MENDEL'S LAWS OF INHERITANCE AND EXCEPTIONS TO THE LAWS

History

The assertion that life can instantaneously arise from non living matter is called spontaneous generation. Here are the critical experiments that busted the myth. Although today we understand that living things arise from other living things, the idea of spontaneous generation was entrenched in the minds of man throughout most of history. Spontaneous generation is the belief that, on a daily basis, living things arise from non living material. This debunked belief is not the same as abiogenesis, the study of how life on earth could have arisen from inanimate matter billions of years ago.

Aristotle and Spontaneous Generation (383-322)

Aristotle was one of the first to record his conclusions on the possible routes to life. He saw beings as arising in one of three ways, from sexual reproduction, asexual reproduction or nonliving matter. According to Aristotle, it was readily observable that aphids arise from the dew on plants, fleas from putrid matter, and mice from dirty hay; and this belief remained unchallenged for more than two thousand years.

Francesco Redi's Experiments (late 1600s)

Redi was and Italian physician and one of the first to formally challenge the doctrine of spontaneous generation. Redi's question was simple, "Where do maggots come from?" According to spontaneous generation, one would conclude that maggots came from rotting food. Redi hypothesized that maggots came from flies and designed an experiment, elegant in its simplicity, to challenge spontaneous generation.

Redi put meat into three separate jars:

- Jar #1 he left open. He observed flies laying eggs on the meat and the eventual development of maggots.
- Jar #2 he covered with netting. Flies laid their eggs on the netting and maggots soon appeared.
- Jar #3 he sealed. Flies were not attracted to this jar and no maggots developed on the meat.

This seems to be a clear demonstration of life giving rise to life. Yet it took another two hundred years for people to accept spontaneous generation as a fallacy.

Anthony van Leeuwenhoek's "Animalcules" (1600-1700s)

Leeuwenhoek was a Dutch cloth merchant, and due to his trade, he frequently used lenses to examine cloth. Rather than employing lenses made by others, he ground his own, and the expertise that he gained through lens crafting combined with a curious mind eventually led

to an interest in microscopy. During his life, Leeuwenhoek assembled more than 250 microscopes, some of which magnified objects 270 times. Through magnification, he discovered presence of “micro” organisms - organisms so tiny that they were invisible to the naked eye. He called these tiny living things “animalcules,” and was the first to describe many microbes and microscopic structures, including bacteria, protozoans and human cells.

John Needham & Lazzaro Spallanzani (1700s)

The debate over spontaneous generation was reignited with Leeuwenhoek’s discovery of animalcules and the observation that these tiny organisms would appear in collected rainwater within a matter of days. John Needham and Lazzaro Spallazani both set out to examine Leeuwenhoek's animalcules.

Needham’s Experiment

John Needham was a proponent of spontaneous generation, and his beliefs were confirmed when, after boiling beef broth to kill all microbes, within the span of a few days, cloudiness of the broth indicated the respawning of microscopic life.

Spallazani’s Experiment

Lazzaro Spallazani noted a flaw in Needham’s experiment. The containers holding Needham’s beef broths had not been sealed upon boiling. So Spallazani modified Needham’s experiment, boiling infusions, but immediately upon boiling he melted the necks of his glass containers so that they were not open to the atmosphere. The microbes were killed and did not reappear unless he broke the seal and again exposed the infusion to air.

Louis Pasteur (1800s)

Pasteur, a French scientist who made great contributions to our understanding of microbiology and for whom the process of “pasteurization” is named, repeated experiments similar to those of Spallazani’s and brought to light strong evidence that microbes arise from other microbes, not spontaneously.

Pasteur’s Swan-Necked Flasks

Pasteur created unique glass flasks with unusual long, thin necks that pointed downward. These “swan-necked” flasks allowed air into the container but did not allow particles from the air to drift down into the body of the flask.

The End of Spontaneous Generation

After boiling his nutrient broths, Pasteur found that these swan-necked containers would remain free of microbes until he either broke the necks of the flasks, allowing particles from the air to drift in, or until he tilted the flask so that the liquid came in contact with dust that had accumulated at the opening of the flask. It was these carefully controlled experiments of Pasteur

that finally put to rest the debate over spontaneous generation.

Preformation theory (Swammerdam and Bonnet. 1720 1793)

Preformation theory proposes that the only male and female is responsible for heredity. The male gamete consists of a miniature figure of man's body called as homunculus which is responsible for heredity. Epigenesis (C.f.wolf (1733-1794) and K.E. Von Baer (1792-1876) said that the different organs and tissues of adult plant and animals developed from the uniform embryonic tissue and not from mere growth expansion of the miniature homunculi present in eggs / sperms. Von Baer proposed that they developed through a sequential modification of the embryonic tissue. This concept is universally accepted.

Swammerdam (1637-1680), for example, thought that a tiny preformed frog occurred in the animal hemisphere of the frog egg and that became simply larger by feeding on the food stored in the vegetal hemisphere of the egg. Another biologist, Hartsoeker (1695) published a figure showing a miniature man known as mankin or homunculus in the head of the human spermatazoa. Such preformation theories had been supported by Leeuwenhoek (1632-1723), Malpighi (1673), Reaumur, Bonnet (1720- 1793), Spallanzani (1729-1799) and other workers of 17th and early 18th centuries. With the development of improved microscopy and other cytological techniques in 17th and 18th centuries, it became clear to biologists that neither the egg nor the sperm contained a preformed individual but that each was a relatively uniform, homogeneous mass of protoplasm.

