CHAPTER 13 ARTHROPODS STUDY GUIDE

13.1 A Winning Combination

- **A.** Insects cause staggering economic losses every year, far more than human wars.
- **B.** Insects are the dominant group of animals on the Earth today.
- **C.** The diversity of insects is far greater than all other taxa combined.
- **D.** There are an estimated 200 million insects alive for every human today.

13.1 Characteristics

- **A. Introduction**
  1. Arthropoda includes spiders, scorpions, ticks, mites, crustaceans, millipedes, centipedes, insects, and some smaller groups
     – they are the most abundant and diverse of all animals
  2. There is a rich fossil record extending back to the mid-Cambrian period (Figure 13.1A, B).
  3. Arthropods are **eucoelomate protostomes** with well-developed organ systems, and a chintinized cuticular exoskeleton.
  4. Segments have coalesced into **tagmata.**
  5. They range in size from 0.1mm to 3.7 m.
  6. Arthropods compete with us for food and spread disease; they also produce silk, honey, and beeswax.
- **B. Ecological Relationships**
  1. Found in all environments and virtually all altitudes and latitudes.
  2. Species are adapted to land and to fresh, brackish, and marine water.
  3. Most species fly to favored habitats.
  4. All modes of feeding occur among arthropods though the majority are herbivorous.
  5. Aquatic species generally feed on algae; land species generally feed on plants.
  6. Nothing rivals their diversity.
- **C. Position in the Animal Kingdom and Biological Contributions**
- **D. Characteristics of Phylum Arthropoda** (see Inset, page 237).

13.3 Why Have Arthropods Achieved Such Great Diversity and Abundance?

- **A. Structural and Physiological Patterns**
  1. **Versatile Exoskeleton** (Figure 13.2)
     - a. The **cuticle** is highly protective but is **jointed,** providing mobility in a **flexible exoskeleton.**
     - b. It consists of an inner thick **procuticle** and an outer thin **epicuticle**.
     - c. The outer epicuticle is composed of proteins and lipids; a tanning process stabilizes and hardens the protein.
     - d. Procuticle has an **exocuticle** secreted before a molt and an **endocuticle** secreted after molting.
     - e. Both layers of procuticle contain **chitin** bound with protein.
     - f. Chitin is a tough resistant nitrogenous polysaccharide insoluble in water.
     - g. Thus the procuticle is lightweight, flexible, and provides protection against dehydration.
     - h. Impregnation with **calcium salts** makes the procuticle very hard in lobsters and crabs.
     - i. As the cuticle is thin between segments, it allows movement at the joints
     - j. Muscles attach to the cuticle.
     - k. The cuticle also folds inward to line the foregut, hindgut, and trachea.
     - l. **Ecdysis**, at the end of molting, is the process of shedding its outer exoskeleton.
     - m. Arthropods typically molt four to seven times; exoskeleton weight is a limit to body size.
  2. **Segmentation and Appendages for Efficient Locomotion**
     - a. Usually each somite bears a pair of jointed appendages.
     - b. Segments and appendages are then modified for various adaptive functions.
     - c. Limb segments are hollow levers with internal striated muscles.
     - d. Appendages may function in sensing, food handling, walking or swimming.
  3. **Air Piped Directly to Cells**
     - a. Terrestrial arthropods use an efficient tracheal system that delivers oxygen directly to cells.
     - b. Aquatic arthropods respire by various forms of efficient gills.
  4. **Highly Developed Sensory Organs**
     - a. Eyes vary from a simple light sensitive ocelli to a compound mosaic eye.
     - b. Other senses accomplish touch, smell, hearing, balancing and chemical reception.
  5. **Complex Behavior Patterns**
     - a. Arthropods surpass most other invertebrates in complex and organized activities.
     - b. Most behavior is innate or unlearned but some is learned.
  6. **Reduced Competition through Metamorphosis**
     - a. Many arthropods have metamorphic changes that result in different larval and adult stages.

    b. Larvae and adults eat different foods and occupy different habitat and avoid competition.
7. a. Most biologists accept Arthropoda as monophyletic.
    b. Previous additions divide arthropods into four subphyla – Trilobita, Chelicerata, Crustacea, and Uniramia.
    c. Uniramia share appendages with a single branch and include insects and myriopods.
    d. Recent works supports the division of Uniramia into the subphyla Myriapoda and Hexapoda.
    e. Hexapoda contain the class Insecta.

12.4 **Subphylum Trilobita**

1. Trilobites arose before the Cambrian, flourished, and then became extinct 200 million years ago.
2. They have a trilobed body shape due to a pair of longitudinal grooves.
3. They were bottom dwellers and probably were scavengers (Figure 13.1A).
4. Ranging from 2 to 67 centimeters long, they could roll up like pill bugs.
5. Their exoskeleton contained chitin strengthened by calcium carbonate.

12.5 Subphylum Chelicerata

A. Characteristics

1. Chelicerates have **six pairs of appendages** including **chelicerae, pedipalps and four pair of legs**.
2. They lack mandibles and antennae.
3. Most suck liquid food from prey.

B. Class Merostomata: Subclass Euryptida

1. Eurypterids (giant water scorpions) were the largest of all fossil arthropods at three meters in length (Figure 13.1B).
2. Their fossils occur in rocks from the Ordovician to the Permian periods, 200 to 500 million years ago.
3. They resemble both marine horseshoe crabs and terrestrial scorpions.

C. Class Merostomata: Subclass Xiphosurida, Horseshoe Crabs

1. The modern horseshoe crab (e.g., ***Limulus)*** is nearly unchanged from ancestors in the Triassic period (Figure 13.5A,B).
2. Five species in three genera survive.
3. Most live in shallow water.
4. **Structures**
    a. An unsegmented shield or **carapace** covers the body in front of a broad abdomen
    b. A **telson** or spinelike tail
    c. The cephalothorax has five pairs of walking legs and a pair of **chelicerae**.
    d. **Book gills** are exposed on some of the abdominal appendages.
5. They walk with their walking legs and swim with abdominal plates.
6. They feed at night on worms and small molluscs.

D. Class Pycnogonida: Sea Spiders

1. Sea spiders vary from a few millimeters to larger sizes; all have small, thin bodies.
2. Some males may have a subsidiary pair of legs **(ovigers)** to carry developing eggs (Figure 13.6).
3. The mouth, at the tip of a proboscis, sucks juices from cnidarians and soft-bodied animals.
4. They have a greatly reduced abdomen attached to an elongated **cephalothorax.**
5. Four pairs of long, thin walking legs are present.

