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# The important role of processes such as synapsis and recombination during meiosis in sexual reproduction

Wenjia Zhang*

Qingdao No. 2 High School of Shandong Province, Qingdao, Shandong, 266071, China

**Abstract:** Sexual reproduction is a process that involves the fusion of sperm and egg cells, producing genetic diversity and enhancing the ability of species to adapt to environmental changes. During the fertilization process, the formation of gametes is significant, and it is closely related to meiosis. Meiosis consists of seven major processes: two rounds of division, cytokinesis, crossing over, chromosome condensation, nuclear envelope breakdown and reconstruction, and spindle formation. Among these, the pairing, synapsis, and recombination of chromosomes can increase genetic diversity and are the central focus of meiosis. This article reviews the process of meiosis and the research on several related genes.

## 1 Introduction

The alternation of generations is not only of great significance in the phylogeny of plants but also plays a crucial role in their adaptation to environmental changes and survival strategies. Through alternation of generations, plants can combine the rapid reproductive advantages of asexual reproduction with the genetic diversity brought about by sexual reproduction, enhancing the adaptability and survival capacity of the population.

Double fertilization is an important junction connecting two generations. In seed plants, pollen grains and embryo sacs serve as the gametophytes of flowering plants, containing male and female gametes, respectively, produced through meiosis. The concept of meiosis was originally proposed by August Weismann, the founder of the "germ plasm theory," who discovered that polar bodies and egg cells arise from the division of oocytes and carry only half the genetic material. This phenomenon is referred to as "reducing division." Later, in 1905, J. R. Farmer defined the two successive divisions occurring in the formation of gametes as "meiosis"[1]. Thus, the concept of meiosis was officially established.

## 2 Sexual reproduction of plants

The sexual reproduction process of plants increases genetic diversity in offspring by combining genetic material from different parents. This sexual reproduction helps populations adapt to various environmental pressures, allowing plants to maximize their reproductive success by producing a large number of offspring with different genetic traits. Sexual reproduction is a crucial stage in the plant life cycle and is essential for the reproduction and survival of species.

The process of sexual reproduction leads to the formation of a fertilized egg. Before the fertilized egg is formed, gametes need to fuse. Organisms produce gametes through meiosis, and the resulting gametes are haploid, meaning they contain half the number of chromosomes. The gametes combine through sexual reproduction to form a diploid zygote, which marks the beginning of a new life cycle. The zygote further undergoes cell division and growth through mitosis. In the reproductive process of angiosperms, first, the sporophyte proliferates through mitosis. Then, the spore mother cell prepares to undergo meiosis, and after two rounds of meiosis, the male and female gametes begin to develop. When the sperm reaches the ovule, it combines with the egg cell to form a fertilized egg; this process is called double fertilization. In the process of double fertilization, one sperm combines with the egg cell to form a fertilized egg, which then develops into an embryo and ultimately grows into a new plant. Meanwhile, the other sperm merges with the polar nucleus to form the primary endosperm nucleus, which subsequently develops into the endosperm that provides nutrition for the seed. Throughout the entire process of reproduction in angiosperms, meiosis plays an important role (figure 1). [2]

