Nutrition, Digestion, Excretion

- Nutritional Ecology
  - Essential nutrients
- The Digestive System
- The Excretory System

What nutrients are essential for insects?

- Water
- Energy
- Essential amino acids
- Essential lipids
- Vitamins & growth factors
- Minerals

Water

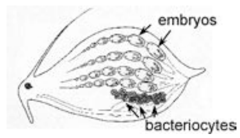
- This is the ultimate challenge for many terrestrial insects.
  - Drinking or moisture in food.
  - Oxidative metabolism.
  - Absorption of water vapor.

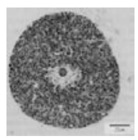
Energy

- Oxidation of carbohydrates, fats, organic acids, suitable amino acids.
- Each are variably available to different types of insects.
- Requirements can be quite high: Certain insect flight muscles convert more energy per unit weight than any other animal tissue.

Essential Amino Acids

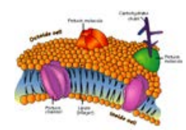
- Insects need at least the same 10 amino acids in their diet as we do.
  - Predators have little problem with this.
  - Phytophagous insects more of a problem.
  - Particularly sap-suckers.





Essential Lipids

- Insects are unable to synthesize polyunsaturated fatty acids
  - Involved in formation of phospholipids of cell membranes.
- Also **sterols** (unlike mammals).
  - Required for many hormones.
  - Derived from cholesterols (animal food) or β-sitosterol (plant food)



Vitamins and Growth factors

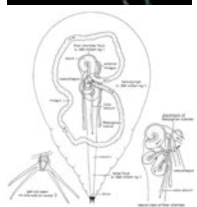
- Vitamin Bs particularly important.
- Vertebrate blood is particularly low in these (which insects care?)
- How do they get it?

Minerals

- Requirements essentially the same across animal kingdom (e.g. we cannot synthesize them).

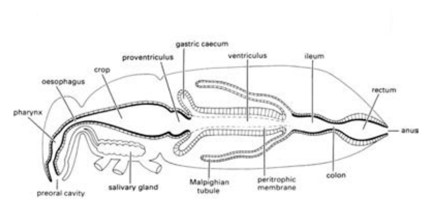
The Insect Gut

- The insect's digestive system & excretory system will reflect the diet in much the same way that mouthparts do.



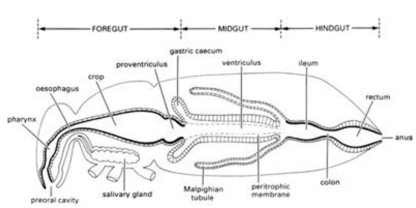
Gross Gut Morphology

- Foregut: Processing and storage of food.
- Midgut: Digestion and absorption of food.
- Hindgut: Absorption of water, salts, elimination of wastes.



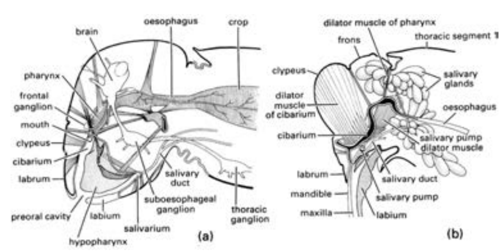
Gross Gut Morphology

- Note that the foregut and the hindgut are lined with cuticle (derived from ectoderm).
- **Midgut** is not, instead lined with **peritrophic membrane** (derived from endoderm).



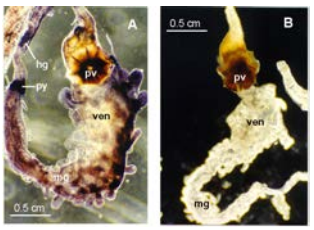
Foregut

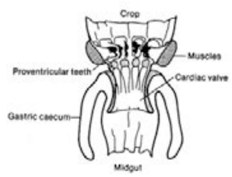
- Mouth and oral cavity: consumption of food.
  - Ventral glandular salivarium
  - Dorsal muscular cibarium



Foregut

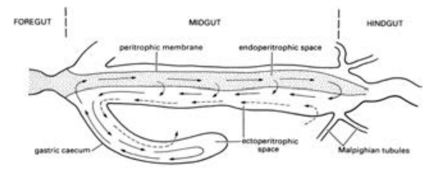
- Mechanical processing of food in pharynx and proventriculus (gizzard).
- Storage in crop.





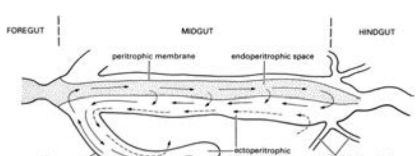
Midgut

- Most digestion of food occurs here.
- Two main areas:
  - **Gastric caeca** often house endosymbionts.
  - **Ventriculus** where most digestion occurs.