E. Class Arachnida

1. There is a great diversity among scorpions, mites, ticks, daddy longlegs and others.
2. Of 50,000 described species, most are free living and more common in warm, dry regions.
3. Arachnids are divided into a cephalothorax and abdomen.
4. **Order Araneae: Spiders**
    a. About 35,000 species of spiders are known.
    b. The body consists of an unsegmented cephalothorax and abdomen joined by a slender **pedicel** (Figure 13.7A).
    c. The anterior appendages are a pair of chelicerae with terminal fangs.
    d. Four pairs of walking legs terminate in claws (Figure 13.7A).
    e. All spiders are predaceous, mostly on insects, which are dispatched by poison and fangs.
    f. The injected venom liquefies and digests the tissues; this is sucked into the spider's stomach.
    g. Spiders breathe by **book lungs and/or tracheae** (Figure 13.7C).
        1) **Book lungs** are unique to spiders; parallel air pockets extend into a blood-filled chamber.
        2) Air enters the chamber through a slit in the body wall.
        3) The tracheae system is less extensive than in insects; it carries air directly to tissues.
        4) Spiracles are openings to the trachea.
    h. Spiders and insects have **Malpighian tubules** for an excretory system (Figure 13.7C).
        1) Potassium, other solutes and waste molecules are secreted into the tubules.

2) **Rectal glands** reabsorb the potassium and water, leaving wastes and uric acid for excretion.
3) This recycling process conserves water and permits the organisms to live in dry regions.
4) Many spiders have **coxal glands** that are modified nephridia at the base of some legs.

i. **Sensory Systems**
1) Most spiders have eight simple eyes, each with a lens, optic rods and a retina (see Figure 13.7B).
2) They detect movement and may form images.
3) Sensory setae detect air currents, web vibrations, and other stimuli.

j. **Web-Spinning Habits**
1) Spinning silk is a critical ability for spiders and some other arachnids (Figure 13.8)..
2) Two or three pairs of **spinnerets** contain microscopic tubes that run to **silk glands**.
3) A liquid **scleroprotein** secretion hardens as it is extruded from the spinnerets.
4) Silk threads are very strong and will stretch considerably before breaking.
5) Spiders are often camouflaged or cryptic (Figure 13.9A).
6) Jumping spiders have excellent vision and stalk prey (Figure 13.9B).
7) Silk is used for orb webs, lining burrows, forming egg sacs, and wrapping prey (Figures 13.8, 13.10, 13.12A).
8) The fisher spider, *Dolomedes triton,* feeds on minnows (Figure 13.8).
9) Wolf spiders, jumping spiders, and fisher spiders chase and catch their prey.

k. **Reproduction**
1) Before mating, the male spins a small web, deposits a drop of sperm on it, and then stores the
package in his pedipalps.
2) Mating involves inserting the pedipalps into the female genital openings and depositing the **spermatophore**.
3) Sperm are stored in a seminal receptacle for weeks or months until eggs are ready.
4) A courtship ritual is often required before the female will allow mating.
5) Eggs may develop in a cocoon in the web or may be carried by the female.
6) The young hatch in few weeks and may molt before leaving the cocoon.

l. **Are spiders really dangerous?**
1) Most fear spiders without good reason.
2) Spiders are allies of humans in our battle with insects.
3) American tarantulas rarely bite and the bite is not dangerous (Figure 13.11).
4) Species of **black widow** spiders are dangerous; the venom is neurotoxic (Figure 13.12A).
5) The **brown recluse** spider has hemolytic venom that destroys tissue around the bite (Figure 13.12B).
6) Some Australian and South American spiders are the most dangerous and aggressive.

5. **Order Scorpionida: Scorpions**
a. Scorpions are more common in tropical and subtropical zones but do occur in temperate areas.
b. They are nocturnal and feed largely on insects and spiders (Figure 13.13A).
c. Sand-dwelling scorpions locate prey by detecting surface waves with their leg sensillae.
d. The cephalothorax has the appendages, a pair of medial eyes and 2-5 lateral eyes.
e. The abdomen contains a broad preabdomen and a postabdomen.
e. The postabdomen has the long, slender tail of five segments that ends in a **stinging apparatus**.
f. The **stinger** on the last segment has venom that varies from mildly painful to dangerous.
g. Scorpions bear live young carried on the mother's back.

6. **Order Opiliones: Harvestmen**
a. Harvestmen or daddy longlegs are common, particularly in tropical regions (Figure 13.13B).
b. Unlike spiders, their abdomen and cephalothorax join broadly without a narrow pedicel.
c. They can lose one or more legs of their eight legs without ill effect.
d. Their chelicerae are pincer-like and they feed more as scavengers than do spiders.

7. **Order Acari: Ticks and Mites**
a. Acari are medically and economically the most important arachnids.
b. About 25,000 species have been described; many more are estimated to exist.
c. They are both aquatic and terrestrial; some parasitize vertebrates and invertebrates.
d. Most mites are less than 1 millimeter long; ticks may range up to 2 cm.
e. Acarines have complete fusion of cephalothorax and abdomen with no sign of external segmentation (Figure 13.14A).
f. Mouthparts are on the tip of the anterior **capitulum**.

g. Adult mites and ticks possess four pairs of legs.
h. Acarines may transfer sperm directly or by spermatophores.
i. The egg hatches, releasing a six-legged larva; eight-legged nymphal stages follow.
j. **Diversity**
   1) House dust mites are free-living and often cause allergies (Figure 13.14B).
   2) Spider mites are one of many important agricultural pest mites that suck out plant nutrients.
   3) Chiggers are larval *Trombicula* mites; they feed on dermal tissues and cause skin irritation (see Inset, page 245).
   4) The hair follicle mite ***Demodex*** is harmless but other species cause mange in domestic animals (Figure 13.14C).
   5) Tick species of *Ixodes* carry Lyme disease (see Inset, page 245).
   6) Tick species of *Dermacentor* transmit Rocky Mountain spotted fever.
   7) The cattle tick transmits Texas cattle fever.

12.6 Subphylum Crustacea

A. Classification: Traditionally in the subphylum Mandibulata, along with insects and myriapods.

B. Characteristics: Members of all of these groups have at least 1 pair of antennae, mandibles, and maxillae on the head

1. The 67,000 species include lobsters, crayfish, shrimp, crabs, and copepods.
2. Most are aquatic, and free living; many are sessile, commensal, or parasitic.
3. The main distinguishing characteristic of crustaceans is that they have **two pairs of antennae.**
4. The head also has a **pair of mandibles** and **two pairs of maxillae** (Figure 12.14).
5. There is one pair of appendages on each of the additional somites; some somites may lack appendages.
6. All appendages, except perhaps the first antennae, are **biramous** (they have two main branches) (Figure 13.3).
7. Primitive crustaceans may have up to 60 somites; derived crustaceans have fewer segments.
8. The tagmata are usually **head**, **thorax** and **abdomen** but they are not homologous across taxa.
9. The dorsal covering is the **carapace**; it may cover most of the body or just the cephalothorax.

