

13.1 How Does Meiosis Occur?

To understand meiosis, it is important to grasp some key ideas about chromosomes. For example, when cell biologists began to study the cell divisions that lead to gamete formation, they made an important observation: Each organism has a characteristic number of chromosomes.

Organisms Have Unique Chromosome Compositions

Chromosomes Come in Distinct Sizes and Shapes

Consider the drawings in [Figure 13.1](#), which are based on research begun by the American cell biologist Nettie Maria Stevens in 1906. Stevens was the first person to study chromosomes during the cell divisions leading up to the formation of egg and sperm. Using the fruit fly *Drosophila melanogaster*, a major model organism (see [BioSkills 9](#)), she identified a total of eight chromosomes in *Drosophila* cells. Your cells have 46 chromosomes, chickens have more (78), and corn has fewer (20).

Figure 13.1 Cells Contain Different Types of Chromosomes That Often Come in Pairs.



Numbers and letters designate the types of *Drosophila* chromosomes. The X chromosome is sometimes called chromosome 1.

Source: Adapted from Calvin Bridges, 1915, 1916, in the public domain.

Stevens found each *Drosophila* cell has eight chromosomes, but just five distinct types, distinguished by their size and shape. Three of these chromosomes always occurred in pairs and are labelled chromosomes 2–4 in [Figure 13.1](#). One of the chromosomes had a pair in females but not males. This chromosome was named X for mysterious. Another chromosome was found only in males—she gave this chromosome the next letter in the alphabet, Y. Chromosomes found in two copies in both males and females are called **autosomes** while those that are not are called **sex chromosomes**.

Many animal and some plant species also have sex chromosomes. Humans, for example, have 24 different chromosomes: an X, a Y, and 22 autosomes named 1 to 22. Females have two of each autosome and two X chromosomes. This is written as 46,XX where 46 is the number of all chromosomes and the two Xs are the sex chromosomes present in this number. Males are 46,XY and have the same autosomes but one of each sex chromosome. These summaries of a species, number and types of chromosomes is known as its **karyotype** ("nucleus form").

Chickens (*Gallus gallus*) also have sex chromosomes but these are named Z and W instead of X and Y. Males have two of the same chromosome, in this case two Z chromosomes. Females have two different sex chromosomes, a Z and a W. Both sexes also have 38 pairs of autosomes for a total of 78 chromosomes. Other birds have different numbers of autosomes but the same Z and W chromosomes.

Corn (*Zea mays*) has only autosomes. Thus every corn plant has the same 10 pairs of autosomes. These examples are typical. Most animals and plants fall into one of three categories:

1. autosomes plus X and Y sex chromosomes (*Drosophila* and mammals, for example);
2. autosomes plus Z and W sex chromosomes (chickens and other birds);
3. only autosomes (corn and most other plants).

Chromosomes Carry Genes

Chromosomes that are the same size and shape are called **homologous chromosomes** ("same proportion") or **homologs**, and the pair is called a homologous pair. Later work showed that homologous chromosomes are similar in content as well as in size and shape. Homologous chromosomes carry the same genes. A **gene** is a section of DNA that influences some hereditary trait in an individual. For example, each copy of chromosome 2 found in *Drosophila* carries genes that influence eye colour, wing size and shape, and bristle size.

The versions of a gene found on homologous chromosomes may differ, however. Biologists use the term **allele** to denote different versions of the same gene. For example, the allele for an eye-colour gene on one homolog of chromosome 2 may be associated with red eyes, the normal colour in *Drosophila*, whereas the allele of the same eye-colour gene on the other homolog may be associated with purple eyes ([Figure 13.2](#)); the particular alleles of the bristle-size gene will influence whether the fly's bristles are long or short, and so on.

Figure 13.2 Homologous Chromosomes May Contain Different Alleles of the Same Gene.

The homologs of *Drosophila* chromosome 2 are shown; the location of only one of many genes is indicated.

To sum up, homologous chromosomes are not identical, even though they carry the same genes in the same positions, because each homolog may contain different alleles of any particular gene.

A thing to watch for as you develop the vocabulary of meiosis and genetics is the sometimes imprecise use of terms by both biologists and the media. This is especially true of the words "gene" and "allele." For instance, you might read about the discovery of a new breast cancer gene. What's really meant is that a particular allele of a gene has been discovered. The normal function of the gene isn't to cause breast cancer. For this reason, you'll often need to pay attention to know whether the discussion really is about an allele or a gene.

The Concept of Ploidy

Most Eukaryotic Species Are Diploid

Humans, corn, and most other multicellular eukaryotes have two copies of each autosome. This makes them **diploid** (double form). Diploid cells have two alleles of each gene—one on each of the homologous pairs of chromosomes. Although a diploid individual can carry only two different alleles of a gene, there can be many different alleles in a population.

Yeast and other unicellular eukaryotic species are similar. Diploid cells produce haploid cells

possess a single chromosome, so in this respect they are similar to haploid eukaryotic cells. Biologists use a compact notation to indicate the number and source of the chromosomes present

- The letter n stands for the number of chromosomes present in a gamete and is called the **haploid number**. Human sperm and egg cells, for example, are both $n = 23$. Eggs have one

- Animals are the result of two gametes joining together (a topic that will be discussed later in this chapter). The gamete from the mother carries the **maternal chromosomes**, while the gamete from the father carries the **paternal chromosomes**.
 - Each cell in an animal has twice the number of chromosomes as a gamete, for a total number of chromosomes of $2n$. Using humans as an example again, the cells in our body are $2n = 46$ (see chapter opening figure in [Chapter 16](#)).

If you understand these terms, you should be able to apply them to domestic cats (*Felis catus*). This species has 18 autosomes plus X and Y sex chromosomes. Complete this statement: Adult cats are $n =$ and have copies of each gene. Are adult cats haploid or diploid?

A few species (or types) of plants and fish are **polyploid** (many form) and have more than two of each chromosome. Bread wheat (*Triticum aestivum*), for example, is a hexaploid species. Each

it has seven different chromosomes, each adult cell contains 42 chro-

How can we modify our notation system to include polyploid species? There are different ways, but the preferred method is to continue to use n as the number of chromosomes present in a gamete but to use another letter, x (called the **basic number**^D), to be the number of distinct types of chromosomes.

chromosomes as spores, 6 copies of each chromosome, and 42 chromosomes in total. Hexaploid bread wheat is just one example of a polyploid species. Other examples include seedless bananas ($3x$, triploid), salmon and trout ($4x$, tetraploid), and *Dahlia* plants ($8x$, octoploid).

This system can also work with diploid plants. Corn is $2n = 2x = 20$, for example. Note that for

If you understand these terms, you should be able to describe Durum wheat (*Triticum durum*; flour from this species is used to make pasta). There are 7 distinct chromosomes present in this

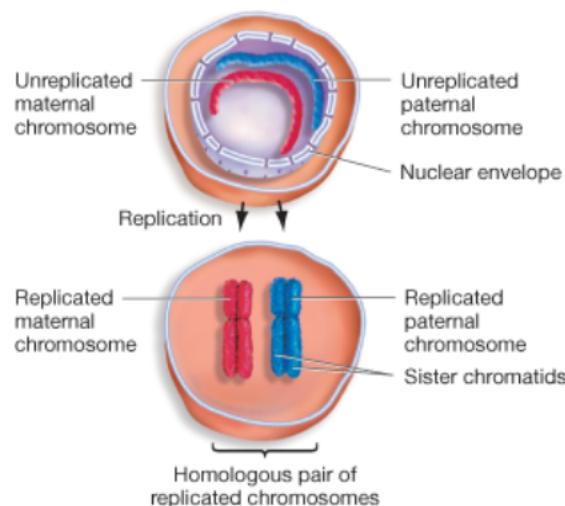
wheat is $n =$ $x =$ and has copies of each gene. Which type of polyploid is this species?

