# **10** MEIOSIS AND SEXUAL REPRODUCTION

## Why Sex?

Single-celled eukaryotes started to engage in sex many hundreds of millions of years ago, although no one knows how. An unsolved puzzle is why they did it at all.

Asexual reproduction by way of mitotic cell division is easier and faster. Evolutionarily speaking, one individual alone parcels out its DNA to offspring, which are just like their parent. Without sex, that one individual has all of its DNA represented in the new generation. The advantages are evident among most of the protists and fungi, which reproduce asexually most of the time. They quickly give rise to huge populations of cells just like themselves. The advantages are evident among many plants and many invertebrates, including corals, sea stars, and flatworms. Even after bits of these organisms bud or break off, or if the body splits in two, the parts grow into complete copies of the parent. How can the costs of sexual reproduction such as all of the energy required to construct and use special mate-attracting body parts—beat that?

Sexual reproduction can be an alternative adaptation in changing environments. Consider the plant-sucking insects called aphids. In spring and summer, when plant juices are plentiful, a female aphid reproduces by parthenogenesis. In one day she can give birth to as many as five females, all from unfertilized eggs (Figure 10.1*a*). Aphid population sizes soar until autumn, when food dwindles. Males now form from eggs, aphids engage in sex, and large fertilized eggs are laid that can withstand winter conditions. Next spring, the eggs develop into asexually oriented females.

Alternative adaptations to the environment also may be why we find a few all-female species of fishes, reptiles, and birds—not mammals—in nature. Not content to let it go at that, University of Tokyo researchers recently fused two mouse eggs in a test tube and made an embryo with no DNA from a male. The embryo developed into Kaguya, the world's first fatherless mammal (Figure 10.1*b*). The female mouse grew up, engaged in sex with a male mouse, and gave birth to offspring. But back to the big picture:

Sexual reproduction also has advantages when other organisms change. This is especially apparent when we consider the interactions between predators and prey, or between hosts and the parasites or pathogens that infect them. An intriguing idea, the Red Queen hypothesis, may explain the connection between these interactions and sexual reproduction.

In Lewis Carroll's book *Through the Looking Glass*, the Queen of Hearts tells Alice, "Now here, you see, it takes all the running you can do, to keep in the same place." When mutation introduces a better defense against a predator, parasite, or pathogen, we can comfortably predict that natural selection will favor it. However, we also can predict that selection will favor individual predators, parasites, or pathogens that have a novel means to overcome the new defense. The interacting species coevolve; each is running as fast as it can to keep up with the ongoing changes in the other. Talk about an evolutionary treadmill.

Applying the Red Queen hypothesis to our questions, sexual reproduction endures because individuals that practice it can come up with far more variety in heritable defenses compared to the ones that do not. Remember the chromosomes? Sexual reproducers typically have a diploid chromosome number; they inherit two of each type, from two parents. Their two sets of chromosomes



**Figure 10.1** Reproductive moments. (**a**) Aphid giving birth. Like females of some other sexually reproducing species, this one reproduces asexually in spring but engages in sex before winter. (**b**) A fatherless mouse. (**c**) Poppy plant being helped by a beetle, which makes pollen deliveries for it. (**d**) Mealybugs mating.

## IMPACTS, ISSUES

generally hold information about the same traits, but the information about a given trait is not always *exactly* the same on both of them. Some of it might even be bad under prevailing conditions but might be useful in the future. As you will see shortly, meiosis and fertilization mix up information, so that a tremendous variety of novel traits is tried out among the offspring of each new generation. The capacity for rapid, adaptive responses to abiotic and biotic conditions may well be present somewhere in the expressed range of variation.

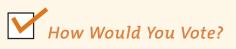
Asexual reproduction cannot shuffle information into novel combinations. It puts out the same versions of traits again and again into the environmental testing ground. Doing so works well enough—as long as the organism is already equipped to handle change.

With this chapter, we turn to mechanisms of sexual reproduction. Three interconnected events—meiosis, the formation of gametes, and fertilization—are hallmarks of this reproductive mode. The outcome is the production of offspring that display novel combinations of traits. As you will see throughout the book, that outcome has

contributed immensely to the range of diversity, past and present.

Watch the video online!

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Japanese researchers have successfully created a "fatherless" mouse that contains the genetic material from the eggs of two females. The mouse is healthy and fully fertile. Do you think researchers should be allowed to try the same process with human eggs? See BiologyNow for details, then vote online.

## Key Concepts

#### SEXUAL VERSUS ASEXUAL REPRODUCTION

By asexual reproduction, one parent alone transmits genetic information to offspring. By sexual reproduction, offspring inherit novel combinations of information from more than one parent, because those parents typically differ in their alleles. Alleles are slightly different molecular forms of a gene that specify different versions of the same trait. Section 10.1

#### OVERVIEW OF MEIOSIS

Meiosis, a nuclear division mechanism, divides the parental chromosome number by half. It occurs only in cells set aside for sexual reproduction. Section 10.2

## STAGES OF MEIOSIS

Meiosis sorts out a reproductive cell's chromosomes into four new nuclei. After it ends, gametes form by way of cytoplasmic division and other events. Section 10.3

## CHROMOSOME RECOMBINATIONS AND SHUFFLINGS

During meiosis, each pair of chromosomes swaps segments and exchanges alleles. Also, one of each pair is randomly aligned for distribution into a new nucleus. Which ends up in a given gamete is a matter of chance. Chromosomes are shuffled again at fertilization. These events contribute to variation in traits among offspring. Section 10.4

## SEXUAL REPRODUCTION IN THE LIFE CYCLES

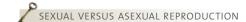
In animals, gametes form by different mechanisms in males and females. In most plants, spore formation and other events intervene between meiosis and gamete formation. Spores store and protect hereditary information through times that predictably do not favor survival of offspring. Section 10.5

#### MITOSIS AND MEIOSIS COMPARED

Recent molecular evidence suggests that meiosis originated through mechanisms that already existed for mitosis and, before that, for repairing damaged DNA. Section 10.6



For this chapter, you will be drawing on your sense of the dynamic nature of microtubule assembly and disassembly (Sections 4.10, 4.11, 9.2). Be sure you have a clear picture of the structural organization of chromosomes (9.1) and that you can define chromosome number (9.2). Reflect on how a bipolar spindle made of microtubules moves chromosomes during nuclear division (9.3), and how the cytoplasm gets divided following nuclear division (9.4). You will be revisiting the checkpoint gene products that monitor and repair chromosomal DNA during the cell cycle (9.5).





