Meiosis: Stages, Duration and Significance

Meaning of Meiosis:

Chromosome number remains constant between the generations in asexually reproducing organisms since reproduction in them is based on mitosis. But in most species sexual reproduction does take place; it involves fertilization, i.e. fusion of male and female gametes.

Therefore, a mechanisms to reduce the number of chromosomes to half of the normal for the species during the formation of gametes has evolved in such organisms. Thus the life cycle alternates between two phases: haplophase and diplophase. The spores and gametes are haploid and represent the haplophase which falls between meiosis and fertilization.

The zygote (result of fertilization) and the organism derived from it through mitosis are in diplophase which falls between fertilization and meiosis. Somatic cells of most of the animal and plant species are diploid, but several lower organisms, such as, fungi, are haploid for most of their life cycle.

In these organisms, fertilization does occur and haploid sex cells fuse to form a diploid zygote, but the zygote gives rise to haploid cells through meiosis. Meiosis may be defined as a special kind of cell division where the nucleus divides two times successively, while there is only one round of replication as well as division of chromosomes; this results in four haploid nuclei from a single diploid parent nucleus.

The first division of meiosis is called heterotypic or reductional division since there is separation of homologous segments of non-sister chromatids; this is commonly denoted as meiosis I. Chromosome number, as a result, is reduced to half in this division.

The second division is similar to mitosis, and is called hoinotypic or equational division as there is separation of homologous segments of sister chromatids; it is generally referred to as meiosis II. In absence of crossing over, the first meiotic division is reductional, while the second division is equational.

But when crossing over has taken place, the centromere and the segment between the centromere and first chiasma is considered reductional in the first division. Contrary to this, the first division is equational for the segment beyond the first chiasma because this region of sister chromatids separates as mitosis. For these segments, the second meiotic division is reductional.

There are special tissues in the organisms where meiosis occurs. In plants (spermatophytes), microspores (pollen grains) are produced from pollen mother cells (PMC) located in anthers – the microsporangium. Similarly, megaspores are produced from megaspore mother cells (MMC) situated in ovules – the mega sporangium.

Gametogenesis in male animals, i.e., spermatogenesis occurs in testes, while that in females, i.e., oogenesis, occurs in ovaries.

Stages of Meiosis:

Meiosis is divided into several different stages and sub-stages as given below (Fig. 10.1).

Meiosis I:

1. Prophase I

(i) Leptotene

(ii) Zygotene

(iii) Pachytene

(iv) Diplotene

(v) Diakinesis

2. Metaphase I

3. Anaphase I

4. Telophase I

Interkinesis

Meiosis II:

1. Prophase II

2. Metaphase II

3. Anaphase II

4. Telophase II

Pre-Meiotic Interphase:

The pre-meiotic interphase consists of $G_{1;}$ S and G_2 phases, like the interphase of mitosis, and chromosomes replicate. Often, the G_2 phase may be very short or almost absent. The S phase is usually longer than the mitotic S phase. A unique type of histone called the meiotic histone, differing from those in somatic tissues is found in anther cells; its synthesis occurs in S phase and it may have certain function in the regulation of meiosis.

Prophase I:

Prophase I of meiosis takes a larger duration as compared to the prophase of mitosis; it varies from few hours to few days in the different species (Table 10.1). The nucleus, through hydration, becomes several times larger than the mitotic interphase nucleus.

Some very important and specific events taking place during this stage are: synapsis of homologous chromosomes, crossing over and chiasma formation, and repulsion and chiasmaterminalization. Prophase I is divided into five sub-stages, namely, leptotene (leptonema), zygonema, (zygonema), pachytene (pachynema), diplotene (diplonema), and diakinesis (Fig. 10.1).

Leptotene:

Chromosomes are visible as long and slender threads, they are much finer than those in mitotic prophase. Although, each chromosome has replicated and consists of two sister chromatids, these chromatids are not visible so that the chromosomes generally appear as single and individual structure.

