmic body, probably protein in composition, which with other genes makes up the greater part of the chromosomes. Each gene is the *determiner* of some adult character. Genes are also called *factors*. The character "tallness" in peas is due to the presence in the zygote of a definite body, the gene for "tallness." The gene itself is not "tall" — but the plant into which that zygote develops will be tall, due to the presence of the gene. The conception that the gametes uniting in a zygote contain the genes of all the characteristics of an individual is known as the *theory of the gene* or the *factor hypothesis*.

For example, the following are believed on good evidence to be *factors* in human inheritance — a certain type of color blindness, immunity to disease, blue eyes, red hair.

Professor Biffen in England found by experiment that the following are factors in wheat: beardlessness, red grain, early ripening, thick stem, immunity to rust. In other words each of the above cited characters are represented in the gametes by definite particles called "genes."

Independent Assortment of Factors. A Dihybrid Ratio. This is an extension of the law of segregation. Mendel investigated several pairs of allelomorphs and found when he carried on experiments in which two forms differed in two or more of these, that the inheritance of any one pair of allelomorphs was *independent* of the inheritance of any other pair (Fig. 361). Inheritance of stature is independent of seed color and both of these independent of smoothness of seed coat. An example of this will be cited and studied in some detail. Let us inbreed a pea plant having round-yellow seeds with one having wrinkled-green seeds. Round is dominant over wrinkled and yellow dominant over green. The hybrids will appear round-yellow. Let us now cross these *hybrid* round-yellows. We find four classes of offspring in *definite* proportions.

$\frac{9}{16}$ round-yellow; $\frac{3}{16}$ round-green; $\frac{3}{16}$ wrinkled-yellow; $\frac{1}{16}$ wrinkled-green. Recall that when round-wrinkled hybrids are crossed, the F_2 generation would be $\frac{3}{4}$ round to $\frac{1}{4}$ wrinkled.

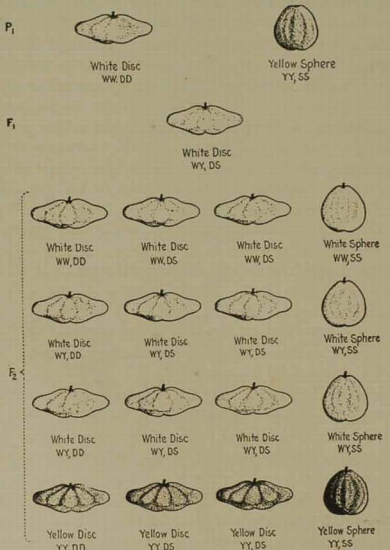


FIG. 361. — Mendelian dihybrid ratio. Two pairs of characters are involved. In summer squashes, *disc* shape is dominant over *sphere* shape and *white* color over *yellow*. White disc crossed with yellow sphere gives an F_1 generation, in which all offspring are white disc. When these hybrids are interbred, the F_2 generation consists of about: $\frac{9}{16}$ white disc; $\frac{3}{16}$ white sphere; $\frac{3}{16}$ yellow disc and $\frac{1}{16}$ yellow sphere. (From Sinnott, *Botany — Principles and Problems*, Revised edition. McGraw-Hill Book Co. Reprinted by permission.)

When hybrid yellow-greens are crossed, the F_2 generation would be $\frac{3}{4}$ yellow to $\frac{1}{4}$ green. Now if the theory of independent assortment is true and if both crossings are made simultaneously, we should find $\frac{3}{4}$ round $\times$ $\frac{3}{4}$ yellow, or $\frac{9}{16}$ round-yellow; $\frac{3}{4}$ round $\times$

$\frac{1}{4}$ green, or $\frac{3}{16}$ round-green; $\frac{3}{4}$ yellow $\times$ $\frac{1}{4}$ wrinkled, or $\frac{3}{16}$ yellow-wrinkled; $\frac{1}{4}$ green $\times$ $\frac{1}{4}$ wrinkled, or $\frac{1}{16}$ green-wrinkled. But this tells us nothing of the genetic constitution of these forms. We can, theoretically at least, determine this by diagramming according to the Mendelian hypothesis what took place in the F_2 generation. There would be four types of male gametes and four similar types of female gametes.