## Introducing Alleles

Asexual reproduction produces genetically identical copies of a parent. Sexual reproduction introduces variation in the details of traits among offspring.

When an orchid or aphid reproduces by itself, what sort of offspring does it get? By the process of **asexual reproduction**, all offspring inherit the same number and kinds of genes from a single parent. **Genes** are sequences of chromosomal DNA. The genes for each species contain all the heritable information necessary to make new individuals. Rare mutations aside, then, asexually produced individuals can only be *clones*, or genetically identical copies of the parent.

Inheritance gets far more interesting with **sexual reproduction**, a process involving meiosis, formation of gametes, and fertilization—a union of two gametes. In most sexual reproducers, such as humans, the first cell of a new individual holds *pairs of genes* on pairs of chromosomes. Usually, one of each pair is maternal and the other paternal in origin (Figure 10.2).

If information in all pairs of genes were identical down to the last detail, sexual reproduction would also produce clones. Just imagine—you, every person you know, the entire human population might be a clone, with everybody looking alike. But the two genes of a pair might *not* be identical. Why not? The molecular structure of any gene can change permanently; it can mutate. So two genes that happen to be paired in an individual's cells may "say" slightly different things about a trait. Each unique molecular form of the same gene is called an **allele**.

Such tiny differences affect thousands of traits. For instance, whether your chin has a dimple depends on which pair of alleles you inherited at one chromosome location. One kind of allele at that location says "put a dimple in the chin." Another kind says "no dimple." Alleles are one reason why the individuals of sexually reproducing species do not all look alike. *With sexual reproduction, offspring inherit new combinations of alleles, which lead to variations in the details of their traits.* 

Figure 10.2 A maternal and a paternal chromosome. Any gene on one might be slightly different structurally than the same gene on the other.

This chapter gets into the cellular basis of sexual reproduction. More importantly, it starts you thinking about far-reaching effects of gene shufflings at certain stages of the process. The process introduces variations in traits among offspring that are typically acted upon by agents of natural selection. Thus, *variation in traits is a foundation for evolution*.

Sexual reproduction introduces variation in traits by bestowing novel combinations of alleles on offspring.

OVERVIEW OF MEIOSIS

## 10.2 What Meiosis Does

*Meiosis* is a nuclear division process that divides a parental chromosome number by half in specialized reproductive cells. Sexual reproduction will not work without it.

## THINK "HOMOLOGUES"

Think back to the preceding chapter and its focus on mitotic cell division. Unlike mitosis, meiosis sorts out chromosomes into parcels not once but *twice*. Unlike mitosis, it is the first step leading to the formation of gametes. Male and female gametes—such as sperm and eggs—fuse to form a new individual. In most multicelled eukaryotes, cells that form in specialized reproductive structures or organs are the forerunners of gametes. Figure 10.3 gives three examples of where cells that give rise to gametes originate.

As you know, the **chromosome number** is the sum total of chromosomes in cells of a given type. If a cell has a **diploid number** (2n), it has a *pair* of each type of chromosome, often from two parents. Except for a pairing of nonidentical sex chromosomes, each pair has the same length, shape, and assortment of genes, and they line up with each other at meiosis. We call them **homologous chromosomes** (*hom*– means alike).

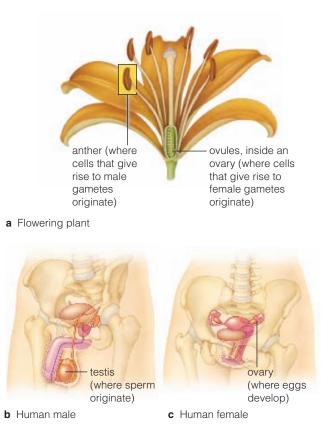
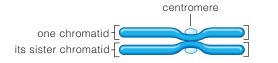


Figure 10.3 Examples of reproductive organs, where cells that give rise to gametes originate.

The body cells of humans are diploid, with 23 + 23 homologous chromosomes (Figure 10.4). So are human germ cells that give rise to gametes. Following meiosis, every gamete normally gets 23 chromosomes—one of each type. Meiosis reduced the parental chromosome number by half, to a **haploid number** (*n*).

## TWO DIVISIONS, NOT ONE

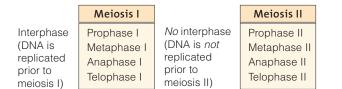
Bear in mind, meiosis *is* similar to mitosis in certain respects. As in mitosis, a germ cell duplicates its DNA in interphase. The two DNA molecules and associated proteins stay attached at the centromere, the notably constricted region along their length. For as long as they remain attached, we call them **sister chromatids**:



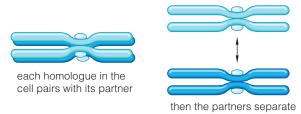
one chromosome in the duplicated state

As in mitosis, the microtubules of a spindle apparatus move the chromosomes in prescribed directions.