*Corresponding author's e-mail: 15192497327@163.com

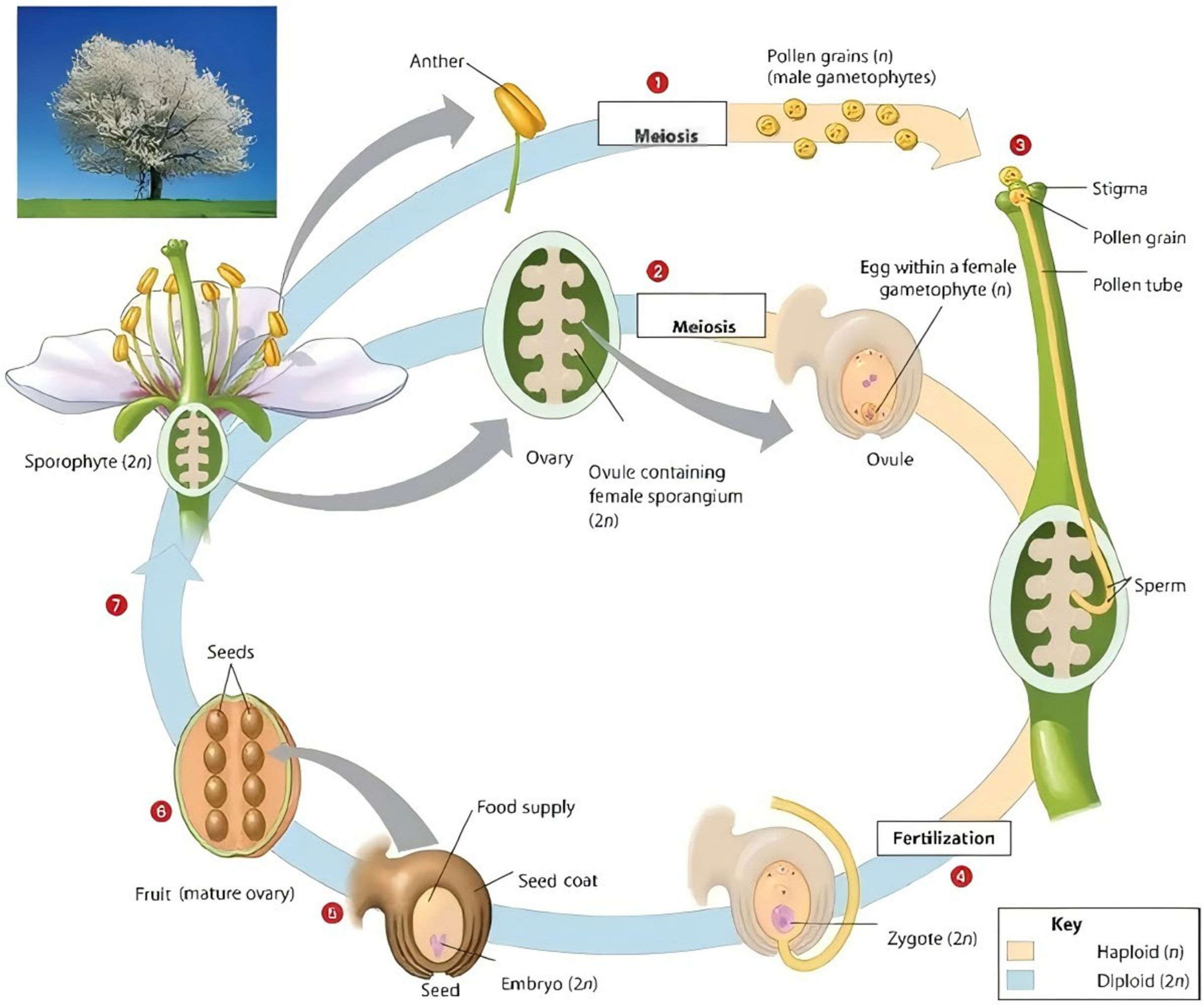


**Figure 1.** The process of sexual reproduction in angiosperms.

## 3 The process of meiosis

Meiosis is the process of cell division through which sexually reproducing organisms form gametes. It includes the first meiotic division in primary spermatocytes and the second meiotic division in secondary spermatocytes. The characteristic events occur during prophase I of the first meiotic division (Zhang et al., 2019). In male mammals, after sexual maturation, spermatogonial stem cells (SSCs) begin meiosis in response to retinoic acid (RA) stimulation. Following two consecutive divisions, the chromosomal content in the cells is halved. Similar to mitosis in SSCs, the progression of meiosis is regulated by both intracellular and extracellular factors. Furthermore, the characteristic events occurring during prophase I impose more complex requirements on the synthesis and interactions of functional proteins within the cell (Ishiguro et al., 2020).[3]

