Chapter 12: Sexual Reproduction and Meiosis

Chapter Synopsis

Meiosis and syngamy constitute a cycle of sexual reproduction. Fertilization would double the chromosome number of each subsequent generation except that the gametes possess only a haploid complement of DNA. Thus the resultant zygote inherits genetic material from both its father and its mother, in the case of humans, twenty-three chromosomes from each. Sexual reproduction produces offspring that are genetically different from either parent while asexual reproduction produces progeny that are genetically identical to the parent cell. The specific events of sexual reproduction varies from kingdom to kingdom. For example, in most unicellular eukaryotes, the individual cells function directly as gametes. In plants, specific haploid cells are produced by meiosis, these cells then divide mitotically to form a multicellular haploid phase which further produces eggs and/or sperm. In animals special gamete-producing cells differentiate from the other somatic cells early on in development. Only these cells are able to undergo meiosis to create haploid eggs or sperm.

Gamete-producing cells differentiate from somatic cells early in development. While they themselves are diploid, their products are haploid as a result of meiosis. Although meiosis and mitosis share many features, including microtubule formation, meiosis is unique for three reasons: synapsis, homologous recombination and reduction division. During synapsis homologous chromosomes physically pair along their length. In homologous recombination genetic exchange, called crossing over, occurs between the homologues. Reduction division is the two separate rounds of nuclear division that occur in the remainder of the process. In the first division, homologous chromosomes pair, exchange material, and separate. No genetic replication occurs before the second division when the non-identical sister chromatids separate into individual gametes. Each division is composed of prophase, metaphase, anaphase, and telophase, additionally labeled I or II.

Some of the most important events of meiosis occur during prophase I, itself further divided into leptotene, zygotene, pachytene, diplotene, and diakinesis. The ends of the sister chromatids attach to specific sites on the nuclear envelope. The attachment sites for the two homologues are near one another ensuring that each chromosome associates closely with its homologue. Each gene corresponds with its partner forming the synaptonemal complex. Certain genes are exchanged between homologues, an event called crossing over. The homologues are released from the membrane but remain tightly connected to one another. The homologues line up along the central plate of the cell during metaphase I. Only one face of each centromere is accessible to microtubule attachment, thus each homologue attaches to only one polar spindle fiber. The microtubules shorten at anaphase I and pull the homologues apart to opposite ends of the cell. Each pole ends up with a complete set of haploid chromosomes. Telophase I finishes division I, cytokinesis may or may not occur.

Meiosis II is essentially a mitotic process. During metaphase II, the still connected sister chromatids line up along their new metaphase plate with spindle fibers from each pole attached to each centromere. During anaphase II, the centromeres split and the sister chromatids are drawn to opposite poles. The result is four cells containing a haploid complement of genetic material.

Sexual reproduction is advantageous to species that benefit from genetic variability. However, since evolution occurs because of changes in an individual's DNA, crossing over and chromosome segregation is likely to result in progeny that are less well-adapted than their parents. On the other hand, asexual reproduction ensures the production of progeny as fit as the parent since they are identical to the parent. Remember the adage, "if it's not broken, don't fix it." There are several hypotheses regarding the evolution of sexual reproduction. One is associated with repairing double-stranded DNA breaks induced by radiation or chemicals. The contagion hypothesis suggests that sex arose from infection by mobile genetic elements. The Red Queen hypothesis theorizes that sex is needed to store certain recessive alleles in case they are needed

in the future. Along similar lines, eukaryotic cells build up large numbers of harmful mutations. Sex, as explained by Miller's rachet hypothesis, may simply be a way to reduce these mutations. The "whole truth" is likely a combination of these factors. Regardless of how and why, the great diversity of vertebrates and higher plants and their ability to adapt to the highly varied terrestrial habitats is indeed a result of their sexual reproduction.

CHAPTER OBJECTIVES

- Explain why both meiosis and syngamy are necessary for continued sexual reproduction.
- Differentiate between haploid and diploid in terms of genetic composition and indicate whether associated with somatic or gametic cells.
- Discuss the three major features that differentiate meiosis and mitosis.
- Identify the stages of meiosis I and the characteristic events of each stage.
- Describe the characteristic events of each stage of meiosis II and indicate how these events resemble mitosis.
- Explain how the homologues are held together during prophase I.
- Understand the genetic consequences of synaptonemal crossing over.
- Describe how the spindle-fiber attachment to chromosomes differs between mitosis and meiosis.
- Understand how and at what stage(s) chromosomes assort independently during meiosis.
- Understand how sexual reproduction is different from asexual reproduction.
- Indicate the evolutionary advantages and disadvantages of sexual reproduction and describe the most current explanations for its development.
- Understand the ultimate genetic and evolutionary consequences of meiosis and sexual reproduction.

