We have just finished looking at the process of mitosis, a process that produces cells genetically identical to the original cell. Mitosis ensures that each cell of an organism has the same DNA as the original fertilized egg or zygote.

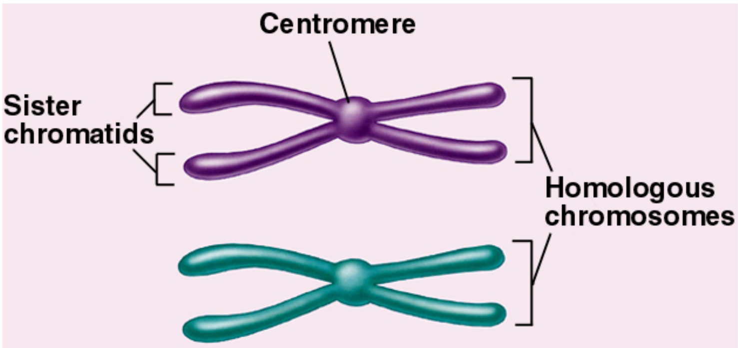
Passing chromosomes and genetic information from generation to generation is equally important. A critical role of heredity is to maintain and obtain variation among members of a species. These variations are the result of the specific genes we inherit from our parents through sexual reproduction.

However, chromosome number doesn't double with each generation. Each generation of a species has the same chromosome number as the preceding generations. **Meiosis** is the process that ensures that each new generation has the same chromosome number as the preceding generation.

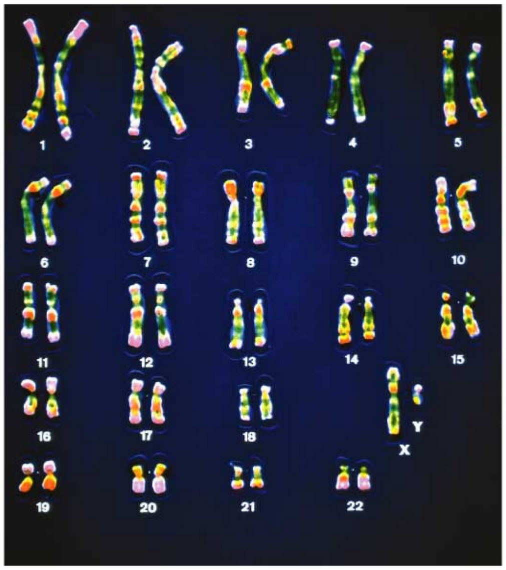
Meiosis is a process that reduces chromosome number by half and occurs at just one stage in an organism's life cycle (to form gametes in animals, or to start the gamete producing stage in plants, or for some organisms to restore the appropriate chromosome number for the assimilative stage of its life history). **Sexual reproduction** or more properly, **fertilization,** then restores the "typical" number of chromosomes for the next generation.

Meiosis and Chromosome Number

Before discussing meiosis we need to go back and re-examine chromosomes, this time with reference to the genetic information carried in the DNA of each chromosome. When we look at the chromosomes of most eukaryotic organisms carefully, it can be seen that for each individual chromosome, a second chromosome can be found that physically matches it in length and shape. Closer inspection of the DNA shows that the matching chromosomes have very similar, but **not identical** DNA which carries equivalent genetic information, or genes. These matching chromosomes, called **homologous chromosome**s, with their similar DNA, form the basis of the variation we see in the genetic traits, or genes, of living organisms.



A display of homologous chromosome pairs is called a **karyotype**. The human karyotype has 23 pairs of chromosomes.



Human Male karyotype

Cells that contain pairs of homologous chromosomes are called **diploid**. For humans, the diploid number of chromosomes is 46. These 46 chromosomes are comprised of 23 homologous pairs of chromosomes. Each pair is physically similar and has equivalent genetic information. As we shall discuss later, the genes on homologous chromosomes do not have to be identical (although they can be). We know for example, that you can inherit either brown eyes or blue eyes; a tongue that curls, or one that cannot curl. The alternative forms that genes can take are called **alleles**. Inheritance looks at how these pieces of DNA interact to produce the traits expressed in individuals.

When chromosome number is reduced during meiosis, the product cells are called **haploid,** having half as many chromosomes as the diploid cells of the organism. "Ploid" as a general term means a "set", so we can also say that a diploid cell has two sets of chromosomes, or two of each kind of chromosome. A haploid cell has no pairs of chromosomes, just one of each kind. (It's possible to have more than 2 chromosomes of each kind. Polyploids are quite common in agriculture as a result of plant breeding. Polyploids are less common in animals.)

