# Chapter 6

# Cell Division and Reproduction

## 6.1 Lesson 6.1: Chromosomes and the Cell Cycle

### Lesson Objectives

- Describe the properties of cell division in prokaryotes.
- Describe cell division in eukaryotes. Explain the main differences between cell division in prokaryotic and eukaryotic cells.
- Describe the basic properties of chromosomes.
- Describe the key steps in the cell cycle.
- Identify and describe the main processes in mitosis.
- Describe how the cell cycle is controlled and define cancer.

### Introduction

You are made of many different types of cells. Nerve cells, skin cells, muscle cells, and many more. These cells obviously have many different functions, yet they all develop from the first cell that makes you. So do they all have the same DNA? Are all the cells in your body genetically identical? How does the first cell of an organism know to become two cells, then four cells, and so on? What tells these cells what to do? Your body produces about 25 million genetically identical cells every second. These new cells are formed when older cells divide, a process called cell division or cell reproduction.

Cell division is the final step in the life of a cell, otherwise known as the cell cycle. Eukaryotic cells and prokaryotic cells complete this process by a number of different mechanisms. The cell cycle is a repeating series of events, during which the eukaryotic cell carries out its necessary functions, including metabolism, cellular growth, and division, resulting in two genetically identical daughter cells. To produce two genetically identical daughter cells, the chromosomes need to replicate and the nucleus and cytoplasm need to divide. These are key events in the life of a cell.

## Cell Division in Prokaryotes

Prokaryotic organisms reproduce asexually by **binary fission**, a process that produces identical offspring (**Figure** 6.1). In asexual reproduction, a single parent produces genetically identical offspring. As prokaryotes do not have a nucleus, and have only one circular chromosome, they do not need to reproduce by the same mechanism as eukaryotic cells. Prokaryotic cell division is a much simpler process. In prokaryotic cell division, after the single chromosome is copied, the cell grows larger. Eventually the two chromosomes separate and move to opposite ends of the cell. Newly formed cell membrane then grows into the center of the cell, separating the two chromosomes, and forming two genetically identical daughter cells. The formation of two daughter cells is called cytokinesis.

Under ideal conditions, reproduction in bacteria is extremely efficient, with some bacteria reproducing every 20 minutes. This makes bacteria an extremely effective tool for the molecular biologist. However, bacteria do not usually live in ideal conditions; otherwise, bacteria would grow and divide extremely rapidly, eventually covering the surface of Earth. Bacterial growth is limited by nutrients and water, predation, and by their own wastes.

## Cell Division in Eukaryotes

Cell division in eukaryotic organisms is very different from that in prokaryotes, mainly because of the many chromosomes in the nuclei of eukaryotic cells. Cell division in eukaryotic organisms is necessary for development, growth, and repair. This cell division ensures that each resulting daughter cell receives a complete copy of the organism's entire genome. Remember that all of an organism's DNA must be present in each somatic, or body, cell. This DNA contains the information necessary for that cell to perform its functions, and to give that organism its traits. Therefore, prior to cell division, the eukaryotic cell's complete genome must be copied, ensuring that each daughter cell receives a complete set of the genome.

The formation of **gametes**, an organism's reproductive cells, such as sperm and egg cells, involves a completely different method of cell division. This cell division ensures that each gamete receives half the amount of an organism's DNA.

## DNA, Chromosomes, and Genes

As previously discussed (in the *Foundations of Life Science* chapter), DNA contains the information necessary to make proteins, direct a cell's activities, and give an organism its traits. This information is organized into structural units scattered along the length of the

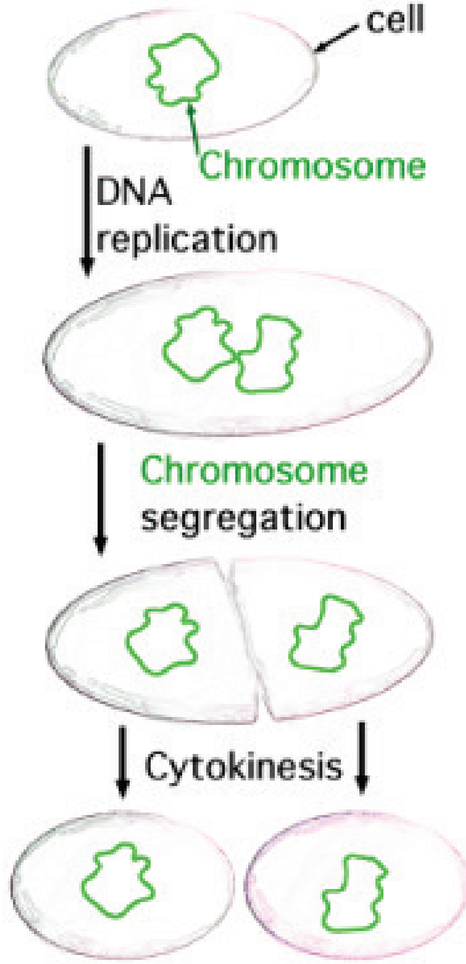


Figure 6.1: Binary fission. In binary fission, the single chromosome is copied and eventually separates into two separate chromosomes, the cell grows larger, and two identical cells form by cytokinesis. (14)

DNA molecule. These units are known as **genes**. A gene contains the information necessary to encode an RNA molecule or a protein. A single DNA molecule contains hundreds to thousands of genes. Different cell types use the information in different genes to make different proteins. This process gives different cell types distinct activities. Thus, a liver cell will have many different proteins than a kidney cell, giving the two cells types distinct activities. When a cell is using the information within a gene, the segment of DNA containing that gene is unwound, exposing the double helix to the cell machinery needed to use that information.

Prior to cell division, the DNA must duplicate itself in a process called DNA replication. This ensures that each resulting cell receives a complete set of the organism's genome. But how is the replicated DNA divided up evenly? What guarantees that each new cell will receive a complete set of DNA? It was the identification of chromosomes that allowed this process to be characterized. As a eukaryotic cell prepares to divide, the DNA and associated proteins (histones) coil into a structure, known as a **chromosome** (**Figure** 6.2). The DNA copies itself prior to this process, so the chromosome that forms consists of two identical chromatids, known as **sister chromatids**, identical copies of DNA. The two chromatids are attached at a region called the **centromere.** The chromatids separate from each other when the nucleus divides just prior to cell division. Thus, each new cell that results after cell division will have the complete amount of genetic material, identical to the original, or parent, cell. In human cells, this amounts to 46 chromosomes. These chromosomes come in pairs (one from each pair inherited from each parent). So these 46 chromosomes are actually two sets of 23 chromosomes each. For an animation of how the DNA coils into a chromosome, see http://www.hhmi.org/biointeractive/media/DNAi_packaging_vo2-sm.mov.

Each human somatic cell (a body cell, or every cell other than a gamete) normally has two sets of chromosomes, one set inherited from each parent. Each set contains 23 chromosomes, for a total of 46 chromosomes. Each chromosome differs in size, from over 250 million nucleotide pairs to less than 50 million nucleotide pairs. Each chromosome contains a specific set of genes, making each chromosome essential to survival.

Each pair of chromosomes consists of two chromosomes that are similar in size, shape, and genes. These pairs of chromosomes are known as **homologous chromosomes**, or **homologues**. Upon fertilization, a **zygote** is formed (**Figure** 6.3). A zygote is the first cell of a new individual. In humans, a zygote contains 23 pairs (or two sets) of chromosomes. Any cell containing two sets of chromosomes is said to be **diploid**. The zygote forms from the fusion of two **haploid** gametes. A haploid cell contains one set of chromosomes. In humans, a haploid gamete contains 23 chromosomes. Biologists use the symbol $n$ to represent one set of chromosomes, and $2n$ to represent two sets. In humans, each set of chromosomes contains 22 **autosomes** and 1 sex chromosome. Autosomes are chromosomes that are not directly involved in determining the sex of an individual. The sex chromosomes contain genes that determine the sex of an individual.