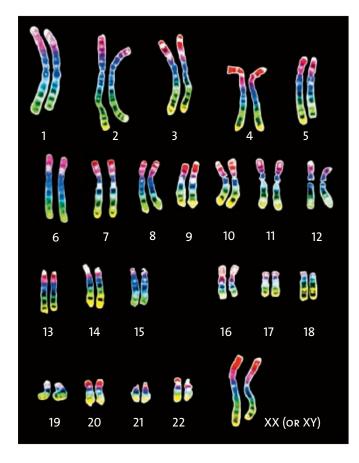
With meiosis, however, chromosomes go through <u>two</u> consecutive divisions that end with the formation of four haploid nuclei. The germ cell does not enter interphase between the two nuclear divisions, which are known as meiosis I and meiosis II:



In meoisis I, each duplicated chromosome aligns with its partner, *homologue to homologue*. After the two chromosomes of every pair have lined up with each other, they are moved apart:

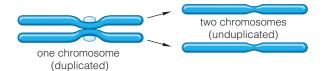


The cytoplasm typically starts to divide at some point after each homologue detaches from its partner. The two daughter cells formed this way are haploid, with *one* of each type of chromosome. Don't forget, these chromosomes are still in the duplicated state.



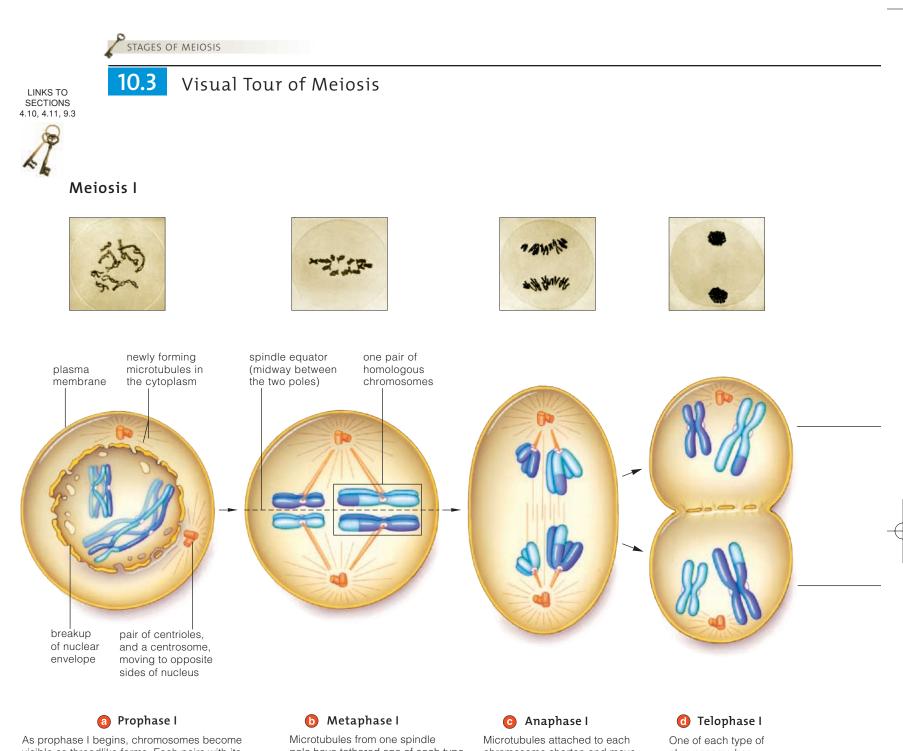
**Figure 10.4** Another look at the twenty-three pairs of homologous human chromosomes. This example is from a human female, with two X chromosomes. Human males have a different pairing of sex chromosomes (XY). These chromosomes have been labeled with fluorescent markers.

Next, during meiosis II, the two sister chromatids of each chromosome are separated from each other:



There are now four parcels of 23 chromosomes, and each has one chromosome of each type. New nuclear envelopes enclose them, as four nuclei. Typically the cytoplasm divides once more, so the outcome is four haploid (n) cells. Figure 10.5 on the next two pages puts these chromosomal movements in the context of the sequential stages of meiosis.

Meiosis, a nuclear division mechanism, reduces a parental cell's chromosome number by half—to a haploid number (n).



As prophase r begins, chromosomes become visible as threadlike forms. Each pairs with its homologue and usually swaps segments with it, as indicated by the breaks in color in the large chromosomes. Microtubules are forming a bipolar spindle (Section 9.3). If two pairs of centrioles are present, one pair is moved to the opposite side of the nuclear envelope, which is starting to break up.

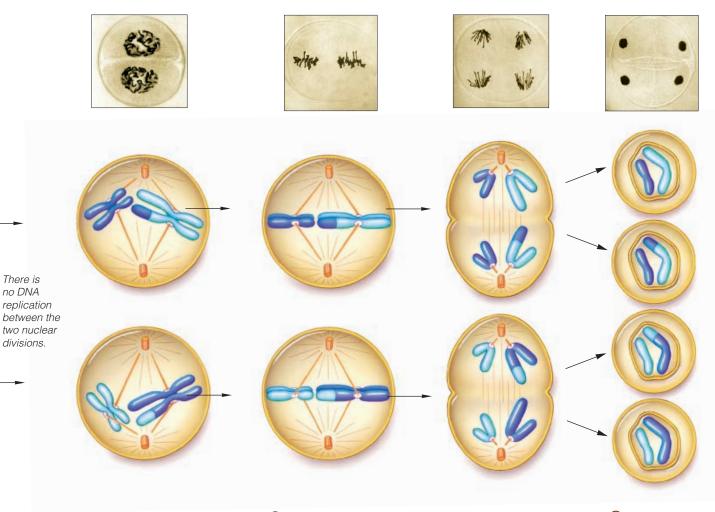
Microtubules from one spinale pole have tethered one of each type of chromosome; microtubules from the other pole have tethered its homologue. By metaphase I, a tug-of-war between the two sets of microtubules has aligned all chromosomes midway between the poles. Microtubules attached to each chromosome shorten and move it toward a spindle pole. Other microtubules, which extend from the poles and overlap at the spindle equator, ratchet past each other and push the two poles farther apart. Motor proteins drive the ratcheting.