Meiosis includes two consecutive stages of cell division: meiosis I and meiosis II. This process reduces the chromosome number by half, producing gametes (sperm and egg cells) with a haploid chromosome number. Prophase I of meiosis includes leptotene, zygotene, pachytene, and diplotene stages. During leptotene, chromosomes begin to condense and appear thread-like. In the zygotene stage, homologous chromosomes pair up, forming a double-stranded structure called a bivalent. During pachytene, homologous chromosomes are closely paired and chromosome exchange occurs. In the diplotene stage, homologous chromosomes begin to separate but remain connected at chiasmata. In the mid-stage, the second-order bodies are arranged on the equatorial plane of the cell, forming the "equatorial plate." In the later stage, homologous chromosomes are pulled toward the two poles of the cell, but the two chromatids of each chromosome remain connected. In the final stage, cytokinesis occurs, resulting in the formation of two cells with a haploid number of chromosomes, each containing two chromatids of the chromosomes. Meiosis II will process haploid cells. In prophase, the chromosomes condense again, and the nuclear membrane and nucleolus disappear. During metaphase, the chromosomes are arranged on the equatorial plane of the cell. In anaphase, the staining monomer is pulled to the two poles of the cell. In telophase, the cytoplasm divides, forming four cells with a haploid number of chromosomes, which will ultimately become gametes. [4]

The result of meiosis is the production of four genetically distinct gametes, each containing half the number of chromosomes. When the gametes combine during fertilization, they restore the chromosome number to diploid levels, thereby maintaining the chromosomal stability of the species. This process not only ensures the transmission of genetic information but also increases genetic diversity through chromosomal recombination (figure 2).[5]