The experiment would be represented diagrammatically as follows:

MALE GAMETES

FEMALE GAMETES	RY	Ry	rY	ry
RY	RY RY Round Yellow	Ry RY Round Yellow	rY RY Round Yellow	ry RY Round Yellow
Ry	RY Ry Round Yellow	Ry Ry Round Green	rY Ry Round Yellow	ry Ry Round Green
rY	RY rY Round Yellow	Ry rY Round Yellow	rY rY Wrinkled Yellow	ry rY Wrinkled Yellow
ry	RY ry Round Yellow	Ry ry Round Green	rY ry Wrinkled Yellow	ry ry Wrinkled Green

Genotype and Phenotype. Any zygote that has at least *one gene* for round (the dominant character) will *appear* round and any zygote that has at least one gene for yellow will *appear* yellow. As previously estimated, *these* sixteen combinations fall into four groups; *i.e.*, $\frac{9}{16}$ round-yellow; $\frac{3}{16}$ round-green; $\frac{3}{16}$ wrinkled-yellow and $\frac{1}{16}$ wrinkled-green. Thus, there are four different lots so far as *external appearance* goes. These are called *phenotypes.* However, if we examine the gene composition of *all* the members of any one group we find different combinations of genes, although all in the group have the same external appearance. For example, in the round-yellow phenotype group we find the following different gene combinations: RRYY: RRYy: RrYY: RrYy.

These are called *genotypes, i.e.,* in this case the phenotype round-yellow has four genotypes. The round-green phenotype contains the following genotypes, RRyy : Rryy. The wrinkled-yellow phenotype has two genotypes, rrYY, rrYy. Finally, the wrinkled-green is a phenotype *and* a genotype also. It is more important to know the genotype rather than the phenotype because if we interbred phenotypes, we could not necessarily produce similar offspring. For example, if we interbred the Round-yellow phenotypes RRYY × RRYy, the offspring would all appear round yellow while if we interbred the round-yellow phenotypes RrYY × RrYy, there would be round yellows and wrinkled yellow. If we interbred similar genotypes, all the progeny would be like the parents. To test this we will diagram two more experiments. First let us inbreed the following genotypes belonging to the round-yellow phenotype group.

GENETIC COMPOSITION OF MALE ZYGOTE — RRYY

MALE GAMETES

GENETIC COMPOSITION OF FEMALE ZYGOTE—RRYy

FEMALE GAMETES

	RY	RY	RY	RY
RY	RY RY Round Yellow	RY RY Round Yellow	RY RY Round Yellow	RY RY Round Yellow
Ry	RY Ry Round Yellow	RY Ry Round Yellow	RY Ry Round Yellow	RY Ry Round Yellow
RY	RY RY Round Yellow	RY RY Round Yellow	RY RY Round Yellow	RY RY Round Yellow
Ry	RY Ry Round Yellow	RY Ry Round Yellow	RY Ry Round Yellow	RY Ry Round Yellow

The phenotype is named in each square.

In this case two different genotypes of the same phenotype class are interbred. All the offspring are *similar phenotypically* to the parents, for all have at least one dominant factor for shape, *i.e.,* round and also at least one dominant factor for color, *i.e.,* yellow. And yet the same two genotypes still appear, *i.e.,* RRYY and RRYy. But promiscuous inbreeding of *any similar pheno-*

types will not *always* give us the same results. This is shown in the second case. Let us now interbreed two other zygotes of the same phenotype class as before but which are different genotypes, namely, RrYY and RrYy.

GENETIC COMPOSITION OF MALE ZYGOTE — RrYY

Male Gametes

GENETIC COMPOSITION OF FEMALE ZYGOTE — RrYy

Female Gametes

	RY	RY	rY	rY
ry	RY ry Round Yellow	RY ry Round Yellow	rY ry Wrinkled Yellow	rY ry Wrinkled Yellow
rY	RY rY Round Yellow	RY rY Round Yellow	rY rY Wrinkled Yellow	rY rY Wrinkled Yellow
Ry	RY Ry Round Yellow	RY Ry Round Yellow	rY Ry Round Yellow	rY Ry Round Yellow
RY	RY RY Round Yellow	RY RY Round Yellow	rY RY Round Yellow	rY RY Round Yellow

The phenotype is named in each square.

In this example two different genotypes of the same phenotype class are interbred. In this case the *offspring* belong to *two* phenotype classes, namely, round-yellow and wrinkled-yellow. It will be noted that all zygotes have at least one factor for yellow which is dominant. Some of the zygotes are wrinkled because some classes of male *and* female gametes *both* carry this recessive factor.

A Trihybrid Ratio. In the next place let us diagram what would be produced if we inbred two parents, each of which is a hybrid tall-dwarf, yellow-green and round-wrinkled. The table on the following page shows the results.

Phenotypes are as follows: Out of the 64 classes of zygotes there are $\frac{27}{64}$ RYT; $\frac{9}{64}$ RYt; $\frac{9}{64}$ RyT; $\frac{9}{64}$ rYT; $\frac{3}{64}$ Ryt; $\frac{3}{64}$ rYt; $\frac{3}{64}$ ryT; $\frac{1}{64}$ ryt. There are 27 different genotypes.