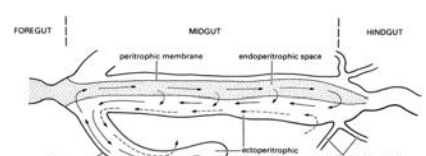
Peritrophic membrane

- Secreted by microvillate columnar epithelial cells.
- Made up of an amorphous sheet of polysaccharide, chitin, glycoprotein, and protein.
- Tubular film that surrounds the bolus and within which considerable digestion occurs.
- **Why would insects do this?**



Peritrophic membrane

- Protects against abrasion (re: no chitin).
- Serves as mucus (e.g. polysaccharides).
- Forms a barrier against **diseases**, plant **secondary metabolites** (e.g. tannins).
- Lined with pores that are selectively permeable: control movement of food out and enzymes in.



Peritrophic membrane

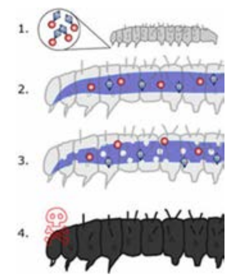
- Numerous insect pathogens center activity on peritrophic membrane.
- Including **Bt**: genetically derived insecticide from *Bacillus thuringiensis.*

A 12-day-old cotton bollworm larva raised on a diet containing Bt proteins. Source: USDA

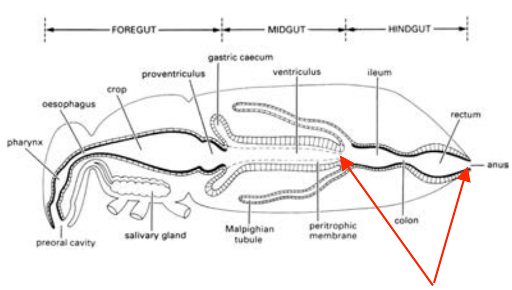
A 12-day-old cotton bollworm larva raised on a diet with no Bt. Source: USDA

Peritrophic membrane

1. Insect eats *Bt* crystals and spores. Enzymes are activated by proteolytic enzymes in the insect gut.
2. The toxin binds to specific receptors in the gut and the insects stops eating.
3. The crystals cause pores to open in the peritrophic membrane, allowing spores and normal gut bacteria to enter the body.
4. The insect dies as spores and gut bacteria proliferate in the body.



Hindgut & Malpighian Tubules: Water conservation and excretion.

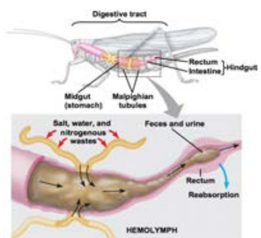


Hindgut & Malpighian Tubules: Water conservation and excretion.

- Intimately involved in **osmoregulation** and elimination of wastes (especially nitrogenous).
- Re: insects have open circulatory system, therefore, no kidney or nephridia.
- Aquatic insects also have chloride cells to actively pump in ions.

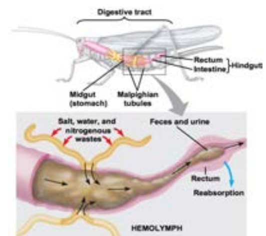
Malphigian Tubules

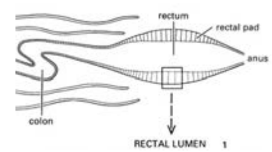
- Outgrowth of hindgut, ectodermal in origin.
- Dead end tips open into hemolymph
- Transport epithelium secretes nitrogenous wastes and solutes **into** tubules: the **filtrate**.
- Water follows, how?
- These are delivered to the hindgut.



The Hindgut

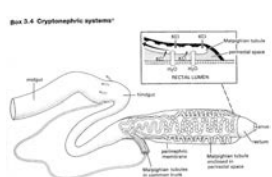
- Parts of rectal epithelium are thickened to form **rectal pads**.
- These are specialized for absorption of water from feces before defecation.
- Active transport of ions across these cells sets up osmotic gradient, water is reabsorbed.
- How are nitrogenous wastes excreted?





Cryptonephridia

- Some desert insects have intimate association between Malpighian tubules and hindgut.
- Bounded by **perinephric** membrane.
- Allows extreme conservation of water, including absorption of water from humid air in the rectum.



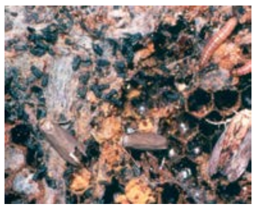
Some unusual diets…

- Insects can digest some abundant, yet resistant compounds.
- Some moths and beetles can feed on keratin.
  - Requires enzyme, low oxygen environment to reduce sulfur bonds, and reducing agent.

Clothes moths (Tineidae) are also known to scavenge horn, hooves, and even tortoise shells.

Some unusual diets…

- Beeswax is ordinarily resistant to digestion.
- But wax moths can eat it: have a highly **basic** gut.