Along the length of chromosomes, bead like structures called chromomeres may be seen. The arrangement of chromosomes in the nucleus is not always random. In some plants, the chromosomes are clumped to one side of the nucleus leaving the remaining part of the nucleus clear; this is called synizesis.

In animals, the chromosomes appear polarized where the ends of chromosomes are drawn together towards that part of the nuclear membrane close to the centriole and they seem to be attached with the envelope. Such polarization called bouquet stage may persist until pachytene.

It is now well known that each chromosome is attached at both of its ends to the nuclear envelope via a specialized structure called an attachment plaque.

TABLE 10.1. Duration (hours) of various stages of meiosis in different plant species (Data from Bennet, M.D. and Smith, J.B. 1972. Proc. Roy. Soc. London. Ser. B., Biol. Sci. 181 : 81–107; Bennet, M.D. 1972. Proc Roy. Soc. I ,nd., Ser. B., Biol. Sci. 181 : 109-135)

Stage of meiosis	Plant species with ploidy level				
	Hordeum vulgare (2x)	*Secale cereale* (2x)	*S. cereale* (4x)	*Triticum eastivum* (6x)	*Triticale* (*X. triticosecale*) (8x)
Prophase I :					
Leptotene	12.0	20.0	13.0	10.4	7.4
Zygotene	9.0	11.4	9.0	3.4	3.0
Pachytene	8.8	8.0	6.4	2.2	2.3
Diplotene	2.2	1.0	1.0	0.6	1.0
Diakinesis	0.6	0.6	0.6	0.4	0.5
Metaphase I	1.6	2.0	1.8	1.6	1.8
Anaphase I	0.5	1.0	0.7	0.5	0.5
Telophase I	0.5	1.0	0.7	0.5	0.5
Dyads	2.0	2.5	2.0	2.0	1.5
Matephase II	1.2	1.7	1.4	1.4	1.3
Anaphase II	0.5	1.0	0.7	0.5	0.5
Telophase II	0.5	1.0	0.7	0.5	0.5
Total duration (hours)	39.4	51.2	38.0	24.0	20.8

Zygotene:

Zygotene stage is considered to begin when intimate pairing (synapsis) between the homologous chromosomes is initiated. Pairing often starts when the homologous ends of the chromosomes are brought together on the nuclear envelope, and continues inwards in a zipper like fashion.

In other cases, synapsis may begin at any or several contact points, called zygomeres, and proceeds from these points in both the directions. Synapsis is highly precise and specific and occurs between all homologous sections leading to **“gene-to-gene pairing”.**

If homologous segments are present on non-homologous chromosomes, as in case of interchanges, they pair together forming a multivalent. In case of inversion, gene-to-gene pairing occurs through loop formation.

If there are more than two homologous chromosomes (auto-polyploids, polysomics), they all may pair to form a multivalent, but at any given point, pairing is, as a rule, two-by-two. It is not known exactly what causes the homologous parts of the chromosomes to become precisely aligned during zygotene.

It has been suggested that the specificity for pairing is mediated by the axes of chromosomes which are involved in the formation of a specialized structure called synaptinemal complex (or synaptonemal complex).