Whereas autosomes are found as homologous pairs in somatic cells, sex chromosomes come in two different sizes, shapes, and contain different genes. In many organisms, including

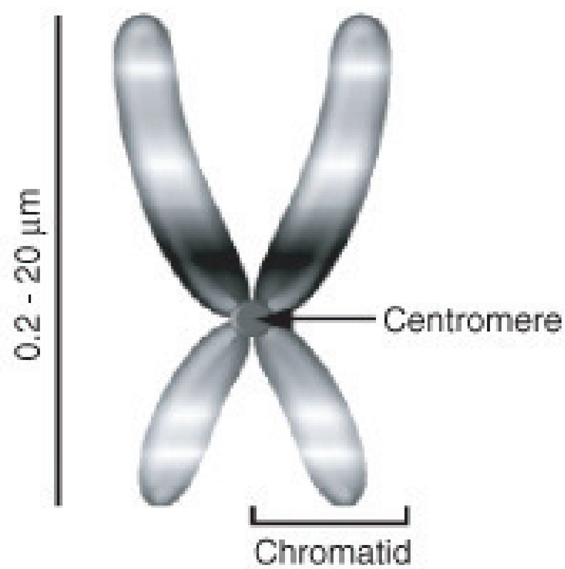


Figure 6.2: A representation of a condensed eukaryotic chromosome, as seen after the DNA has been copied. The chromosome is made of two identical, or sister, chromatids held together by a centromere. (5)

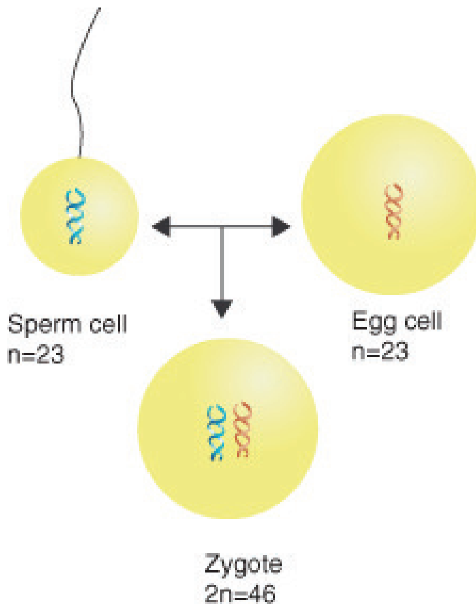


Figure 6.3: Upon fertilization a diploid zygote is formed. In humans, a zygote has 46 chromosomes, 23 inherited from each parent. The gametes, sperm and eggs, are haploid cells, with 23 chromosomes each. (7)

humans, the sex chromosomes are known as the X and Y chromosomes. The Y chromosome contains genes that cause male development. Therefore, any individual with a Y chromosome is male, and a male will have both an X and Y chromosome (XY). Females, without a Y chromosome, will have two X chromosomes (XX). As females have two X chromosomes, they must pass an X chromosome to all of their children. As males have both an X chromosome (inherited from their mother) and a Y chromosome, they can give either chromosome to their children. If a child inherits a Y from his father, he will be male; if a child inherits an X from her father, she will be female. It therefore is the male gamete that determines the sex of the offspring.

## The Cell Cycle

Cell division in eukaryotic cells is much more complex than in prokaryotic cells because of the many chromosomes within the nucleus. Both the cytoplasm and the genetic material must be divided, ensuring that each resulting daughter cell receives 46 separate chromosomes. To ensure this, in addition to the cell performing its necessary functions, the DNA must be copied, as must many organelles, prior to cell division.

The life of a eukaryotic cell is a cycle, known as the **cell cycle** (**Figure** 6.4). The cell cycle is a repeating series of cellular growth and division. The cell cycle has five phases: the first growth ($G_1$) phase, the synthesis (S) phase, the second growth ($G_2$) phase, mitosis, and cytokinesis, though many consider mitosis and cytokinesis to be combined into one phase. The cell spends the majority of the cycle in the first three phases of the cycle, collectively known as **interphase**. After cytokinesis, two genetically identical daughter cells are formed.

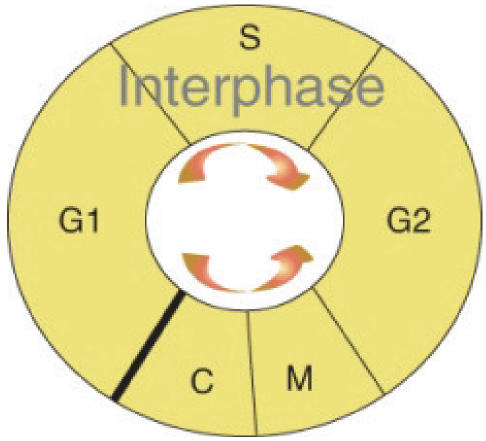


Figure 6.4: The Cell Cycle. The cell cycle depicts the life of an eukaryotic cell. The cell cycle has five phases: the first growth ($G_1$) phase, the synthesis (S) phase, the second growth ($G_2$) phase, mitosis (M), and cytokinesis (C). The cell spends the majority of the cycle in the first three phases ($G_1$, S, $G_2$) of the cycle, collectively known as interphase. After cytokinesis, two genetically identical daughter cells are formed. Many consider the cell cycle to only have four phases, with mitosis and cytokinesis combined. http://www.cellsalive.com/cell_cycle.htm has an excellent animation of the cell cycle. (3)

The first growth ($G_1$) phase: The cell spends most of its life in the $G_1$ phase. During this phase, a cell undergoes rapid growth and the cell performs its routine functions. If a cell is not dividing, the cell remains in this phase.

The synthesis (S) phase: For two genetically identical daughter cells to be formed, the cell's DNA must be copied or replicated. When the DNA is replicated, both strands of the double helix are used as templates to produce two new complementary strands. These new strands then hydrogen bond to the template strands and two double helices form.

The second growth ($G_2$) phase is a shortened growth period in which many organelles are reproduced or manufactured. Parts necessary for cell division are made during $G_2$.

**Mitosis** is the phase of nuclear division, in which one nucleus divides and becomes two nuclei. After mitosis is **cytokinesis**, in which the cytoplasm divides in half, producing two daughter cells, each containing a complete set of genetic material.

## Mitosis

Mitosis is the division of the cell's nucleus, the final step before two daughter cells are produced. The cell enters mitosis as it approaches its size limitations. Four distinct phases of mitosis have been recognized: *prophase, metaphase, anaphase, and telophase,* with each phase merging into the next one (**Figure** 6.5).

