Chapter 20
Terrestrial Mandibulates

I. Diversity & Characteristics

A. Uniramia

- controversial taxon including the millipedes, centipedes, & insects
- Uniramians are primarily terrestrial with a few freshwater

B. Characteristics

- Myriapods include centipedes, millipedes, pauropods, & symphylans
- insects have reduced their body tagmata to head, thorax, & abdomen
    a. abdominal appendages greatly reduced or absent
    b. common ancestor of insects probably resembled the myriapod body form
- uniramia only have **one pair of antenna** & appendages are always **uniramous**
- gills in aquatic larvae are not homologous w/ crustacean gills
- tracheae distribute respiratory gases, similar to annelids
- excretion usually involves **Malpighian tubules**

II. Subphylum Uniramia
Class Chilopoda

A. Characteristics

- Centipedes are terrestrial
- flattened bodies with up to 177 somites
- each somite, except 1st behind head & last two, bear a pair of jointed legs
- appendages of 1st body segment form **poison claws**
- head has one pair of antennae, pair of mandibles, & one/two pairs of maxillae
- eyes on either side of head consist of groups of **ocelli**
- salivary glands empty into anterior end of straight digestive tract
- two pairs of Malpighian tubules empty into the hind intestine
- elongated heart has pair of arteries in each somite; ostia provide return flow of hemolymph
- pair of spiracles in each somite allows air to diffuse through branched air tubes of the tracheae
- nervous system includes a portion that serves as a visceral nervous system

B. Reproduction

- sexes separate w/ unpaired gonads & paired ducts
- some lay eggs; others are viviparous
- young resemble adults

C. Natural History

- found under logs, bark, & stones
- carnivorous, eat earthworms, cockroaches, & other insects
- house centipede has 15 pairs of long legs & common in bathrooms & damp cellars
- most are harmless to humans, but few large, tropical species of dangerous

III. Subphylum Uniramia
Class Diplopoda

A. Characteristics

- millipedes have **two pairs of legs** per somite, probably fusion of two segments
- cylindrical bodies have from 25 to 100 somites
- head has 2 clusters of simple eyes & pair of each antennae, mandibles & maxillae
- each abdominal somite has two pairs of spiracles opening into air chambers & tracheal air tubes

B. Reproduction

- 7^{th} somite specialized for copulatory organ
- female lays eggs in nest & guards them
- larvae have only one pair of legs to each somite

C. Natural History

- less active than centipedes; walk gracefully rather than wriggling
- most eat decayed plants, few eat living plant tissue
- most are slow moving & roll into coil for defense
- some secrete toxic or repellant fluids from special **repugnatorial glands** on side of body

IV. Subphylum Uniramia
Class Insecta

A. Diversity

- most diverse & abundant of all arthropods
- number of known species estimated over one million
- continued evolution among modern insects; fossil records indicates they are a stable group
- play major medical & economic roles w/ humans; critical to animal ecology

B. Characteristics

- **three pair of legs** & often **two pair of wings** on thorax
- insects range from less than 1mm to 20cm in length; larger insects are tropical

C. Distribution

- found in nearly all habitats except the sea
- common in freshwater, brackish, & salt marshes
- abundant in soils, forest canopy, deserts, & wastelands
- most animals & plants have insects as parasites externally & internally
- adaptive traits:
    a. flight & small size makes insects widely distributed
    b. well-protected eggs withstand rigorous conditions & are readily dispersed
    c. wide variety of structural & behavioral adaptations gains them access to every possible niche

D. Adaptability

- most structural modifications are in wings, legs, antennae, mouthparts, & alimentary canal
- specialization for eating only one part of a host plant allows many insect species to coexist on one plant
- hard & protective exoskeleton well adapted to life in desert regions
- exoskeleton holds in water; along w/ metabolism that saves water also good in desert
- exoskeleton made of complex plates (sclerites) connected by hinge joints
    a. muscles attaching sclerites allow precise movement
    b. rigidity due to scleroproteins & not mineral matter; lightness allows flight

E. External Form & Function

- more homogenous tagmatization than variable crustaceans
- cuticle composed of a dorsal notum, ventral sternum, & pair a lateral pleura
- Head
    a. usually pair of large compound eyes
    b. one pair of antennae vary greatly in form (feel, taste, & hear)
    c. mouthparts consist of a labrum, pair of mandibles & maxillae, a labium & a hypopharynx

- Thorax
    a. consists of prothorax, mesothorax, metathorax; each has a pair of legs

    b. Wings
        1. if present, 2 pairs on meso & metathorax
        2. wings consist of double membrane
        3. veins serve to strengthen wing; pattern used to identify insect taxa

    c. Legs
        1. walking legs end in terminal pads & claws
        2. hindlegs of grasshoppers & crickets enlarged for jumping
        3. mole crickets front legs adapted for burrowing
        4. forelegs praying mantis allow it to grasp prey
        5. honeybees have leg adaptations for pollen collection
- Abdomen
    a. insect abdomen has from 9 to 11 segments; last reduced to a pair of cerci
    b. larval & nymphal forms may have abdominal appendages lacking in adults
    c. external genitalia are usually at end of abdomen