C. Form and Function

1. **Appendages**
   a. Crayfish and lobsters (class Malacostraca) exhibit appendage modifications.
   b. Crayfish appendages have evolved into walking legs, mouthparts, swimmerets, etc., from modification of the basic biramous appendage.
   c. **Swimmerets** or abdominal appendages, retain the primitive biramous condition and consist of an **endopod** and **exopod** which are attached to one or more **basal segments** collectively called a **protopod** (Figure 13.18).
   d. Three pairs of thoracic appendages are called **maxillipeds;** first pair of walking legs called **chelipeds;** last pair of appendages are called **uropods** (Figure 13.19).
   e.. The evolutionary trend is reduction and modification of appendages.
   f. Appendages may be foliaceous (leaflike), biramous, or uniramous as found in walking legs.
   g. Abdominal swimmertes are used in locomotion; the first pair are named gonopods.
   h. Gonopods in males are modified for copulation, females attach eggs and young to them.
   i. Uropods serve as paddles for swift backward movement.
   j. The telson also protects eggs and young on the swimmerets.
2. **Internal Features** (Figure 13.22)
   a. Muscular and nervous systems and segmentation show the **metamerism** of annelid-like ancestors.
   b. **Hemocoel**
      1) The major body space in arthropods is not a coelom but a **blood-filled hemocoel.**
      2) Vestigial coelomic sacs are lost within the space between mesoderm, ectoderm and yolk.
      3) The spaces that develop as hemocoel are not lined by mesodermal peritoneum.
      4) In crustaceans, coelomic compartments remain as end sacs of excretory organs and gonads.
   c. **Muscular System**
      1) **Striated muscles** make up a major portion of the crustacean body.
      2) Most muscles are arranged as antagonistic groups; **flexors** draw a limb toward the body and **extensors** straighten a limb out.
      3) Abdominal flexors of a crayfish allow it to swim backward.
      4) Strong muscles located on each side of the stomach control the mandibles.

3. **Ecdysis**

a. **The Molting Process**

1) Molting is necessary for a crustacean to increase in size; the exoskeleton does not grow.
2) The physiology of molting affects reproduction, behavior and many metabolic processes.
   a) Inorganic salts are withdrawn from the old cuticle during **premolt**.
   b) The underlying epidermis secretes the cuticle.
   c) Epidermal cells enlarge before ecdysis then secrete a new inner epicuticle layer.
   d) Enzymes released into the area above the new epicuticle dissolve the old endocuticle (Figure 13.20 sequence).
   e) When only the old exocuticle and epicuticle remain, the animal swallows water or air to expand and burst the old cuticle (Figure 13.21).
   f) The new soft new cuticle stretches and then hardens with the deposition of inorganic salts during **postmolt**.
   g) Molting occurs often in young animals, and may cease in adults.
3) Temperature, day length or other stimuli trigger the central nervous system to begin ecdysis.
4) The central nervous system decreases production of **molt-inhibiting hormone** by the **X-organ.**
5) This promotes release of molting hormone from the **Y-organs** and leads to ecdysis.

4. **Other Endocrine Functions**

1) Pigments in epidermal chromatophores give body color to crustaceans.
2) Chromatophores change color by concentrating or dispersing pigment in cells.
3) Removing eyestalks accelerates molting and prevents color changes to match the background.
4) Hormones from **neurosecretory cells** in the eyestalk (see Inset, page 248) control dispersal of cell pigment.
5) Neurosecretions from the pericardial organs cause an increase in heartbeat.
6) **Androgenic glands** in male amphipods stimulate expression of male characteristics.

5. **Feeding Habits**

1. Vary widely with many adaptations.
2. Many can shift from one type of feeding to another, depending on food availability.
3. Mandibles and maxillae ingest food; maxillipeds hold and crush food.
4. The same fundamental mouthparts are adapted to a wide array of feeding habits.
5. **Suspension feeders** generate water currents in order to eat plankton, detritus and bacteria.
6. Predators consume larvae, worms, crustaceans, snails and fishes.
7. The shrimp-like *Lygiosquilla* pierces prey with a specialized digit on a walking leg.
8. The pistol shrimp, *Alpheus*, catches prey with a large chela that snaps shut.
9. **Scavengers** eat dead animal and plant matter.
10. Crayfishes have a two-part stomach; a **gastric mill** grinds up food in the first compartment.

6. **Respiration, Excretion, and Circulation**

a. **Respiration, Excretion, and Circulation**

1) Gills vary in shape, attach to appendages, and contain blood vessels and sinuses.
2) The carapace protects brachial chambers.
3) Excretory and osmoregulatory glands are located in the head.
4) These **antennal or maxillary glands** open at the base of the antenna or maxilla.
5) Decapods have antennal glands called **green glands** (figure 13.22).
6) Waste products consist of ammonia with some urea and uric acid.
7) Crustaceans and other arthropods have an "open" circulatory system; there is no system of veins
   to separate blood from interstitial fluid.
8) Hemolymph leaves the heart by arteries but washes through a hemocoel to return to the heart via sinuses.
9) This contrasts with annelids that have a closed system, as do vertebrates.
10) Movement of organs and limbs circulate blood in the open sinuses, less reliance on heartbeats.
11) Hemocyanin and/or hemoglobin are respiratory pigments; clotting also occurs.

7. Nervous and Sensory Systems (Figure 13.22)

1) A brain or cerebral ganglion connects to anterior sense organs and the subesophageal ganglion.

2) A double ventral nerve cord with segmental ganglia connects to viscera, appendages, and muscles;
giant fibers are also present.
3) A **median** or nauplius eye and compound eyes are present.
4) The median eye consists of three pigment cups, retinal cells, and maybe a lens.
5) Crustacean compound eyes are similar to insect eyes.
6) Attached to moveable stalks, compound eyes detect motion and analyze polarized light.
7) Their corneal surfaces covers a wide visual field.
8) Compound eyes are composed of ommatidia that varies from a few to many thousands (Figure 13.23).
9) Crustacean ommatidia are adapted to bright or dim light or to both conditions.
10) Statocysts, tactile setae, and chemosensitive setae are also present.