Wax moths (Pyralidae) are considered a pest by beekeepers

Some unusual diets…

- Wood regularly consumed by some wood-boring beetles, termites, wood-feeding roaches, and silverfish.
  - Some endogenous production of cellulases (wood-roaches, termites).
  - Most endosymbiotic interactions with bacteria or fungi.
  - Some exogenous consumption of fungi to obtain cellulases.

Termites and wood-roaches are the only insects known to convincingly produce their own cellulolytic enzymes

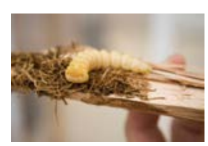
Asian longhorn beetle house an endosymbiotic fungus that produces cellulolytic enzymes

Bark Beetle Infestations

Some unusual diets…

- Wood regularly consumed by some wood-boring beetles, termites, wood-feeding roaches, and silverfish.
- Some endogenous production of cellulases (wood-roaches, termites).
- Most endosymbiotic interactions with bacteria or fungi.
- Some exogenous consumption of fungi to obtain cellulases.
- Some only consume rare starch, sugar, or whole cell walls in wood tissue, not lignin itself.

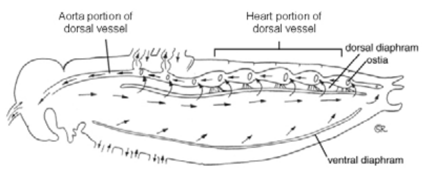
Termites and wood-roaches are the only insects known to convincingly produce their own cellulolytic enzymes



Asian longhorn beetle house an endosymbiotic fungus that produces cellulolytic enzymes

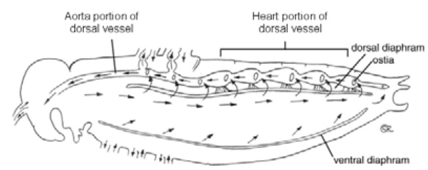
The Insect Circulatory System

- Insects have an "open" circulatory system.
  - The **hemocoel** (body cavity) is filled with **hemolymph** (blood) that bathes the organs.
- Does this mean that blood does not circulate?



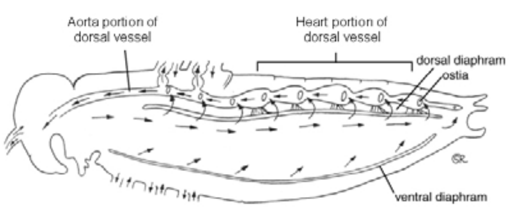
Insect Circulatory Organs

- Multichambered 'heart' = dorsal blood vessel
  - Chambers vary across lineages: cockroaches have 13, house flies have 3.
  - Each chamber has a pair of **ostia**: inlet valves that draw hemolymph into the heart.



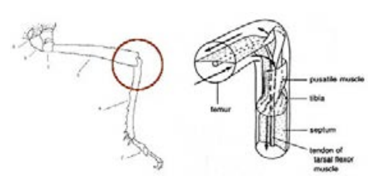
Insect Circulatory Organs

- <u>**Dorsal diaphragm**</u> is a horizontal membrane in the abdomen that separates hemocoel into two regions
  - Above is the pericardial sinus: hemolymph enters the heart.
  - Blood pumped anteriorly via peristaltic action to the head.
  - Below is abdominal hemocoel, blood flows posteriorly there.



Insect Circulatory Organs

- The leg muscles need to eat, too.
- Are divided by a septum.
- Insects have local **pulsatile** organs at the bases of appendages that pump hemolymph.



Hemolymph

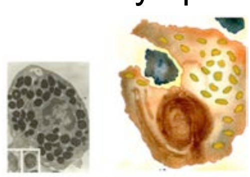
- Largely a colorless liquid that bathes tissues
  - (separated from cells by basement membrane; what purpose does this serve?)
  - Makes up 15-30% of total body weight and 15-70% of total body volume.
- More than nine cell types, all **nucleate**: **hemocytes**
- Function of many still unknown.
- Most common are **plasmatocytes**: phagocytic on bacteria and other foreign microorganisms.

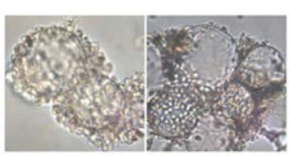
Functions of the hemolymph

- Transport of nutrients, wastes, hormones.
- Water storage
- Lubrication of internal organs
- Heat exchange
- Hydraulics

Functions of the hemolymph

- Immune reaction
- Phagocytosis
  - Plasmatocytes phagocytose bacteria, other foreign particles.
- Immunity proteins
  - Still poorly understood
- Encapsulation
  - Lamellocytes encase parasitic wasp eggs that bind to the surface of cells and cannot be phagocytosed



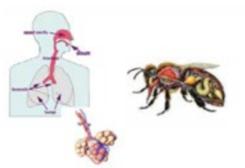


Functions of the hemolymph

- Clots and wound repair.
  - Less risk of bleeding because of weak blood pressure.
  - Coagulocytes and prohemocytes seal wound.