An Overview of Meiosis

Cells replicate each of their chromosomes before starting meiosis. At the beginning of meiosis, chromosomes are in the same state they are in at the start of mitosis.

Recall that an unreplicated eukaryotic chromosome consists of a single, long DNA double helix organized around proteins called histones (Chapter 12). During S phase of the cell cycle the DNA is replicated, and therefore each chromosome is also replicated. A replicated chromosome consists of two **sister chromatids** (Figure 13.3). Each sister chromatid contains an identical copy of the DNA double helix that was present in the unreplicated chromosome before S phase. Therefore, each sister chromatid contains the same genetic information. Sister chromatids remain physically joined along their entire length during much of meiosis.

Figure 13.3 Each Chromosome Replicates before Undergoing Meiosis.

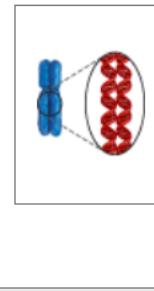
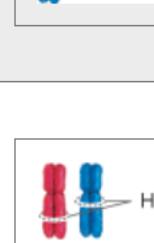
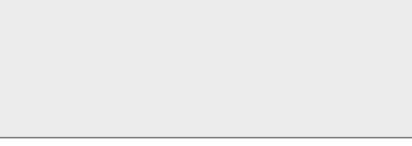
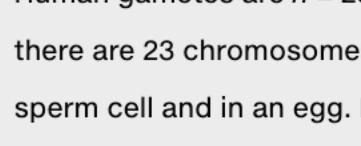
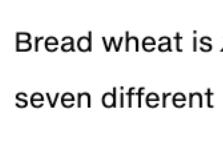


Unreplicated chromosomes (top) are shown as visible structures, but they are not actually condensed at this stage.

To understand meiosis, it is important to understand the relationship between chromosomes and sister chromatids. The trick is to recognize that an unreplicated chromosome and a replicated chromosome are both *single* chromosomes, even though the replicated chromosome contains *two* sister chromatids. This makes sense if you consider that a chromosome carries a particular set of genetic information in its DNA and that the amount of *unique* information is the same whether there is one copy of it present or two. It's similar to thinking about the amount of information present in one copy of a book or two copies—the two copies may have more pages, but there's no more new information. Don't fall into the mistake of thinking that every time DNA replicates, the number of chromosomes doubles.

By convention, an unreplicated chromosome is never called a chromatid; the term "chromatid" is used only to describe the structures in a replicated chromosome. Table 13.1 summarizes the terms that biologists use to describe chromosomes and illustrates the relationship between chromosomes and chromatids. **CAUTION If you understand the relationship between chromosomes and chromatids, you should be able to draw one chromosome in both an unreplicated and replicated state, label the sister chromatids, indicate the number of double-helical molecules of DNA present in each drawing, and explain why both of your drawings represent single chromosomes.**

Summary Table 13.1 Terms for Describing Chromosomes

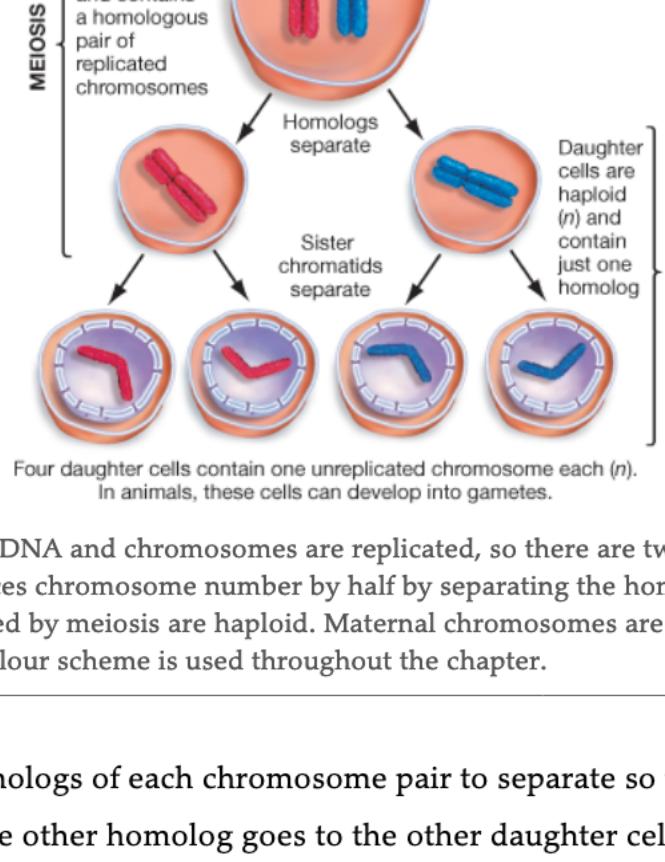
Term	Definition	Example or Comment
Chromosome	Structure made up of DNA and proteins; carries the cell's hereditary information (genes)	Eukaryotes have linear chromosomes; most bacteria and archaea have just one circular chromosome
• Sex chromosome	A chromosome not present in two copies in both males and females	X and Y chromosomes of humans (males are XY, females XX); Z and W chromosomes of birds butterflies (males are ZZ, females ZW)
• Autosome	A chromosome present in two copies in all individuals in a species	Chromosomes 1–22 in humans
Unreplicated chromosome	A chromosome that consists of one double-helical molecule of DNA packaged with proteins (not shown) for compactness.	
Replicated chromosome	A chromosome after DNA replication. Consists of two identical chromatids, each containing one double-helical DNA molecule packaged with proteins (not shown) for compactness	
Sister chromatids	The two identical chromatid copies in a replicated chromosome	
Homologous chromosomes (homologs)	Chromosomes that have the same genes in the same position and are the same size and shape. (Because the alleles of particular genes are often different between the homologs, homologs are not called identical chromosomes.)	
Non-sister chromatids	Chromatids on different members of a homologous chromosome pair. (To be non-sister chromatids, one of the chromatids is on one homolog and the other chromatid is on the other homolog.)	
Bivalent	Homologous replicated chromosomes that are joined together during prophase I and metaphase I of meiosis	
Haploid number	The number of chromosomes present in a gamete or spore, symbolized as n	Human gametes are $n = 23$, so there are 23 chromosomes in a sperm cell and in an egg. Bread wheat spores are $n = 21$, so each contains 21 chromosomes
Basic number	The number of distinct chromosomes in a polyploid species, symbolized as x	Bread wheat is $x = 7$, so it has seven different chromosomes
Ploidy	The number of each type of chromosome present	The number of haploid chromosome sets present; shown by the number in front of n (for example, $2n$)
• Haploid	Having one set of chromosomes	Bacteria and archaea are haploid all of the time; unicellular eukaryotes are haploid most of the time; most plants spores and animal gametes are haploid
• Diploid	Having two sets of chromosomes	Unicellular eukaryotes are diploid some of the time; most adult plants and animals are diploid
• Polyploid	Having more than two chromosome sets; species can be triploid ($3x$), tetraploid ($4x$), hexaploid ($6x$), and so on	Seedless bananas are triploid, salmon are tetraploid, bread wheat is hexaploid

Meiosis Consists of Two Cell Divisions

Two back-to-back cell divisions occur in meiosis, **meiosis I** and **meiosis II**. As Figure 13.4

shows, these divisions differ sharply.

