Unit - II

Embryology - Structure of mature anther and ovule. Fertilization (double fertilization and triple fusion). Structure, types and functions of endosperm. Structure of a mature dicot embryo (*Capsella bursa-pastoris).*

Genetics - Mendelism - Monohybrid and Dihybrid ratios - Laws of dominance, Segregation and Independent assortment.

Embryology

Structure mature of anther (microsporangium):

(a) Development of micro-sporangia is eusporangiate type (i.e, from a group of initial cells)

(b) Few cells in the hypodermal region become differentiated as archesporial cells. In Boerhavia and Dionaea, there is only one archesporial cell.

(c) The archesporial cell divides periclinally (along the periphery) to form outer – primary parietal layer and inner – sporogenous layer.

(d) The primary parietal layer lies just beneath the epidermis and divides again periclinally to form 3-5 concentric layers. These layers give raise the wall of the sporangium, along with epidermis.

(e) The innermost layer of the wall is called tapetum, which serves to provide nourishment to the developing pollen grains.

(f) The layer just below the epidermis is called endothecium.

(g) The sporogenous layer may function directly as pollen mother cell or it may divide to form many pollen mother cells.

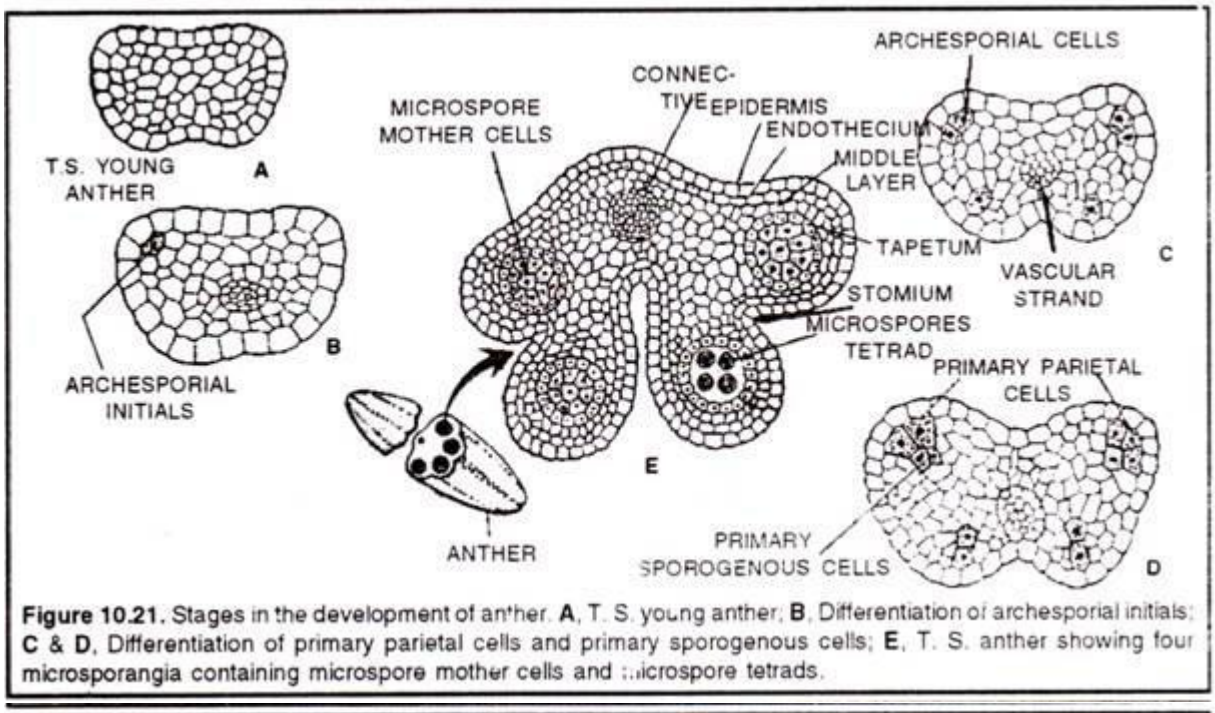


Figure 10.21. Stages in the development of anther. **A**, T. S. young anther; **B**, Differentiation of archesporial initials; **C & D**, Differentiation of primary parietal cells and primary sporogenous cells; **E**, T. S. anther showing four microsporangia containing microspore mother cells and microspore tetrads.

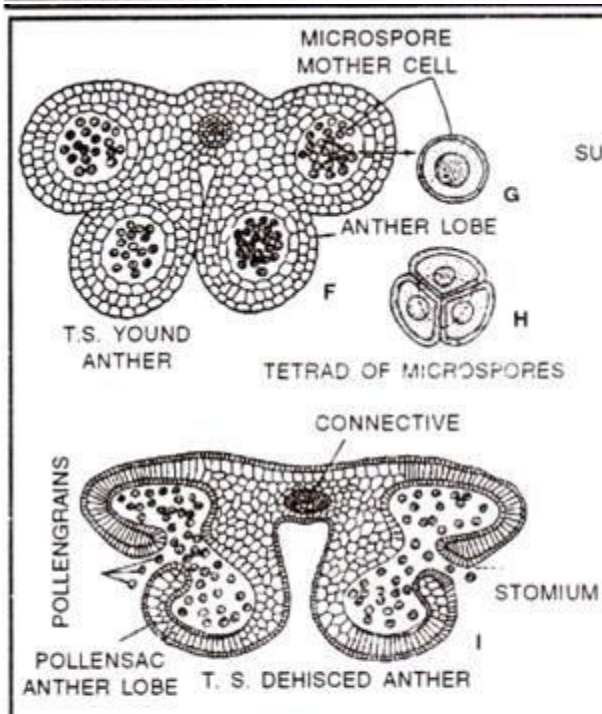


Figure 10.22. Development of pollen-grains (microspores) and dehiscence of anther.