Remember: "Sister" Chromatids are not pairs; they are the two identical parts of one duplicated chromosome. You must make this distinction! The pairs are the homologous chromosomes. Homologous pairs of chromosomes function together during meiosis, as we shall discuss. All chromosomes are independent in mitosis.

Meiosis and Genetic Variation

Meiosis is necessary to ensure that each new generation has the same chromosome number as the preceding generation, but meiosis has a second function for living organisms: maintaining **genetic variation**. Each time meiosis occurs, followed by, at some point, sexual reproduction, the new individual formed is genetically different from either parent. Because meiosis is involved with genetic variation and is needed for sexual reproduction, we need to mention a few things about genetic inheritance and sexual reproduction to better understand why meiosis is so important.

During **meiosis** there is some shifting and recombining of alleles so that gene combinations always occur in the gametes that are different from the parent.

Each parent typically has two "genes" (or more correctly, two alleles of a gene) for each genetic characteristic (one on each of the homologous chromosomes). Each parent passes one of each of its homologous chromosomes (with its particular alleles) to the offspring by meiosis and fertilization. The fertilized egg (**zygote**) will then have two genes (alleles) for each trait, one from each parent. It's important to note that each individual will have a **paternal** set of chromosomes and a **maternal** set of chromosomes. Each homologous pair of chromosomes has one paternal and one maternal origin.

Since parents are not genetically identical, their haploid gametes will have different combinations of genes. Each egg and each sperm (or each spore) is genetically different from the parent's DNA (having only half as much).

At fertilization, two haploid gametes fuse, each containing one of each type of homologous chromosome, which restores the diploid number of chromosomes. The zygote will now have homologous chromosomes, but one from each of the parents. Since each gamete has a unique combination of chromosomes, each zygote will be unique.

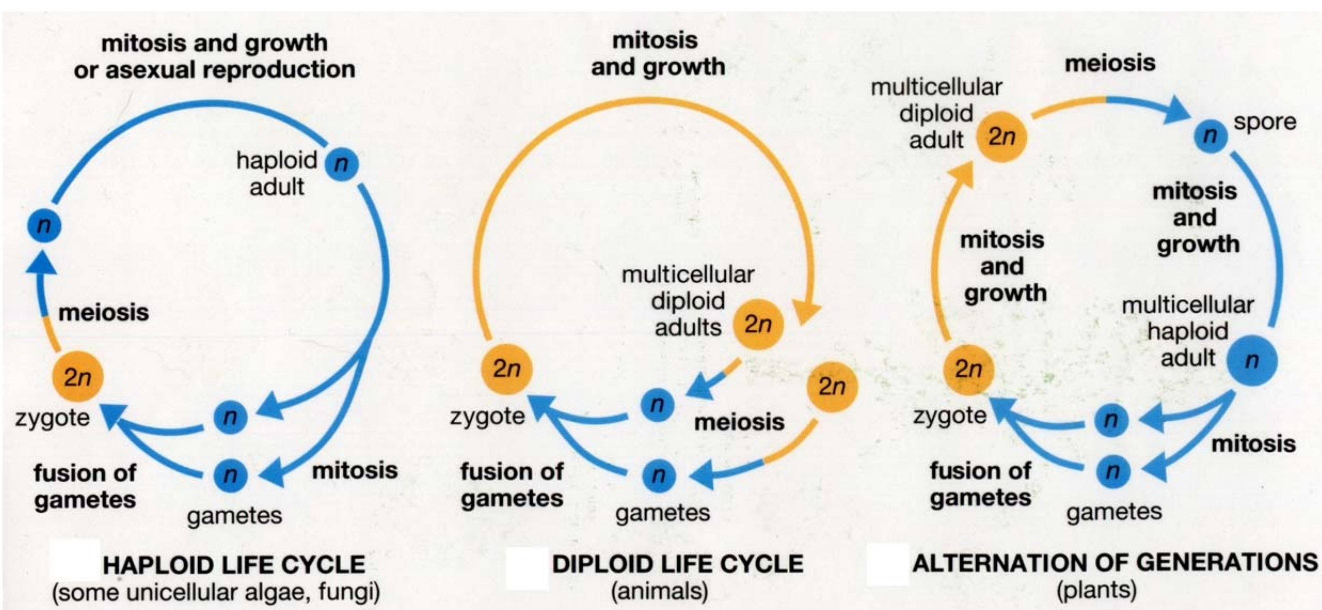
The offspring (children) formed by sexual reproduction will have genetic variation, important for the long-term response of species to their environment. Such variations among offspring lead to physical, behavioral and physiological differences. These differences may be more or less useful in the surroundings of that organism, and are subject to the agents of selection. This variation is an important basis for evolutionary change, which will be discussed later.

