

12

Sexual Reproduction and Meiosis

Concept Outline

12.1 Meiosis produces haploid cells from diploid cells.

Discovery of Reduction Division. Sexual reproduction does not increase chromosome number because gamete production by meiosis involves a decrease in chromosome number. Individuals produced from sexual reproduction inherit chromosomes from two parents.

12.2 Meiosis has three unique features.

Unique Features of Meiosis. Three unique features of meiosis are synapsis, homologous recombination, and reduction division.

12.3 The sequence of events during meiosis involves two nuclear divisions.

Prophase I. Homologous chromosomes pair intimately, and undergo crossing over that locks them together.

Metaphase I. Spindle microtubules align the chromosomes in the central plane of the cell.

Completing Meiosis. The second meiotic division is like a mitotic division, but has a very different outcome.

12.4 The evolutionary origin of sex is a puzzle.

Why Sex? Sex may have evolved as a mechanism to repair DNA, or perhaps as a means for contagious elements to spread. Sexual reproduction increases genetic variability by shuffling combinations of genes.

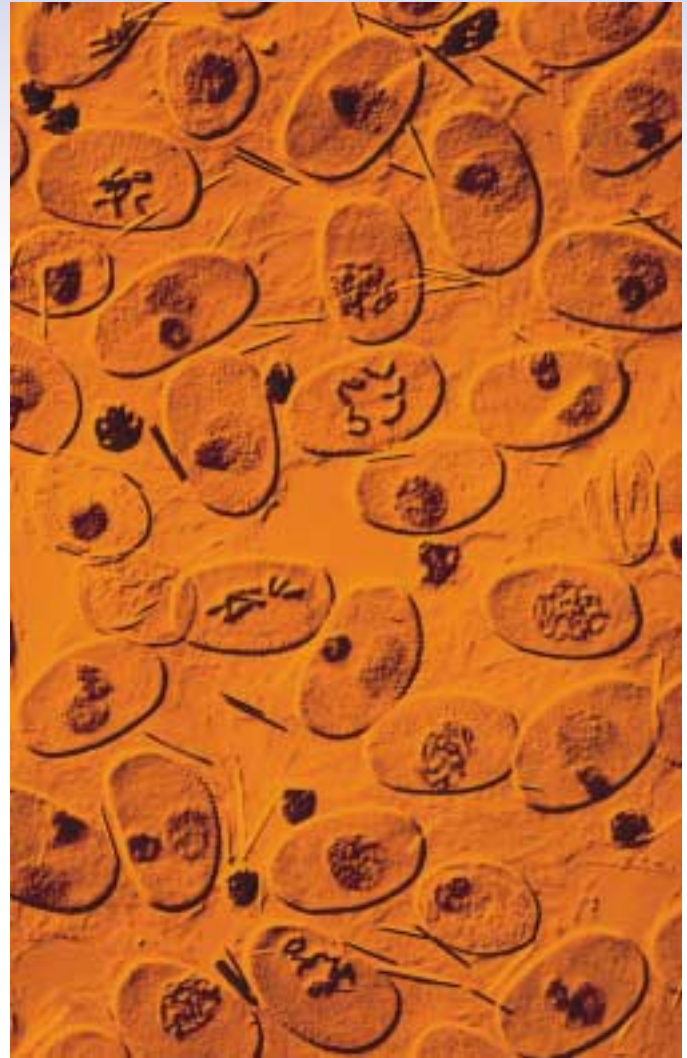


FIGURE 12.1

Plant cells undergoing meiosis (600 \times). This preparation of pollen cells of a spiderwort, *Tradescantia*, was made by freezing the cells and then fracturing them. It shows several stages of meiosis.

Most animals and plants reproduce sexually. Gametes of opposite sex unite to form a cell that, dividing repeatedly by mitosis, eventually gives rise to an adult body with some 100 trillion cells. The gametes that give rise to the initial cell are the products of a special form of cell division called meiosis (figure 12.1), the subject of this chapter. Far more intricate than mitosis, the details of meiosis are not as well understood. The basic process, however, is clear. Also clear are the profound consequences of sexual reproduction: it plays a key role in generating the tremendous genetic diversity that is the raw material of evolution.

12.1 Meiosis produces haploid cells from diploid cells.

Discovery of Reduction Division

Only a few years after Walther Fleming's discovery of chromosomes in 1882, Belgian cytologist Pierre-Joseph van Beneden was surprised to find different numbers of chromosomes in different types of cells in the roundworm *Ascaris*. Specifically, he observed that the **gametes** (eggs and sperm) each contained two chromosomes, while the **somatic** (nonreproductive) cells of embryos and mature individuals each contained four.

Fertilization

From his observations, van Beneden proposed in 1887 that an egg and a sperm, each containing half the complement of chromosomes found in other cells, fuse to produce a single cell called a **zygote**. The zygote, like all of the somatic cells ultimately derived from it, contains two copies of each chromosome. The fusion of gametes to form a new cell is called **fertilization**, or **syngamy**.

Reduction Division

It was clear even to early investigators that gamete formation must involve some mechanism that reduces the number of chromosomes to half the number found in other cells. If it did not, the chromosome number would double with each fertilization, and after only a few generations, the

number of chromosomes in each cell would become impossibly large. For example, in just 10 generations, the 46 chromosomes present in human cells would increase to over 47,000 (46×2^{10}).

The number of chromosomes does not explode in this way because of a special reduction division that occurs during gamete formation, producing cells with half the normal number of chromosomes. The subsequent fusion of two of these cells ensures a consistent chromosome number from one generation to the next. This reduction division process, known as **meiosis**, is the subject of this chapter.

The Sexual Life Cycle

Meiosis and fertilization together constitute a cycle of reproduction. Two sets of chromosomes are present in the somatic cells of adult individuals, making them **diploid** cells (Greek *diploos*, “double” + *eidos*, “form”), but only one set is present in the gametes, which are thus **haploid** (Greek *haploos*, “single” + *plion*, “vessel”). Reproduction that involves this alternation of meiosis and fertilization is called **sexual reproduction**. Its outstanding characteristic is that offspring inherit chromosomes from *two* parents (figure 12.2). You, for example, inherited 23 chromosomes from your mother, contributed by the egg fertilized at your conception, and 23 from your father, contributed by the sperm that fertilized that egg.

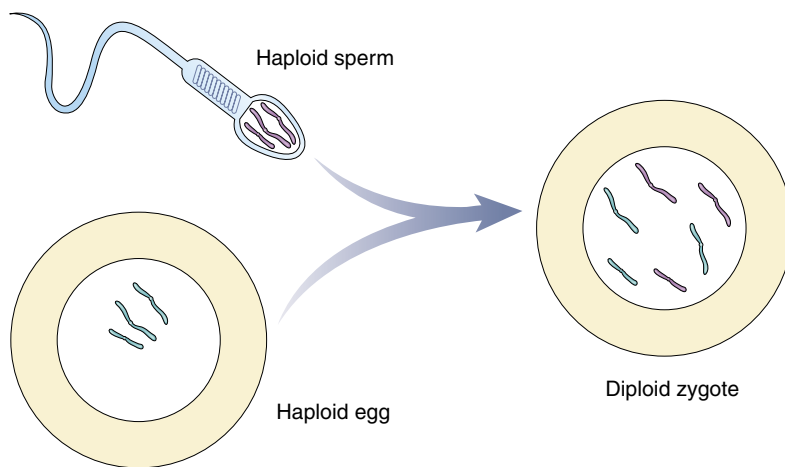


FIGURE 12.2

Diploid cells carry chromosomes from two parents. A diploid cell contains two versions of each chromosome, one contributed by the haploid egg of the mother, the other by the haploid sperm of the father.