The insect respiratory system

- How do insects get oxygen to tissues?
- Hemolymph does not bind oxygen (with some exceptions).
- Respiration is via direct ventilation of tissues via **tracheal system**.



Spiracles

- External openings
- Hypothetically one per segment;
- Normally occur on meso-, metathorax, and abdominal segments 1-8 (none in head, prothorax or genital segments)

Spiracles

- Have a chamber or pit = **atrium**.
- Protected by **valve** which can be opened or closed.
- What do these do?
- These lead to tracheae

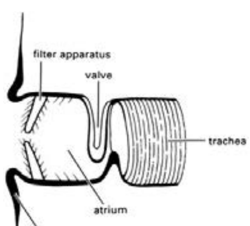
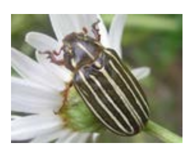


Figure 3.10a from book

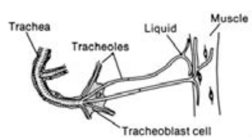
Trachea

- Series of air-filled tubes; unique to insects
- Entirely separate from the circulatory system.
- Lined with cuticle
- Extensively branched
  - 39% of body volume of the June beetle
- **Taenidia**: spiral cuticular thickening running through trachea
  - Prevent tubes from collapsing under reduced pressure.



Tracheoles

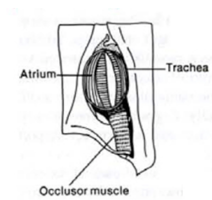
- **Tracheoles**: smallest diameter tubes.
  - <1 micron in diameter
  - No cell in an insect is more than 1 cell away from a tracheole.
  - In flight muscles where O_2 consumption is high, tracheoles extend *between* muscle fibers.
  - Tips of tracheoles are fluid-filled at rest, but air-filled during activity (for maximum gas diffusion)
  - In the 5th instar silkworm, each spiracle gives rise to 103,000 tracheoles (~1.5 million altogether).



Ventilation in Insects

Two types: passive and active

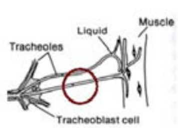
- Occlusor muscle influenced by CO_2 level
- Spiracle opens and air comes in.
- Air passes through atrium.

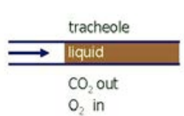


Ventilation in Insects

Two types: passive and active

- Air passes trachea, reaches tracheoles.
- Air exchange in tracheole.
- Muscle takes O_2.





Ventilation in Insects

Two types: passive and active

- Only type of ventilation in smaller insects.
- Based on simple diffusion, not active pumping.
- Continuous O_2 uptake and CO_2 storage causes 'suction'.
- CO_2 is expelled in cyclical bursts--every 20 min. in termites, every 6 hr in moth pupae.
- In between CO_2 is stored in the hemolymph as bicarbonate.
- This creates negative pressure and air is sucked into the trachea.
- When CO_2 concentration in the trachea >6.5%, spiracles relax and CO_2 is expelled.

Ventilation in Insects

Two types: passive and <u>active</u>

- Large insects must physically move air in and out of the tracheal system.
- Close forward spiracles and force air out of rear ones via blood pressure, muscle contraction.
- Creates negative pressure (vacuum) up front when rear spiracles closed.

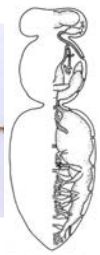


Figure 3.11b from Book

Ventilation in Insects

Two types: passive and <u>active</u>

- <u>Tracheal air sacs</u> (flying insects) can increase tidal flow and reduce density of the insect.

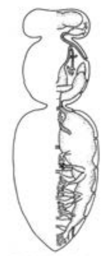


Figure 3.11b from Book

Arrangements of the Spiracles

(modifications)

- Mosquito larvae: only abdominal segment 9 spiracle functional.
- No spiracles:
  - mayfly, damselfly nymphs use abdominal 'tracheal gills'
  - Dragonfly uses gills in a modified hindgut.

Adaptations in other aquatic insects

- Giant water bugs (Belastomatidae) and water scorpions (Nepidae): breathe through a pair of 'siphons' at the posterior end of the abdomen.
- Diving beetles (Dytiscidae): trap an air bubble between the elytra and the abdominal terga: spiracles have moved (evolutionarily) to the dorsal surface of the abdomen.
- Waterboatmen (Corixidae): hairs on the abdomen hold a thin, continuous air bubble in place, giving the abdomen a silvery appearance.

Atracheate insects

- All gas exchange takes place through the integument.
- Examples are Collembola (springtails) and some parasitic hymenopterous larvae.