TRIHYBRID RATIO

Trihybrid Male Zygote's Genetic Composition = TYRtyr

MALE GAMETES

Genetic Composition of Female Trihybrid Zygote — TYRtyr

FEMALE GAMETES

	TYR	TyR	TYr	Tyr	tYR	tyR	tYr	tyr
TYR	TYR TYR	TyR TYR	TYr TYR	Tyr TYR	tYR TYR	tyR TYR	tYr TYR	tyr TYR
TyR	TYR TyR	TyR TyR	TYr TyR	Tyr TyR	tYR TyR	tyR TyR	tYr TyR	tyr TyR
TYr	TYR TYr	TyR TYr	TYr TYr	Tyr TYr	tYR TYr	tyR TYr	tYr TYr	tyr TYr
Tyr	TYR Tyr	TyR Tyr	TYr Tyr	Tyr Tyr	tYR Tyr	tyR Tyr	tYr Tyr	tyr Tyr
tYR	TYR tYR	TyR tYR	TYr tYR	Tyr tYR	tYR tYR	tyR tYR	tYr tYR	tyr tYR
tyR	TYR tyR	TyR tyR	TYr tyR	Tyr tyR	tYR tyR	tyR tyR	tYr tyR	tyr tyR
tYr	TYR tYr	TyR tYr	TYr tYr	Tyr tYr	tYR tYr	tyR tYr	tYr tYr	tyr tYr
tyr	TYR tyr	TyR tyr	TYr tyr	Tyr tyr	tYR tyr	tyR tyr	tYr tyr	tyr tyr

We observe, from a comparison of the types of experiments cited, namely, (*a*) those in which *one pair* of characters alone was considered; (*b*) where *two* allelomorphs were used in the same experiment and (*c*) where *three* allelomorphs were inbred in the same experiment, that the number of different types of gametes is greater in each successive case; the number of phenotypes increases and also the number of genotypes. Let us represent the number of allelomorphs or factor pairs by the letter "n." The following formula is useful. The number of kinds of gametes (male or female) is 2^n; the number of phenotypes is 2^n; the number of genotypes is 3^n.

Let us take the example in which three allelomorphs were used in a single experiment. This is a trihybrid ratio. In this case we crossed two plants that are each hybrid, *i.e.*, RYTryt × RYTryt. The number of factor pairs is three, namely, R-r; Y-y; T-t. According to the formula, there must be 2^3 gametes

of each sex, or 8; there must be 8 phenotypes and 27 genotypes. The preceding table confirms this.

Mendel worked with seven pairs of allelomorphs. If he obtained hybrids embodying combinations of all of the above, then there would have been 2^7 or 128 different kinds of gametes; there would have been as many phenotypes and 2187 or 3^7 genotypes.

It is said that man possesses 24 pairs of chromosomes. Theoretically each chromosome carries many genes. If each chromosome pair carried only one distinctive allelomorphic pair according to the above formulae, there would be 16,777,216 different male and female gametes and just as many phenotypes and 3^{24} genotypes. But chromosomes are far, far more complicated than this, so that *great variation* in children follows. Children are *like* their parents in *some* respects and *unlike* them in *other* respects.

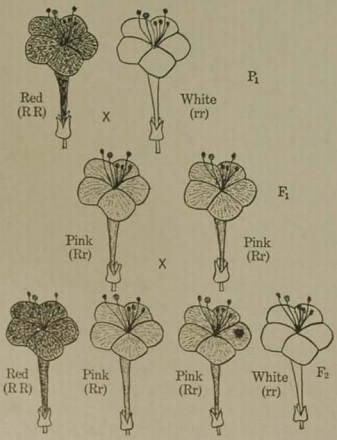


FIG. 362 *A*. — Lack of Dominance — illustrated by interbreeding Red and White Four O'clocks.

Presence-Absence Hypothesis, or Absence of Dominance. Many of the earlier simple conceptions of Mendel have been modified, due to experiments with a great variety of plants and animals. Exceptions to the so-called law of dominance were soon found by later workers, and now it is not considered essential to Mendelian theory. For example (Fig. 362 *A*), when *red* Four O'clock plants are crossed with *white* Four O'clocks, the flowers of the hybrids are *pink*, showing that the law of dominance does not hold here. When the hybrid pinks are inbred, there are three classes of offspring, namely, 25% reds; 50% pinks; 25% whites.

To explain this, the presence-absence hypothesis was advanced. According to this idea, red is due to the presence of a double set of color-determining factors, *i.e.*, R-R; while white is due to the absence of these, *i.e.*, r-r. A zygote that contains R-R in its body cells has red flowers; one that has r-r in its body cells is white flowered and one that has the combination R-r will be pink flowered. We can see that if R-r is crossed with R-r, the resulting offspring will be 25% R-R; 50% R-r; 25% r-r, as stated above.

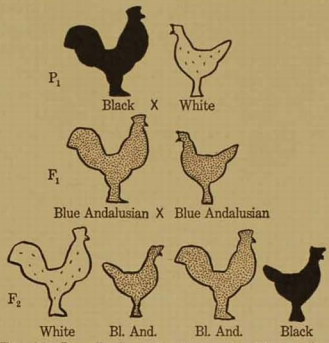


FIG. 362 *B*. — Lack of Dominance in Blue Andalusian Fowls.