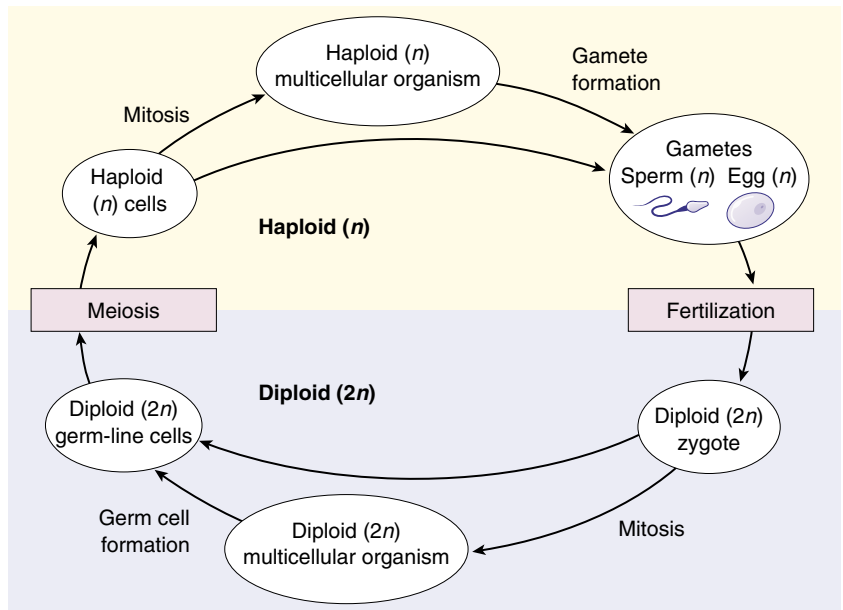


FIGURE 12.3
Alternation of generations. In sexual reproduction, haploid cells or organisms alternate with diploid cells or organisms.

Somatic Tissues. The life cycles of all sexually reproducing organisms follow the same basic pattern of alternation between the diploid and haploid chromosome numbers (figures 12.3 and 12.4). After fertilization, the resulting zygote begins to divide by mitosis. This single diploid cell eventually gives rise to all of the cells in the adult. These cells are called somatic cells, from the Latin word for “body.” Except when rare accidents occur, or in special variation-creating situations such as occur in the immune system, every one of the adult’s somatic cells is genetically identical to the zygote.

In unicellular eukaryotic organisms, including most protists, individual cells function as gametes, fusing with other gamete cells. The zygote may undergo mitosis, or it may divide immediately by meiosis to give rise to haploid individuals. In plants, the haploid cells that meiosis produces divide by mitosis, forming a multicellular haploid phase. Certain cells of this haploid phase eventually differentiate into eggs or sperm.

Germ-Line Tissues. In animals, the cells that will eventually undergo meiosis to produce gametes are set aside from somatic cells early in the course of development. These cells are often referred to as germ-line cells. Both the somatic cells and the gamete-producing germ-line cells are diploid, but while somatic cells undergo mitosis to form genetically identical, diploid daughter cells, gamete-producing germ-line cells undergo meiosis, producing haploid gametes.

Meiosis is a process of cell division in which the number of chromosomes in certain cells is halved during gamete formation. In the sexual life cycle, there is an alternation of diploid and haploid generations.

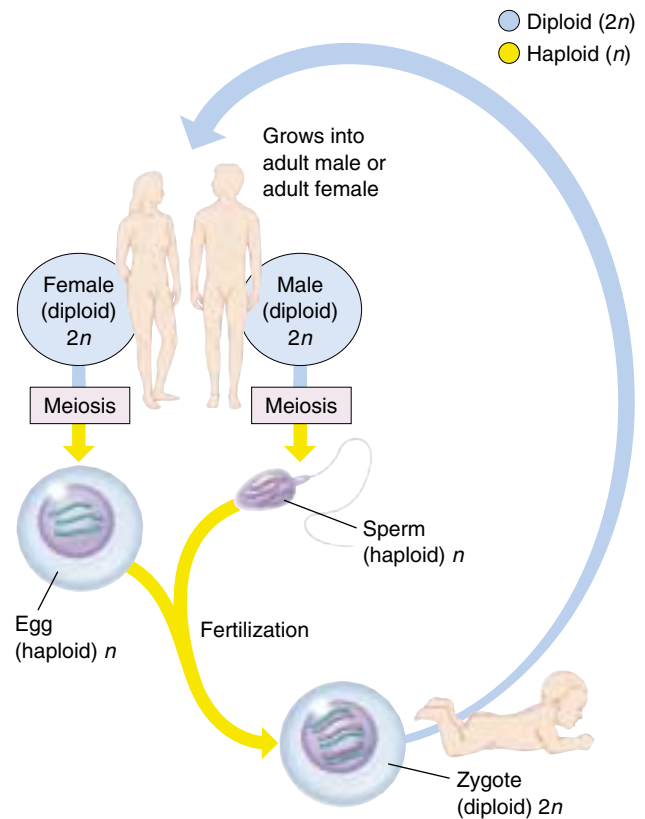


FIGURE 12.4
The sexual life cycle. In animals, the completion of meiosis is followed soon by fertilization. Thus, the vast majority of the life cycle is spent in the diploid stage.

12.2 Meiosis has three unique features.

Unique Features of Meiosis

The mechanism of cell division varies in important details in different organisms. This is particularly true of chromosomal separation mechanisms, which differ substantially in protists and fungi from the process in plants and animals that we will describe here. Meiosis in a diploid organism consists of two rounds of division, mitosis of one. Although meiosis and mitosis have much in common, meiosis has three unique features: synapsis, homologous recombination, and reduction division.

Synapsis

The first unique feature of meiosis happens early during the first nuclear division. Following chromosome replication, *homologous chromosomes*, or *homologues* (see chapter 11), *pair all along their length*. The process of forming these complexes of homologous chromosomes is called **synapsis**

Homologous Recombination

The second unique feature of meiosis is that *genetic exchange occurs between the homologous chromosomes* while they are thus physically joined (figure 12.5a). The exchange process that occurs between paired chromosomes is called **crossing over**. Chromosomes are then drawn together along the equatorial plane of the dividing cell; subsequently, homologues are pulled by microtubules toward opposite poles of the cell. When this process is complete, the cluster of chromosomes at each pole contains one of the two homologues of each chromosome. Each pole is haploid, containing half the number of chromosomes present in the original diploid cell. Sister chromatids do not separate from each other in the first nuclear division, so each homologue is still composed of two chromatids.

Reduction Division

The third unique feature of meiosis is that *the chromosomes do not replicate between the two nuclear divisions*, so that at the end of meiosis, each cell contains only half the original complement of chromosomes (figure 12.5b). In most respects, the second meiotic division is identical to a normal mitotic division. However, because of the crossing over that occurred during the first division, the sister chromatids in meiosis II are not identical to each other.

Meiosis is a continuous process, but it is most easily studied when we divide it into arbitrary stages. The stages of meiosis are traditionally called meiosis I and meiosis II. Like mitosis, each stage is subdivided further into prophase, metaphase, anaphase, and telophase (figure 12.6). In meiosis, however, prophase I is more complex than in mitosis.

In meiosis, homologous chromosomes become intimately associated and do not replicate between the two nuclear divisions.