Meiosis and the Life Cycles of Organisms
Meiosis is something that takes place at just one point in any sexually reproducing organism's life cycle. In animals, meiosis generally occurs to form gametes: sperm or eggs. In many other types of organisms, meiosis occurs at some different point in the life cycle, and the products of meiosis may be spores, (as in plants) or the first cells of the next generation (for most protists and most fungi). At some point however, all organisms that sexually reproduce will make haploid gametes. Although we are familiar with, and comfortable with the animal life cycle, it's good to know how different organisms fit meiosis into their life cycles.

Similarly, **fertilization** occurs at one point in an organism's life history. Fertilization occurs between two different haploid cells, called gametes, to form the **zygote**, or fertilized egg. The zygote obtains half its chromosomes from the sperm and half from the egg or from different gametes, the more general term.

Fusion of gametes restores the diploid number, and in so doing, also restores homologous chromosomes (one of each kind being provided by the sperm and one of each kind coming from the egg). Since each gamete has a unique combination of chromosomes, each zygote will be unique, and genetic variation is both maintained and obtained within the species.

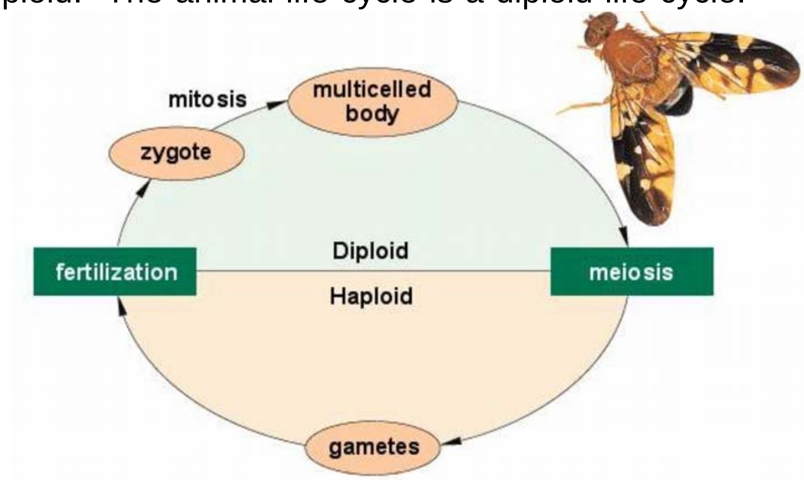
We will now discuss typical life cycle patterns and look at the timing of meiosis in the life cycle.



Overview of Life Cycle Variations

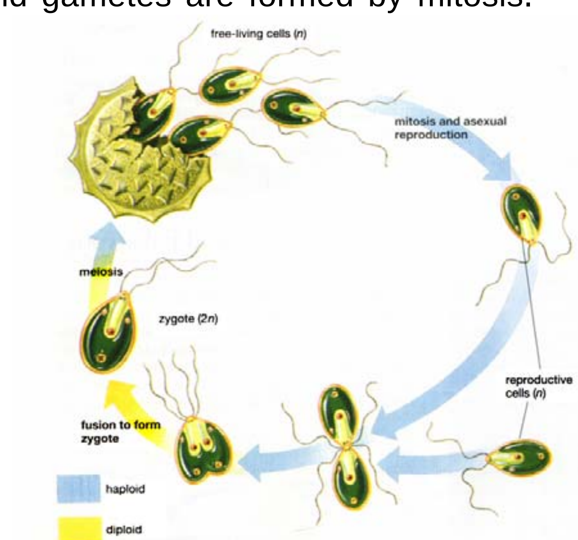
Diploid Life Cycle

- In animals, meiosis generally produces just haploid sex cells, which at fertilization start the next generation. The only haploid cells of the animal are egg or sperm, and the respective maturation processes are called oogenesis and spermatogenesis.
- When gametes fuse, the zygote grows by mitosis producing the adult stage. All cells will be diploid. The animal life cycle is a diploid life cycle.