Particulate Theory

A French biologist Maupertius in 1698-1759 discards the preformation theory and forwarded the concept of biparental through many tiny particles. According to him both the parents produce the semen, which composed of many tiny particles. The semen of both the parents unite and the embryo formed each organ of the embryo was supposed to be formed by two particles. Each of which came from each parent. In the year 1732-1806 J.C. Koelreuter was the first person to get fertile hybrids by artificial crossing two species of tobacco and concluded that the gametes were the physical basis of heredity.

Pangenesis

Charles Darwin proposed this theory. According to pangenesis that each organ of an individual produces very small almost invisible identical copies of itself called gemmules or pangenes. These gemmules from various parts collected into the blood stream of animals. The blood transports the gemmules into the reproductive organ, which produce gametes. Male and female gametes unite to form zygotes. When these gives rise to a new organism, the gemmules of different parts of the body give rise to the same kind of organs, tissues and cells, which

produced them in the parents.

Lamarckism

A French biologist Lamark (1774-1829) considered the inheritance of acquired characters to be the most important, if not the sole, mechanism of evolutionary changes. According to urgent need, use and disuse of organs, the modification thus acquired will be transmitted to their off spring.

Germplasm theory August Weismanís (1834-1914)

Germplasm theory explains that body of individual consists of two distinct types of tissues, (1) somatoplasm (2) germplasm. Somatoplasm consists of all body tissues, which do not contribute to the sexual reproduction. The germplasm on the other hand produces gametes that are the basis of heredity. It is only applied to animals and plants in which distinction between soma and germ can be made. Weismannís famous experiment of cutting off the tail of mice for 22 generations and observing that the progeny still had tail of normal length, proved that the somatoplasm is not responsible for transmission of characters.

Cell Theory(1838)

Schleiden and Schwann proposed cell theory 1838. They concluded that all plant and animal tissues were made of cells. It was also postulated that cell is the functional unit of living organism. In 1846 Negeli said that all cells originated from preexisting cells. Virchow 1853 elaborated this and referred it as cell linkage theory.

Mendelian concept of hereditary

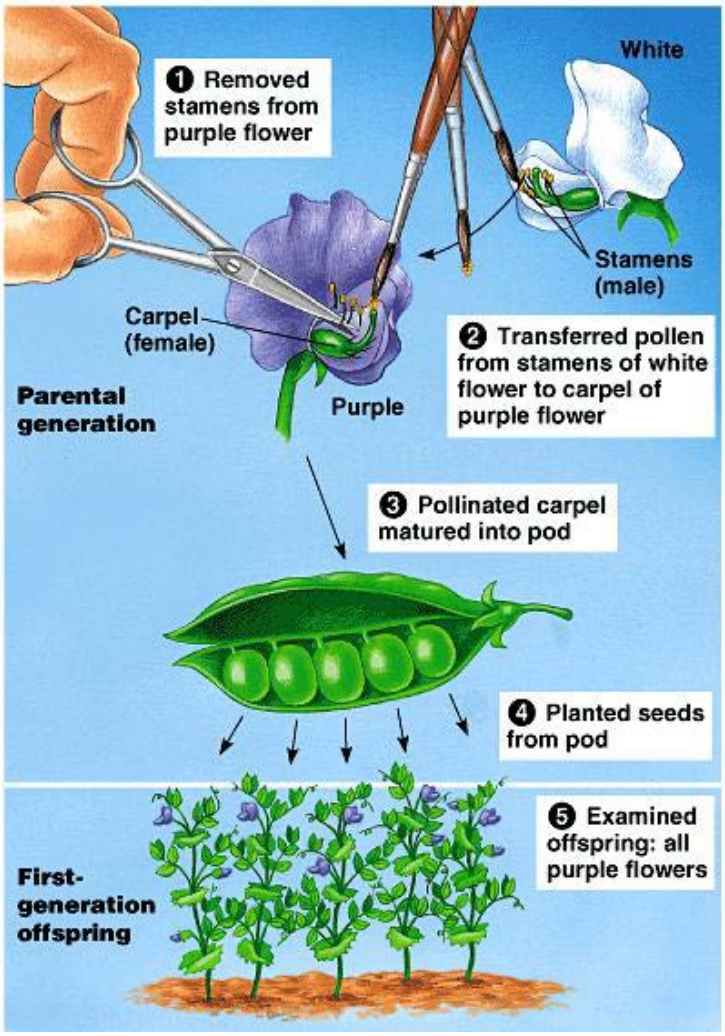
The laws of inheritance were derived by Gregor Mendel, a 19th century monk conducting hybridization experiments in garden peas (*Pisum sativu*m). Between 1856 and 1863, he cultivated and tested some 29,000 pea plants. From these experiments he deduced two generalizations which later became known as *Mendel's Laws of Heredity* or *Mendelian inheritance*. He described these laws in a two part paper, "Experiments on Plant Hybridization" that he read to the Natural History Society of Bruno on February 8 and March 8, 1865, and which was published in 1866.

Mendel's findings allowed other scientists to predict the expression of traits on the basis of mathematical probabilities. A large contribution to Mendel's success can be traced to his decision to start his crosses only with plants he demonstrated were true-breeding. He also measured only absolute (binary) characteristics, such as color, shape, and position of the offspring, rather than quantitative characteristics. He expressed his results numerically and subjected them to statistical analysis. His method of data analysis and his large sample size gave credibility to his data. He also had the foresight to follow several successive generations

(f2, f3) of his pea plants and record their variations. Finally, he performed "test crosses" (back-crossing descendants of the initial hybridization to the initial true-breeding lines) to reveal the presence and proportion of recessive characters. Without his careful attention to procedure and detail, Mendel's work could not have had the impact it made on the world of genetics.

