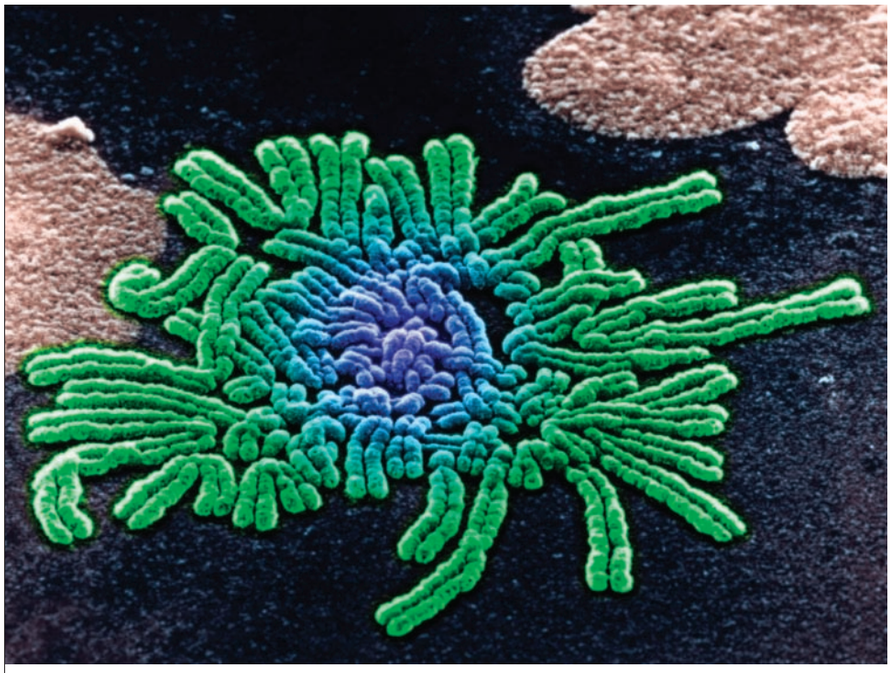


Adrian T. Sumner/Science Photo Library/Photo Researchers, Inc.

Chromosomes aligned during metaphase of the first division of meiosis, the process that produces gametes such as eggs and sperm (colorized SEM).

11 Meiosis: The Cellular Basis of Sexual Reproduction

Study Plan

11.1 The Mechanisms of Meiosis

Meiosis is based on the interactions and distribution of homologous chromosome pairs

The meiotic cell cycle produces four genetically different daughter cells with half the parental number of chromosomes

11.2 Mechanisms That Generate Genetic Variability

Variability generated by recombination depends on chromosome pairing and physical exchanges between homologous chromatids

Random segregation of maternal and paternal chromosomes is the second major source of genetic variability in meiosis

Random joining of male and female gametes in fertilization adds additional variability

11.3 The Time and Place of Meiosis in Organismal Life Cycles

In animals, the diploid phase is dominant, the haploid phase is reduced, and meiosis is followed directly by gamete formation

In most plants and fungi, generations alternate between haploid and diploid phases that are both multicellular

In some fungi and other organisms, the haploid phase is dominant and the diploid phase is reduced to a single cell

Why It Matters

A couple clearly shows mutual interest. First, he caresses her with one arm, then another—then another, another, and another. She reciprocates. This interaction goes on for hours; a hug here, a squeeze there. At the climactic moment, the male reaches deftly under his mantle and removes a packet of sperm, which he inserts under the mantle of the female. For every one of his sperm that successfully performs its function, a fertilized egg can develop into a new octopus.

For the octopus, sex is an occasional event, preceded by a courtship ritual that involves intermingled tentacles. For another marine animal, the slipper limpet, sex is a lifelong group activity. Slipper limpets are relatives of snails. Like many other animals, a slipper limpet passes through a free-living immature stage before it becomes a sexually mature adult. When the time comes for an immature limpet to transform into an adult, it settles onto a rock or other firm surface. If the limpet settles by itself, it develops into a female. If instead it settles on top of a female, it develops into a male. If another slipper limpet settles down on that male, it, too, becomes a male. Adult slipper limpets almost always live in such piles, with the one on the bottom always being a female. All the male limpets continually contribute sperm that fertilize

eggs shed by the female. If the one female dies, the surviving male at the bottom of the pile changes into a female and reproduction continues.

These octopuses and slipper limpets are engaged in forms of **sexual reproduction**, the production of offspring through union of male and female **gametes**—for example, eggs and sperm cells in animals. Sexual reproduction depends on **meiosis**, a specialized process of cell division that produces gametes. Meiosis reduces the number of chromosomes, producing gametes with half the number of chromosomes present in the **somatic cells** (body cells) of a species. The derivation of the word *meiosis* (*meioun* = to diminish) reflects this reduction. At **fertilization**, the nuclei of an egg and sperm cell fuse, producing a cell called the **zygote**, in which the chromosome number typical of the species is restored. Without the halving of chromosome number by the meiotic divisions, fertilization would double the number of chromosomes in each subsequent generation.

Both meiosis and fertilization also mix genetic information into new combinations; thus, none of the offspring of a mating pair is likely to be genetically identical. By contrast, asexual reproduction generates genetically identical offspring because they are the products of mitotic divisions (asexual reproduction is discussed in Chapter 10). Sexual reproduction generates the variability that is the basis of most inherited differences among individual sexually reproducing organisms. This variability is the source of raw material for the process of evolution.

The halving of the chromosome number and mixing of genetic information into new combinations—both by meiosis—and the restoration of the chromosome number by fertilization, are the biological foundations of sexual reproduction. Intermingled tentacles in octopuses, communal sex among limpets, and the courting and mating rituals of humans, are nothing more or less than variations of the means for accomplishing fertilization.

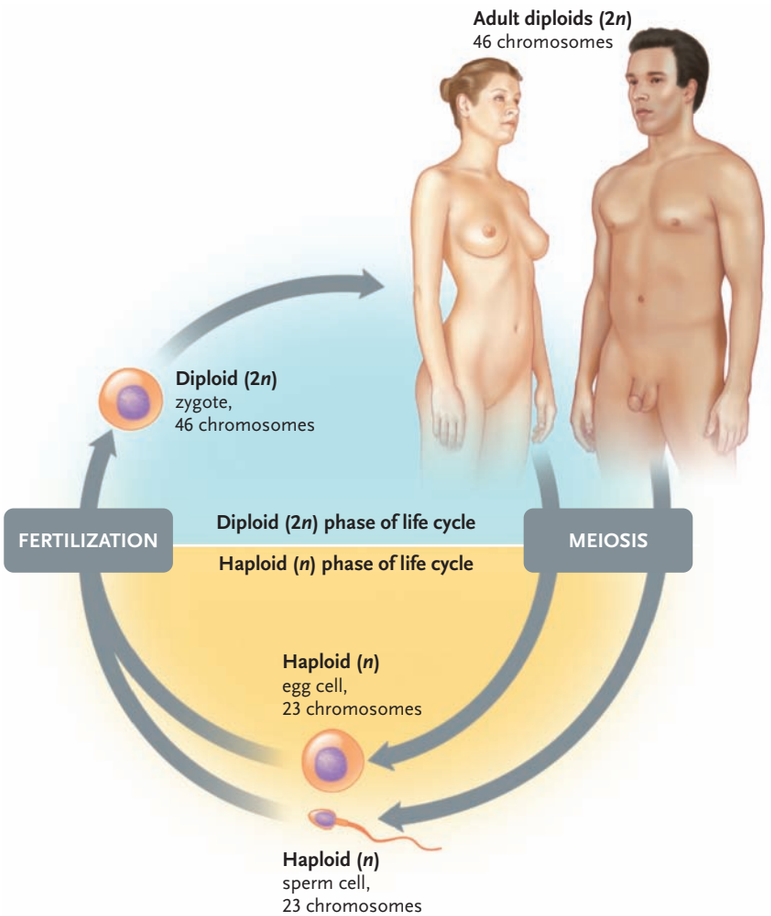


Figure 11.1
The cycle of meiosis and fertilization. Meiosis reduces the chromosome number from the diploid level of two representatives of each chromosome to the haploid level of one representative of each chromosome. Fertilization restores the chromosome number to the diploid level.

11.1 The Mechanisms of Meiosis

Meiosis occurs only in eukaryotes that reproduce sexually and only in organisms that are at least diploid—that is, organisms that have at least two representatives of each chromosome.

Meiosis Is Based on the Interactions and Distribution of Homologous Chromosome Pairs

To follow the steps of meiosis, you must understand clearly the significance of the chromosome pairs in diploid organisms. As discussed in Section 10.1, the two representatives of each chromosome in a diploid cell constitute a *homologous pair*—they have the same genes, arranged in the same order in the DNA of the chromosomes. One chromosome of each homologous pair, the **paternal chromosome**, is derived from the male parent of the organism, and the other chromosome, the **maternal chromosome**, is derived from its female parent.