One of each type of chromosome has now arrived at the spindle poles. For most species, the cytoplasm divides at some point, forming two haploid cells. All chromosomes are still duplicated.

**Figure 10.5** *Animated!* Meiosis in one type of animal cell. This is a nuclear division mechanism. It reduces the parental chromosome number in immature reproductive cells by half, to the haploid number, for forthcoming gametes. To keep things simple, we track only two pairs of homologous chromosomes. Maternal chromosomes are shaded *purple* and paternal chromosomes *blue*.

Of the four haploid cells that form by meiosis and cytoplasmic divisions, one or all may develop into gametes and function in sexual reproduction. In plants, the cells that form may develop into spores, a stage that precedes gamete formation in the life cycle.

## Meiosis II



## Prophase II

A new bipolar spindle forms in each haploid cell. Microtubules have moved one member of the pair of centrioles to the opposite end of each cell. One chromatid of each chromosome becomes tethered to one spindle pole, and its sister chromatid becomes tethered to the opposite pole.

## Metaphase II

Microtubules from both spindle poles have assembled and disassembled in a tug-of-war that ended at metaphase II, when all chromosomes are positioned midway between the poles.

## O Anaphase II

The attachment between sister chromatids of each chromosome breaks. Each is now a separate chromosome but is still tethered to microtubules, which move it toward a spindle pole. Other microtubules push the poles apart. A parcel of unduplicated chromosomes ends up near each pole. One of each type of chromosome is present in each parcel.

## h Telophase II

In telophase II, four nuclei form as a new nuclear envelope encloses each cluster of chromosomes. After cytoplasmic division, each of the resulting daughter cells has a haploid (*n*) number of chromosomes. CHROMOSOME RECOMBINATIONS AND SHUFFLINGS

## **10.4** How Meiosis Introduces Variations in Traits

As Sections 10.2 and 10.3 make clear, the basic function of meiosis is the reduction of a parental chromosome number by half. In evolutionary terms, two other functions are as important: Prophase I crossovers and the random alignment of chromosomes at metaphase I contribute greatly to the variation in traits among offspring.

The preceding section mentioned in passing that pairs of homologous chromosomes swap parts of themselves during prophase I. It also showed how a homologous chromosome becomes aligned with its partner during prophase I. Both events introduce new combinations of alleles into the gametes that form at some point *after* meiosis. Along with the chromosome shufflings that occur during fertilization, they contribute to variation in traits that occur among new generations of offspring in sexually reproducing species. Later in the book, you will explore how variation in traits has evolutionary and ecological consequences. We suggest that you read this section closely. It will serve you well later on.

## CROSSING OVER IN PROPHASE I

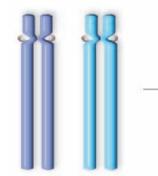
Figure 10.6*a* is a simple sketch of a pair of duplicated chromosomes, early in prophase I of meiosis. Notice how they are in threadlike form. All chromosomes in a germ cell condense this way. When they do, each is drawn close to its homologue. The chromatids of one become stitched point by point along their length to the chromatids of the other, with little space between them. This tight, parallel orientation favors **crossing over**, a molecular interaction between a chromatid of one chromosome and a chromatid of the homologous partner. DNA strands break and seal in complex ways, but the outcome is that the two "nonsister" chromatids exchange corresponding segments; they swap genes.

 This maternal chromosome (*purple*) and paternal chromosome (*blue*) were duplicated in interphase. They appear in microscopes early in prophase I, when they are starting to condense to threadlike form. Sister chromatids of each chromosome are positioned so close together that they look like a single thread. (We pulled them apart a bit in this sketch so you can distinguish between them.)

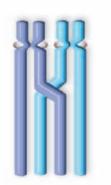


Each chromosome now becomes zippered up with its homologous partner, so all four chromatids are tightly aligned. If the two sex chromosomes have different forms (such as X paired with Y), they still get tightly aligned, but only in a tiny region at their ends.

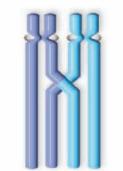




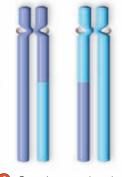
Here is the simplest way to think about crossing over. However, don't forget that the chromosomes are not really rod-shaped during early prophase I. They are still condensing to threadlike form, and each is tightly aligned with its homologous partner.



 The intimate contact encourages crossovers at various intervals along the length of nonsister chromatids. Here we show the location of just one crossover.



Nonsister chromatids exchange segments at the crossover site. They keep on condensing into thicker, rodlike forms. They will be fully unzippered from each other by metaphase I.



Crossing over breaks up the old combinations of alleles and puts new ones together in homologous chromosomes. It mixes up maternal and paternal information about traits.

**Figure 10.6** *Animated!* Key events of prophase I, the first stage of meiosis. For clarity, we show only one pair of homologous chromosomes and one crossover. More than one crossover usually occurs in each chromosome pair. *Blue* signifies a paternal chromosome, and *purple*, its maternal homologue.

Gene swapping would be pointless if each type of gene never varied. But remember, a gene can come in slightly different forms—alleles. You can predict that a number of the alleles on one chromosome will *not* be identical to their partner alleles on the homologous chromosome. Each crossover event is a chance to swap slightly different versions of heritable information on gene products.

We will look at the mechanism of crossing over in later chapters. For now, just remember this: *Crossing* over leads to recombinations among genes of homologous chromosomes, and eventually to variation in traits among offspring.

