

VU Medical Zone

Admin:

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Principles of Animal Life-II

ZOO 203 Merge ppt

Lecture 1 to 36

EUKARYOTIC CHROMOSOMES

Structural Levels Of Eukaryotic Chromosomes

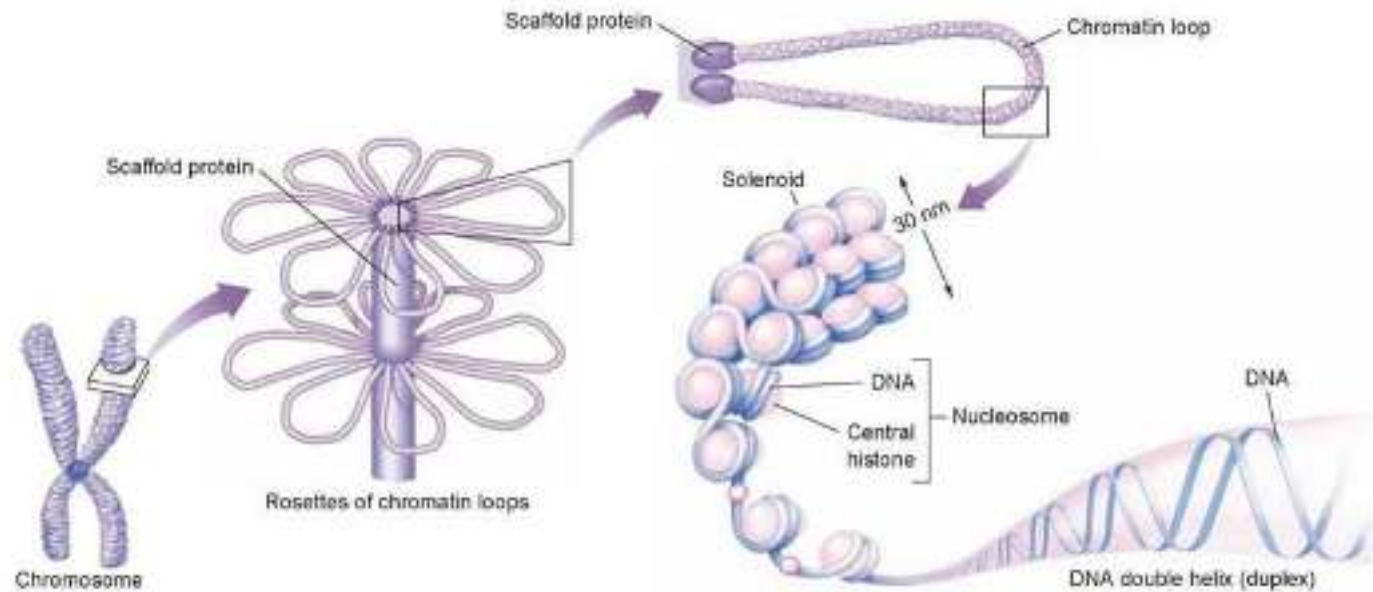
Eukaryotic Chromosomes

- ▶ DNA is the genetic material, and it exists with protein in the form of chromosomes in eukaryotic cells.
- ▶ During most of the life of a cell, chromosomes are in a highly dispersed state called **chromatin**.
- ▶ During these times, units of inheritance called **genes** may actively participate in the formation of protein.
- ▶ When a cell is dividing, however, chromosomes exist in a highly folded and condensed state that allows them to be distributed between new cells being produced.

Eukaryotic Chromosomes

- ▶ **Chromatin** consists of DNA and histone proteins.
- ▶ This association of DNA and protein helps with the complex jobs of packing DNA into chromosomes (chromosome condensation) and regulating DNA activity.
- ▶ There are five different histone proteins.
- ▶ The amino acid composition of these proteins creates positive charges that attract the negative charges of DNA's phosphate groups.
- ▶ Some of these proteins form a core particle.
- ▶ DNA wraps in a coil around the proteins, a combination called a **nucleosome** .
As shown in figure below:

Eukaryotic Chromosomes



Eukaryotic Chromosomes

- ▶ **Organization of Eukaryotic Chromosomes:** The above figure shows that Chromosomes consist of long DNA molecules that wrap histone proteins. The DNA and histone complex is called a nucleosome, and the chain of nucleosomes is coiled into a solenoid. The solenoid is then looped into rosettes around a scaffold protein. Further compaction results in the eukaryotic chromosome.

Eukaryotic Chromosomes

- ▶ The fifth histone, sometimes called the linker protein, is not needed to form the nucleosome but may help anchor the DNA to the core and promote the winding of the chain of nucleosomes into a solenoid.
- ▶ Higher-order folding forms chromatin loops, rosettes, and the final chromosome. The details of this higher-order folding are still under investigation.
- ▶ Inactive portions of chromosomes produce dark banding patterns with certain staining procedures and thus are called **heterochromatic regions**, whereas active portions of chromosomes are called **euchromatic regions**.

Eukaryotic Chromosomes

- ▶ Alterations of chromatin structure including the addition of chemical groups to histone proteins and DNA, removal or repositioning nucleosomes, and hypercondensation of chromatin can control chromatin activity.

EUKARYOTIC CHROMOSOMES

Sex Chromosomes and Autosomes

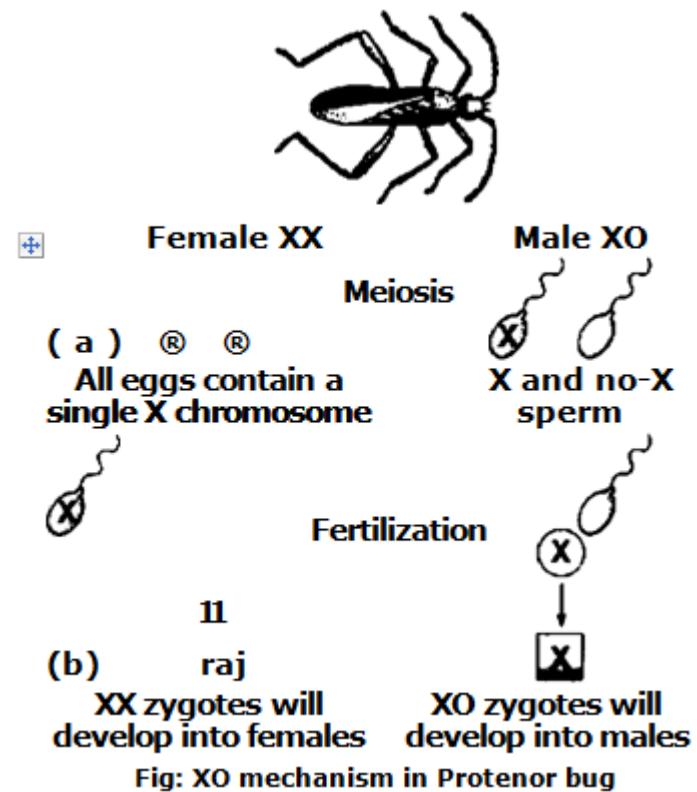
Sex Chromosomes and Autosomes

- ▶ In the early 1900s, attention turned to the cell to find a chromosomal explanation for the determination of maleness or femaleness.
- ▶ Some of the evidence for a chromosomal basis for sex determination came from work with the insect *Protenor*.
- ▶ One darkly staining chromosome of *Protenor*, called the **X chromosome**, is represented differently in males and females.
- ▶ All somatic (body) cells of males have one X chromosome (XO), and all somatic cells of females have two X chromosomes (XX).

Sex Chromosomes and Autosomes

- ▶ Similarly, half of all sperm contain a single X, and half contain no X, whereas all female gametes contain a single X.
- ▶ This pattern suggests that fertilization involving an X-bearing sperm will result in a female offspring and that fertilization involving a sperm with no X chromosome will result in a male offspring.
- ▶ As figure below shows, this sex determination system explains the approximately 50:50 ratio of females to males in this insect species.

Sex Chromosomes and Autosomes



Sex Chromosomes and Autosomes

- ▶ **X-O System of Sex Determination for the Insect Protenor:** The figure shows that (a) Protenor belfragei belongs to a family of plant bugs that feed on plant juices of grasses and sedges. (b) In females, all cells except gametes possess two X chromosomes. During meiosis, homologous X chromosomes segregate, and all eggs contain one X chromosome. Males possess one X chromosome per cell. Meiosis results in half of all sperm cells having one X, and half of all sperm cells having no X. (c) Fertilization results in half of all offspring having one X chromosome (males), and half of all offspring having two X chromosomes (females).

Sex Chromosomes and Autosomes

- ▶ Chromosomes that are represented differently in females than in males and function in sex determination are **sex chromosomes**.
- ▶ Chromosomes that are alike and not involved in determining sex are **autosomes** (Gr. autos, self 1 soma, body).
- ▶ The **system of sex determination** described for *Protenor* is called the **X-O system**.
- ▶ It is the simplest system for determining sex because it involves only one kind of chromosome.
- ▶ Many other animals (e.g., humans and fruit flies) have an **X-Y system** of sex determination.

Sex Chromosomes and Autosomes

- ▶ In the X-Y system, males and females have an equal number of chromosomes, but the male is usually XY, and the female is XX.
- ▶ (In birds, the sex chromosomes are designated Z and W, and the female is ZW.)
- ▶ Even though the X and Y chromosomes are called “**sex chromosomes**,” they also help determine non-sex-related traits.
- ▶ This is especially true for the X chromosome of most animals.
- ▶ It is very large and has genes that code for many traits. Similarly, autosomal chromosomes frequently carry genes that influence sexual characteristics.

Sex Chromosomes and Autosomes

- ▶ This mode of sex determination also results in approximately equal numbers of male and female offspring:

Sperm

X Y

Egg X XX XY

1 female : 1 male

EUKARYOTIC CHROMOSOMES

Number of Chromosome

Number of Chromosome

- ▶ Even though the number of chromosomes is constant within a species, chromosome number varies greatly among species.
- ▶ The chromosome number of animals usually varies between 10 and 50.

Number of Chromosome

- ▶ Chromosomes are present in sets, with the number in a set being characteristic of each kind of animal and expressed as “N.”
- ▶ N identifies the number of different kinds of chromosomes. Most animals have two sets, or $2N$ chromosomes.
- ▶ This is the **diploid** (Gr. di, two 1 eoides, doubled) **condition**.
- ▶ Some animals have only one set, or N chromosomes (like gametes) and are **haploid** (Gr. hapl, single) (e.g., male honeybees and some rotifers).

Number of Chromosome

- ▶ Very few animals (e.g., brine shrimp, snout beetles, some flatworms, and some sow bugs) have more than the diploid number of chromosomes, a condition called **polyploidy** (Gr. polys, more).
- ▶ The upset in numbers of sex chromosomes apparently interferes with reproductive success.
- ▶ Asexual reproduction often accompanies polyploidy.

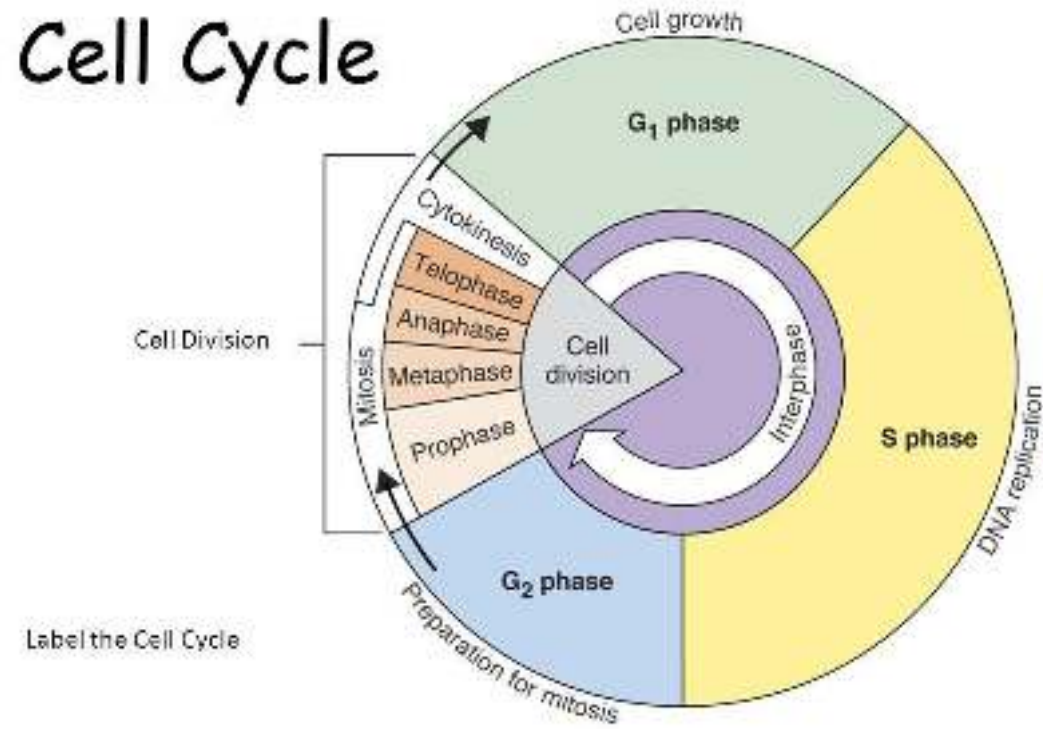
Cell Division

Cell Cycle

Cell Cycle

- ▶ The life of a cell begins when a parent cell divides to produce the new cell.
- ▶ The new cell then goes through maintenance and growth processes until it matures and ultimately divides to produce another generation of two cells.
- ▶ The life of a cell, from its beginning until it divides to produce the new generation of cells, is called the **cell cycle**.

Cell Cycle



Cell Cycle

- ▶ **Life Cycle of a Eukaryotic Cell:** The figure shows that during the G1 phase, cell components are synthesized and metabolism occurs, often resulting in cell growth. During the S (synthesis) phase, the chromosomes replicate, resulting in two identical copies called sister chromatids. During the G2 phase, metabolism and growth continue until the mitotic phase is reached. This drawing is generalized, and the length of different stages varies greatly from one cell to the next

Cell Cycle

- ▶ **Mitosis** (Gr. mitos, thread) is the distribution of chromosomes between two daughter cells, and **cytokinesis** (Gr. kytos, hollow vessel 1 kinesis, motion) is the partitioning of the cytoplasm between the two daughter cells.
- ▶ **Interphase** (L. inter, between) is the time between the end of cytokinesis and the beginning of the next mitotic division.
- ▶ It is a time of cell growth, DNA synthesis, and preparation for the next mitotic division.

Cell Cycle

- ▶ The **G1** (first growth or gap) phase represents the early growth phase of the cell. During the **S (DNA synthesis) phase**, growth continues, but this phase also involves DNA replication.
- ▶ The **G2** (second growth or gap) phase prepares the cell for division.
- ▶ It includes replication of the mitochondria and other organelles, synthesis of microtubules and protein that will make up the mitotic spindle fibers, and chromosome condensation.

Cell Cycle

- ▶ The **M** (mitotic) phase includes events associated with partitioning chromosomes between two daughter cells and the division of the cytoplasm (cytokinesis).

Cell Division

Interphase: Replicating the Hereditary Material

Interphase: Replicating the Hereditary Material

- ▶ Interphase typically occupies about 90% of the total cell cycle. The first portion of interphase is **gap phase 1 (G1)**.
- ▶ It is usually the longest interval of interphase and is a period of cell growth and the metabolic activities characteristic of the particular cell type.
- ▶ G1 ends with the beginning of the S phase.

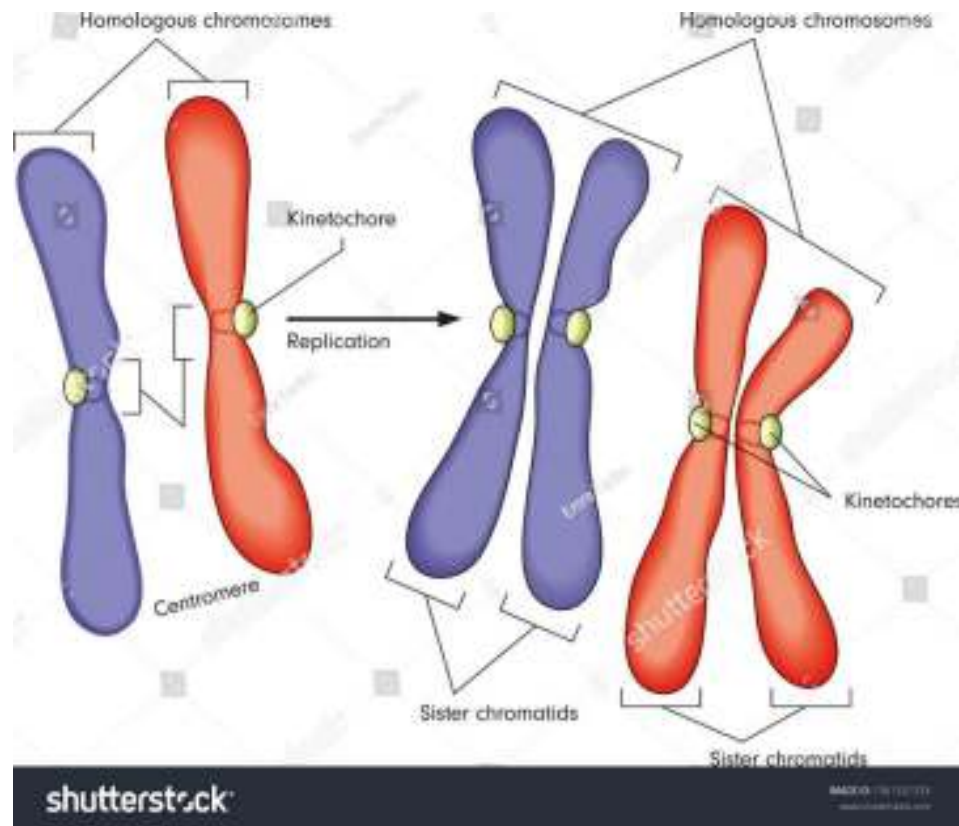
Interphase: Replicating the Hereditary Material

- ▶ Before a cell divides, an exact copy of the DNA is made during the S (synthesis) phase. This process is called **replication**, because the double-stranded DNA makes a replica, or duplicate, of itself.
- ▶ **Replication** is essential to ensure that each daughter cell receives identical genetic material to that present in the parent cell.
- ▶ The result is a pair of identical sister chromatids .
- ▶ A **chromatid** is a copy of a chromosome produced by replication. Each chromatid attaches to its other copy, or sister, at a point of constriction called a **centromere**.