Although the two chromosomes of a homologous pair contain the same genes, arranged in the same order, different versions of the genes, called **alleles**, may be present in either member of the pair. The alleles of a gene have different DNA sequences and encode distinct versions of the same protein, which may have different structures, different biochemistry, or both.

For example, humans normally have 46 chromosomes in their cells, which make up 23 homologous pairs (see Figure 10.7). However, each individual (except for identical twins, identical triplets, and so forth) has a unique combination of the alleles in the two chromosomes of each homologous pair. The distinct set of alleles, arising from the mixing mechanisms of meiosis and fertilization, gives each individual his or her unique combination of inherited traits, including such attributes

as height, hair and eye color, susceptibility to certain diseases, and even aspects of personality and intelligence.

Meiosis separates the homologous pairs, thereby reducing the diploid or 2*n* number of chromosomes to the **haploid** or *n* number **(Figure 11.1).** Each gamete produced by meiosis receives only one member of each homologous pair. For example, a human egg or sperm cell contains 23 chromosomes, one of each pair. When the egg and sperm combine in sexual reproduction to produce the zygote—the first cell of the new individual—the diploid number of 46 chromosomes (23 pairs) is regenerated. The processes of DNA replication and mitotic cell division ensure that this diploid number is maintained in the body cells as the zygote develops.

The Meiotic Cell Cycle Produces Four Genetically Different Daughter Cells with Half the Parental Number of Chromosomes

Meiosis is a two-part (**meiosis I** and **meiosis II**) process of cell division in sexually reproducing organisms. In meiosis, the duplicated chromosomes in the parental cell are distributed to four daughter cells, each of which, therefore, has half the number chromosomes as does the parental cell. By contrast, in mitosis, each chromosome duplication is followed by a division. Consequently, the chromosome number remains constant from one cell generation to the next.

The meiotic cell cycle begins with a premeiotic interphase in which DNA replicates and the chromosomal proteins are duplicated. (This interphase passes through G_1, S, and G_2 stages as does a premitotic interphase.) As in a premitotic interphase, the two resulting copies are the identical *sister chromatids* of each chromosome **(Figure 11.2).** Following premeiotic interphase, cells enter the two meiotic divisions, meiosis I and meiosis II. Homologous chromosomes pair during meiosis I and undergo an exchange of chromosome segments; this process is called *recombination*. The homologous chromosomes separate after recombination as the cell continues through the first division. Completion of meiosis I produces two cells, each with the haploid number of chromosomes, with each chromosome still consisting of two chromatids. During the second meiotic division, meiosis II, the sister chromatids separate and segregate into different cells. A total of four cells, each with the haploid number of chromosomes, is the result of the two meiotic divisions.

For convenience, biologists separate each meiotic division into the same key stages as mitosis: *prophase, prometaphase, metaphase, anaphase,* and *telophase*. The stages are identified as belonging to the two divisions, meiosis I and meiosis II, by a *I* or *II,* as in *prophase I* and *prophase II*. A brief interphase called **interkinesis** separates the two meiotic divisions, *but no DNA replication occurs during interkinesis*.

Prophase I. At the beginning of prophase I, the replicated chromosomes, each consisting of two sister chromatids, begin to fold and condense into threadlike structures in the nucleus (**Figure 11.3,** step 1). The two

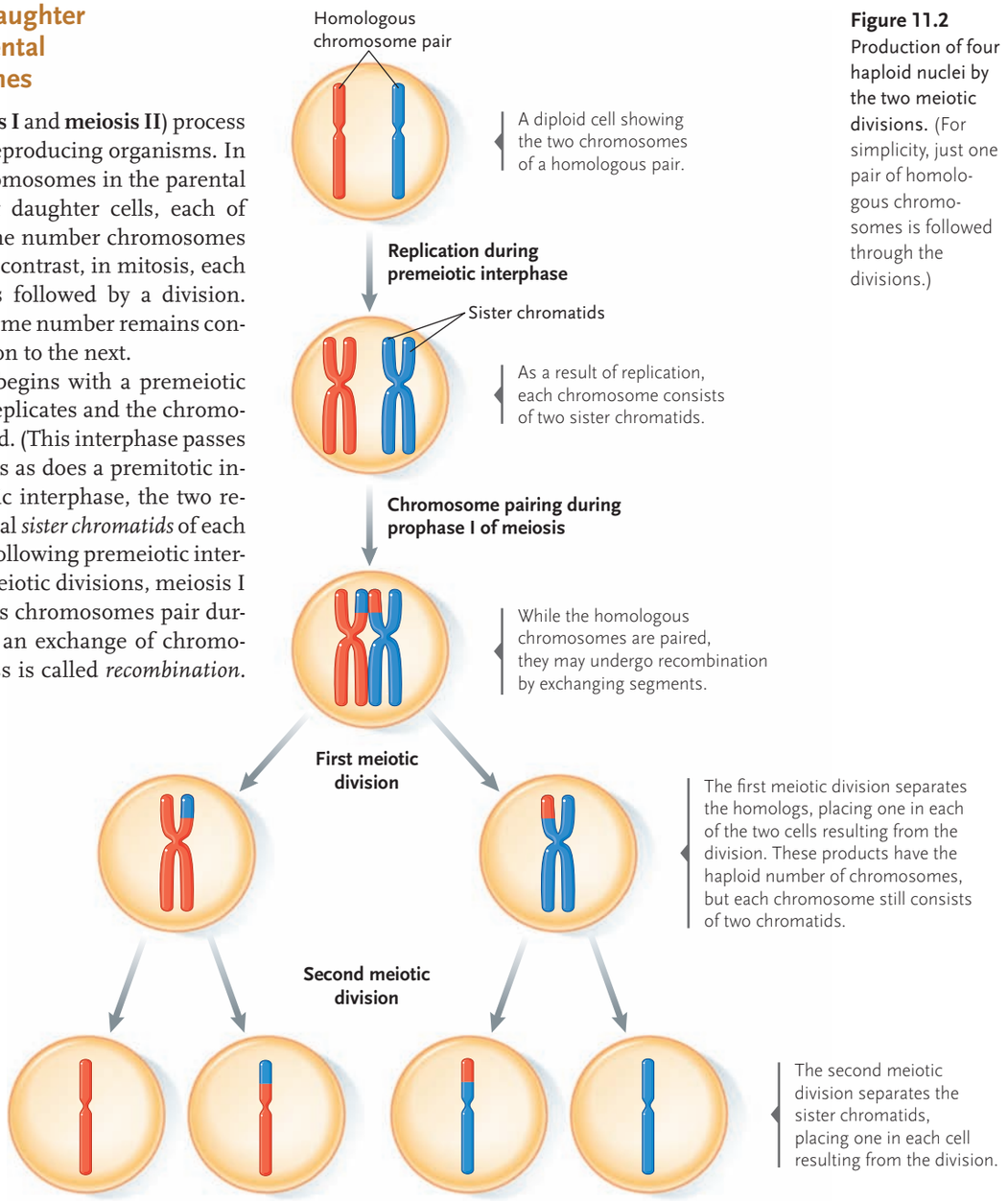


Figure 11.2 Production of four haploid nuclei by the two meiotic divisions. (For simplicity, just one pair of homologous chromosomes is followed through the divisions.)