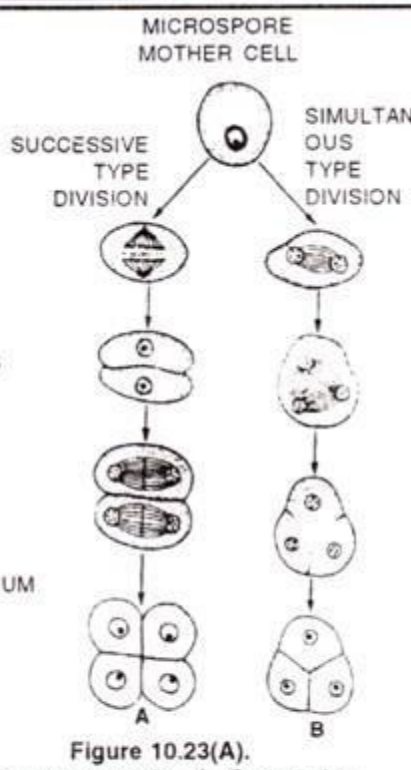


Figure 10.23(A). Microsporogenesis—**A**. Successive type in monocotyledonous plants. **B**. Simultaneous type in dicotyledonous plants.

Figure 10.23(B). Different types of microspore tetrads.

Anther wall:

(a) The mature anther wall comprises of an epidermis, followed by an endothecium, 2-3 middle layers and innermost tapteum.

(b) Endothecium consists of radially elongated cells, which possess fibrous bands and these are hygroscopic (moisture absorbing) in nature. These help in dehiscence of anther (splitting of anther to release spores).

Tapetum:
It is the innermost nourishing layer of the anther wall present below the middle layer. It is usually single layered and is rich in reserve food material.

It is polyploidy & serves to provide food to the developing sporogenous tissue (microspores) based on its behaviour, tap turn is of two type:
A. Glandular (or secretory) tapetum:
It is also called parietal tapetum. In this type the tapetum cells remains as such in their original position, throughout the microspore development. These cells secrete nutrient materials which are given to the developing spores. It is more common in angiosperms. In the initial stages of the development, the cells of the glandular tapetum, contains, small bodies, called pro-ubisch bodies, which are involved in the external thickening of the exine of the spore wall.

B. Amoeboid tapetum:
In this type, the breakdown of the inner and radial walls take place and the cytoplasm, containing food material moves into the inner anther cavity and forms the peri-plasmodium mass, which provide nourishment of the sporogenous cells. It is found usually in hydrophytes.

2. Formation of microspores or pollen grains (micro-sporogenesis):
(a) The sporogenous tissues, formed by archesporial cells divide many times to form pollen mother cells (or microspore mother cells) these are diploid cells.

(b) Each such cell divides meiotically (by meiosis) and forms four haploid microspores or pollen grains.

(c) The division is of two types in various angiosperms – simultaneous type and successive type.

(d) In simultaneous division, the M_1 of meiosis is not followed by cytokinesis, wall formation takes place only after the completion of both Mi (Meiosis-I) and M_2 (Meiosis-ll).

(e) On the other hand, in successive type of division, cytokinesis occurs after both divisions M_1 as well as M_2

Microspore mother cells $\rightarrow M_1$ 2 haploid cell $\rightarrow M_2$4 Microspore (pollen grain)

The microspore so formed, remain associated with each other for some time. This group of 4n (pollen grains) is called microspore tetrad. Different plants represent 5 types of tetrads -1. Tetrahedral tetrad (most common),

2. Isobilateral tetrad,

3. Decussate tetrad,

4. Inverted T shaped tetrad and

5. Linear tetrad.

In Aristolochiaelegans, all the 5 types of microspore tetrads are found. The enzyme callase disintegrates the callose (polysaccharide) present in pollen tetrad.

Structure of (microspore) pollen grain (microspore):

(a) Microspores (or pollen grains) are the unicellular, uni-cleated, haploid and spherical structures, which develop to give rise to male gametophyte. Smallest pollen are present in myosotis and largest pollens are present in Mirabilis.

(b) Microspores represent the first cell of male gametophyte.

(c) Microspores are surrounded by a two-layered wall.

(d) The outer layer is called exine, which is thick and cuti-cularised layer.

(e) The inner layer is called intine, which is smooth, thin and cellulosic.

(f) The exine shows different types of outgrowths. It contains a resistant fatty substance, called sporopollenin. Exine consists of extexine (outer) and endexine (inner) Extectine further coisists of a foot layer, baculate layer(middle) and an outermost tectum. Tectum characteristic texture to exine. The morphology and texture of exine is important from taxonomic point of view. The study of pollen and its exine structure is called palynology. Father of palynology is Erdtman & Indian palynology is P.K. Nair.

(g) Chemically the pollen grains are composed with carbohydrates (25-48%), protein (7-26%), and water (7-16%), Fats (1-15%).

(h) The germ pores are important because these mark the origin of pollen tube,

(f) Normally there are three germ pores in dicots, while only one in monocots.

Structure of ovule (mega sporangium):

(a) Each ovule is attached to the inner wall of the ovary (placenta), by a slender stalk, called funicle.

(b) The point of attachment of ovule to its funicle is called hilum.

(c) Main body of the ovule is formed by inner central mass i.e., nucellus. Nucellus consists of living parenchymatous cells.

(d) Each mature ovules the nucellus serves to cover and provide nutrition to the embryo sac (female gametophyte).

(e) Each ovule has two distinct ends-a micropyle end (it also called opening of ovule during fertilisation) and b. Chalaza end (the posterior end, opposite to micropylarend).

(f) Externally the nucellus is covered by one or two protective covers, called integuments. These integuments arise from the chalazal end.

(g) When only one integument is present, the ovule is called unitegmic, and if the ovule consists of two integuments, it is called bitegmic very rarely tri-tegmic (with three integuments) is present in plants like Asphodelus. In some plants such as Santalum, etc, ategmic (no integument) condition may be present.

(h) In mature ovules, the female gametophyte or embryo sac is present in the centre. The embryosac consists of egg cell (female gamete), synergid cells, antipodal cells and polar nuclei, (this is described a little later).