Interphase: Replicating the Hereditary Material

- ▶ The centromere is a specific DNA sequence of about 220 nucleotides and has a specific location on any given chromosome.
- ▶ Bound to each centromere is a disk of protein called a **kinetochore**, which eventually is an attachment site for the microtubules of the mitotic spindle.

Interphase: Replicating the Hereditary Material



Interphase: Replicating the Hereditary Material

- ▶ The final stage of interphase is **gap phase 2 (G2)**.
- ▶ As the cell cycle moves into the G2 phase, the chromosomes begin condensation.
- ▶ During the G2 phase, the cell also begins to assemble the structures that it will later use to move the chromosomes to opposite poles (ends) of the cell.
- ▶ For example, centrioles replicate, and there is extensive synthesis of the proteins that make up the microtubules.

Interphase: Replicating the Hereditary Material

- ▶ The time spent by a cell in interphase varies greatly depending on the cell.
- ▶ Rapidly dividing embryonic cells move very quickly through G1 to S, and again quickly through G2 to M.
- ▶ The entire cell cycle may occur within a few minutes time.
- ▶ Rapidly dividing cells produce a many-celled embryo from a single fertilized egg within hours.

Interphase: Replicating the Hereditary Material

- ▶ On the other hand, maturing cells spend relatively more time in G1 because they are growing and taking on functions of adult cells.
- ▶ Many adult cells are not dividing.
- ▶ Mature bone, muscle, and nerve cells enter G1 and pause.
- ▶ They may remain in this G0 phase indefinitely or until cell division is required, for example, to repair an injury.

Cell Division

M-Phase: Mitosis

M-Phase: Mitosis

- ▶ **Mitosis** is divided into five phases:
- ▶ Prophase
- ▶ Prometaphase
- ▶ Metaphase
- ▶ Anaphase
- ▶ Telophase

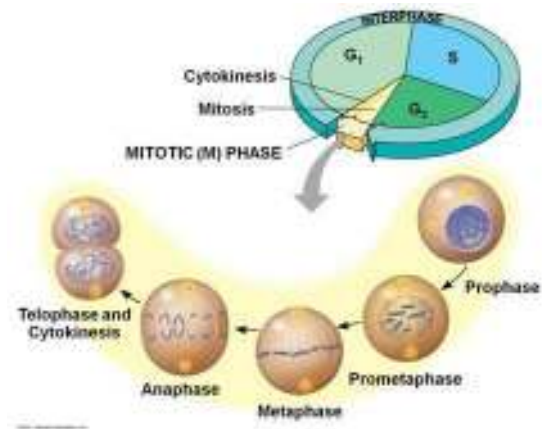
M-Phase: Mitosis

- ▶ The first phase of mitosis, **prophase** (Gr. pro, before 1 phase), begins when chromosomes become visible with the light microscope as threadlike structures.
- ▶ The nucleoli and nuclear envelope begin to break up, and the two centriole pairs move apart.
- ▶ By the end of prophase, the centriole pairs are at opposite poles of the cell.
- ▶ The centrioles radiate an array of microtubules called asters (L. aster, little star), which brace each centriole against the plasma membrane.
- ▶ Between the centrioles, the microtubules form a spindle of fibers that extends from pole to pole.
- ▶ The asters, spindle, centrioles, and microtubules are collectively called the mitotic spindle (or mitotic apparatus).

M-Phase: Mitosis

- ▶ **Prometaphase** follows the break-up of the nuclear envelope.
- ▶ A second group of microtubules attach at one end to the kinetochore of each chromatid and to one of the poles of the cell at the other end of the microtubule.
- ▶ This bipolar attachment of spindle fibers to chromatids is critical to the movement of the chromatids of each chromosome to opposite poles of the cell in subsequent phases of mitosis.

M-Phase: Mitosis



M-Phase: Mitosis

- ▶ As the dividing cell moves into **metaphase** (Gr. meta, after 1 phase), the chromatids (replicated chromosomes) begin to align in the center of the cell, along the spindle equator.
- ▶ Toward the end of metaphase, the centromeres divide and detach the two sister chromatids from each other, although the chromatids remain aligned next to each other.
- ▶ After the centromeres divide, the sister chromatids are considered fullfledged chromosomes (called daughter chromosomes).

M-Phase: Mitosis

- ▶ During **anaphase** (Gr. ana, back again 1 phase), the shortening of the microtubules in the mitotic spindle, and perhaps the activity of motor proteins of the kinetochore, pulls each daughter chromosome apart from its copy and moves it toward its respective pole.
- ▶ Anaphase ends when all the daughter chromosomes have moved to the poles of the cell.
- ▶ Each pole now has a complete, identical set of chromosomes.

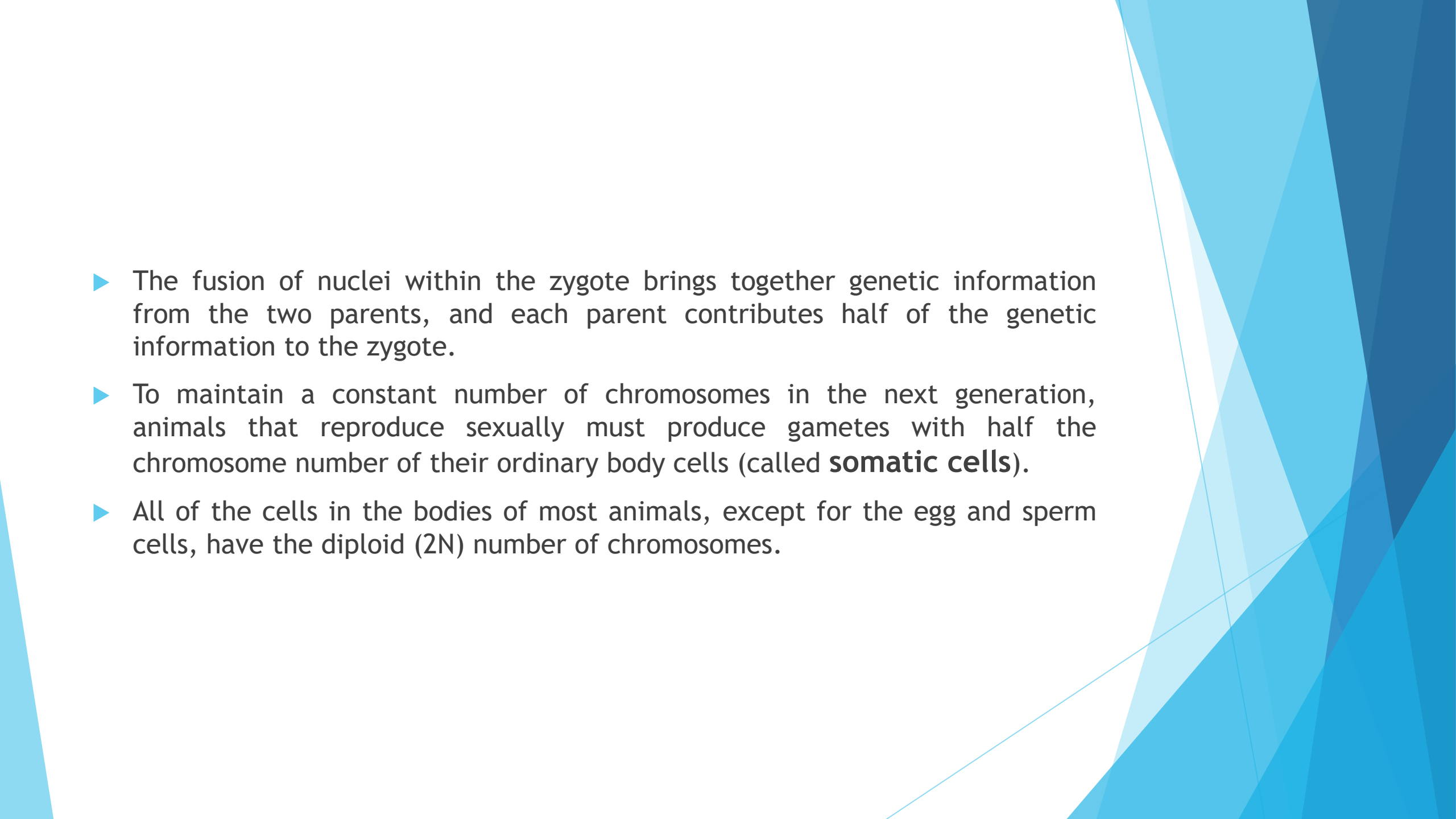
M-Phase: Mitosis

- ▶ **Telophase** (Gr. telos, end 1 phase) begins once the daughter chromosomes arrive at the opposite poles of the cell.
- ▶ During telophase, the mitotic spindle disassembles.
- ▶ A nuclear envelope re-forms around each set of chromosomes, which begin to uncoil for gene expression, and the nucleolus is resynthesized.
- ▶ The cell also begins to pinch in the middle.
- ▶ Mitosis is over, but cell division is not.

Cell Division

MEIOSIS: THE BASIS OF SEXUAL REPRODUCTION

- ▶ **Sexual reproduction** requires a genetic contribution from two different sex cells.
- ▶ Egg and sperm cells are specialized sex cells called gametes (Gr. gamete, wife; gametes, husband).
- ▶ In animals, a male gamete (sperm) unites with a female gamete (egg) during fertilization to form a single cell called a **zygote** (Gr. zygotos, yoked together).
- ▶ The **zygote** is the first cell of the new animal.

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- The background of the slide features abstract, overlapping geometric shapes in various shades of blue, ranging from light sky blue to deep navy blue. These shapes are primarily located on the right side and bottom of the slide, creating a modern, dynamic aesthetic.
- ▶ The fusion of nuclei within the zygote brings together genetic information from the two parents, and each parent contributes half of the genetic information to the zygote.
 - ▶ To maintain a constant number of chromosomes in the next generation, animals that reproduce sexually must produce gametes with half the chromosome number of their ordinary body cells (called **somatic cells**).
 - ▶ All of the cells in the bodies of most animals, except for the egg and sperm cells, have the diploid ($2N$) number of chromosomes.

- ▶ Gametes are produced by cells set aside for that purpose early in development.
- ▶ These cells are called **germ-line cells** and eventually undergo a type of cell division called **meiosis** (Gr. meiosis, diminution).
- ▶ Meiosis occurs in germ-line cells of the ovaries and testes and reduces the number of chromosomes to the haploid ($1N$) number.
- ▶ The nuclei of the two gametes combine during fertilization and restore the diploid number.

- ▶ Meiosis begins after the G2 phase in the cell cycle— after DNA replication.
- ▶ Two successive nuclear divisions, designated meiosis I and meiosis II, take place.
- ▶ The two nuclear divisions of meiosis result in four daughter cells, each with half the number of chromosomes of the parent cell.
- ▶ Moreover, these daughter cells are not genetically identical.
- ▶ Like mitosis, meiosis is a continuous process, and biologists divide it into the phases that follow only for convenience.

M-Phase: Cytokinesis

- ▶ The final phase of cell division is **cytokinesis**, in which the cytoplasm divides.
- ▶ **Cytokinesis** usually starts sometime during late anaphase or early telophase.
- ▶ A contracting belt of microfilaments called the **contractile ring** pinches the plasma membrane to form the cleavage furrow.
- ▶ The furrow deepens, and two new, genetically identical, daughter cells form.

Cell Division

The First Meiotic Division

The First Meiotic Division

- ▶ In **prophase I**, chromatin folds and chromosomes become visible under a light microscope.
- ▶ Because a cell has a copy of each type of chromosome from each original parent cell, it contains the diploid number of chromosomes.
- ▶ **Homologous chromosomes** (homologues) carry genes for the same traits, are the same length, and have a similar staining pattern, making them identifiable as matching pairs.

The First Meiotic Division

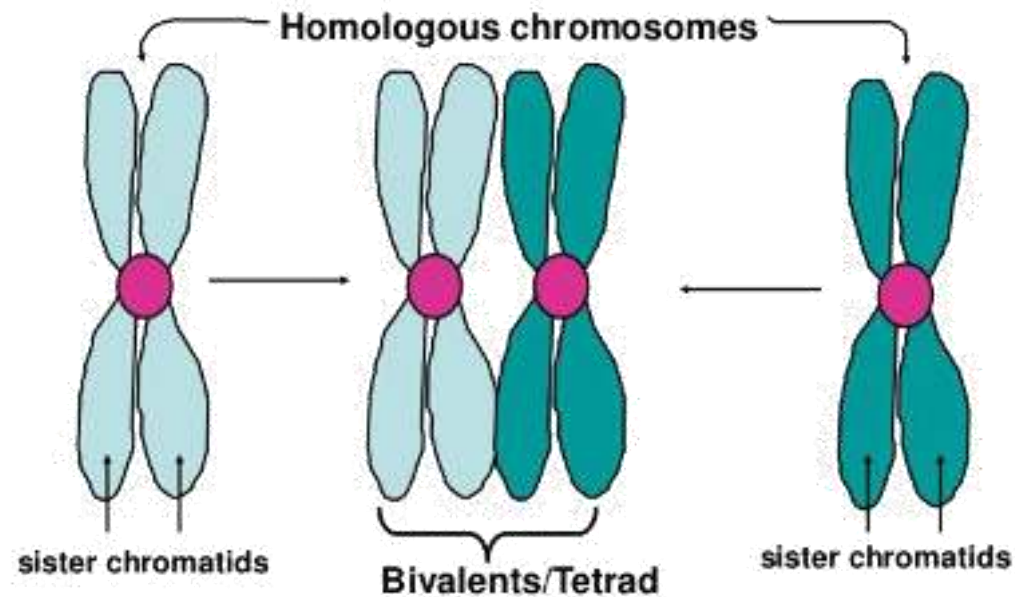
- ▶ During prophase I, homologous chromosomes line up side-by-side in a process called **synapsis** (Gr. synapsis, conjunction), forming a tetrad of chromatids (also called a bivalent).
- ▶ The tetrad thus contains the two homologous chromosomes, one is maternal in origin and one is paternal in origin.
- ▶ An elaborate network of protein is laid down between the two homologous chromosomes.
- ▶ This network holds the homologous chromosomes in a precise union so that corresponding genetic regions of the homologous chromosomes are exactly aligned.

The First Meiotic Division

- ▶ Synapsis also initiates a series of events called **crossingover**, whereby the nonsister chromatids of the two homologous chromosomes in a tetrad exchange DNA segments.
- ▶ This process effectively redistributes genetic information among the paired homologous chromosomes and produces new combinations of genes on the various chromatids in homologous pairs.
- ▶ Thus, each chromatid ends up with new combinations of instructions for a variety of traits.
- ▶ **Crossingover** is a form of genetic recombination and is a major source of genetic variation in a population of a given species.

The First Meiotic Division

**Synapsis during prophase I:
process by which bivalents/tetrad form**



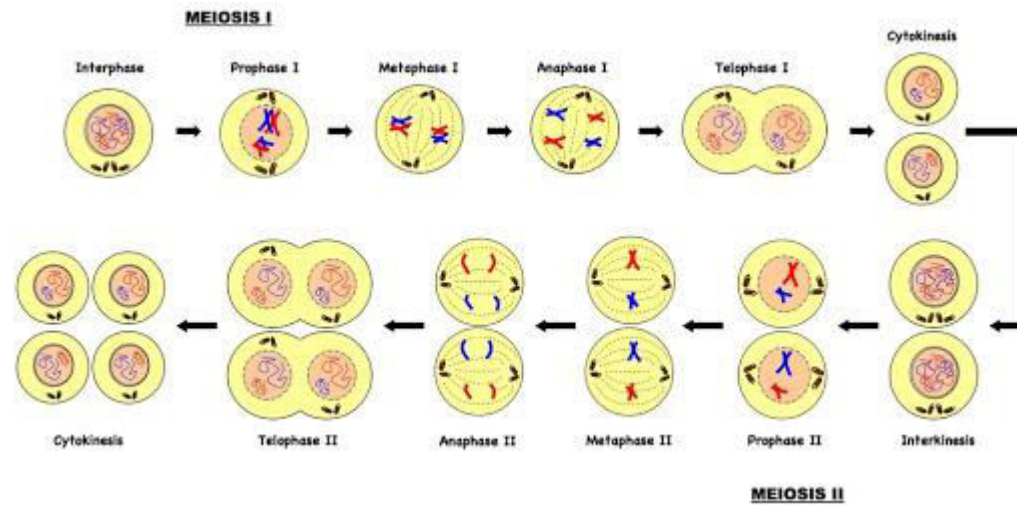
The First Meiotic Division

- ▶ In metaphase I, the microtubules form a spindle apparatus just as in mitosis.
- ▶ However, unlike mitosis, where homologous chromosomes do not pair, each pair of homologues lines up in the center of the cell, with centromeres on each side of the spindle equator.
- ▶ Anaphase I begins when homologous chromosomes separate and begin to move toward each pole.
- ▶ Because the orientation of each pair of homologous chromosomes in the center of the cell is random, the specific chromosomes that each pole receives from each pair of homologues are also random.