- Variations in Body Form
    a. land beetles are thick & shielded
    b. aquatic beetles are streamlined
    c. cockroaches are flat & live in crevices
    d. antennae vary widely from long to short; plumed to knobbed

- Walking
    a. insects walk using 1st & last leg on one side & middle leg on opposite side in alternation w/ reverse; provides stability
    b. water striders have non-wetting footpads that don't break the surface water tension

- Power of Flight
    a. wings are not homologous w/ other flyers
    b. wings are outgrowths of cuticle from mesothorax & metathorax segments
    c. most flying insects have 2 pairs of wings; Diptera (flies) have one pair
    d. halteres are reduced wings that provide the fly w/ balance during flight
    e. modification of wings
        - direct flight muscles attach to wing directly
        - indirect alter the shape of thorax to cause wing movement
        - wing hinged on pleural process that forms fulcrum, all insects cause the upstroke w/ indirect muscles that pull the tergum downward
        - dragonflies & cockroaches contract direct muscles to pull the wing downward
        - bees, wasps, flies arch the tergum to cause the downstoke indirectly
        - beetles & grasshoppers use a combo of direct & indirect muscles to move wings

f. flight muscle contraction
- synchronous muscle control uses a single volley of nerve impulses to stimulate stroke
- asynchronous muscles stretch antagonistic muscle & cause it to contract in response
- asynchronous muscles only need occasional nervous stimulation
- wing beats may vary from a slow 4/sec in butterflies to over 1000/sec in midges

g. wing thrust
- direct flight muscles alter angle wings to twist leading edge provide thrust
- figure 8 movement moves insect forward
- fast flight requires long, narrow wings & strong tilt (dragonflies & horse flies)

F. Internal Form & Function

1. Nutrition

a. Digestive System
- foregut consists of mouth w/ salivary glands, esophagus, crop, gizzard
- digestion occurs in crop as salivary enzymes mix w/ food (no absorption)
- gizzard grinds food before entering midgut
- midgut main site for digestion & absorption
- ceca increases digestive & absorptive area
- hindgut primary site for water reabsorption

- many are specialists:
  - plant tissues or juices (herbivores)
  - partition plant parts between larvae & adults
  - cultivate fungus gardens
  - saprophagus eat dead matter
  - parasitic (specialized mouth parts - sucking)

2. Circulation
- tubular heart in pericardial cavity moves hemolymph foreword through dorsal aorta
- heartbeat is a peristaltic wave
- accessory pulsatile organs help move hemolymph into wings & legs
- hemolymph has plasma & amebocytes (don't carry O_2)

3. Gas Exchange
- terrestrial living dilemma (exchange gases but prevent water loss)
- **tracheal system**, network of thin-walled tubes that branch throughout the body
- **spiracles** open to tracheal trunks, 2 on thorax, 7-8 on abdomen
- valve on spiracle cuts down water loss
- tracheae composed of a single layer of cells lined w/ cuticle that is shed at each molt
- **taenidia** (thickenings of cuticle) prevent tracheae from collapsing
- tracheae branch out into fluid-filled tubules = **tracheoles**
- tracheoles reach individual body cells; providing gases w/out the need for O_2-carrying pigments
- muscular movements assist in moving air in/out
- air sacs in insects are dilated tracheae w/out taenidia

- variations:
    diving insects (beetles) use abdominal hairs to capture air bubbles & store under wings
        "artificial gill"

    mosquito larva use short breathing tubes to snorkel air

    very small insects use simple diffusion

    aquatic nymphs use tracheal gills or rectal gills

4. Excretion & Water Balance
- utilize Malpighian tubules in conjunction w/ rectal glands (like spiders)
- malpighian tubules vary in #, join between midgut & hindgut
- blind ends of tubules float free in hemocoel bathed in hemolymph
- main waste product is **Uric Acid**

5. Nervous System
- resembles that of larger crustaceans, w/ fusion of ganglia (Fig. 20-13)
- some have a giant fiber system
- neurosecretory cells in brain function in controlling molt & metamorphosis