Figure 13.4 Meiosis First Separates Homologs and Then Separates Sister Chromatids.



Before undergoing meiosis, DNA and chromosomes are replicated, so there are two chromatids per chromosome. Meiosis reduces chromosome number by half by separating the homologous pairs. In diploid organisms, the cells produced by meiosis are haploid. Maternal chromosomes are shown in red; paternal chromosomes, blue. This colour scheme is used throughout the chapter.

Meiosis I causes the homologs of each chromosome pair to separate so that one homolog goes to one daughter cell and the other homolog goes to the other daughter cell. At the end of meiosis I, each of the two daughter cells has one of each type of chromosome instead of two, and thus half as many chromosomes as the parent cell had. Put another way: During meiosis I, the diploid ($2n$) parent cell produces two haploid (n) daughter cells. Notice, however, that each chromosome still consists of *two sister chromatids*—chromosomes are in their replicated form at the end of meiosis I.

During meiosis II, the sister chromatids of each chromosome separate. One sister chromatid goes to one daughter cell; the other sister chromatid goes to the other daughter cell. Each separated sister chromatid is called a daughter chromosome. Remember that each haploid cell that started meiosis II had only one of each type of chromosome, but each chromosome was still in its replicated form consisting of two sister chromatids. The cells produced by meiosis II also have one of each type of chromosome and are haploid, but now the daughter chromosomes each consist of a single double-helical molecule of DNA and so are said to be unreplicated.

To reiterate, sister chromatids separate into daughter chromosomes during meiosis II. This is just what happens during mitosis. Meiosis II is actually equivalent to mitosis in a haploid cell. In meiosis I, on the other hand, sister chromatids stay together. This sets meiosis I apart from both mitosis and meiosis II.

As in mitosis, chromosome movement during meiosis I and II is coordinated by microtubules of the spindle apparatus that attach to kinetochores located at the centromere of each chromosome. Recall that the centromere is a region on the chromosome; kinetochores are protein-based structures that form on that region (see [Chapter 12](#)). Chromosome movement is driven by fraying of the ends of microtubules at each kinetochore, just as it is in mitosis (see [Figure 12.7](#)).

Meiosis I Is a Reduction Division

A host of early cell biologists worked out the sequence of events in meiosis I and II by carefully observing cells with the light microscope. They came to a key realization: Meiosis I reduces chromosome number. For this reason, meiosis I is known as a reduction division. Reduction is another important way in which meiosis I differs from meiosis II and mitosis.

In most plants and animals, the original cell entering meiosis is diploid and the four final daughter cells are haploid. In animals, the haploid daughter cells, each containing one of each homologous chromosome, may eventually go on to form egg cells or sperm cells to complete the process of **gametogenesis** ("gamete origin"; see [Chapter 47](#)). In plants, yeast, and many other eukaryotes, the haploid spores may divide by mitosis and even go on to produce a haploid multicellular organism.

When two haploid gametes fuse during fertilization, the full diploid complement of chromosomes is restored ([Figure 13.5](#)). The diploid cell that results from fertilization is called a **zygote**, and it is the first cell of a new individual. In this way, each diploid individual receives a haploid chromosome set from its mother and a haploid set from its father.

Figure 13.5 Fertilization Restores a Diploid Set of Chromosomes.

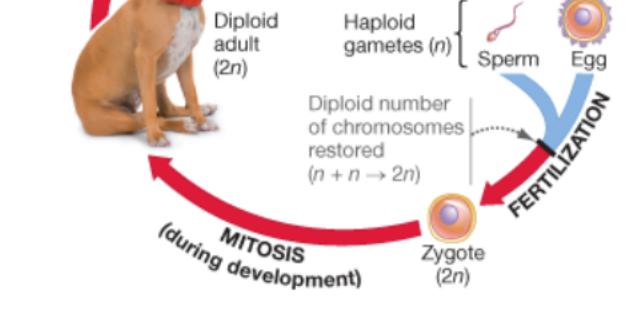


Figure 13.6 puts these events into the context of a **life cycle**—the sequence of events that occurs over the life of an individual, from fertilization to the production of offspring. As you study the figure, note how **ploidy** changes as the result of meiosis and fertilization. In the case of the dog illustrated here, meiosis in a diploid adult results in the formation of haploid gametes, which combine to form a diploid zygote. The zygote marks the start of a new generation, and through mitotic divisions during development, the zygote goes on to form the adult. The dog life cycle is typical of familiar animals. However, life cycles of other types of organisms can be very different (see, for example, [Chapters 29](#) and [30](#)).

CAUTION If you understand the events of meiosis, you should be able to predict how many double-helical molecules of DNA will be present in the gametes of the fruit fly *Drosophila*, a diploid organism that has eight replicated chromosomes in each cell that enters meiosis.

Figure 13.6 Ploidy Changes during the Life Cycle of an Animal.

Diploid ($2n$) MEIOSIS Number of chromosomes reduced by half ($2n \rightarrow n$)

Haploid gametes (n) { Sperm Egg

Diploid number of chromosomes restored ($n + n \rightarrow 2n$)

Zygote ($2n$)

(during development)

The dog life cycle is typical of most familiar animals, because most of it involves diploid cells.