The First Meiotic Division

- ▶ This random distribution of members of each homologous pair to the poles of the cell, along with the genetic recombination between homologous chromosomes that occurs during crossing-over (prophase I), means that no two daughter cells produced by meiotic cell division will be identical.
- ▶ Meiotic telophase I is similar to mitotic telophase.
- ▶ The transition to the second nuclear division is called **interkinesis**.
- ▶ Cells proceeding through interkinesis do not replicate their DNA. After a varying time period, meiosis II occurs.

The First Meiotic Division

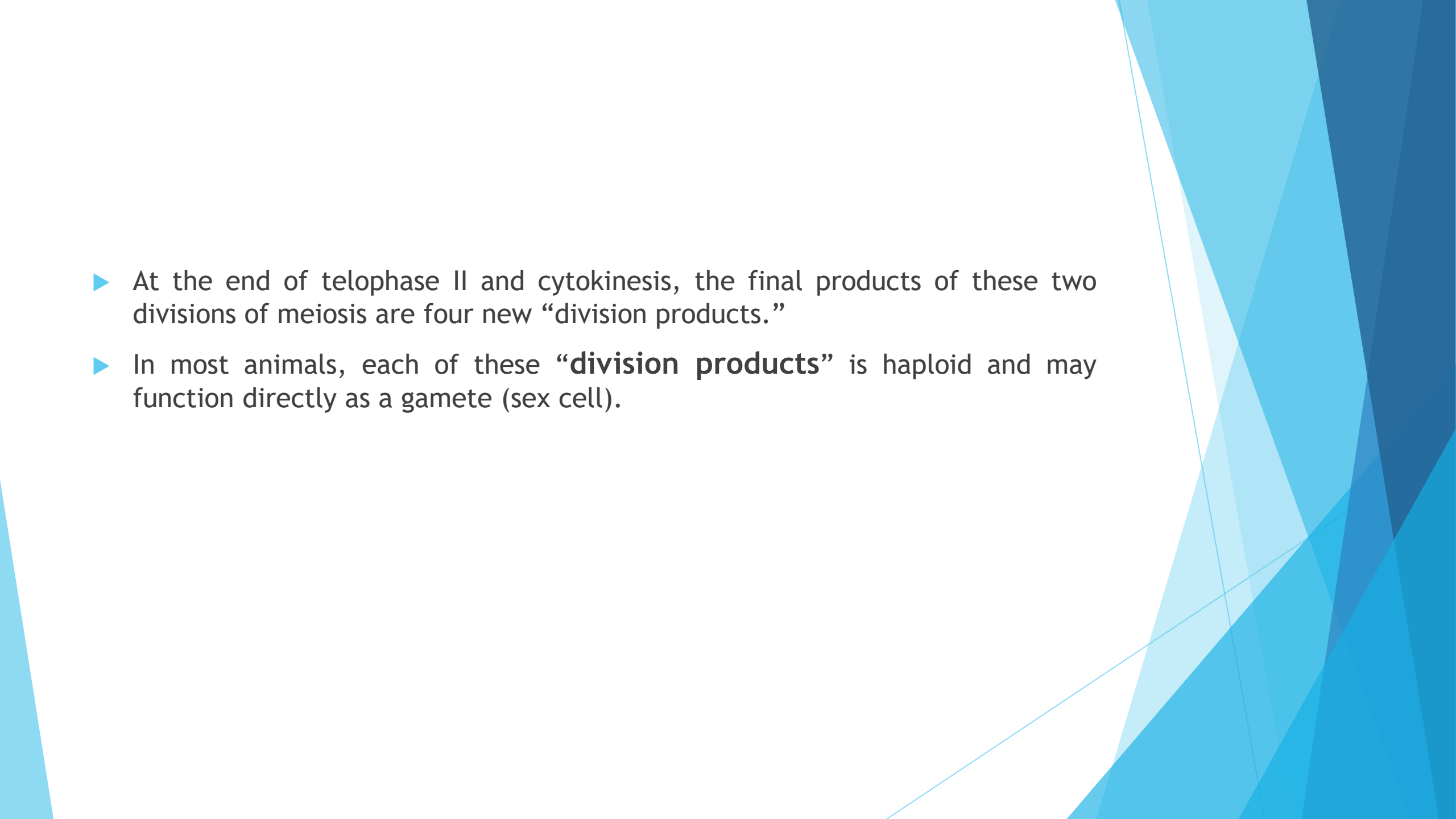


Cell Division

The Second Meiotic Division

The Second Meiotic Division

- ▶ The second **meiotic division** (meiosis II) resembles an ordinary mitotic division, except that the number of chromosomes has been reduced by half.
- ▶ The phases are listed below:
- ▶ Prophase II
- ▶ Metaphase II
- ▶ Anaphase II
- ▶ Telophase II

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- The background of the slide features abstract, overlapping geometric shapes in various shades of blue, ranging from light sky blue to deep navy blue. These shapes are primarily located on the right side and bottom of the slide, creating a modern, dynamic aesthetic.
- ▶ At the end of telophase II and cytokinesis, the final products of these two divisions of meiosis are four new “division products.”
 - ▶ In most animals, each of these “**division products**” is haploid and may function directly as a gamete (sex cell).

Spermatogenesis and Oogenesis

- ▶ The result of meiosis in most animals is the formation of sperm and egg cells.
- ▶ **Spermatogenesis** produces mature sperm cells and follows the sequence previously described.
- ▶ All four products of meiosis often acquire a flagellum for locomotion and a caplike structure that aids in the penetration of the egg.

Spermatogenesis and Oogenesis

- ▶ **Oogenesis** produces a mature ovum or egg. It differs from spermatogenesis in that only one of the four meiotic products develops into the functional gamete.
- ▶ The other products of meiosis are called **polar bodies** and eventually disintegrate.
- ▶ In some animals the mature egg is the product of the first meiotic division and only completes meiosis if it is fertilized by a sperm cell.

Cell Division

Control of the Cell Cycle

Control of the Cell Cycle

- ▶ It is essential that daughter cells be exact duplicates of the parent cell.
- ▶ Mistakes in the duplication or distribution of the chromosomes lead to mutations that may be passed forward to every new cell produced from the abnormal cell.
- ▶ To prevent a compromised cell from continuing to divide, there are internal control mechanisms that operate at three main **cell cycle checkpoints** at which the cell cycle can be stopped until conditions are favorable.

Control of the Cell Cycle

- ▶ The first checkpoint (G_1) determines whether all conditions are favorable for cell division to proceed.
- ▶ This checkpoint is the point at which the cell irreversibly commits to the cell-division process. In addition to adequate reserves and cell size, there is a check for damage to the genomic DNA.
- ▶ A cell that does not meet all the requirements will not be released into the S phase.

Control of the Cell Cycle

- ▶ The second checkpoint (G_2) bars the entry to the mitotic phase if certain conditions are not met.
- ▶ The most important role of this checkpoint is to ensure that all of the chromosomes have been replicated and that the replicated DNA is not damaged.
- ▶ The final checkpoint (M) occurs in the middle of mitosis.
- ▶ This checkpoint determines if all of the copied chromosomes are arranged appropriately to be separated to opposite sides of the cell.
- ▶ If this doesn't happen correctly, incorrect numbers of chromosomes can be partitioned into each of the daughter cells, which would likely cause them to die.

REGULATOR MOLECULES OF THE CELL CYCLE

- ▶ In addition to the internally controlled checkpoints, there are two groups of intracellular molecules that regulate the cell cycle. These regulatory molecules either promote progress of the cell to the next phase (positive regulation) or halt the cycle (negative regulation).
- ▶ Regulator molecules may act individually, or they can influence the activity or production of other regulatory proteins.
- ▶ Therefore, it is possible that the failure of a single regulator may have almost no effect on the cell cycle, especially if more than one mechanism controls the same event.
- ▶ It is also possible that the effect of a deficient or non-functioning regulator can be wide-ranging and possibly fatal to the cell if multiple processes are affected.

POSITIVE REGULATION OF THE CELL CYCLE

- ▶ Two groups of proteins, called **cyclins** and **cyclin-dependent kinases (Cdks)**, are responsible for the progress of the cell through the various checkpoints.
- ▶ Increases in the concentration of cyclin proteins are triggered by both external and internal signals.
- ▶ After the cell moves to the next stage of the cell cycle, the cyclins that were active in the previous stage are degraded.
- ▶ Cyclins regulate the cell cycle only when they are tightly bound to Cdks.

POSITIVE REGULATION OF THE CELL CYCLE

- ▶ To be fully active, the Cdk/cyclin complex must also be phosphorylated in specific locations.
- ▶ Like all kinases, Cdks are enzymes (kinases) that phosphorylate other proteins. Phosphorylation activates the protein by changing its shape.
- ▶ The proteins phosphorylated by Cdks are involved in advancing the cell to the next phase.
- ▶ The levels of Cdk proteins are relatively stable throughout the cell cycle; however, the concentrations of cyclin fluctuate and determine when Cdk/cyclin complexes form.
- ▶ The different cyclins and Cdks bind at specific points in the cell cycle and thus regulate different checkpoints.

POSITIVE REGULATION OF THE CELL CYCLE

- ▶ Since the cyclic fluctuations of cyclin levels are based on the timing of the cell cycle and not on specific events, regulation of the cell cycle usually occurs by either the Cdk molecules alone or the Cdk/cyclin complexes.
- ▶ Without a specific concentration of fully activated cyclin/Cdk complexes, the cell cycle cannot proceed through the checkpoints.

Cell Division

Control of Cell Cycle (Part II)

NEGATIVE REGULATION OF THE CELL CYCLE

- ▶ The second group of cell cycle regulatory molecules are **negative regulators**.
- ▶ In positive regulation, active molecules such as CDK/cyclin complexes cause the cell cycle to progress. In negative regulation, active molecules halt the cell cycle.
- ▶ **Negative regulatory molecules** are as follows:
 - ▶ Retinoblastoma protein (Rb)
 - ▶ p53
 - ▶ p21

NEGATIVE REGULATION OF THE CELL CYCLE

- ▶ Much of what is known about cell cycle regulation comes from research conducted with cells that have lost regulatory control.
- ▶ All three of these regulatory proteins were discovered to be damaged or non-functional in cells that had begun to replicate uncontrollably (became cancerous).
- ▶ In each case, the main cause of the unchecked progress through the cell cycle was a faulty copy of the regulatory protein.
- ▶ For this reason, Rb and other proteins that negatively regulate the cell cycle are sometimes called **tumor suppressors**.

NEGATIVE REGULATION OF THE CELL CYCLE

- ▶ Rb, p53, and p21 act primarily at the G_1 checkpoint.
- ▶ **p53** is a multi-functional protein that has a major impact on the commitment of a cell to division because it acts when there is damaged DNA in cells that are undergoing the preparatory processes during G_1 .
- ▶ If damaged DNA is detected, p53 halts the cell cycle and recruits enzymes to repair the DNA.
- ▶ If the DNA cannot be repaired, p53 can trigger apoptosis, or cell suicide, to prevent the duplication of damaged chromosomes.

NEGATIVE REGULATION OF THE CELL CYCLE

- ▶ As p53 levels rise, the production of **p21** is triggered.
- ▶ **p21** enforces the halt in the cycle dictated by p53 by binding to and inhibiting the activity of the Cdk/cyclin complexes.
- ▶ As a cell is exposed to more stress, higher levels of p53 and p21 accumulate, making it less likely that the cell will move into the S phase.

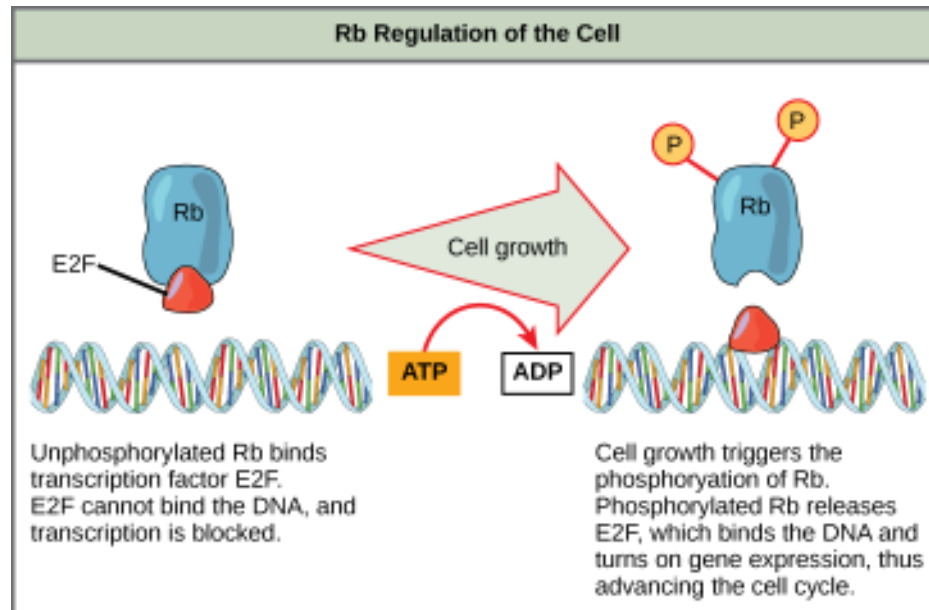
NEGATIVE REGULATION OF THE CELL CYCLE

- ▶ **Rb** exerts its regulatory influence on other positive regulator proteins. Chiefly, Rb monitors cell size.
- ▶ In the active, dephosphorylated state, Rb binds to proteins called transcription factors.
- ▶ Transcription factors “turn on” specific genes, allowing the production of proteins encoded by that gene.
- ▶ When Rb is bound to transcription factors, production of proteins necessary for the G_1/S transition is blocked.

NEGATIVE REGULATION OF THE CELL CYCLE

- ▶ As the cell increases in size, Rb is slowly phosphorylated until it becomes inactivated.
- ▶ Rb releases the transcription factors, which can now turn on the gene that produces the transition protein, and this particular block is removed.
- ▶ For the cell to move past each of the checkpoints, all positive regulators must be “turned on,” and all negative regulators must be “turned off.”

NEGATIVE REGULATION OF THE CELL CYCLE



DNA: THE GENETIC MATERIAL

DNA: THE GENETIC MATERIAL

- ▶ A molecule that serves as the genetic material must have certain characteristics to explain the properties of life:
- ▶ First, the genetic material must be able to code for the sequence of amino acids in proteins and control protein synthesis.
- ▶ Second, it must be able to replicate itself prior to cell division.
- ▶ Third, the genetic material must be in the nuclei of eukaryotic cells.
- ▶ Fourth, it must be able to change over time to account for evolutionary change.
- ▶ Only one molecule, DNA (deoxyribonucleic acid), fulfills all of these requirements.

The Double Helix Model

- ▶ Two kinds of molecules participate in protein synthesis.
- ▶ Both are based on a similar building block, the nucleotide, giving them their name—nucleic acids.
- ▶ One of these molecules, deoxyribonucleic acid or DNA, is the genetic material, and the other, ribonucleic acid or RNA, is produced in the nucleus and moves to the cytoplasm, where it participates in protein synthesis.
- ▶ The study of how the information stored in DNA codes for RNA and protein is **molecular genetics**.

The Double Helix Model

- ▶ DNA and RNA are large molecules made up of subunits called **nucleotides**.
- ▶ A **nucleotide** consists of a nitrogen- containing organic base in the form of either a double ring (purine) or a single ring (pyrimidine).
- ▶ Nucleotides also contain a pentose (five-carbon) sugar and a phosphate (2PO₄) group.
- ▶ DNA and RNA molecules, however, differ in several ways.

The Double Helix Model

- ▶ Both DNA and RNA contain the purine bases adenine and guanine, and the pyrimidine base cytosine.
- ▶ The second pyrimidine in DNA, however, is thymine, whereas in RNA it is uracil.
- ▶ A second difference between DNA and RNA involves the sugar present in the nucleotides.
- ▶ The pentose of DNA is deoxyribose, and in RNA it is ribose.
- ▶ A third important difference between DNA and RNA is that DNA is a double-stranded molecule and RNA is single stranded, although it may fold back on itself and coil.