Additional functions of the tracheal system

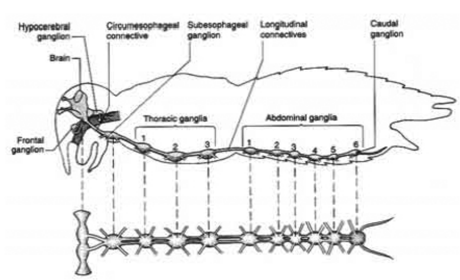
- Suspend internal organs (especially during movement).
- Air pressure needed for ecdysis.
- Thermoregulation--insulating layer of trachea around flight muscles.
- Pathway for development of nervous system.
- Weight reduction--hollow structures.
- Sound perception--tympanum is modified from tracheal system.
- Defense--spittlebug froth, defensive secretions from some grasshoppers & moths.

Nervous System Organization

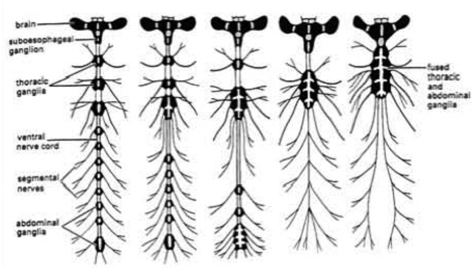
Three Major Regions

1. Central Nervous System (CNS)
   - Chain of ganglia
   - Brain

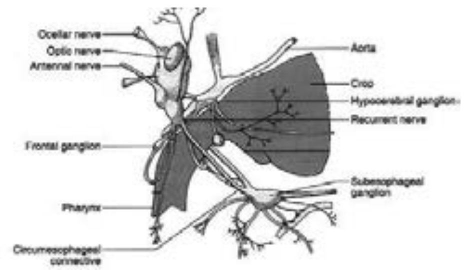
Insect Nervous System



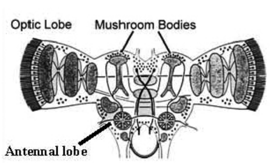
Insect Nervous System



Insect Nervous System



The Brain



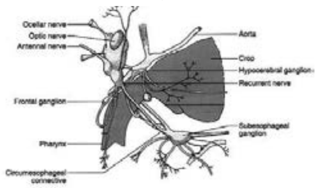
- Protocerebrum
  - Optic lobes
  - Ocellar lobes
  - Mushroom bodies
- Deuterocerebrum
  - Antennal lobes
- Tritocerebrum
  - Connections to frontal & subesophageal ganglia

Nervous System Organization

Three Major Regions

1. Central Nervous System (CNS)
   - Chain of ganglia
   - Brain
2. Visceral Nervous System (VNS)
   - Stomatogastric (stomodeal)

Stomatogastric nervous system = ‘mouth & gut’



- Frontal ganglion
- Hypocerebral ganglion
  - Corpora allata
  - Corpora cardiaca

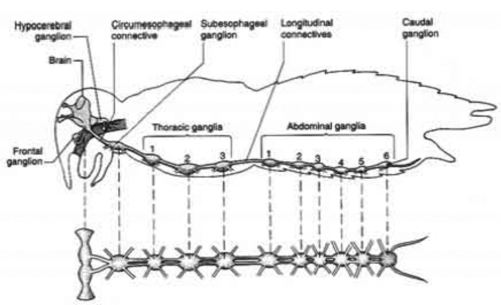
Endocrine Organs

Nervous System Organization

Three Major Regions

1. Central Nervous System (CNS)
   - Chain of ganglia
   - Brain
2. Visceral Nervous System (VNS)
   - Stomatogastric (stomodeal)
   - Ventral visceral
   - Caudal visceral

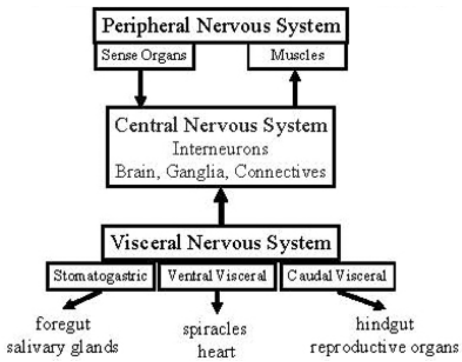
Nervous System Organization



Nervous System Organization

Three Major Regions

1. Central Nervous System (CNS)
   - Chain of ganglia
   - Brain
2. Visceral Nervous System (VNS)
   - Stomatogastric (stomodeal)
   - Ventral visceral
   - Caudal visceral
3. Peripheral Nervous System (PNS)