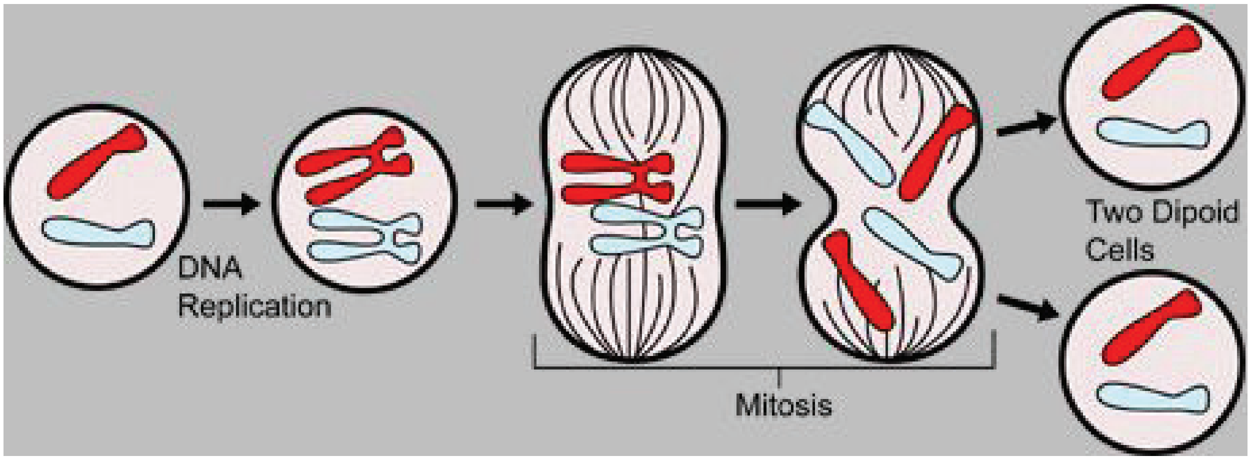


Figure 6.5: During mitosis, the nucleus divides, paving the way for two cells to be produced after cell division, each with a complete makeup of genetic material. `http://www.biology.arizona.edu/Cell_bio/tutorials/cell_cycle/MitosisFlash.html` has an excellent animation of mitosis. (1)

Prophase is the first and longest phase of mitosis. During prophase, the DNA coils up into visible chromosomes, each made up of two sister chromatids held together by the centromere. The nucleus disappears as the nuclear envelope and nucleolus break apart. The centrioles begin to move to opposite ends, or poles, of the cell. As the centrioles migrate, the fiber-like spindle begins to elongate between the centrioles. The spindle is a thin, cage-like structure made out of microtubules. In plant cells, the spindle forms without centrioles. The spindle plays an essential role moving chromosomes and in the separation of sister chromatids.

During metaphase the spindle attaches to the centromere of each chromosome. Helped by the spindle, the chromosomes line up at the center, or equator, of the cell, also known as the metaphase plate. Each sister chromatid is attached to a separate spindle fiber, with one fiber extending to one pole, and the other fiber extending to the other pole. This ensures that the sister chromatids separate and end up in distinct cells after cell division.

Anaphase is the phase in which the sister chromatids separate. The sister chromatids are pulled apart by the shortening of the microtubules of the spindles, similar to the reeling in of a fish by the shortening of the fishing line. One sister chromatid moves to one pole of the cell, and the other sister chromatid moves to the opposite pole. At the end of anaphase, each pole of the cell has a complete set of chromosomes, identical to the amount of DNA at the beginning of $G_1$ of the cell cycle.

Telophase is essentially the opposite of prophase. The chromosomes begin to unwind in preparation to direct the cell's metabolic activities. The spindle begins to break down, allowing a new nucleus to form. This is followed by cytokinesis, the division of the cytoplasm, resulting in two genetically identical cells, ready to enter $G_1$ of the next cell cycle. The phases of mitosis are summarized in **Figure** 6.6.

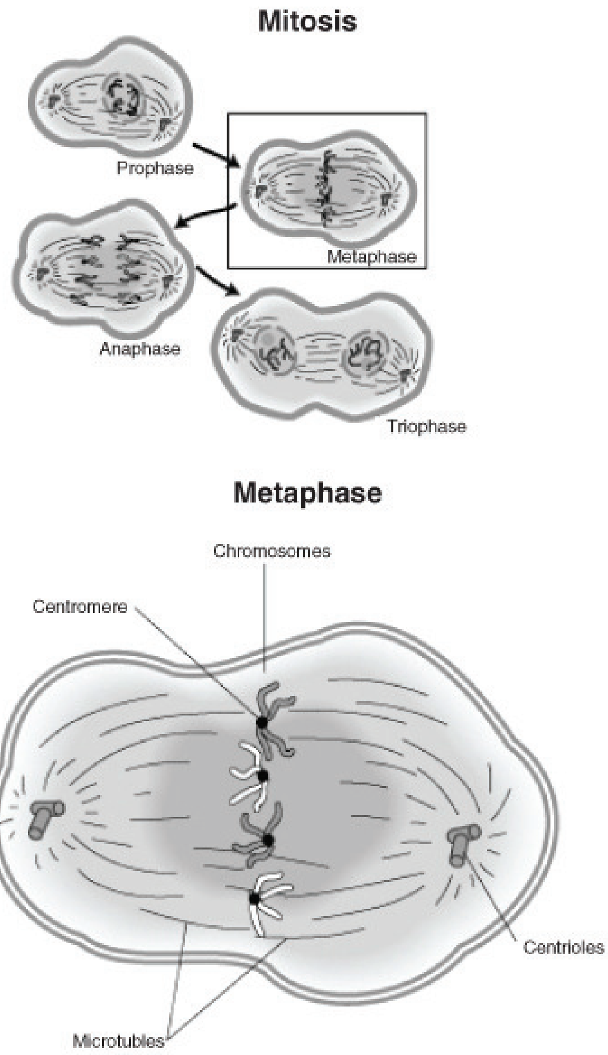


Figure 6.6: Mitosis. The phases of mitosis are depicted. The second phase, metaphase, is shown with the chromosomes lined up at the equator of the cell and the microtubule spindle fibers extending from the centrioles to the centromeres of the chromosomes. (10)

Cytokinesis (**Figure** 6.7) differs between plant and animal cells. In animal cells, the plasma membrane pinches inward along the cell's equator until two cells are formed. In plant cells, a cell plate forms along the cells equator. A new membrane grows along each side of the cell plate, with a new cell wall forming on the outside of each new membrane.

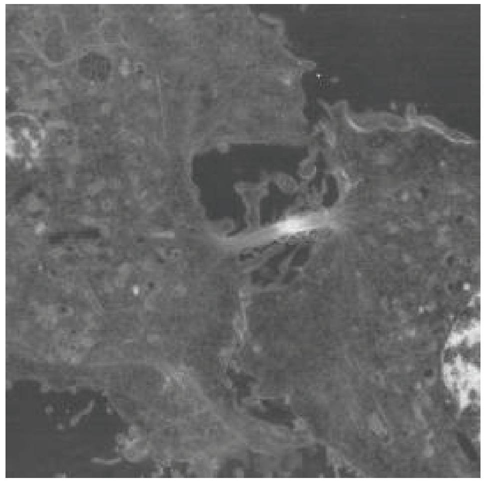

Figure 6.7: Cytokinesis. In this electron micrograph of a cell, two formation of two new cells is almost complete, as new membrane grows and divides the parent cell. (15)

## Control of the Cell Cycle

How does the cell know when to divide? How does the cell know when to replicate the DNA? The answers to these questions have to do with the control of the cell cycle. But how is the cell cycle controlled?

The cell cycle is controlled by a number of protein-controlled feedback processes. Two types of proteins involved in the control of the cell cycle are kinases and cyclins. Cyclins activate kinases. Cyclins are a group of proteins that is rapidly produced at key stages in the cell cycle. Kinases activate other target molecules. It is this precise regulation of proteins that triggers advancement through the cell cycle.