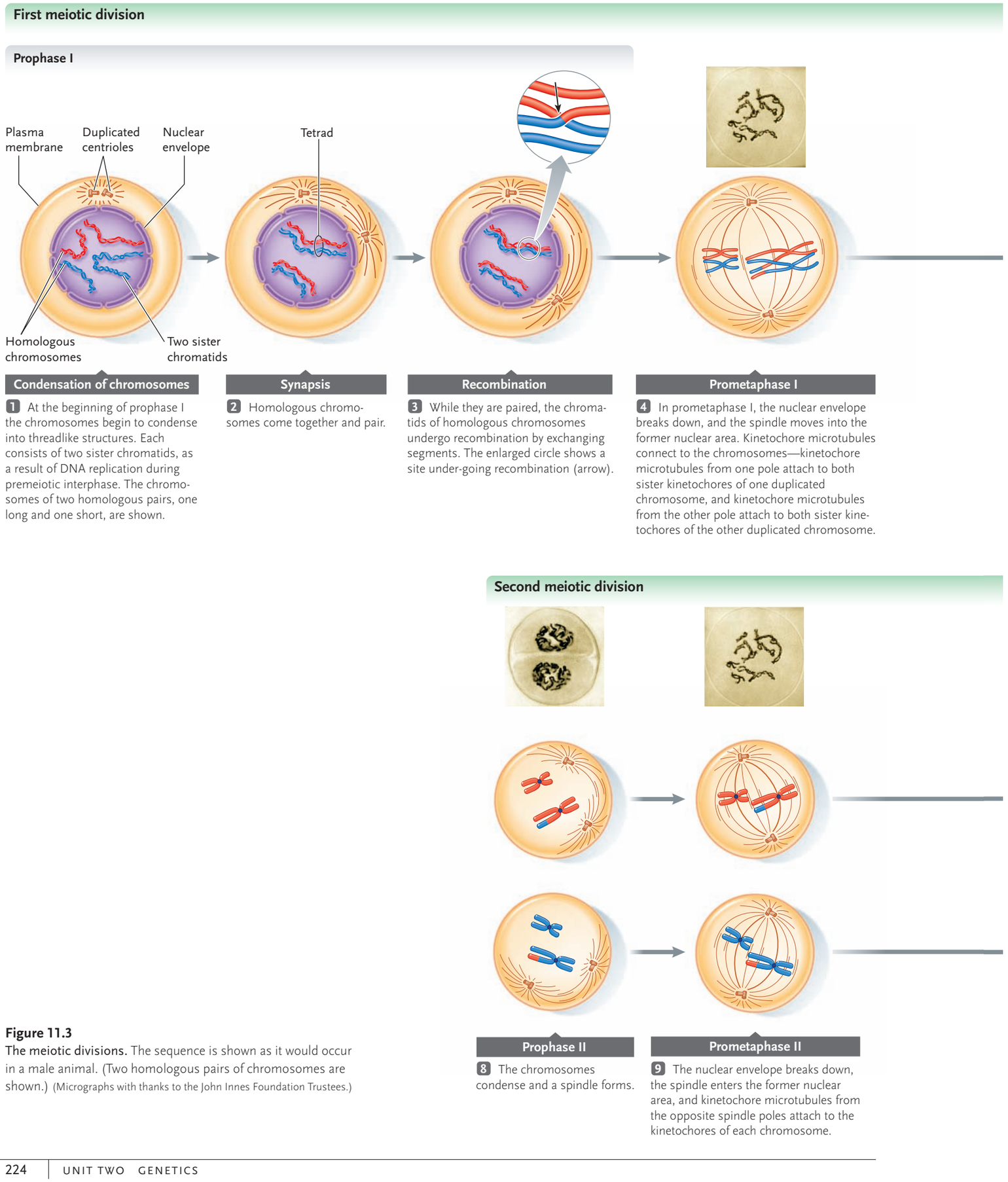
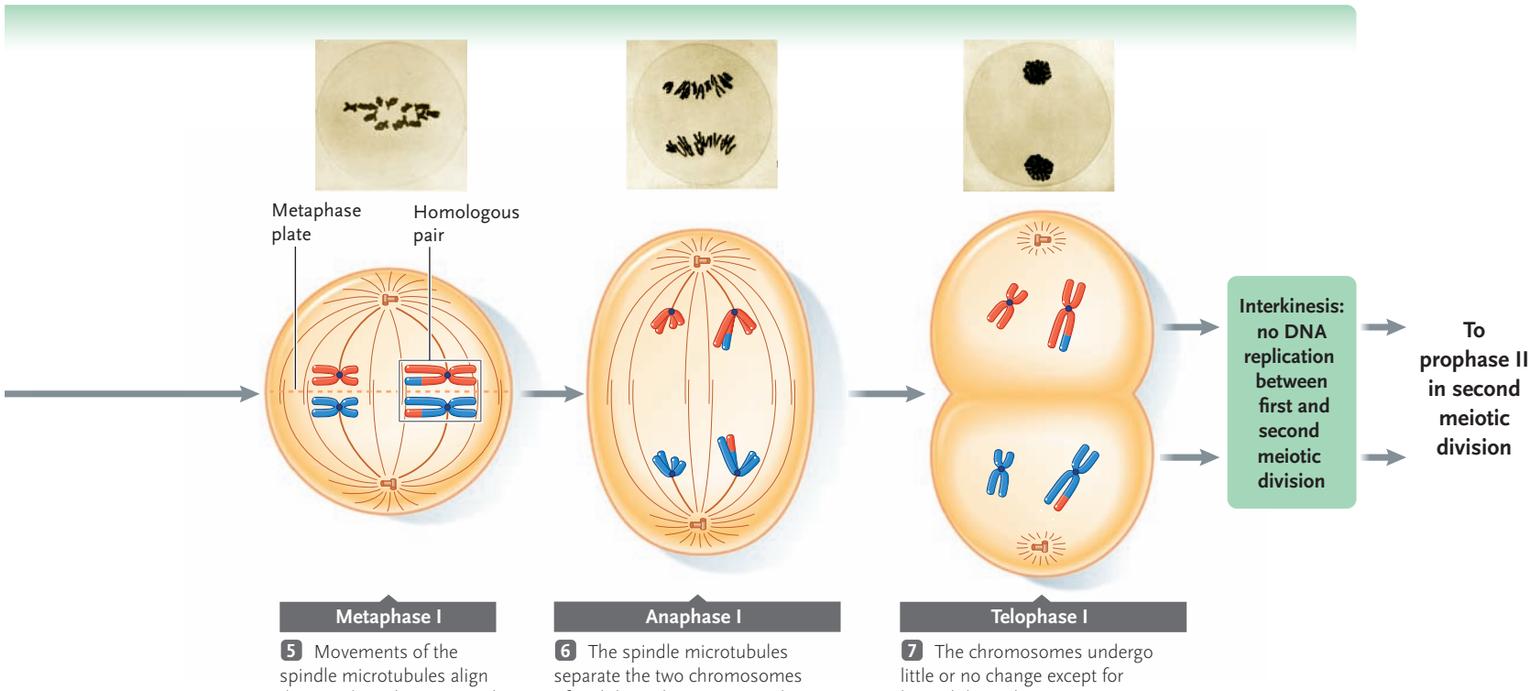


Figure 11.3
The meiotic divisions. The sequence is shown as it would occur in a male animal. (Two homologous pairs of chromosomes are shown.) (Micrographs with thanks to the John Innes Foundation Trustees.)



Metaphase I

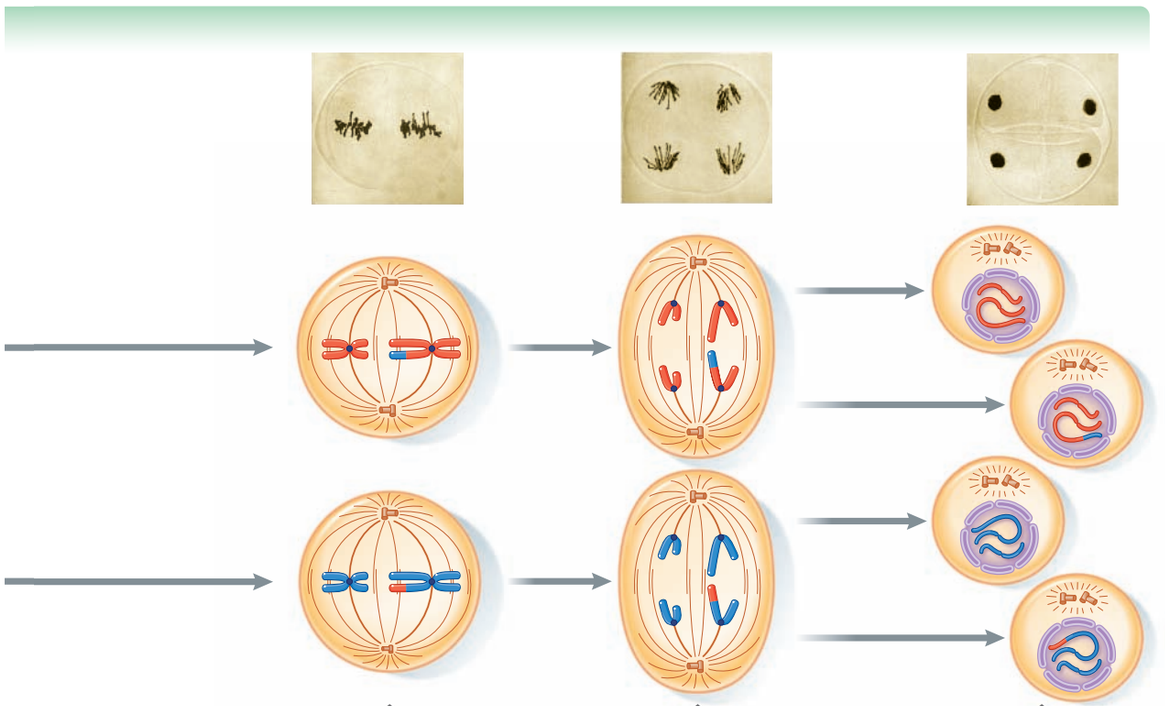
5 Movements of the spindle microtubules align the tetrads in the equatorial plane–metaphase plate–between the two spindle poles.

Anaphase I

6 The spindle microtubules separate the two chromosomes of each homologous pair and move them to opposite spindle poles. The poles now contain the haploid number of chromosomes. However, each chromosome at the poles still contains two chromatids.

Telophase I

7 The chromosomes undergo little or no change except for limited decondensation or unfolding in some species. The spindle of the first meiotic division disassembles, and two new spindles form for the second division.