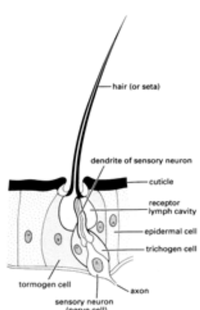


Insect senses

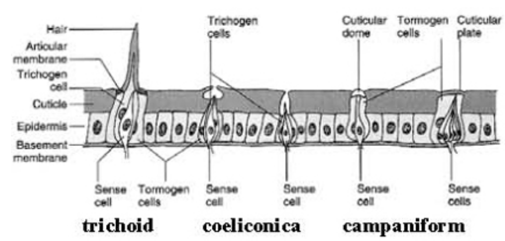
- Mechanoreception
  - Tactile
  - Proprioreception
  - Auditory
- Chemoreception
  - Olfaction
  - Gustation
- Photoreception

Sense Organs

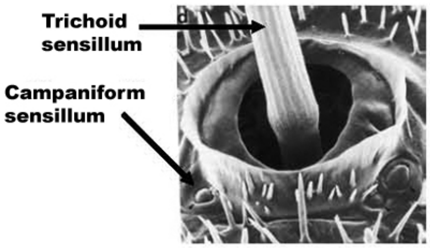
- External Sense Organs
  - Derived from setae
    - Trichogen cell
    - Tomogen cell
    - Sensory neurons (bipolar)
  - Classified based on shape
    - Trichoid sensillae (hair-like)
    - Coeloconica sensillae (cone in pits)
    - Campaniform sensillae (plate)



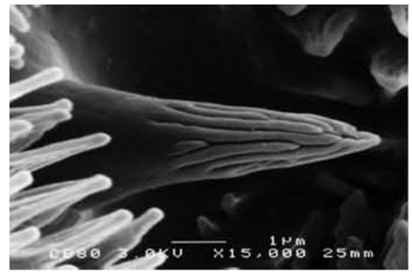
Sensillae



Sensillae



Sensillae



Coeloconica sensillum

Mechanoreception

- Tactile
  - Trichoid sensillae
    - Cerci
    - Directionally sensitive

Mechanoreception

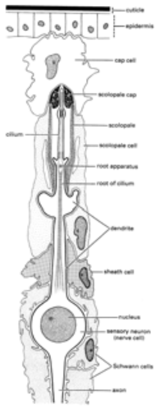
- Tactile
  - Trichoid sensillae
  - Proprioreceptors
    - External
    - Hair plates

Ant antenna hair plate

Dipteran haltere

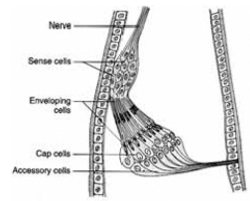
Mechanoreception

- Tactile
  - Trichoid sensillae
  - Proprioreceptors
    - External
    - Internal
      - Chordotonal organs
      - Scolopidia: bipolar neuron, solopale cells with cap, attachment cell
      - Between internal integument



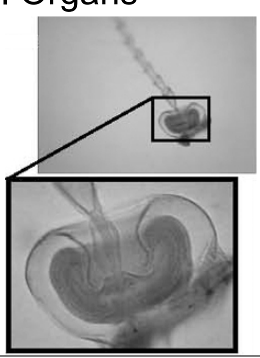
Chordotonal Organs

- Subgenual Organ
  - Below femoral-tibial joint
  - Vibrations



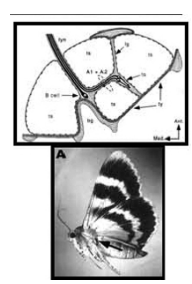
Chordotonal Organs

- Subgenual Organ
- Johnston's Organ
  - Pedicel
  - Wind speed
  - Sound reception

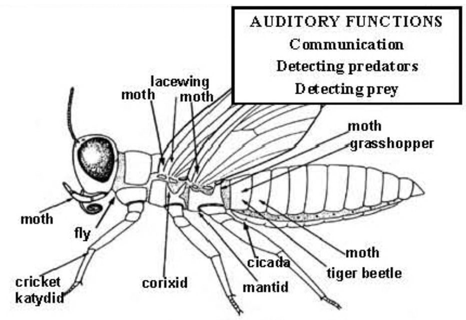


Chordotonal Organs

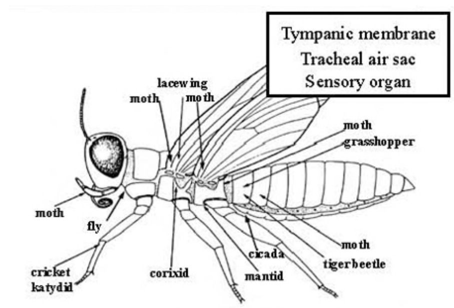
- Subgenual Organ
- Johnston's Organ
- Tympanic Organ
  - Hearing
    - Communication
    - Predators
    - Prey/Host