#### METAPHASE I ALIGNMENTS

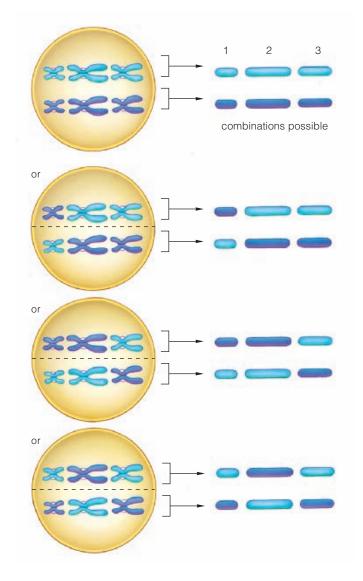
Major shufflings of intact chromosomes start during the transition from prophase I to metaphase I. Suppose this is happening right now in one of your germ cells. Crossovers have already made genetic mosaics of the chromosomes, but put this aside in order to simplify tracking. Just call the twenty-three chromosomes you inherited from your mother the *maternal* chromosomes and the twenty-three you inherited from your father the *paternal* chromosomes.

At metaphase I, microtubules from both poles have now aligned all of the duplicated chromosomes at the spindle equator (Figure 10.5*b*). Have they tethered all maternal chromosomes to one pole and all paternal chromosomes to the other? Maybe, but probably not. When the microtubules were growing, they latched on to the first chromosome they contacted. Because the tethering was random, there is no particular pattern to the metaphase I positions of maternal and paternal chromosomes.

Now carry this thought one step further. During anaphase I, when a duplicated chromosome is moved away from its homologous partner, *either partner* can end up at either spindle pole.

Think of the possibilities while tracking just three pairs of homologues. By metaphase I, these three pairs may be arranged in any one of four possible positions (Figure 10.7). This means that eight combinations (2<sup>3</sup>) are possible for forthcoming gametes.

Cells that give rise to human gametes have twentythree pairs of homologous chromosomes, not three. Thus, every time a human sperm or egg forms, there is a total of *8,388,608* (or 2<sup>23</sup>) possible combinations of maternal and paternal chromosomes! Moreover, in a sperm or an egg, many hundreds of alleles inherited from the mother might not "say" the exact same thing about hundreds of different traits as alleles inherited



**Figure 10.7** *Animated!* Possible outcomes for the random alignment of merely three pairs of homologous chromosomes at metaphase I. The three types of chromosomes are labeled 1, 2, and 3. With four alignments, eight combinations of maternal chromosomes (*purple*) and paternal chromosomes (*blue*) are possible in gametes.

from the father. Are you getting an idea of why such fascinating combinations of traits show up among the generations of your own family tree?

Crossing over, an interaction between a pair of homologous chromosomes, breaks up old combinations of alleles and puts new ones together during prophase I of meiosis.

The random tethering and subsequent positioning of each pair of maternal and paternal chromosomes at metaphase *I* lead to different combinations of maternal and paternal traits in each new generation. SEXUAL REPRODUCTION IN THE LIFE CYCLES

## **10.5** From Gametes to Offspring

LINK TO SECTION 9.4 What happens to the gametes that form after meiosis? Later chapters have specific examples. Here, simply focus on where they fit in the life cycles of plants and animals.

Gametes are not all the same in their details. Human sperm have one tail, opossum sperm have two, and roundworm sperm have none. Crayfish sperm look like pinwheels. Most eggs are microscopic in size, yet an ostrich egg inside its shell is as big as a football. A flowering plant's male gamete is just a sperm nucleus.

#### GAMETE FORMATION IN PLANTS

The life cycle of most plant species alternates between sporophyte and gametophyte stages. A *sporophyte* is a multicelled spore-producing body that makes sexual spores by way of meiosis (Figure 10.8*a*). In plants, each **spore** is a haploid reproductive cell that is not a gamete and that does not take part in fertilization. At some point, the spore undergoes mitotic cell divisions that give rise to a *gametophyte*. One or more gametes do form inside this multicelled haploid body.

Pine trees are examples of sporophytes, and their female gametophytes form on the scales of pinecones. Rose bushes and fuschias also are sporophytes, and gametophytes form inside their flowers. You will be focusing on plant life cycles in Chapters 23 and 32.

## GAMETE FORMATION IN ANIMALS

In animals, diploid germ cells give rise to gametes. In a male reproductive system, a germ cell develops into a primary spermatocyte. This large, immature cell enters meiosis and cytoplasmic divisions. Four haploid cells result and develop into spermatids (Figure 10.9). Each cell undergoes changes, such as the formation of a tail, and becomes a **sperm**, a type of mature male gamete.

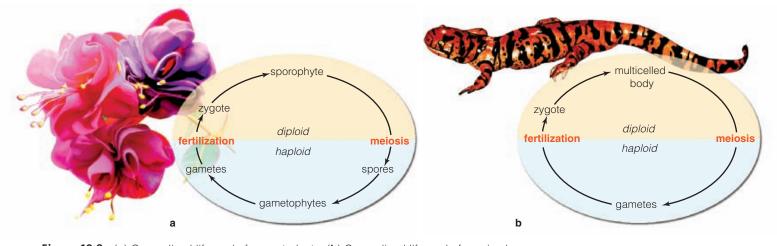
In female animals, a germ cell becomes a primary oocyte, which is an immature egg. Unlike sperm, the primary oocyte increases in size and stockpiles many cytoplasmic components. In addition, its four daughter cells differ in size and function (Figure 10.10).

When the primary oocyte divides after meiosis I, one daughter cell—the secondary oocyte—gets nearly all of the cytoplasm. The other cell, a first polar body, is exceedingly small. Later, both of these haploid cells enter meiosis II, then cytoplasmic division. One of the secondary oocyte's daughter cells becomes the second polar body. The other daughter cell gets most of the cytoplasm and develops into a gamete. The mature female gamete is an ovum (plural, ova). An ovum also is known informally as an egg.