The cell cycle has key checkpoints. When the cell receives key signals or information (feedback regulation), the cell can begin the next phase of the cell cycle. The cell can also receive signals that delay passage to the next phase of the cell cycle. These signals allow the cell to complete the previous phase before moving forward. Three key checkpoints are the cell growth ($G_1$) checkpoint, the DNA synthesis ($G_2$) checkpoint, and the mitosis checkpoint.

The cell growth ($G_1$) checkpoint allows the cell to proceed into the S phase of the cell cycle and continue on to divide. The cell spends most of the cycle in the $G_1$ phase. $G_1$ is where the cell carries out its main functions. If the cell has performed its functions and has grown to significant size to be divided in half, key proteins will stimulate DNA replication to begin. If the cells are not to divide, such as some muscle and nerve cells, the cell will stop at this checkpoint and move into a resting phase. Some cells may stay in this resting period permanently, never dividing.

The DNA synthesis ($G_2$) checkpoint determines if the cell is ready for mitosis. DNA repair enzymes check the replicated DNA at this point. If the checkpoint is passed, the many molecular mechanisms and processes needed for mitosis will begin.

The mitosis checkpoint determines the end of one cycle and the beginning of the next. This checkpoint signals the end of mitosis, allowing the cell to prepare for the beginning of $G_1$ of the next cell cycle.

## Cancer and the Cell Cycle

Many cancers result from uncontrolled cell division, when the regulation of the cycle is lost (**Figure** 6.8). Cancerous cells divide much more rapidly than healthy cells. These cells use the blood and nutrients that other cells need and they can stress the environment of the healthy cells. As cancerous cells do not provide any useful function to the organism, they are extremely harmful. If cancerous cells are allowed to grow uncontrolled, they will kill the host organism. Many cancerous cells are the products of normal cells that have lost the ability to regulate the cell cycle. The genes that encode the proteins involved in cell cycle regulation have mutations. One category of genes, called oncogenes, accelerate the cell cycle. Many cancers can be inherited, such as breast cancer. Others are triggered by an environmental stimulus, such as through the relationship between tobacco smoke and lung cancer, or ultraviolet radiation and skin cancer.

## Lesson Summary

- The cell cycle is a repeating series of events, characterizing the life of a eukaryotic cell.
- Binary fission is a form of cell division in prokaryotic organisms that produces identical offspring.
- As a eukaryotic cell prepares to divide, the DNA and associated proteins coil into a structure, known as a chromosome.
- The DNA copies during the S phase of the cell cycle, resulting in a chromosome that consists of two identical chromatids, known as sister chromatids, attached at a region called the centromere.
- Any cell containing two sets of chromosomes is said to be diploid; the zygote forms from the fusion of two haploid gametes.
- The cell cycle has five phases: the first growth ($G_1$) phase, the synthesis (S) phase, the second growth ($G_2$) phase, mitosis, and cytokinesis.
- Mitosis is the division of the nucleus; four distinct phases of mitosis have been recognized: prophase, metaphase, anaphase, and telophase.
- Cytokinesis is the division of the cytoplasm.
- The cell cycle is controlled through feedback mechanisms.
- Cancer results from uncontrolled cell division, due to the loss of regulation of the cell cycle.

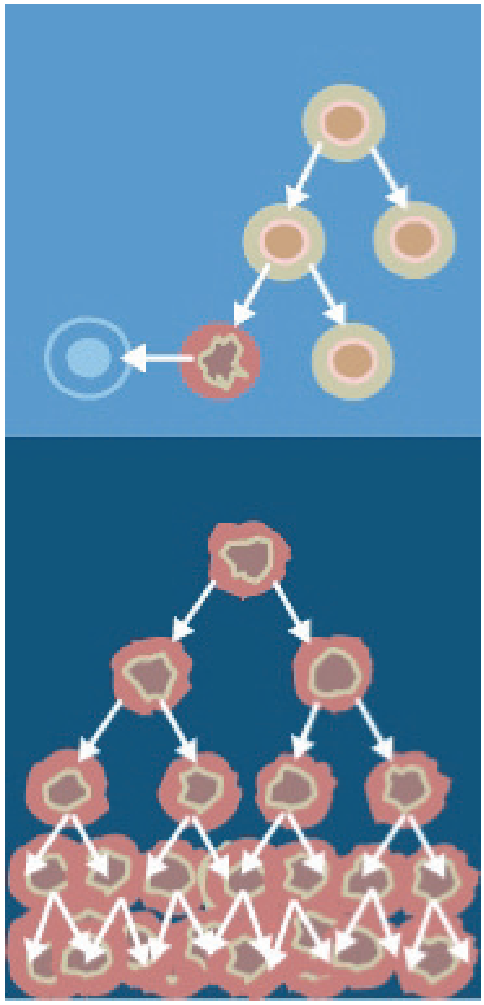

Figure 6.8: When normal cells are damaged beyond repair, they are eliminated. (A) diagrams damaged cells being destroyed. Cancer cells avoid elimination and, because of uncontrolled cell division, continue to multiply in an unregulated manner. (B) depicts damaged cells dividing in an uncontrolled fashion. (12)

## Review Questions

1. How does cell division in bacteria differ from mitosis in eukaryotes?
2. Describe the structure of a chromosome in prophase of mitosis.
3. What is cytokinesis and when does it occur?
4. What is a centromere?
5. Describe interphase.
6. Describe the main steps of mitosis.
7. What is binary fission?
8. Define a gene.

## Further Reading / Supplemental Links

- http://www.genome.gov
- http://www.cellsalive.com/mitosis.htm
- http://www.cellsalive.com/cell_cycle.htm
- http://biology.clc.uc.edu/courses/bio104/mitosis.htm
- http://nobelprize.org/educational_games/medicine/2001

## Vocabulary

**autosomes** Chromosomes that are not directly involved in determining the sex of an individual.

**binary fission** Asexual reproduction in prokaryotic organisms; produces identical offspring.

**cancer** Disease that can result from uncontrolled cell division, when the regulation of the cycle is lost.

**cell cycle** A repeating series of events, during which the eukaryotic cell carries out its necessary functions, including metabolism, cellular growth, and division, resulting in two genetically identical daughter cells.

**cell division** Process of cell formation from the division of older cells.

**cell plate** Forms during cytokinesis in plant cells; a new membrane grows along each side of the cell plate, with a new cell wall forming on the outside of each new membrane.

**centriole** Structure from which spindle fibers originate.

**centromere** Region that attaches two sister chromatids; approximately near the middle of a chromosome.

**chromosome** Coiled structure of DNA and histone proteins; allows for the precise separation of replicated DNA; forms during prophase of mitosis and meiosis.

**cyclins** A group of proteins that is rapidly produced at key stages in the cell cycle; activate kinases; participate in the regulation of the cell cycle.

**cytokinesis** Division of the cytoplasm, forming two daughter cells.

**diploid** A cell containing two sets of chromosomes; in human cells, two sets contains 46 chromosomes.

**DNA replication** Process by which the DNA is copied, resulting in two identical copies.

**gametes** An organism's reproductive cells, such as sperm and egg cells.

**gene** A segment of DNA that contains the information necessary to encode an RNA molecule or a protein.

**haploid** A cell containing one set of chromosomes; in human gametes, one set is 23 chromosomes.

**homologous chromosomes** A pair of chromosomes (one from each parent) consisting of two chromosomes that are similar in size, shape, and genes; also known as homologues.

**interphase** The first three phases of the cell cycle; the cell spends the majority of its time here.

**kinases** Proteins involved in the regulation of the cell cycle; activated by cyclins; activate other target molecules.