8. **Reproduction and Life Cycles**

a. **Diversity of Reproduction**

1) Crustaceans have separate sexes with specializations for copulation.
2) Barnacles are **monoecious** but generally cross-fertilize.
3) In some ostracods, males are scarce and reproduction is by parthenogenesis.
4) Most crustaceans brood eggs in **brood chambers**, in **brood sacs** attached to the abdomen, or attached to abdominal appendages (see Figure 13.25).
5) Crayfishes develop directly without a larval form.
6) Most crustaceans have a larva unlike the adult in form, and undergo metamorphosis.
7) The **nauplius** is a common larval form with uniramous first antennae, biramous second antennae, and mandibles that all aid in swimming (Figure 13.24).

12.7. Brief Survey of Crustaceans

A. Class Branchiopoda (Figure 13.25A)

1. There are four orders in this class.
   a. Order **Anostraca** includes fairy shrimp and brine shrimp that lack a carapace.
   b. Order **Notostraca** includes tadpole shrimp; the carapace forms a large dorsal shield.
   c. Order **Conchostraca** includes clam shrimp enclosed by a bivalved carapace.
   d. Order **Cladocera** includes water fleas with a carapace that encloses the body but not the head.
2. All have flattened and leaf-like legs (**phyllopodia**) that are the chief respiratory organs.
3. Legs assist in suspension feeding and, except for cladocerans, function in locomotion.
4. Most are freshwater organisms; cladocerans are an important part of the freshwater **zooplankton.**

B. Class Maxillopoda

1. Maxillopods include a number of groups that form a clade within Crustacea.
   a. The general body plan has five cephalic, six thoracic and four abdominal somites plus a telson.
   b. Reductions from this body plan are common; there are no appendages on the abdomen.
   c. When present, the eye of the nauplius is unique in structure and is called a **maxillopodan eye.**
2. **Subclass Ostracoda**
   a. Ostracods, enclosed in a bivalve carapace, resemble tiny clams, 0.25-8.0 mm long (Figure 13.25B).
   b. There is considerable fusion of trunk somites; thoracic appendages are reduced to two or one.
   c. Most live on the bottom or climb onto plants, but some are planktonic, parasitic or burrowing.
3. **Subclass Copepoda**
   a. This group is second to Malacostraca in numbers of species.
   b. They lack a carapace and retain the simple, median, nauplius eye in the adult (Figure 13.25C).
   c. They have four pairs of flattened, biramous, thoracic swimming appendages.
   d. Parasitic forms are highly modified and reduced, often unrecognizable as arthropods.
   e. Free-living copepods may be the dominant primary consumer in aquatic communities.
4. **Subclass Branchiura** (Figure 13.26A,B)
   a. Branchiurans lack gills; most are **parasites** of fish.
   b. Found on both marine and freshwater fish, they are 5-10 mm long.
   c. They have a broad, shield-like carapace, compound eyes, four biramous thoracic swimming appendages
   and a short unsegmented abdomen.
   d. The second maxillae are modified as **suction cups** to hold on to the host fish.
5. **Subclass Pentastomida** (Figure 13.27C)
   a. Tongue worms
   b. parasites in the vertebrate lungs, e.g. reptiles & small canines & felines
6. **Subclass Cirripedia** (Figure 13.27A,B)

a. Cirripedia includes **barnacles** in order Thoracica and three orders of burrowing or parasitic forms.
b. Barnacle adults are sessile and attach directly **(acorn barnacles)** or by a stalk **(goose barnacles)** to the substrate ((Figure 13.27A,B).
c. The carapace surrounds the body and secretes a set of calcareous plates.
d. The head is reduced, the abdomen is absent and the thoracic legs are long with hair-like setae.
e. The many-jointed **cirri** that bear the setae are extended from the plates to feed on small particles.

C. Class Malacostraca

1. This is the largest and most diverse class of Crustacea found in marine and freshwater.
2. Four of 12 to 13 orders are discussed in the text.
3. Malacostracans have eight thoracic and six abdominal segments each with paired appendages.
4. **Order Isopoda**
   a. They are dorsoventrally flattened, lack a carapace and have sessile compound eyes.
   b. Abdominal appendages bear gills.
   c. Common land forms include the **sow bugs** and **pill bugs** (Figure 13.28A,B).
   d. Some isopods are highly modified as parasites of fish or crustaceans (Figure 12.29).
5. **Order Amphipoda** (Figure 13.30)
   a. Amphipods resemble isopods; they lack a carapace, have sessile compound eyes, and one pair of maxillipeds
   b. However, they are compressed laterally and gills are in the thoracic position.
   c. Many are marine; others are beach-dwelling, freshwater or parasitic.
6. **Order Euphausiacea** (Figure 13.31)
   a. This order only has about 90 species but includes the important ocean plankton called "krill."
   b. They form a major component of the diet of baleen whales and of many fishes.
   c. Most are 3 to 6 cm long.
7. **Order Decapoda**
   a. Decapods have three pairs of maxillipeds and five pairs of walking legs, the first forming pincers or **chelae** (see Figures 13.19A,B).
   b. They range from a few millimeters to the largest arthropod, a Japanese crab with a 4-meter leg-span.
   c. True crabs have a broader cephalothorax and reduced abdomen, compared to crayfish or lobsters.
   d. Fiddler crabs have a reduced abdomen and burrow in the sand (figures 13.32C).
   e. Hermit crabs are adapted to live in snail shells (Figure 13.32B).

12.8 Subphylum Myriapoda

A. Characteristics

1. The myriapods include the centipedes, millipedes, pauropods and symphylans.
2. Several classes have two tagmata – a head and trunk with paired appendages on the trunk.
3. Myriapods only have **one pair of antennae, mandibles, and maxillae.**
4. Legs are always **uniramous.**
5. Respiration occurs through the body surface, trachea, or gills in juveniles.

12.9 Class Chilopoda: Centipedes

A. Characteristics

1. Centipedes are terrestrial predators with flattened bodies with up to 177 somites (Figure 13.15A).
2. Each somite, except the one behind the head and the last two, bears a pair of **jointed legs.**
3. Appendages of the first body segment form **poison claws** (Figure 13.15B).
4. The head has **one pair of antennae**, a **pair of mandibles** and one or **two pairs of maxillae**.
5. Eyes on either side of the head consist of groups of **ocelli**.
6. A pair of spiracles in each somite allows air to diffuse through branched air tubes of the tracheae.

B. Life History

1. Sexes are separate, all are oviparous.
2. Young resemble adults.
3. Centipedes are found under logs, bark and stones.
4. They are **carnivorous**, eating earthworms, cockroaches and other insects.
5. The house centipede has 15 pairs of long legs and is common in bathrooms and damp cellars.
6. Most are harmless to humans but a few large, tropical centipedes are dangerous.