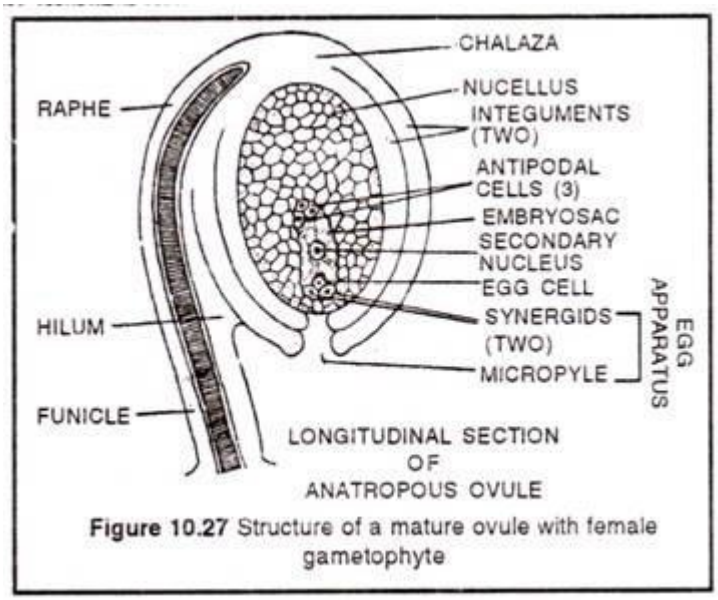


Figure 10.27 Structure of a mature ovule with female gametophyte

Fertilization:

On, penetrating the nucellus, whether through the micropyle, or, by a round about way through the chalaza, or, by piercing the integuments, the pollen tube penetrates the embryo sac and enters the egg apparatus. Ultimately, the tip of the pollen tube bursts and both the gametes are discharged. Probably the synergids play little or no role in this act. One of these gametes fuses with the egg cell of the egg apparatus.

The other gamete fuses with the secondary fusion nucleus. This behaviour of the two male gametes is termed **double fertilization** which was first observed by Nawaschin (1898) in *Lilium and Fritilaria* species. As a result of the first fertilization the oospore cell is formed which is the mother cell of the embryo and is a diploid cell containing 2n complement of chromosomes whereas the microspore and all nuclei of male and female gametophytes are haploid with n complement of chromosomes.

The secondary fusion nucleus of the embryo sac, however, normally becomes 2n at the time of the fusion undergone by it. (Exceptions to this have already been mentioned in connection with female gametophyte development). So, the fusion of this nucleus with the second male

gamete is **triple fusion** and the resultant nucleus is triploid or 3n. This is the first nucleus of the endosperm.

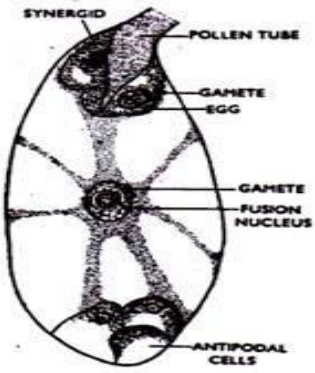


FIG. 419. Fertilization. The pollen tube has discharged the two male gametes. One male gamete is fertilizing the egg nucleus and the other is fusing with the secondary fusion nucleus.

In the post-fertilizational changes within the ovule, the embryo and the endosperm are seen to develop simultaneously (Fig. 420). The oospore forms the embryo while the fertilized fusion nucleus (product of triple fusion) develops the endosperm. The other nuclei or cells within the embryo sac (synergids, antipodal cells) may behave differently but are destined to disorganise sooner or later.

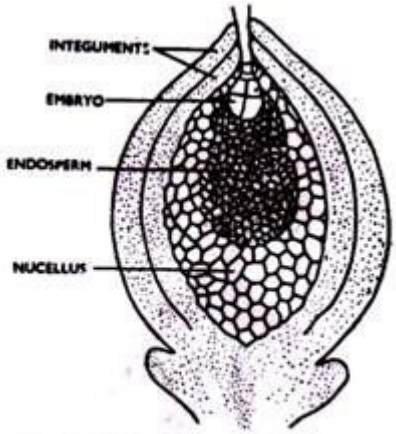


FIG. 420. Development of the embryo and the endosperm (diagrammatic).

Development of the Endosperm:

The Angiospermic endosperm, except in special cases, is a triploid (3n) tissue as it is a product of triple fusion involving double fertilization. It is, thus, distinct from the endosperm of Gymnosperms and heterosporous Pteridophytes where the endosperm is a simple haploid (n) tissue of the gametophyte not involving any complication like polar fusion or fertilization.

The real function of the endosperm is supplying nutrition to the growing embryo.

There are at least two families, Orchidaceae and Podostemonaceae, where the product of double fertilization soon disintegrates and endosperm development is completely suppressed.

In other plants, three types of endosperm development, nuclear, cellular and helobial, are usual:

(1) Nuclear Type:

This is the common type of endosperm development. Here, the endosperm nucleus gives rise to a number of free nuclei (Figs. 421 a, 424) which remain in the peripheral layer of embryo sac cytoplasm surrounding a large central vacuole. The nuclei, usually, become cut off by cell walls at a later stage if they be not already absorbed by the growing embryo. Such cell wall formation usually begins from the basal periphery.

The cells soon organise into an endosperm tissue and goes on increasing further. Development of the nuclear endosperm in Capsella bursa-pastoris (Fig. 424) is described later. In some cases the central vacuole may not be filled up even in the mature seed. This is seen in the palms. In coconut, the central cavity full of coconut water is the original embryo sac vacuole while the nuclei around it form the peripheral endosperm kernel.

(2) Cellular Type:

In a number of plants belonging to Annonaceae, Gentianaceae, etc., and in Adoxa, *Peperomia, Villarsia* (Fig. 421B), etc., division of the original endosperm nucleus is immediately followed by wall formation so that the endosperm is cellular from the beginning although some cells may enclose more than one nucleus.

(3) Helobial Type:

Among members of Helobiales (e.g., *Vallisneria, Eremurus, Limnophyton*, etc.) there is a type of endosperm development which is intermediate between the nuclear and the cellular types. Here, a partition wall develops between the two nuclei resulting from the first division of the endosperm nucleus so that the embryo sac is divided into two compartments.

A large number of free nuclei is now developed in the upper chamber while the lower nucleus forms a few of them or may not divide at all (Fig. 421C).