Another early case that appeared was that of the Blue Andalusian fowl. Breeders could never get this to breed true and were at a loss to know why. Breeding experiments after the Mendelian fashion (Fig. 362 *B*) revealed the fact that the Blue Andalusian is a hybrid between certain black and white parent breeds. The case is similar to the above Four O'Clock example. Other cases examined indicated that although dominance of a sort is present it differs in degree and that other factors sometimes influence dominance.

Modification of Factors. Not all breeding experiments show as simple definite results as those of Mendel. It has been found that factor pairs in combination with each other in some cases produce a modification of what occurs when inbred separately.

Certain breeds of poultry have what is known as a "rose" comb; other breeds, a "pea" comb; and still others, a "single" comb. Each type breeds true. But when "rose" was crossed with "single," there was a distinct separation into two classes as follows: ¾ "rose" and ¼ "single," the monohybrid ratios already familiar to us. Again, when "pea" was crossed with "single," the result was ¾ "pea" and ¼ "single." "Rose" is dominant over "single" and "pea" is dominant over "single" also.

But Bateson and Punnett found that when they crossed "rose" and "pea," neither proved to be dominant but a new type of comb called "walnut" appeared. This had previously been found in an unrelated breed of fowls. Then they inbred the hybrid "walnuts," and in the F_2 generation there were $\frac{9}{16}$ "walnut," $\frac{3}{16}$ "rose," $\frac{3}{16}$ "pea" and $\frac{1}{16}$ "single." This resembles a dihybrid ratio, but not the ordinary sort. "Walnut" is a new phenotype. It was found that when the "singles" obtained were inbred, they produced "singles." This indicated that "single" depends on the interaction of the recessives of "rose" and "pea." The $\frac{9}{16}$ group of phenotypes obtained in an ordinary dihybrid ratio contain at least one factor for each of the dominant allelomorphic pairs. Hence we may assume that "walnut" in this case is effected when a phenotype possesses at least one factor for "rose" *and* one for "pea." Fig. 363 depicts the above explanation. "Walnut" appears to express a reaction between *two* distinct dominant characters. "Single" occurs when the genetic constitution is a double recessive, *i.e.*, "rrpp."

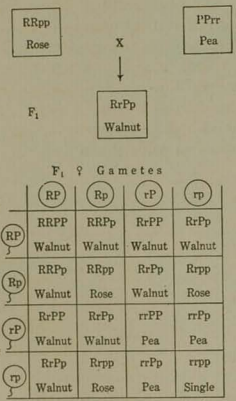


FIG. 363. — Modification of Dominant Factors in combination — shown here by inbreeding Rose-comb and Pea-comb fowls.

Complementary Factors. As new types of experiments were performed, new complications appeared and new explanations were devised to bring them in line with orthodox Mendelian hypothesis. One of these resembles the last case but differs in that no *new* character appears as the result of the interaction of factors. When purple sweet peas are crossed with white sweet peas, the result is *usually* $\frac{3}{4}$ purple (P) and $\frac{1}{4}$ white (p), and when white is crossed with white, the result is usually white. Bateson and Punnett found at times that white × white gave purple.

When the latter were crossed, they gave $\frac{9}{16}$ purple and $\frac{7}{16}$ white. This can be explained as follows: The proportions suggest a dihybrid ratio and that two allelomorphs are present. Moreover, purple may be due to two *complementary factors*, one for purple and the other for color — possibly a *potential* purple *pigment* activated by a color *enzyme*. We can postulate *two* allelomorphs then, one pair being *purple pigment* (P) and its alternate, absence of pigment (p); the other pair being *color activator* (C) and its absence (c). It would follow that both P and C would have to be in the same zygote to get a purple flower. Suppose we treat these allelomorphs as we did in the dihybrid ratio in peas. The following diagram indicates our hypothesis. In the lower part of each square is indicated the hypothetical color of the flower.

FEMALE GAMETES

MALE GAMETES	CP	Cp	cP	cp
CP	CP CP Purple	Cp CP Purple	cP CP Purple	cp CP Purple
Cp	CP Cp Purple	Cp Cp White	cP Cp Purple	cp Cp White
cP	CP cP Purple	Cp cP Purple	cP cP White	cp cP White
cp	CP cp Purple	Cp cp White	cP cP White	cp cp White

Zygotes are $\frac{9}{16}$ Purple and $\frac{7}{16}$ White.

Nine of these zygotes ($\frac{9}{16}$) contain at least one factor for color and one factor for purple pigment; the other seven contain (1) neither, (2) or only one or the other, (3) or possibly two of the same positive factor, (4) but not *both* C and P. We can understand now why the interbreeding of certain whites would produce purple. Inheritance similar to this occurs in a number of other cases and the above explanation fits there as well. The complementary factor hypothesis throws light on the reappearance, after many generations, of characters that have been latent. These are known as reversions.