12.10 Class Diplopoda

A. Characteristics

1. Millipedes have many legs but not a thousand as suggested by their name.
2. Two pairs of legs are present per somite, probably from fusion of two segments (Figure 13.16).

3. Their cylindrical bodies have from 25 to 100 somites.
4. Each abdominal somite has two pairs of spiracles opening into air chambers and tracheal air tubes.
5. After copulation, the female lays eggs in a nest and guards them.
6. Larvae have only one pair of legs to each somite.
7. Most eat decayed plants but a few eat living plant tissue.

12.11 Class Pauropoda

A. Characteristics

1. Pauropods are soft-bodied, small (2 mm or less) myriapods.
2. Almost 500 species are known.
3. The head lacks eyes, has branched antennae, and a pair of sense organs.
4. The 12 trunks segments bear nine pairs of legs but none on the last two segments.
5. A tergal plate covers each two segments.
6. They lack tracheae, spiracles and a circulatory system.
7. Pauropods are probably most closely related to diplopods.

B. Life History

1. Pauropods live in moist soil, leaf litter, decaying vegetation, or under bark and debris.
2. They are the least well known of myriapods.

12.12 Class Symphyla

A. Characteristics

1. Symphylans are small (2-10 mm) with centipede-like bodies.
2. They are soft-bodied with 14 segments; 12 segments bear legs and one bears a pair of spinnerets.
3. Antennae are long and unbranched.
4. About 160 species are known.
5. They are eyeless with sensory pits at the base of the antennae.
6. The tracheal system connects to a pair of spiracles on the head and tracheal tubes to the anterior only.

B. Life History and Reproduction

1. They live in humus, leaf mold and debris.
2. The male ***Scutigerella*** places a spermatophore at the end of a stalk.
3. The female stores the sperm in special pouches; she removes eggs and smears them with sperm before attaching them to moss or lichen.
4. Young hatch with only six or seven pairs of legs.

12.13 Subphylum Hexapoda

1. Characteristics include six uniramous legs and three tagmata – head, thorax, and abdomen.
2. Abdominal appendages are greatly reduced or absent.
3. Bases of mouthparts are enclosed within the head capsule in the Class Entognatha.
4. Class Insecta mouthpart bases are visible outside of the head capsule.

12.14 Class Insecta

A. Diversity

1. Insecta are the **most diverse and abundant** of all arthropods, indeed, all taxa at this level of classification (Figure 13.33 & 13.34).
2. The number of known species is nearly **one million**; there may be many more.
3. Insects play major medical and economic roles with humans, and are critical to animal ecology.
4. The study of insects is called **entomology**.

B. Characteristics

1. Insects have three pair of legs and often two pair of wings on the thoracic region of the body (Figure 13.35A,B).
2. Insects range from less than 1 mm to 20 cm in length; the larger insects are tropical.

C. Distribution

1. Insects are found in nearly all habitats, a few are marine.
2. Insects are common in fresh water, brackish water and salt marshes.
3. Insects are abundant in soils, forest canopies, and can be found in deserts and wastelands.
4. Most animals and plants have insects as parasites externally and internally.
5. Adaptive Traits
    a. Flight, small size, and adaptable nature makes insects widely distributed.
    b. Their well-protected eggs withstand rigorous conditions and are readily dispersed.
    c. Structural and behavioral adaptations include:
        1) A waxy cuticle and the ability to close spiracles thereby minimizing water loss.
        2) Maximal fluid is extracted from food and fecal material.
        3) Water is also retained in oxidative metabolism.
        4) Many enter diapause or dormancy during unfavorable conditions.

E. External Features

1. There are more than 30 orders of insects. (pages 271-273)
2. Insect tagmata are the head, thorax, and abdomen.
3. The cuticle of a somite is composed of a dorsal notum, a ventral sternum and a pair of lateral pleura.
4. **Head**
   a. Usually there is a pair of large compound eyes and three ocelli.
   b. One pair of antennae is present.
   c. Mouthparts consist of a labrum, a pair of mandibles and maxillae, a labium, and a hypopharynx.
5. **Thorax**
   a. **Thorax:** consists of the **prothorax, mesothorax** and **metathorax**; each has a pair of legs.
   b. **Wings:**
      1) If two pairs of wings are present, they are on the **mesothorax** and **metathorax.**
      2) Wings consist of a double membrane with cuticular veins.
      3) Veins serve to strengthen the wing; the vein pattern is used to identify insect taxa.
   c. **Legs:**
      1) Walking legs end in terminal pads and claws.
      2) Houseflies walk upside down with sticky pads.
      3) Hindlegs of grasshoppers and crickets are enlarged for jumping (Figure 13.35).
      4) Mole crickets have front legs adapted for burrowing in the ground.
      5) Forelegs of the praying mantis allow it to grasp prey (Figure 13.36).
      6) Honeybees have leg adaptations for collecting pollen.
      7) Waterbugs swim with paddle-shaped appendages.
6. **Wings and the Flight Mechanism**
   a. Insect wings are not homologous with bird and flying mammal wings.
   b. Insect wings are outgrowths of cuticle from the mesothoracic and metathoracic segments.
   c. Most flying insects have two pairs of wings; the Diptera (true flies) have one pair (Figure 13.38).
   d. **Halteres** are reduced wings that provide the fly with balance during flight.
   e. Non-reproductive ants and termites are wingless; lice and fleas have also lost their wings.
   f. **Modifications of Wings**
      1) Wings for flight are thin and membranous.
      2) The thick and horny front wings of beetles are protective.
      3) Butterflies have wings covered with scales; caddisflies have wings covered with hairs.
   g. **Flight Muscles of Insects**
      1) **Direct flight muscles** attach to a wing directly (Figure 13.38A).
      2) **Indirect flight muscles** alter the shape of the thorax to cause wing movement (Figure 13.38B).
      3) The wing is hinged on a pleural process that forms a fulcrum; all insects pull the tergum downward with indirect muscles causing the upstroke (Figure 13.38B).
      4) Dragonflies and cockroaches contract direct muscles to pull the wing downward.
      5) Bees, wasps and flies arch the tergum to cause the downstroke indirectly.
      6) Beetles and grasshoppers use a combination of direct and indirect muscles to move wings.
   h. **Flight Muscle Contraction**
      1) **Synchronous muscle** control uses a single volley of nerve impulses to stimulate a wing stroke.
      2) **Asynchronous muscles** stretch the antagonistic muscle and cause it to contract in response.
      3) Asynchronous muscles only need occasional nervous stimulation.
      4) Potential energy can be stored in resilient tissues.
      5) Wing beats may vary from a slow 4/second in butterflies to over 1000/second in midges.
   i. **Wing Thrust**
      1) Direct flight muscles also alter the angle of wings to twist the leading edge to provide thrust.
      2) This figure-8 movement moves the insect forward (Figure 13.38AC).
      3) Fast flight requires long, narrow wings and a strong tilt, as in dragonflies and horse flies.
      4) Monarch butterflies (*Danaus plexippus)* migrate from the northern United States and the southern provinces of Canada, at times exceeding 2100 miles to precise locations for overwintering in Mexico.