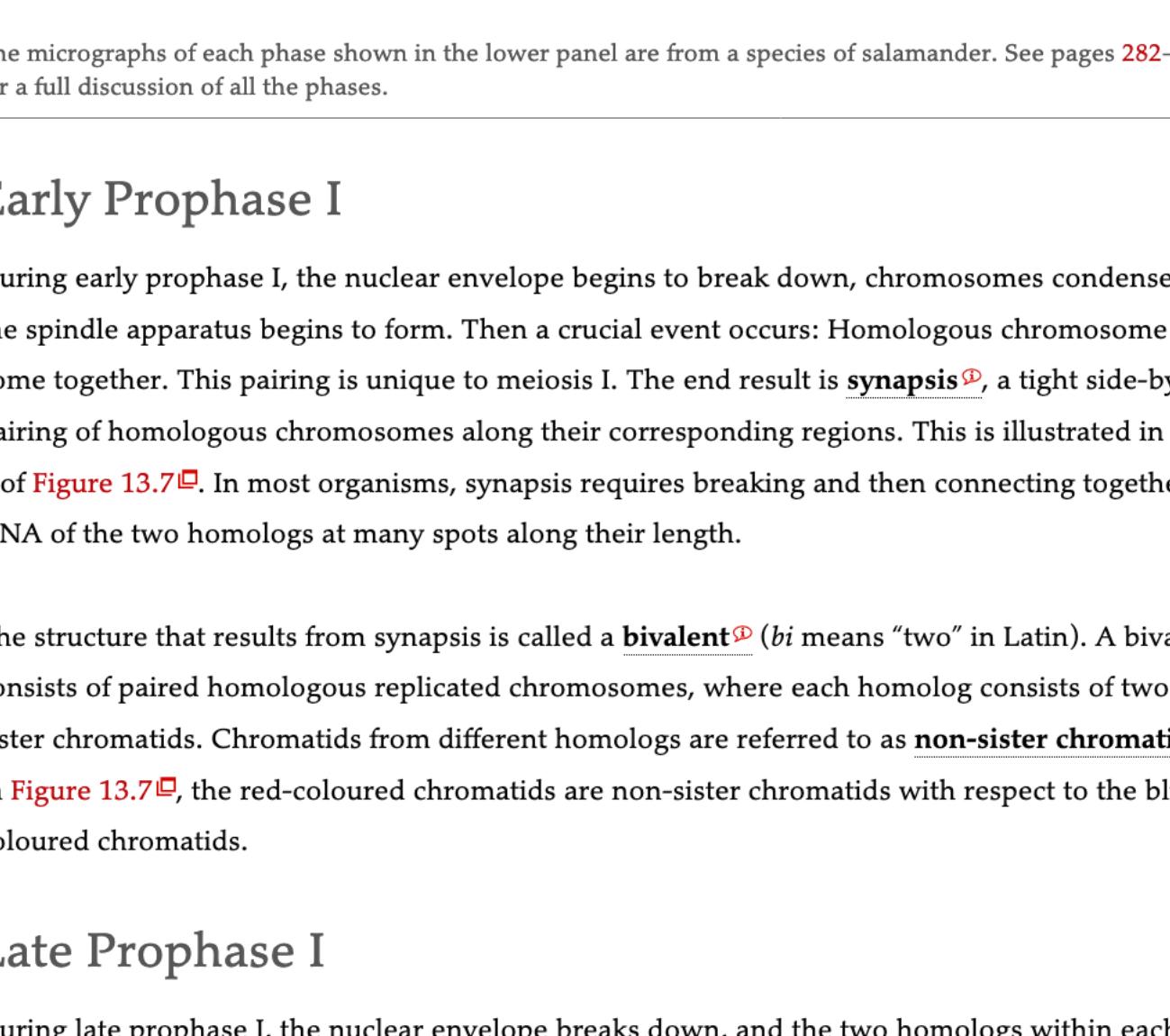
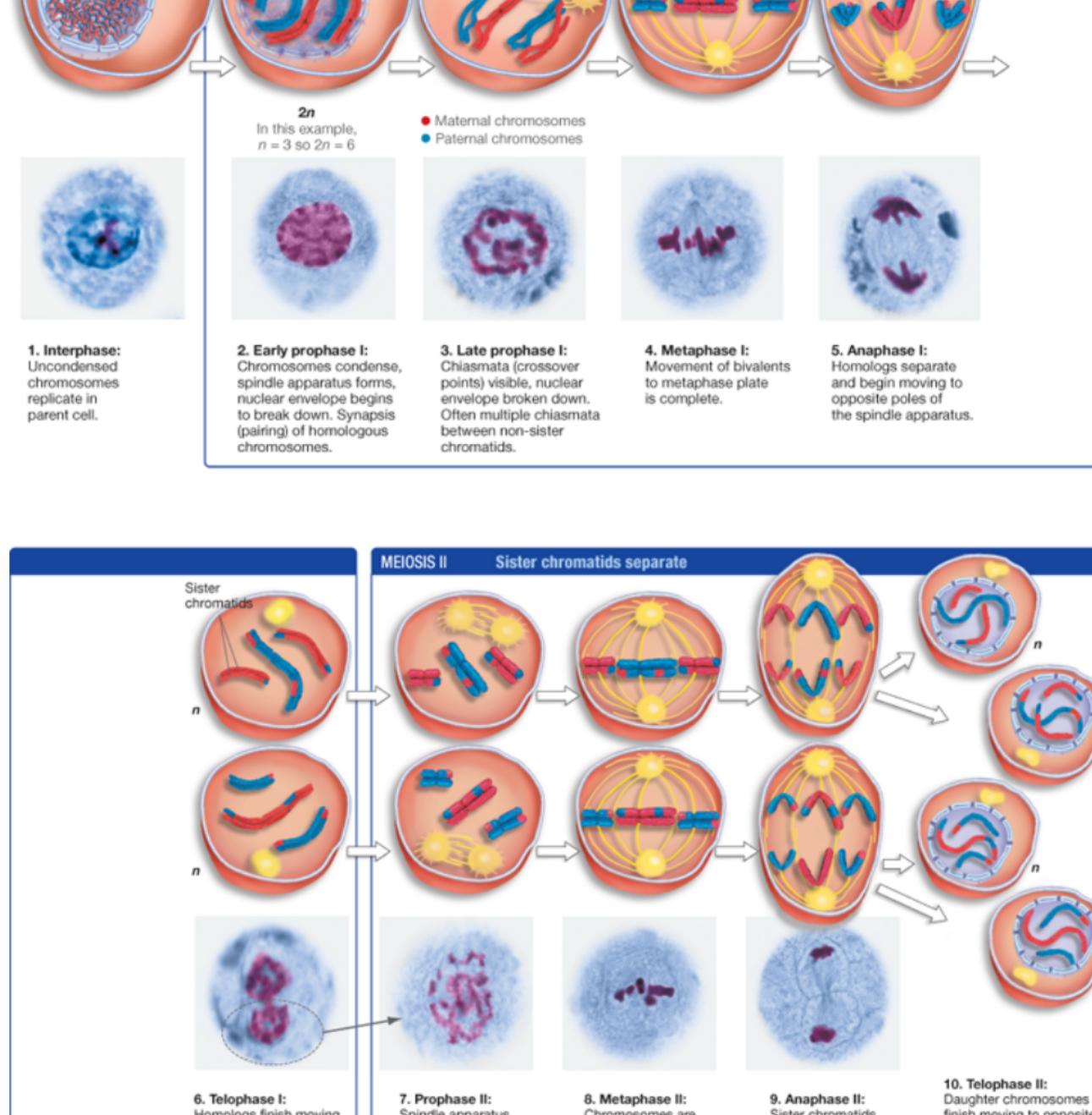
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Once early research had filled in the details of meiosis and the accompanying changes in ploidy, the mystery of fertilization was solved. To appreciate the consequences of meiosis fully, let's analyze the events in more detail.

The Phases of Meiosis I

Meiosis begins after chromosomes are replicated during S phase and the cell moves through G₂ phase (see Chapter 12). Just as for mitosis, before the start of meiosis, chromosomes are extended and not visible under a light microscope. The major steps that occur during meiosis are shown in Figure 13.7.

Figure 13.7 Meiosis Can Be Divided into Phases.



The micrographs of each phase shown in the lower panel are from a species of salamander. See pages 282–284 for a full discussion of all the phases.