Metaphase II

10 Movements of the spindle microtubules align the chromosomes on the metaphase plate.

Anaphase II

11 The spindle microtubules separate the two chromatids of each chromosome and deliver them to opposite spindle poles.

Telophase II

12 The chromosomes begin decondensing, the spindles disassemble, and new nuclear envelopes form.

Insights from the Molecular Revolution

Fertile Fields in the Human Y Chromosome

Part of the human Y chromosome contains active genes and pairs with homologous regions of the X chromosome during meiosis. The remainder of the Y, which does not pair with the X, was once thought to be an inert region containing no functional genes. However, researchers have identified several genes in this region. One gene is *SRY,* which governs formation of the testes in developing male embryos. Other genes include a recently discovered cluster of eight "housekeeping" genes—that is, genes that encode proteins with basic functions, such as protein synthesis, that occur in all cells. Housekeeping genes are well known on the X chromosome and other, nonsex chromosomes, but it was a surprise to find them in the nonpairing region of the Y.

This unexpected discovery led two investigators at the Massachusetts Institute of Technology, Bruce T. Lahn and David C. Page, to question whether other genes might be in the nonpairing region of the Y. One clue that more genes might exist there is that deletions in this region often lead to infertility and testicular tumors in male individuals, suggesting that the Y chromosome contains sequences that are vital to male fertility.

To focus on possible unknown genes, Lahn and Page first used genetic analysis techniques to eliminate noncoding regions of the Y chromosome, which do not contain genes, as well as genes that were already known. A small set of chromosome fragments potentially containing previously unidentified genes remained. Molecular analysis of these fragments showed the presence of 12 genes, all of which are in the nonpairing region of the Y. Lahn and Page used a computer program to compare the amino acid sequences encoded by the 12 genes with data banks of known protein sequences. The comparison showed that five of the genes are housekeeping genes—for example, one gene encodes a ribosomal protein. Each of these five genes is also on the X chromosome.

The proteins encoded in the seven remaining genes showed no clear relationships to any known proteins. However, most of them contain combinations of amino acids that are characteristic of proteins that bind to DNA or RNA sequences or to chromatin (the DNA-protein fibers of chromosomes). These characteristics suggest that the proteins encoded in these genes may regulate genes or stabilize DNA, RNA, or chromatin; thus, that they may have a role in the developmental processes that produce viable sperm cells.

Lahn and Page's research shows that regions of the Y chromosome once thought to be genetic wastelands actually contain functional genes, including some that may be required for normal male fertility. Identification of the functions of these genes may lead to treatments for male infertility resulting from defects in their functions.

chromosomes of each homologous pair then come together and line up side-by-side in a zipperlike way; this process is called **pairing** or **synapsis** (step 2). The fully paired homologs are called **tetrads,** referring to the fact that each homologous pair consists of four chromatids. No equivalent of chromosome pairing exists in mitosis.

While they are paired, the chromatids of homologous chromosomes physically exchange segments (step 3). This physical exchange, called **recombination,** is the step that mixes the alleles of the homologous chromosomes into new combinations and contributes to the generation of variability in sexual reproduction (see later in this chapter for details of the recombination mechanism).

As prophase I finishes, a spindle forms in the cytoplasm by the same basic mechanisms described in Section 10.3.

Prometaphase I. In prometaphase I, the nuclear envelope breaks down and the spindle enters the former nuclear area (Figure 11.3, step 4). The two chromosomes of each pair attach to kinetochore microtubules leading to opposite spindle poles. That is, both sister chromatids of one homolog attach to microtubules leading to one spindle pole, whereas both sister chromatids of the other homolog attach to microtubules leading to the opposite pole.

Metaphase I and Anaphase I. At metaphase I, movements of the spindle microtubules have aligned the tetrads on the equatorial plane—the *metaphase plate*—between the two spindle poles (Figure 11.3, step 5). Then, the two chromosomes of each homologous pair separate and move to opposite spindle poles as the spindle microtubules contract during anaphase I (step 6). The movement segregates homologous pairs, delivering a haploid set of chromosomes to each pole of the spindle. However, all the chromosomes at the poles are still double structures composed of two sister chromatids.

Rarely, chromosome segregation fails. For example, both chromosomes of a homologous pair may connect to the same spindle pole in anaphase I. In the resulting **nondisjunction,** as it is called, the spindle fails to separate the homologous chromosomes of the tetrad. As a result, one pole receives both chromosomes of the homologous pair, whereas the other pole has no copies of that chromosome. Zygotes that receive an extra chromosome because of nondisjunction have three copies of one chromosome instead of two. In humans, most zygotes of this kind do not result in live births. One exception is Down syndrome, which results from three copies of chromosome 21 instead of the normal two copies. Down syndrome involves characteristic alterations in body and facial structure, mental retardation,

and significantly reduced fertility (see Chapter 13 for a more detailed discussion of Down syndrome.)

Telophase I and Interkinesis. Telophase I is a brief, transitory stage in which there is little or no change in the chromosomes (Figure 11.3, step 7). New nuclear envelopes form in some species but not in others. Telophase I is followed by an interkinesis in which the single spindle of the first meiotic division disassembles and the microtubules reassemble into two new spindles for the second division.

Prophase II, Prometaphase II, and Metaphase II. The second meiotic division, meiosis II, is similar to a mitotic division. During prophase II, the chromosomes condense and a spindle forms (Figure 11.3, step 8). During prometaphase II, the nuclear envelope breaks down, the spindle enters the former nuclear area, and spindle microtubules leading to opposite spindle poles attach to the two kinetochores of each chromosome (step 9). At metaphase II, movements of the spindle microtubules have aligned the chromosomes on the metaphase plate (step 10).

Anaphase II and Telophase II. Anaphase II begins as the spindles separate the two chromatids of each chromosome and pull them to opposite spindle poles (Figure 11.3, step 11). At the completion of anaphase II, the chromatids—now called chromosomes—have been segregated to the two poles. During telophase II, the chromatids decondense to the extended interphase state, the spindles disassemble, and new nuclear envelopes form around the masses of chromatin (step 12). The result is four haploid cells, each with a nucleus containing half the number of chromosomes present in a G_1 nucleus of the same species.

Sex Chromosomes in Meiosis. In many eukaryotes, including most animals, one or more pairs of chromosomes, called the **sex chromosomes,** are different in male and female individuals of the same species. For example, in humans, the cells of females contain a pair of sex chromosomes called the *XX* pair (the sex chromosomes are visible in Figure 10.7). Male humans contain a pair of sex chromosomes that consist of one X chromosome and a smaller chromosome called the *Y chromosome*. The two X chromosomes in females are fully homologous, whereas the male X and Y chromosomes are homologous only through a short region. However, an X chromosome from the mother is able to pair up with either an X or a Y from the father and follow the same pathways through the meiotic divisions as the other chromosome pairs.

As a result of meiosis, a gamete formed in females may receive either member of the X pair. A gamete formed in males receives either an X or a Y chromosome. (*Insights from the Molecular Revolution* outlines studies that identify a key sex-determining gene on the mammalian Y chromosome.)

The sequence of steps in the two meiotic divisions accomplishes the major outcomes of meiosis: the generation of genetic variability and the reduction of chromosome number. (**Figure 11.4** reviews the two meiotic divisions and compares them with the single division of mitosis.)

Study Break

1. How does the outcome of meiosis differ from that of mitosis?
2. What is recombination, and in what stage of meiosis does it occur?
3. Which of the two meiotic divisions is similar to a mitotic division?

11.2 Mechanisms That Generate Genetic Variability

The generation of genetic variability is a prime evolutionary advantage of sexual reproduction. The variability increases the chance that at least some offspring will be successful in surviving and reproducing in changing environments.

The variability produced by sexual reproduction is apparent all around us, particularly in the human population. Except for identical twins (or identical triplets, identical quadruplets, and so forth), no two humans look alike, act alike, or have identical biochemical and physiological characteristics, even if they are members of the same immediate family. Other species that reproduce sexually show equivalent variability arising from meiosis.

During meiosis and fertilization, genetic variability arises from three sources: (1) recombination, (2) the differing combinations of maternal and paternal chromosomes segregated to the poles during anaphase I, and (3) the particular sets of male and female gametes that unite in fertilization. The three mechanisms, working together, produce so much total variability that no two gametes produced by the same or different individuals and no two zygotes produced by union of the gametes are likely to have the same genetic makeup. Each of these sources of variability is discussed in further detail in the following sections.

Variability Generated by Recombination Depends on Chromosome Pairing and Physical Exchanges between Homologous Chromatids

Recombination, the key genetic event of prophase I, starts when homologous chromosomes pair (**Figure 11.5,** step 1). As the homologous chromosomes pair, they are held together tightly by a protein framework

called the **synaptonemal complex (Figure 11.6).** Supported by this framework, regions of homologous chromatids exchange segments, producing new combinations of alleles (Figure 11.5, step 2). The exchange process is very precise and involves the breakage and rejoining of DNA molecules by enzymes. Each recombination event involves two of the four chromatids; the other two chromatids are not involved. When meiosis is completed, each of the four nuclei produced by the meiotic divisions receives one of the four chromatids (Figure 11.5, step 3); two receive unchanged chromatids, and two receive chromatids that have new combinations of alleles due to recombination. When the exchange is complete toward the end of prophase I, the synaptonemal complex disassembles and disappears.