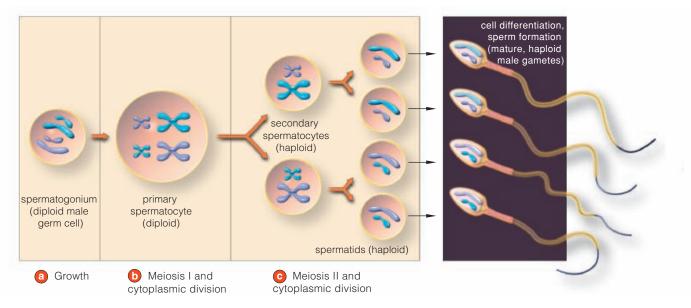
And so we have one egg. The three polar bodies that formed don't function as gametes and aren't rich in nutrients or plump with cytoplasm. In time they degenerate. But their formation assures that the egg will have a haploid chromosome number. Also, by getting most of the cytoplasm, the egg holds enough metabolic machinery to support early cell divisions of the new individual, as Chapters 43 and 44 explain.

#### MORE SHUFFLINGS AT FERTILIZATION

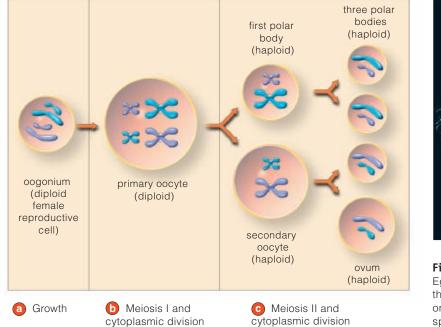
The chromosome number characteristic of the parents is restored at **fertilization**, a time when a female and male gamete unite and their haploid nuclei fuse. If meiosis did not precede fertilization, the chromosome number would double in each generation. Doublings would disrupt hereditary information, usually for the worse. Why? That information is like a fine-tuned set



**Figure 10.8** (a) Generalized life cycle for most plants. (b) Generalized life cycle for animals. The zygote is the first cell to form when the nuclei of two gametes fuse at fertilization.



**Figure 10.9** *Animated!* Generalized sketch of sperm formation in animals. Figure 44.4 shows a specific example (how sperm form in human males).





**Figure 10.10** *Animated!* Animal egg formation. Eggs are far larger than sperm and larger than the three polar bodies. The painting above, based on a scanning electron micrograph, depicts human sperm surrounding an ovum.

of blueprints that must be followed exactly, page after page, to build a normal individual.

Fertilization also adds to variation among offspring. Reflect on the possibilities for humans alone. During prophase I, every human chromosome undergoes an average of two or three crossovers. In addition to the crossovers, random positioning of pairs of paternal and maternal chromosomes at metaphase I results in one of millions of possible chromosome combinations in each gamete. And of all male and female gametes that form, *which* two actually get together is a matter of chance. The sheer number of combinations that can exist at fertilization is staggering!

The distribution of random mixes of chromosomes into gametes, random metaphase chromosome alignments, and fertilization contribute to variation in traits of offspring.

MITOSIS AND MEIOSIS COMPARED

## **10.6** Mitosis and Meiosis—An Ancestral Connection?

LINKS TO SECTIONS 9.2, 9.5 This chapter opened with hypotheses about the survival advantages of asexual and sexual reproduction. It seems like a giant evolutionary step from producing clones to producing genetically varied offspring. But was it?

Figure 10.11 shows an obvious parallel between the four stages of mitosis and meiosis II. The same kind of bipolar spindle assorts duplicated chromosomes into parcels in very similar ways. Recent studies also reveal striking similarities at the molecular level.

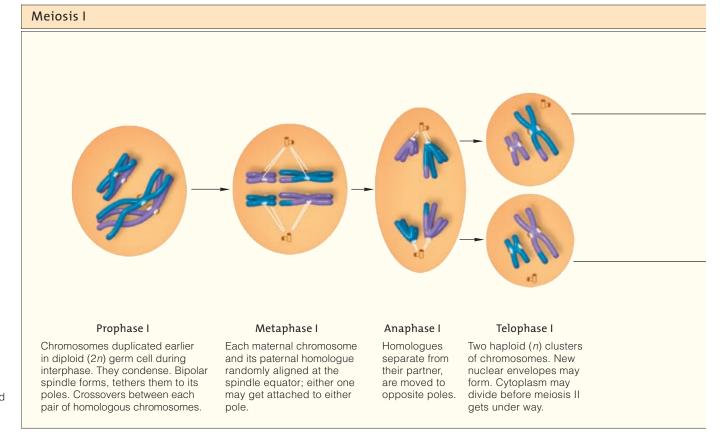
In all organisms, from prokaryotes to mammals, certain genes code for proteins that can recognize and repair breaks in the double-stranded DNA molecules of chromosomes. Such damage, recall, is monitored by products of checkpoint genes while DNA is being replicated during the cell cycle (Sections 9.2 and 9.5). If they detect a problem, there is a pause in the cycle until it is repaired. Even in bacteria—the most ancient lineages on Earth—a mechanism exists that may well have been recruited for mitosis and meiosis.

Some highly conserved gene products often repair breaks and odd rearrangements in chromosomal DNA that occur during mitosis. They also put chromosomal DNA back together in prophase I, after homologous chromosomes exchange segments. This outcome—a form of genetic recombination—could have been part of the evolution of sexual reproduction.

Is *Giardia intestinalis* one model? This descendent of one of the earliest eukaryotic lineages does not have mitochondria, and it does not form a bipolar spindle during mitosis. This single-celled parasite has never been observed to reproduce sexually. Yet it has gene products that serve in meiosis in higher eukaryotes.