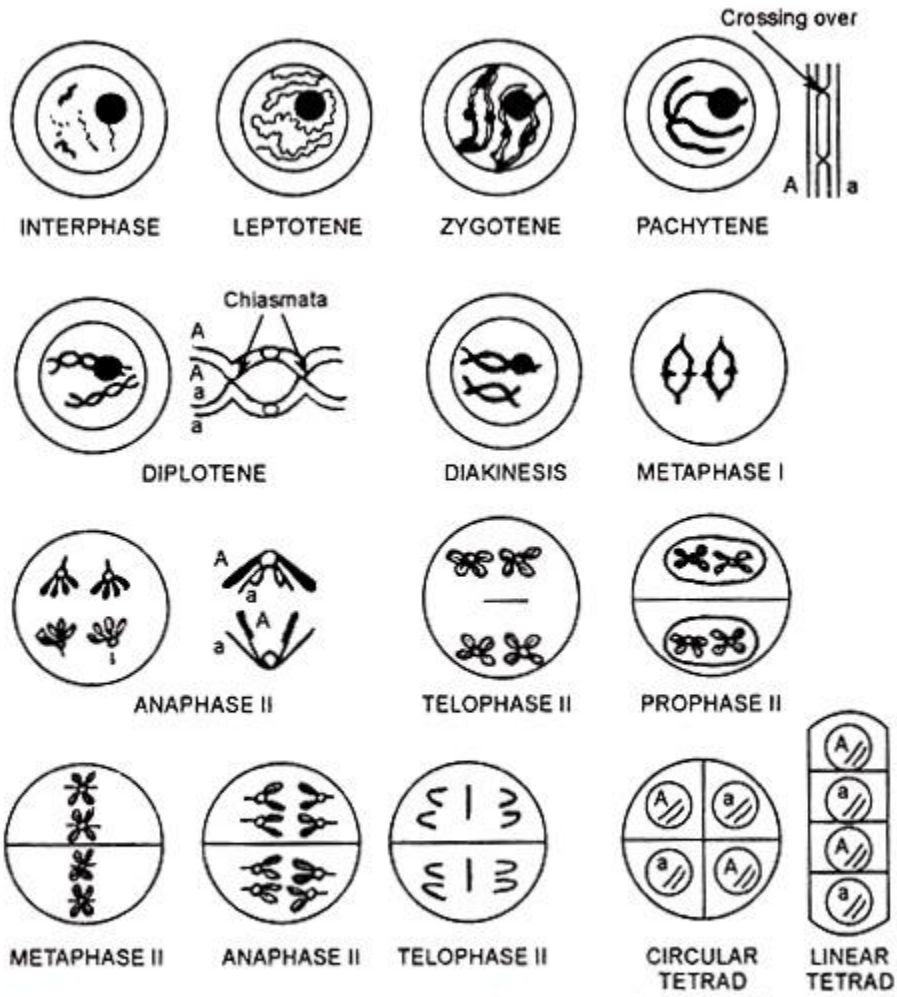

Fig. 10.1. Diagrammatic representation of meiotic cell division. Additional figures with pachytene, diplotene and anaphase I represent some detailed structures. Alleles A, a are shown to explain the results of the genetic exchange.

It has been shown that total DNA is not replicated during the S phase of pre-meiotic interphase. The completion of synthesis of the remaining part (about 0.3%) of DNA occurs during zygotene; it is believed to play role in chromosome pairing.

Pachytene:

Contraction of chromosomes continues. Pachytene stage begins just when the synapsis has completed. The paired chromosome structures are called bivalents. If there are more than two homologues in paired condition, they are called **"multivalents",** e.g., trivalents, quadrivalents, pentavalents etc.

The unpaired chromosomes are called univalents. Each bivalent has four strands (2 chromatids of each of the two chromosomes), therefore, it is also called "tetrad". However, it is not possible to see the four strands of the bivalents.

Chromosomes are visible along the length of bivalents; their pattern can be used to identify specific bivalents or their segments. Synaptinemal complex can be observed between synapsed chromosomes with the help of electron microscope.

At pachytene stage, recombination nodules appear at intervals on the synaptinemal complex, and they are thought to mediate crossing over. Exchange of chromatids is invisible at this stage but they subsequently result in chiasmata (Fig. 10.1).

Nucleoli are observable during pachytene; in many species they are united to form one large nucleolus. A very small amount of DNA replication (ca. 0.3%) occurs during pachytene; this is believed to be a form of repair replication related to the process of crossing over.

Diplotene:

After pachytene, the paired homologues begin to move apart; this stage is called diplotene. Synaptinemal complex dissolves but the two homologous chromosomes in each bivalent remain joined by one or more chiasmata which represent the sites where crossing over has taken place (Fig. 10.1).

The number of chiasmata per bivalent depends on the species and on the length of chromosomes. In Viciafaba upto 12 chiasmata have been observed in the long chromosomes. At this stage, the chromatids in each chromosome become visible.