KEY TERMS

asexual reproduction
chiasma (chiasmata)
crossing over
diakinesis
diploid
diplotene
fertilization
gamete
haploid
independent assortment
leptotene
meiosis
pachytene
parthenogenesis
recombinant nodule
sexual reproduction
somatic
synapsis
syngamy
zygote
zygotene

CHAPTER OUTLINE

12.0 Introduction

I. MOST CELLS REPRODUCE SEXUALLY

A. Gametes Are a Product of Special Division Called Meiosis fig 12.1

B. Sexual Reproduction Generates Genetic Diversity

12.1 Meiosis produces haploid cells from diploid cells

I. DISCOVERY OF REDUCTION DIVISION

A. Different Chromosome Numbers Are Found in One Organism
1. van Beneden examined cells in the roundworm *Ascaris*
   a. Gametes contained 2 chromosomes
   b. Somatic cells contained four chromosomes

B. Fertilization
1. Zygotes are produced by fusion of gametes
   a. Each gamete contains a single complement of genetic material
   b. The zygote contains two copies of each chromosome
2. Fusion of gametes is called fertilization or syngamy

C. Reduction Division
1. Fusion of body cells would sequentially increase chromosome number
2. Special reduction division serves to stabilize the chromosome number
3. Meiosis ensures constant chromosome number from one generation to next

D. The Sexual Life Cycle
1. Fertilization and meiosis constitute a cycle of sexual reproduction fig 12.2
   a. Body cells of adult are diploid and possess two sets of chromosomes
   b. Gametes are haploid and possess a single set of genetic material
   c. An individual inherits genes from its father and its mother, 23 each
2. Somatic tissues
   a. Life cycles show pattern of alternating chromosome numbers
   b. Alternate between diploid and haploid number fig 12.3, 4
   c. After syngamy, the zygote divides by mitosis
   d. All adult somatic cells are genetically identical to the zygote
   e. Unicellular organisms
      1) Individual cells function directly as gametes
      2) Zygote may divide mitotically or meiotically
3. Germ-line tissues
   a. Cells that become meiotic cells are isolated early in development
   b. Called germ-line cells, are diploid like somatic cells
   c. Somatic cells undergo mitosis, producing genetically identical diploid cells
   d. Germ-line cells undergo meiosis, producing haploid gametes

12.2 Meiosis has three unique features

I. UNIQUE FEATURES OF MEIOSIS

A. Meiosis Consists of Two Rounds of Nuclear Division
1. Process has much in common with mitosis
2. Meiosis has two unique features
   a. Synapsis
   b. Homologous recombination
   c. Reduction division

B. Synapsis
1. Homologous chromosomes (homologues) pair along their length
2. Process of forming complexes of homologues is called synapsis

C. Homologous Recombination
1. Genetic exchange occurs between homologues while joined fig 12.5a
2. Process called crossing over
3. Chromosomes come together along equatorial plate
4. Homologues pulled to opposite poles by microtubules
5. Clusters of chromosomes at poles are haploid
6. Each chromosome still composed of two chromatids

D. Reduction Division
1. Chromosomes do not replicate between divisions
2. After two divisions, cell contains half the chromosomal complement fig 12.5b
3. Second division is nearly identical to mitosis
4. Sister chromatids dissimilar because of crossing over
5. Process is continual, arbitrarily divided into stages
6. Two stages called meiosis I and meiosis II
7. Each stage divided into prophase, metaphase, anaphase, and telophase fig 12.6
8. Meiosis prophase I more complex than mitosis prophase

12.3 The sequence of events during meiosis involves two nuclear divisions

I. PROPHASE I

A. Preparation for Division
1. Already replicated DNA coils even tighter
2. Individual chromosomes become visible under light microscopy
3. Chromosomes consist of two sister chromatids joined at centromeres
4. Homologous chromosomes undergo synapsis, cross over segments, and separate