We invite you to think about these possibilities as you read later chapters in the book. We invite you to explore likely connections on your own. For instance, when you look at *Chlamydomonas*, a single-celled alga of freshwater habitats, mull over the fact that haploid *Chlamydomonas* cells reproduce asexually by mitotic cell division. But two cells of different mating strains also can function as *gametes*; they can fuse and form a diploid individual. Do such cells offer more clues to the origin of sexual reproduction? Maybe.

Recombination mechanisms that are vital for reproduction of eukaryotic cells might have evolved from DNA repair mechanisms in prokaryotic ancestors.



**Figure 10.11** Comparative summary of key features of mitosis and meiosis, starting with a diploid cell. Only two paternal and two maternal chromosomes are shown. Both were duplicated in interphase, prior to nuclear division. Both use a bipolar spindle made of microtubules to sort out and move the chromosomes.

Mitosis maintains the parental chromosome number. Meiosis halves it, to the haploid number.

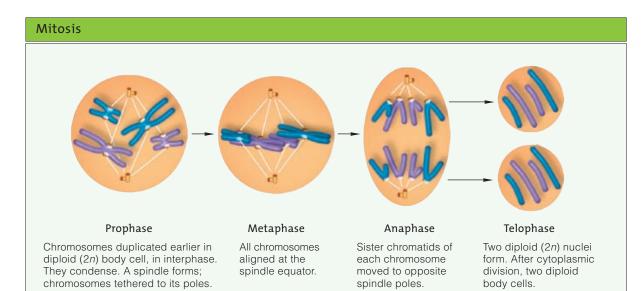
Mitotic cell division is the basis of asexual reproduction among eukaryotes. It is the basis of growth and tissue repair of multicelled eukaryotic species.

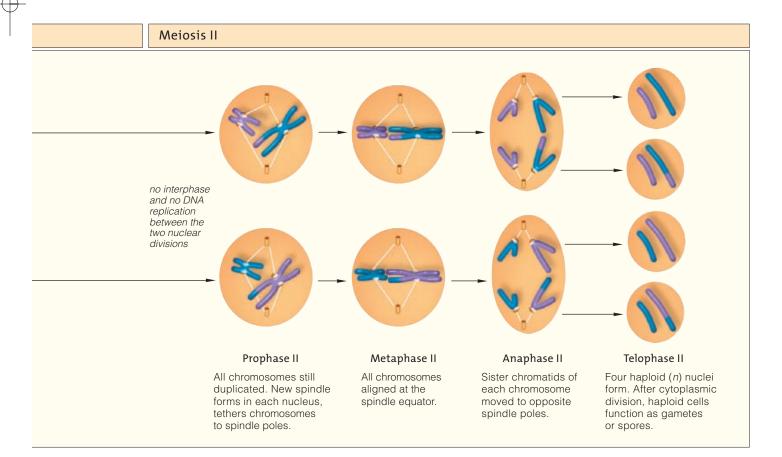
Meiotic cell division is a required step before the formation of gametes or sexual spores.

## CONNECTIONS









## http://biology.brookscole.com/starr11

## Summary

**Section 10.1** Life cycles of eukaryotic species often have asexual and sexual phases.

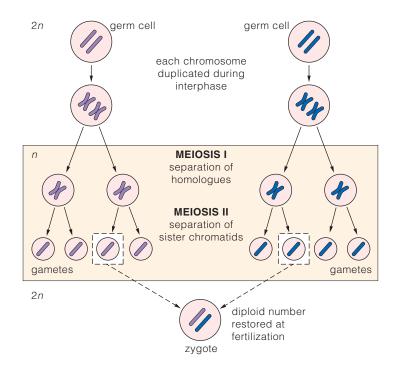
Asexual reproduction by way of mitosis yields a clone, or offspring that are genetically the same as one parent. Compared with sexual modes, it is easier, requires less energy, and gives rise to huge populations in far less time.

Sexual reproduction involves two parents that engage in meiosis, gamete formation, and fertilization. It leads to novel allele combinations in offspring. Compared to asexual reproduction, the expressed range of variation offers a far greater capacity for rapid, adaptive response to novel changes in abiotic and biotic conditions.

Alleles are slightly different molecular forms of the same gene that specify different versions of the same gene product. Meiosis and fertilization mix up the alleles (and forms of traits) in each generation of offspring.

**Section 10.2** Meiosis, a nuclear division process, precedes gamete formation. It divides the chromosome number characteristic of a species by half, so that fusion of two gametes at fertilization restores the chromosome number (Figure 10.12).

Offspring of most sexual reproducers inherit pairs of chromosomes, one from a maternal and one from a paternal parent. Except in individuals that have inherited



**Figure 10.12** Summary of changes in chromosome number at different stages of sexual reproduction, using two diploid (2*n*) germ cells as the example. During two nuclear divisions, meiosis reduces the chromosome number by half (*n*). The union of haploid nuclei of two gametes at fertilization restores the diploid number.

are duplicated in interphase, prior to meiosis. Meiosis sorts out duplicated chromosomes twice, in two divisions (meiosis I and II) that are not separated by interphase.

nonidentical sex chromosomes (e.g., X with Y), the pairs

are homologous (alike); each pair has the same length,

In meiosis I, the first nuclear division, homologous chromosomes are partitioned into two clusters, both with one of each type of chromosome.

Prophase I. Chromosomes condense into threadlike form, and each pair of homologues typically undergoes crossing over. Microtubules start forming a bipolar spindle. One of two pairs of centrioles, if present, is moved to the opposite side of the nucleus. The nuclear envelope breaks up, so microtubules growing from both spindle poles can penetrate the nuclear region and tether the chromosomes.

Metaphase I. A tug-of-war between microtubules from both poles has positioned all pairs of the tethered homologous chromosomes at the spindle equator.