Due to the forces that repel the homologous chromosomes, the chiasmata slowly shift towards the telomeres and decline in number; this process is called chiasmaterminalization. Therefore, at later stages of diplotene, the actual position and number of crossovers can not be determined. The terminalization process may be complete, partial of absent; in the last case, chiasmata are called localized chiasmata.

Classification of single chiasmata was made by Darlington in the following manner:
(i) Interstitial chiasma: There is a length of chromatid on each side of chiasma.

(ii) Lateral chiasma: Chiasma is terminal as to two chromatids and interstitial as to others.

(iii) Terminal chiasma: Chiasma is localized at the ends of the pairing partners.

(iv) Multiple chiasma: A terminal chiasma in which 3 or 4 pairs of chromatids participate as in multivalent.

(v) Imperfect or incomplete chiasma: A chiasma in which one of the four crosswise associations is broken prior to anaphase.

For explanation of chiasmaterminalization, three main hypotheses have been proposed:

(i) Electrostatic hypothesis:
This hypothesis, proposed by Darlington and coworkers, assumes that the movement of chiasma to the chromosome ends is caused by two separate repulsion forces, (a) the force that repels the centromeres, i.e., localized repulsion, and (b) the force that repels the entire chromosomes apart, i.e., generalized repulsion.

(ii) Coiling hypothesis:
According to Swanson, the movement of chiasma occurs due to the mechanical tension developed by coiling and shortening of chromosomes.

(iii) Elastic chromosome repulsion hypothesis:
Ostergren proposed that chiasmata are pushed towards chromosome ends by the repulsion forces and thus the tension caused by chiasmata to the chromosomes is reduced. Meiosis is blocked in the diplotene stage in oocytes of certain vertebrates including human, and in primary spermatocytes of some insects. This stage may persist for a long time, e.g., for days, months or years.

De-condensation of chromosomes occurs, they increase in length and form thin loops transverse to the main axis of the chromosomes. These chromosomes are called lamp brush chromosomes due to their special appearance. In the mammalian oocytes, this stage is called dictyotene. These loops support active mRNA synthesis.

Diakinesis:

Contraction of chromosomes continues and it reaches the maximum at the end of this stage. Chiasmaterminalization is complete and all the chiasmata are normally located at chromosome ends (Fig. 10.1). Bivalents may take various forms, such as, open ring, closed ring, rod, and cross bivalents.

At the end of diakinesis, nucleolus begins to disappear. Bivalents move close to the nuclear membrane and become evenly distributed. Therefore, diakinesis is an ideal stage for counting the chromosomes.

Metaphase I:

Chromosomes are coiled to the maximum extent, and they appear smooth in outline. Nucleolus is absent and the nuclear membrane has disappeared, its components becoming a part of the endoplasmic reticulum. Chiasmaterminalization has already been completed.

Spindle is formed and the centromeres of the two chromosomes is each bivalent are attached with the chromosomal fibres of opposite poles. Bivalents move towards equatorial plate mainly due to the contraction and relaxation of the chromosomal fibres.

The stage between the start of spindle activity and the equilibrium state of the bivalents at the metaphase plate is called prometaphase I, while once the state of equilibrium is achieved, it is known as metaphase I.

The two chromosomes of each bivalent coronet in such a way that their centromeres point towards the opposite poles and lie on either side of the equatorial plate, while the chiasmata lie on the plate itself (Fig. 10.1). Thus the two homologous centromeres in each bivalent are located at equal distance from the equatorial plate and their respective poles.

Although the centromere of each chromosome is divided into two parts, it functions as a single centromere. The metaphase I (MI) differs from the metaphase of mitosis in many respects. In mitosis, single chromosomes are arranged on equatorial plate and the sister chromatids are held together by functionally undivided centromeres to which the spindle fibres are attached on both the sides.

But in meiosis, spindle fibres are attached on only one side of the centromere of each chromosome of the bivalent. Kinetochore fibres of sister chromatids point in the same direction in contrast to mitosis where they point towards opposite poles.

With the exception of preferential segregation, the orientation of each chromosome of a bivalent with respect to the poles is random. This leads to the random segregation of chromosomes which is the basis for the Law of Independent Assortment of Mendel; it is assumed that the two genes under consideration are located on different bivalents (Fig. 10.2).