Lethal Factors. Sometimes offspring possess characters that cause early death. These are known as *lethal* factors. Apparently these must be present in a double dose in the zygote to be effective, *i.e.*, to be lethal. In other words, the zygote must be homozygous in respect to this factor; if it is heterozygous, the lethal factor is not effective. However, it may be conceived that if *both* parents are each heterozygous with regard to this factor, then there is a possibility of *some* offspring being homozygous in respect to it and so destined to an early death.

Sex Determination. What are the factors which determine the sex of an individual? This question has long interested many inquiring minds. Many untenable theories have been advanced. It remained for the Mendelian and cytologist to make substantial contributions to the solution of this age-long mystery. It occurred to many experimenters that sex is inherited in the Mendelian fashion. Let us assume that the case is similar to that in which hybrid tall-dwarf peas were crossed with pure dwarfs, *i.e.*, Tt $\times$ tt and where the result was 50% *heterozygous* dominant and 50% *homozygous* recessive. In sex inheritance, the offspring are about 50% male and 50% female. Furthermore, the male appears to be heterozygous and the female homozygous in this type of inheritance. In that case the male would produce two kinds of gametes and the female but one type of gamete. Cytological studies of gonad cells, of spermatogenesis, oogenesis and of germ cells reveal chromosomal conditions which confirm the above assumptions and together with Mendelian experiments permit the construction of a theory of sex determination more satisfactory than any hitherto advanced.

About twenty-five years ago examination of the gametes of certain insects indicated two kinds of sperm. One had an *extra* chromosome which was lacking in the other type of sperm. All the eggs had the extra chromosome. Moreover, the primitive germ cells and body cells of the female had *two* of these "*accessory*" chromosomes in addition to a certain number of other chromosomes, now called "*autosomes.*" The cells of the male body and its primitive germ cells also had the same number of *autosomes* and but *one accessory* chromosome. McClung, in 1902, suggested the relation between sex determination and these accessory chromosomes, now called *sex chromosomes.* Extensive work on many forms, principally insects, revealed the same general con-

dition. The evidence from chromosomes supports the theory that sex is determined *at the time of fertilization* by the egg combining with a *male-determining* or a *female-determining* sperm, and that so far as we know the type of sperm involved depends on chance.

Let us represent the cells of the female body by the formula " AAXX " (Fig. 364), that is, they are homozygous. All female gametes would be represented by the formula " AX." The male

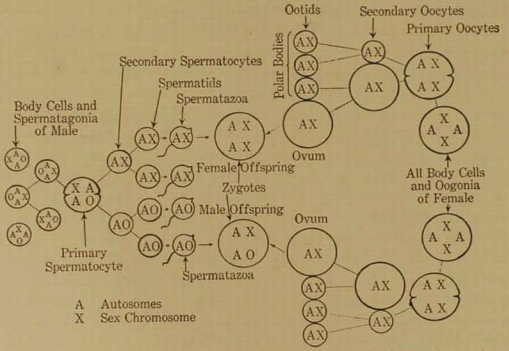


FIG. 364. — Relation of Sex Determination to Oogenesis, Spermatogenesis and Sex chromosomes. (*a*) All eggs are alike as to sex chromosomes; (*b*) two types of sperm as to sex chromosome; (*c*) equal numbers of male and female offspring.

body cells would be represented by the formula " AAXO " and there would be two types of gametes, namely, " AX " and " AO." If a zygote is formed from an egg " AX " and a sperm " AX," then all the developing body cells would be " AAXX," which is exactly the formula of the female body cells. However, if an egg, " AX," united in fertilization with the other type of sperm, " AO," the zygote and all developing cells would have the formula " AAXO," which is the formula *found* in male body cells. Therefore the facts support the theory.

In some cases, the sex chromosome or " X " chromosome has a mate, called the " Y " chromosome, which is supposed to carry but a few or *no* unit characters. The " Y " chromosome is of *different*

shape and usually pairs with the "X" chromosome in synapsis. The "Y" chromosome of Drosophila (Fig. 365) is larger than its companion, the "X" chromosome, and is of different form. A series of forms of animals has been found in which the "Y" chromosome is smaller than the "X" chromosome, and forms are found in which there is no mate and where the condition in the body cells of males may be represented by the formula "AAXO." Variations in the "X" chromosomes also occur. In certain moths and butterflies and possibly in birds the situation is reversed. In these cases, the female is heterozygous as to sex chromosomes and produces two types of gametes, (*a*) those having the "AY" chromosome outfit and (*b*) those having the "AX" type, while all the sperm are of the "AX" type.