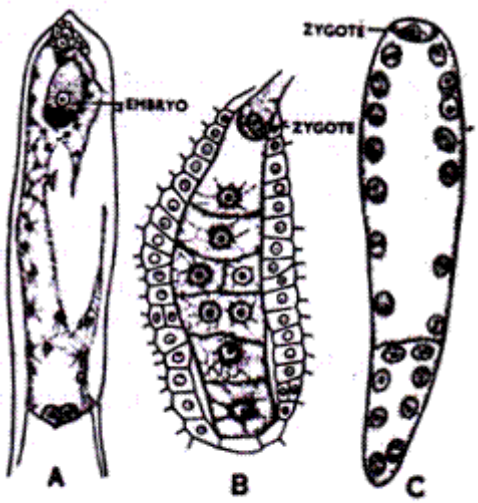


FIG. 421. TYPES OF ENDOSPERM DEVELOPMENT, A. Nuclear. B. Cellular in *Villarsia* (after Stolt). C. Helobial in *Eremurus* (after Stenar).

Development of the Embryo:

Side by side with the development of the endosperm, the zygote or oospore is developing the embryo. Both dicotyledons and monocotyledons begin embryo development in the same way but, there is considerable difference in later differentiation. In all Angiosperms the zygote (Fig. 422A) divides to develop a. two-celled proembryo (Fig. 422B). In most plants the first wall between the two cells is transverse while only in a few cases the first wall is more or less vertical (Piperad type, Fig. 423A_1).

Of the two cells the one near the micropyle is termed the basal cell while the one pointing towards the centre of the embryo sac is called the terminal cell. The basal cell usually forms the suspensor and may or may not contribute towards the future embryo in whose development the terminal cell takes the main part.

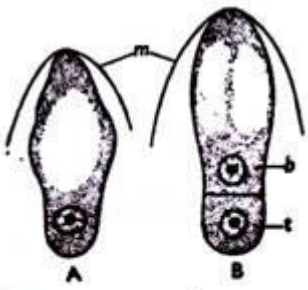


FIG. 422. A. Zygote, *m* = embryo sac membrane. B. 2-celled proembryo with transverse partition wall. *b* = basal cell (micropylar end), *t* = terminal cell.

Johansen (1950) recognizes six types of embryo development among the Angiosperms according to the manner of differentiation of the basal and terminal cells:

A. Zygote divides by a more or less vertical wall (Fig. 423A)

.. **1. Piperad type**
viz., *Peperomia, Balanophora*

B. Zygote divides by a transverse wall

I. Terminal cell divides by a vertical wall forming a ⊥-shaped proembryo (Figs. 423B, 424B, 425B)

(*a*) The basal cell plays little or no part in the formation of the embryo

.. **2. Onagrad** or **Crucifer type**
viz., Onagraceae, Cruciferae, Ranunculaceae, Rutaceae, Liliaceae, Juncaceae, etc., may be considered as the typical mode of embryo development.

(*b*) Both basal and terminal cells contribute to the formation of the embryo

.. **3. Asterad type**
viz., Compositae, *Polygonum*, etc.

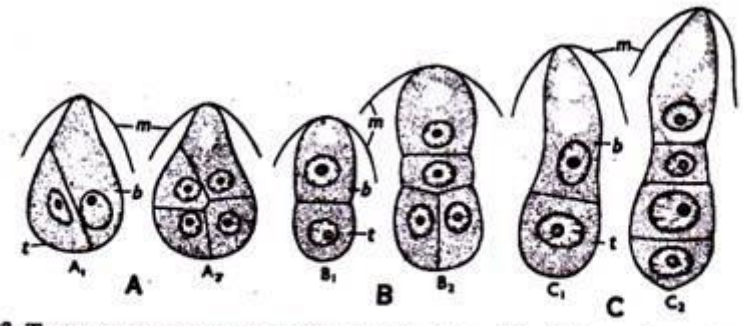


FIG. 423. TYPES OF EMBRYO DEVELOPMENT. A_1 & A_2. 2- and 4-celled proembryo of *Scabiosa* of *Piperad type* (after Souèges). B_1 & B_2. 2- and ⊥-shaped, 4-celled proembryo of *Onagrad type* (after Johansen). C_1 & C_2. 2- and straight 4-celled proembryo of *Nicotiana* of *Solanad type* (after Souèges).

II. Terminal cell divides by a transverse wall forming a straight proembryo (Fig. 423C)

(*a*) Basal cell plays little part in the future embryo

(*i*) Basal cell undergoes no further division but becomes a large suspensor cell

.. **4. Caryophyllad type**
viz., Caryophyllaceae, *Saxifraga, Medicago, Myriophyllum*, etc.

(*ii*) Basal cell forms suspensor of 2 or more cells

.. **5. Solanad type**
viz., Solanaceae, *Papaver, Linum*, etc.

(*b*) Both basal and terminal cells contribute to the formation of the embryo

.. **6. Chenopodiad type**
viz., Chenopodiaceae, *Myosotis*, etc.

Although there is no essential difference between the embryogeny of monocotyledons and that of dicotyledons in the early stages, later differentiation makes the two embryos

(1) Typical development of dicotyledonous embryo (*Capsella bursa-pastoris* type):

The classical example of dicotyledonous embryo development is the plant Capsella bursa-pastoris of Cruciferae. The ovule is campylotropous so that the embryo sac and the later developed endosperm as well as embryo are horseshoe-shaped.

Moreover the micropyle being pointed downwards, the embryo looks upside down. Embryo development here is of the typical Onagrad or Crucifer type described above.

The oospore (Fig. 424A) divides by a transverse wall forming a large basal cell and a smaller terminal cell (Fig. 424B). The basal cell now divides transversely while the terminal cell divides by a vertical wall developing a ⊥ -shaped 4-celled proembryo (Fig. 424B).
Next, the second basal cell quickly divides by a number of transverse walls giving rise to a row of cells called the suspensor (Fig. 424C). The lowest (micropylar) cell of the suspensor remains disproportionately large. As the suspensor increases in length, it pushes down the terminal embryonal cells deeper into the embryo sac. The embryonal cell, meanwhile, divides by three walls at right angles to one another giving rise to eight cells or octants (Fig. 424C).