F. **Internal Form and Function**

1. **Nutrition**
   a. **Digestive System**
      1) Digestive system proper consists of a **foregut** (mouth with salivary glands, **esophagus, crop** for storage and **proventriculus** for grinding), **midgut** (stomach and gastric caeca), and **hindgut (intestine, rectum**, and **anus)** (Figure 13.39).
      2) The foregut and hindgut is lined with cuticle; absorption occurs in the midgut.

   b. **Feeding Strategies**
      1. Most insects feed on plant tissues or juices and are herbivorous or **phytophagous**.
      2. Many caterpillars are specialized to eat only certain species of plants (Figure 13.43A).
      3. Certain ants and termites cultivate fungus gardens for food.
      4. Many beetles and other insect larvae eat dead animals and are **saprophagous**.
      5. Some insects are **predaceous** on other insects or other animals.
      6. Many species are **parasitic** as adults and/or larvae (Figure 13.40).
      7. Lice are parasitic throughout their life cycle (Figures 13.41, 13.42).
      8. Many parasitic insects, in turn, have parasites, which is a condition called **hyperparasitism**.
      9. **Parasitoids** live inside a host until they eventually kill the host; they are important in pest control (Figure 13.43B).

   C. **Mouthparts** (Figures 13.44A,B,C,D)
      1) **Sucking mouthparts** form a tube to pierce tissues of animals or plants.
      2) Houseflies and blowflies have **sponging mouthparts;** the soft lobes at the tip absorb food.
      3) Mosquitoes **pierce** with needlelike stylets then suck food through a channel.
      4) The **biting** and **chewing mouthparts** of grasshoppers can seize and crush food.
      5) The honey bee labium forms a flexible tongue that moves back and forth when plunged into nectar.
      6) Butterflies and moths use a sucking proboscis to draw nectar from flowers.

2. **Circulation**
   a. A tubular heart in the **pericardial cavity** moves hemolymph forward through the dorsal aorta (see Figure 13.39).
   b. The heartbeat is a peristaltic wave.
   c. Accessory pulsatile organs help move the hemolymph into wings and legs.
   d. **Hemolymph** has plasma and amebocytes but does not function with oxygen transport.
   e. The tracheal system transports oxygen directly to each cell by tubes.

3. **Gas Exchange** (Figure 13.45)
   a. Terrestrial animals are faced with the dilemma of exchanging gases but preventing water loss.
   b. The **tracheal system** is a network of thin-walled tubes that branch throughout the insect body.
   c. **Spiracles** open to the tracheal trunks; there are two on the thorax and 7-8 on the abdomen.
   d. A valve on the spiracle often cuts down on water loss.
   e. **Tracheae** are composed of a single layer of cells lined with cuticle that is shed at each molt.
   f. Spiral thickenings of cuticle, called **taenidia**, prevent the tracheae from collapsing.
   g. The tracheae branch out into fluid-filled tubules called t**racheoles** that reach individual body cells.
   h. This system provides gas transport without use of oxygen-carrying pigments.
   i. Diving beetles use abdominal hairs to maintain a bubble under their wings—an “artificial gill.” (see Inset, page 262).
   j. Muscular movements may assist in moving air in and out of air sacs in larger insects.
   k. Very small insects transport all gases by simple diffusion.
   l. Aquatic insect nymphs may use **tracheal gills** or rectal gills for gas exchange.

4. **Excretion and Water Balance** (see Figure 13.39)
   a. Both insects and spiders utilize **Malpighian tubules** in conjunction with **rectal glands**.
   b. The main waste product is uric acid, water is conserved.
   c. Insects in dry environments absorb nearly all water from the rectum.
   d. Leaf-feeding insects excrete large quantities of water.
   e. Freshwater larvae excrete water and conserve salts.

5. **Nervous System**
   a. Insect nervous systems resemble that of larger crustaceans, with fusion of **ganglia** (see Figure 13.39).
   b. Some have a giant fiber system.
   c. A **visceral system** corresponds to the autonomic system of vertebrates.

   d. **Neurosecretory cells** in the brain have an endocrine function and control molting and metamorphosis.
6. **Sense Organs**
   a. Many insects have keen sensory perception.
   b. Most sense organs are microscopic and located in the body wall or on appendages.
   c. Different organs respond to mechanical, auditory, chemical, visual and other stimuli.
   d. **Photoreception**
      1) Insects have two types of eyes: **ocelli** and **compound**.
      2) Compound eyes may contain thousands of **ommatidia**.
      3) Ommatidia structure is similar to that of crustaceans.
      4) Visual acuity in insects is lower than human eye acuity.
      5) Flying insects have a higher flicker-fusion rate; they distinguish 200-300 flashes per second.
      6) Most insects have three ocelli on their head and dermal light receptors on their body
   e. **Mechanoreception**
      1) Touch, pressure, and vibration are picked up by sensilla or sensory cells in the epidermis.
      2) A sensillum may be a single hair-like seta or a complex organ.
   f. **Auditory Reception**
      1) Sensitive setae (hair sensilla) or tympanal organs may detect airborne sounds.
      2) Sensilla are cuticular modifications supplied with one more neurons.
      3) Tympanal organs occur in Orthoptera, Homoptera and Lepidoptera.
   g. **Chemoreception**
      1) Chemoreceptive sensilla are peglike or setae.
      2) They occur on mouthparts, antennae, and legs.
   i. **Other Senses**
      1) Insects are very sensitive to temperature, especially by cells in antennae and legs.
      2) Insects also detect humidity, proprioception, gravity and other physical properties.
7. **Reproduction**
   a. Sexes are separate in insects and fertilization is usually internal.
   b. **Parthenogenesis** is common in Homoptera and Hymenoptera.
   c. **Sexual Attraction**
      1) Female moths secrete a powerful **pheromone** to attract males from a great distance.
      2) Fireflies use flashes of light to detect mates.
      3) Some insects use sounds, color signals and other courtship behaviors.
   d. Many insects deposit sperm in the vagina during copulation.
   e. In some orders, spermatophores are transferred or deposited on substrate.
   f. During evolution from aquatic to terrestrial life, spermatophores were used first.
   g. The female may only mate once and store the sperm to fertilize eggs throughout her life.
   h. Females may lay a few eggs and provide care of young, or lay huge numbers.
      1) A queen honey bee may lay more than 1 million eggs during her life time.
      2) Some flies are ovoviviparous and bring forth one offspring at a time.
   i. Butterflies and moths must lay eggs on a specific host plant if the caterpillars are to survive
   k. Wasps may have to locate a specific larva in which her young will live as internal parasites. (Figure 13.46).