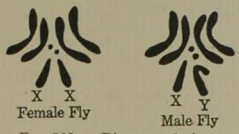


FIG. 365. — Diagram of chromosomes of male and female Drosophila (after Bridges). (From Morgan, *Critique of Theory of Evolution*. Princeton University Press. Reprinted by permission.)

Painter has come to the conclusion that the somatic cells of men contain 46 autosomes and another pair, namely, "XY" chromosomes, and that the body cells of women contain 46 autosomes and "XX" pair of chromosomes. Human ova thus possess 23 autosomes plus one "X" chromosome. There are two types of human sperm which occur in equal numbers: (1) 23 autosomes + one "Y" chromosome and (2) the 23 autosomes + one "X" chromosome. The student can readily see that fertilization of an egg by the first type of sperm would produce the chromosome equipment which body cells of males possess, while fertilization by the other type of sperm would produce the chromosome equipment shown by female body cells. A peculiar case is that of the honey bee. The somatic cells of the queen bee have 32 chromosomes and her egg cells 16. In our account of the honeybee we found that drones develop from unfertilized eggs. Theoretically, the body cells of drones should have 16 chromosomes, which is the case. There is no regular reducing division in sperm-cell formation in the drone, so that its sperm cells have 16 chromosomes. The drone mates with a queen, and thus, in case of fertilization, an egg with 16 chromosomes unites with a sperm having 16 chromosomes and produces a zygote with 32 chromosomes, which is the body cell number of the queen.

Modification of Sex. Recent work by Riddle and others indicates that although sex may be *determined* as outlined above at the time of fertilization, yet this is merely a tendency which may be later modified by physiological conditions. For example, the female of a certain variety of pigeon lays two eggs at a time, one of which usually develops after fertilization into a female and the other into a male. The eggs differ in appearance. The *female* egg is larger, has more nutriment and the rate of metabolism is lower than in the *male* egg. If eggs are removed from the pigeon as soon as they are laid, the pigeon lays oftener than normally. It is found after a time that both of these *later* eggs develop into females. Riddle suggests that excessive egg laying changes the metabolic rate of the *male* egg to the level of the *female* egg so that both develop into females.

When twins in cattle are of the same sex, they are normal. At times, however, calves appear of which one is a normal male while the other, called a *free-martin*, resembles a female in some respects but is otherwise a male. F. R. Lillie, after investigation of many specimens obtained at different stages of development, noted different embryological modifications and decided that the free-martin began life as a female. However, the sex organs of its male companion developed earlier, and the foetal testes of the male twin secreted the hormone which normally causes the development of the secondary sex organs. In this peculiar instance, the male hormone circulates in the blood system common to *both* twin foetuses and not only interferes with the development of some female secondary sex structures of the female calf, but also brings about, in the female, the development of certain structures of the male sex.

The effect of the loss of female hormones is evidenced by the much-quoted experiment of Goodale. He removed the ovary from a female Rouen duck. It gradually developed the distinctive male plumage. Similar effects are noted in other forms in which the sexes differ in appearance. An extreme case has been described by Dr. F. A. Crew of Edinburgh. A hen of a pedigreed stock (Fig. 344) had been known to lay eggs from which chicks had been hatched. She stopped laying and developed certain secondary male sex characters. Her behavior became that of a male. This metamorphosed female mated with another female and fertilized the eggs of the latter and from them chicks developed. In

this case the change not only affected the secondary sex characters but *also the gonads.* Examination after death indicated that the ovaries had degenerated and testes had developed in place of them.

Forms intermediate between male and female and called intersexes have been found in a number of cases. Goldschmidt found them in crosses between different varieties of moths. In the past, differences rather than resemblances between the sexes in the human species have been overemphasized. The popular conception is probably greatly influenced by literary ideas rather than scientific observations. Social customs served to further accentuate the differences. But after all the body possesses not only organs of reproduction but also those of metabolism and adjustment and these are very similar in both sexes.

Linkage. The principle of the independent assortment of factors when two or more pairs of characters were inbred has been stated to be a corollary of Mendel's law of *segregation.* It has been tested in experiments with various plants and animals with positive results. But many *other* experiments have indicated an association or *linkage* of characters in heredity. T. H. Morgan is largely responsible for the development of this principle, now regarded as one of the fundamental laws of heredity.

It has been evidenced in experiments with insects, cats, rats, rabbits, fowls, man, peas, corn, beans, cotton, tomatoes and many other forms. Morgan suggested that linkage of factors in heredity was due to their genes being present in the same chromosome. If, in germ-cell formation, such a chromosome is delivered intact to a gamete, then the characters developed from such linked genes would appear associated in the offspring. Examples of linkage are: (1) In the sweet pea, purple flowers with long pollen grains; (2) primrose, short style with magenta corolla; (3) garden pea, late flowering with colored flowers; (4) tomato, green foliage with two-celled fruit; (5) beans, seed pattern with vine habit; (6) rat, albinism with red eye.