Haploid Life Cycle

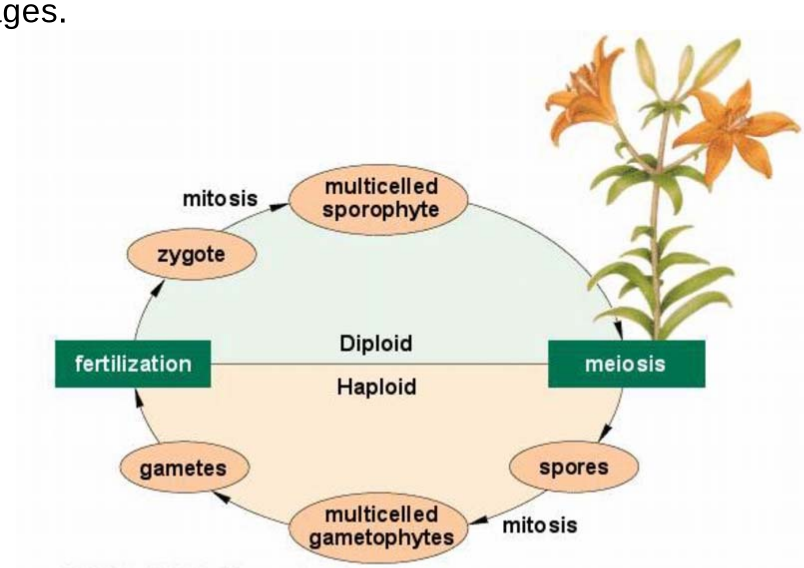
- In many protists, and some fungi, haploid gametes fuse to form a zygote, but the zygote immediately does meiosis forming single haploid cells.
- In protists, which remain single cell organisms, the nucleus is then haploid.
- At some time, the single cells may just decide to become gametes and fuse with another to make a zygote, or haploid cells may do mitosis to make more individuals asexually.
- Haploid life cycles can be more complex. Fungi, and some algae may make multicellular haploid organisms from single-celled meiotic product, by mitosis. At some time, special areas of the haploid body will become gamete-making structures, and haploid gametes are formed by mitosis.



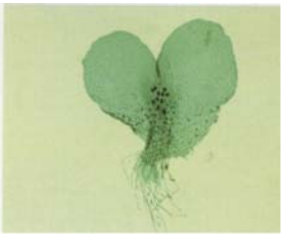
Alternation of Generations

- Most plants have both a multicellular haploid stage and a multicellular diploid stage in their life histories. This is called the alternation of generations.
- In plants, the structure in which meiosis occurs is called a **sporangium.**
- Meiosis does not directly produce gametes, but produces haploid cells, called **spores** that in turn, grow, by mitosis, into multicellular haploid structures called **gametophytes** (gamete-making plant). Gametophytes eventually produce and contain gametes. (The multicellular diploid structures that produce sporangia are called **sporophytes**.)

Which stage (sporophyte or gametophyte) is predominant in the life of a plant varies with different types of plants. Most "higher" plants have predominant sporophytes. A pollen grain of pine tree or flower, for example is the male gametophyte stage of those plants. In ferns, both gametophyte and sporophyte are photosynthetic, but the gametophyte is short-lived and very small. Mosses, in contrast, have predominant gametophyte stages.



Alternation of Generations in Plants



Fern Sporangia Fern Gametophyte

Non-Sexual Reproduction

As discussed, many organisms have both sexual and non-sexual means of increasing the numbers of individuals. Asexual reproduction can be a good strategy in an environment that is consistent, if a species is well-suited to those conditions. Without sexual reproduction, however, there is no genetic variation to adapt to change.

The Process of Meiosis

Homologous chromosome pairs are essential to how meiosis works. In meiosis the homologous chromosomes literally pair up prior to the reduction of chromosome number. In meiosis, one of each type of chromosome (one of each homologous pair) is distributed to each meiotic product, so that the meiotic products have half as many chromosomes as the "parent" cell. This is the crucial difference between mitosis and meiosis, and explains why we can reduce chromosome number and still have all of the genetic information needed to form a new organism. **The homologous pairs of chromosomes in diploid organisms do not interact during mitosis; each chromosome is on its own.**

After meiosis, the meiotic products have a **haploid** (half the parental) number of chromosomes, and **no pairs of homologous chromosomes**. Haploid also refers to the cell when there is just one of each kind of chromosome, or the "n" number of chromosomes. (Diploid is the 2n number of chromosomes.)