The sites where recombination occurs can be seen later in prophase I, when increased condensation of the chromosomes thickens the chromosomes enough to make them visible under the light microscope (see Figure 11.3, steps 3 and 4). The sites, called **crossovers** or **chiasmata** (singular, *chiasma* = crosspiece), clearly show that two of the four chromatids have exchanged segments. Because of the shape produced, the recombination process is also called **crossing over.**

Recombination takes place largely at random, at almost any position along the chromosome arms, between any two of the four chromatids of a homologous pair. One or more additional recombination events may occur in the same chromosome pair and involve the same or different chromatids exchanging segments in the first event. In most species, recombination occurs at two or three sites in each set of paired chromosomes.

Random Segregation of Maternal and Paternal Chromosomes Is the Second Major Source of Genetic Variability in Meiosis

Random segregation of chromosomes of maternal and paternal origin accounts for the second major source of genetic variability in meiosis. Recall that metaphase I is the stage of meiosis in which the homologous pairs of chromosomes attach to the spindle poles. The maternal and paternal chromosomes of each pair typically carry different alleles of many of the genes on that chromosome. For each homologous pair, one chromosome makes spindle connections leading to one pole and the other chromosome connects to the opposite pole. In making these connections, all the maternal chromosomes may connect to one pole and all the paternal chromosomes may connect to the opposite pole. Or, as is most likely, any random combination of connections between these possibilities may be made. As a result, any combination of chromosomes of maternal and paternal origin may be segregated to the spindle poles **(Figure 11.7).** The second meiotic division segregates these random combinations of chromosomes to gamete nuclei.

The number of possible combinations depends on the number of chromosome pairs in a species. For example, the 23 chromosome pairs of humans allow 2^{23} different combinations of maternal and paternal chromosomes to be delivered to the poles, producing potentially 8,388,608 genetically different gametes from this source of variability alone.

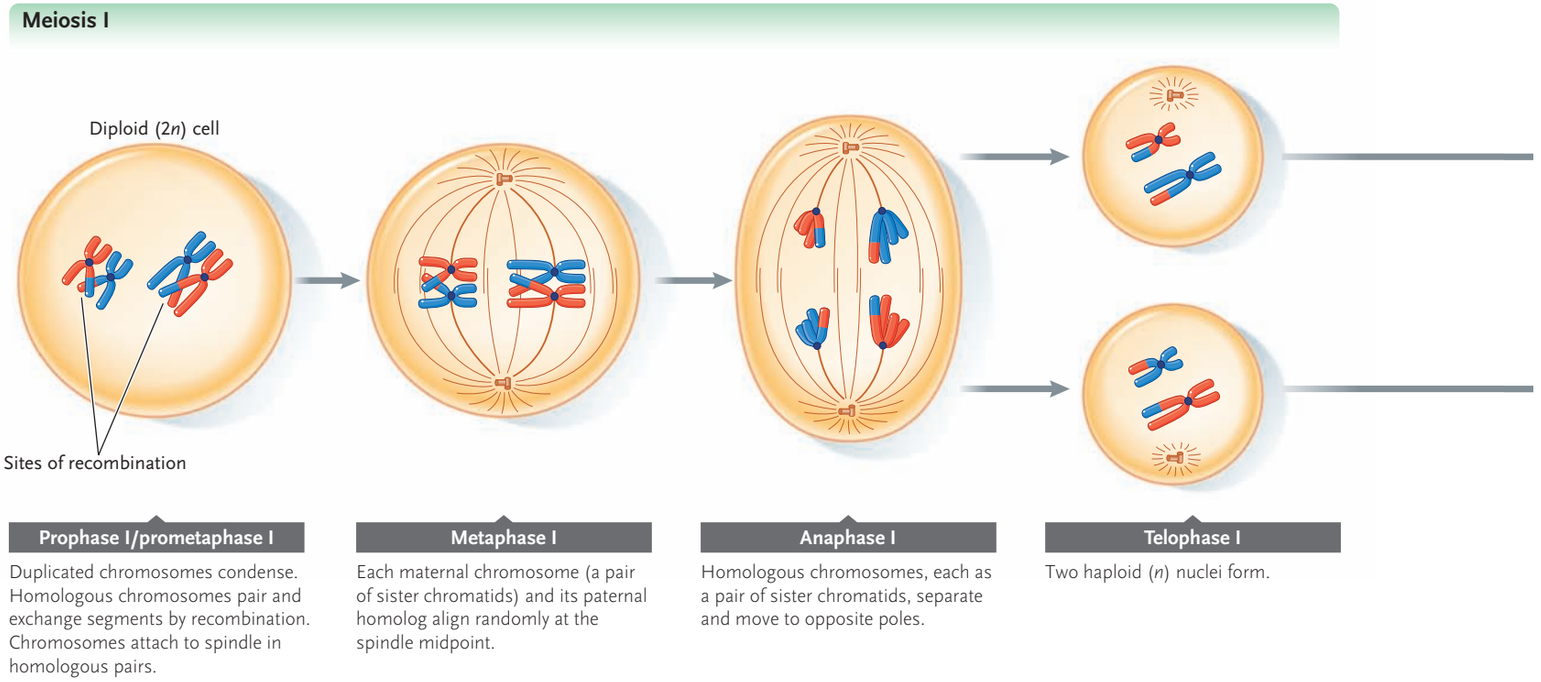
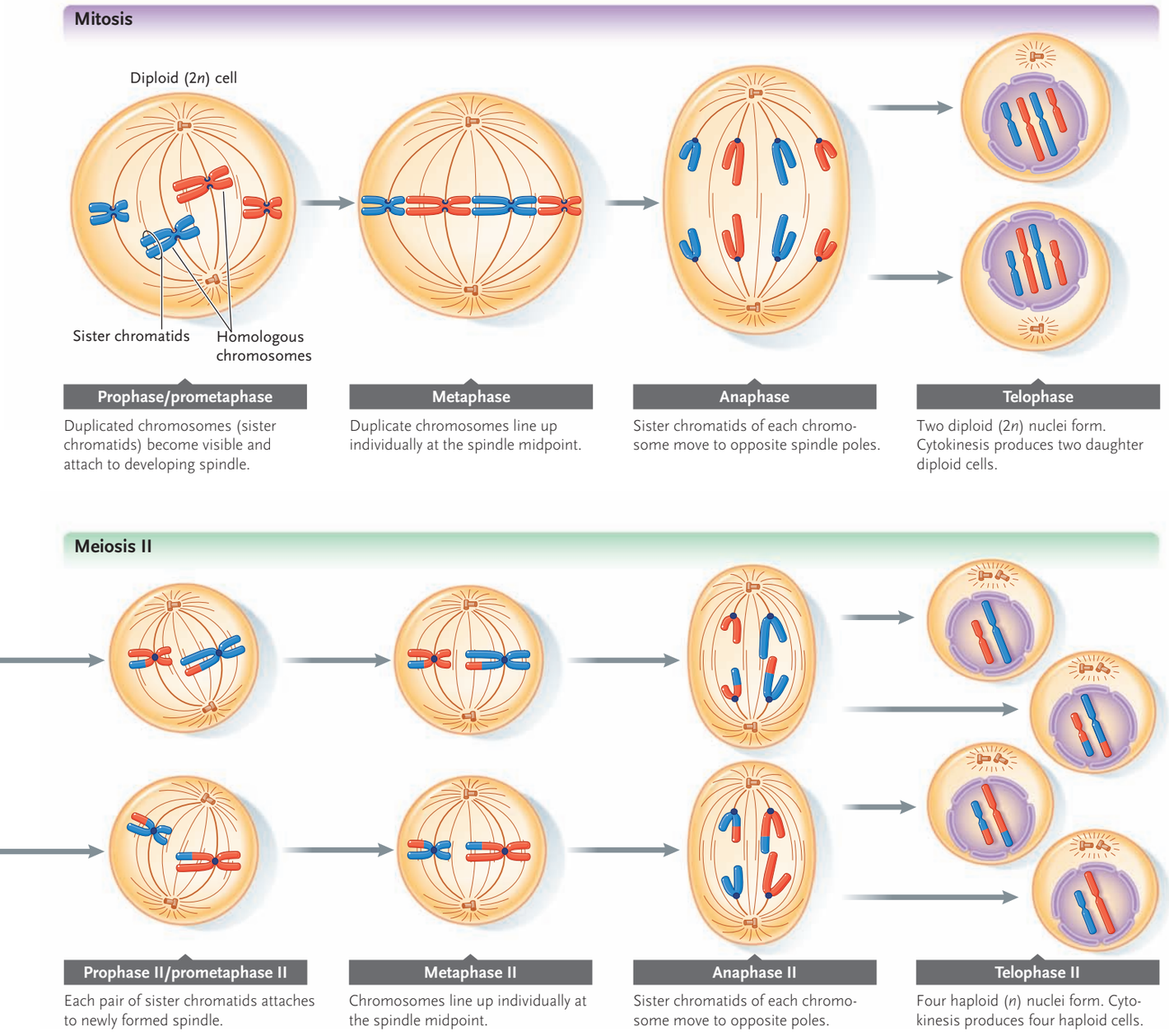


Figure 11.4
Comparison of key steps in meiosis and mitosis. Both diagrams use an animal cell as an example. Maternal chromosomes are shown in red; paternal chromosomes are shown in blue.