This is called the embryonal mass. The lowest cell of the suspensor is called the hypo physis. The embryonal mass, along with the hypophysis, divides further (Fig. 424 D & E).

Ultimately, the four terminal octants form the two cotyledons, the four micropylar octants form the hypocotyl and the core of the radicle while the hypophysis forms the cortex and the epidermis of the radicle as well as the root-cap (Fig. 424 F & G). In the final stage (Fig. 424H) we find the mature embryo with the plumule developed also out of the four terminal octants. The suspensor gradually withers as the radicle is developed.

As the embryo is developing, the endosperm also keeps pace. Endosperm development, in this case, is strictly nuclear. The endosperm mother nucleus rapidly gives rise to a number of free nuclei which are arranged in the cytoplasm lining the periphery of the embryo sac while the centre is occupied by a big vacuole (Fig. 424D).

Gradually, cell wall formation begins from the periphery (Fig. 424F). The antipodal cells, in this, case, form a tissue which is short-living. The endosperm supplies nutrition to the embryo mainly through the suspensor. As the embryo of Capsella increases, the endosperm presses upon and sucks in plenty of food material from the nucellus which is soon consumed.

In the final stage (Fig. 424H) the nucellus has been completely consumed and most of the endosperm has also been consumed by the embryo. In the mature seed even this remnant of endosperm disappears so that the seed becomes exalbuminous.

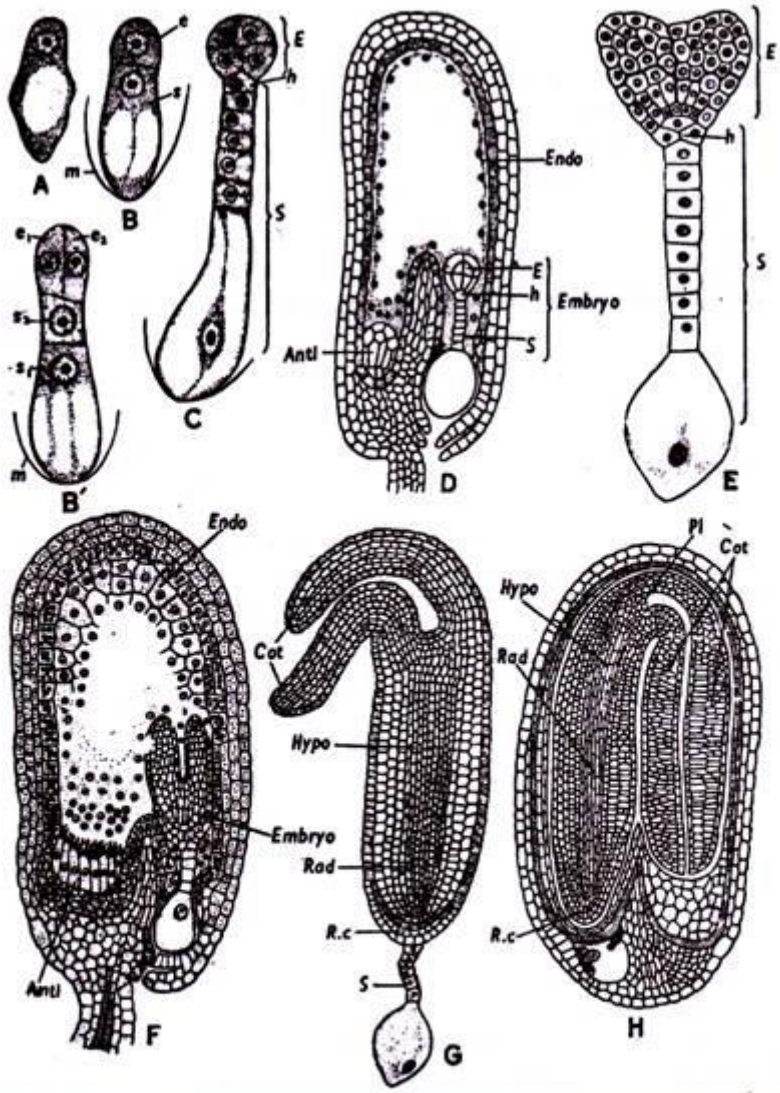


FIG. 424. Embryogeny in *Capsella bursa-pastoris* of Cruciferae (Dicot). A. The oospore. B. Transverse division of oospore forming 2-celled proembryo. *e* = terminal cell; *s* = basal cell; *m* = embryo sac membrane. B′. 4-celled T-shaped proembryo; e_1, e_2 are from terminal cell; s_1, s_2 are from basal cell. C. Further development of embryo. *S* = suspensor; *h* = hypophysis; *E* = embryonal mass. D. L.s. of ovule. *Endo* = endosperm in free-nuclear stage. *Anti* = antipodal tissue. *Embryo* = developing embryo. E. Embryo showing further development of embryonic octants and hypophysis. F. L.s. of ovule. Endosperm becoming cellular. G. Embryo. *Cot* = cotyledons; *Hypo* = hypocotyl; *Rad* = radicle; *R.c* = root-cap. H. Mature seed. *Pl* = plumule. Endosperm has been consumed almost completely.

GENETICS:

Mendelian inheritance is a type of biological inheritance that follows the principles originally proposed by Gregor Mendel in 1865 and 1866, re-discovered in 1900 and popularized by William Bateson.[1] These principles were initially controversial. When Mendel's theories were integrated with the Boveri–Sutton chromosome theory of inheritance by Thomas Hunt Morgan in 1915, they became the core of classical genetics. Ronald Fisher combined these ideas with the theory of natural selection in his 1930 book *The Genetical Theory of Natural Selection*, putting evolution onto a mathematical footing and forming the basis for population genetics within the modern evolutionary synthesis.[2]