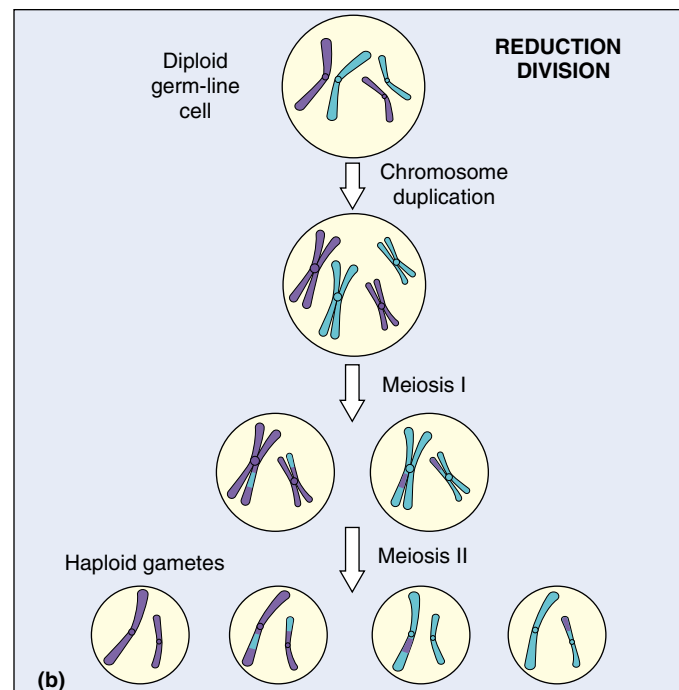
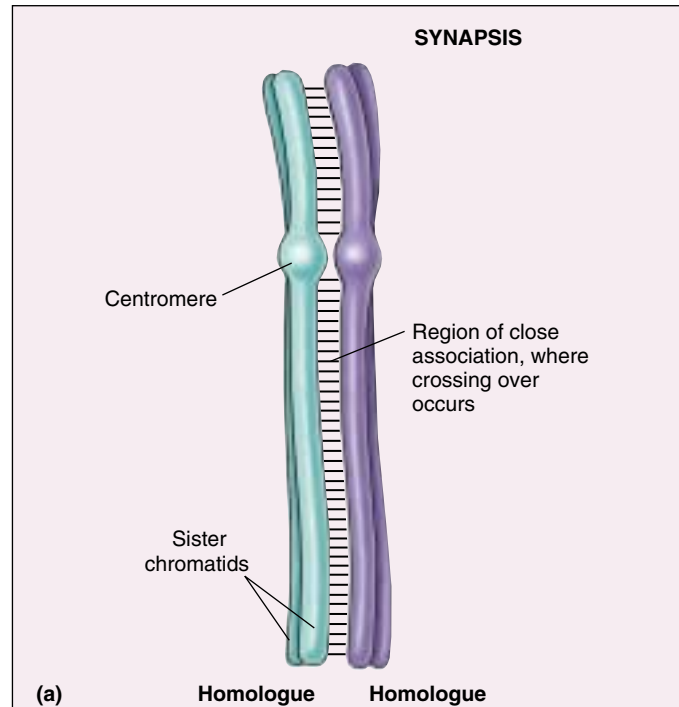


FIGURE 12.5

Unique features of meiosis. (a) Synapsis draws homologous chromosomes together, creating a situation where the two chromosomes can physically exchange parts, a process called crossing over. (b) Reduction division, by omitting a chromosome duplication before meiosis II, produces haploid gametes, thus ensuring that chromosome number remains stable during the reproduction cycle.

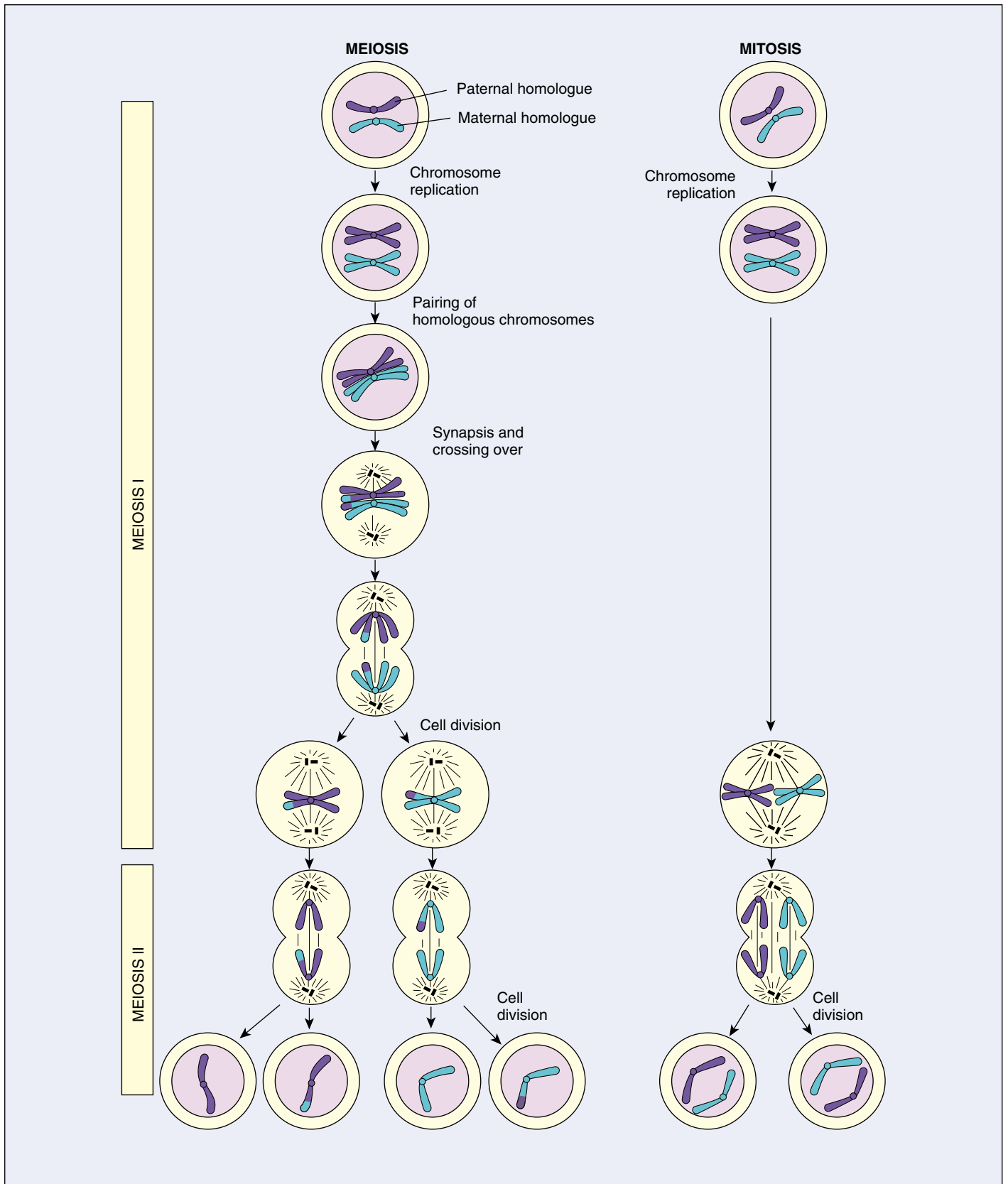


FIGURE 12.6
A comparison of meiosis and mitosis. Meiosis involves two nuclear divisions with no DNA replication between them. It thus produces four daughter cells, each with half the original number of chromosomes. Crossing over occurs in prophase I of meiosis. Mitosis involves a single nuclear division after DNA replication. It thus produces two daughter cells, each containing the original number of chromosomes.