Mendel's Laws

Mendel discovered that by crossing white flower and purple flower plants, the result was not a hybrid offspring. Rather than being a mix of the two, the offspring was purple flowered. He then conceived the idea of heredity units, which he called "factors", one which is a recessive characteristic and the other dominant. Mendel said that factors, later called genes, normally occur in pairs in ordinary body cells, yet segregate during the formation of sex cells. Each member of the pair becomes part of the separate sex cell. The dominant gene, such as the purple flower in Mendel's plants, will hide the recessive gene, the white flower. After Mendel self-fertilized the F1 generation and obtained the 3:1 ratio, he correctly theorized that genes can be paired in three different ways for each trait; AA, aa, and Aa. The capital **A** represents the dominant factor and lowercase **a** represents the recessive.



Mendel stated that each individual has two factors for each trait, one from each parent. The two factors may or may not contain the same information. If the two factors are identical, the individual is called **homozygous** for the trait. If the two factors have different information, the individual is called **heterozygous**. The alternative forms of a factor are called **alleles**. The genotype of an individual is made up of the many alleles it possesses. An individual's physical appearance, or phenotype, is determined by its alleles as well as by its environment. An individual possesses two alleles for each trait; one allele is given by the female parent and the other by the male parent. They are passed on when an individual matures and produces gametes: egg and sperm. When gametes form, the paired alleles separate randomly so that each gamete receives a copy of one of the two alleles. The presence of an allele doesn't promise that the trait will be expressed in the individual that possesses it. In heterozygous individuals the only allele that is expressed is the dominant. The recessive allele is present but its expression is hidden. Mendel summarized his findings in two laws; the **Law of Segregation** and the **Law of Independent Assortment**.

Law of Segregation (The "First Law")

The Law of Segregation states that when any individual produces gametes, the copies of a gene separate, so that each gamete receives only one copy. A gamete will receive one allele or the other. The direct proof of this was later found when the process of meiosis came to be known. In meiosis the paternal and maternal chromosomes get separated and the alleles with the characters are segregated into two different gametes.

Law of Independent Assortment (The "Second Law")

The Law of Independent Assortment, also known as **"Inheritance Law"**, states that alleles of different genes assort independently of one another during gamete formation. While Mendel's experiments with mixing one trait always resulted in a 3:1 ratio between dominant and recessive phenotypes, his experiments with mixing two traits (dihybrid cross) showed 9:3:3:1 ratios. But the 9:3:3:1 table shows that each of the two genes are independently inherited with a 3:1 ratio. Mendel concluded that different traits are inherited independently of each other, so that there is no relation, for example, between a cat's color and tail length. This is actually only true for genes that are not linked to each other.

Independent assortment occurs during meiosis I in eukaryotic organisms, specifically metaphase I of *meiosis*, to produce a gamete with a mixture of the organism's maternal and paternal chromosomes. Along with chromosomal crossover, this process aids in increasing genetic diversity by producing novel genetic combinations.

In independent assortment the chromosomes that end up in a newly-formed gamete are randomly sorted from all possible combinations of maternal and paternal chromosomes. Because gametes end up with a random mix instead of a pre-defined "set" from either parent, gametes are therefore considered assorted independently. As such, the gamete can end up with any combination of paternal or maternal chromosomes. Any of the possible combinations of gametes formed from maternal and paternal chromosomes will occur with equal frequency. For human gametes, with 23 pairs of chromosomes, the number of possibilities is 2^23 or 8,388,608 possible combinations. The gametes will normally end up with 23 chromosomes, but the origin of any particular one will be randomly selected from paternal or maternal chromosomes. This contributes to the genetic variability of progeny.

Rediscovery of Mendelís work

Mendel's conclusions were largely ignored. Although they were not completely unknown to biologists of the time, they were not seen as generally applicable, even by Mendel himself, who thought they only applied to certain categories of species or traits. A major block to understanding their significance was the importance attached by 19th century biologists to the apparent blending of inherited traits in the overall appearance of the progeny, now known to be due to multigene interactions, in contrast to the organ-specific binary characters studied by Mendel. In 1900, however, his work was "re-discovered" by three European scientists, Hugo de Vries, Carl Correns, and Erich von Tschermak. The exact nature of the "re-discovery" has been somewhat debated: De Vries published first on the subject, mentioning Mendel in a footnote, while Correns pointed out Mendel's priority after having read De Vries's paper and realizing that he himself did not have priority. De Vries may not have acknowledged truthfully how much of his knowledge of the laws came from his own work, or came only after reading Mendel's paper. Later scholars have accused Von Tschermak of not truly understanding the results at all. Regardless, the "re-discovery" made Mendelism an important but controversial theory. Its most vigorous promoter in Europe was William Bateson, who coined the term "genetics", "gene", and "allele" to describe many of its tenets.

The model of heredity was highly contested by other biologists because it implied that heredity was discontinuous, in opposition to the apparently continuous variation observable for many traits. Many biologists also dismissed the theory because they were not sure it would apply to all species, and there seemed to be very few true Mendelian characters in nature. However, later work by biologists and statisticians such as R.A. Fisher showed that if multiple Mendelian factors were involved in the expression of an individual trait, they could produce the diverse results observed. Thomas Hunt Morgan and his assistants later integrated the

theoretical model of Mendel with the chromosome theory of inheritance, in which the chromosomes of cells were thought to hold the actual hereditary material, and create what is now known as classical genetics, which was extremely successful and cemented Mendel's place in history.