**metaphase plate** The center (equator) of a cell during mitosis; chromosomes line up at the metaphase plate to ensure the proper separation of the chromatids.

**mitosis** The division of the nucleus into two genetically identical nuclei.

**oncogene** Cancer causing gene; can accelerate the cell cycle.

**resting phase** Phase associated with the $G_1$ phase of the cell cycle; cells that do not divide are in a resting phase and do not continue to the S phase.

**S phase** Synthesis phase; the phase of the cell cycle in which the DNA is replicated (copied).

**sex chromosomes** Contain genes that determine the sex of an individual.

**sister chromatid** Identical copies of a DNA molecule; a chromosome at the start of mitosis and meiosis has two sister chromatids.

**spindle** Thin, cage-like fibers made out of microtubules; used to move chromosomes and to separate the sister chromatids during mitosis.

**zygote** The first cell of a new individual.

## Points to Consider

- A human cell has 46 chromosomes, while a bacterial cell has only one chromosome. Would you think that the number of chromosomes relates to the complexity of the cell or organism?
- Mitosis and cytokinesis produce two genetically identical daughter cells. Think about how a cell with half as much DNA, such as a sex cell, may form.
- As not every species has members of the opposite sex, such as bacteria, yet all organisms must reproduce to stay alive, think about how these sexless organisms may reproduce.

# 6.2 Lesson 6.2: Meiosis

## Lesson Objectives

- Describe asexual reproduction; explain the genetic relationship between parent and offspring.
- Describe sexual reproduction; explain the genetic relationship between parent and offspring.
- Identify and describe the main steps of meiosis, distinguishing between the quantity of genetic material in the parent and resulting cells.
- Describe gametogenesis and identify the key differences between oogenesis and spermatogenesis.
- Distinguish between the three types of sexual life cycles.

## Introduction

Some organisms look and act exactly like their parent. Others share many similar traits, but they are definitely unique individuals. Some species have two parents, whereas others have just one. How an organism reproduces determines the amount of similarity the organism will have to its parent. Asexual reproduction produces an identical individual, whereas sexual reproduction produces a similar, but unique, individual. In sexual reproduction, meiosis produces haploid gametes that fuse during fertilization to produce a diploid zygote (**Figure** 6.9 and **Figure** 6.11).

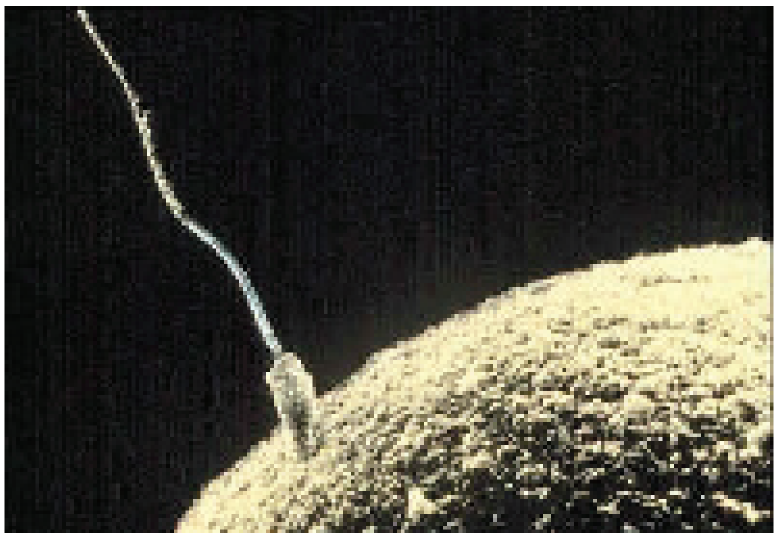

Figure 6.9: Fertilization of an egg cell by a sperm cell. In sexual reproduction, haploid gametes fuse to produce a diploid zygote. (4)

## Asexual Reproduction

Are there male and female bacteria? How could you tell? Remember, bacteria have just one chromosome; they do not have an X or Y chromosome. So they probably have a very simplified form of reproduction. Asexual reproduction, the simplest and most primitive method of reproduction, produces a **clone**, an organism that is genetically identical to its parent. Haploid gametes are not involved in asexual reproduction. A parent passes all of its genetic material to the next generation. All prokaryotic and many eukaryotic organisms reproduce asexually.

There are a number of types of asexual reproduction including fission, fragmentation and budding. In fission, a parent separates into two or more individuals of about equal size. In fragmentation, the body breaks into several fragments, which later develop into complete adults. In budding, new individuals split off from existing ones. The bud may stay attached or break free from the parent. Eukaryotic organisms, such as the single cell yeast and multicellular hydra, undergo budding (**Figure** 6.10).

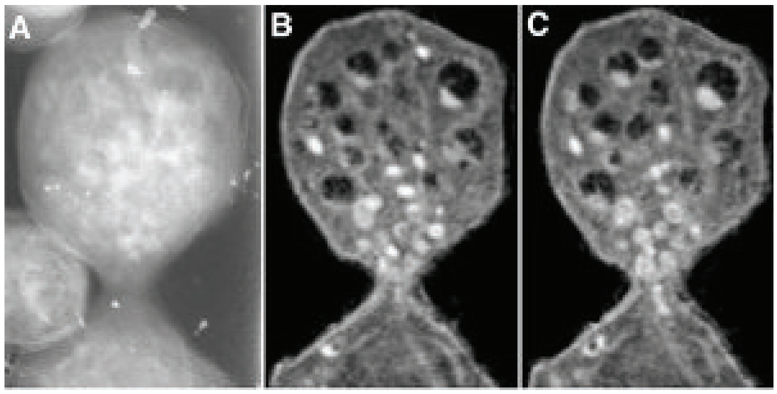


Figure 6.10: Magnification of a budding yeast. (8)

## Sexual Reproduction and Meiosis

Why do you look similar to your parents, but not identical? First, it is because you have two parents. Second, it is because of sexual reproduction.

Whereas asexual reproduction produces genetically identical clones, sexual reproduction produces genetically diverse individuals. As both parents contribute half of the new organism's genetic material, the offspring will have traits of both parents, but will not be exactly like either parent.

Organisms that reproduce sexually by joining gametes, a process known as fertilization, must have a mechanism to produce haploid gametes. This mechanism is meiosis, a type of cell division that halves the number of chromosomes. During meiosis the pairs of chromosomes separate and segregate randomly to produce gametes with one chromosome from each pair. Meiosis involves two nuclear and cell divisions without an interphase in between, starting with one diploid cell and generating four haploid cells (**Figure** 6.11). Each division, named meiosis I and meiosis II, has four stages: prophase, metaphase, anaphase, and telophase. These stages are similar to those of mitosis, but there are distinct and important differences.

Prior to meiosis, the cell's DNA is replicated, generating chromosomes with two sister chromatids. A human cell prior to meiosis will have 46 chromosomes, 22 pairs of homologous autosomes, and 1 pair of sex chromosomes. Homologous chromosomes are similar in size, shape, and genetic content. You inherit one chromosome of each pair from your mother and the other one from your father.

The 8 stages of meiosis are summarized below. The stages will be described for a human cell, starting with 46 chromosomes.