Early Prophase I

During early prophase I, the nuclear envelope begins to break down, chromosomes condense, and the spindle apparatus begins to form. Then a crucial event occurs: Homologous chromosome pairs come together. This pairing is unique to meiosis I. The end result is **synapsis** (a tight side-by-side pairing of homologous chromosomes along their corresponding regions. This is illustrated in step 2 of Figure 13.7. In most organisms, synapsis requires breaking and then connecting together DNA of the two homologs at many spots along their length.

The structure that results from synapsis is called a **bivalent** (bi means “two” in Latin). A bivalent consists of paired homologous replicated chromosomes, where each homolog consists of two sister chromatids. Chromatids from different homologs are referred to as **non-sister chromatids**. In Figure 13.7, the red-coloured chromatids are non-sister chromatids with respect to the blue-coloured chromatids.

Late Prophase I

During late prophase I, the nuclear envelope breaks down, and the two homologs within each bivalent become attached to microtubules coming from opposing poles of the spindle apparatus—that is, each homolog in the bivalent is attached to a different pole. This form of attachment is unique to meiosis I, and it is essential for separating the homologous pairs.

The homologs that were so closely paired in synapsis now begin to separate at many points along their length. They stay joined, however, by X-shaped structures called **chiasmata** (singular: **chiasma**). (In the Greek alphabet, the letter “X” is called chi.) Normally, at least one chiasma forms in every pair of homologous chromosomes, and there are often several chiasmata. The chiasmata mark particular sites of DNA breakage and rejoining between homologs early in prophase I.

What are the reasons for these events? There are two. As step 3 of Figure 13.7 shows, the chromatids that meet to form a chiasma are always non-sister chromatids. Chiasmata help hold the homologous chromosomes together during meiosis I. Notice how they hold together the blue and the red chromosomes.

At each chiasma there is an exchange of parts of chromosomes between paternal and maternal homologs. These reciprocal exchanges between different homologs create chromatids that have both paternal and maternal segments. This process of chromosome exchange is called **crossing over**. Step 4 of Figure 13.7 illustrates that crossing over produces chromosomes with a combination of maternal (red) and paternal (blue) segments. Consequently, these chromosomes have a mixture of maternal and paternal alleles.

Chiasmata therefore have two functions:

1. They help hold homologous chromosomes together during meiosis I.
2. They are one way in which meiosis creates genetic diversity, a point we will return to.

Metaphase I

In metaphase I, the kinetochore microtubules move the pairs of homologous chromosomes (bivalents) to a region called the **metaphase plate** (step 4). The metaphase plate is not a physical structure but an imaginary plane midway between the poles of the spindle apparatus.

Here are two key points about chromosome movement: (1) In metaphase I, each bivalent straddles the metaphase plate with one homolog on one side and the other homolog on the other; and (2) the alignment of each bivalent is independent of any other bivalent. This means that if one bivalent has a maternal homolog above the metaphase plate and the paternal homolog below the metaphase plate, the alignment of this pair of homologs has no influence on how any other bivalent will align. The independent alignment of bivalents may seem a trivial detail, but it accounts for the most fundamental principles of genetics (see Chapter 14).

Anaphase I and Telophase I

Sister chromatids of each chromosome remain together. The unique attachment of the kinetochores of each homolog to microtubules that come from one spindle pole means that each homolog in the pair is attached to a different spindle pole. This allows the homologous chromosomes in each bivalent to separate from each other during anaphase I as they are moved to opposite poles of the spindle apparatus (step 5). Meiosis I concludes with telophase I, when the homologs finish moving to opposite sides of the spindle (step 6). When meiosis I is complete, **cytokinesis** (division of cytoplasm) occurs and two haploid daughter cells form.

Meiosis I: A Recap

Meiosis I results in daughter cells that have only one chromosome of each homologous pair. A reduction in chromosome number has occurred: The daughter cells produced by meiosis I are haploid, having only one copy of each type of chromosome. The sister chromatids remain attached in each chromosome, however, meaning that the haploid daughter cells at the end of meiosis I still contain replicated chromosomes.

It is important to note that the chromosomes in each cell are a random assortment of maternal and paternal chromosomes as a result of (1) crossing over and (2) the random distribution of maternal and paternal homologs to daughter cells.

Chromosome movement occurs through the dynamic assembly and disassembly of the microtubules attached to the kinetochore. When meiosis I is complete, the cell divides and two haploid daughter cells are produced.

The Phases of Meiosis II

Recall that chromosome replication occurred before meiosis I. An important feature of the period between meiosis I and II is that there is no DNA replication and therefore no chromosome replication. Meiosis II works to separate the sister chromatids of the replicated chromosomes into separate cells. Each of these cells will contain unreplicated daughter chromosomes.

During prophase II, a spindle apparatus forms in both daughter cells (step 7 of [Figure 13.7](#)). If nuclear envelopes had formed at the end of meiosis I, they now break apart. Microtubules that polymerize from the two spindle poles attach to kinetochores on opposite sides of every chromosome and begin moving the chromosomes toward the middle of each cell. This attachment is exactly the same as observed in mitosis.

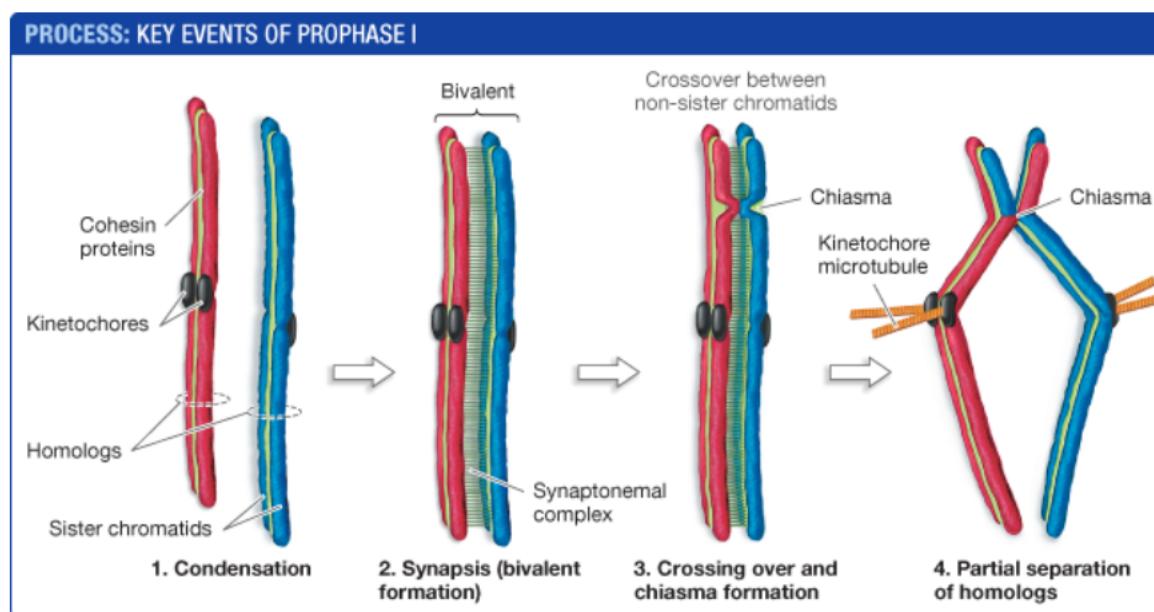
In metaphase II, the chromosomes are lined up at the metaphase plate (step 8). In contrast to metaphase I, each chromosome is attached by microtubules to both of the poles. The sister chromatids of each chromosome are separated during anaphase II (step 9) and move to different daughter cells during telophase II (step 10). Once they are separated, each chromatid is considered an independent daughter chromosome. At the end of meiosis II, there are four haploid cells, each with one daughter chromosome of each type in the chromosome set.