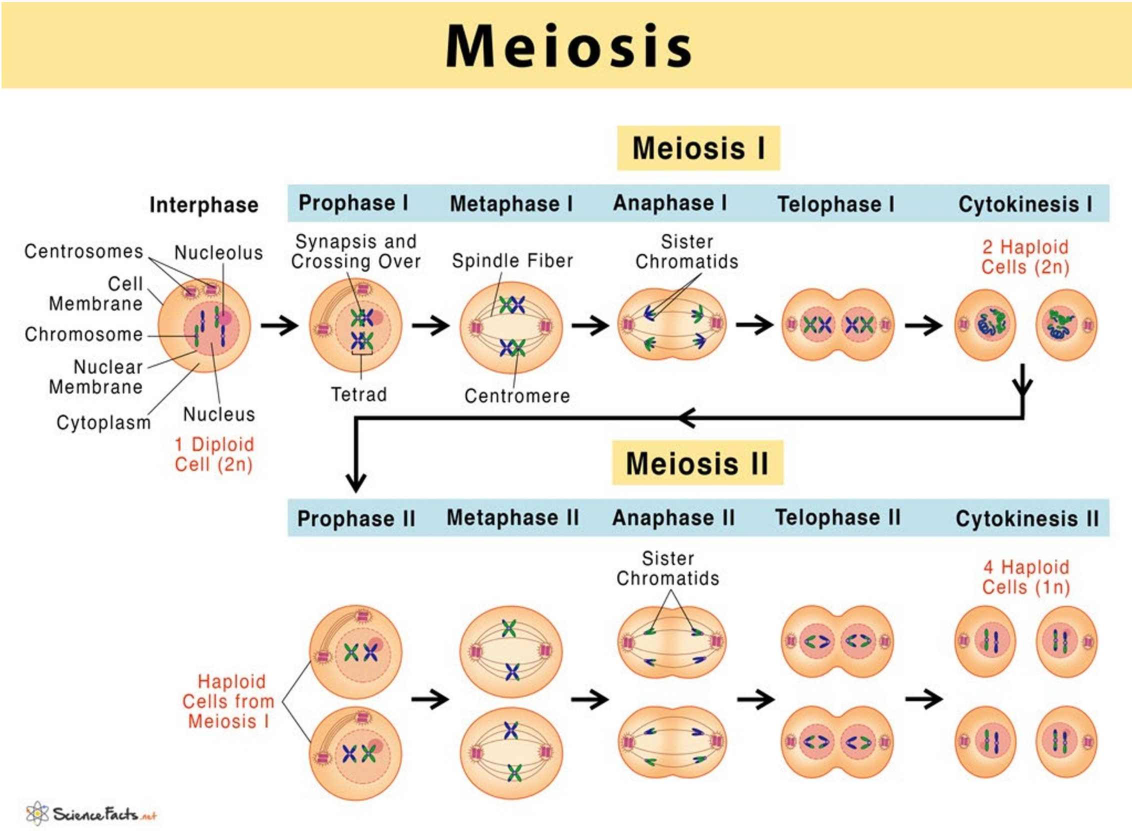


**Figure 2.** Meiosis Process

## 4 Pairing, synapsis, and recombination increase genetic diversity.

### 4.1 Pairing

The pairing occurs during the zygotene stage of prophase I of meiosis when homologous chromosomes (a pair of chromosomes, one from the mother and one from the father, which are similar in morphology and genetic sequence) begin to pair up. Pairing is a prerequisite for synapsis, allowing homologous chromosomes to accurately recognize and pair with each other.[6]

Taking plants as an example, Ph1 (Pairing homoeologous1) is an early discovered gene controlling chromosome pairing in plants. This gene was found in the study of homologous chromosome pairing in wheat nucleosomes. It can inhibit the pairing between some homologous chromosomes to ensure the correct pairing and synapsis of homologous chromosomes. Phs1 (Poor homologous synapsis 1) is a gene reported in maize that is involved in coordinating chromosome pairing, synapsis, and recombination. In the mutants of this gene, the pairing between homologous chromosomes is completely replaced by non-homologous chromosomes, suggesting that it plays an important role in the recognition of homologous chromosomes and affects subsequent chromosome synapsis and pairing. Later, Ronceret et al. identified Phs1 in Arabidopsis and further defined its role in coordinating chromosome pairing and recombination. In the phs1 mutation of Arabidopsis thaliana, the MRN complex proteins RAD50 and MRE11 are missing, resulting in extensive chromosome pairing defects and the loss of synapsis. The study also demonstrated that Phs1 regulates the transport of RAD50 from the cytoplasm to the nucleus. It is speculated that during double-strand break repair, RAD51 and DMC1 proteins have a limited amount of single-stranded DNA ends, leading to failed homologous searches and producing non-homologous chromosome ectopic pairing. Pair1 (Homologous pairing aberration in rice meiosis 1), Pair2, and Pair3 are genes associated with meiotic pairing in rice. Pair1 is mainly expressed in the early stage of meiosis, and the mutant phenotype first appears in the zygotene stage. In pair1 mutants, homologous chromosomes do not pair throughout the entire meiosis process. Similar to pair1, the mutant of pair2 also does not have chromosome pairing early in meiosis and ultimately cannot undergo synapsis. Pair3 is also necessary for homologous chromosome pairing and synapsis in rice. Like the pair1 and pair2 mutants, the pair3 mutant cannot form bivalents, ultimately leading to plant sterility. Unlike the pair1 and pair2 mutants, the pair3 mutant shows normal cytokinesis and can produce tetrads. Pair1 and Pair3 do not interact in the yeast two-hybrid system, so they belong to different protein complexes and play roles in different pathways of chromosome pairing and association. Early studies have also demonstrated that homologous chromosome pairing and association begin at the telomeres, which is why telomere bouquets are considered the initiation of homologous chromosome pairing and association. Due to the scarcity of mutants, no related genes have been cloned as of now, so the mechanisms in this regard remain unclear.[7]

### 4.2 Synapsis

"synapsis" refers to homologous chromosomes that are paired and closely linked, forming a bivalent. "synapsis" refers to homologous chromosomes that are paired and closely linked, forming a bivalent. In a bivalent, the non-sister chromatids of homologous chromosomes are arranged side by side. The synapsis provides the physical basis for the exchange of genetic material between chromosomes, serving as a prerequisite for recombination.