12.3 The sequence of events during meiosis involves two nuclear divisions.

Prophase I

In prophase I of meiosis, the DNA coils tighter, and individual chromosomes first become visible under the light microscope as a matrix of fine threads. Because the DNA has already replicated before the onset of meiosis, each of these threads actually consists of two sister chromatids joined at their centromeres. In prophase I, homologous chromosomes become closely associated in synapsis, exchange segments by crossing over, and then separate.

An Overview

Prophase I is traditionally divided into five sequential stages: leptotene, zygotene, pachytene, diplotene, and diakinesis.

Leptotene. Chromosomes condense tightly.

Zygotene. A lattice of protein is laid down between the homologous chromosomes in the process of synapsis, forming a structure called a *synaptonemal complex* (figure 12.7).

Pachytene. Pachytene begins when synapsis is complete (just after the synaptonemal complex forms; figure 12.8), and lasts for days. This complex, about 100 nm across, holds the two replicated chromosomes in precise register, keeping each gene directly across from its partner on the homologous chromosome, like the teeth of a

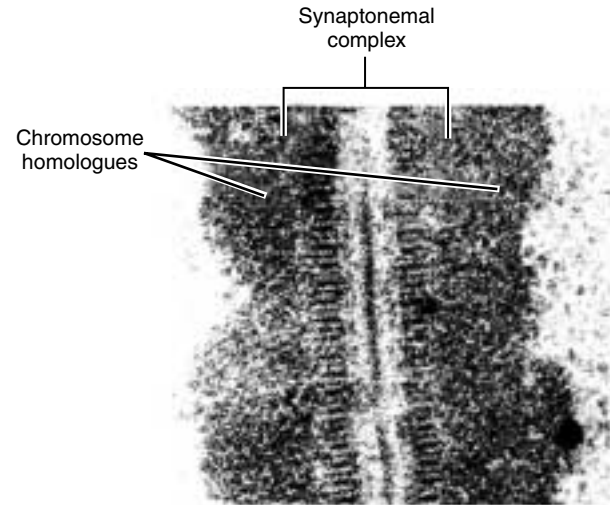


FIGURE 12.7
Structure of the synaptonemal complex. A portion of the synaptonemal complex of the ascomycete *Neotiella rutilans*, a cup fungus.

zipper. Within the synaptonemal complex, the DNA duplexes unwind at certain sites, and single strands of DNA form base-pairs with complementary strands *on the other homologue*. The synaptonemal complex thus provides the structural framework that enables crossing over between the homologous chromosomes. As you

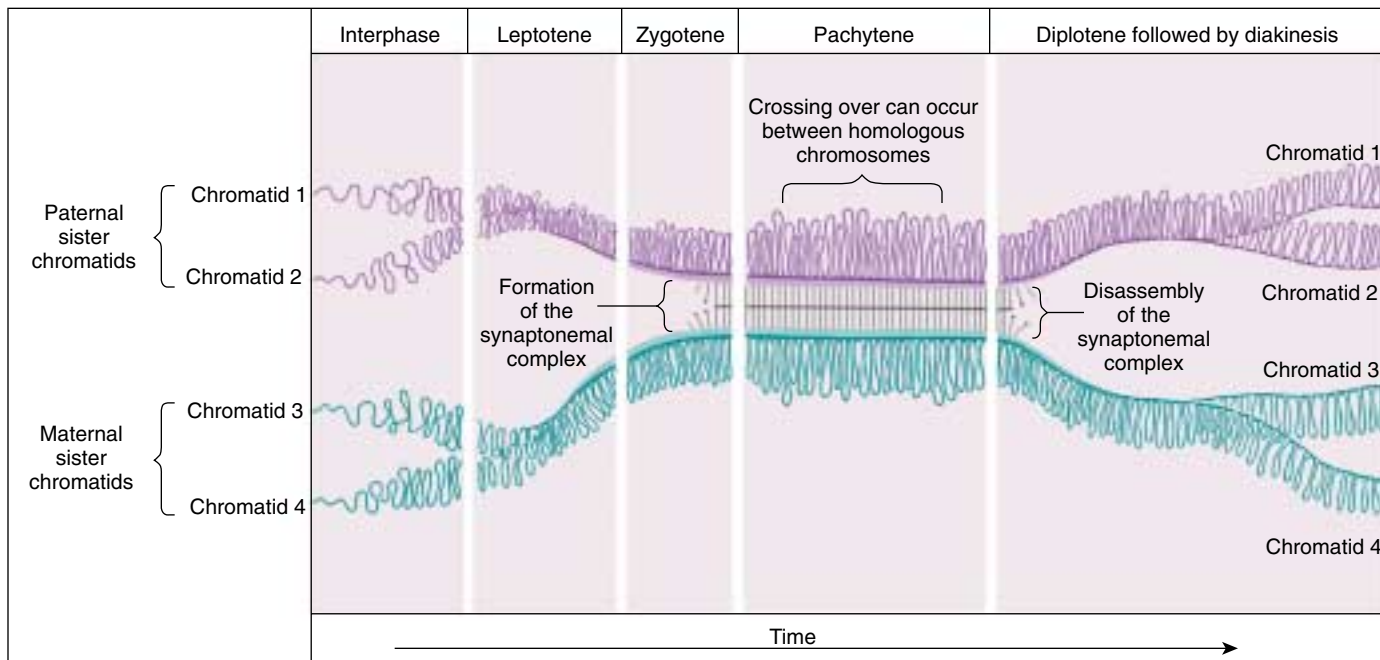


FIGURE 12.8
Time course of prophase I. The five stages of prophase I represent stages in the formation and subsequent disassembly of the synaptonemal complex, the protein lattice that holds homologous chromosomes together during synapsis.

will see, this has a key impact on how the homologues separate later in meiosis.

Diplotene. At the beginning of diplotene, the protein lattice of the synaptonemal complex disassembles. Diplotene is a period of intense cell growth. During this period the chromosomes decondense and become very active in transcription.

Diakinesis. At the beginning of diakinesis, the transition into metaphase, transcription ceases and the chromosomes recondense.



FIGURE 12.9
Chiasmata. This micrograph shows two distinct crossovers, or chiasmata.

Synapsis

During prophase, the ends of the chromatids attach to the nuclear envelope at specific sites. The sites the homologues attach to are adjacent, so that the members of each homologous pair of chromosomes are brought close together. They then line up side by side, apparently guided by heterochromatin sequences, in the process called synapsis.

Crossing Over

Within the synaptonemal complex, recombination is thought to be carried out during pachytene by very large protein assemblies called **recombination nodules**. A nodule's diameter is about 90 nm, spanning the central element of the synaptonemal complex. Spaced along the synaptonemal complex, these recombination nodules act as large multienzyme "recombination machines," each nodule bringing about a recombination event. The details of the crossing over process are not well understood, but involve a complex series of events in which DNA segments are exchanged between nonsister or sister chromatids. In humans, an average of two or three such crossover events occur per chromosome pair.

When crossing over is complete, the synaptonemal complex breaks down, and the homologous chromosomes are released from the nuclear envelope and begin to move away from each other. At this point, there are four chromatids for each type of chromosome (two homologous chromosomes, each of which consists of two sister chromatids). The four chromatids do not separate completely, however, because they are held together in two ways: (1) the two sister chromatids of each homologue, recently created by DNA replication, are held near by their common centromeres; and (2) the paired homologues are held together at the points where crossing over occurred within the synaptonemal complex.