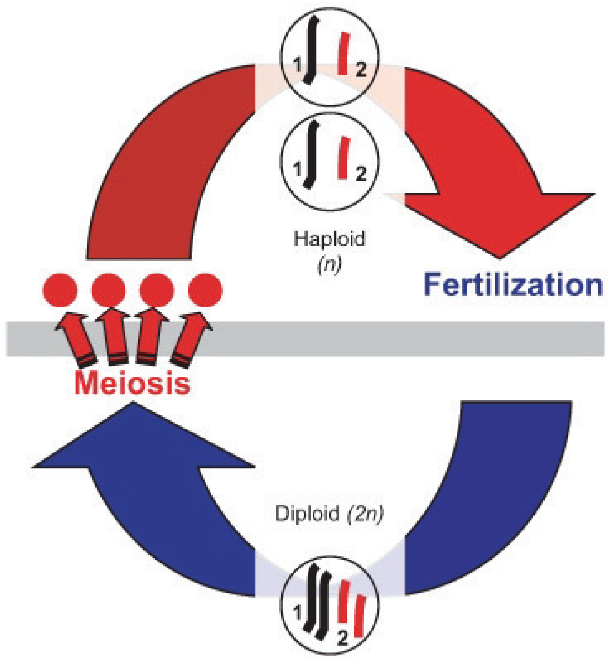


Figure 6.11: During meiosis the number of chromosomes is reduced from a diploid number (2n) to a haploid number (n). During fertilization, haploid gametes come together to form a diploid zygote and the original number of chromosomes (2n) is restored. (9)

Prophase I: prophase I is very similar to prophase of mitosis, but with one very significant difference. In Prophase I, the nuclear envelope breaks down, the chromosomes condense, and the centrioles begin to migrate to opposite poles of the cell, with the spindle fibers growing between them. During this time, the homologous chromosomes form pairs. These homologous chromosomes line up gene-for-gene down their entire length, allowing crossing-over to occur. This is an important step in creating genetic variation and will be discussed later.

Metaphase I: In metaphase I, the 23 pairs of homologous chromosomes line up along the equator of the cell. During mitosis, 46 individual chromosomes line up during metaphase. Some chromosomes inherited from the father are facing one side of the cell, and some are facing the other side.

Anaphase I: During anaphase I the spindle fibers shorten, and the homologous chromosome pairs are separated from each other. One chromosome from each pair moves toward one pole, with the other moving toward the other pole, resulting in a cell with 23 chromosomes at one pole and the other 23 at the other pole. The sister chromatids remain attached at the centromere. Because human cells have 23 pairs of chromosomes, this independent assortment of chromosomes produces $2^{23}$, or 8,388,608 possible configurations. More on independent assortment of chromosomes will be presented in the chapter on Mendelian Genetics.

Telophase I: The spindle fiber disassembles and the nucleus reforms. This is quickly followed by cytokinesis and the formation of two haploid cells, each with a unique combination of chromosomes, some from the father and the rest from the mother. After cytokinesis, both cells immediately enter meiosis II; the DNA is not copied in between. Meiosis II is essentially the same as mitosis, separating the sister chromatids from each other.

Prophase II: Once again the nucleus breaks down, and the spindle begins to reform as the centrioles move to opposite sides of the cell.

Metaphase II: The spindle fibers align the 23 chromosomes, each made out of two sister chromatids, along the equator of the cell.

Anaphase II: The sister chromatids are separated and move to opposite poles of the cell. As the chromatids separate, each is known as a chromosome. Anaphase II results in a cell with 23 chromosomes at each end of the cell; each chromosome contains half as much genetic material as at the start of anaphase II.

Telophase II: The nucleus reforms and the spindle fibers break down. Each cell undergoes cytokinesis, producing four haploid cells, each with a unique combination of genes and chromosomes.

- An excellent animation depicting meiosis can be viewed at

http://www.youtube.com/watch?v=D1_-mQS_FZ0&feature=related.

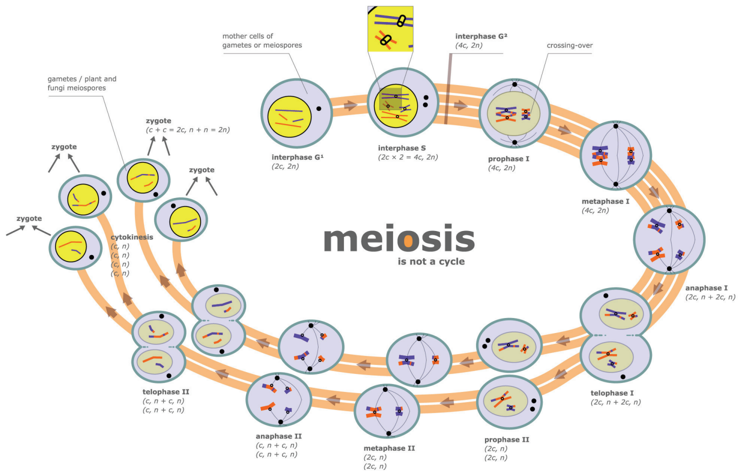


Figure 6.12: Meiosis is a process in which a diploid cell divides itself into four haploid cells. *c* represents the number of chromosomes, *n* represents a haploid cell, *2n* represents a diploid cell. (16)

## Meiosis and Genetic Variation

Sexual reproduction results in infinite possibilities of genetic variation. This occurs through a number of mechanisms, including crossing-over, the independent assortment of chromosomes during anaphase I, and random fertilization.

Crossing-over occurs during prophase I. Crossing-over is the exchange of genetic material between non-sister chromatids of homologous chromosomes. Recall during prophase I, homologous chromosomes line up in pairs, gene-for-gene down their entire length, forming a configuration with four chromatids, known as a **tetrad**. At this point, the chromatids are very close to each other and some material from two chromatids switch chromosomes, that is, the material breaks off and reattaches at the same position on the homologous chromosome (**Figure** 6.13). This exchange of genetic material can happen many times within the same pair of homologous chromosomes, creating unique combinations of genes. This process is also known as **recombination**.

As mentioned above, in humans there are over 8 million configurations in which the chromosomes can line up during metaphase I. It is the specific processes of meiosis, resulting in four unique haploid cells, that results in these many combinations. **Figure** 6.14 compares mitosis and meiosis. This independent assortment, in which the chromosome inherited from either the father or mother can sort into any gamete, produces the potential for tremendous genetic variation. Together with random fertilization, more possibilities for genetic variation exist between any two people than individuals alive today. Sexual reproduction is the random fertilization of a gamete from the female using a gamete from the male. In humans, over 8 million ($2^{23}$) chromosome combinations exist in the production of gametes in both the male

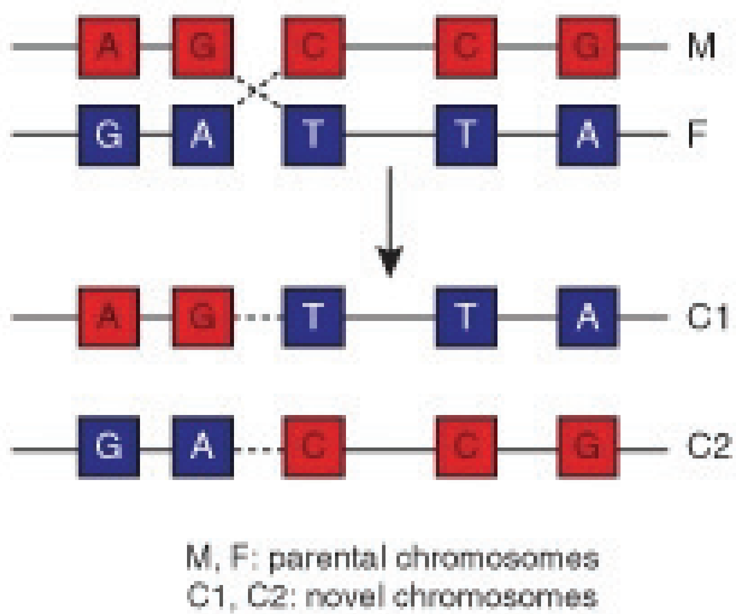


Figure 6.13: Crossing-over. A maternal strand of DNA is shown in red. Paternal strand of DNA is shown in blue. Crossing over produces two chromosomes that have not previously existed. The process of recombination involves the breakage and rejoining of parental chromosomes (M, F). This results in the generation of novel chromosomes (C1, C2) that share DNA from both parents. (2)

and female. A sperm cell, with over 8 million chromosome combinations, fertilizes an egg cell, which also has over 8 million chromosome combinations. That is over 64 trillion unique combinations, not counting the unique combinations produced by crossing-over. In other words, each human couple could produce a child with over 64 trillion unique chromosome combinations.