Random Joining of Male and Female Gametes in Fertilization Adds Additional Variability

The male and female gametes produced by meiosis are genetically diverse. Which two gametes join in fertilization is a matter of chance. This chance union of gametes amplifies the variability of sexual reproduction. Considering just the variability from random separation of homologous chromosomes and that from fertilization, the possibility that two children of the same parents could receive the same combination of maternal and paternal chromosomes is 1 chance out of $(2^{23})^2$ or 1 in 70,368,744,000,000 (~70 trillion), a number that far exceeds the number of people in the entire human population. The further variability introduced by recombination makes it practically impossible for humans and most other sexually reproducing organisms to produce genetically identical gametes or offspring. The only exception is identical twins (or identical triplets, identical quadruplets, and so forth), which arise not from the combination of identical gametes during fertilization but from mitotic division of a single fertilized egg into separate cells that give rise to genetically identical individuals.



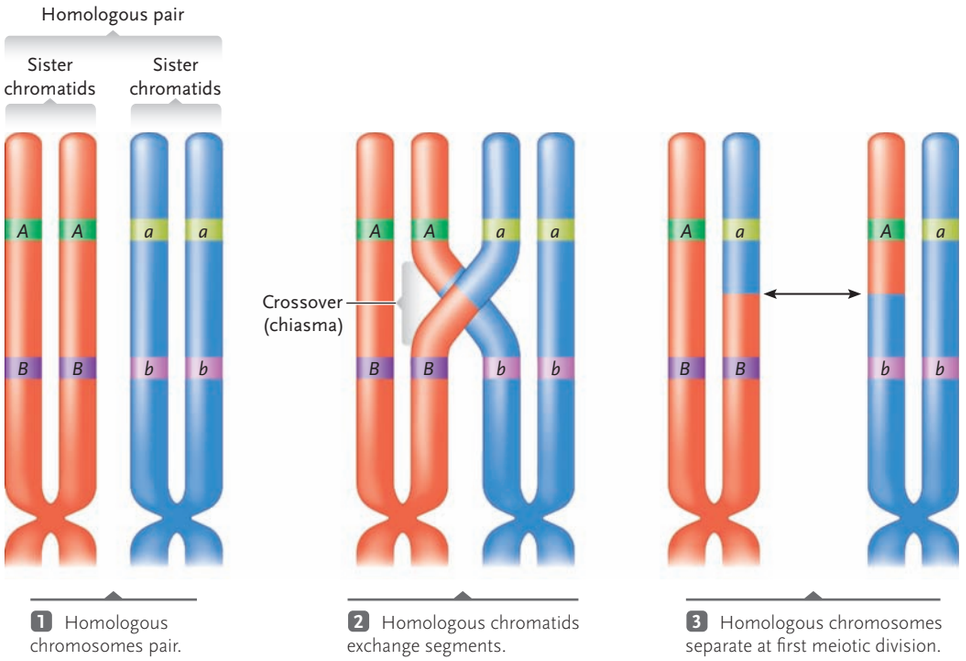


Figure 11.5
Effects of the exchanges between chromatids that accomplish genetic recombination. The letters indicate two alleles, *A* and *a*, of one gene, and two alleles, *B* and *b*, of another gene. The parents have these alleles in the combinations *A-B* and *a-b;* as a result of the recombination, two of the chromatids—the recombinants—have the new combinations *a-B* and *A-b*.

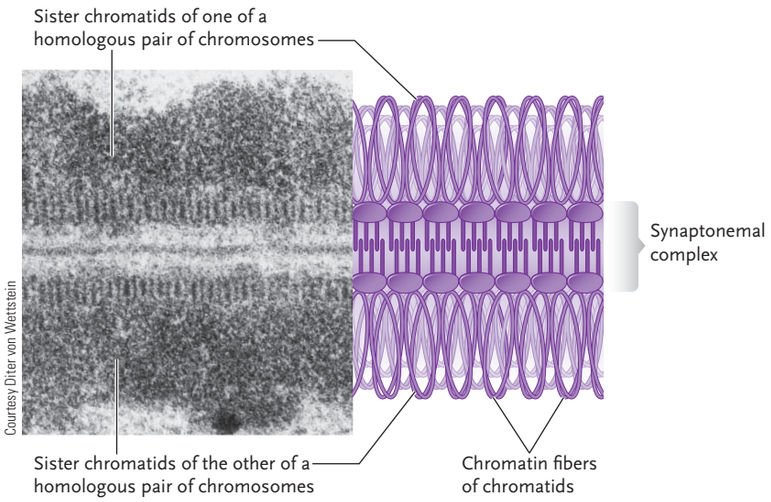


Figure 11.6
The synaptonemal complex as seen in a meiotic cell of the fungus *Neotiella*. The relationship of the complex to the chromatin fibers of the paired chromosomes is shown.

Study Break

1. What are the three ways in which sexual reproduction generates genetic variability?
2. Consider an animal with six pairs of chromosomes; one set of six chromosomes is from this animal's male parent, and the homologous set of six chromosomes is from this animal's female parent. When this animal produces gametes, what proportion of these gametes will have chromosomes, all of which originate from the animal's female parent?

11.3 The Time and Place of Meiosis in Organismal Life Cycles

The time and place at which meiosis occurs follows one of three major patterns in the life cycles of eukaryotes **(Figure 11.8).** The differences reflect the portions of the life cycle spent in the haploid and diploid phases and whether mitotic divisions intervene between meiosis and the formation of gametes.

In Animals, the Diploid Phase Is Dominant, the Haploid Phase Is Reduced, and Meiosis Is Followed Directly by Gamete Formation

Animals follow the pattern (see Figure 11.8a) in which the diploid phase dominates the life cycle, the haploid phase is reduced, and meiosis is followed directly by gamete formation. In male animals, each of the four nuclei produced by meiosis is enclosed in a separate cell by cytoplasmic divisions, and each of the four cells differentiates into a functional sperm cell. In female animals, only one of the four nuclei becomes functional as an egg cell nucleus.

Fertilization restores the diploid phase of the life cycle. Thus, animals are haploids only as sperm or eggs, and no mitotic divisions occur during the haploid phase of the life cycle.

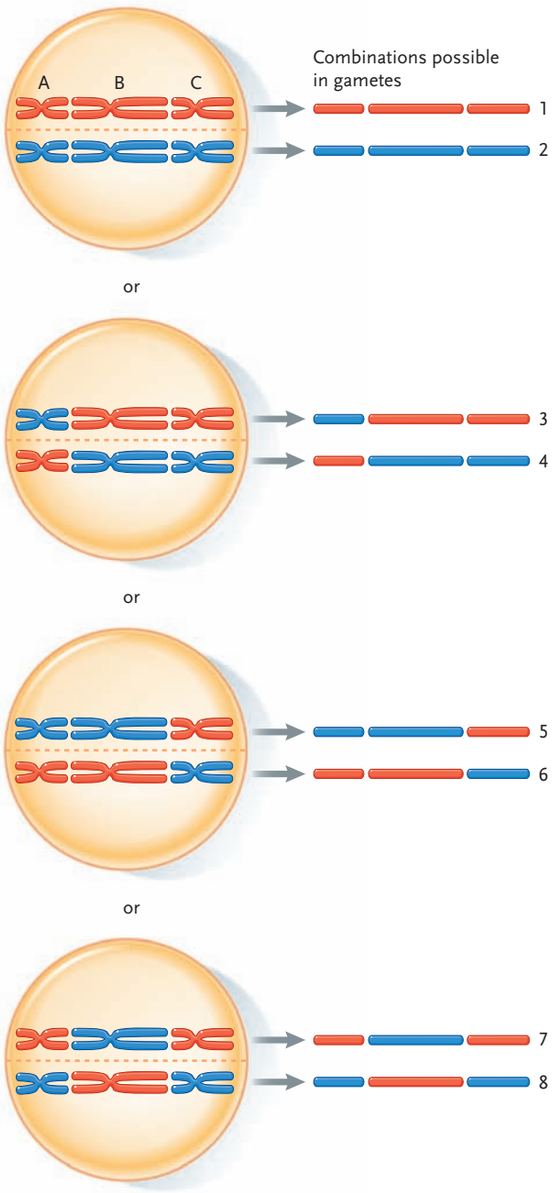


Figure 11.7
Possible outcomes of the random spindle connections of three pairs of chromosomes at metaphase I of meiosis. The three types of chromosomes are labeled A, B, and C. Maternal chromosomes are red; paternal chromosomes are blue. There are four possible patterns of connections, giving eight possible combinations of maternal and paternal chromosomes in gametes (labeled 1–8).