History of genetics

The principles of Mendelian inheritance were named for and first derived by Gregor Johann Mendel,[3] a nineteenth-century Moravian monk who formulated his ideas after conducting simple hybridisation experiments with pea plants (*Pisum sativum)* he had planted in the garden of his monastery.[4] Between 1856 and 1863, Mendel cultivated and tested some 5,000 pea plants. From these experiments, he induced two generalizations which later became known as *Mendel's Principles of Heredity* or *Mendelian inheritance*. He described his experiments in a two-part paper, *Versuche über Pflanzen-Hybriden* (*Experiments on Plant Hybridization*),[5] that he presented to the Natural History Society of Brno on 8 February and 8 March 1865, and which was published in 1866.[6][7][8][9]

Mendel's results were largely ignored by the vast majority. 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 many inherited traits in the overall appearance of the progeny, now known to be due to multi-gene interactions, in contrast to the organ-specific binary characters studied by Mendel.[4] 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 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' 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 and how much came only after reading Mendel's paper. Later scholars have accused Von Tschermak of not truly understanding the results at all.[4][10][11][12]

Regardless, the "re-discovery" made Mendelism an important but controversial theory. Its most vigorous promoter in Europe was William Bateson, who coined the terms "genetics" and "allele" to describe many of its tenets. The model of heredity was 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. However, later work by biologists and statisticians such as Ronald Fisher showed that if multiple Mendelian factors were involved in the expression of an individual trait, they could produce the diverse results observed, and thus showed that Mendelian genetics is compatible with natural selection. Thomas Hunt Morgan and his assistants later integrated Mendel's theoretical model with the chromosome theory of inheritance, in which the chromosomes of cells were thought to hold the actual hereditary material, and created what is now known as classical genetics, a highly successful foundation which eventually cemented Mendel's place in history.

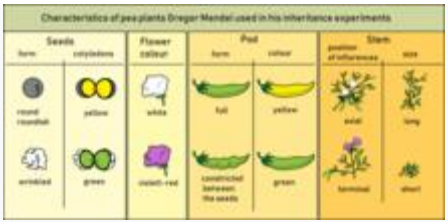
Mendel's findings allowed scientists such as Fisher and J.B.S. Haldane to predict the expression of traits on the basis of mathematical probabilities. An important aspect of Mendel's success can be traced to his decision to start his crosses only with plants he demonstrated were true-breeding. He only measured discrete (binary) characteristics, such as color, shape, and position of the seeds, rather than quantitatively variable 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 had the foresight to follow several successive generations (P, F_1, F_2, F_3) of pea plants and record their variations. Finally, he performed "test crosses" (backcrossing descendants of the initial hybridization to the initial true-breeding lines) to reveal the presence and proportions of recessive characters.

Mendel's genetic discoveries

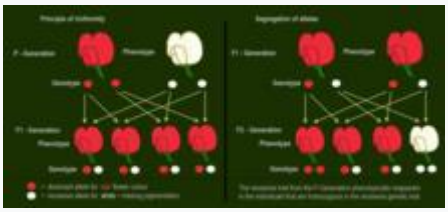
Five parts of Mendel's discoveries were an important divergence from the common theories at the time and were the prerequisite for the establishment of his rules.

1. Characters are unitary, that is, they are discrete e.g: purple *vs*. white, tall *vs*. dwarf. There is no medium sized plant or light purple flower.
2. Genetic characteristics have alternate forms, each inherited from one of two parents. Today, we call these alleles.
3. One allele is dominant over the other. The phenotype reflects the dominant allele.
4. Gametes are created by random segregation. Heterozygotic individuals produce gametes with an equal frequency of the two alleles.
5. Different traits have independent assortment. In modern terms, genes are unlinked.

According to customary terminology we refer here to the principles of inheritance discovered by Gregor Mendel as Mendelian laws, although today's geneticists also speak of *Mendelian rules* or *Mendelian principles*,[13][14] as there are many exceptions summarized under the collective term Non-Mendelian inheritance.



Characteristics Mendel used in his experiment[



P-Generation and F_1-Generation: The dominant allele for purple-red flower hides the phenotypic effect of the recessive allele for white flowers. F_2-Generation: The recessive trait from the P-Generation phenotypically reappears in the individuals that are homozygous with the recessive genetic trait.

Myosotis: Colour and distribution of colours are inherited independently.

Mendel selected for the experiment the following characters of pea plants:

- Form of the ripe seeds (round or roundish, surface shallow or wrinkled)
- Colour of the seed–coat (white, gray, or brown, with or without violet spotting)
- Colour of the seeds and cotyledons (yellow or green)
- Flower colour (white or yellow)
- Form of the ripe pods (simply inflated, not contracted, or constricted between the seeds and wrinkled)
- Colour of the unripe pods (yellow or green)
- Position of the flowers (axial or terminal)
- Length of the stem

When he crossed purebred white flower and purple flower pea plants (the parental or P generation) by artificial pollination, the resulting flower colour was not a blend. Rather than being a mix of the two, the offspring in the first generation (F_1-generation) were all purple-flowered. Therefore, he called this biological trait dominant. When he allowed self-fertilization in the uniform looking F_1-generation, he obtained both colours in the F_2 generation with a purple flower to white flower ratio of 3 : 1. In some of the other characters also one of the traits was dominant.

He then conceived the idea of heredity units, which he called hereditary "factors". Mendel found that there are alternative forms of factors—now called genes—that account for

variations in inherited characteristics. For example, the gene for flower color in pea plants exists in two forms, one for purple and the other for white. The alternative "forms" are now called alleles. For each trait, an organism inherits two alleles, one from each parent. These alleles may be the same or different. An organism that has two identical alleles for a gene is said to be homozygous for that gene (and is called a homozygote). An organism that has two different alleles for a gene is said be heterozygous for that gene (and is called a heterozygote).

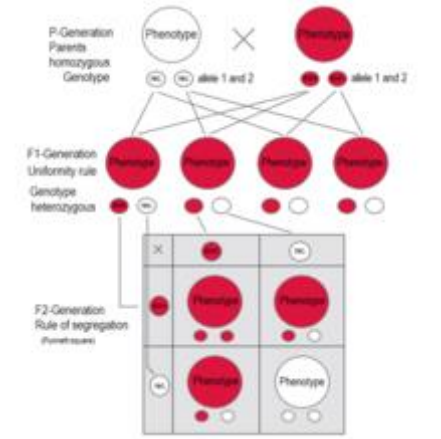
Mendel hypothesized that allele pairs separate randomly, or segregate, from each other during the production of the gametes in the seed plant (egg cell) and the pollen plant (sperm). Because allele pairs separate during gamete production, a sperm or egg carries only one allele for each inherited trait. When sperm and egg unite at fertilization, each contributes its allele, restoring the paired condition in the offspring. Mendel also found that each pair of alleles segregates independently of the other pairs of alleles during gamete formation.