The Double Helix Model

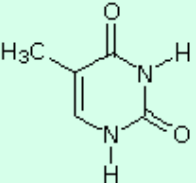
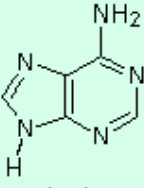
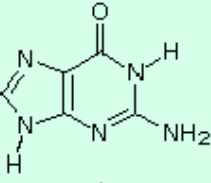
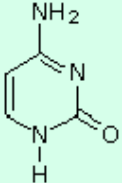
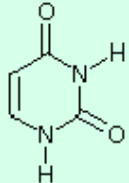
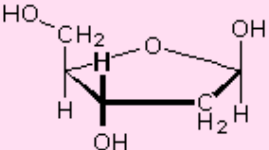
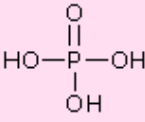
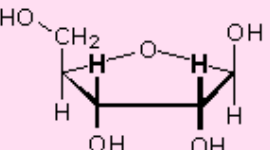
- ▶ The key to understanding the function of DNA is knowing how nucleotides link into a three-dimensional structure.
- ▶ The DNA molecule is ladderlike, with the rails of the ladder consisting of alternating sugar-phosphate groups.
- ▶ The phosphate of a nucleotide attaches at the fifth (5') carbon of deoxyribose.
- ▶ Adjacent nucleotides attach to one another by a covalent bond between the phosphate of one nucleotide and the third (3') carbon of deoxyribose.
- ▶ The pairing of nitrogenous bases between strands holds the two strands together.

The Double Helix Model

- ▶ Adenine (a purine) is hydrogen bonded to its complement, thymine (a pyrimidine), and guanine (a purine) is hydrogen bonded to its complement, cytosine (a pyrimidine).
- ▶ Each strand of DNA is oriented such that the 3' carbons of deoxyribose in one strand are oriented in the opposite directions from the 5' carbons in the other strand.
- ▶ Thus, the two strands of DNA have opposite polarity and the DNA molecule is said to be antiparallel (Gr. anti, against 1 para, beside 1 allelon, of one another).
- ▶ The entire molecule is twisted into a right-handed helix, with one complete spiral every 10 base pairs.

The Double Helix Model

Components of Nucleic Acids

	DNA only	DNA & RNA			RNA only
Nitrogen Bases	 Thymine	 Adenine	 Guanine	 Cytosine	 Uracil
Sugars & Phosphate	 2-Deoxyribose	 Phosphate			 Ribose

DNA: The Genetic Material

DNA Replication in Prokaryotes

DNA Replication in Prokaryotes

- ▶ DNA replication has been extremely well studied in prokaryotes primarily because of the small size of the genome and the mutants that are available.
- ▶ *E. coli* has 4.6 million base pairs in a single circular chromosome and all of it gets replicated in approximately 42 minutes, starting from a single origin of replication and proceeding around the circle in both directions.
- ▶ This means that approximately 1000 nucleotides are added per second. The process is quite rapid and occurs without many mistakes.

DNA Replication in Prokaryotes

- ▶ DNA replication employs a large number of proteins and enzymes, each of which plays a critical role during the process.
- ▶ One of the key players is the enzyme DNA polymerase, also known as DNA pol, which adds nucleotides one by one to the growing DNA chain that are complementary to the template strand.
- ▶ The addition of nucleotides requires energy; this energy is obtained from the nucleotides that have three phosphates attached to them, similar to ATP which has three phosphate groups attached.
- ▶ When the bond between the phosphates is broken, the energy released is used to form the phosphodiester bond between the incoming nucleotide and the growing chain.
- ▶ In prokaryotes, three main types of polymerases are known: DNA pol I, DNA pol II, and DNA pol III.
- ▶ It is now known that DNA pol III is the enzyme required for DNA synthesis; DNA pol I and DNA pol II are primarily required for repair.

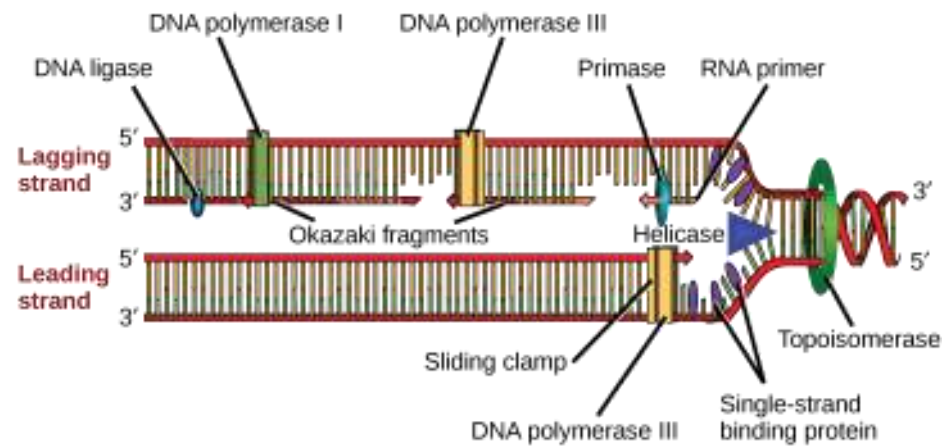
DNA Replication in Prokaryotes

- ▶ How does the replication machinery know where to begin?
- ▶ It turns out that there are specific nucleotide sequences called origins of replication where replication begins.
- ▶ In *E. coli*, which has a single origin of replication on its one chromosome (as do most prokaryotes), it is approximately 245 base pairs long and is rich in AT sequences.
- ▶ The origin of replication is recognized by certain proteins that bind to this site.
- ▶ An enzyme called helicase unwinds the DNA by breaking the hydrogen bonds between the nitrogenous base pairs.
- ▶ ATP hydrolysis is required for this process.
- ▶ As the DNA opens up, Y-shaped structures called replication forks are formed.
- ▶ Two replication forks are formed at the origin of replication and these get extended bi-directionally as replication proceeds.
- ▶ Single-strand binding proteins coat the single strands of DNA near the replication fork to prevent the single-stranded DNA from winding back into a double helix.

DNA Replication in Prokaryotes

- ▶ DNA polymerase is able to add nucleotides only in the 5' to 3' direction (a new DNA strand can be only extended in this direction).
- ▶ It also requires a free 3'-OH group to which it can add nucleotides by forming a phosphodiester bond between the 3'-OH end and the 5' phosphate of the next nucleotide.
- ▶ This essentially means that it cannot add nucleotides if a free 3'-OH group is not available.
- ▶ Then how does it add the first nucleotide?
- ▶ The problem is solved with the help of a primer that provides the free 3'-OH end.
- ▶ Another enzyme, RNA primase, synthesizes an RNA primer that is about five to ten nucleotides long and complementary to the DNA.
- ▶ Because this sequence primes the DNA synthesis, it is appropriately called the primer.
- ▶ DNA polymerase can now extend this RNA primer, adding nucleotides one by one that are complementary to the template strand

DNA Replication in Prokaryotes



DNA Replication in Prokaryotes

- ▶ The replication fork moves at the rate of 1000 nucleotides per second.
- ▶ DNA polymerase can only extend in the 5' to 3' direction, which poses a slight problem at the replication fork.
- ▶ As we know, the DNA double helix is anti-parallel; that is, one strand is in the 5' to 3' direction and the other is oriented in the 3' to 5' direction.
- ▶ One strand, which is complementary to the 3' to 5' parental DNA strand, is synthesized continuously towards the replication fork because the polymerase can add nucleotides in this direction.

DNA Replication in Prokaryotes

- ▶ This continuously synthesized strand is known as the **leading strand**.
- ▶ The other strand, complementary to the 5' to 3' parental DNA, is extended away from the replication fork, in small fragments known as **Okazaki fragments**, each requiring a primer to start the synthesis.
- ▶ **Okazaki fragments** are named after the Japanese scientist who first discovered them.
- ▶ The strand with the Okazaki fragments is known as the **lagging strand**.

DNA: The Genetic Material

DNA Replication in Eukaryotes

DNA Replication in Eukaryotes

- ▶ Eukaryotic genomes are much more complex and larger in size than prokaryotic genomes.
- ▶ The human genome has three billion base pairs per haploid set of chromosomes, and 6 billion base pairs are replicated during the S phase of the cell cycle.
- ▶ There are multiple origins of replication on the eukaryotic chromosome; humans can have up to 100,000 origins of replication.
- ▶ The rate of replication is approximately 100 nucleotides per second, much slower than prokaryotic replication.
- ▶ In yeast, which is a eukaryote, special sequences known as **Autonomously Replicating Sequences** (ARS) are found on the chromosomes.
- ▶ These are equivalent to the origin of replication in *E. coli*.

DNA Replication in Eukaryotes

- ▶ The number of DNA polymerases in eukaryotes is much more than prokaryotes:
- ▶ 14 are known, of which five are known to have major roles during replication and have been well studied.
- ▶ They are known as pol α , pol β , pol γ , pol δ , and pol ϵ .

DNA Replication in Eukaryotes

- ▶ The essential steps of replication are the same as in prokaryotes. Before replication can start, the DNA has to be made available as template.
- ▶ Eukaryotic DNA is bound to basic proteins known as **histones** to form structures called nucleosomes.
- ▶ The chromatin (the complex between DNA and proteins) may undergo some chemical modifications, so that the DNA may be able to slide off the proteins or be accessible to the enzymes of the DNA replication machinery.
- ▶ At the origin of replication, a pre-replication complex is made with other initiator proteins.
- ▶ Other proteins are then recruited to start the replication process

DNA Replication in Eukaryotes

- ▶ A helicase using the energy from ATP hydrolysis opens up the DNA helix. Replication forks are formed at each replication origin as the DNA unwinds.
- ▶ The opening of the double helix causes over-winding, or supercoiling, in the DNA ahead of the replication fork.
- ▶ These are resolved with the action of topoisomerases.
- ▶ Primers are formed by the enzyme primase, and using the primer, DNA pol can start synthesis.
- ▶ While the leading strand is continuously synthesized by the enzyme pol δ , the lagging strand is synthesized by pol ϵ .

DNA Replication in Eukaryotes

- ▶ A sliding clamp protein known as **PCNA** (Proliferating Cell Nuclear Antigen) holds the DNA pol in place so that it does not slide off the DNA.
- ▶ RNase H removes the RNA primer, which is then replaced with DNA nucleotides.
- ▶ The Okazaki fragments in the lagging strand are joined together after the replacement of the RNA primers with DNA.
- ▶ The gaps that remain are sealed by DNA ligase, which forms the phosphodiester bond

Telomere replication

- ▶ Unlike prokaryotic chromosomes, eukaryotic chromosomes are linear.
- ▶ As you've learned, the enzyme DNA pol can add nucleotides only in the 5' to 3' direction.
- ▶ In the leading strand, synthesis continues until the end of the chromosome is reached.
- ▶ On the lagging strand, DNA is synthesized in short stretches, each of which is initiated by a separate primer.
- ▶ When the replication fork reaches the end of the linear chromosome, there is no place for a primer to be made for the DNA fragment to be copied at the end of the chromosome.
- ▶ These ends thus remain unpaired, and over time these ends may get progressively shorter as cells continue to divide.

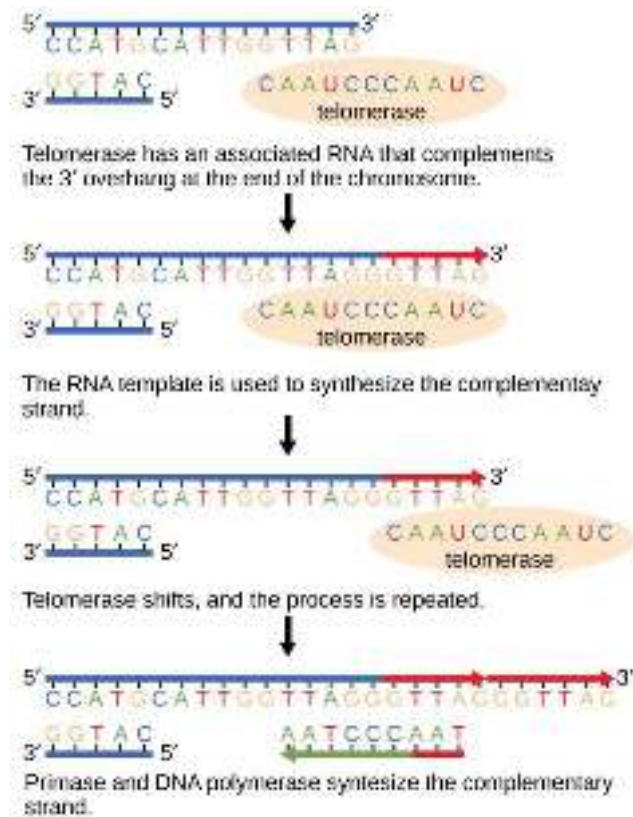
Telomere replication

- ▶ The ends of the linear chromosomes are known as **telomeres**, which have repetitive sequences that code for no particular gene.
- ▶ In a way, these telomeres protect the genes from getting deleted as cells continue to divide.
- ▶ In humans, a six base pair sequence, TTAGGG, is repeated 100 to 1000 times.
- ▶ The discovery of the enzyme telomerase helped in the understanding of how chromosome ends are maintained.

Telomere replication

- ▶ The telomerase enzyme contains a catalytic part and a built-in RNA template.
- ▶ It attaches to the end of the chromosome, and complementary bases to the RNA template are added on the 3' end of the DNA strand.
- ▶ Once the 3' end of the lagging strand template is sufficiently elongated, DNA polymerase can add the nucleotides complementary to the ends of the chromosomes.
- ▶ Thus, the ends of the chromosomes are replicated.

Telomere replication



Telomere replication

- ▶ Telomerase is typically active in germ cells and adult stem cells. It is not active in adult somatic cells. For her discovery of telomerase and its action, Elizabeth Blackburn received the Nobel Prize for Medicine and Physiology in 2009.

DNA Replication in Prokaryotes

- ▶ The leading strand can be extended by one primer alone, whereas the lagging strand needs a new primer for each of the short Okazaki fragments.
- ▶ The overall direction of the lagging strand will be 3' to 5', and that of the leading strand 5' to 3'.
- ▶ A protein called the **sliding clamp** holds the DNA polymerase in place as it continues to add nucleotides.
- ▶ The sliding clamp is a ring-shaped protein that binds to the DNA and holds the polymerase in place.
- ▶ Once the chromosome has been completely replicated, the two DNA copies move into two different cells during cell division.

Table 14.4.1 14.4.1: Prokaryotic DNA Replication: Enzymes and Their Function

Enzyme/protein	Specific Function
DNA pol I	Exonuclease activity removes RNA primer and replaces with newly synthesized DNA
DNA pol II	Repair function
DNA pol III	Main enzyme that adds nucleotides in the 5'-3' direction
Helicase	Opens the DNA helix by breaking hydrogen bonds between the nitrogenous bases
Ligase	Seals the gaps between the Okazaki fragments to create one continuous DNA strand
Primase	Synthesizes RNA primers needed to start replication
Sliding Clamp	Helps to hold the DNA polymerase in place when nucleotides are being added
Topoisomerase	Helps relieve the stress on DNA when unwinding by causing breaks and then resealing the DNA
Single-strand binding proteins (SSB)	Binds to single-stranded DNA to avoid DNA rewinding back.

DNA: The Genetic Material

Control of Gene Expression in Eukaryotes (Part I)

Genes in Action/ Gene Expression

- ▶ A **gene** can be defined as a sequence of bases in DNA that codes for the synthesis of one polypeptide, and genes must somehow transmit their information from the nucleus to the cytoplasm, where protein synthesis occurs.
- ▶ The synthesis of an RNA molecule from DNA is called **transcription** and the formation of a protein from RNA at the ribosome is called **translation**.

Three Major Kinds of RNA

- ▶ Each of the three major kinds of RNA has a specific role in protein synthesis and is produced in the nucleus from DNA.
- ▶ **Messenger RNA** (mRNA) is a linear strand that carries a set of genetic instructions for synthesizing proteins to the cytoplasm.
- ▶ **Transfer RNA** (tRNA) picks up amino acids in the cytoplasm, carries them to ribosomes, and helps position them for incorporation into a polypeptide.
- ▶ **Ribosomal RNA** (rRNA), along with proteins, makes up ribosomes.

Transcription

- ▶ The genetic information in DNA is not translated directly into proteins, but is first transcribed into mRNA.
- ▶ Transcription involves numerous enzymes that unwind a region of a DNA molecule, initiate and end mRNA synthesis, and modify the mRNA after transcription is complete.
- ▶ Unlike DNA replication, only one or a few genes are exposed, and only one of the two DNA strands is transcribed.
- ▶ One of the important enzymes of this process is RNA polymerase.

Transcription

- ▶ After a section of DNA is unwound, RNA polymerase recognizes a specific sequence of DNA nucleotides.
- ▶ RNA polymerase attaches and begins joining ribose nucleotides, which are complementary to the 3' end of the DNA strand.
- ▶ In RNA, the same complementary bases in DNA are paired, except that in RNA, the base uracil replaces the base thymine as a complement to adenine.
- ▶ Newly transcribed mRNA, called the primary transcript, must be modified before leaving the nucleus to carry out protein synthesis.

Transcription

- ▶ Some base sequences in newly transcribed mRNA do not code for proteins. RNA splicing involves cutting out noncoding regions so that the mRNA coding region can be read continuously at the ribosome.