Because meiosis II occurs in both daughter cells produced by meiosis I, the overall process results in four daughter cells from each parent cell. To summarize meiosis, one diploid cell with replicated chromosomes gives rise to four haploid cells with unreplicated chromosomes.

A Closer Look at Synapsis and Crossing Over

The pairing of homologs and crossing over in prophase I are both important events unique to meiosis. [Figure 13.8](#) provides a closer look at how chromosomes come together and exchange parts during meiosis I.

Figure 13.8 Synapsis and Crossing Over Are Key Events of Prophase I.



Step 1 At the entry to prophase I, chromosomes begin to condense. Sister chromatids are held together along their full length by proteins known as cohesins.

Step 2 Homologs pair in a process called synapsis and are held together by a network of proteins called the synaptonemal complex.

Step 3 In most organisms, one or more breaks are made in the DNA. At least one of these breaks eventually leads to a crossover between non-sister chromatids. Crossover points are visible as chiasmata.

Step 4 The synaptonemal complex disassembles in late prophase I. The two homologs are held together only at chiasmata. Chiasmata are eventually broken to restore individual, unconnected chromosomes.

At a chiasma, the non-sister chromatids from each homolog are *attached to each other at corresponding points*. When chiasmata are broken, corresponding segments of maternal and paternal chromosomes are exchanged. This figure also shows that some proteins are required to hold the chromatids together. Some of these are cohesin proteins, the same proteins that play an important role in mitosis (see [Chapter 12](#)). Other proteins are responsible for the crossover events that occur between non-sister chromatids. Synaptonemal complex proteins are the subject of [Canadian Research 13.1](#) at the end of this section.

Mitosis versus Meiosis

How do mitosis and meiosis compare? Table 13.2 summarizes some important similarities and differences. A key difference between the two processes is that homologous chromosomes pair early in meiosis but do not pair at all during mitosis. Because homologs in prophase of meiosis I are connected by chiasmata, they can migrate to the metaphase plate together. In meiotic prophase I, the unique attachment of each homolog to microtubules coming from only one pole allows for the separation of homologs during anaphase of meiosis I. This results in a reduction division. If you understand key differences between meiosis and mitosis, you should be able to explain why mitosis in a triploid ($3x$) cell can occur easily but meiosis is difficult.

Summary Table 13.2 Key Differences between Mitosis and Meiosis

Feature	Mitosis	Meiosis
Number of cell divisions	One	Two
Number of chromosomes in daughter cells compared with parent cell	Same	Half
DNA content of daughter cells compared with parent cell	Reduced to 1/2 as chromosomes go from replicated S unreplicated	Reduced to 1/4 as chromosomes go from replicated diploid sets S replicated haploid sets (meiosis I) S unreplicated haploid sets (meiosis II)
Synapsis of homologs	No	Yes
Microtubule attachment	Individual chromatids in each chromosome attach to microtubules from different spindle poles.	Both chromatids in each chromosome attach to microtubules from the same spindle pole.
Number of crossing-over events	None	One or more per pair of homologous chromosomes
Makeup of chromosomes in daughter cells	Identical	Different—various combinations of maternal and paternal chromosomes, paternal and maternal segments mixed within chromosomes
Role in organism life cycle	Asexual reproduction in some eukaryotes; cell division for growth and wound healing	Halving of chromosome number in cells that will produce gametes

See Figure 13.9 for a visual summary of these two processes. Given that mitosis works perfectly well for cell division, why does meiosis exist at all? What are its consequences?

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Check Your Understanding

If you understand that ...

- Meiosis is called a reduction division because the total number of chromosomes present is cut in half.
- During meiosis, a single diploid parent cell with replicated chromosomes gives rise to four haploid daughter cells with unreplicated chromosomes.

You should be able to ...

1. Identify the event that makes meiosis a reduction division and explain how it reduces chromosome number.
2. **CAUTION** Explain how DNA content is reduced by half in both meiosis I and meiosis II, yet chromosome number is reduced only in meiosis I.

Answers are available in Appendix A.

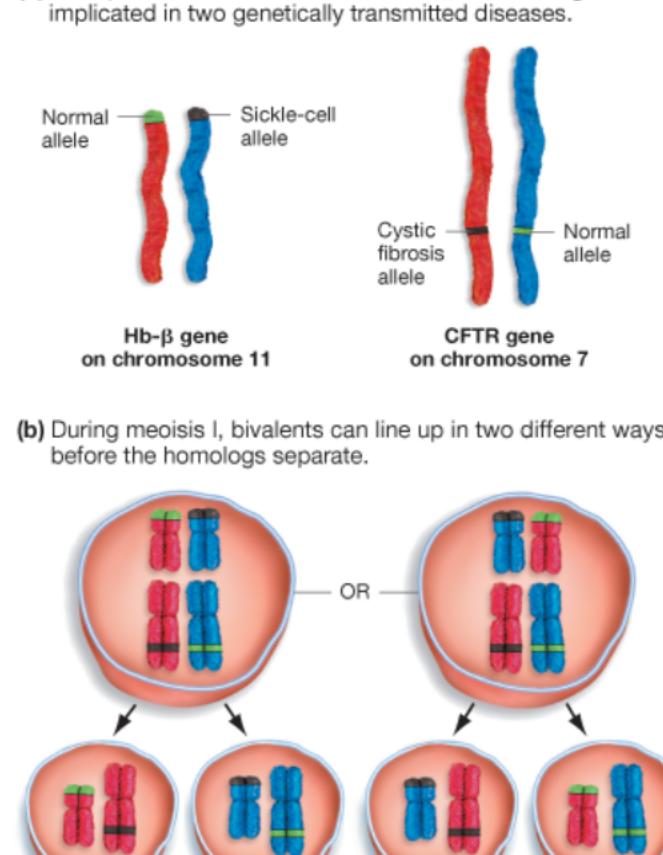
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The Role of Independent Assortment

Section 13.2 Meiosis promotes genetic variation

Each somatic cell in your body contains 23 homologous pairs of chromosomes, or 46 chromosomes in total. Half of these chromosomes came from your mother, and half from your father. Each chromosome contains genes, and genes influence particular traits. For example, one gene that affects the type of hemoglobin in your red blood cells is located on chromosome 11 while a gene that affects the form of an ion channel protein is located on chromosome 7 (Figure 13.11a). Why are the type of hemoglobin and the specific form of ion channel important? It's because abnormal forms of these two proteins can lead to sickle-cell disease and cystic fibrosis, respectively. These are relatively common and very serious genetic diseases.

Figure 13.11 Independent Assortment of Homologous Chromosomes Results in Varied Combinations of Maternal and Paternal Alleles.



Maternal chromosomes are shown in red; paternal in blue. CFTR stands for the ion channel protein that causes cystic fibrosis when cells possess two copies of the defective allele; Hb- β is an abbreviation for a gene that determines the type of hemoglobin. Sickle-cell disease occurs when there are two copies of the defective Hb- β allele.