G. Metamorphosis and Growth

1. Various forms of **metamorphosis** produce degrees of change among different insect groups.
   a. Most insects change form after hatching from an egg.
   b. Each stage between molts is called an **instar**.
2. **Holometabolous Metamorphosis** (see Figure 13.47)
   a. About 88% of insects undergo this complete metamorphosis: **egg, larva, pupa, adult.**
   b. Metamorphosis separates the physiology of larval growth, pupa differentiation and adult reproduction.
   c. Larvae and adults often live in completely different environments and therefore do not compete.
   d. After several larval instars, the larva of a moth forms a **pupa,** sometimes within a silken cocoon,
   whereas a butterfly typically constructs a naked pupa called a **chrysalis**.
   e. Pupae often pass the winter in this stage; the final molt occurs and the adult emerges in spring.
   f. Stages are **egg-larva-pupa-adult.**
3. **Hemimetabolous Metamorphosis** (Figures 13.48; 13.49A,B, C)

a. Some insects undergo a **gradual metamorphosis**.
b. Grasshoppers, cicadas, mantids, true bugs, mayflies and dragonflies exhibit this metamorphosis.
c. Young are called **nymphs**.
d. Bud-like growths in early instars show where the adult wings will eventually develop.
e. Stages are **egg-nymph-adult.**

4. **Direct Development**
   a. Silverfish and springtails have young similar to adults except in size and sexual maturation.
   b. Stages **are egg-juveniles-adult.**
   c. These are primitively wingless insects.
5. **Physiology of Metamorphosis (in Instructor's Guide only; no text counterpart)**
   a. **Hormones** regulate insect metamorphosis.
   b. The brain and nerve cord ganglia produce **brain hormone** or **ecdysiotropin.**
   c. The prothoracic gland produces molting hormone or **ecdysone** in response.
   d. Ecdysone starts the molting process
   e. The corpora allata produces juvenile hormone.
   f. **Molting continues as long as juvenile hormone (neotenine) is sufficiently present.**
   g. In later instars, the corpora allata release less and less juvenile hormone.
   h. When juvenile hormone reaches a low level, the larva molts to become a pupa.
   i. Cessation of juvenile hormone production in the pupa leads to an adult at the last molt.
   j. In hemimetabolous insects, cessation of juvenile hormone occurs in the last nymphal instar.
   k. In adults, the corpora allata becomes active again in normal egg production.
   l. The prothoracic glands degenerate in adult insects and adults do not molt.

H. Diapause (Figure 13.50)
1. Any stage (eggs, larvae, pupae or adults) may remain dormant to survive adverse conditions.
2. This allows them to synchronize with the environment.
3. Diapause is genetically determined but it may be triggered by environmental cues such as day length.
4. Diapause always occurs at the end of an active growth stage; the insect is then ready for another molt.

J. Behavior and Communication
1. Due to very sensitive perception, insects respond to many environmental stimuli.
2. Responses are governed by both the physiological state of the animal and its nerve pathways.
3. A moth attracted to a light or carrion flies attracted to the odor of dead flesh are simple responses.
4. Many insect behaviors are complex sequences of responses (Figure 13.51).
   a. A Dung beetle chews off a piece of dung and rolls it into a ball.
   b. The beetle next rolls the ball to a burial site after laying eggs in it.
   c. A potter wasps scoops up clay pellets and carries them to her building site.
   d. The pellets are fashioned into clay pots and provisioned with caterpillars.
   e. Eggs are laid in the clay pots with well-stocked food.
5. Most insect behavior is innate but some involves simple learning.
   a. A potter wasp must learn where she left her pots to fill them with caterpillars.
   b. Social insects are capable of basic learning.
   c. Insects are not capable of insight learning (the ability to solve a new problem).
6. **Chemical Signals: Pheromones**
   a. These chemicals are secreted by one individual to affect the behavior of another individual.
   b. Pheromones attract the opposite sex, signal alarm, fend off aggression, and mark trails.
   c. Bees, wasps and ants can recognize nestmates and signal an alarm if strangers enter the nest.
7. **Sound Production and Reception**
   a. Sounds are used as warning devices, advertisement of territory, and courtship songs.
   b. Crickets chirp for courtship and aggression.
   c. The male cicada vibrates paired membranes on its abdomen to attract females.
8. **Tactile and Visual Communication**
   a. Tactile communication involves tapping, stroking, grasping and antennae touching.
   b. Some beetles, flies and springtails use **bioluminescence** as visual signals or mate attractors.
   c. Some female fireflies mimic another species' flash pattern and attract males and then eat them (Figure 13.52).
9. **Social Behavior**
   a. Some social communities are temporary and uncoordinated (Figure 13.53).
   b. Other social groups are **highly organized** and depend on chemical and tactile communication.
   c. Honeybees, ants, and termites have complex societies with division of labor.

d. Parents remain with young and share duties in a cooperative manner.
e. **Caste differentiation** is common in the most organized social groups.
f. **Honeybees**
1) Honeybees have a few male **drones**, a fertile female **queen,** and many **sterile female workers** (Figure 13.54).
2) Workers care for young, secrete wax for honeycomb cells, gather pollen, and guard the hive.
3) One or more drones fertilize the queen during the mating flight.
4) Males come from unfertilized eggs; fertilized eggs produce queens and workers in this haplodiploid system.
5) Castes are determined by what is fed to larvae.
6) The development of a fertile queen occurs because she is fed **royal jelly**.
7) A queen secretes "**queen substance**" to prevent workers from maturing.
8) A honeybee hive of 60,000-70,000 individuals continues indefinitely.
9) Honeybees have a communication system; scouts can inform workers on the location of food.

g. **Termites** (Figure 13.55A,B).
1) A fertile **king** and **queen** fly away to start a new colony; they mate and lose their wings.
2) Sterile members are wingless and become **workers** and **soldiers**.
3) **Soldiers** have large heads and defend the colony.
4) Reproductive individuals secrete inhibiting pheromones that produce sterile workers.
5) Nymphs feed from each other in **trophallaxis**, thus spreading the pheromone about.
6) Worker castes also produce worker and soldier substances; drops in these pheromone levels result in more of the needed caste developing in the next generation.

h. **Ants**
1) Ants differ from termites; ants are darker, hard-bodied and have a thread-like waist.
2) In ant colonies, the male ant dies after mating.
3) Ants have wingless soldiers and workers that gather food, care for the young, and protect the colony.
4) Ants have also evolved slavery, fungus farming, sewing nests together, tool use, and Herding.
5) Weaver ants sew their nests together with silk.