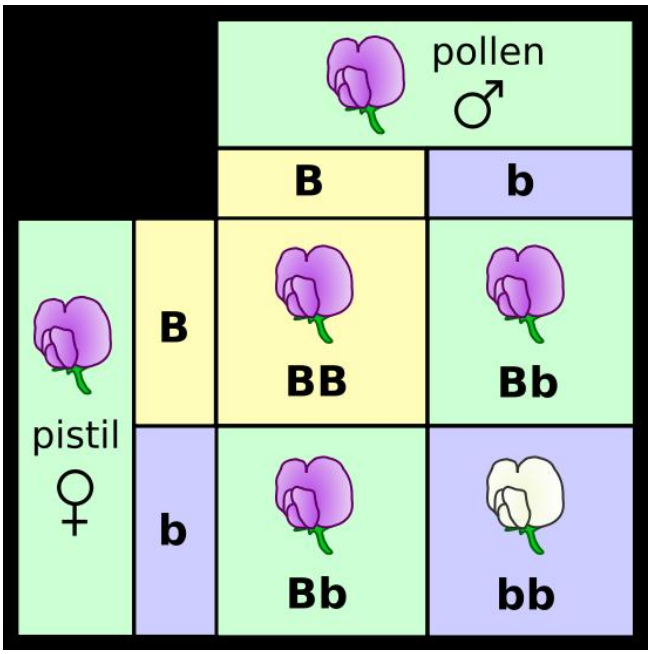
Mendel's Laws of Inheritance

Mendel postulated three laws, which are now called after his name as Mendel's laws of heredity. These are:

1. Law of dominance and recessive
2. Law of segregation
3. Law of independent assortment

1. Law of Dominance

Definition: When two homozygous individuals with one or more sets of contrasting characters are crossed, the characters that appear in the F_1 hybrids are dominant characters and those do not appear in F_1 are recessive characters.



Law of dominance- If there are two alleles coding for the same trait and one is dominant it will show up in the organism while the other won't

Explanation : The dominance and recessive of genes can be explained on the basis of enzymatic functions of genes. The dominant genes - are capable of synthesizing active polypeptides or proteins that form functional enzymes, whereas the recessive genes (mutant

genes) code for incomplete or non-functional polypeptides. Therefore, the dominant genes produce a specific phenotype while the recessive genes fail to do so. In the heterozygous condition also the dominant gene is able to express itself, so that the heterozygous and homozygous individuals have similar phenotype.

Critical appreciation of Law of Dominance

Scientists conducted cross-breeding experiments to find out the applicability of law of dominance. The experiments were conducted by Correns on peas and maize, Tschermak on peas, by De Vries on maize etc., by Bateson and his collaborators on a variety of organisms, by Davenport on poultry, by Furst on rabbits, by Toyama on silk moth and by many others. These scientists observed that a large number of characters in various organisms are related as dominant and recessive.

Importance of law of dominance

The phenomenon of dominance is of practical importance as the harmful recessive characters are masked by the normal dominant characters in the hybrids. In Human beings a form of idiocy, diabetes, haemophilia etc. are recessive characters. A person hybrid for all these characteristics appears perfectly normal. Thus harmful recessive genes can exist for several generations without expressing themselves.

Exceptions to Law of Dominance is the Incomplete Dominance. After Mendel several cases were recorded by scientists, where F_1 hybrids exhibited a blending of characters of two parents. These hybrids were found to be midway between the two parents. This is known as incomplete dominance or blending inheritance. It means that two genes of the allelomorphic pair are not related as dominant and recessive, but each of them expresses itself partially. As for example, in four-o'clock plant, *Mirabilis jalapa,* when plants with red flowers (RR) are crossed with plants having white flowers (rr), the hybrid F_1 plants (Rr) bear pink flowers. When these F_1 plants with pink flowers are self-pollinated they develop red (RR), pink (Rr) and white (IT) flowered plants in the ratio of 1 : 2 : 1 (F_2 generation).

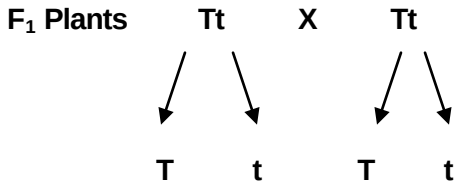
2. Law of Segregation (Purity of Gametes)

Explanation - The law of segregation states that when a pair of contrasting factors or genes or allelomorphs are brought together in a heterozygote (hybrid) the two members of the allelic pair remain together without being contaminated and when gametes are formed from the hybrid, the two separate out from each other and only one enters each gamete.

Example - Pure tall plants are homozygous and, therefore/possess genes (factors) TT; similarly dwarf possess genes tt. The tallness and dwarfness are two independent but contrasting factors or

determiners. Pure tall plants produce gametes all of which possess gene T and dwarf plants t type of gametes.

During cross fertilization gametes with T and t unite to produce hybrids of F_1 generation. These hybrids possess genotype Tt. It means F_1 plants, though tall phenotypically, possess one gene for tallness and one gene for dwarfness. Apparently, the tall and dwarf characters appear to have become contaminated developing only tall character. But at the time of gamete formation, the genes T (for tallness) and t (for dwarfness) separate and are passed on to separate gametes. As a result, two types of gametes are produced from the heterozygote in equal numerosity. 50% of the gametes possess gene T and other 50% possess gene t. Therefore, these gametes are either pure for tallness or for dwarfness. (This is why the law of segregation is also described as Law of purity of gametes).



Gametes unite at random and when gametes are numerous all possible combinations can occur, with the result that tall and dwarf appear in the ratio of 3 :1. The results are often represented by Punnett square as follows:

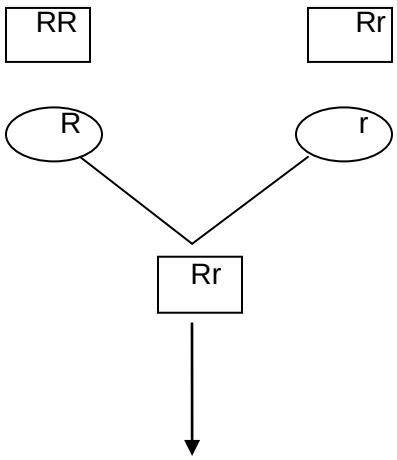
Critical appreciation of law of segregation

It has been confirmed by cytological studies that dominance or no dominance, the law of segregation holds good to all cases. Its far reaching applicability has made it rare biological generalization.