In Most Plants and Fungi, Generations Alternate between Haploid and Diploid Phases That Are Both Multicellular

Most plants and some algae and fungi follow the life cycle pattern shown in Figure 11.8b. These organisms alternate between haploid and diploid generations in which, depending on the organism, either generation may dominate the life cycle, and mitotic divisions oc-

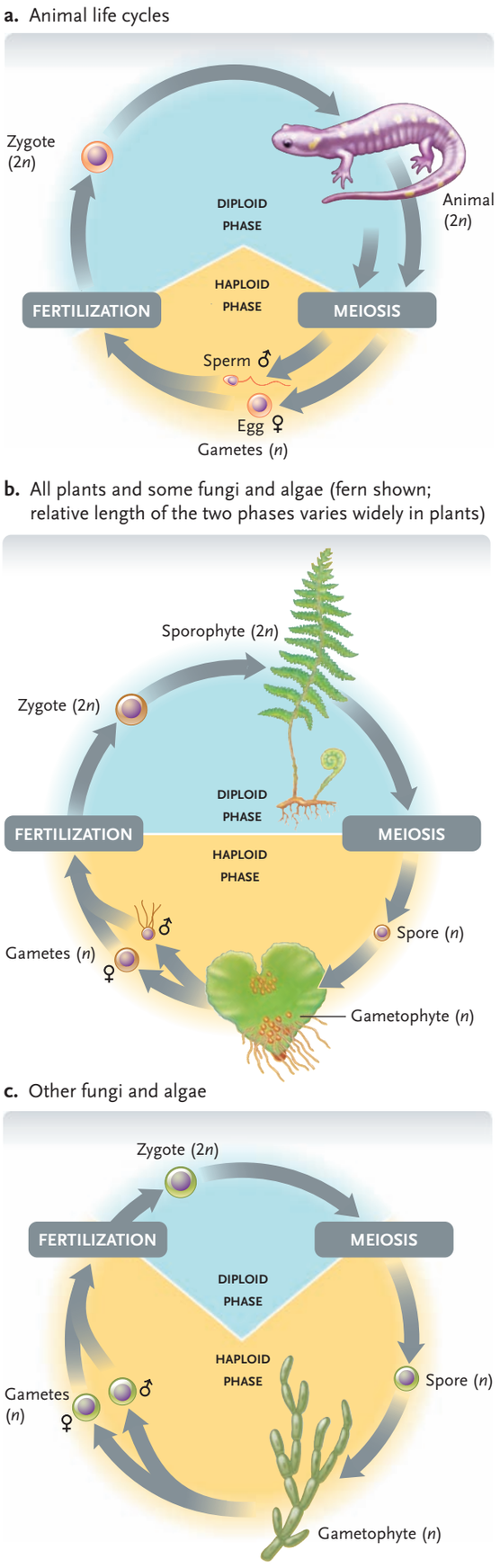


Figure 11.8
Variations in the time and place of meiosis in eukaryotes. The diploid phase of the life cycles is shaded in green; the haploid phase is shaded in yellow. n = haploid number of chromosomes; $2n$ = diploid number. **(a)** Meiosis in animal life cycles. **(b)** Meiosis in most plants and some fungi and algae. **(c)** Meiosis in other fungi and algae.

cur in both phases. In these organisms, fertilization produces the diploid generation, in which the individuals are called **sporophytes** (*spora* = seed; *phyta* = plant). After the sporophytes grow to maturity by mitotic divisions, some of their cells undergo meiosis, producing haploid, genetically different, reproductive cells called **spores.** The spores are not gametes; they germinate and grow directly by mitotic divisions into a generation of haploid individuals called **gametophytes** (*gameta* = gamete). At maturity, the nuclei of some cells in gametophytes develop into egg or sperm nuclei. All the egg or sperm nuclei produced by a particular gametophyte are genetically identical because they arise through mitosis; meiosis does not occur in gametophytes. Fusion of a haploid egg and sperm nucleus produces a diploid zygote nucleus that divides by mitosis to produce the diploid sporophyte generation again.

In many plants, including most bushes, shrubs, trees, and flowers, the diploid sporophyte generation is the most visible part of the plant. The gametophyte generation is reduced to an almost microscopic stage that develops in the reproductive parts of the sporophytes—in flowering plants, in the structures of the flower. The female gametophyte remains in the flower; the male gametophyte is released from flowers as microscopic pollen grains. When pollen contacts a flower of the same species, it releases a haploid nucleus that fertilizes a haploid egg cell of a female gametophyte in the flower. The resulting cell reproduces by mitosis to form a sporophyte.

In Some Fungi and Other Organisms, the Haploid Phase Is Dominant and the Diploid Phase Is Reduced to a Single Cell

The life cycle of some fungi and algae follows the third life cycle pattern (see Figure 11.8c). In these organisms, the diploid phase is limited to a single cell, the zygote, produced by fertilization. Immediately after fertilization, the diploid zygote undergoes meiosis to produce the haploid phase. Mitotic divisions occur only in the haploid phase.

During fertilization, two haploid gametes, usually designated simply as positive (+) or negative (−) because they are similar in structure, fuse to form a diploid nucleus. This nucleus immediately enters meiosis, producing four haploid cells. These cells develop directly or after one or more mitotic divisions into haploid spores. These spores germinate to produce haploid individuals, the gametophytes, which grow or in-

Unanswered Questions

The overall mechanism and outcomes of meiosis have been known for a long time, since the turn of the twentieth century. However, despite the fundamental importance of meiosis in sexual reproduction, the biochemical, genetic, and molecular mechanisms of meiosis are poorly understood. For example, how do homologous chromosomes recognize their appropriate pairing partners? How do they become aligned in a configuration that allows the formation of crossovers? How is the number of crossover events regulated to ensure that each chromosome pair will have a crossover? Developing a deeper understanding of the molecular mechanisms that regulate meiosis is highly important in human biology, because mis-segregation of chromosomes during meiosis I is a major cause of birth defects and the leading cause of miscarriages.

What molecular interactions initiate the chromosome pairing process, and what forces bring the chromosomes together?

Before pairing begins in prophase I, the chromosomes of homologous pairs are separated widely in the nucleus. During pairing, the chromosomes move together. What molecular interactions initiate the pairing process, and what forces bring the chromosomes together? Abby Dernburg at Lawrence Berkeley National Laboratory and her collaborators are studying these questions using as a model organism, the nematode *Caenorhabditis elegans.* She and her colleagues have found that there are regions called pairing centers near one end of each chromosome. During meiosis, the pairing centers stabilize a previously unrecognized intermediate in the pairing process, and they promote synapsis. However, intermediates can form, even when two chromosomes are not a perfect match and do not recombine. Their working model to explain this occurrence is that the pairing centers hold a pair of chromosomes together long enough for the quality of the molecular match to be assessed, and those with a good match then proceed to synapsis. How the molecular match is assessed is unknown and is the subject of current investigations. The researchers are also searching for and characterizing specific genes that are involved in pairing center function.

What are the genetic and molecular controls of meiosis?

Many unanswered questions surround the regulatory controls that switch cells from mitosis and that control the many individual steps of the division process. Both the yeast *Saccaromyces cerevisiae* and the fruit fly, *Drosophila melanogaster,* have been used widely in this research. Researchers have discovered a large number of mutant genes—well over a hundred in the two species combined—with effects in meiosis. Many of the genes identified are related to genes in humans. Many questions surround the control and operation of these genes and the identity and functions of the proteins they encode. For instance, Michael Lichten at the National Cancer Institute, National Institutes of Health, is using yeast in a project to describe the molecular steps of meiotic recombination from start to finish, including the chromosomal structure changes that occur when homologous chromosomes pair and recombine. For example, one of Lichten's research projects is using genomics scale techniques to study gene expression changes related to chromosomal structure during meiosis. That is, he is surveying all the genes in the genome to determine which ones increase or decrease gene expression during chromosome condensation, recombination, and segregation during meiosis.

Peter J. Russell

crease in number by mitotic divisions. Eventually positive and negative gametes are formed in these individuals by differentiation of some of the cells produced by the mitotic divisions. Because the gametes are produced by mitosis, all the gametes of an individual are genetically identical.

In this chapter, we have seen that meiosis has three outcomes that are vital to sexual reproduction. Meiosis reduces the chromosomes to the haploid number so that the chromosome number does not double at fertilization. Through recombination and random separation of maternal and paternal chromosomes, meiosis produces genetic variability in gametes; further variability is provided by the random combination of gametes in fertilization. The next chapter shows how the outcomes of meiosis and fertilization underlie the inheritance of traits in sexually reproducing organisms.