The genotype of an individual is made up of the many alleles it possesses. The phenotype is the result of the expression of all characteristics that are genetically determined by its alleles as well as by its environment. The presence of an allele does not mean that the trait will be expressed in the individual that possesses it. If the two alleles of an inherited pair differ (the heterozygous condition), then one determines the organism's appearance and is called the dominant allele; the other has no noticeable effect on the organism's appearance and is called the recessive allele.

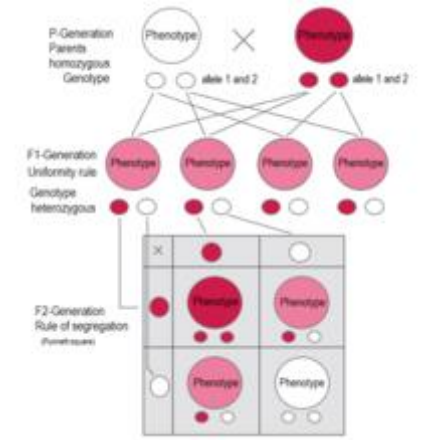
Mendel's laws of inheritance

Law	Definition
Law of dominance and uniformity	Some alleles are dominant while others are recessive; an organism with at least one dominant allele will display the effect of the dominant allele.[18]
Law of segregation	During gamete formation, the alleles for each gene segregate from each other so that each gamete carries only one allele for each gene.
Law of independent assortment	Genes of different traits can segregate independently during the formation of gametes.

Law of Dominance



F_1 generation: All individuals have the same genotype and same phenotype expressing the dominant trait (red).
F_2 generation: The phenotypes in the second generation show a 3 : 1 ratio.
In the genotype 25 % are homozygous with the dominant trait, 50 % are heterozygous genetic carriers of the recessive trait, 25 % are homozygous with the recessive genetic trait and expressing the recessive charakter.



In Mirabilis jalapa and Antirrhinum majus are examples for intermediate inheritance.[19][20] As seen in the F_1-generation, heterozygous plants have "light pink" flowers—a mix of "red" and "white". The F_2-generation shows a 1:2:1 ratio of red : light pink : white

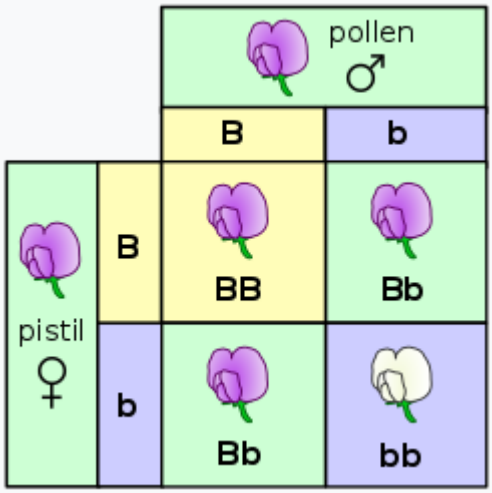
If two parents are mated with each other who differ in one genetic characteristic for which they are both homozygous (each pure-bred), all offspring in the first generation (F_1) are equal to the examined characteristic in genotype and phenotype showing the dominant trait.
This *uniformity rule* or *reciprocity rule* applies to all individuals of the F_1-generation.[21]

The principle of dominant inheritance discovered by Mendel states that in a heterozygote the dominant allele will cause the recessive allele to be "masked": that is, not expressed in the phenotype. Only if an individual is homozygous with respect to the recessive allele will the recessive trait be expressed. Therefore, a cross between a homozygous dominant and a homozygous recessive organism yields a heterozygous organism whose phenotype displays only the dominant trait.

The F_1 offspring of Mendel's pea crosses always looked like one of the two parental varieties. In this situation of "complete dominance," the dominant allele had the same phenotypic effect whether present in one or two copies.

But for some characteristics, the F_1 hybrids have an appearance *in between* the phenotypes of the two parental varieties. A cross between two four o'clock (*Mirabilis jalapa*) plants shows an exception to Mendel's principle, called *incomplete dominance*. Flowers of heterozygous plants have a phenotype somewhere between the two homozygous genotypes. In cases of intermediate inheritance (incomplete dominance) in the F_1-generation Mendel's principle of uniformity in genotype and phenotype applies as well. Research about intermediate inheritance was done by other scientists. The first was Carl Correns with his studies about Mirabilis jalapa.

Law of Segregation of genes



A Punnett square for one of Mendel's pea plant experiments – self-fertilization of the F1 generation

The Law of Segregation of genes applies when two individuals, both heterozygous for a certain trait are crossed, for example hybrids of the F_1-generation. The offspring in the F_2-generation differ in genotype and phenotype, so that the characteristics of the grandparents (P-generation) regularly occur again. In a dominant-recessive inheritance an average of 25% are homozygous with the dominant trait, 50% are heterozygous showing the dominant trait in the phenotype (genetic carriers), 25% are homozygous with the recessive trait and therefore express the recessive trait in the phenotype. The genotypic ratio is 1 : 2 : 1, the phenotypic ratio is 3 : 1.

In the pea plant example, the capital "B" represents the dominant allele for purple blossom and lowercase "b" represents the recessive allele for white blossom. The pistil plant and the pollen plant are both F_1-hybrids with genotype "B b". Each has one allele for purple and one allele for white. In the offspring, in the F_2-plants in the Punnett-square, three combinations are possible. The genotypic ratio is 1 *BB* : 2 *Bb* : 1 *bb*. But the phenotypic ratio of plants with purple blossoms to those with white blossoms is 3 : 1 due to the dominance of the allele for purple. Plants with homozygous "b b" are white flowered like one of the grandparents in the P-generation.