12.15 Insects and Human Welfare

A. Beneficial Insects
1. Insects produce honey, beeswax, silk and shellac.
2. Of more economic importance, bees pollinate **$10 billion** worth of food crops in the U.S. annually.
3. Pollinating insects and flowering plants are tightly co-evolved.
4. Predaceous and parasitoid insects are vital in controlling many pest insect populations (Figure 13.57A,B, C).
5. Dead animals are rapidly consumed by fly maggots.
6. Insects are critical components of most **food chains** and a central food for many fish and birds.

B. Harmful Insects (Figure 13.58A,B, C)
1. Harmful insects eat and destroy our plants and fruits.
2. Nearly every cultivated crop has several insect pests; this requires substantial money for insect control.
3. Bark beetles, spruce budworms, the gypsy moth and others are serious forest pests.
4. Insects also destroy food, clothing and property.
5. **Medically important insects** include vectors for disease agents.
   a. Warble and bot flies attack humans and domestic livestock.
   b. **Malaria** is carried by *Anopheles* mosquitoes and is the most common major world disease (Figure 13.59).
   c. **Yellow fever** and lymphatic filariasis are also mosquito-borne.
   d. Fleas carry **plague**, a disease that changed human history in the Middle Ages.
   e. Lice carry **typhus fever**.
   f. The tsetse fly carries **African sleeping sickness.**
   g. The common house fly carrier of >100 pathogens (Figure 13.37).

C. Control of Insects
1. Broad-spectrum insecticides damage beneficial insect populations along with the targeted pest.
2. Some chemical pesticides persist in the environment and accumulate as the move up the food chain.

3. Some strains of insects have evolved a **resistance** to common insecticides.
4. **Biological control** is the use of natural agents, including diseases, to suppress an insect population.
5. ***Bacillus thuringiensis*** is a bacterium that controls lepidopteran pests; the gene coding for the "B.t." toxin
   has been introduced to other bacteria and transferred to crop plants themselves.
6. Some natural predators or parasites of insect pests can be raised and released to control the pest.
7. Release of sterile males can eradicate the few insect species that only mate once.
8. Pheromones can monitor pests and hormones may have a role in disrupting their life cycle.
9. **Integrated pest management** is the combined use of all possible, practical techniques listed above, to reduce the reliance on chemical insecticides.

D. Classification of Subphylum Hexapoda

Class Entognatha

Order Protura
Order Diplura
Order Collembola

Class Insecta

Order Thysanura (Figure 12.60)
Order Ephemeroptera (Figure 12.61)
Order Odonata
Order Orthoptera
Order Isoptera
Order Mallophaga
Order Anoplura
Order Hemiptera
Order Homoptera (Figure 12.62)
Order Neuroptera (Figure 12.63)
Order Coleoptera
Order Lepidoptera
Order Diptera
Order Trichoptera
Order Siphonaptera
Order Hymenoptera

E. **Phylum Arthropoda**

Subphylum Trilobita

Subphylum Chelicerata

Class Merostomata
Class Arachnida

Subphylum Crustacea

Class Malacostraca
Class Branchiopoda
Class Maxillopoda
Class Pycnogonida

Subphylum Myriapoda

Class Chilopoda
Class Diplopoda
Class Pauropoda
Class Symphyla

Subphylum Hexapoda

Class Insecta
Class Entognatha

12.16 Phylogeny and Adaptive Radiation (Figure 12.64)

A. **Phylogeny**

1. Whether Arthropoda is monophyletic or polyphyletic is also controversial.
2. **"Arthropodization"** is a crucial development.
   a. The hardening of the cuticle led to most arthropod features.
3. Molecular data indicates Hexapoda and Myriapoda are considered subphyla.
4. Crustaceans were traditionally allied with insects and myriapods in the Mandibulata.
   a. Critics argue mandibles are so different in these groups they could not have been inherited from a common ancestor.
   b. Advocates of the "mandibulate hypothesis" believe in a common ancestral mandible.
5. Crustaceans and insects share ommatidia and heads composed of five segments with appendages.
6. Crustaceans and hexapods may or may not be sister groups.
7. Pancrustacea includes crustaceans and hexapods.
8. Phylogenetic placement of the subplylum Myriapoda is also controversial.
   a. This text portrays polytomy (figure 12.64).
9. **Evolution of hexapods** (Figure 12.65):

a. Three postcephalic somites become thoracic segments.
b. Reduction of appendages was another evolutionary trend.
c. Diplura, Collembola and Protura are endognathous, with mouthparts in deep pouches.
d. Thysanura are ectognathous, with mandibles and maxillae external.
e. Wings unite the remaining ectognathous orders.
f. Metamorphosis also distinguished insects by the Permian period.
    1) Hemimetabolous metamorphosis, chewing mouthparts and cerci group the Orthoptera, Dermaptera, Isoptera and Embioptera.
    2) Hemimetabolous metamorphosis and sucking mouthparts group the Thysanoptera, Hemiptera, Homoptera and perhaps the Psocoptera, Zoraptera, Mallophaga and Anoplura.
    3) Other orders have holometabolous metamorphosis and are the most specialized.

10. Classically, annelids and arthropods originated from a line of **coelomate segmented protostomes**.
    a. Divergence led to a protoannelid line with laterally located parapodia.
    b. One or more protoarthropod lines had ventrally located appendages.
    c. However, molecular evidence aligns annelids and arthropods with separate superphyla.
    d. Recognition of **Ecdysozoa** and **Lophotrochozoa** would mean that metamerism arose independently.
11. **Tardigrada** may be sister taxa to arthropods.
12. Phylogeny of Chelicerata is also controversial, especially relationships of Pycnogonida

B. Adaptive Radiation

1. In contrast to annelids, arthropods have pronounced **tagmatization** by fusion of somites.
2. Modification of exoskeleton and appendages allowed variation in feeding and movement.