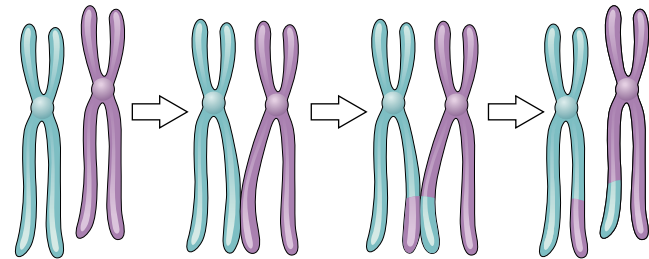


FIGURE 12.10
The results of crossing over. During crossing over, nonsister (shown above) or sister chromatids may exchange segments.

Chiasma Formation

Evidence of crossing over can often be seen under the light microscope as an X-shaped structure known as a **chiasma** (Greek, "cross"; plural, **chiasmata**; figure 12.9). The presence of a chiasma indicates that two chromatids (one from each homologue) have exchanged parts (figure 12.10). Like small rings moving down two strands of rope, the chiasmata move to the end of the chromosome arm as the homologous chromosomes separate.

Synapsis is the close pairing of homologous chromosomes that takes place early in prophase I of meiosis. Crossing over occurs between the paired DNA strands, creating the chromosomal configurations known as chiasmata. The two homologues are locked together by these exchanges and they do not disengage readily.

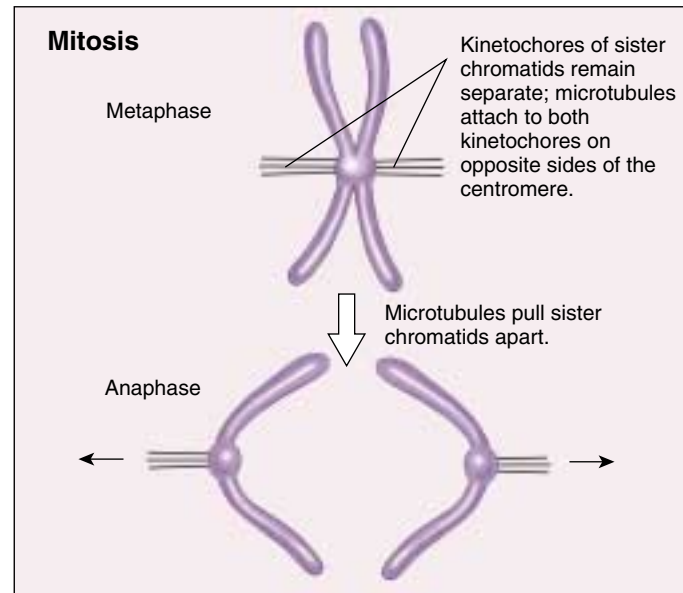
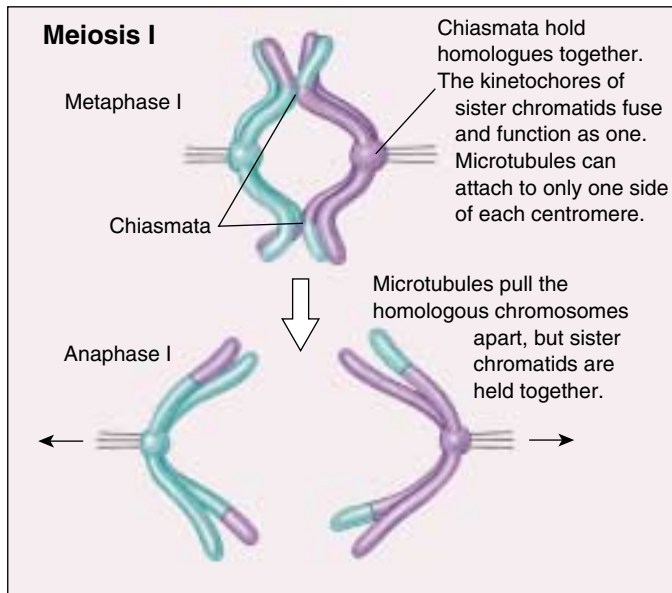


FIGURE 12.11

Chiasmata created by crossing over have a key impact on how chromosomes align in metaphase I. In the first meiotic division, the chiasmata hold one sister chromatid to the other sister chromatid; consequently, the spindle microtubules can bind to only one side of each centromere, and the homologous chromosomes are drawn to opposite poles. In mitosis, microtubules attach to *both* sides of each centromere; when the microtubules shorten, the sister chromatids are split and drawn to opposite poles.

Metaphase I

By metaphase I, the second stage of meiosis I, the nuclear envelope has dispersed and the microtubules form a spindle, just as in mitosis. During diakinesis of prophase I, the chiasmata move down the paired chromosomes from their original points of crossing over, eventually reaching the ends of the chromosomes. At this point, they are called terminal chiasmata. Terminal chiasmata hold the homologous chromosomes together in metaphase I, so that only one side of each centromere faces outward from the complex; the other side is turned inward toward the other homologue (figure 12.11). Consequently, spindle microtubules are able to attach to kinetochore proteins only on the outside of each centromere, and the centromeres of the two homologues attach to microtubules originating from opposite poles. This one-sided attachment is in marked contrast to the attachment in mitosis, when kinetochores on *both* sides of a centromere bind to microtubules.

Each joined pair of homologues then lines up on the metaphase plate. The orientation of each pair on the spindle axis is random: either the maternal or the paternal homologue may orient toward a given pole (figure 12.12). Figure 12.13 illustrates the alignment of chromosomes during metaphase I.

Chiasmata play an important role in aligning the chromosomes on the metaphase plate.