The diploid number of chromosomes will be restored when two gametes (egg and sperm) unite in sexual fertilization.

The Process of Meiosis - Details

Prior to any cell division, chromosomes must undergo DNA duplication. To achieve the reduction in chromosome number and appropriate distribution of chromosomes, meiosis requires **two divisions**, called **Meiosis I** and **Meiosis II**. At the completion of the second division, four cells will typically be produced. The stages of meiosis resemble those of mitosis; the differences occur in the matching or pairing of the homologous chromosomes, which occurs during the first division prophase.

Some Notes:

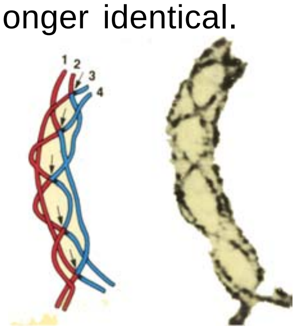
- "Sister" Chromatids are not pairs; they are the two identical parts of one duplicated chromosome. You must make this distinction to understand how the process of meiosis works!

- A pair of duplicated homologous chromosomes will have a total of 4 chromatids, two chromatids for each homologue. It's just a fact that prior to any cell division, chromosomes duplicate, so meiosis starts with duplicated chromosomes.

The Meiosis Stages (Or how we break up a continuous process into chunks)
Pre-Meiotic Interphase
The DNA of the cell* that will do meiosis replicates. (DNA replication must precede any cell division.) The identical sister chromatids of each replicated chromosome are attached at their centromeres and have their kinetochores.

* Again, cells that do meiosis are restricted to sex organs, such as the ovary and the testis of animals; or anther and ovule of "higher" plants; or sporangia of "lower" plants. The sex organs are diploid, just as is the rest of the organism. Only the products of meiosis (gametes or gamete-producing structures) are haploid. For organisms that have a haploid life cycle, meiosis immediately follows the formation of the zygote. The haploid cells produced are the first cells of the next generation, which grow by mitosis to become adults.

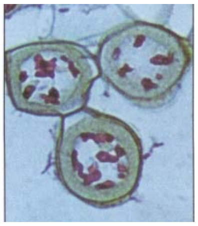
Meiosis I
Prophase I
- Homologous chromosomes pair up at the start of prophase I in a process called **synapsis**. This uses proteins along the chromosomes to join the homologues together. The homologues literally join at several points (called **chiasmata**). All four chromatids of the homologous pair are aligned together.
- This arrangement allows for a process of genetic importance to occur. The intertwined chromatids of the homologous chromosomes break at one or more places and exchange equivalent bits of DNA with each other. This exchange is called **crossing over.** This occurs between the non-sister chromatids, and is mediated by enzymes. If the alleles of the homologues were different forms of the genes, than **recombination** occurs. The sister chromatids now have some genetic variation; they are no longer identical.



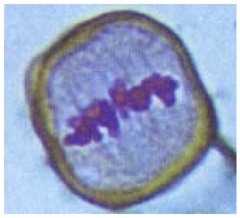
Crossing Over

- After crossing over takes place, the still-joined homologues pull apart slightly, although the chromosomes are still attached at the chiasmata.
- All things that we normally think of taking place in a prophase also occur in prophase I of meiosis, including attaching spindle fibers to each chromosome of the attached homologous pairs.

Early Prophase I



Synapsed Homologous Pairs



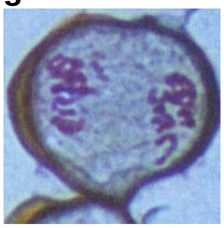
Metaphase I

Metaphase I

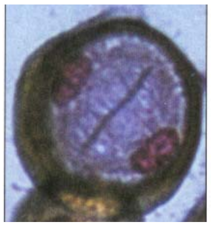
- Synapsed homologous pairs of chromosomes are moved to the equator by the spindle complex.
- The alignment is random; some maternal chromosomes will orient facing one pole along the equator; others face the opposite pole. The random alignment of homologous pairs of chromosomes at metaphase increases genetic variation.