6. Sense Organs
- Many have keen sensory perception
- most sense organs microscopic, located in body wall
- different organs respond to different stimuli:

a. Mechanoreception
- touch, pressure, vibration picked up by **sensilla**
- sensillum may be single hair-like seta or complex
- distributed widely over antennae, legs, body

b. Auditory Reception
- sensitive **setae** (hair sensilla) or **tympanal organs** detect airborne sounds
- tympanal organs occur in Orthoptera, Homoptera, Lepidoptera
- organs in legs detect vibrations in substrate

c. Chemoreception
- bundles of sensory cell processes located in sensory pits
- occur in mouthparts, antennae, legs
- some insects detect odors several km away
- feeding, mating, habitat selection are mediated through chemical senses

d. Visual Reception
- Insects have 2 types of eyes: simple & compound
- **Ocelli** monitor light intensity but don't form images
- compound eyes contain thousands of **ommatidia** similar to crustaceans
- insects can see simultaneously in almost every direction; image is myopic & fuzzy
- have a higher flicker-fusion rate; distinguish 200-300 flashes per second
- bees can distinguish ultraviolet light, but cannot detect shades of red

7. Reproduction
- sexes separate; fertilization usually internal
- parthenogenesis common in Homoptera & Hymenoptera
- sexual attraction:
    female moths secrete powerful pheromones over great distances
    fireflies use flashes on light to detect mates

    some use sounds, color signals, & other courtship behaviors

- deposit sperm into female vagina or use spermatophores
- many females mate only once, store sperm to fertilize eggs throughout her life
- number of eggs laid varies greatly

G. Metamorphosis & Growth

1. Various forms of metamorphosis produce degrees of change among different groups
   - most insects change form after hatching form egg
   - each stage between molts is called an **instar**
   - wings develop during last stage where they are useful in reproduction
   - hormones regulate insect metamorphosis

2. **Holometabolous** Metamorphosis
   - 88% of insects undergo this type
   - stages: **egg-larva-pupa-adult**
   - larvae & adults live separate lives & don't compete

3. **Hemimetabolous** Metamorphosis
   - gradual metamorphosis seen in grasshoppers, cicadas, mantids, true bugs, mayflies, & dragonflies
   - young called nymphs; wings appear as buds in early instars
   - stages: **egg-nymph-adult**

H. Diapause

- period of dormancy in annual life cycle, independent of conditions
- winter dormancy called **hibernation**; summer dormancy called **estivation**
- any stage may remain dormant to survive adverse conditions
- allows them to synchronize w/ environment
- genetically determined but may be triggered by environmental cues (day length, temp)
- Diapause always occurs at end of an active growth stage; insect is then ready for a molt

I. Behavior, Communication, & Defense

- Behaviors range from simple to complex, most innate but some involve simple learning

a. Pheromones

- chemicals secreted by one individual to affect behavior of another
- attract opposite sex, trigger aggression, fend off aggression & mark trails
- recognition of nestmates (bees, wasps) or signal alarm if strangers enter
- used to trap insects in monitoring populations

b. Sound Production & Reception

- sounds used as warning devices, advertisement of territory, & courtship songs
- crickets chirp for courtship & aggression
- male cicada vibrate paired membranes on abdomen

c. Tactile Communication
- involved tapping, stroking, grasping & antennae touching
- bioluminescence (beetles, flies, springtails)
- female fireflies mimic other species flash patterns, lure males in and eat them

d. Social Behavior
- temporary & uncoordinated to highly organized
- many use chemical & tactile communication to organize
- caste differentiation common in most

1. Honeybees:
- Male drones (haploid)
- Sterile Female workers (diploid)
- Fertile Female Queen

Queen secretes "queen substance" to prevent workers from maturing or feeding larvae "royal jelly"

Hives of 60,000-70,000 individuals continue Indefinitely

Communicate: scouts inform workers of food location using several dances

2. Ants:
- Fertile male mates then dies & Queen starts new colony
- Sterile wingless workers & soldiers
- Some species evolved slavery, fungus farming, tool use & herding

III. Phylogeny & Classification

A. Fossil Record

1. 1st terrestrial arthropods were scorpions & millipedes that appeared in the Silurian period
2. 1st insects were wingless & appeared in Devonian
3. Several orders of winged insects evolved in the Carboniferous period

B. Possible Phylogenies

1. Some researchers believe Myriapoda paraphyletic Diplopoda/Pauropoda may be sister groups
2. Molecular data suggests insects & myriapods are remotely related & insects arose within the Crustaceans

C. Classification of Classes:

Order Protura
Order Diplura
Order Collembola
Order Thysanura
Order Ephemeroptera
Order Odonata
Order Orthoptera
Order Dermaptera
Order Plecoptera
Order Isoptera
Order Embioptera
Order Psocoptera
Order Zoraptera
Order Mallophaga
Order Anoplura
Order Hemiptera
Order Homoptera
Order Neuroptera
Order Coleoptera
Order Stepsiptera
Order Mecoptera
Order Lepidoptera
Order Diptera
Order Trichoptera
Order Siphonaptera
Order Hymenoptera
Order Thysanoptera