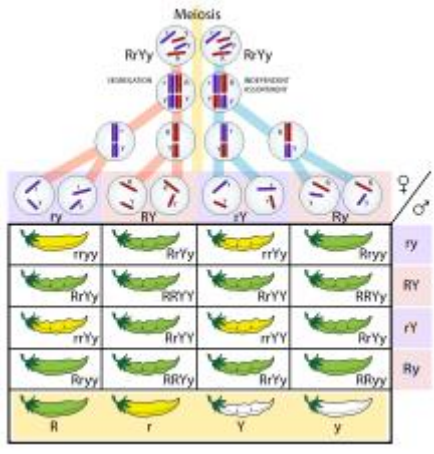
In cases of incomplete dominance the same segregation of alleles takes place in the F_2-generation, but here also the phenotypes show a ratio of 1 : 2 : 1, as the heterozygous are different in phenotype from the homozygous because the genetic expression of one allele

compensates the missing expression of the other allele only partially. This results in an intermediate inheritance which was later described by other scientists.

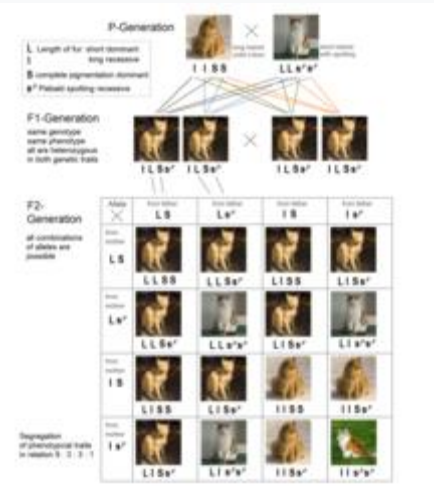
In some literature sources the principle of segregation is cited as "first law". Nevertheless, Mendel did his crossing experiments with heterozygous plants after obtaining these hybrids by crossing two purebred plants, discovering the principle of dominance and uniformity at first

Molecular proof of segregation of genes was subsequently found through observation of meiosis by two scientists independently, the German botanist Oscar Hertwig in 1876, and the Belgian zoologist Edouard Van Beneden in 1883. Most alleles are located in chromosomes in the cell nucleus. Paternal and maternal chromosomes get separated in meiosis, because during spermatogenesis the chromosomes are segregated on the four sperm cells that arise from one mother sperm cell, and during oogenesis the chromosomes are distributed between the polar bodies and the egg cell. Every individual organism contains two alleles for each trait. They segregate (separate) during meiosis such that each gamete contains only one of the alleles.[27] When the gametes unite in the zygote the alleles—one from the mother one from the father—get passed on to the offspring. An offspring thus receives a pair of alleles for a trait by inheriting homologous chromosomes from the parent organisms: one allele for each trait from each parent Heterozygous individuals with the dominant trait in the phenotype are genetic carriers of the recessive trait.

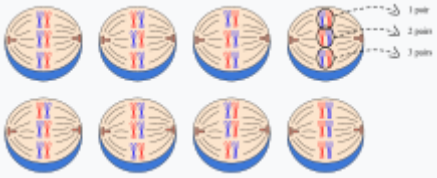
Law of Independent Assortment



Segregation and independent assortment are consistent with the chromosome theory of inheritance.



When the parents are homozygous for two different genetic traits (**llSS** and **LL** s_P s_P), their children in the F_1 generation are heterozygous at both loci and only show the dominant phenotypes (**Ll S** s_P). P-Generation: Each parent possesses one dominant and one recessive trait purebred (homozygous). In this example, solid coat color is indicated by **S** (dominant), Piebald spotting by s_P (recessive), while fur length is indicated by **L** (short, dominant) or **l** (long, recessive). All individuals are equal in genotype and phenotype. In the F_2 generation all combinations of coat color and fur length occur: 9 are short haired with solid colour, 3 are short haired with spotting, 3 are long haired with solid colour and 1 is long haired with spotting. The traits are inherited independently, so that new combinations can occur. Average number ratio of phenotypes 9:3:3:1



For example 3 pairs of homologous chromosomes allow 8 possible combinations, all equally likely to move into the gamete during meiosis. This is the main reason for independent assortment. The equation to determine the number of possible combinations given the number of homologous pairs = 2^x (x = number of homologous pairs)

The Law of Independent Assortment states that alleles for separate traits are passed independently of one another. That is, the biological selection of an allele for one trait has nothing to do with the selection of an allele for any other trait. Mendel found support for this law in his dihybrid cross experiments. In his monohybrid crosses, an idealized 3:1 ratio between dominant and recessive phenotypes resulted. In dihybrid crosses, however, he found a 9:3:3:1 ratios. This shows that each of the two alleles is inherited independently from the other, with a 3:1 phenotypic ratio for each.

Independent assortment occurs in eukaryotic organisms during meiotic metaphase I, and produces a gamete with a mixture of the organism's chromosomes. The physical basis of the independent assortment of chromosomes is the random orientation of each bivalent chromosome along the metaphase plate with respect to the other bivalent chromosomes. Along with crossing over, independent assortment increases genetic diversity by producing novel genetic combinations.

There are many deviations from the principle of independent assortment due to genetic linkage.

Of the 46 chromosomes in a normal diploid human cell, half are maternally derived (from the mother's egg) and half are paternally derived (from the father's sperm). This occurs as sexual reproduction involves the fusion of two haploid gametes (the egg and sperm) to produce a zygote and a new organism, in which every cell has two sets of chromosomes (diploid). During gametogenesis the normal complement of 46 chromosomes needs to be halved to 23 to ensure that the resulting haploid gamete can join with another haploid gamete to produce a diploid organism.

In independent assortment, the chromosomes that result are randomly sorted from all possible maternal and paternal chromosomes. Because zygotes end up with a mix instead of a pre-defined "set" from either parent, chromosomes are therefore considered assorted

independently. As such, the zygote can end up with any combination of paternal or maternal chromosomes. For human gametes, with 23 chromosomes, the number of possibilities is 2^{23} or 8,388,608 possible combinations.[31] This contributes to the genetic variability of progeny. Generally, the recombination of genes has important implications for many evolutionary processes