RR have only gene for round

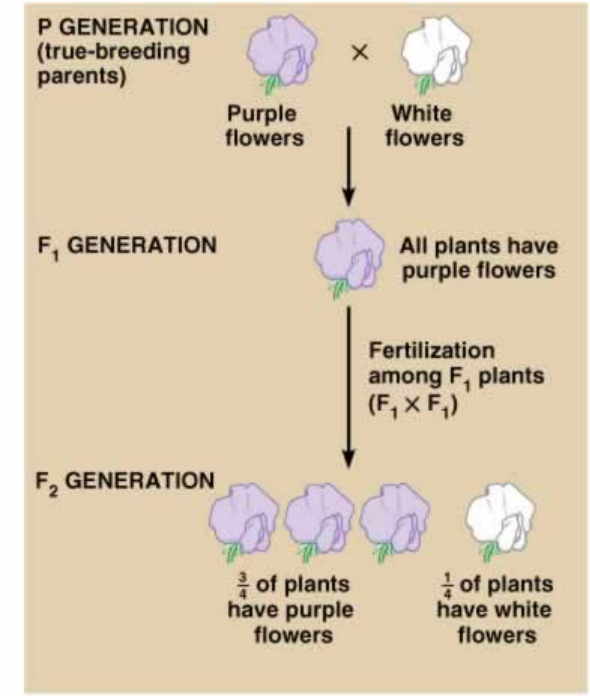
Rr, rR have gene for round and wrinkle

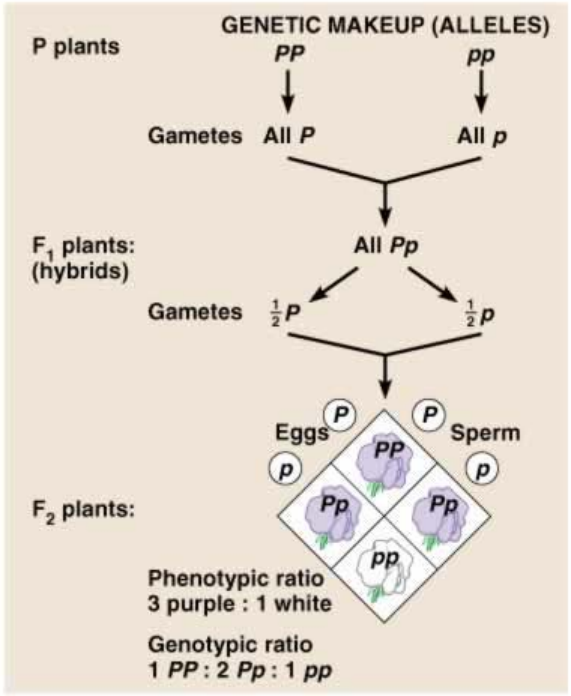
Rr have only wrinkeld gene



	R	r
R	RR	Rr
r	Rr	Rr

Round, Wrinkled - 3:1 ratio





3. Law of Independent Assortment

Definition: The inheritance of more than one pair of characters (two pairs or more) is studied simultaneously, the factors or genes for each pair of characters assort out independently of the other pairs. Mendel formulated this law from the results of a dihybrid cross.

Explanation: The cross was made between plants having yellow and round cotyledons and plants having green and wrinkled cotyledons.

The F_1 hybrids all had yellow and round seeds. When these F_1 plants were self fertilized they produced four types of plants in the following proportion:

(i) Yellow and round 9

(ii) Yellow and wrinkled 3

(iii) Green and round 3

(iv) Green and wrinkled 1

The above results indicate that yellow and green seeds appear in the ratio of 9 + 3 : 3 + 1 = 3 : 1. Similarly, the round and wrinkled seeds appear in the ratio of 9 + 3 : 3 +1 = 12:4 or 3 :1. This indicates that each of the two pairs of alternative characters *viz.* yellow-green cotyledon colour is inherited independent of the round-wrinkled character of the cotyledons. It means at the time of gamete formation the factor for yellow colour enters the gametes independent of R or r, i.e, gene Y can be passed on to the gametes either with gene R or r.

Cytological explanation of the results: In the above experiment yellow and round characters are dominant over green and wrinkled characters which can be represented as follows:

(i) gene for yellow colour of cotyledons Y

(ii) gene for green colour of cotyledons y

(iii) gene for round character of cotyledons R

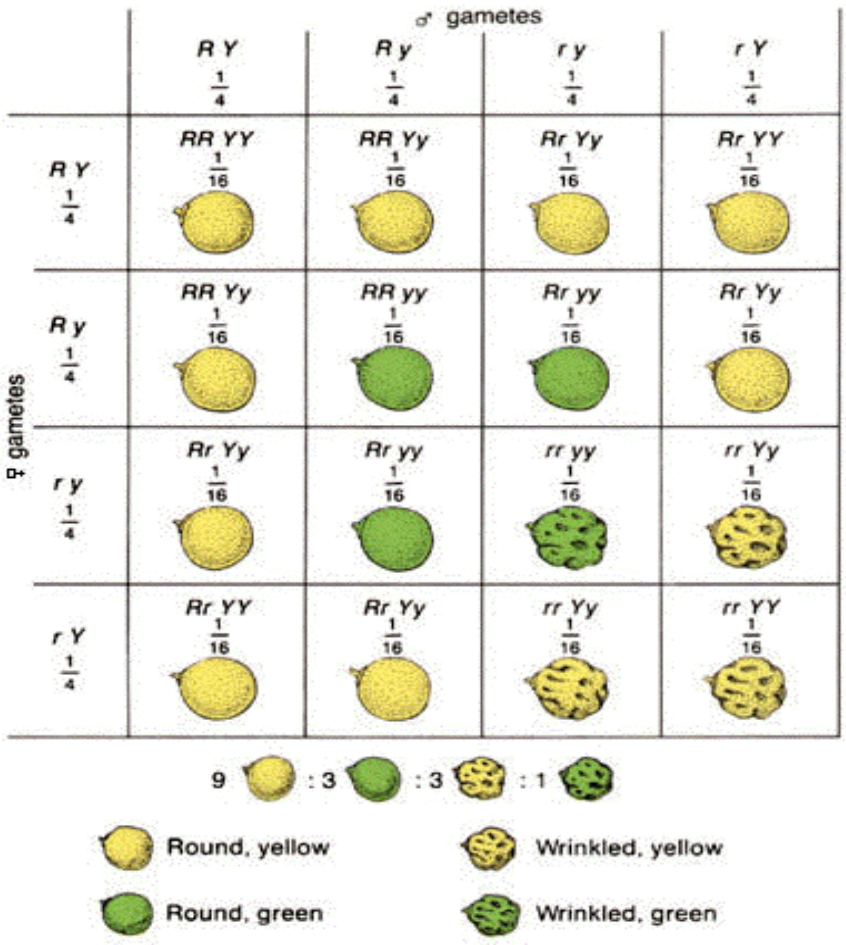
(iv) gene for wrinkled character of colyledons r

Therefore, plants with yellow and round cotyledons will have their genotype YYRR and those with green and wrinkled cotyledons will have a genotype yyrr. These plants will produce gametes with gene YR and yr respectively. When these plants are cross pollinated, the union of these gametes will produce F_1 hybrids with YyRr genes. When these produce gametes all the four genes have full freedom to assort independently and, therefore, there are possibilities of four combinations in both male and female gametes.

(i)*RY* (ii) Ry (iii) rY (iv) ry

This shows an excellent example of independent assortment. These gametes can unite at random producing in all 16 different combinations of genes, but presenting four phenotypes in the ratio of 9: 3: 3: 1.

Dihybrid ratio : RR yy - Round, yellow seeded ; Rr yy - Wrinkled and greed seeded



Test cross

F1 Rr Yy x rr yy (recessive)

1:1:1:1

Critical appreciation of law of Independent Assortment-

The law of independent assortment fails to have a universal applicability. Cytological studies have revealed that only those allelomorphs assort independently during meiosis, which are located in different homologous pairs of chromosomes. But, if the allelomorphs for different characters are present in the same homologous pair of chromosomes, these are passed on to the same gamete. Law of independent assortment does not apply to such cases.

BIOLOGICAL SIGNIFICANCE OF MENDEL'S LAWS

Mendel's work remained burried for about three decades, but after its rediscovery, the laws are being used for the various branches of breeding. These are use for improving the varieties of fowls and their eggs; in obtaining rust-resistant and disease-resistant varieties of grains. Various new breeds of horses and

dogs are obtained by cross breeding experiments. The science of Eugenics is the outcome of Mendelism, which deals with the betterment of human race.

Mendelian deviation

Mendelian deviations or exceptions or anomalies includes

1) Incomplete dominance

2) Codominance

3) Lethal genes etc.

1. Incomplete dominance

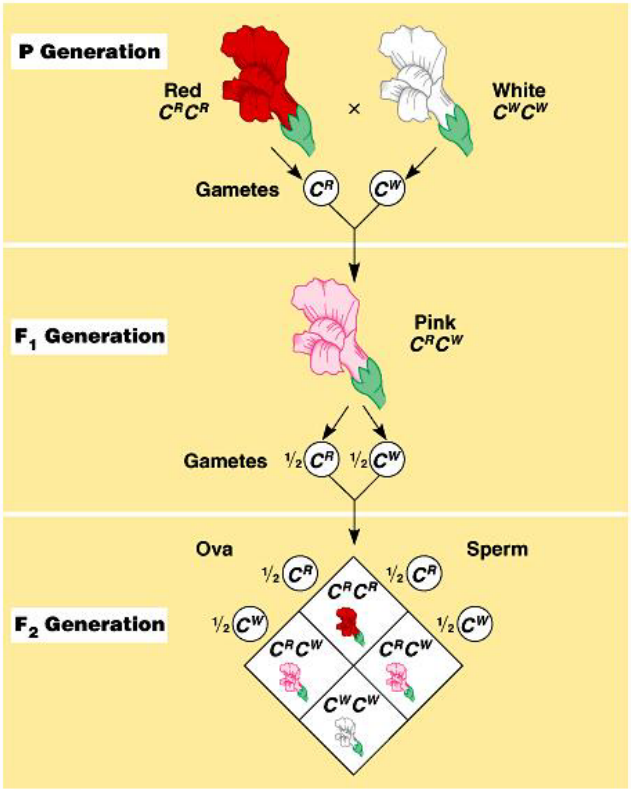
Mendel always observed complete dominance of one allele over the other for all the seven characters, which he studied, in garden pea. Later on cases of incomplete dominance were reported. For example, in four ëoí clock plant (Mirabilis jalapa) there are two types of flower viz., red and white. A cross between red and white flowered plants produced plants with intermediate flower colour i.e. pink colour in F1 and a modified ratio of 1 red: 2 pink: 1 White in F2.