The shape of the bivalents at metaphase I may vary according to the number and presence or absence of chiasma and the centromere position in the chromosome: it may be a closed ring, open ring or rod shaped.

Anaphase I:

The anaphase I (AI) begins when the chromosome ends of bivalents loose their connections and the two homologues forming a bivalent move towards opposite poles, i.e., disjunction of homologous chromosomes occurs. The chromosome separation is **"reductional"** when crossing over has not occurred.

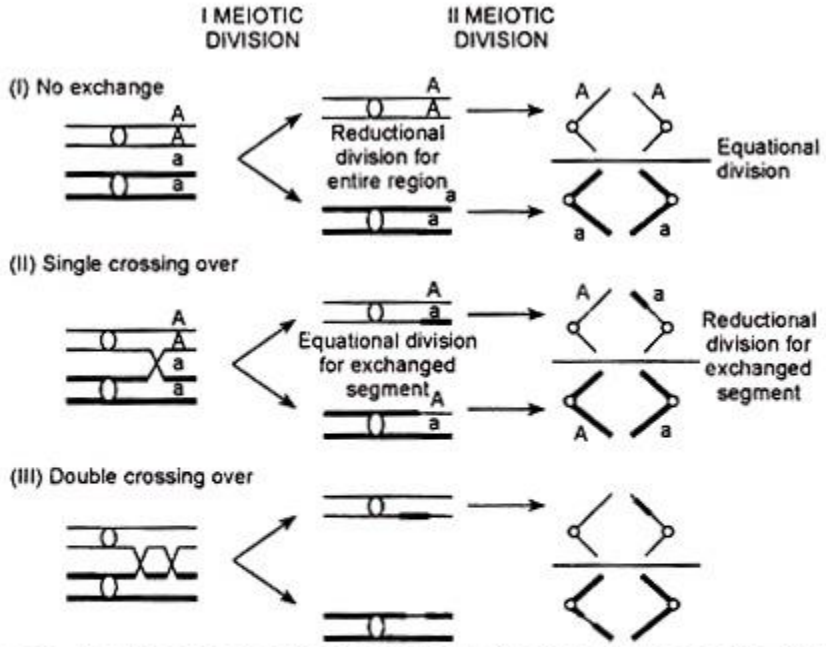

Fig. 10.3. Diagram showing reductional and equational divisions during meiosis. (*i*) In absence of exchange, I meiotic division is reductional, while the II meiotic division is equational. (*ii*) In case of one crossing over, I meiotic division is reductional for the region between the centromere and the crossover point, while equational for the exchanged region. The II meiotic division is equational for the region between the centromere and the crossover point and reductional for the exchanged segment. (*iii*) In case of 2-strand double crossing over the region between the two chiasmata shows equational division while the rest of the regions show reductional division at meiosis I.

But if crossing over has occurred, the separation is reductional only for the region between the centromere and the first chiasma; it is "equational" for the region distal to the first chiasma. If double crossing over involving the same two chromatids (2-strand double crossing over) occurs,

the region between the two chiasmata shows equational division, while the rest of the regions show reductional division at meiosis I (Fig. 10.3).

The number of chromosomes reaching each pole is half of the somatic number (2n) and is called the haploid or gametic chromosome number (n). The somatic number is expressed as 2n irrespective of the ploidy level (2x, 4x, etc.), while the gametic number is denoted by "n".

Telophase I:
When the chromosomes reach the poles, telophase I is considered to begin. Each pole receives half the number of somatic chromosomes. This stage is quite variable in different species. During this stage, the chromosomes may be partly uncoiled and the nuclear membrane may be formed.

Later, cytokinesis may produce two cells which remain attached together; they are called dyad, e.g., in barley, maize, Tradescantia, grasshopper etc. In other cases, telophase I is absent and the two groups of chromosomes at anaphase I directly pass on to prophase II, e.g., in Trillium. In Paeonia, chromosome coiling is retained and cytokinesis is postponed until after the second meiotic division.