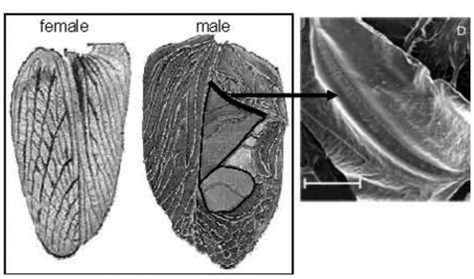
Diversity of Insect Ears



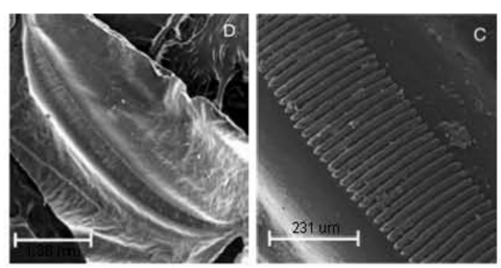
Insect Ears



Sound Production
Cricket Tegmina



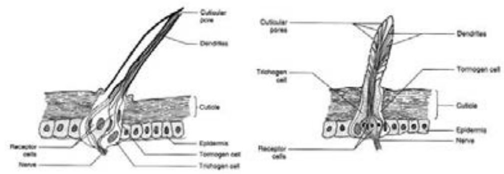
Sound Production
Stridulatory Files



Chemoreception

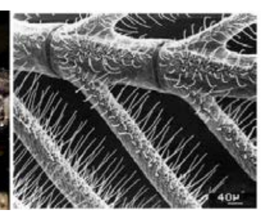
- Olfaction (distance chemoreception)
  - Gaseous
  - Low concentrations
  - High specificity
- Gustation (contact chemoreception)
  - Liquid
  - High concentrations
  - Low specificity

Chemoreceptors



Chemoreceptors

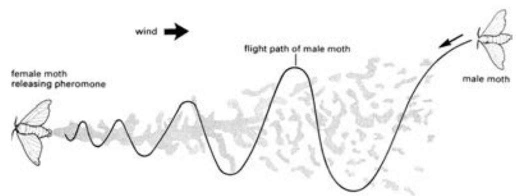
Chemoreceptors



Semiochemicals

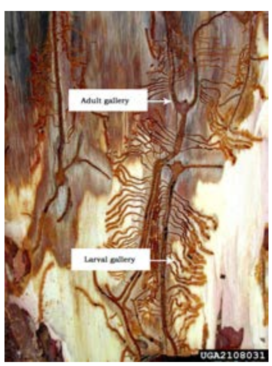
- Intraspecific communication
- Pheromones
  - Exocrine glands--secrete externally
  - Sex pheromones

Semiochemicals



Semiochemicals

- Also…
  - Aggregation pheromones
  - Spacing pheromones



Semiochemicals

- Also…
  - Aggregation pheromones
  - Spacing pheromones
  - Trail marking
  - Alarm pheromones

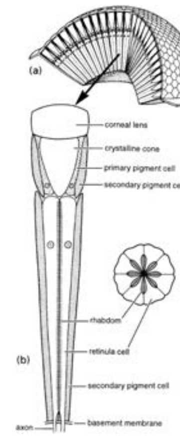
"The defendant had the motive, he had the opportunity, and let's face it, he's a killer bee."

Photoreception

- Many insects have photoreceptive cells throughout their body.
- Most photoreception occurs in the **compound eyes** and **ocelli**.

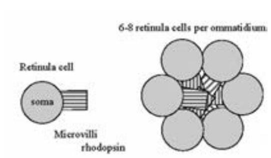
Compound Eyes

- Composed of 10 to 20,000 ommatidia.
- Two portions:
  - Dioptric apparatus
    - Lens & Cone
    - Focus light
  - Receptor apparatus
    - Rhabdom
      - Retinula cell & microvilli
    - Converts light energy into neural signal



The Rhabdom

- The Receptor Apparatus.
- Light is focused by diotric apparatus to rhabdom.
- 6-10 retinula cells per ommatidium.
- Microvilli with visual pigments excited by different wavelengths.



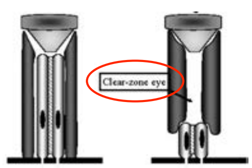
Transverse section of rhabdom

The Apposition Eye

- In normal **apposition eyes**, each cluster of retinula cells is surrounded by pigment.
- Therefore insect vision is composed of many, many apposed facets.
- Is there a problem with having a very, very small diameter of lens?

The Superposition Eye

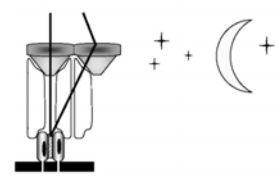
- Insects that fly in low-light have an adaptation called the **superposition eye**.
- Clear zone separates dioptric apparatus from receptor apparatus.
- Why?