Parents Red flower x White flower

RR x rr

F1 Rr pink flower

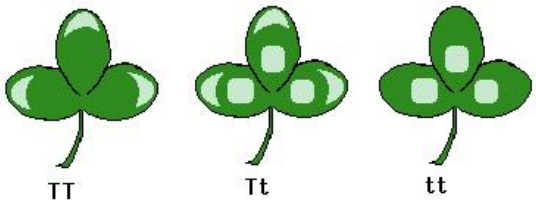
F2 1 Red (Rr) **:** 2 Pink (RR) **:** 1 White (rr)



Incomplete dominance in flowers of *Mirabilis jalapa*

2. Codominance

In case of codominance both alleles express their phenotypes in heterozygote greater than an intermediate one. The example is AB blood group in human. The people who have blood type AB are heterozygous exhibiting phenotypes for both the IA and IB alleles. In other words, heterozygotes for codominant alleles are phenotypically similar to both parental types. The main difference between codominance and incomplete dominance lies in the way in which genes act. In case of codominance both alleles are active while in case of incomplete dominance both alleles blend to make an intermediate one.



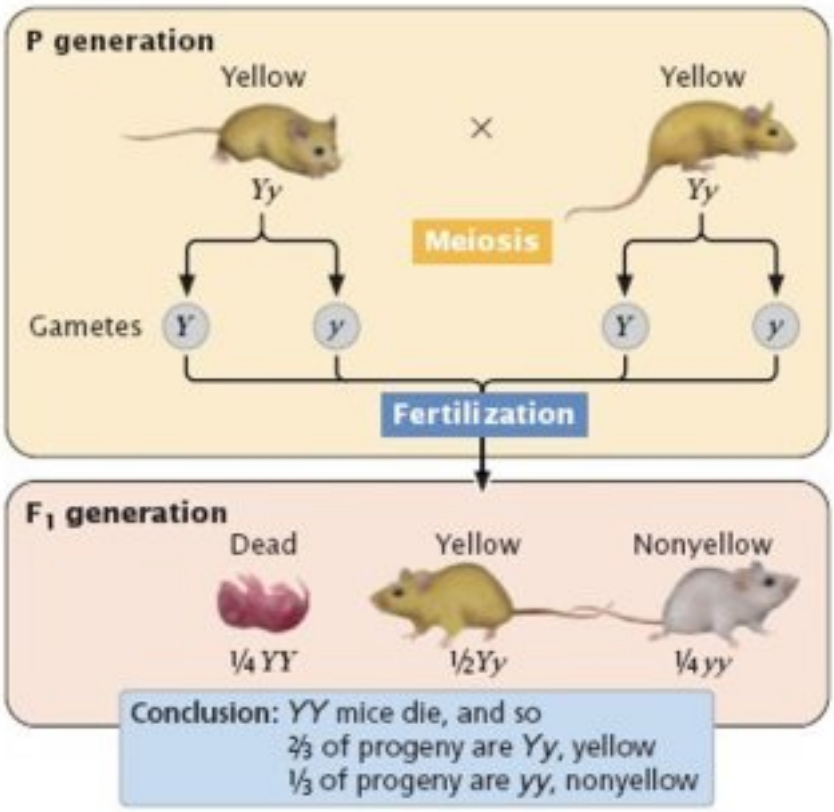
Codominance - both genes fully expressed

3. Lethal genes

Gene, which causes the death of its carrier when in homozygous condition is called lethal gene. Mendel's findings were based on equal survival of all genotypes. In normal segregation ratio of 3:1 is modified into 2:1 ratio. Lethal genes have been reported in both animals as well as plants. In mice allele for yellow coat colour is dominant over grey. When a cross is made between yellow and grey a ratio of 1:1 for yellow and gray mice was observed. This indicated that yellow mice are always heterozygous. Because yellow homozygotes are never born because of homozygous

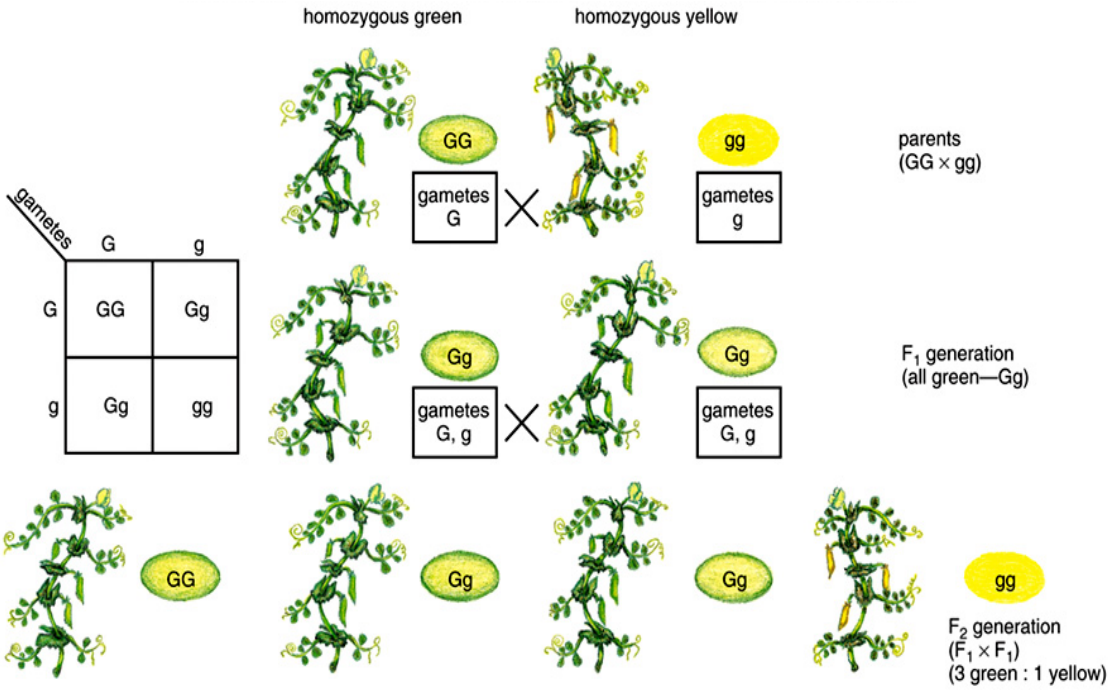
lethality. Such genes were not observed by Mendel. He always got 3:1 ratio in F2 for single gene characters.