Interkinesis:
The stage between telophase I and prophase II is called interkinesis. During this stage, DNA replication does not occur; the chromosomes have already replicated during the pre-meiotic interphase. A little despiralization is observed in the chromosomes. In many caises, interkinesis is absent and the cell in telophase I directly comes into prophase II.

Second meiotic division:
The second meiotic division is similar to mitosis, hence it is sometimes called meiotic mitosis. This division is also called the "equational division" because the sister chromatids of chromosomes separate and move to opposite poles and the chromosome number of the daughter nuclei remains the same as of the parent nucleus. This division is divided into the following four stages, viz., prophase II, metaphase II, anaphase II and telophase II. (Fig. 10.1).

Prophase II:
In several organisms this stage is absent. Chromatids of each chromosome are distinctly visible; chromosomes appear as crosses (X) because there is no relational coiling between the sister chromatids. Chromosomes are much condensed. In case of heterozygotes, the crossover

chromatids are genetically dissimilar to this sister chromatids in relation to the exchanged segments.

Metaphase II:
Spindle is organised in both the cells of dyad if formed. In species where dyad is not formed, each area of the cytoplasm organizes a spindle. Nuclear membrane and nucleolus are absent.

Chromosomes in the two dyad cells are arranged on the equatorial plate. Spindle fibres are attached to the centromeres of the sister chromatids of each chromosome on both sides.

Anaphase II:
The centromeres of each chromosome are structurally divided during the first meiotic division itself but they behave as single centromeres till the beginning of anaphase II. The two sister centromeres of each chromosome separate and move away to the opposite poles, dragging along with the concerned chromatids.

Telophase II:
When the sister chromatids reach the opposite poles, they begin to uncoil. Nuclear envelope reorganizes, typical interphase nucleus is formed and the nucleolus reappears.

Cytokinesis:
When the cytoplasm divides to form two daughter cells, it is called bi-partitioning, and when it divides to form four daughter cells, it is called quadri-partitioning. Cytoplasm of each cell of the dyad divides to produce two haploid cells (bi-partitioning) and thus four haploid cells make a quartet.

If the cytokinesis had not occurred at the end of the first meiotic division, there become 4 haploid nuclei in the same cell at the end of the second meiotic division, e.g., in Trillium and Viciafaba. In these plants, cytokinesis occurs at the end of telophase II giving rise to four haploid cells (quadri-partitioning).

In plants, the PMC forms cross-shaped or radial tetrad (quartet) (Fig. 10.1). These quartets differentiate into 4 haploid (n) microspores. The megaspore mother cell (MMC) produces a linear tetrad forming 4 megaspores of which 3 degenerate and one develops to form the embryo sac.

In male animals, four spermatids are produced through meiosis in the spermatocytes and they differentiate into 4 sperms by the process of spermiogenesis (spermiohistorogenesis). In female animals, the first meiotic division in the oocyte produces two dyad cells of which one cell degenerates to form the first polar body.

The second meiotic division of the remaining cell produces two daughter cells. Here again, one cell degenerates and forms the second polar body, while the remaining one nucleus forms the egg nucleus.

Duration of Meiosis:

Duration of meiosis vanes due to certain factors, such as, type of organism, sex, ploidy level, DNA content and environment etc.

(i) Organism:

The duration of meiosis differs in different organisms, from hours to days, months and years. In triticale (X Triticosecale), it takes 20.8 h, in Haplopappusgracilis and Triticumaestivum, it takes 24 h, while in Trillium it takes 274 h to complete meiosis (Table 10.1, 10.2). In general, meiotic duration is greater in animal species as compared to plant species (Table 10.3) In human female, meiosis starts in late prenatal stage and completes at the time of ovulation, thereby taking 12 to 50 years to complete meiosis.