As a result of long-continued breeding experiments with the little fruit fly, Drosophila, Morgan came to the conclusion that — "In Drosophila it has been demonstrated . . . that there are exactly as many groups of characters that are inherited together, as there are pairs of chromosomes." The Morgan "Fly Squad" found four groups of such characters. The members of any one group are inherited together. The members of any one group

appear to be inherited independently of the members of any other group. There are four pairs of chromosomes. There are three large groups of characters and three pairs of large chromosomes; there is one small group of characters and one pair of small chromosomes. The distribution of linked characters in successive generations agrees with the chromosome distribution. The Drosophila investigators have made a map (Fig. 366) of many of the genes showing that each has a definite location on a particular chromosome. The genes are arranged in a linear fashion along the chromosomes as the linkage theory would indicate. However the position of a gene bears no relation to the location of that character in the adult.

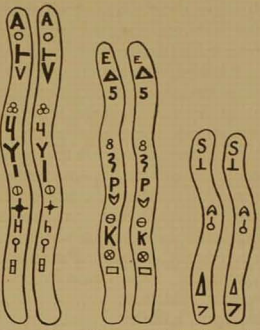


FIG. 366. — Diagram illustrating the theory of arrangement and distribution of genes (factors) in chromosomes. This imaginary animal has three pairs of chromosomes. According to the diagram, homozygous characters are represented by equal-sized figures within the chromosomes; while heterozygous characters are represented by unequal-sized figures. The larger figure in that case represents the dominant condition.

Crossing Over. In some cases the usual association of characters in heredity is departed from. New combinations appear. The hypothesis called *crossing over*, attempts to explain this. Cytological examination of germ cell formation in such cases reveals that in synapsis the chromosomes appear (Fig. 367) twisted around each other and so when they part company in the reduction division, the twisted chromosomes might *break* at the crossing points, and thus a new alignment of chromosome pieces *may be* effected. This aids in ex-

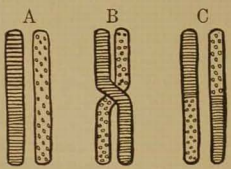


FIG. 367. — Crossing Over Hypothesis. When germ cells are formed homologous chromosomes come together in synapsis as in A.; At times they bend around one another as in B.; When they separate, in that case, they may have a new alignment of genes, as shown in C.

plaining the origin of many cases of new combinations or groups of characters in certain hybrids.

Sex-Linked Inheritance. Many cases have been found which indicate linkage between sex and some other character. One of the first examples was observed by Morgan. Drosophila is normally red-eyed. A white-eyed form appeared. When such a white-eyed male was mated with a red-eyed female, the results were different than when a white-eyed female was mated with a red-eyed male. Plumage peculiarities in fowls are associated with sex. Many other examples are known. Two interesting examples occur in man. First: Hemophilia or the tendency for the blood *not* to clot, possessed by certain individuals popularly known as "bleeders." Second: Daltonism, a kind of color blindness which appears to be associated with inheritance of sex. We will consider this in detail. The sons of a color-blind man are never color-blind nor are his daughters, but some of the sons of the latter are color-blind. Color-blindness seems to cross from one sex to the other from generation to generation. A color-blind female produces color-blind offspring oftener than a color-blind male. There are fewer color-blind females than males. A normal-eyed male never has color-blind descendants, but a normal-eyed female may have color-blind descendants.

These facts suggest that the factor for color-blindness is associated with the factor for sex. Therefore the two are carried by the same chromosome, namely, the "X" chromosome, although this does not imply that the "X" chromosome *always* carries the factor for color-blindness. Since man has but one "X" chromosome, the factor for color-blindness when present is associated with this chromosome and not the "Y" chromosome. The factor for color-blindness is not carried by the "Y" chromosome because color-blindness is transmitted by females, and these do not possess the "Y" chromosome. When a normal-eyed female produces some color-blind descendants, this indicates that although she is homozygous for sex she is heterozygous for color-blindness; that is, this factor is carried on one of the two "X" chromosomes. Finally, in order to be color-blind herself, she must have this factor linked with both her "X" chromosomes. A theoretical formula of the various conditions is presented diagrammed below. Let "X" represent a normal sex or accessory chromosome, and "x" when this chromosome carries the factors for

both sex and color-blindness. We will omit the autosomes since they appear to have nothing to do with the matter. " XY " represent the sex chromosomes of a normal-eyed man and " xY " those of a color-blind man. " XX " would be the sex chromosomes of a normal-eyed woman who has no genes for color-blindness linked with the sex chromosomes.

Let us consider a few possible marriages.

First. A normal woman marries a color-blind man.

P_1	♀	X	X			x	Y	♂
Gametes		♀	X		X			
		♂	x		Y			
F_1			2 Xx		2 XY			

None of the children is color-blind. The sons are genetically normal. Marriages with normal women never produce color-blind offspring. *These* daughters, however, though homozygous for sex are heterozygous as to color-blindness. Half their eggs will be normal and half will carry color-blindness.