Anaphase I. Microtubules pull each chromosome away from its homologue, to opposite spindle poles. Other microtubules that overlap at the spindle equator ratchet past each other to push the poles farther apart. There are now two parcels of duplicated chromosomes, one near each spindle pole.

Telophase I. Two haploid nuclei form around the parcels. Cytoplasmic division typically follows.

In meiosis II, the second nuclear division, the sister chromatids of each chromosome are pulled away from each other and partitioned into two clusters. This occurs in both haploid nuclei that formed in meiosis I. By the end of telophase II, there are four nuclei, each with a haploid chromosome number.

When the cytoplasm divides, there are four haploid cells. One or all may serve as gametes or, in plants, as spores that will give rise to gamete-producing bodies.

## Biology 🔊 Now

*Explore what happens during each stage of meiosis with the animation on BiologyNow.* 

**Section 10.4** Novel combinations of alleles and of maternal and paternal chromosomes arise through events in prophase I and metaphase I.

*Non*sister chromatids of homologous chromosomes undergo crossing over during prophase I. They break and exchange segments, so that each ends up with allelic combinations that were not present in either parent.

Maternal and paternal chromosomes get tethered randomly to one spindle pole or the other. Thus they are positioned at random when they are aligned at the spindle equator at metaphase I, so alleles of either one may end up in a new nucleus, then in a gamete.

## Biology 🔊 Now

Study how crossing over and metaphase I alignments affect allele combinations with the animation on BiologyNow.

**Section 10.5** Life cycles of plants and animals have sexual phases. Sporophytes are a multicelled plant body that produces sexual spores. Such plant spores give rise to gametophytes, in which haploid gametes form.

In most animals, germ cells in reproductive organs give rise to sperm or eggs. Fusion of a sperm and egg nucleus at fertilization results in a zygote, the first cell of a new individual.

## **Biology** SNow

Learn how gametes form with the animation on BiologyNow.

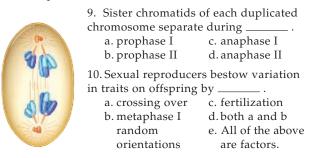
**Section 10.6** Like mitosis, meiosis uses a bipolar spindle to move and sort duplicated chromosomes. But meiosis occurs only in sex cells and does not produce clones of the parent; it reduces the parental chromosome number by half. Crossing over and random alignments of different mixes of maternal and paternal chromosomes for distribution to gametes occur only in meiosis. These events, and the chance of any two gametes meeting at fertilization, contribute to enormous variation in traits among offspring.

## Self-Quiz

Answers in Appendix II

- 1. Meiosis and cytoplasmic division function in . a. asexual reproduction of single-celled eukaryotes b. growth, tissue repair, often asexual reproduction c. sexual reproduction d. both b and c
- 2. A duplicated chromosome has \_ chromatid(s). b. two c. three d.four a. one
- 3. A somatic cell having two of each type of chromosome \_ chromosome number. has a(n).
- a. diploid b. haploid c. tetraploid d.abnormal 4. Sexual reproduction requires
- a. meiosis c. spore formation b. fertilization d a and b
- 5. Generally, a pair of homologous chromosomes a. carry the same genes c. interact at meiosis b. are the same length, shape d. all of the above
- the parental chromosome number. 6. Meiosis a. doubles b. halves c. maintains d. corrupts
- 7. Meiosis ends with the formation of . a. two cells c. eight cells b. two nuclei d. four nuclei

8. The cell in the diagram below is in anaphase I rather than anaphase II. I know this because \_





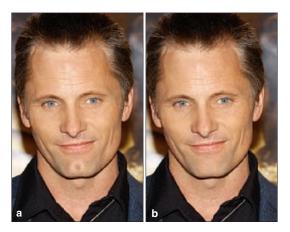


Figure 10.13 Bdelloid rotifer.

Figure 10.14 Viggo Mortensen (a) with and (b) without a chin dimple.

11. Match each term with its description.

chromosome	a. differe
number	of the
alleles	b. none l
metaphase I	c. all chi
interphase	at spir

ent molecular forms same gene between meiosis I, II romosomes aligned indle equator d. sum total of all chromosomes in cells of a given type

Additional questions are available on **Biology** SNow

## Critical Thinking

1. Why can you predict that meiosis will give rise to genetic variation between parent cells and daughter cells in fewer cell cycles than mitosis?

2. The bdelloid rotifer lineage started at least 40 million years ago (Figure 10.13). About 360 known species of these tiny animals live in many aquatic habitats worldwide. All are female. Do some research to identify conditions in the physical and biological environments to which they might be reproductively adapted.

3. Actor Viggo Mortensen inherited a gene that makes his chin dimple. Figure 10.14b shows what he might have looked like if he inherited a different form of that gene. What is the name for alternative forms of the same gene?

4. Assume you can measure the amount of DNA in the nucleus of a primary oocyte, and then in the nucleus of a primary spermatocyte. Each gives you a mass *m*. What mass of DNA would you expect to find in the nucleus of each mature gamete (egg and sperm) that forms after meiosis? What mass of DNA will be (1) in the nucleus of a zygote that forms at fertilization and (2) in that zygote's nucleus after the first DNA

duplication?

5. The diploid chromosome number for the somatic cells of several eukaryotic species are listed at right. Write down the number of chromosomes that normally end up in gametes of each species. Then write what the number would be after three generations if meiosis did not occur before gamete formation.

Fruit fly, Drosophila melanogaster	8
Garden pea, Pisum sativum	14
Corn <i>, Zea mays</i>	20
Frog, Rana pipiens	26
Earthworm, Lumbricus terrestris	36
Human, <i>Homo sapiens</i>	46
Chimpanzee, Pan troglodytes	48
Amoeba, <i>Amoeba</i>	50
Horsetail, Equisetum	216