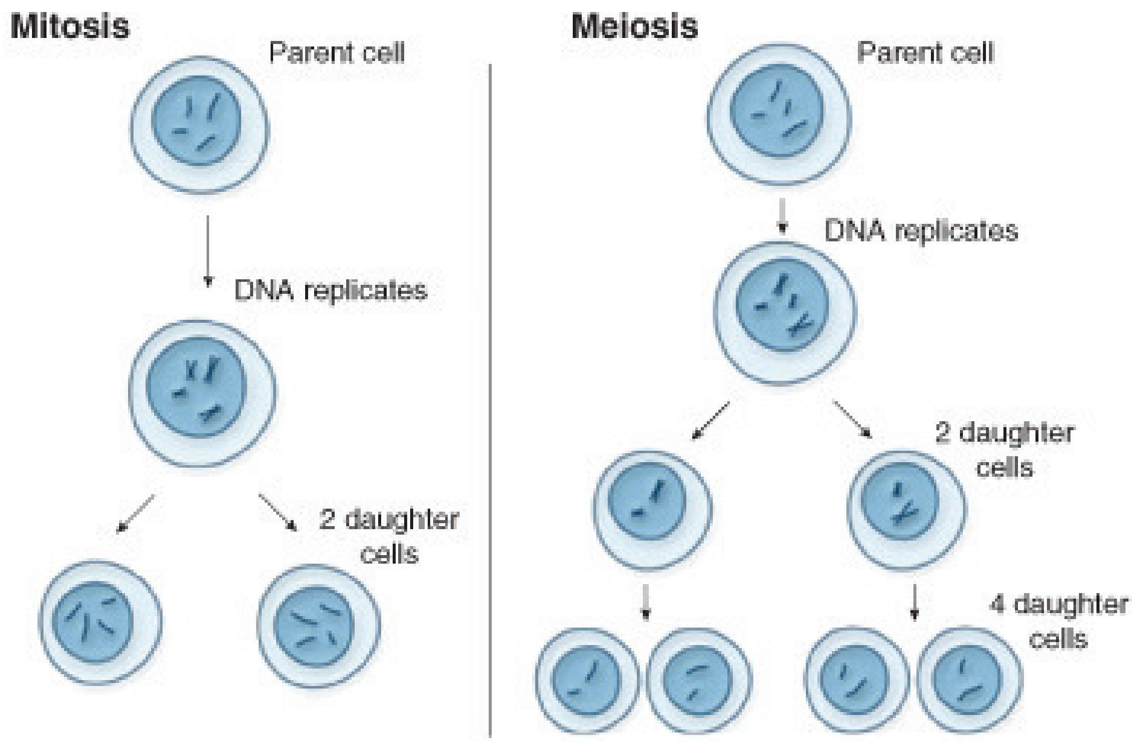


Figure 6.14: Mitosis vs. Meiosis Comparison. Mitosis produces two diploid daughter cells, genetically identical to the parent cell. Meiosis produces four haploid daughter cells, each genetically unique. See How Cells Divide: Mitosis vs. Meiosis (www.pbs.org/wgbh/nova/miracle/divide.html) for an animation comparing the two processes. (13)

## Gametogenesis

At the end of meiosis, haploid cells are produced. These cells need to further develop into mature gametes capable of fertilization, a process called **gametogenesis** (**Figure** 6.15).

Gametogenesis differs between the sexes. In the male, the production of mature sperm cells, or **spermatogenesis**, results in four haploid gametes, whereas, in the female, the production of a mature egg cell, **oogenesis**, results in just one mature gamete.

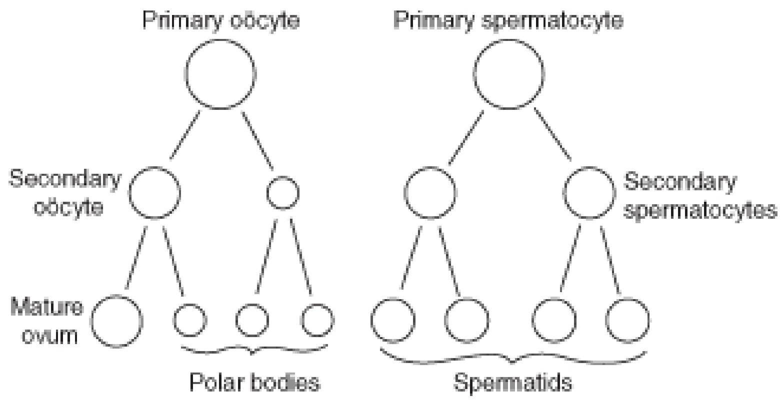


Figure 6.15: Analogies in the process of maturation of the ovum and the development of the spermatids. Four haploid spermatids form during meiosis from the primary spermatocyte, whereas only 1 mature ovum, or egg forms during meiosis from the primary oocyte. Three polar bodies may form during oogenesis. These polar bodies will not form mature gametes. (11)

During spermatogenesis, primary spermatocytes go through the first cell division of meiosis to produce secondary spermatocytes. These are haploid cells. Secondary spermatocytes then quickly complete the meiotic division to become spermatids, which are also haploid cells. The four haploid cells produced from meiosis develop a flagellum tail and compact head piece to become mature sperm cells, capable of swimming and fertilizing an egg. The compact head, which has lost most of its cytoplasm, is key in the formation of a streamlined shape. The middle piece of the sperm, connecting the head to the tail, contains many mitochondria, providing energy to the cell. The sperm cell essentially contributes only DNA to the zygote.

On the other hand, the egg provides the other half of the DNA, but also organelles, building blocks for compounds such as proteins and nucleic acids, and other necessary materials. The egg, being much larger than a sperm cell, contains almost all of the cytoplasm a developing embryo will have during its first few days of life. Therefore, oogenesis is a much more complicated process than spermatogenesis.

Oogenesis begins before birth and is not completed until after fertilization. Oogenesis begins when an oogonia (singular, oogonium), which are the immature eggs that form in the ovaries before birth, with the diploid number of chromosomes undergoes mitosis to form primary oocytes, also with the diploid number. It proceeds as a primary oocyte undergoes the first cell division of meiosis to form secondary oocytes with the haploid number of chromosomes. A secondary oocyte undergoes the second meiotic cell division to form a haploid ovum if it is fertilized by a sperm. The one egg cell that results from meiosis contains most of the cytoplasm, nutrients, and organelles. This unequal distribution of materials produces one large cell, and one cell with little more than DNA. This other cell, known as a **polar body**, eventually breaks down. The larger cell undergoes meiosis II, once again producing a large cell and a polar body. The large cell develops into the mature gamete, called an ovum.