DNA: The Genetic Material

Control of Gene Expression in Eukaryotes
(Part II)

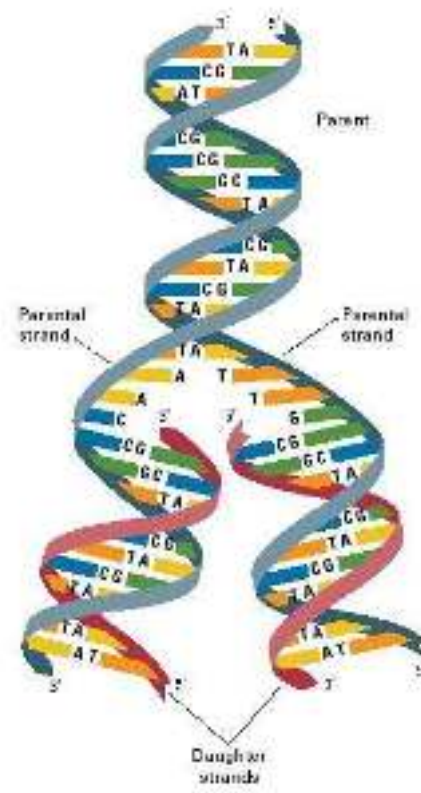
Translation

- ▶ **Translation** is protein synthesis at the ribosomes in the cytoplasm, based on the genetic information in the transcribed mRNA.
- ▶ Another type of RNA, called transfer RNA (tRNA), is important in the translation process.
- ▶ It brings the different amino acids coded for by the mRNA into alignment so that a polypeptide can be made.
- ▶ Complementary pairing of bases across the molecule maintains tRNA's configuration.
- ▶ The presence of some unusual bases (i.e., other than adenine, cytosine, guanine, or uracil) disrupts the normal base pairing and forms loops in the molecule.

Translation

- ▶ The center loop (the “anticodon loop”) has a sequence of three unpaired bases called the **anticodon**.
- ▶ During translation, pairing of the mRNA codon with its complementary anticodon of tRNA appropriately positions the amino acid that tRNA carries.
- ▶ Ribosomes, the sites of protein synthesis, consist of large and small subunits that organize the pairing between the codon and the anticodon.
- ▶ Several sites on the ribosome are binding sites for mRNA and tRNA.
- ▶ At the initiation of translation, mRNA binds to a small, separate ribosomal subunit.

Translation



- ▶ Attachment of the mRNA requires that the initiation codon (AUG) of mRNA be aligned with the P (peptidyl) site of the ribosome.
- ▶ A tRNA with a complementary anticodon for methionine binds to the mRNA, and a large subunit joins, forming a complete ribosome.
- ▶ Polypeptide formation can now begin.
- ▶ Another site, the A (aminoacyl) site, is next to the P site.
- ▶ A second tRNA, whose anticodon is complementary to the codon in the A site, is positioned.

Translation

- ▶ Two tRNA molecules with their attached amino acids are now side-by-side in the P and A sites.
- ▶ This step requires enzyme aid and energy, in the form of guanine triphosphate (GTP).
- ▶ An enzyme (peptidyl transferase), which is actually a part of the larger ribosomal subunit, breaks the bond between the amino acid and tRNA in the P site, and catalyzes the formation of a peptide bond between that amino acid and the amino acid in the A site.

Translation

- ▶ The mRNA strand then moves along the ribosome a distance of one codon.
- ▶ The tRNA with two amino acids attached to it that was in the A site is now in the P site.
- ▶ A third tRNA can now enter the exposed A site.
- ▶ This process continues until the entire mRNA has been translated, and a polypeptide chain has been synthesized.
- ▶ Translation ends when a termination codon (e.g., UAA) is encountered.

DNA: The Genetic Material

Gene Mutation

Gene Mutation

- ▶ The genetic material of a cell can change, and these changes increase genetic variability and help increase the likelihood of survival in changing environments.
- ▶ These changes include alterations in the base sequence of DNA and changes that alter the structure or number of chromosomes.

Point Mutations

- ▶ Genetic material must account for evolutionary change.
- ▶ **Point mutations** are changes in nucleotide sequences and may result from the replacement, addition, or deletion of nucleotides.
- ▶ Mutations are always random events.
- ▶ They may occur spontaneously as a result of base-pairing errors during replication, which result in a substitution of one base pair for another.
- ▶ Although certain environmental factors (e.g., electromagnetic radiation and many chemical mutagens) may change mutation rates, predicting what genes will be affected or what the nature of the change will be is impossible.

Point Mutations

- ▶ Mutations are the only source of new genetic material.
- ▶ For individuals, mutations can be a source of great suffering because mutations in genes that disturb the structure of proteins that are the products of millions of years of evolution are usually negative and cause many of our genetic diseases.
- ▶ The majority of mutations arise in body cells.
- ▶ These often remain hidden and cause no problems for the individual because either they are within a gene that is not being expressed in the cell or they may be altering the structure of DNA that is not coding for a protein.
- ▶ We all harbor hundreds of millions of these somatic mutations.
- ▶ The only mutations that affect future generations are those that arise in germ cells of the testes or ovaries.

Variation in Chromosome Number

- ▶ Changes in chromosome number may involve entire sets of chromosomes.
- ▶ Aneuploidy, on the other hand, involves the addition or deletion of one or more chromosomes, not entire sets. The addition of one chromosome to the normal $2N$ chromosome number ($2N + 1$) is a **trisomy**, and the deletion of a chromosome from the normal $2N$ chromosome number ($2N - 1$) is a **monosomy**.
- ▶ Errors during meiosis usually cause **aneuploidy**. Nondisjunction occurs when a homologous pair fails to segregate during meiosis I or when chromatids fail to separate at meiosis II.
- ▶ Gametes produced either lack one chromosome or have an extra chromosome. If one of these gametes is involved in fertilization with a normal gamete, the monosomic or trisomic condition results. Aneuploid variations usually result in severe consequences involving mental retardation and sterility.

Variation in Chromosome Structure

- ▶ Some changes may involve breaks in chromosomes.
- ▶ After breaking, pieces of chromosomes may be lost, or they may reattach, but not necessarily in their original position.
- ▶ The result is a chromosome that may have a different sequence of genes, multiple copies of genes, or missing genes.
- ▶ All of these changes can occur spontaneously.
- ▶ Various environmental agents, such as ionizing radiation and certain chemicals, can also induce these changes. The effects of changes in chromosome structure may be mild or severe, depending on the amount of genetic material duplicated or lost.

INHERITANCE PATTERNS

Mendelian genetics

INHERITANCE PATTERNS

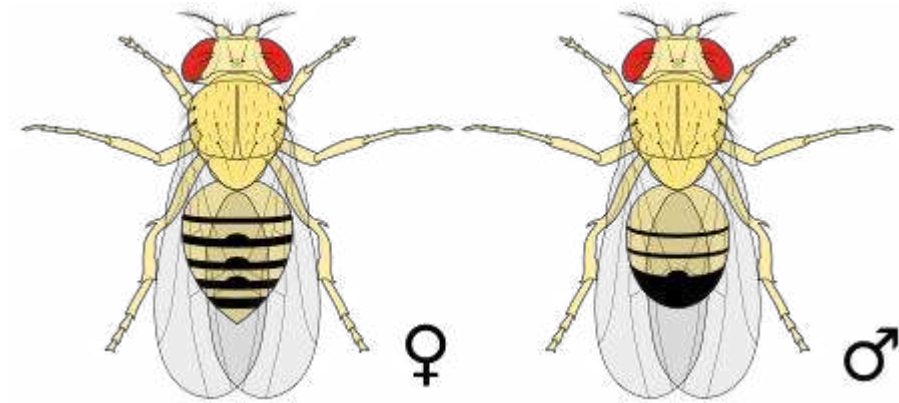
- ▶ Classical genetics began with the work of **Gregor Mendel** and remains an important basis for understanding gene transfer between generations of animals.
- ▶ Understanding these genetics principles helps us predict how traits will be expressed in offspring before these offspring are produced, something that has had profound implications in agriculture and medicine.

- ▶ One of the challenges of modern genetics is to understand the molecular basis for these inheritance patterns.
- ▶ The fruit fly, *Drosophila melanogaster*, is a classic tool for studying inheritance patterns.
- ▶ Its utility stems from its ease of handling, short life cycle, and easily recognized characteristics.

INHERITANCE PATTERNS

- ▶ Studies of any fruit-fly trait always make comparisons to a wild-type fly.
- ▶ If a fly has a characteristic similar to that found in wild flies, it is said to have the wild-type expression of that trait.
- ▶ (In the examples that follow, wild-type wings lay over the back at rest and extend past the posterior tip of the body, and wild-type eyes are red.)
- ▶ Numerous mutations from the wild-type body form, such as vestigial wings (reduced, shriveled wings) and sepia (dark brown) eyes, have been described.

INHERITANCE PATTERNS



INHERITANCE PATTERNS

Segregation

Segregation

- ▶ During gamete formation, genes in each parent are incorporated into separate gametes. During anaphase I of meiosis, homologous chromosomes move toward opposite poles of the cell, and the resulting gametes have only one member of each chromosome pair.
- ▶ Genes carried on one member of a pair of homologous chromosomes end up in one gamete, and genes carried on the other member are segregated into a different gamete.
- ▶ The **principle of segregation** states that pairs of genes are distributed between gametes during gamete formation.
- ▶ Fertilization results in the random combination of gametes and brings homologous chromosomes together again.

Segregation

- ▶ A cross of wild-type fruit flies with flies having vestigial wings illustrates the principle of segregation.
- ▶ (The flies come from stocks that have been inbred for generations to ensure that they breed true for wild-type wings or vestigial wings.)
- ▶ The offspring (progeny) of this cross have wild-type wings and are the first generation of offspring, or the first filial (F1) generation.
- ▶ If these flies are allowed to mate with each other, their progeny are the second filial (F2) generation.

Segregation

- ▶ Approximately a fourth of these F2 generation of flies have vestigial wings, and three-fourths have wild-type wings.
- ▶ Note that the vestigial characteristic, although present in the parental generation, disappears in the F1 generation and reappears in the F2 generation.
- ▶ In addition, the ratio of wild-type flies to vestigial-winged flies in the F2 generation is approximately 3:1.
- ▶ Reciprocal crosses, which involve the same characteristics but a reversal of the sexes of the individuals introducing a particular expression of the trait into the cross, yield similar results.

Segregation

- ▶ Genes that determine the expression of a particular trait can exist in alternative forms called **alleles** (Gr. allelos, each other).
- ▶ In the fruit-fly cross, the vestigial allele is present in the F1 generation, and even though it is masked by the wild-type allele for wing shape, it retains its uniqueness because it is expressed again in some members of the F2 generation.
- ▶ **Dominant alleles** hide the expression of another allele; **recessive alleles** are those whose expression can be masked.
- ▶ In the fruit-fly example, the wild-type allele is dominant because it can mask the expression of the vestigial allele, which is therefore recessive.

Segregation

- ▶ The visual expression of alleles may not always indicate the underlying genetic makeup of an organism.
- ▶ This visual expression is the **phenotype**, and the genetic makeup is the **genotype**.
- ▶ In the example, the flies of the F1 generation have the same phenotype as one of the parents, but they differ genotypically because they carry both a dominant and recessive allele.
- ▶ They are **hybrids**, and because this cross concerns only one pair of genes and a single trait, it is a monohybrid cross (monos, one 1 and hybrida, offspring of two kinds of parents).

Segregation

- ▶ An organism is **homozygous** (Latin: homo, same 1 Greek: zygon, paired) if it carries two identical genes for a given trait and **heterozygous** (Greek: heteros, other) if the genes are different (alleles of each other).
- ▶ Thus, in the example, all members of the parental generation are homozygous because only truebreeding flies are crossed.
- ▶ All members of the F1 generation are heterozygous.
- ▶ Crosses are often diagrammed using a letter or letters descriptive of the trait in question.

Segregation

- ▶ The first letter of the description of the dominant allele commonly is used.
- ▶ In fruit flies, and other organisms where all mutants are compared with a wild-type, the symbol is taken from the allele that was derived by a mutation from the wild condition.
- ▶ A superscript “1” next to the symbol represents the wild-type allele.
- ▶ A capital letter means that the mutant allele being represented is dominant, and a lowercase letter means that the mutant allele being represented is recessive.
- ▶ Geneticists use the Punnett square to help predict the results of crosses.

INHERITANCE PATTERNS

Independent Assortment

Independent Assortment

- ▶ It is also possible to make crosses using flies with two pairs of characteristics:
- ▶ flies with vestigial wings and sepia eyes, and flies that are wild for these characteristics.
- ▶ Sepia eyes are dark brown, and wild-type eyes are red.

Independent Assortment

- ▶ Note that flies in the parental generation are homozygous for the traits in question and that each parent produces only one kind of gamete.
- ▶ Gametes have one allele for each trait. Because each parent produces only one kind of gamete, fertilization results in offspring heterozygous for both traits.
- ▶ The F1 flies have the wild-type phenotype; thus, wild-type eyes are dominant to sepia eyes.
- ▶ The F1 flies are hybrids, and because the cross involves two pairs of genes and two traits, it is a dihybrid cross (Gr. di, two 1 L. hybrida, offspring of two kinds of parents).

Independent Assortment

- ▶ The 9:3:3:1 ratio is typical of a dihybrid cross.
- ▶ During gamete formation, the distribution of genes determining one trait does not influence how genes determining the other trait are distributed.
- ▶ In the example, this means that an F1 gamete with a *vg1* gene for wing condition may also have either the *se* gene or the *se1* gene for eye color.

Independent Assortment

- ▶ Note that all combinations of the eye color and wing condition genes are present, and that all combinations are equally likely.
- ▶ This illustrates the **principle of independent assortment**, which states that, during gamete formation, pairs of factors segregate independently of one another.

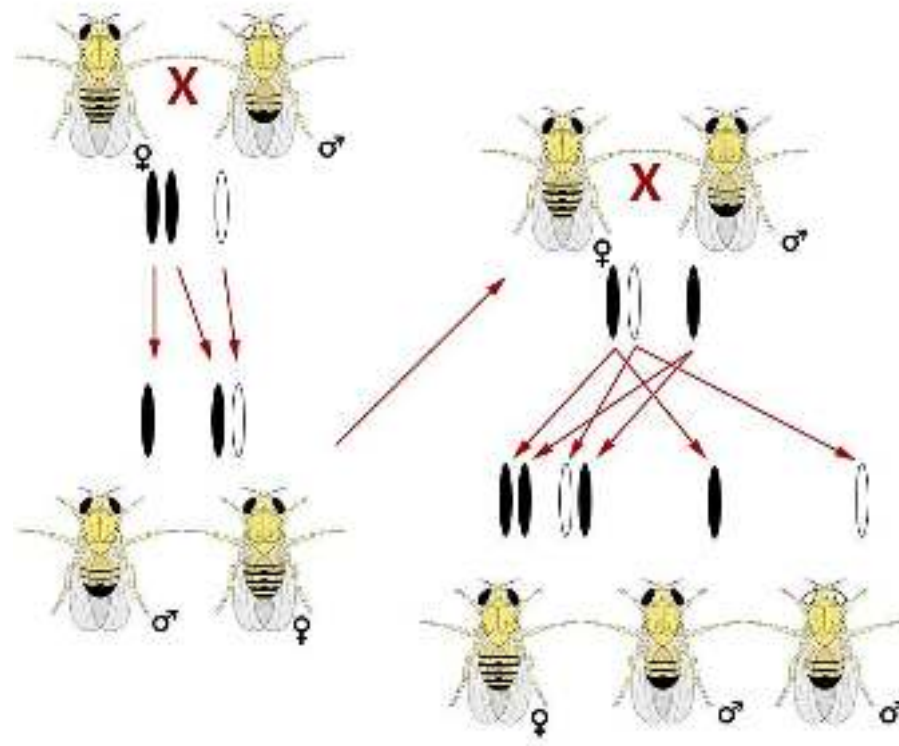
Independent Assortment

- ▶ The events of meiosis explain the principle of independent assortment.
- ▶ Cells produced during meiosis have one member of each homologous pair of chromosomes.
- ▶ Independent assortment simply means that when homologous chromosomes line up at metaphase I and then segregate, the behavior of one pair of chromosomes does not influence the behavior of any other pair.
- ▶ After meiosis, maternal and paternal chromosomes are distributed randomly among cells.

Independent Assortment

- ▶ This independent assortment of maternal and paternal chromosomes is the third source of genetic variation covered in this chapter.
- ▶ Independent assortment as well as crossing over and point mutations provide the genetic variation upon which evolutionary processes act.

Segregation



Inheritance Patterns

Multiple Alleles

Multiple Alleles

- ▶ The traits considered thus far have been determined by two genes, where one allele is dominant to a second.
- ▶ In this section, you learn that there are often many alleles in a population and that not all traits are determined by an interaction between a single pair of dominant or recessive genes.

Multiple Alleles

- ▶ Two genes, one carried on each chromosome of a homologous pair, determine traits in one individual.
- ▶ A population, on the other hand, may have many different alleles with the potential to contribute to the phenotype of any member of the population. These are called **multiple alleles**.

- ▶ Genes for a particular trait are at the same position on a chromosome.
- ▶ The gene's position on the chromosome is called its **locus** (L. loca, place). Numerous human loci have multiple alleles.
- ▶ Three alleles, symbolized I^A , I^B , and i , determine the familiar ABO blood types.
- ▶ Table 1.1 shows the combinations of alleles that determine a person's phenotype.
- ▶ Note that i is recessive to I^A and to I^B . I^A and I^B , however, are neither dominant nor recessive to each other. When I^A and I^B are present together, both are expressed.

Incomplete Dominance and Codominance

- ▶ **Incomplete dominance** is an interaction between two alleles that are expressed more or less equally, and the heterozygote is different from either homozygote.
- ▶ For example, in cattle, the alleles for red coat color and for white coat color interact to produce an intermediate coat color called roan.
- ▶ Because neither the red nor the white allele is dominant, uppercase letters and a prime or a superscript are used to represent genes.
- ▶ Thus, red cattle are symbolized RR, white cattle are symbolized R⁹R⁹, and roan cattle are symbolized RR⁹.