Study Break

How does the place of meiosis differ in the life cycles of animals and most plants?

Review

Go to ThomsonNOW™ at www.thomsonedu.com/login to access quizzing, animations, exercises, articles, and personalized homework help.

11.1 The Mechanisms of Meiosis

- The major cellular processes that underlie sexual reproduction are the halving of chromosome number by meiosis and restoration of the number by fertilization. Meiosis and fertilization also produce new combinations of genetic information (Figure 11.1).
- Meiosis occurs only in eukaryotes that reproduce sexually and only in organisms that are at least diploid—that is, organisms that have at least two representatives of each chromosome.
- DNA replicates and the chromosomal proteins are duplicated during the premeiotic interphase, producing two copies, the sister chromatids, of each chromosome.
- During prophase I of the first meiotic division (meiosis I), the replicated chromosomes condense and come together and pair. While they are paired, the chromatids of homologous chromosomes undergo recombination by exchanging segments. While these events are in progress, the spindle forms in the cytoplasm (Figures 11.2 and 11.3).
- During prometaphase I, the nuclear envelope breaks down, the spindle enters the former nuclear area, and kinetochore microtubules leading to opposite spindle poles attach to one kinetochore of each pair of sister chromatids of homologous chromosomes (Figure 11.3).
- At metaphase I, spindle microtubule movements have aligned the tetrads on the metaphase plate, the equatorial plane between the two spindle poles. The connections of kinetochore microtubules to opposite poles ensure that the homologous pairs separate and move to opposite spindle poles during anaphase I, reducing the chromosome number to the haploid value. Each chromosome at the poles still contains two chromatids.
- Telophase I and interkinesis are brief and transitory stages; no DNA replication occurs during interkinesis. During these stages, the single spindle of the first meiotic division disassembles and the microtubules reassemble into two new spindles for the second division.
- During prophase II, the chromosomes condense and a spindle forms. During prometaphase II, the nuclear envelope breaks down, the spindle enters the former nuclear area, and spindle microtubules leading to opposite spindle poles attach to the two kinetochores of each chromosome. At metaphase II, the chromosomes become aligned on the metaphase plate. The connections of kinetochore microtubules to opposite spindle poles ensure that during anaphase II, the chromatids of each chromosome are separated and segregate to those opposite spindle poles.
- During telophase II, the chromosomes decondense to their extended interphase state, the spindles disassemble, and new nuclear envelopes form. The result is four haploid cells, each containing half the number of chromosomes present in a G_1 nucleus of the same species.

Animation: Gamete-producing organs

Animation: Meiosis step-by-step

Animation: Meiosis I and II

Animation: Comparing mitosis and meiosis

11.2 Mechanisms That Generate Variability

- Recombination is the first source of the genetic variability produced by meiosis (Figures 11.5 and 11.6). During recombination, chromatids generate new combinations of alleles by physically exchanging segments. The exchange process involves precise breakage and joining of DNA molecules. It is catalyzed by enzymes and occurs while the homologous chromosomes are held together tightly by the synaptonemal complex.
- The crossovers visible between the chromosomes at late prophase I reflect the exchange of chromatid segments that occurred during the molecular steps of genetic recombination.
- The random segregation of homologous chromosomes is the second source of genetic variability produced by meiosis. The homologous pairs separate at anaphase I of meiosis, segregating random combinations of maternal and paternal chromosomes to the spindle poles (Figure 11.7).
- Random joining of male and female gametes in fertilization is the third source of genetic variability.

Animation: Crossing over

Animation: Random alignment

11.3 Time and Place of Meiosis in Organismal Life Cycles

- The time and place of meiosis follow one of three major pathways in the life cycles of eukaryotes, which reflect the portions of the life cycle spent in the haploid and diploid phases and whether mitotic divisions intervene between meiosis and the formation of gametes (Figure 11.8).
- In animals, the diploid phase dominates the life cycle; mitotic divisions occur only in this phase. Meiosis in the diploid phase gives rise to products that develop directly into egg and sperm cells without undergoing mitosis (Figure 11.8a).
- In most plants and fungi, the life cycle alternates between haploid and diploid generations that both grow by mitotic divisions. Fertilization produces the diploid sporophyte generation; after growth by mitotic divisions, some cells of the sporophyte un-

dergo meiosis and produce haploid spores. The spores germinate and grow by mitotic divisions into the gametophyte generation. After growth of the gametophyte, cells develop directly into egg or sperm nuclei, which fuse in fertilization to produce the diploid sporophyte generation again (Figure 11.8b).

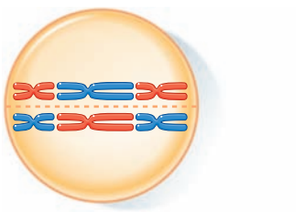
- In some fungi and protists, meiosis occurs immediately after fertilization, producing a haploid phase, which dominates the life cycle; mitosis occurs only in the haploid phase. At some point in the life cycle, haploid cells differentiate directly into gametes, which fuse together as pairs to produce the brief diploid phase (Figure 11.8c).

Animation: Generalized life cycles

Questions

Self-Test Questions

1. The diploid number of this individual is 6.



This figure represents:
   a. mitotic metaphase.
   b. meiotic metaphase I.
   c. meiotic metaphase II.
   d. a gamete.
   e. six nonhomologous chromosomes.

2. Which of the following is *not* associated with meiosis?
   a. daughter cells identical to the parent cell
   b. variety in resulting cells
   c. chromosome number halved in resulting cells
   d. four daughter cells arising from one parent cell
   e. 23 chromosomes in the human egg or sperm

3. Chiasmata:
   a. form during metaphase II of meiosis.
   b. occur between two nonhomologous chromosomes.
   c. represent chromosomes independently assorting.
   d. are sites of DNA exchange between homologous chromatids.
   e. ensure the resulting cells are identical to the parent cell.

4. If $2n$ is four, the number of possible combinations in the resulting gametes is:
   a. 1. b. 2. c. 4. d. 8. e. 16.

5. The number of human chromosomes in a cell in prophase I of meiosis is ___ and in telophase II is ___.
   a. 92; 46
   b. 46; 23
   c. 23; 23
   d. 23; 16
   e. 4; 2

6. In meiosis:
   a. homologous chromosomes pair up at prophase II.
   b. chromosomes separate from their homologous partners at anaphase I.
   c. the centromeres split at anaphase I.
   d. a female gamete has two X chromosomes.
   e. reduction of chromosome number occurs in meiosis II.

7. The DNA content in a diploid cell in G_2 is X. If that cell goes into meiosis at its metaphase II, the DNA content would be:
   a. 0.1X. b. 0.5X. c. X. d. 2X. e. 4X.

8. Metaphase in mitosis is similar to what stage in meiosis?
   a. prophase I
   b. prophase II
   c. metaphase I
   d. metaphase II
   e. crossing over

9. In the human gamete:
   a. there must be one chromosome of each type, except for the sex chromosomes, where both an X and a Y chromosome are present.
   b. a chromosome must be represented from each parent.
   c. there must be an unequal mixture of chromosomes from both parents.
   d. there must be representation of chromosomes from only one parent.
   e. there is the possibility of 2^{46} different combinations of maternal and paternal chromosomes.

10. In plants, the adult diploid individuals are called:
   a. spores.
   b. sporophytes.
   c. gametes.
   d. gametophytes.
   e. zygotes.

Questions for Discussion

1. You have a technique that allows you to measure the amount of DNA in a cell nucleus. You establish the amount of DNA in a sperm cell of an organism as your baseline. Which multiple of this amount would you expect to find in a nucleus of this organism at G_2 of premeiotic interphase? At telophase I of meiosis? During interkinesis? At telophase II of meiosis?
2. One of the human chromosome pairs carries a gene that influences eye color. In an individual human, one chromosome of this pair has an allele of this gene that contributes to the formation of blue eyes. The other chromosome of the pair has an allele that contributes to brown eye color (other genes also influence eye color in humans). After meiosis in the cells of this individual, what fraction of the nuclei will carry the allele that contributes to blue eyes? To brown eyes?
3. Mutations are changes in DNA sequence that can create new alleles. In which cells of an individual, somatic or meiotic cells, would mutations be of greatest significance to that individual? What about to the species to which the individual belongs?

Experimental Analysis

Design experiments to determine whether a new pesticide on the market adversely affects egg production and fertilization in frogs.

Evolution Link

Explain aspects of the processes of mitosis and meiosis that would lead you to conclude that they are evolutionarily related processes. Do you think that mitosis evolved from meiosis, or did the opposite occur? Explain your conclusion.

How Would You Vote?

Japanese researchers have successfully created a "fatherless" mouse that contains the genetic material from the eggs of two females. The mouse is healthy and fully fertile. Do you think researchers should be allowed to try the same process with human eggs? Go to www.thomsonedu.com/login to investigate both sides of the issue and then vote.