TABLE 10.2. Comparison of durations of mitosis and meiosis in some plant species

Species	Chromosomes (2n)	Duration (hours)	
		Mitosis	Meiosis
Pisum sativum	14	10.0	30.0
Haplopappus gracilis	4	11.9	24.0
Secale cereale	14	12.75	51.2
Vicia faba	12	13.0	72.0
Allium cepa	16	17.4	96.0
Tradescantia paludosa	12	20.0	126.0
Lilium longiflorum	24	24.0	192.0
Trillium erectum	10	29.0	274.0

(ii) Sex:

Meiotic duration is also affected by the sex. In some plants, such as, barley and wheat, meiosis takes nearly similar time in pollen mother cells and embryo sac mother cells.

In Tradescantiapaludosa, meiotic duration in pollen mother cells is larger (120 h) than that in embryo sac mother cell (80 h). Meiotic duration in animal females is generally greater than that in males.

(iii) Ploidy Level:

When compared randomly among different genera and species, the meiotic duration increases with ploidy level. But within the same genus or species, meiosis is faster in polyploids. For example, meiotic durations in Triticummonococcum (2x), T. dicoccum (4x) and T. aestivum (6x) are 42, 30 and 24 h, respectively. In Secalecereale, meiosis completes in 51.2 h in diploids, while it takes only 38 h in tetraploid (Table 10.1).

(iv) DNA Content:

In general, the duration of meiosis is positively associated with DNA content per cell, especially for diploids (Table 10.3). The same is true for mitosis also.

(v) Environment:

Meiosis in the same organism is affected by environmental conditions, especially temperature. The process of meiosis becomes slow at lower temperatures (Table 10.4). In Endymion (animal species), it takes 864 h at 0°C while only 19.9 h at 30°C to complete the meiotic process. In Secalecereale meiotic durations in PMC's were 87.6, 50.88 and 39.12 hours at the temperatures 15°C, 20°C and 25°C, respectively.

TABLE 10.3. Duration of male meiosis and DNA content per cell in certain plant and animal species

Organism	Meiotic duration	DNA content per cell ($pg = 10^{-12}$ g)
PLANT SPECIES (Duration in hours)		
Vicia sativa	24	8.2
Pisum sativum	30	14.8
Triticum monococcum	42	21.0
Vicia faba	72	44.0
Tradescantia paludosa	126	54.0
Trillium erectum	274	120.0
ANIMAL SPECIES (Duration in days)		
Drosophila melanogaster	1–2	0.085
Lacusta migratoria	7–8	12.8
Triturus viridescens	12–13	72.0
Mus musculus	12	5.0
Homo sapiens	24	6.0

TABLE 10.4. Effect of temperature on duration of meiosis

Organism		Temperature and meiotic duration						
Endymion	Temperature (°C)	0	5	10	15	20	25	30
	Duration (h)	864	360	168	84	48	30	19.9
Schistocerca gregaria (grasshopper)	Temperature (°C)	30	32	38	40			
	Duration (h)	336	264	180	144			
Secale cereale	Temperature (°C)	15	20	25				
	Duration (h)	87.6	50.88	39.12				
Trillium erectum	Temperature (°C)	1	2	5	15			
	Duration (h)	2160	1680	960	384			

In general, mitosis is of shorter duration than meiosis. A comparison of both the cell divisions regarding duration in certain plant species is presented in Table 10.2.

Significance of Meiosis:

Sexually reproducing organisms exhibit alternation of generations during which the following two important event take place:

(1) The somatic chromosome number (2n) is reduced to half and haploid (n) gametes are produced through meiotic cell division.

(2) Fertilization involves the fusion of haploid female and male gametes to form the 2n zygote; this zygote produces embryo in the higher organisms. However, in lower organisms, the 2n zygote directly undergoes meiosis. In this way, the chromosome number of sexually reproducing species remains constant over generations.

During meiosis, recombination between linked genes, segregation of the alleles of a gene and independent assortment of genes located on different chromosome occur and new gene combinations arise that lead to the appearance of genetic variation.

In case of asexual reproduction, there is no alternation of generations, and the number of chromosomes remains constant over generations due to reproduction through mitotic divisions only. Recombination and segregation do not occur and new gene combinations do not arise. Therefore, genetic variation is not released in the progeny of asexually reproducing organisms.