Incomplete Dominance and Codominance

- ▶ Codominance occurs when the heterozygote expresses the phenotypes of both homozygotes.
- ▶ Thus, in the ABO blood types, the $I^A I^B$ heterozygote expresses both alleles.

TABLE 3.1

GENOTYPES AND PHENOTYPES IN THE ABO BLOOD GROUPS

Phenotype	Genotype
O	ii
A	I ^A I ^A or I ^A i
B	I ^B I ^B or I ^B i
AB	I ^A I ^B

Applications of Genetic Technologies

Recombinant DNA

Overview of Biotechnology

- ▶ **Biotechnology** is the use of biological techniques and engineered organisms to make products or plants and animals that have desired traits.
- ▶ People have used biotechnology processes, such as selectively breeding animals and fermentation, for thousands of years.
- ▶ Late 19th and early 20th century discoveries of how microorganisms carry out commercially useful processes and how they cause disease led to the commercial production of vaccines and antibiotics.
- ▶ Improved methods for animal breeding have also resulted from these efforts.
- ▶ Scientists in the San Francisco Bay Area took a giant step forward with the discovery and development of recombinant DNA techniques in the 1970s.

Overview of Biotechnology

- ▶ The field of biotechnology continues to accelerate with new discoveries and new applications expected to benefit the economy throughout the 21st century.
- ▶ In its broadest definition, **biotechnology** is the application of biological techniques and engineered organisms to make products or modify plants and animals to carry desired traits.
- ▶ This definition also extends to the use of various human cells and other body parts to produce desirable products.
- ▶ Bioindustry refers to the cluster of companies that produce engineered biological products and their supporting businesses.

Applications of Genetic Technologies

- ▶ **Genetic engineering** means the manipulation of organisms to make useful products and it has broad applications.
- ▶ Genetic engineering, also called **genetic modification**, is the direct manipulation of an organism's genome using biotechnology.
- ▶ New DNA may be inserted in the host genome by first isolating and copying the genetic material of interest, using molecular-cloning methods to generate a DNA sequence; or by synthesizing the DNA, and then inserting this construct into the host organism.
- ▶ Genes may be removed, or “knocked out”, using a nuclease.

Applications of Genetic Technologies

- ▶ **Gene targeting** is a different technique that uses homologous recombination to change an endogenous gene, and can be used to delete a gene, remove exons, add a gene, or introduce point mutations.
- ▶ Genetic engineering has applications in medicine, research, industry and agriculture and can be used on a wide range of plants, animals and microorganisms.
- ▶ Genetic engineering has produced a variety of drugs and hormones for medical use.
- ▶ For example, one of its earliest uses in pharmaceuticals was gene splicing to manufacture large amounts of insulin, made using cells of *E. coli* bacteria.

Applications of Genetic Technologies

- ▶ **Interferon**, which is used to eliminate certain viruses and kill cancer cells, also is a product of genetic engineering, as are tissue plasminogen activator and urokinase, which are used to dissolve blood clots.
- ▶ Another byproduct is a type of **human growth hormone**; it's used to treat dwarfism and is produced through genetically-engineered bacteria and yeasts.
- ▶ The evolving field of **gene therapy** involves manipulating human genes to treat or cure genetic diseases and disorders.
- ▶ Modified plasmids or viruses often are the messengers to deliver genetic material to the body's cells, resulting in the production of substances that should correct the illness.

Applications of Genetic Technologies

- ▶ Sometimes cells are genetically altered inside the body; other times scientists modify them in the laboratory and return them to the patient's body.
- ▶ Since the 1990s, gene therapy has been used in clinical trials to treat diseases and conditions such as AIDS, cystic fibrosis, cancer, and high cholesterol.
- ▶ Drawbacks of gene therapy are that sometimes the person's immune system destroys the cells that have been genetically altered, and also that it is hard to get the genetic material into enough cells to have the desired effect.
- ▶ Biotechnology refers to the use of the biological sciences (such as gene manipulation), often in combination with other sciences (such as materials sciences, nanotechnology, and computer software), to discover, evaluate and develop products for bioindustry.

Applications of Genetic Technologies

- ▶ Biotechnology products have made it easier to detect and diagnose illnesses.
- ▶ Many of these new techniques are easier to use and some, such as pregnancy testing, can even be used at home.
- ▶ More than 400 clinical diagnostic devices using biotechnology products are in use today.
- ▶ The most important are screening techniques to protect the blood supply against contamination by AIDS and the hepatitis B and C viruses.

Applications of Genetic Technologies

Recombinant DNA (Part II)

Recombinant DNA

- ▶ An important tool in this technology is a series of enzymes called **restriction endonucleases**.
- ▶ Each of these enzymes, derived from bacteria, cleaves double-stranded DNA at particular sites determined by their base sequences.
- ▶ Many of these endonucleases cut the DNA strands so that one has several bases projecting farther than the other strand (Figure 5.24), leaving what are called “sticky ends.”
- ▶ When these DNA fragments are mixed with others that have been cleaved by the same endonuclease, their sticky ends tend to anneal (join) by the rules of complementary base pairing.
- ▶ The ends are sealed into their new position by the enzyme DNA ligase in a process called ligation.

Recombinant DNA

- ▶ If DNA from a foreign source (such as a mammal) is ligated into a plasmid (see preceding note), the product is recombinant DNA.
- ▶ To produce the recombinant DNA in large quantities, the modified plasmid must be cloned in bacteria.
- ▶ The bacteria are treated with dilute calcium chloride to make them more susceptible to entry by the recombinant DNA, but plasmids do not enter most bacterial cells.

Recombinant DNA

- ▶ Bacterial cells that have acquired the recombinant DNA can be identified if the plasmid has a marker, for example, resistance to an antibiotic.
- ▶ Then, only bacteria that can grow in the presence of the antibiotic are ones that have absorbed the recombinant DNA.
- ▶ Some bacteriophages (bacterial viruses) also are used as carriers for recombinant DNA.
- ▶ Plasmids and bacteriophages that carry recombinant DNA are called vectors.
- ▶ The vectors retain the ability to replicate in the bacterial cells; therefore the recombinant insert is produced in large quantities, a process called amplification.

Polymerase Chain Reaction

- ▶ Recent advances permit a specific gene to be cloned enzymatically from any organism as long as part of the sequence of that gene is known.
- ▶ The technique is called the polymerase chain reaction (PCR).
- ▶ Two short chains of nucleotides called primers are synthesized; primers are complementary to different DNA strands in the known sequence at opposite ends of the gene to be cloned.
- ▶ A large excess of each primer is added to a sample of DNA from the organism, and the mixture is heated to separate the double helix into single strands.

Polymerase Chain Reaction

- ▶ When the mixture is cooled, there is a much greater probability that each strand of the gene of interest will anneal to a primer than to the other strand of the gene—because the primer is present in a much higher concentration.
- ▶ A heat-stable DNA polymerase and the four deoxyribonucleotide triphosphates are added to the reaction mixture.
- ▶ DNA synthesis proceeds from the 3' end of each primer, extending the primer in the 5' to 3' direction.
- ▶ Primers are designed so that the free 3' end of each faces toward the gene whose sequence is to be cloned.

Polymerase Chain Reaction

- ▶ Entire new complementary strands are synthesized, and the number of copies of the gene has doubled (Figure 5.25).
- ▶ The reaction mixture is then reheated and cooled again to allow more primers to bind original and new copies of each strand.
- ▶ With each cycle of DNA synthesis, the number of copies of the gene doubles.
- ▶ Since each cycle can take less than five minutes, the number of copies of a gene can increase from one to over one million in less than two hours!
- ▶ The PCR allows cloning a known gene from an individual patient, identification of a drop of dried blood at a crime scene, or cloning DNA of a 40,000-year-old woolly mammoth.
- ▶

Polymerase Chain Reaction

- ▶ Recombinant DNA technology and PCR are currently being used to engineer crop plants, including soybeans, cotton, rice, corn, and tomato.
- ▶ Transgenic mice are commonly used in research, and gene therapy for human genetic diseases is being developed.
- ▶

Animal Behaviour

Four approaches to animal behaviour

- ▶ In 1973, the Nobel Prize in Physiology or Medicine was awarded to three pioneering zoologists, Karl von Frisch, Konrad Lorenz, and Niko Tinbergen (Figure 38-1).
- ▶ The citation stated that these three were the principal architects of the new science of ethology, the scientific study of animal behavior, particularly under natural conditions.
- ▶ It was the first time any contributor to the behavioral sciences was so honored, and it meant that the discipline of animal behavior, which really has its roots in the work of Charles Darwin, had arrived.

Proximate and Ultimate Causes

- ▶ Behavioral biologists have traditionally asked two kinds of questions about behavior: how animals behave and why they behave as they do.
- ▶ “How” questions are concerned with **immediate or proximate causation**.
- ▶ For example, a biologist might wish to explain the singing of a male whitethroated sparrow in the spring in terms of hormonal or neural mechanisms.
- ▶ Such physiological or mechanistic causes of behavior are **proximate factors**.

Proximate and Ultimate Causes

- ▶ Alternatively, a biologist might ask what function singing serves the sparrow, and then seek to understand those events in the ancestry of birds that led to springtime singing.
- ▶ These are “why” questions that focus on **ultimate causation**, the evolutionary origin and purpose of a behavior.
- ▶ These are really independent approaches to behavior, because understanding how the sparrow sings does not depend on what function singing serves, and vice versa.
- ▶ Students of animal behavior consider this distinction significant.
- ▶ Studies of proximate and ultimate causation are both important, but each may be of limited value in understanding the other.

Comparative Psychology

- ▶ The study of animal behavior has arisen from several different historical roots, and there is no universally accepted term for the whole subject.
- ▶ **Comparative psychology** emerged from efforts to find general laws of behavior that would apply to many species, including humans.
- ▶ Early research that depended heavily on inference was later replaced by replicable experimental approaches that concentrated on a few species, particularly white rats, pigeons, dogs, and occasionally primates.

Ethology

- ▶ The aim of a second approach, **ethology**, has been to describe the behavior of an animal in its natural habitat.
- ▶ Most ethologists have been zoologists. Their laboratory has been the out-of-doors, and early ethologists gathered their data by field observation.
- ▶ They also conducted experiments, often with nature providing the variables, but increasingly ethologists have manipulated the variables for their own purposes by using animal models, playing recordings of animal vocalizations and altering the habitat.

Ethology

- ▶ Modern ethologists also conduct many experiments in the laboratory where they can test their predictions under closely controlled conditions.
- ▶ However, ethologists usually take pains to compare laboratory observations with observations of free-ranging animals in undisturbed natural environments.
- ▶ Ethology emphasizes the importance of ultimate factors affecting behavior.
- ▶ One of the great contributions of von Frisch, Lorenz, and Tinbergen was to demonstrate that behavioral traits are measurable entities like anatomical or physiological traits.
- ▶ This was to become the central theme of ethology: behavioral traits can be isolated and measured and they have evolutionary histories.

Ethology

- ▶ Sociobiology, the ethological study of social behavior, originated with the 1975 publication of E. O. Wilson's *Sociobiology: The New Synthesis*.
- ▶ Wilson describes social behavior as reciprocal communication of a cooperative nature (transcending mere sexual activity) that permits a group of organisms of the same species to become organized in a cooperative manner.
- ▶ In a complex system of social interactions, individuals are highly dependent on others for their daily living.

Ethology

- ▶ While social behavior appears in many groups of animals, Wilson identified four “pinnacles” of complex social behavior.
- ▶ These are as follows:
- ▶ **Colonial invertebrates**, such as the Portuguese man-of-war, which is a tightly-knit composite of individual organisms
- ▶ **Social insects**, such as ants, bees, and termites, which have developed sophisticated systems of communication
- ▶ **Nonhuman mammals**, such as dolphins, elephants, and some primates, which have highly developed social systems
- ▶ **Humans**

Animal Behavior

Anthropomorphism

Anthropomorphism

- ▶ **Anthropomorphism** (pronounced ann-throw-poe-MORF-ism) is giving human traits or attributes to animals, inanimate objects or other non-human things. It comes from the Greek words *anthropo* (human) and *morph* (form).
- ▶ This could be very obvious: for example, a rock shaped like a human being would be considered anthropomorphic. But anthropomorphism is usually more figurative than that.

Examples of Anthropomorphism

- ▶ Anthropomorphism can also be a *mistake*. For example, some people think that eagles and other birds of prey look angry.
- ▶ But of course that's just because of the way their eyes are shaped. Birds don't have the same facial expressions as human beings, so it's an error to look at an eagle's eyes and conclude that she is angry - this is anthropomorphizing the bird.
- ▶ An entire organization might be described through an anthropomorphic analogy or metaphor if its various members were thought of as body parts.

Examples of Anthropomorphism

- ▶ For example, the brains of the organization would be its leader; the muscle would be a tough henchman; and the eyes and ears would be the organization's spy network.
- ▶ (This would be an analogy if there were explicit “comparing” words - otherwise, it would be a metaphor.)
- ▶ Sometimes, we anthropomorphize parts of our own bodies. For example, the common expression “listen to your heart” suggests that the heart speaks to us, which of course is not *literally*. Similarly, people describe conversations between the head and the heart, which is an example of anthropomorphizing (or personifying) these two organs.

Types of Anthropomorphism

a. Literal Anthropomorphism

- ▶ The simplest form of anthropomorphism is when something is just literally shaped like a human, or literally shown as acting human.
- ▶ A cartoon animal who wears clothes is an example of literal anthropomorphism.
- ▶ Similarly, animals playing the piano or trees talking to each other would be examples of literal anthropomorphism.

Types of Anthropomorphism

b. Metaphorical Anthropomorphism (personification)

- ▶ **Personification** is a popular literary trope in which an inanimate object is described as if it were a person. This is one particular form of anthropomorphism, and also a form of metaphor.
- ▶ Example of personification include:
- ▶ The wind hawled

Types of Anthropomorphism

c. Anthropomorphic Analogy

- ▶ In an anthropomorphic analogy, you're saying that something is *like* a human being in some way.
- ▶ This is distinguished from personification by the presence of *comparing language* - words like "as" or "like."
- ▶ By comparing something to a human being, you may be able to illustrate its qualities or behavior more clearly, or make an abstract idea come off the page.

Types of Anthropomorphism

d. Symbolic Anthropomorphism

- ▶ This is when a human (or human-like) character stands in symbolically for something else. Unlike personification, this isn't *just* a metaphor - it's an extended symbol that goes to the essence of who the character is.
- ▶ For example, the Greek god Poseidon is an anthropomorphic (human-formed) symbol for the sea, and similarly Aeolus is an anthropomorphic symbol for the wind.
- ▶ So, the sentence "the wind howled" is personification; if there's an actual *character* standing in for the wind, such as Aeolus, then it's not personification but symbolic anthropomorphism.
- ▶ Many theologians and religious scholars argue that the God of Christianity, Judaism, and Islam is an anthropomorphic symbol for benevolence, compassion, or transcendence.

The Importance of Anthropomorphism

- ▶ Human beings are hardwired to understand human behavior and react to it in certain ways - generally, we respond to anthropomorphism in a visceral and emotional way.
- ▶ Writers can tap into this by using anthropomorphism in their descriptions and comparisons.
- ▶ Think of how much more powerful your mental image is if the author describes “an angry, bitter storm” rather than just “a strong storm.”

The Importance of Anthropomorphism

- ▶ Anthropomorphism can also make a story more accessible to children.
- ▶ No one's quite sure why, but children generally love to see animals and inanimate objects (such as cars or kitchen implements) behave like people.
- ▶ Perhaps it's just that such anthropomorphism makes the story seem more imaginative and whimsical.

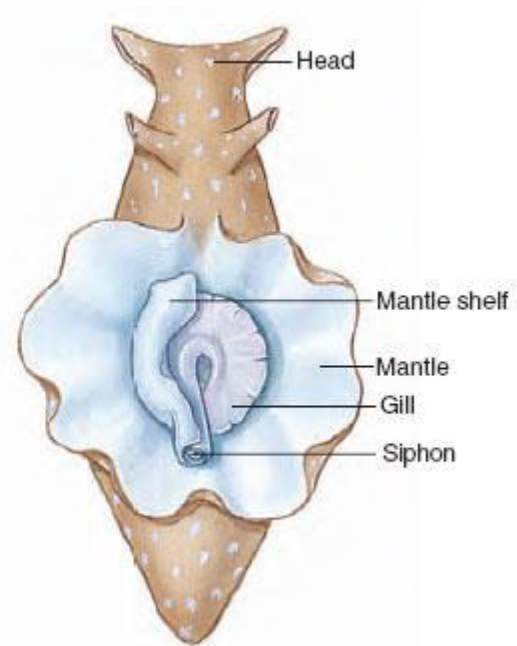
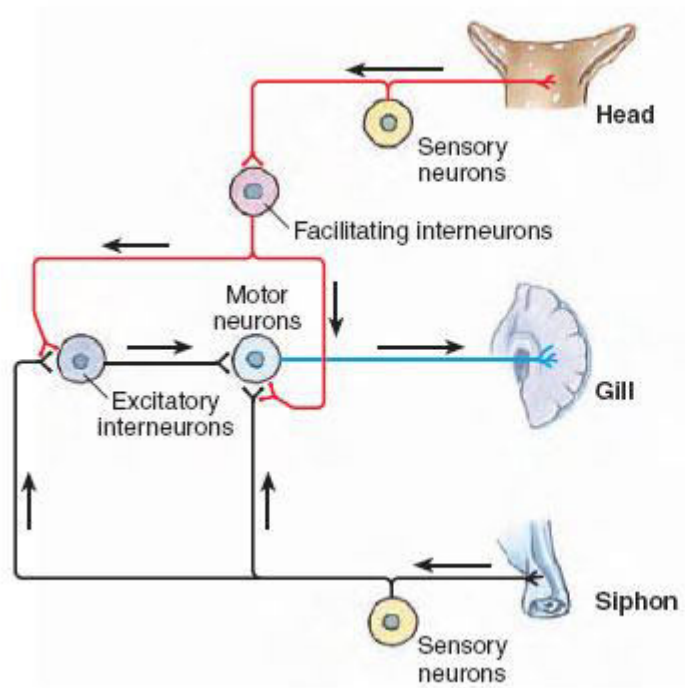
Development of Behavior

Learning

Learning

- ▶ Another aspect of behavior is **learning**, which we define as the modification of behavior through experience.
- ▶ An excellent model system for studying learning processes has been the marine opisthobranch snail *Aplysia*, a subject of intense experimentation by E. R. Kandel and his associates.
- ▶ The gills of *Aplysia* are partly covered by the mantle cavity and open to the outside by a siphon.
- ▶ If one prods the siphon, *Aplysia* withdraws its siphon and gills and folds them in the mantle cavity.