Lethal genes can be recessive, as in the aforementioned mouse experiments. Lethal genes can also be dominant, conditional, semilethal, or synthetic, depending on the gene or genes involved.



MONOHYBRID CROSS

A cross is made between two true-breeding parents differing for a single trait, producing an F1 generation. These plants are intercrossed to produce an F2 generation.



Dihybrid Crosses

The following legends were described for peas by Mendel:

T- Tall

tt - dwarf

G - green (pod)

gg- yellow

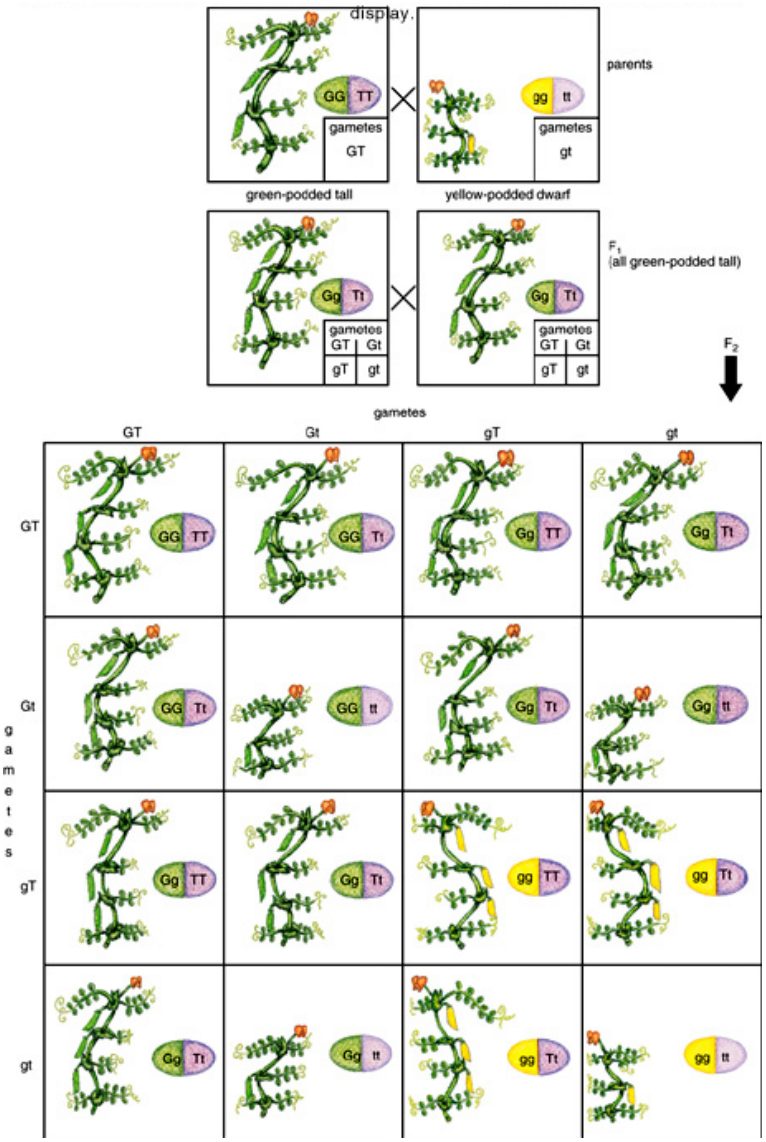
Pure breeding parents can be crossed to produce a dihybrid meaning that 2 genes affecting different traits are heterozygous (segregating) in all the f1 progeny.

Examples: TT, GG X tt, gg ⟶ Tt, Gg

TT, gg X tt, GG ⟶ Tt, Gg

When the F1 is self fertilized (plants) or crossed with another Tt, Gg individual, the progeny will show the expected 3 dominant : 1 recessive phenotypic ratio for each trait. If the two traits are independent, the two 3 : 1 ratios will interact to give a ratio based on 16ths.

#	**Genotypes**	**Phenotypes**
9	T_, G_	Tall, Green
3	T_, gg	Tall, yellow
3	tt, G_	Dwarf, Green
1	tt, gg	Dwarf, Yellow



Backcross

Backcrossing is a crossing of a hybrid with one of its parents or an individual genetically similar to its parent, in order to achieve offspring with a genetic identity which is closer to that of the parent.

The Testcross

Because some alleles are dominant over others, the phenotype of an organism does not always reflect its genotype. A recessive phenotype (yellow) is only expressed with the organism is homozygous recessive (gg). A pea plant with green pods may be either homozygous dominant (GG) or heterozygous (Gg). To determine whether an organism with a dominant

phenotype (e.g. green pod color) is homozygous dominant or heterozygous, you use a *testcross*.

The breeding of an organism of unknown genotype with a homozygous recessive. If all the progeny of the testcross have green pods, then the green pod parent was probably homozygous dominant since a GG x gg cross produces Gg progeny. If the progeny of the testcross contains both green and yellow phenotypes, then the green pod parent was heterozygous since a Gg x gg cross produces Gg and gg progeny in a 1:1 ratio. The testcross was devised by Mendel and is still an important tool in genetic studies.