B. An Overview
1. Divided into five sequential stages
2. Leptotene: Chromosomes condense tightly
3. Zygotene
   a. Homologues line up side by side in synapsis fig 12.7
   b. Forms resultant synaptonemal complex held together by protein latticework
4. Pachytene
   a. Begins when synapsis is complete fig 12.8
   b. Each gene held in precise register with its corresponding gene
   c. DNA duplexes unwind
   d. Single strands of DNA pair with complementary strand from other homologue
5. Diplotene
   a. Protein lattice disassembles
   b. Period of intense cell growth
   c. Chromosomes decondense, active transcription occurs
6. Diakinesis
   a. Transition into metaphase
   b. Transcription stops, chromosomes recondense

C. Synapsis
1. Ends of chromatids attach to nuclear envelope at specific sites
   a. Membrane sites of homologues are adjacent
   b. Members of homologous pairs brought close together
2. Homologues line up side-by-side
   a. Guided by heterochromatin sequences
   b. Process called synapsis

D. Crossing Over
   1. Recombination nodules are very large protein assemblages
      a. Nodule spans central element of synaptonemal complex
      b. Act as large multienzyme recombination machines
   2. Complex series of events where DNA segments are exchanged between sister chromatids
   3. Two to three events per chromosome pair in humans
   4. When process is complete, synaptonemal complex breaks down
   5. Homologous chromosomes released from the nuclear membrane
   6. Homologues do not separate completely
      a. Sister chromatids held together by their common centromere
      b. Paired homologues held together at points of crossing over

E. Chiasma Formation
   1. Points of crossing over may be visible as X-shaped chiasma fig 12.9
   2. Chiasma indicates that two chromatids have exchanged parts fig 12.10
   3. Chiasma move to ends of arms as chromosomes separate

II. METAPHASE I

A. Events of the Second Stage of Meiosis I
   1. Nuclear envelope disperses, microtubules form spindle as in mitosis
   2. Formation of terminal chiasmata
      a. Position of chiasma when reaches it ends of chromosome
      b. One side of centromere faces outward
      c. One side of centromere faces other homologue fig 12.11
      d. Spindle microtubules only attach to kinetochore proteins on outer face of centromere
      e. Centromere of each homologue attached to only one pole
      f. In mitosis, kinetochores on both sides attach to microtubules
   3. Joined homologues line up on metaphase plate
   4. Attachment of homologue to a pole is random fig 12.12
   5. Alignment of chromosomes during metaphase I fig 12.13

III. COMPLETING MEIOSIS

A. Anaphase I
   1. With completion of spindle attachment, microtubules shorten
   2. Chiasma broken, centromeres pulled toward each pole
      a. Chromosomes dragged along
      b. Individual centromeres not pulled apart
      c. Sister chromatids do not separate
   3. Each pole has a complete set of haploid chromosomes
      a. Each set contains one member of each homologous pair
      b. Poles receive homologues randomly
   4. Genes on different chromosomes assort independently

B. Telophase I
   1. Each pole has full complement of chromosomes clustered at poles
   2. Nuclear membrane reforms around each new cluster
   3. Each chromosome exists as sister chromatids joined by centromere
   4. Chromatids are not identical because of crossing over fig 12.14
   5. Cytokinesis may or may not occur at this point

C. The Second Meiotic Division
1. Is a simple mitotic division using the products of meiosis I
2. Prophase II: Nuclear envelope breaks down, new spindle forms
3. Metaphase II: Spindle apparatus binds to sides of centromeres
4. Anaphase II
   a. Spindle fibers contract
   b. Centromeres divide
   c. Sister chromatids drawn to opposite poles
5. Telophase II: Nuclear envelopes reform

D. Completion of the Process fig 12.15
1. End result is four haploid complements of chromosomes
2. In animals, cells develop into gametes
3. In plants, fungi, and protists cells may proliferate via mitotic divisions

12.4 The evolutionary origin of sex is a puzzle

I. WHY SEX?

A. Not All Reproduction Is Sexual
1. Asexual reproduction
   a. Individual inherits all chromosomes from one parent
   b. Individual is genetically identical to parent
2. Bacterial cells reproduce by binary fission
3. Protists divide asexually unless under stress
4. Plants and multicellular organisms frequently reproduce asexually
5. Animals may reproduce by budding off localized masses of cells
6. Development from an unfertilized egg via parthenogenesis
   a. Example: Bees
      1) Fertilized eggs become diploid females
      2) Unfertilized eggs become haploid males
   b. Examples: Lizards, fish, amphibians

B. Recombination Can Be Destructive
1. Problems associated with sexual reproduction
   a. Advantage to species which benefit from genetic variability
   b. Evolution occurs because of changes at level of the individual
2. Recombination is evolutionarily both constructive and destructive
   a. Segregation of chromosomes disrupts beneficial gene combinations
   b. Diverse progeny will be less well-adapted than parents
   c. Complex adaptations are less likely to benefit from recombination