Learning



Learning

- ▶ This simple protective response, called **gill withdrawal reflex**, will be repeated when Aplysia extends its siphon again.
- ▶ But if the siphon is touched repeatedly, Aplysia decreases the gill withdrawal response and finally comes to ignore the stimulus altogether.
- ▶ This behavior modification illustrates a widespread form of learning called **habituation**.

Learning

- ▶ If now *Aplysia* is given a noxious stimulus (for example, an electric shock) to the head at the same time the siphon is touched, it becomes sensitized to the stimulus and withdraws its gills as completely as it did before habituation occurred.
- ▶ **Sensitization**, then, can reverse any previous habituation.
- ▶ The mechanisms of habituation and sensitization in *Aplysia* are known because these behaviors constitute a rare instance in which the nervous pathways involved have been completely revealed.

Learning

- ▶ Receptors in the siphon are connected through sensory neurons to motor neurons that control the gill-withdrawal muscles and muscles of the mantle cavity.
- ▶ **Kandel** found that repeated stimulation of the siphon diminished the release of synaptic transmitter from the sensory neurons.
- ▶ Sensory neurons continue to fire when the siphon is probed but, with less neurotransmitter being released into the synapse, the system becomes less responsive.

Learning

- ▶ Sensitization requires the action of a different kind of neuron called a **facilitating interneuron**.
- ▶ These interneurons make connections between sensory neurons in the animal's head and motor neurons that control muscles of the gill and mantle. When sensory neurons in the head are stimulated by an electric shock, they fire the facilitating interneurons, which end on the synaptic terminals of the sensory neurons.
- ▶ These endings in turn cause an increase in the amount of transmitter released by the siphon sensory neurons.
- ▶ This release increases the state of excitation in the excitatory interneurons and motor neurons leading to the gill and mantle muscles.

Learning

- ▶ The motor neurons now fire more readily than before.
- ▶ The system is now sensitized because any stimulus to the siphon will produce a strong gill-withdrawal response.
- ▶ Kandel's studies indicate that strengthening or weakening of the gill withdrawal reflex involves changes in levels of transmitter in existing synapses.
- ▶ However, we know that more complex kinds of learning may involve formation of new neural pathways and connections, as well as changes in existing circuits.

Development of Behavior

Imprinting

Imprinting

- ▶ Another kind of learned behavior is imprinting, the imposition of a stable behavior in a young animal by exposure to particular stimuli during a critical period in the animal's development.
- ▶ As soon as a newly hatched gosling or duckling is strong enough to walk, it follows its mother away from the nest.
- ▶ After it has followed the mother for some time it follows no other animal.
- ▶ But, if the eggs are hatched in an incubator or if the mother is separated from the eggs as they hatch, the goslings follow the first large object they see.
- ▶ As they grow, the young geese prefer the artificial “mother” to anything else, including their true mother. The goslings are said to be imprinted on the artificial mother.

Imprinting

- ▶ Imprinting was observed at least as early as the first century A.D. when the Roman naturalist Pliny the Elder wrote of “a goose which followed Lacydes as faithfully as a dog.”
- ▶ Konrad Lorenz was the first to study imprinting objectively and systematically.
- ▶ When Lorenz handreared goslings, they formed an immediate and permanent attachment to him and waddled or swam after him wherever he went.
- ▶ They could no longer be induced to follow their own mother or another human being.
- ▶ Lorenz found that the imprinting period is confined to a brief sensitive period in the individual's early life and that once established the imprinted bond usually is retained for life.

Imprinting

- ▶ What imprinting shows is that the brain of the goose (or the brain of numerous other birds and mammals that show imprinting-like behavior) accommodates the imprinting experience.
- ▶ Natural selection favors evolution of a brain that imprints in this way, in which following the mother and obeying her commands are important for survival.
- ▶ The fact that a gosling can be made to imprint to a mechanical toy duck or a person under artificial conditions is a cost to the system that can be tolerated because goslings seldom encounter these stimuli in their natural environment.
- ▶ The disadvantages of the system's simplicity are outweighed by the advantages of its reliability.

Imprinting

- ▶ We will cite one final example to complete our consideration of learning.
- ▶ The males of many species of birds have characteristic territorial songs that identify the singers to the other birds and announce territorial rights to other males of that species.
- ▶ Like many other songbirds, the male white-crowned sparrow must learn the song of its species by hearing the song of its father.
- ▶ If the sparrow is handreared in acoustic isolation in the laboratory, it develops an abnormal song (Figure 38-10).
- ▶ But if the isolated bird is allowed to hear recordings of normal white-crowned sparrow songs during a critical period of 10 to 50 days after hatching, it learns to sing normally.
- ▶ It even imitates the local dialect it hears.

Imprinting



Imprinting

- ▶ It might appear from this result that characteristics of the song are determined by learning alone.
- ▶ However, if during the critical learning period, the isolated male whitecrowned sparrow is played a recording of another species of sparrow, even a closely related one, it does not learn the song.
- ▶ It learns only the song appropriate to its own species.
- ▶ Thus although the song must be learned, the brain is constrained to recognize and to learn vocalizations produced by males of its species alone.
- ▶ Learning the wrong song would result in behavioral chaos, and natural selection favors a system that eliminates such errors.

Control of Behavior

Innate Behavior

Innate Behavior

- ▶ From the beginning, the mostly invariable and predictable nature of stereotyped behavior suggested to behaviorists that they were dealing with inherited, or **innate**, behavior.
- ▶ Many kinds of preprogrammed behavior appear suddenly in animals and are indistinguishable from similar behavior performed by older, experienced individuals.
- ▶ Orb-weaving spiders build their webs without practice, and male crickets court females without lessons from more experienced crickets or by learning from trial and error.

Innate Behavior

- ▶ To such behaviors the term innate, or instinctive, has been applied. Such words suggest that these behavioral patterns are absolutely committed and will develop in the same way regardless of environment.
- ▶ This idea, called **instinct theory**, has fallen out of fashion with behavioral scientists because it cannot be shown that a behavior develops independently of experience.
- ▶ Critics of instinct theory argue that all forms of behavior depend on an interaction of the organism and environment, beginning with the fertilized egg..

Innate Behavior

- ▶ Genes code for proteins and not directly for behavior.
- ▶ Even with webbuilding spiders and courting crickets, the environment is bound to have some influence.
- ▶ Given a different environment in which to develop, the resulting behavior may be different.
- ▶ Nevertheless, it seems incontestable that many complex sequences of behavior in invertebrate animals are largely invariable in their execution, are not learned, and appear to be programmed by rules.
- ▶ It is easy to understand why programmed behavior is important for survival, especially for animals that never know their parents.

Innate Behavior

- ▶ They must be equipped to respond to the world immediately and correctly as soon as they emerge into it.
- ▶ It is also evident that more complex animals with longer lives and with parental care or other opportunities for social interactions may improve or change their behavior by learning.

Control of Behavior

The Genetics of Behavior

The Genetics of Behavior

- ▶ The hereditary transmission of most innate behavior is complex, with many interacting genes regulating each behavioral trait.
- ▶ However, there are a few examples of behavioral differences within species that show simple Mendelian transmission from parents to offspring.
- ▶ Perhaps the most convincing example is the inheritance of hygienic behavior in bees. Honey bees are susceptible to a bacterial disease, American foulbrood (*Bacillus* larvae).
- ▶ A bee larva that catches foulbrood dies.
- ▶ If the bees remove dead larvae from the hive they reduce the chance of the infection spreading.

The Genetics of Behavior

- ▶ Some strains of bees, called “hygienic,” uncap hive cells containing rotting larvae and carry them out of the hive. W. C. Rothenbuhler found that there are two components to this behavior: first removal of cell caps, and second removal of larvae.
- ▶ Hygienic bees have homozygous recessive genotypes for two different genes.
- ▶ Uncapping behavior is performed by individuals homozygous for a recessive allele, *u*, at one gene, and removal behavior is performed by individuals homozygous for a recessive allele, *r*, at a second gene.

The Genetics of Behavior

- ▶ When Rothenbuhler crossed hygienic bees ($u/u \ r/r$) with a nonhygienic strain ($U/U \ R/R$), he found that all the hybrids ($U/u \ R/r$) were nonhygienic.
- ▶ Thus only workers having both genes in the homozygous recessive condition show the complete behavior.
- ▶ Next, Rothenbuhler performed a “backcross” between the hybrids and the hygienic parental strain.
- ▶ As we should expect if hygienic behavior is transmitted by allelic variation of two genes, four different kinds of bees resulted as shown in figure below.

u uncaps cells
U does not uncap cells
r removes diseased larvae
R does not remove diseased larvae

Homozygous
hygienic Homozygous
nonhygienic

♀ *u/u r/r* × ♂ *U/U R/R*

U/u R/r

Nonhygienic hybrids

u/u r/r × *U/u R/r* Backcross of hygienic with
hybrid bees

u/u r/r
Hygienic

U/- r/r
Nonhygienic,
does not uncap
but can remove
dead larvae

u/u R/-
Nonhygienic,
uncaps, leaves
dead larvae
inside cells

U/- R/-
Nonhygienic,
neither uncaps
nor removes
dead larvae



The Genetics of Behavior

- ▶ Approximately one-quarter of the bees were homozygous recessive for both *u* and *r* and showed the complete behavior: they both uncapped the cells and removed the bees.
- ▶ Another quarter of the offspring (*u/u R/r* or *u/u R/R*) uncapped but did not remove dead bees.
- ▶ Another quarter (*U/u r/r* or *U/U r/r*) did not uncap, but would remove the larvae if another worker uncapped the cells.
- ▶ Workers that were homozygous or heterozygous for the dominant allele at both genes (*U/u R/r*) would not perform either part of the cleaning behavior.
- ▶ The results showed clearly that each component of the cleaning behavior was associated with one, independently segregating gene.

The Genetics of Behavior

- ▶ Most inherited behaviors do not show simple segregation and independence; instead, hybrids of subspecies or species commonly show intermediate or confused behavior.
- ▶ A classic study of the effect of cross-breeding on behavior was carried out by W. C. Dilger on nest-building behavior in different species of lovebirds.
- ▶ Lovebirds are small parrots of the genus *Agapornis*. Each species has its own method of courtship and technique for carrying nesting material.
- ▶ Fischer's lovebirds (*A. personata fischeri*) cut long strips of nesting material from vegetation, then carry this to the nest, one strip at a time.

The Genetics of Behavior

- ▶ Peach-faced lovebirds (*A. roseicollis*) carry several strips of torn nesting material at one time by tucking them into feathers of the lower back and rump.
- ▶ Dilger, who was able to cross the two species successfully, found that hybrids displayed a confused conflict between a tendency to carry material in the feathers (inherited from the peach-faced lovebirds) and a tendency to carry material in the bill (inherited from Fischer's lovebird).

The Genetics of Behavior

(after Dilger, 1962)



Peach-faced lovebird



Fischer's lovebird



The Genetics of Behavior

- ▶ The hybrids attempted both feather-tucking and bill-carrying but performed neither behavior correctly.
- ▶ The hybrids had inherited a behavior that was intermediate between that of the parents.
- ▶ With experience hybrids improved their carrying ability by tending to carry the material in their bills, like Fischer's lovebird.

The background features abstract, overlapping geometric shapes in various shades of blue, ranging from light sky blue to deep navy blue. These shapes are primarily located on the left and right sides of the frame, creating a modern, dynamic feel. The central area is a plain, light grayish-white, providing a clean backdrop for the text.

Social Behavior

Social Behavior

- ▶ When we think of “social” animals we are apt to think of highly structured honey bee colonies, herds of antelope grazing on the African plains shown in figure below, schools of herring, or flocks of starlings.
- ▶ But social behavior of animals of the same species living together is by no means limited to such obvious examples in which individuals influence one another.
- ▶ In the broad sense, any interaction resulting from the response of one animal to another of the same species represents social behavior.

Social Behavior



Social Behavior

- ▶ Even a pair of rival males fighting over possession of a female display a social interaction, despite our perceptual bias as people that might encourage us to label it antisocial.
- ▶ Social aggregations are only one kind of social behavior, and indeed not all aggregations of animals are social.
- ▶ Clouds of moths attracted to a light at night, barnacles attracted to a common float, or trout gathering in the coolest pool of a stream are groupings of animals responding to environmental signals.

Social Behavior

- ▶ Social aggregations, on the other hand, depend on signals from the animals themselves.
- ▶ They remain together and do things together by influencing one another.
- ▶ Not all animals showing sociality are social to the same degree.
- ▶ While all sexually reproducing species must at least cooperate enough to achieve fertilization, among some animals breeding is about the only adult sociality to occur.

Social Behavior

- ▶ Alternatively, swans, geese, albatrosses, and beavers, to name just a few, form strong monogamous bonds that last a lifetime.
- ▶ The most persistent social bonds usually form between mothers and their young and, for birds and mammals, these bonds usually terminate at fledging or weaning.

Social Behavior

Advantages of Sociality

Advantages of Sociality

- ▶ Living together may be beneficial in many ways. One obvious benefit for **social aggregations** is defense, both passive and active, from predators.
- ▶ Musk-oxen that form a passive defensive circle when threatened by a wolf pack are much less vulnerable than an individual facing the wolves alone.
- ▶ As an example of active defense, a breeding colony of gulls, alerted by the alarm calls of a few, attack predators en masse; this collective attack is certain to discourage a predator more effectively than individual attacks.

Advantages of Sociality

- ▶ Members of a town of prairie dogs, although divided into social units called **coteries**, cooperate by warning each other with a special bark when danger threatens.
- ▶ Thus every individual in a social organization benefits from the eyes, ears, and noses of all other members of the group.
- ▶ Experimental tests using a wide variety of predators and prey support the notion that the more animals there are in a group, the less likely an individual within the group will be eaten.

Advantages of Sociality

- ▶ Sociality offers several benefits to animals reproduction.
- ▶ It facilitates encounters between males and females, which, for solitary animals, may consume much time and energy.
- ▶ Sociality also helps synchronize reproductive behavior through the mutual stimulation that individuals have on one another.
- ▶ Among colonial birds the sounds and displays of courting individuals set in motion prereproductive endocrine changes in other individuals.

Advantages of Sociality

- ▶ Because there is more social stimulation, large colonies of gulls produce more young per nest than do small colonies.
- ▶ Furthermore, parental care that social animals provide their offspring increases survival of the brood shown in figure below.
- ▶ Social living provides opportunities for individuals to give aid and to share food with young other than their own.
- ▶ Such interactions within a social network have produced some intricate cooperative behavior among parents, their young, and their kin.

Advantages of Sociality



Advantages of Sociality

- ▶ Of the many other advantages of social organization noted by behaviorists, we will mention only a few in this brief treatment:
- ▶ Cooperation in hunting for food
- ▶ Huddling for mutual protection from severe weather
- ▶ Opportunities for division of labor, which is especially well developed in the social insects with their caste systems
- ▶ The potential for learning and transmitting useful information through the society.

Advantages of Sociality

- ▶ Observers of a seminatural colony of macaque monkeys in Japan recount an interesting example of acquiring and passing tradition in a society.
- ▶ The macaques were provisioned with sweet potatoes and wheat at a feeding station on the beach of an island colony.
- ▶ One day a young female of sandy wheat in the water; allowing the sand to sink, she could scoop up the floating wheat to eat.
- ▶ Again, within a few years, wheat-sifting became a tradition in the troop.

The background features abstract, overlapping geometric shapes in various shades of blue, ranging from light sky blue to deep navy blue. These shapes are primarily located on the left and right sides of the frame, creating a modern, dynamic feel. The central area is a plain, light grayish-white, providing a clean backdrop for the text.

Social Behavior

Aggression and Dominance

Aggression and Dominance

- ▶ Many animal species are social because of the numerous benefits that sociality offers.
- ▶ Sociality requires cooperation.
- ▶ At the same time animals, like governments, tend to look out for their own interests.
- ▶ In short, they are in competition with one another because of limitations in the common resources that all require for life.
- ▶ Animals may compete for food, water, sexual mates, or shelter when such requirements are limited in quantity and are therefore worth a fight.