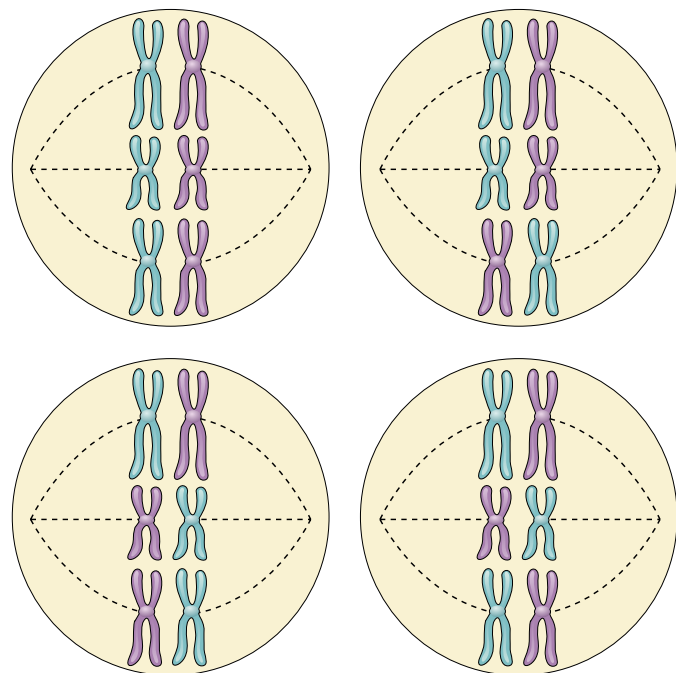
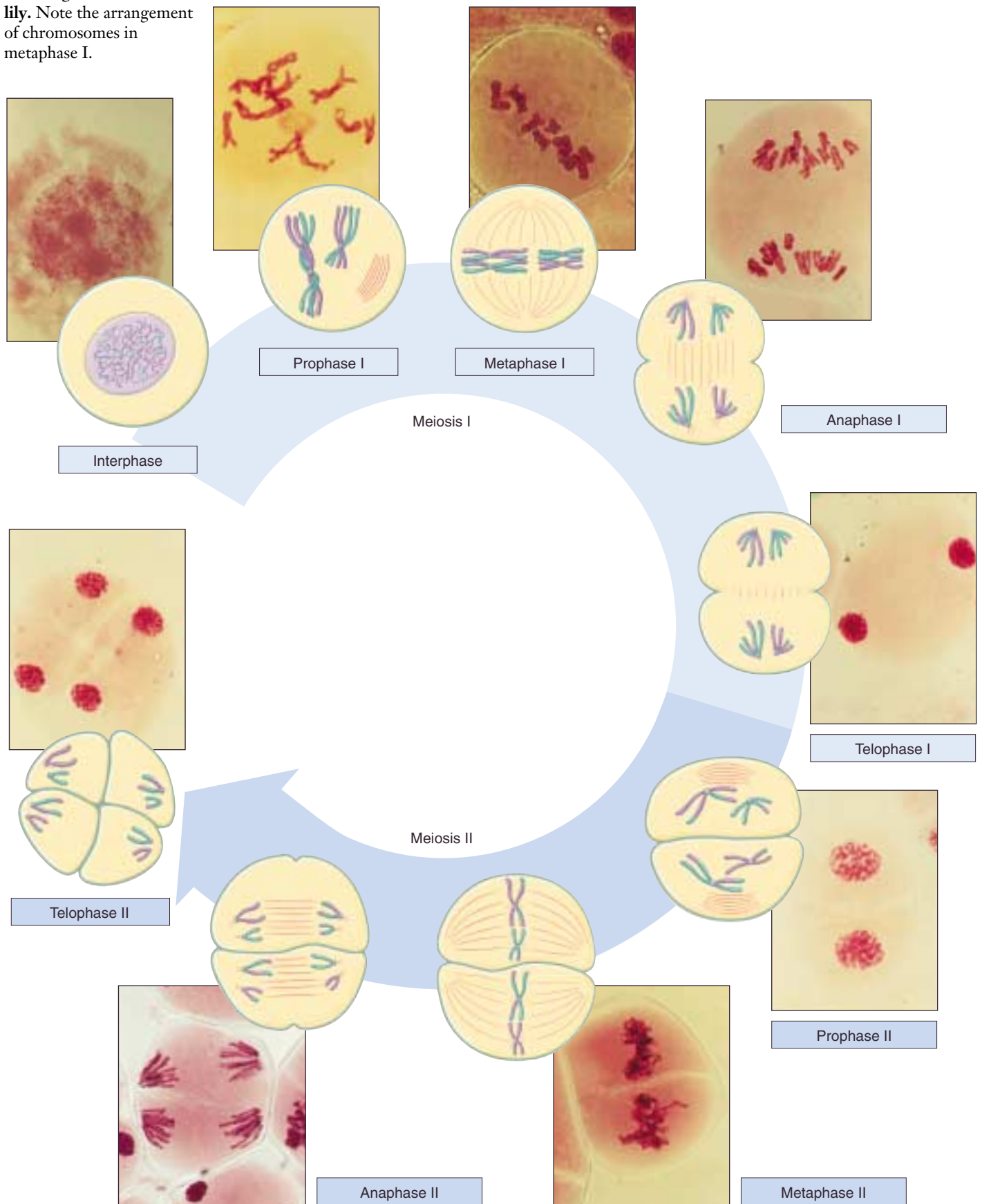


FIGURE 12.12

Random orientation of chromosomes on the metaphase plate.

The number of possible chromosome orientations equals 2 raised to the power of the number of chromosome pairs. In this hypothetical cell with three chromosome pairs, eight (2^3) possible orientations exist, four of them illustrated here. Each orientation produces gametes with different combinations of parental chromosomes.

FIGURE 12.13
The stages of meiosis in a lily. Note the arrangement of chromosomes in metaphase I.



Completing Meiosis

After the long duration of prophase and metaphase, which together make up 90% or more of the time meiosis I takes, meiosis I rapidly concludes. Anaphase I and telophase I proceed quickly, followed—without an intervening period of DNA synthesis—by the second meiotic division.

Anaphase I

In anaphase I, the microtubules of the spindle fibers begin to shorten. As they shorten, they break the chiasmata and pull the centromeres toward the poles, dragging the chromosomes along with them. Because the microtubules are attached to kinetochores on only one side of each centromere, the individual centromeres are not pulled apart to form two daughter centromeres, as they are in mitosis. Instead, the entire centromere moves to one pole, taking both sister chromatids with it. When the spindle fibers have fully contracted, each pole has a complete haploid set of chromosomes consisting of one member of each homologous pair. Because of the random orientation of homologous chromosomes on the metaphase plate, a pole may receive either the maternal or the paternal homologue from each chromosome pair. As a result, the genes on different chromosomes assort independently; that is, meiosis I results in the **independent assortment** of maternal and paternal chromosomes into the gametes.

Telophase I

By the beginning of telophase I, the chromosomes have segregated into two clusters, one at each pole of the cell. Now the nuclear membrane re-forms around each daughter nucleus. Because each chromosome within a daughter nucleus replicated before meiosis I began, each now contains two sister chromatids attached by a common centromere. Importantly, *the sister chromatids are no longer identical*, because of the crossing over that occurred in prophase I (figure 12.14). Cytokinesis may or may not occur after telophase I. The second meiotic division, meiosis II, occurs after an interval of variable length.

The Second Meiotic Division

After a typically brief interphase, in which no DNA synthesis occurs, the second meiotic division begins.

Meiosis II resembles a normal mitotic division. Prophase II, metaphase II, anaphase II, and telophase II follow in quick succession.

Prophase II. At the two poles of the cell the clusters of chromosomes enter a brief prophase II, each nuclear envelope breaking down as a new spindle forms.

Metaphase II. In metaphase II, spindle fibers bind to both sides of the centromeres.



FIGURE 12.14
After meiosis I, sister chromatids are not identical. So-called “harlequin” chromosomes, each containing one fluorescent DNA strand, illustrate the reciprocal exchange of genetic material during meiosis I between sister chromatids.

Anaphase II. The spindle fibers contract, splitting the centromeres and moving the sister chromatids to opposite poles.

Telophase II. Finally, the nuclear envelope re-forms around the four sets of daughter chromosomes.

The final result of this division is four cells containing haploid sets of chromosomes (figure 12.15). No two are alike, because of the crossing over in prophase I. Nuclear envelopes then form around each haploid set of chromosomes. The cells that contain these haploid nuclei may develop directly into gametes, as they do in animals. Alternatively, they may themselves divide mitotically, as they do in plants, fungi, and many protists, eventually producing greater numbers of gametes or, as in the case of some plants and insects, adult individuals of varying ploidy.

During meiosis I, homologous chromosomes move toward opposite poles in anaphase I, and individual chromosomes cluster at the two poles in telophase I. At the end of meiosis II, each of the four haploid cells contains one copy of every chromosome in the set, rather than two. Because of crossing over, no two cells are the same. These haploid cells may develop directly into gametes, as in animals, or they may divide by mitosis, as in plants, fungi, and many protists.