C. The Origin and Maintenance of Sex
1. The DNA repair hypothesis
   a. What are benefits to sexual reproduction?
      1) Meiotic recombination among protists is often absent
      2) In some protists, diploid is transient or only haploid phase exists
         a) With stress, haploids fuse forming diploid zygote
         b) Resulting diploid may not persist
   b. Only diploid cell can repair DNA damage
      1) Particularly double-stranded breaks in DNA
      2) Breaks induced by radiation or chemicals
      3) Repair of such damage is necessary in larger, longer-lived organisms

c. DNA repair through mechanism of synaptonemal complex
   1) Transient diploid stage allows for such repair
   2) Special yeast mutations
      a) Repair system inactivated for double-strand breaks
      b) Crossing over also prevented

2. The contagion hypothesis
   a. Sex arose from infection of eukaryotes by mobile genetic elements
   b. Replicating transposable element infects eukaryotic linage
      1) Propose it possessed genes promoting fusion with uninfected cells and synapsis
      2) Would copy itself onto homologous chromosomes
      3) Rapid spread through population until contained in all members
   c. Explains mating type "alleles" found in many fungi
      1) Matings types not true alleles, but are idiomorphs
         a) Genes that occupy homologous positions on chromosomes
         b) Have dissimilar sequences, not of homologous origin
      2) May be relics of ancient transposable element infections
3. The Red Queen hypothesis
   a. Sex may allow populations to "store" recessive alleles
      1) Under current conditions alleles are bad
      2) May prove useful in future
   b. Selection acts against such alleles
      1) Populations constrained by changing environment
      2) Alleles sheltered in sexually reproducing heterozygotes
   c. Evolution of sexual species keeps pace with ever-changing constraints
   d. Must continually "run to keep in same place"
4. Miller's rachet
   a. Asexual populations incorporate a mutational rachet mechanism
      1) Harmful mutations arise
      2) No way to eliminate them, accumulate over time
   b. Sexual populations use recombination to produce individuals with fewer mutations

D. The Evolutionary Consequences of Sex
1. Three primary mechanisms to generate new genetic combinations
   a. Independent assortment fig 12.16
   b. Crossing over
   c. Random fertilization
2. Evolutionary consequences of sex are profound
   a. Genetic diversity is raw material of evolution
   b. Pace of evolution increased with greater genetic diversity
   c. Example: Thoroughbred race horses
      1) All descended from small number of individuals, limited genetic variability
      2) Winning times in races not improved in recent history
3. Evolutionary process is both revolutionary and conservative
   a. Revolutionary as the pace is quickened by genetic variability
   b. Conservative as variation is not always favored by selection
      1) Acts to preserve existing combinations of genes
      2) Greater in asexual organisms that are not highly mobile
      3) Live in extremely demanding habitats
4. In vertebrates, the evolutionary premium is on versatility, thus sex

INSTRUCTIONAL STRATEGY

PRESENTATION ASSISTANCE:

Meiosis is like roommates splitting up and dividing their belongings. The division is more equitable if the towels are piled together and then divided up, the silverware piled together and divided and so forth, than if things are arbitrarily thrown into one pile or another as they are found. The first method ensures a more even distribution of items and is analogous to homologue pairing.

Differentiating between mitosis and meiosis is like distinguishing between the production of cars and trucks. Each uses the same machinery, but produces an entirely different product.

The evolution of reproduction adds a second step ahead of the first, like the evolution of PS II/PS I photosynthesis. The second division of meiosis is equivalent to the single division of mitosis, chromatids separate from one another. It is slightly different from mitosis in that the sister chromatids are not identical. The first division of meiosis is a new event. The homologues pair, form synaptonemal complexes, and then move to the metaphase plate.

Stress the importance of crossing over and the random assortment of homologues as they relate to producing genetic variation. Meiosis results in (1) genetic variation and (2) the reduction of the genetic complement in preparation for syngamy. It is part of the sexual reproductive process.

A thorough understanding of meiosis is necessary to grasp what occurs in Mendelian genetics. It is amazing that Mendel was able to formulate his ideas without knowledge of either mitosis or meiosis.

VISUAL RESOURCES:

One can utilize similar visuals as in mitosis, but with a distinction between homologues and a resulting halving of the genetic complement.

Construct a model of the chiasmata as indicated in the text using two strands of thick yarn representing the chromosomes and a ring representing the chiasmata.