Aggression and Dominance

- ▶ Much of what animals do to resolve competition is called **aggression**, which we may define as an offensive physical action, or threat, to force others to abandon something they own or might attain.
- ▶ Many behaviorists consider aggression part of a somewhat more inclusive interaction called **agonistic** (Gr. contest) **behavior**, referring to any activity related to fighting, whether it be aggression, defense, submission, or retreat.

Aggression and Dominance

- ▶ Contrary to the widely held notion that aggressive behavior aims at the destruction or at least defeat of an opponent, most aggressive encounters are duels that lack the violence that we usually associate with fighting.
- ▶ Many species possess specialized weapons such as sharpened teeth, beaks, claws, or horns that are used for protection from, or predation on, other species.
- ▶ Although potentially dangerous, such weapons are seldom used in any severely damaging way against members of their own species.

Aggression and Dominance

- ▶ Animal aggression within the species seldom results in injury or death because animals have evolved many symbolic ritualized displays that carry mutually understood meanings.
- ▶ A **ritualized display** is a behavior that has been modified through evolution to make it increasingly effective in serving a communicative function.
- ▶ Through ritualization, simple movements or traits become more intensive, conspicuous, or precise, and acquire the function of a signal.
- ▶ The result of such intensification is to reduce the possibility of misunderstanding.

Aggression and Dominance

- ▶ Fights over mates, food, or territory become ritualized jousts rather than bloody, no-holds-barred battles.
- ▶ When fiddler crabs spar for territory, their large claws usually are only slightly opened, Even in intense fighting when the claws are used, the crabs grasp each other in a way that prevents reciprocal injury.
- ▶ Rival male poisonous snakes engage in stylized bouts by winding themselves together; each attempts to butt the other's head with its own until one becomes so fatigued that it retreats.
- ▶ The rivals never bite each other.

Aggression and Dominance

- ▶ Many species of fish contest territorial boundaries with lateral displays, the males puffing themselves to look as threatening as possible.
- ▶ The encounter is usually settled when either animal perceives itself obviously inferior, folds up its fins, and swims away.
- ▶ Rival giraffes engage in largely symbolic “necking” matches in which two males standing side by side wrap and unwrap their necks around each other shown in figure .
- ▶ Neither uses its potentially lethal hooves on the other, and neither is injured.

Aggression and Dominance



Aggression and Dominance

- ▶ Thus animals fight as though programmed by rules that prevent serious injury.
- ▶ Fights between rival bighorn rams are spectacular to watch, and the sound of clashing horns may be heard for hundreds of meters shown in figure.
- ▶ But the skull is so well protected by the massive horns that injury occurs only by accident.
- ▶ Nevertheless, despite these constraints, aggressive encounters on occasion can be true fights to the death.

Aggression and Dominance



Advantages of Sociality

- ▶ Imo's peers and social inferiors copied her innovations most readily.
- ▶ The adult males, her superiors in the social hierarchy, would not adopt the practice but continued laboriously to pick wet sand grains off their sweet potatoes and scout the beach for single grains of wheat.
- ▶ Social living also has some disadvantages as compared with a solitary existence for some animals.

Advantages of Sociality

- ▶ Species that survive by camouflage from potential predators profit by being dispersed.
- ▶ Large predators benefit from a solitary existence for a different reason, their requirement for a large supply of prey.
- ▶ Thus there is no overriding adaptive advantage to sociality that inevitably selects against the solitary way of life.
- ▶ It depends on the ecological situation.

Social Behavior

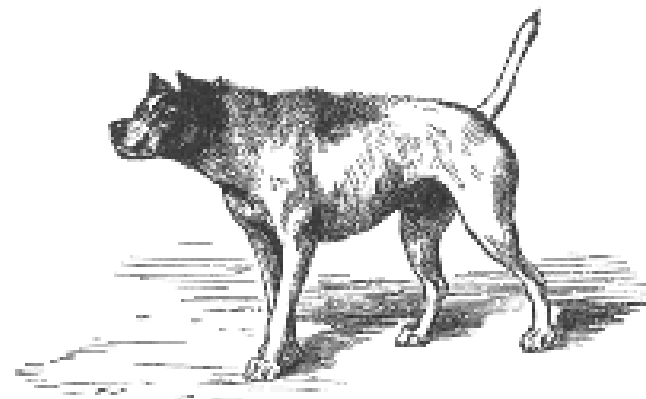
Aggression and Dominance (Part II)

Aggression and Dominance (Part II)

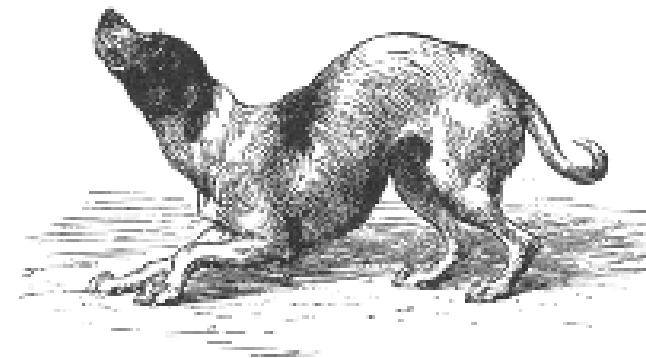
- ▶ If African male elephants are unable to resolve dominance conflicts painlessly with ritual postures, they may resort to incredibly violent battles, with each trying to plunge its tusks into the most vulnerable parts of the opponent's body.
- ▶ More commonly, however, the loser of a ritualized encounter may simply run away, or signal defeat by a specialized subordination ritual.
- ▶ If it becomes evident to him that he is going to lose anyway, he profits by communicating his submission as quickly as possible, thereby avoiding the cost of a real thrashing.

Aggression and Dominance (Part II)

- ▶ Such submissive displays that signal the end of a fight may be almost the opposite of threat displays (Figure 38-16).
- ▶ In his book *Expression of the Emotions in Man and Animals* (1872), Charles Darwin described the seemingly opposite nature of threat and appeasement displays as the “principle of antithesis.”
- ▶ The principle remains accepted by animal behaviorists today.
- ▶ The winner of an aggressive competition is dominant to the loser, the subordinate.



Yorkshire Terrier, standing, facing left, with head turned back. (By permission of the artist.)



Aggression and Dominance (Part II)

- ▶ For the victor, dominance means enhanced access to all contested resources that contribute to reproductive success: food, mates, and territory.
- ▶ In a social species, dominance interactions often take the form of a dominance hierarchy.
- ▶ One animal at the top wins encounters with all other members in the social group; the second in rank wins all but those with the top-ranking individual.

Aggression and Dominance (Part II)

- ▶ However, not all dominance hierarchies have clear-cut dominant and subordinate individuals.
- ▶ In some hierarchies, dominant animals are frequently challenged by subordinates.
- ▶ The subordinates in any social order may be expendable.
- ▶ In many systems they never get a chance to reproduce, and when times get difficult they are often the first to die.

Aggression and Dominance (Part II)

- ▶ During times of food scarcity, death of weaker members helps to protect the resource for stronger members.
- ▶ Rather than sharing food, the excess population is sacrificed.
- ▶ This sacrifice is not viewed by contemporary behaviorists as resulting from some direct, purposeful process ensuring “good for the species”; it is a consequence of the individual advantage that the stronger, dominant individuals possess during such circumstances.

Social Behavior

Territoriality

Territoriality

- ▶ Territorial ownership is another facet of sociality in animal populations.
- ▶ A **territory** is a fixed area from which intruders of the same species are excluded.
- ▶ This exclusion involves defending the area from intruders and spending long periods of time being conspicuous on the site.
- ▶ Territorial defense has been observed in numerous animals: insects, crustaceans, fishes, amphibians, lizards, birds, and mammals, including humans.

Territoriality

- ▶ **Territoriality** is generally an alternative to dominance behavior, although both systems may be observed operating in the same species.
- ▶ A territorial system may work well when the population is low, but it may break down with increasing population density and be replaced with dominance hierarchies in which all animals occupy the same space.
- ▶ Like every other competitive endeavor, territoriality carries both costs and advantages.

Territoriality

- ▶ It is beneficial when it ensures access to limited resources, unless the territorial boundaries cannot be maintained with little effort.
- ▶ The presumed **benefits** of a territory are, in fact, numerous:
- ▶ uncontested access to a foraging area
- ▶ enhanced attractiveness to females thus reducing the problems of pairbonding, mating, and rearing the young
- ▶ reduced disease transmission
- ▶ reduced vulnerability to predators.

Territoriality

- ▶ But the advantages of holding a territory begin to wane if the individual must spend most of the time in boundary disputes with neighbors.
- ▶ Most of the time and energy required for territoriality are expended when the territory is first established.
- ▶ Once the boundaries are located they tend to be respected, and aggressive behavior diminishes as territorial neighbors come to recognize each other.
- ▶ Indeed, neighbors may look so peaceful that an observer who was not present when the territories were established may conclude (incorrectly) that the animals are not territorial.

Territoriality

- ▶ A “beachmaster” sea lion (that is, a dominant male with many females) seldom quarrels with his neighbors who have their own territories to defend.
- ▶ However, he must be constantly vigilant against bachelor bulls who challenge the beachmaster for mating privileges.
- ▶ Birds are conspicuously territorial. Most male songbirds establish territories in the early spring and defend these vigorously against all males of the same species during spring and summer when mating and nesting are at their height.

Territoriality

- ▶ A male song sparrow, for example, has a territory of approximately three-fourths of an acre.
- ▶ In any given area, the number of song sparrows remains approximately the same each year.
- ▶ The population remains stable because the young occupy territories of adults that die or are killed.
- ▶ Any surplus in the song sparrow population is excluded from territories and thus not able to mate or nest.

Territoriality

- ▶ Sea birds such as gulls, gannets, boobies, and albatrosses occupy colonies that are divided into very small territories just large enough for nesting.
- ▶ The territories of these birds cannot include their fishing grounds, since they all forage in the sea where the food is always shifting in location and shared by all.
- ▶ Territorial behavior is not as prominent with mammals as it is with birds.



Territoriality

- ▶ Mammals are less mobile than birds, making it more difficult for them to patrol a territory for trespassers.
- ▶ Instead, many mammals have home ranges.
- ▶ A **home range** is the total area an individual traverses in its activities.
- ▶ It is not an exclusive, defended preserve but overlaps with the home ranges of other individuals of the same species.
- ▶ For example, home ranges of baboon troops overlap extensively, although a small part of each range becomes the recognized territory of each troop for its exclusive use.

Territoriality

- ▶ Home ranges may shift considerably with the seasons.
- ▶ A baboon troop may have to shift to a new range during the dry season to obtain water and better grass.
- ▶ Elephants, before their movements were restricted by humans, made long seasonal migrations across the African savanna to new feeding ranges.
- ▶ However, the home ranges established for each season are remarkably consistent in size.

Social Behavior

Mating Systems

Mating Systems

- ▶ Animals display a diversity of mating systems.
- ▶ Behavioral ecologists generally classify mating systems by the degree to which males and females associate during mating.
- ▶ **Monogamy** is an association between one male and one female at a time.
- ▶ **Polygamy** is a general term that incorporates all multiple mating systems where females and males may have more than one mate.

Mating Systems

- ▶ **Polygyny** refers to a male that mates with more than one female.
- ▶ **Polyandry** is a system in which a female mates with more than one male.
- ▶ There are specific types of polygyny.
- ▶ Resource defense polygyny occurs when males gain access to females indirectly by holding critical resources.
- ▶ For example, female bullfrogs prefer to mate with males who are larger and older.

Mating Systems

- ▶ These males defend territories of higher quality than smaller males because their territories have better temperature regimes for tadpoles to grow or because they are free of predatory leeches.
- ▶ Female defense polygyny occurs when females aggregate and, consequently, are defendable.
- ▶ Thus, when female elephant seals occupy a small island, dominant males can defend and gain access to them for mating relatively easily (as shown in figure).
- ▶ This situation was previously known as a “harem.”

Mating Systems



Mating Systems

- ▶ Male dominance polygyny occurs when females select mates from aggregations of males.
- ▶ For example, some animals form leks.
- ▶ A **lek** is a communal display ground where males congregate to attract and court females.
- ▶ Females choose and mate with the male having the most attractive qualities (shown in figure).

Mating Systems



Mating Systems

- ▶ Leks characterize some birds, including prairie chickens and sage grouse.
- ▶ In these systems, sexual selection is often intense, resulting in evolution of bizarre courtship rituals and exaggerated morphological traits.

Social Behavior

Altruistic Behavior and Kin Selection

Altruistic Behavior and Kin Selection

- ▶ If, as Darwin suggested, animals should behave selfishly and strive to produce as many offspring as possible, why do some animals help others at some risk to themselves?
- ▶ Why do some individuals show utmost cooperation with members of their social group and even forego breeding themselves?
- ▶ Why do some individuals appear to sacrifice themselves so that other members of their group can survive?
- ▶ Until the mid 1960s, scientists had trouble explaining in Darwinian terms how such altruistic behavior could persist in a population.

Altruistic Behavior and Kin Selection

- ▶ Most instances of altruistic behaviors were explained using a groupselection argument.
- ▶ Group selectionists suggested that animals that helped others or that failed to mate did so for the benefit of the other members of the group.
- ▶ Therefore, such behaviors produce increased survivorship of groups whose members behaved altruistically.
- ▶ According to proponents of this argument, selection occurs at the level of the group, not at the level of the individual as Darwin suggested.

Altruistic Behavior and Kin Selection

- ▶ However, the group-selection argument as originally proposed by V. C. Wynne Edwards in 1962 has been rejected by the vast majority of behavioral ecologists for a number of reasons.
- ▶ For example, if in a social group there were randomly distributed genes for a risky altruistic behavior, such as giving calls to warn others of predators, those lacking such genes would flourish.
- ▶ They would be warned with no risk to themselves; their chances of reproduction would be greater and, in time, the “selfish” alleles would eliminate the altruistic ones from the group’s gene pool.

Altruistic Behavior and Kin Selection

- ▶ In 1964, W. D. Hamilton, based largely on his studies of insects, proposed a new way to explain altruistic behavior by modifying Darwin's original concept of fitness.
- ▶ He reasoned that fitness is measured not just by the number of offspring produced but by the increase or decrease in particular alleles in the gene pool.
- ▶ Thus, an individual may act altruistically, even at great risk, if it helps increase representation of its alleles in the gene pool.
- ▶ Alleles are shared by all relatives, including parents and offspring, brothers and sisters, cousins and other relations.

Altruistic Behavior and Kin Selection

- ▶ Alleles that influence altruistic behavior among relatives would persist in future generations.
- ▶ Since the most closely related animals share the most genes by common descent, we expect that altruistic behavior would be most common among closely related individuals.
- ▶ Thus, if everything else were equal, brothers who on average share half their alleles would be more likely to aid one another than they would a cousin who shares on average only 25% of their alleles.

Altruistic Behavior and Kin Selection

- ▶ Hamilton's hypothesis based on this genetic explanation for altruism and cooperation is called **kin selection**.
- ▶ Essentially, **kin selection** is the selection of genes by individuals assisting the survival and reproduction of individuals who possess the same genes by common descent.
- ▶ Hamilton's hypothesis revolutionized evolutionary and behavioral biology.
- ▶ The main criterion of Darwinian fitness is the relative number of an individual's alleles that are passed to future generations.

Altruistic Behavior and Kin Selection

- ▶ Hamilton, however, developed the concept of inclusive fitness, which is the relative number of an individual's alleles that are passed on to future generations either as a result of an individual's own reproductive success or that of related individuals.
- ▶ Thus, kin selection and inclusive fitness may be able to explain many altruistic behaviors that have perplexed biologists for many years.
- ▶ A good example of altruism and kin selection in nature is the remarkable cooperation and coordination among eusocial insects such as ants, bees, and wasps.

Altruistic Behavior and Kin Selection

- ▶ Through haplodiploidy, where males are haploid and females are diploid, sisters are genetically related on average by 75% rather than 50%.
- ▶ Sisters are more closely related to each other than to their own daughters!
- ▶ Therefore, they cooperate with other members of their social group, forego breeding themselves and aid the queen to produce more sisters who are more closely related (75% related) than potential offspring (50% related).
- ▶ Female Belding's ground squirrels, found in the High Sierra of California, give alarm calls when a predator approaches.
- ▶ Alarm calling warns other members of the social group and is risky to the alarm caller.

Altruistic Behavior and Kin Selection

- ▶ However, the benefits to alarm calling outweigh the risks because alarm callers are warning related individuals.
- ▶ Thus, alarm-calling behavior, even if it is risky, may be favored by selection if it increases inclusive fitness of the caller.
- ▶ Kinship theory suggests that animals may evolve an ability to recognize categories of relatives so that cooperation or aid-giving behavior will be directed more efficiently toward relatives.
- ▶ Although kin recognition behavior was discussed by Hamilton, little was known about it until almost 20 years after he wrote his seminal papers.

Altruistic Behavior and Kin Selection

- ▶ Through a number of experimental studies we now know that a variety of species can discriminate between kin and non-kin.
- ▶ Such species are found among invertebrates, including isopods and insects, and vertebrates, including fishes, frog and toad tadpoles, birds, squirrels, and monkeys.
- ▶ Some species can even discriminate between full siblings and half-siblings and between cousins and unrelated individuals.

Altruistic Behavior and Kin Selection

- ▶ Thus, some species have a finely tuned ability to identify relatives of various degrees of relatedness.
- ▶ The cues used in kin recognition vary from species to species.
- ▶ Birds use vocalizations whereas many other species use chemical cues.