MEIOSIS

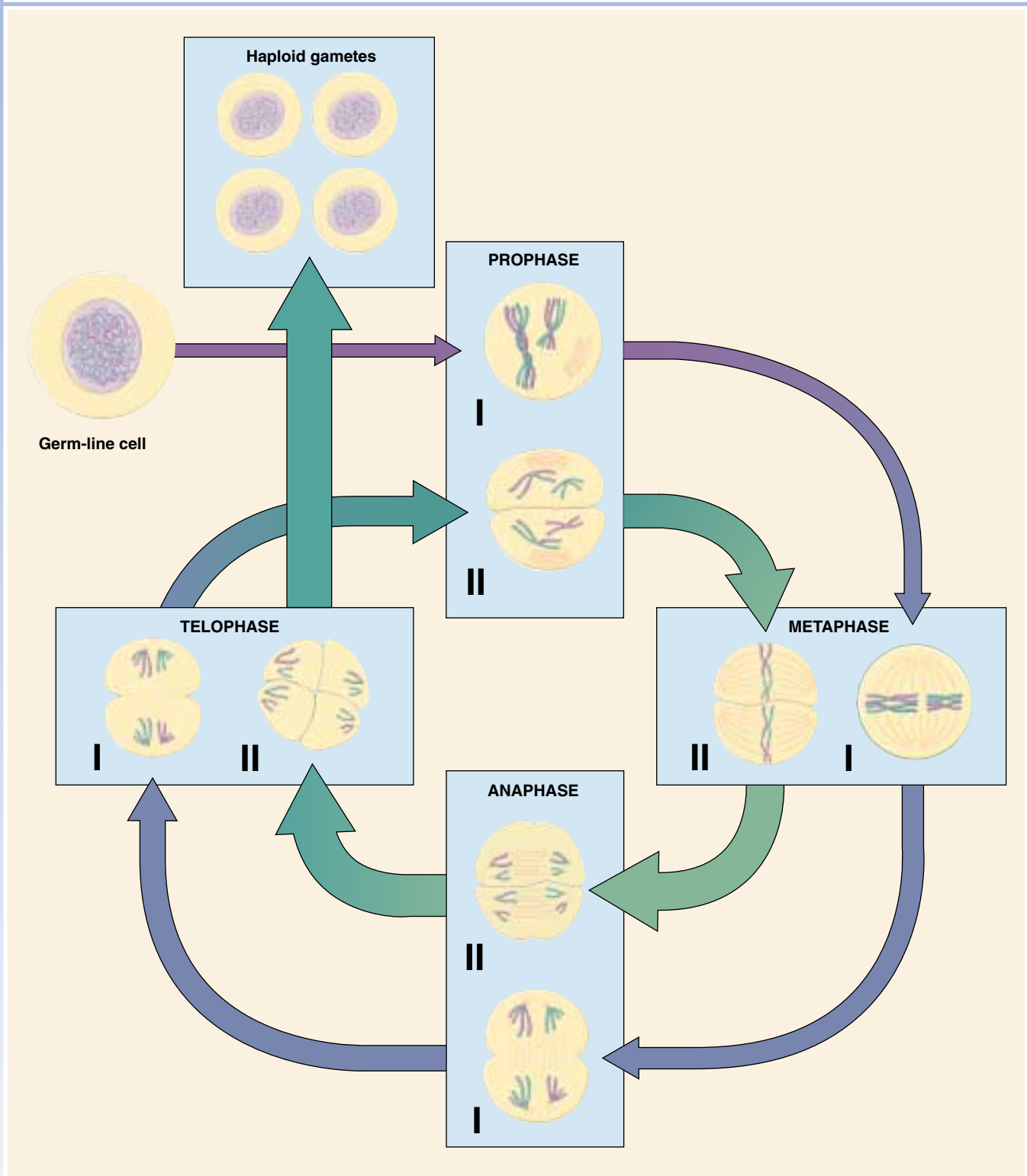


FIGURE 12.15
How meiosis works. Meiosis consists of two rounds of cell division and produces four haploid cells.

12.3 The evolutionary origin of sex is a puzzle.

Why Sex?

Not all reproduction is sexual. In **asexual reproduction**, an individual inherits all of its chromosomes from a single parent and is, therefore, genetically identical to its parent. Bacterial cells reproduce asexually, undergoing binary fission to produce two daughter cells containing the same genetic information. Most protists reproduce asexually except under conditions of stress; then they switch to sexual reproduction. Among plants, asexual reproduction is common, and many other multicellular organisms are also capable of reproducing asexually. In animals, asexual reproduction often involves the budding off of a localized mass of cells, which grows by mitosis to form a new individual.

Even when meiosis and the production of gametes occur, there may still be reproduction without sex. The development of an adult from an unfertilized egg, called **parthenogenesis**, is a common form of reproduction in arthropods. Among bees, for example, fertilized eggs develop into diploid females, but unfertilized eggs develop into haploid males. Parthenogenesis even occurs among the vertebrates. Some lizards, fishes, and amphibians are capable of reproducing in this way; their unfertilized eggs undergo a mitotic nuclear division without cell cleavage to produce a diploid cell, which then develops into an adult.

Recombination Can Be Destructive

If reproduction can occur without sex, why does sex occur at all? This question has generated considerable discussion, particularly among evolutionary biologists. Sex is of great evolutionary advantage for populations or species, which benefit from the variability generated in meiosis by random orientation of chromosomes and by crossing over. However, evolution occurs because of changes at the level of *individual* survival and reproduction, rather than at the population level, and no obvious advantage accrues to the progeny of an individual that engages in sexual reproduction. In fact, recombination is a destructive as well as a constructive process in evolution. The segregation of chromosomes during meiosis tends to disrupt advantageous combinations of genes more often than it creates new, better adapted combinations; as a result, some of the diverse progeny produced by sexual reproduction will not be as well adapted as their parents were. In fact, the more complex the adaptation of an individual organism, the less likely that recombination will improve it, and the more likely that recombination will disrupt it. It is, therefore, a puzzle to know what a well-adapted individual gains from participating in sexual reproduction, as *all* of its progeny could maintain its successful gene combinations if that individual simply reproduced asexually.

The Origin and Maintenance of Sex

There is no consensus among evolutionary biologists regarding the evolutionary origin or maintenance of sex. Conflicting hypotheses abound. Alternative hypotheses seem to be correct to varying degrees in different organisms.

The DNA Repair Hypothesis. If recombination is often detrimental to an individual's progeny, then what benefit promoted the evolution of sexual reproduction? Although the answer to this question is unknown, we can gain some insight by examining the protists. Meiotic recombination is often absent among the protists, which typically undergo sexual reproduction only occasionally. Often the fusion of two haploid cells occurs only under stress, creating a diploid zygote.

Why do some protists form a diploid cell in response to stress? Several geneticists have suggested that this occurs because only a diploid cell can effectively repair certain kinds of chromosome damage, particularly double-strand breaks in DNA. Both radiation and chemical events within cells can induce such breaks. As organisms became larger and longer-lived, it must have become increasingly important for them to be able to repair such damage. The synaptonemal complex, which in early stages of meiosis precisely aligns pairs of homologous chromosomes, may well have evolved originally as a mechanism for repairing double-strand damage to DNA, using the undamaged homologous chromosome as a template to repair the damaged chromosome. A transient diploid phase would have provided an opportunity for such repair. In yeast, mutations that inactivate the repair system for double-strand breaks of the chromosomes also prevent crossing over, suggesting a common mechanism for both synapsis and repair processes.

The Contagion Hypothesis. An unusual and interesting alternative hypothesis for the origin of sex is that it arose as a secondary consequence of the infection of eukaryotes by mobile genetic elements. Suppose a replicating transposable element were to infect a eukaryotic lineage. If it possessed genes promoting fusion with uninfected cells and synapsis, the transposable element could readily copy itself onto homologous chromosomes. It would rapidly spread by infection through the population, until all members contained it. The bizarre mating type "alleles" found in many fungi are very nicely explained by this hypothesis. Each of several mating types is in fact not an allele but an "idiomorph." Idiomorphs are genes occupying homologous positions on the chromosome but having such dissimilar sequences that they cannot be of homologous origin. These idiomorph genes may simply be the relics of several ancient infections by transposable elements.