Suppose that the chromosomes you inherited from your mother contain alleles associated with normal hemoglobin and an abnormal channel protein that causes cystic fibrosis. In contrast, suppose the chromosomes you inherited from your father include the alleles for the abnormal hemoglobin that causes sickle-cell disease and a normal channel protein that does not cause cystic fibrosis. For a person to have either sickle-cell disease or cystic fibrosis, they must possess two copies of the disease-associated allele.

Will some gametes that you produce contain the instructions you inherited from your mother while others contain the instructions you inherited from your father? Figure 13.11b shows that when pairs of homologous chromosomes line up during meiosis I and the homologs separate, different combinations of maternal and paternal chromosomes can result. Each daughter cell gets a random assortment of maternal and paternal chromosomes (which will be reduced from $2n$ to n during meiosis II).

This phenomenon is known as the **principle of independent assortment**. In the example shown in Figure 13.11, meiosis will result in some gametes with alleles for normal hemoglobin (no sickle-cell disease) and for cystic fibrosis, the traits from your mother, as well as some gametes with alleles for sickle-cell disease and normal CFTR (no cystic fibrosis), the traits from your father. But two additional combinations will also occur: gametes having alleles for no sickle-cell disease and no cystic fibrosis, and gametes having alleles for both sickle-cell disease and cystic fibrosis. The creation of new combinations of alleles is called **genetic recombination**. Because the genes in question are on different chromosomes, this was *interchromosomal* genetic recombination. Four different combinations of paternal and maternal chromosomes are possible for two chromosomes distributed to daughter cells during meiosis I.

If you understand independent assortment, you should be able to draw gametes that can be produced by a $2n = 6$ animal. Name its chromosomes: maternal 1, paternal 1, maternal 2, paternal 2, maternal 3, and paternal 3. Use different colours for the maternal and paternal chromosomes.

How many different combinations of maternal and paternal homologs are possible when more chromosomes are involved? With each additional pair of chromosomes, the number of combinations doubles. In general, a diploid organism can produce 2^n combinations, where n is the haploid chromosome number. This means that you ($n = 23$) can produce 2^{23} , or about 8.4 million, gametes that differ in their combination of maternal and paternal chromosome sets—an impressive amount of genetic variation.

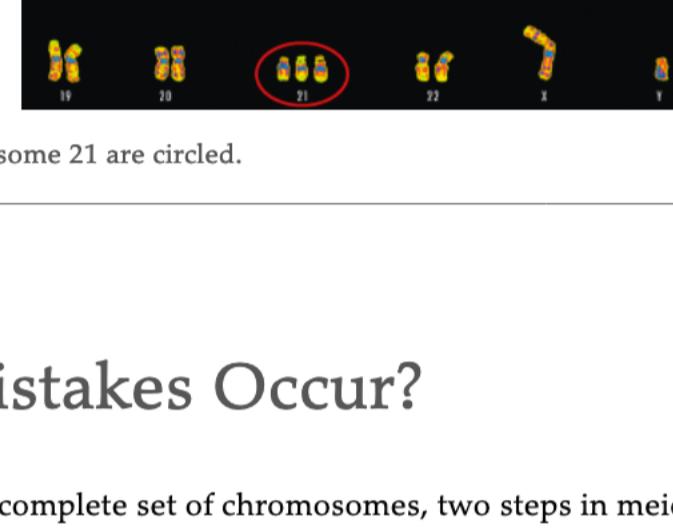
13.3 What Happens When Things Go Wrong in Meiosis?

Errors in meiosis are surprisingly common. If this were like a spelling mistake, it might be only an annoyance. But in humans, a conservative estimate is that a third of conceptions are spontaneously terminated because of problems in meiosis. What are the consequences for offspring if gametes contain an abnormal set of chromosomes?

In 1866, the British physician Langdon Down described a distinctive set of conditions that included mental impairment, a high risk for heart problems and leukemia, and a degenerative brain disorder similar to Alzheimer's disease. **Down syndrome** (see Chapter 16) as the disorder came to be called, is observed in about one infant in every 781 live births in Canada.

For over 80 years the cause of the syndrome was unknown. Then, in the late 1950s, a study of the chromosome sets of nine children with Down syndrome suggested that the condition is associated with an extra copy of chromosome 21. This situation is called **trisomy** ("three bodies")—in this case, trisomy-21—because each cell has three copies of the chromosome. Figure 13.12 shows an example. Human chromosomes are often shown arranged into this pattern, known as a **karyogram** (see Chapter 16). The explanation proposed for the trisomy was that a mistake had occurred during meiosis in either the mother or the father.

Figure 13.12 Chromosomes of an Individual with Down Syndrome.



The three copies of chromosome 21 are circled.

Look at Sciences/Getty Images

How Do Mistakes Occur?

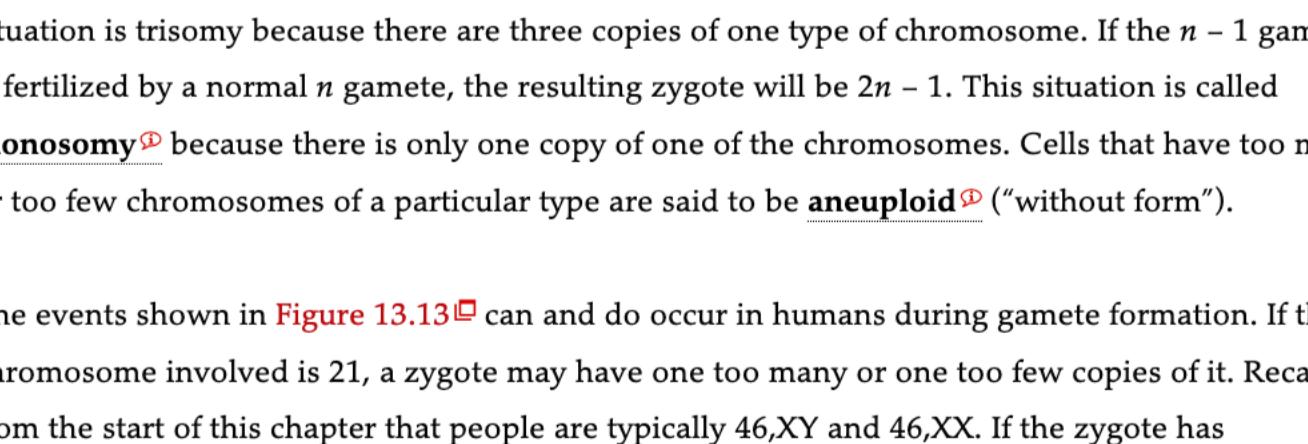
For a gamete to get one complete set of chromosomes, two steps in meiosis must be perfectly executed:

1. The chromosomes in each homologous pair must separate from each other during the first meiotic division, so that only one homolog ends up in each daughter cell.
2. Sister chromatids must separate from each other and move to opposite poles of the dividing cell during meiosis II.

If both homologs in meiosis I or both sister chromatids in meiosis II move to the same daughter cell, the products of meiosis will be abnormal. This sort of meiotic error is referred to as **nondisjunction**, because the homologs or sister chromatids fail to separate, or disjoin.