Second. Let us see what would happen and what does happen when one of these " Xx " women marries a normal man.

P_1	♀	X	x			X	Y	♂
Gametes		♀	X		x			
		♂	X		Y			
F_1			XX + Xx + XY + xY					

Half the daughters are genetically normal as to color-blindness and this is true of half of the sons. Half of the sons are color-blind. They inherited this through a normal-eyed but genetically impure mother from a color-blind grandfather. Half the daughters of the present marriage carry color-blindness on one sex chromosome and will behave in inheritance just like their mother.

Third. Suppose one of these normal-eyed but genetically heterozygous women " Xx " married a color-blind man " xY."

P_1	♀	X	x			x	Y	♂
Gametes		♀	X		x			
		♂	x		Y			
F_1			Xx + xx + XY + xY					

Half the daughters are like the mother, *i.e.*, " Xx," and though normal-eyed, yet are heterozygous as to the character color-blindness. The other daughters " xx " are homozygous as to

color-blindness, *i.e., they are color-blind.* Half the sons are normal and half are color-blind. This type of mating would rarely occur, but when it does, some color-blind daughters appear.

Fourth. Suppose one of the color-blind women married a normal man.

P_1	♀	x	x			X	Y	♂
Gametes			♀	x		x		
			♂	X		Y		
F_1				2 xX		2 xY		

All the sons are color-blind and all the daughters carry color-blindness though functionally normal-eyed. All of these daughters marrying normal men will have some color-blind sons. The theoretical possibilities of inheritance from different kinds of matings, based on the assumption that the factor for color-blindness is linked with that for sex and therefore charted as shown in the above diagrams, are realized in human marriages of the types postulated. The conclusion is that the hypothesis is reasonable.

Hemophilia is more common among men than women. If by chance a woman should be homozygous as to this factor, she would be hemophilic and it *would tend to be lethal at puberty.*

Theory of the Gene. It is true that no one has seen a gene. But the existence of such bodies is considered more than hypothetical. Professor Morgan and his cooperative group consider that the chromosomes of Drosophila contain about 5000 genes. Theoretical evidence of genes has been presented in the preceding pages. The dual nature of somatic chromosomes and the haploid nature of gametic chromosomes, together with the operation of the laws of unit characters, of segregation, of dominance, of independent assortment, of linkage and of the sex chromosomes, all support the theory of the gene. No other interpretation seems possible. The conception of the gene is being extended. For example, attention has been called to a case in which two pairs of allelomorphic genes interact to produce purple color in the sweet pea. Morgan believes that at least twenty-five pairs of genes are responsible for eye color in Drosophila. On the other hand, in some cases it appears that one pair of genes affects more than one character. Finally it appears that the environmental conditions must be of a certain sort in order that the potentiality of the genes be realized in development.

Many of the results of research in genetics throw light on the problem of the generation of species and will be discussed in the chapter on evolution.

Practical Applications of Genetic Principles. It would appear that the discovery of the laws of inheritance, as elucidated by the geneticist, would prove to be of great value to the practical breeder of plants and animals. In spite of a quarter of a century of contributions in pure genetics, however, the practical applications have so far been rather disappointing. There are a number of outstanding exceptions.

For example, Biffen in England combined in one variety of wheat a number of valuable characters appearing in a number of wheats. Shull appropriately calls the result a "*synthetic wheat*" produced as a result of the application of Mendelian principles. Biffen combined the gluten quality, on which good bread making depends; resistance to rust; resistance to mildew; early ripening and resistance to drouth.

It appears that characters in plants are more simple and can be sorted out successfully by the Mendelian method. Only too often, in animals useful to man, the characters desired by the breeder are found to be too complex for this kind of analysis. The breeder follows about the same rule as his predecessors — namely, selection. If he desires to develop a good herd of milk-producing cattle, he uses mothers which have made a high record in milk production. Scientific investigation has shown, however, that the type of male used is also of great importance. The same importance seems to be true in the case of selecting both males and females to secure high egg production. Animal breeders consider the pedigree of the herd of great value because whatever improvement has been achieved is represented somehow in the pedigree.

A few successes are noted here. Immunity to disease appears to be a Mendelian factor in many varieties of plants and so can be incorporated with other useful characters. In corn, resistance to smut and to rust has been discovered. The vigor of certain corn hybrids is greater than that of either parent. This has also been found in the case of other useful plants and in some of our domestic animals. In fact all sorts of domestic varieties of plants and animals are being subjected to the Mendelian type of analysis with some degree of success. The indications are that these

investigations carried out in scientific fashion will bear more fruit in the future, and that much greater progress will be made in this way than by the slower methods of the older selectionists. The advantage of the newer method of approach will be that the phenomena will be better understood and the results more secure. Knowledge of the processes of nature will increase our control.

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