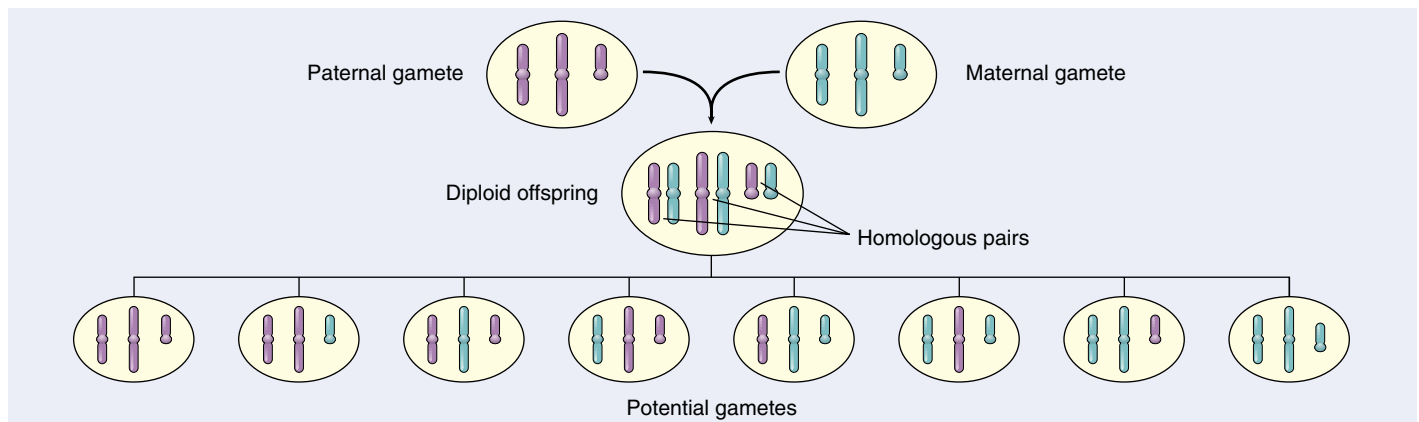


FIGURE 12.16

Independent assortment increases genetic variability. Independent assortment contributes new gene combinations to the next generation because the orientation of chromosomes on the metaphase plate is random. In the cells shown above with three chromosome pairs, eight different gametes can result, each with different combinations of parental chromosomes.

The Red Queen Hypothesis. One evolutionary advantage of sex may be that it allows populations to “store” recessive alleles that are currently bad but have promise for reuse at some time in the future. Because populations are constrained by a changing physical and biological environment, selection is constantly acting against such alleles, but in sexual species can never get rid of those sheltered in heterozygotes. The evolution of most sexual species, most of the time, thus manages to keep pace with ever-changing physical and biological constraints. This “treadmill evolution” is sometimes called the “Red Queen hypothesis,” after the Queen of Hearts in Lewis Carroll’s *Through the Looking Glass*, who tells Alice, “Now, here, you see, it takes all the running you can do, to keep in the same place.”

Miller’s Ratchet. The geneticist Herman Miller pointed out in 1965 that asexual populations incorporate a kind of mutational ratchet mechanism—once harmful mutations arise, asexual populations have no way of eliminating them, and they accumulate over time, like turning a ratchet. Sexual populations, on the other hand, can employ recombination to generate individuals carrying fewer mutations, which selection can then favor. Sex may just be a way to keep the mutational load down.

The Evolutionary Consequences of Sex

While our knowledge of how sex evolved is sketchy, it is abundantly clear that sexual reproduction has an enormous impact on how species evolve today, because of its ability to rapidly generate new genetic combinations. Independent assortment (figure 12.16), crossing over, and random fertilization each help generate genetic diversity.

Whatever the forces that led to sexual reproduction, its evolutionary consequences have been profound. No genetic

process generates diversity more quickly; and, as you will see in later chapters, genetic diversity is the raw material of evolution, the fuel that drives it and determines its potential directions. In many cases, the pace of evolution appears to increase as the level of genetic diversity increases. Programs for selecting larger stature in domesticated animals such as cattle and sheep, for example, proceed rapidly at first, but then slow as the existing genetic combinations are exhausted; further progress must then await the generation of new gene combinations. Racehorse breeding provides a graphic example: thoroughbred racehorses are all descendants of a small initial number of individuals, and selection for speed has accomplished all it can with this limited amount of genetic variability—the winning times in major races ceased to improve decades ago.

Paradoxically, the evolutionary process is thus both revolutionary and conservative. It is revolutionary in that the pace of evolutionary change is quickened by genetic recombination, much of which results from sexual reproduction. It is conservative in that evolutionary change is not always favored by selection, which may instead preserve existing combinations of genes. These conservative pressures appear to be greatest in some asexually reproducing organisms that do not move around freely and that live in especially demanding habitats. In vertebrates, on the other hand, the evolutionary premium appears to have been on versatility, and sexual reproduction is the predominant mode of reproduction by an overwhelming margin.

The close association between homologous chromosomes that occurs during meiosis may have evolved as mechanisms to repair chromosomal damage, although several alternative mechanisms have also been proposed.

**Summary****Questions****Media Resources****12.1 Meiosis produces haploid cells from diploid cells.**

- Meiosis is a special form of nuclear division that produces the gametes of the sexual cycle. It involves two chromosome separations but only one chromosome replication.

1. What are the cellular products of meiosis called, and are they haploid or diploid? What is the cellular product of syngamy called, and is it haploid or diploid?

12.2 Meiosis has three unique features.

- The three unique features of meiosis are synapsis, homologous recombination, and reduction division.

2. What three unique features distinguish meiosis from mitosis?

12.3 The sequence of events during meiosis involves two nuclear divisions.

- The crossing over that occurs between homologues during synapsis is an essential element of meiosis.
- Because crossing over binds the homologues together, only one side of each homologue is accessible to the spindle fibers. Hence, the spindle fibers separate the paired homologues rather than the sister chromatids.
- At the end of meiosis I, one homologue of each chromosome type is present at each of the two poles of the dividing nucleus. The homologues still consist of two chromatids, which may differ from each other as a result of crossing over that occurred during synapsis.
- No further DNA replication occurs before the second nuclear division, which is essentially a mitotic division occurring at each of the two poles.
- The sister chromatids of each chromosome are separated, resulting in the formation of four daughter nuclei, each with half the number of chromosomes that were present before meiosis.
- Cytokinesis typically but not always occurs at this point. When it does, each daughter nucleus has one copy of every chromosome.

3. What are synaptonemal complexes? How do they participate in crossing over? At what stage during meiosis are they formed?

4. How many chromatids are present for each type of chromosome at the completion of crossing over? What two structures hold the chromatids together at this stage?

5. How is the attachment of spindle microtubules to centromeres in metaphase I of meiosis different from that which occurs in metaphase of mitosis? What effect does this difference have on the movement of chromosomes during anaphase I?

6. What mechanism is responsible for the independent assortment of chromosomes?



• Art Activity: Meiosis I



• Meiosis



• Meiosis

12.4 The evolutionary origin of sex is a puzzle.

- In asexual reproduction, mitosis produces offspring genetically identical to the parent.
- Meiosis is thought to have evolved initially as a mechanism to repair double-strand breaks in DNA, in which the broken chromosome is paired with its homologue while it is being repaired.
- The evolutionary significance of meiosis is that it generates large amounts of recombination, rapidly reshuffling gene combinations, producing variability upon which evolutionary processes can act.

7. What is one of the current scientific explanations for the evolution of synapsis?

8. By what three mechanisms does sexual reproduction increase genetic variability? How does this increase in genetic variability affect the evolution of species?



• Evolution of Sex
• Review of Cell Division