Figure 13.13 shows what happens when homologs do not separate correctly during meiosis I. Note that at the end of meiosis, two daughter cells have two copies of the same chromosome, while the other two lack that chromosome entirely. Gametes that contain an extra chromosome are symbolized as $n + 1$; gametes that lack one chromosome are symbolized as $n - 1$.

Figure 13.13 Nondisjunction Leads to Gametes with Abnormal Chromosome Numbers.



If homologous chromosomes fail to separate during meiosis I, the gametes that result will have an extra chromosome or will lack a chromosome. Nondisjunction can also occur during meiosis II if sister chromatids fail to separate.

If an $n + 1$ gamete is fertilized by a normal n gamete, the resulting zygote will be $2n + 1$. This situation is trisomy because there are three copies of one type of chromosome. If the $n - 1$ gamete is fertilized by a normal n gamete, the resulting zygote will be $2n - 1$. This situation is called **monosomy** because there is only one copy of one of the chromosomes. Cells that have too many or too few chromosomes of a particular type are said to be **aneuploid** ("without form").

The events shown in Figure 13.13 can and do occur in humans during gamete formation. If the chromosome involved is 21, a zygote may have one too many or one too few copies of it. Recall from the start of this chapter that people are typically 46,XY and 46,XX. If the zygote has trisomy-21, we can write its karyotype as 47,XY,+21 or 47,XX,+21. There are 47 chromosomes in total, either XX or XY sex chromosomes, and an extra chromosome 21. A zygote with monosomy-21 would be 45,XY,-21 or 45,XX,-21. The consequences of meiotic mistakes are sometimes severe. A zygote with trisomy-21 will become a person with Down syndrome while a zygote with monosomy-21 will not survive.

Why is aneuploidy harmful? Like any other chromosome, human chromosome 21 has genes—about 584 genes in fact. A person with Down syndrome has three copies of these genes instead of two. This upsets the normal formation of their brains and heart during embryogenesis leading to the health problems they experience. Embryos with monosomy-21 only have a single copy of these genes and cannot survive.

At conception, human zygotes may be trisomic or monosomic for any of the autosomes. Almost all are nonviable. Embryos with trisomy-21 live because this is our smallest autosome and it has the fewest genes. In one study of human pregnancies that ended in early embryonic or fetal death, 38 percent of the 119 cases involved atypical chromosome complements that resulted from mistakes in meiosis. Mistakes in meiosis are the leading cause of spontaneous abortion (miscarriage) in humans.

13.4 Why Does Meiosis Exist?

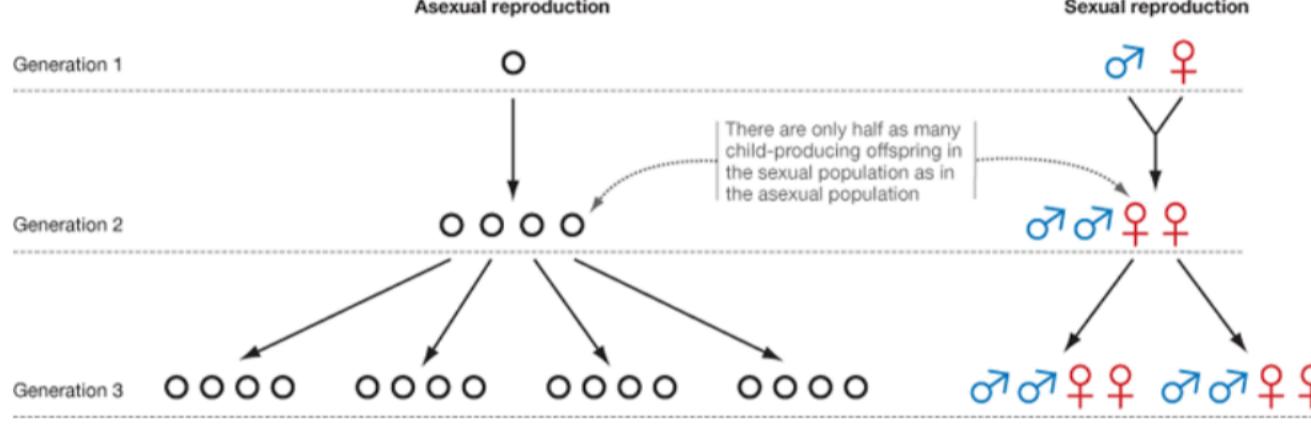
Why sex? Although it seems obvious that sex and therefore meiosis are needed universally for reproduction, that's not the case. Meiosis and sexual reproduction occur in only a small fraction of the lineages on the tree of life. Bacteria and archaea normally undergo only asexual reproduction; most algae, all fungi, and some animals and land plants reproduce both sexually and asexually. Asexual reproduction is even observed in some vertebrates. Several species of guppy in the genus *Poeciliopsis*, for example, reproduce exclusively by mitosis.

Although sexual reproduction plays a central role in the life of most familiar organisms—including us—until recently scientists had no clear idea of why it occurs. In fact, on the basis of theory, biologists had good reason to think that sexual reproduction should *not* exist.

The Paradox of Sex

In 1978, British biologist John Maynard Smith pointed out that the existence of sexual reproduction presents a paradox. Maynard Smith developed a mathematical model showing that because asexually reproducing individuals do not have to produce male offspring, their progeny on average can produce twice as many offspring as individuals that reproduce sexually. [Figure 13.16](#) diagrams this model by showing the number of females (♀), males (♂), and asexually reproducing organisms (\circ) produced over several generations by asexual versus sexual reproduction.

Figure 13.16 Asexual Reproduction Produces More Offspring.



Each female (♀), male (♂), and asexual (\circ) symbol represents an individual. This example assumes that (1) every asexual individual or sexually reproducing couple produces four offspring over the course of a lifetime, (2) sexually reproducing individuals produce half males and half females, and (3) all offspring survive to breed.

QUANTITATIVE In generation 2, there are only two more child-producing individuals in the asexual population than in the sexual population. If the same two-fold difference in reproductive rates were continued, how many more child-producing individuals would there be in the asexual compared to the sexual population of generation 5?

In this example, each asexually reproducing individual and each sexually reproducing couple produces four offspring over the course of their lifetimes. Note that in the sexual population, it takes two individuals—one male and one female—to produce four offspring. Two out of every four children that each female produces are males, who cannot themselves give birth to children. As a result, after one generation (generation 2 in [Figure 13.16](#)) the sexual population has just half as many child-producing individuals as the asexual population. Maynard Smith referred to this result as the “two-fold cost of males.” Asexual reproduction is much more efficient than sexual reproduction because no males are produced.

Based on this analysis, what will happen when asexual and sexual individuals exist in the same population? If all other things are equal, individuals that reproduce asexually should increase in frequency in the population while individuals that reproduce sexually should decline in frequency. In fact, Maynard Smith’s model predicts that sexual reproduction is so inefficient that it should be eliminated.

To resolve this paradox, biologists began examining the assumption “If all other things are equal.” Were there ways that meiosis and outcrossing could lead to the production of offspring that reproduce more than asexually produced individuals do? After decades of debate and analysis, two solid hypotheses to explain the paradox of sex have emerged.