## Sexual Life Cycles

Eukaryotes have three different versions of the sexual life cycle: a haploid life cycle, a diploid life cycle, and a life cycle known as the alternation of generations (**Figure** 6.16). A **life cycle** is the span in the life of an organism from one generation to the next. All species that reproduce sexually follow a basic pattern, alternating between haploid and diploid chromosome numbers. The sexual life cycle depends on when meiosis occurs and the type of cell that undergoes meiosis.

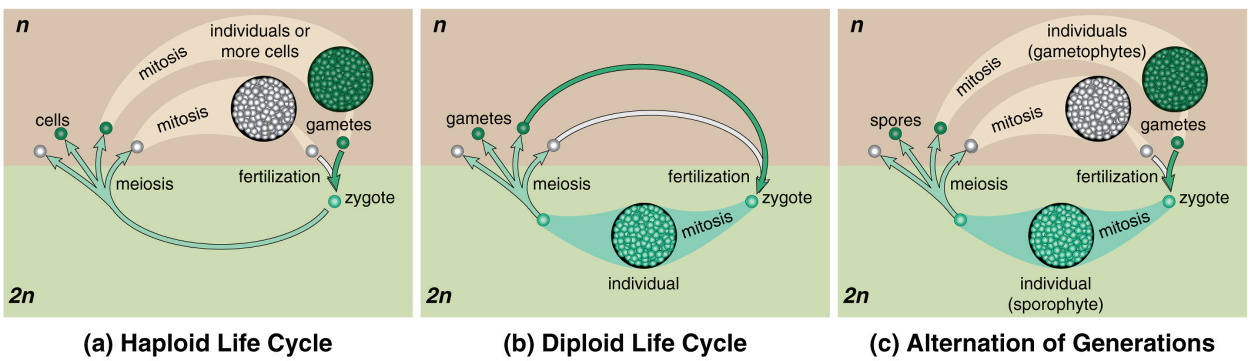


Figure 6.16: Sexual Life Cycles. (6)

### Haploid Life Cycles

The haploid life cycle is the simplest life cycle. Organisms with this life cycle, such as many protists and some fungi and algae, spend the majority of their life cycle as a haploid cell. In fact, the zygote is the only diploid cell. The zygote immediately undergoes meiosis, producing four haploid cells, which grow into haploid multicellular organisms. These organisms produce gametes by mitosis. The gametes fuse through a process called fusion to produce diploid zygotes which undergo meiosis, continuing the life cycle.

### Diploid Life Cycles

Organisms that have a diploid life cycle spend the majority of their lives as diploid adults. All diploid adults inherit half of their DNA from each parent. When they are ready to reproduce, diploid reproductive cells undergo meiosis and produce haploid gametes. These gametes then fuse through fertilization and produce a diploid zygote, which immediately enters $G_1$ of the cell cycle. Next, the zygote's DNA is replicated. Finally, the processes of mitosis and cytokinesis produce two genetically identical diploid cells. Through repeated rounds of growth and division, this organism becomes a diploid adult and the cycle continues.

### Alternation of Generations

Plants, algae, and some protists have a life cycle that alternates between diploid and haploid phases, known as alternation of generations. In plants, the life cycle alternates between the diploid sporophyte and haploid gametophyte. Spore forming cells in the diploid sporophyte undergo meiosis to produce **spores**, a haploid reproductive cell. Spores can develop into an adult without fusing with another cell. The spores give rise to a multicellular haploid gametophyte, which produce gametes by mitosis. The gametes fuse, producing a diploid zygote, which grow into the diploid sporophyte.

## Lesson Summary

- Asexual reproduction produces a clone, an organism that is genetically identical to its parent.
- Asexual reproduction includes fission, fragmentation and budding.
- Sexual reproduction involves haploid gametes and produces a diploid zygote through fertilization.
- Meiosis is a type of cell division that halves the number of chromosomes. There are eight stages of meiosis, divided into meiosis I and meiosis II. DNA is not replicated between meiosis I and meiosis II.
- Crossing-over, the independent assortment of chromosomes during anaphase I, and random fertilization result in genetic variation.
- Meiosis is a step during spermatogenesis and oogenesis. Spermatogenesis produces four haploid sperm cells, while oogenesis produces one mature ovum.
- Eukaryotes have three different versions of the sexual life cycle: a haploid life cycle, a diploid life cycle, and a life cycle known as the alternation of generations. The sexual life cycle depends on when meiosis occurs and the type of cell that undergoes meiosis.

## Review Questions

1. Define crossing-over in meiosis.
2. Describe how crossing-over, independent assortment, and random fertilization lead to genetic variation.
3. Compare and contrast mitosis and meiosis.
4. List the main differences between asexual and sexual reproduction.
5. How many chromosomes does a diploid human cell have? How many chromosomes does a haploid human cell have?

6. Name the three different sexual life cycles. What characterizes the differences between these life cycles?
7. Compare binary fission and asexual reproduction.

## Further Reading / Supplemental Links

- http://www.genome.gov
- http://www.accessexcellence.org/RC/VL/GG/meiosis.html
- http://users.rcn.com/jkimball.ma.ultranet/BiologyPages/M/Meiosis.html
- http://www.emc.maricopa.edu/faculty/farabee/BIOBK/BioBookmeiosis.html

## Vocabulary

**alternation of generations** A life cycle that alternates between diploid and haploid phases.

**asexual reproduction** Reproduction without gametes; the simplest and most primitive method of reproduction; produces a clone, an organism that is genetically identical to its parent.

**budding** Asexual reproduction in which new individuals split off from existing ones; the bud may stay attached or break free from the parent.

**crossing-over** The exchange of genetic material between non-sister chromatids of homologous chromosomes; also known as recombination.

**diploid** A cell containing two sets of chromosomes; in human cells, two sets contains 46 chromosomes.

**fertilization** The joining of gametes during reproduction.

**fission** Asexual reproduction in which a parent separates into two or more individuals of about equal size.

**fragmentation** Asexual reproduction in which the body breaks into several fragments, which later develop into complete adults.

**gametes** An organism's reproductive cells, such as sperm and egg cells.

**gametogenesis** The further maturation of the haploid cells produced by meiosis into mature gametes capable of fertilization.

**gametophyte** Produces gametes by mitosis; in alternation of generation life cycles.

**haploid** A cell containing one set of chromosomes; in human gametes, one set is 23 chromosomes.

**life cycle** The span in the life of an organism from one generation to the next.

**meiosis** A type of cell division that halves the number of chromosomes.

**oogenesis** The production of a mature egg cell; results in just one mature ovum, or egg cell.

**polar body** Cell formed during oogenesis; contains little cytoplasm and eventually breaks down; does not form a gamete.

**sexual reproduction** Reproduction involving the joining of haploid gametes, producing genetically diverse individuals.

**spermatogenesis** The production of mature sperm cells; results in four haploid gametes.

**spore** A haploid reproductive cell; found in plants, algae and some protists; can develop into an adult without fusing with another cell.

**tetrad** A configuration with four chromatids; formed by the pairing of homologous chromosomes during prophase I of meiosis.

## Points to Consider

- The next unit, Genetics, discusses the branch of biology that studies heredity. What is heredity?
- What role do you think meiosis plays in heredity?
- Describe what would happen if gametes were formed by mitosis.
- Human Genetics is an ever increasingly important field of medicine. Explain why this field of medicine is so important.

# Image Sources

(1) NCBI. http://en.wikipedia.org/wiki/Image:MajorEventsInMitosis.jpg. Public Domain.

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(5) http://en.wikipedia.org/wiki/File:Condensed_Eukaryotic_Chromosome.png. GNU-FDL.

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