Mutants related to synapsis are divided into two types: one is the asynaptic variant, where homologous chromosomes are unable to associate properly; the other is the desynaptic variant, where association cannot be maintained normally. The Asy1 in Arabidopsis thaliana is a homologous gene of Hop1 in yeast, and HOP1 is a protein required for the assembly of the synaptonemal complex and normal synapsis in yeast. ASY1 is a lateral component-associated protein of the synaptonemal complex and is an essential component for homologous chromosome synapsis and recombination. Researchers such as Armstrong found that similar to Arabidopsis, cabbage lacks BoAsy1, and the morphology of the synaptonemal complex cannot be built normally. The Pair2 mentioned above is the homologous gene of Asy1 in rice, and homologous chromosome pairing is completely absent in the pair2 mutant. Boden et al. identified the homologous gene TaAsy1 of Asy1 in wheat, and the protein encoded by this gene exhibits a similar localization pattern to ASY1 and PAIR2 in Arabidopsis and rice. Further research indicates that TaAsy1 is essential for chromosome synapsis and can initiate homologous chromosome pairing during meiosis I in wheat. It is worth mentioning that Ph1 can inhibit homologous chromosome pairing by regulating the expression level of TaAsy1, suggesting that TaAsy1 is directly involved in the Ph1-dependent pathway for homologous chromosome pairing.ZYP1 is the transverse filament protein of the synaptonemal complex in Arabidopsis thaliana, and it is also the first synaptonemal complex protein isolated from higher plants.In the absence of ZYP1, the synaptonemal complex cannot form properly, which can lead to a delay in the process of prophase I of meiosis.

The research on the synaptonemal complex is currently focused on some genes related to its components, and there are few studies on how the synaptonemal complex matures. It is generally believed that the elongation of the transverse filament protein in the yeast synaptonemal complex depends on the synaptonemal initiation complex, which is necessary for type I crossover formation. [7]

### 4.3 Recombination

Chromosome crossover or recombination can occur between homologous chromosomes at the pachytene stage of prophase I of meiosis. This involves DNA exchange between non-sister chromatids. Recombination increases genetic diversity because it generates new chromosome combinations that are passed on to offspring during sexual reproduction. [8]

The pattern of the recombination process has been studied fairly well in yeast. First, there is a double-strand break (DSB) in the homologous chromosomes, and the broken double strands are degraded in the 5′to 3′direction, forming 3′end tails. Then, the 3′end tail attacks the intact homologous double-stranded DNA, and their interaction ultimately produces two types of products: crossover recombination and non-crossover recombination. Many genes involved in this process have also been cloned in plants. Some genes are conserved, some genes are not the same as those in yeast, and some genes are plant-specific. [9]

## 5 Conclusion

Recombination leads to new combinations of genes, which means that each gamete ( sperm or egg cell ) has a unique gene combination, thereby increasing the genetic diversity of the population. During sexual reproduction, genetic diversity increases further when different gametes combine to form zygotes, because each zygote will inherit different genetic characteristics from its parents. However, in some species, there is interference between crossover events, which means that the likelihood of another crossover occurring near a crossover on one chromosome is reduced. Interference ensures that genes in different regions of the chromosome can be transmitted to offspring in different combinations, thereby increasing genetic diversity. In addition, each gamete produced by meiosis is independent and has a random combination of chromosomes. This randomness further increases genetic diversity. Through these mechanisms, organisms can produce genetically diverse offspring, which is crucial for the adaptability, survival, and evolution of species. Genetic diversity enables populations to better adapt to environmental changes and to combat diseases and predators.

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