Anaphase I

- The **homologous chromosomes are separated from each other** and pulled toward opposite poles during Anaphase I.
- Replicated chromosomes are not affected during Anaphase I. The sister chromatids are still tightly bound to each other by their centromeres.
- The **chromosome number is officially reduced** at this time because each nucleus that will form at Telophase I will have half the number of chromosomes as the pre-meiotic cell. All of the chromosomes will be replicated. No sister chromatids have separated.
- No homologous chromosome pairs are present at the end of Anaphase I. Each cluster of chromosomes at the respective poles of the cell will have one of each type of homologous chromosome. **The key to reducing chromosome number while maintaining all of the genetic information is the pairing and separation of homologs**.



Anaphase I



Telophase I

Telophase I and Interkinesis

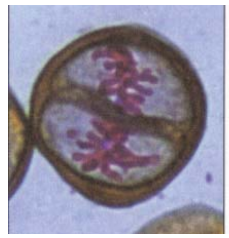
- Typically two new nuclei are formed, each with one set of the homologous chromosomes
- Cytokinesis will form two cells. Each chromosome is still replicated (which occurred in pre-meiotic interphase), and essentially the cells are just preparing for the second division. Some cells do not bother with cytokinesis here, or even form new nuclear envelopes, which will just have to be degraded during meiosis II, anyway.

Meiosis II

Prophase II

- New spindle apparatus is formed in each of the two cells from telophase I.
- The still-replicated chromosomes stretch out and recondense.
- Spindle fibers attach to the kinetochores of each of the sister chromatids, one from each pole.
- Nuclear membranes degrade.


Prophase II


Metaphase II

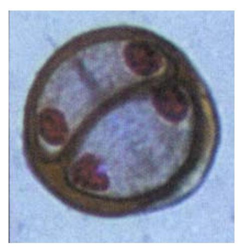
Metaphase II

- The replicated chromosomes are aligned along the equator by the spindle complex.

Anaphase II

- Centromeres of sister chromatids are detached from each other.
- The now non-replicated chromosomes are pulled to the poles of the cells.


Anaphase II


Telophase II

Telophase II and Cytokinesis

- Each new nucleus formed has half the number of the original chromosomes but each nucleus has one of each type of homologous chromosome.
- A total of four new cells will be produced.

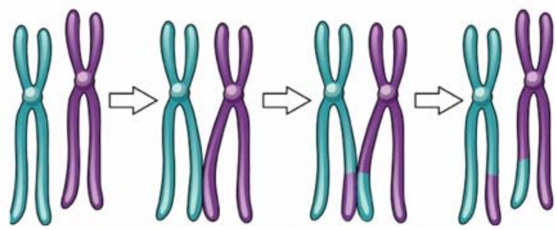
Review of Genetic Importance of Meiosis

To conclude our discussion of meiosis, and to initiate further discussion of genetics and inheritance let us recall that the genetic traits we inherit are in the form of gene alternatives, called alleles. These alleles are located on the homologous chromosomes.

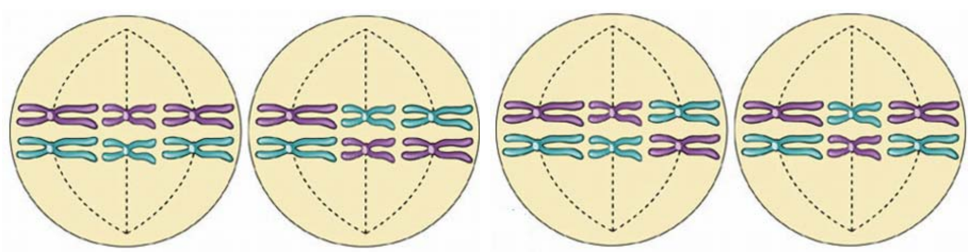
The zygote receives different parental combinations of homologs from the egg and sperm. How these alternatives gets expressed is the study of inheritance.

Meiosis plays the following roles in inheritance:

- Recombination or crossing-over between non-sister chromatids during synapsis (Prophase I) produces gametes with greater variation.



- The independent assortment (or alignment) of maternal and paternal chromosomes at Metaphase I when homologous chromosomes are lined up on the cell equator results in greater genetic variation.



- The fusion of genetically different gametes results in new genetic combinations for each generation.
- Meiosis provides a mechanism to preserve chromosome number from generation to generation.