Apposition Superposition

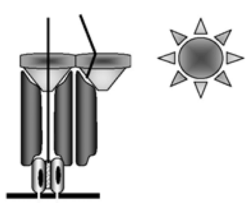
The Superposition Eye

- In low-light, pigment migrates towards lens.
- Receptor apparatus is no longer limited to light from single dioptric apparatus.
- In addition, modified tracheae form **tapetum** at base of retinula.
- What is sacrificed here?


tapetum

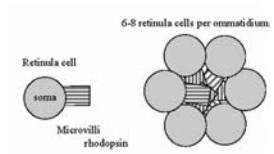
The Superposition Eye

- Can undergo physiological adaptation (NOTE, THIS IS NOT EVOLUTIONARY ADAPTATION).
- Pigment migrates back into pigment cells, rhabdom only receives light from its lens.



Visual pigments

- Colors seen by insects are determined by the visual pigments embedded in the microvilli of a retinula cell.
- Can be sensitive to very different wavelengths.
- What is stimulated controls what the insect perceives.



Transverse section of rhabdom

Visual pigments

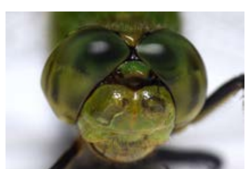
- Humans can see visible light from 380-750 nm.
- Insects range from 310-730 nm.
- Upper end (red) limited to butterflies.
- Most insects can see into the ultraviolet.

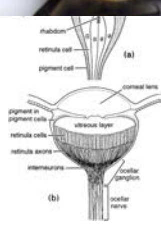
Then there's the nefarious

- Kurup *et al.* 2013. Fluorescent prey traps in carnivorous plants. Plant Botany (Online Early View Version).
- When UV light is blocked out, these become less effective in trapping insects.

Dorsal Ocelli

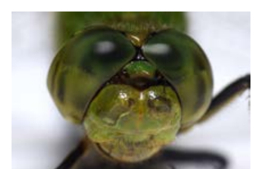
- "Simple Eyes"
- Single lens.
- Many, many photoreceptors.
- Is this good at image forming?
- Or light reception?

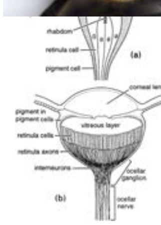




Dorsal Ocelli

- What are these likely used for?



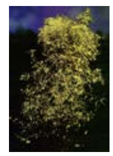


Photoproduction

- Bioluminescence
- **Luciferase** oxidizes **luciferin** in the presence of ATP and oxygen.
- Most prominent in Lampyridae: Lightning Beetles.

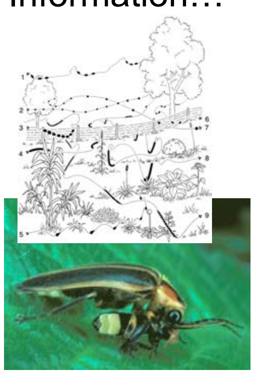
Photoproduction

- Likely originated as aposematic trait.
  - Warning coloration.
- Exapted into species specific signalling.



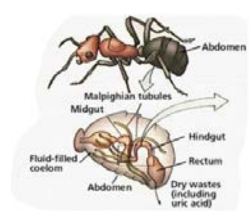
Information is Information…

- *Photinus* fireflies do their species-specific signaling.
- *Photuris* female fireflies mimic *Photinus* female receptive signals.
- What happens when the *Photinus* male thinks he's got it?



Where are insect muscles?

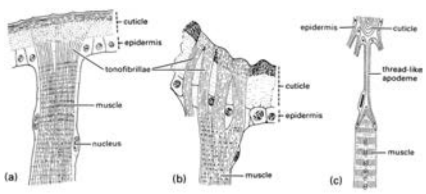
- Skeletal muscles
  - Attached to exoskeleton.
- Visceral muscles
  - Attached to intestines in alimentary canal.



Where are insect muscles?

Muscle attachment

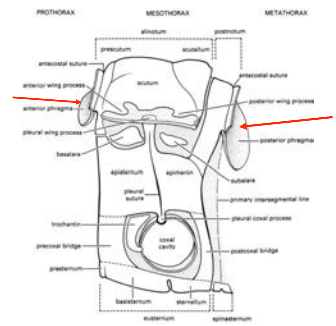
- Attach via **tonofibrillae**
  - Permit fusion of mesoderm (muscle) and ectoderm (cuticle)
- Apodemes & apophyses.
  - Internal ridges; anchors for muscle attachment



Where are insect muscles?

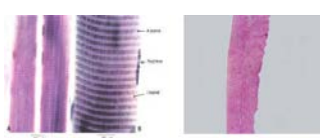
Muscle attachment

- Attach via **tonofibrillae**
  - Permit fusion of mesoderm (muscle) and ectoderm (cuticle)
- Apodemes & apophyses.
  - Internal ridges; anchors for muscle attachment
- Phragma
  - Platelike invagination; flight muscle attachment.

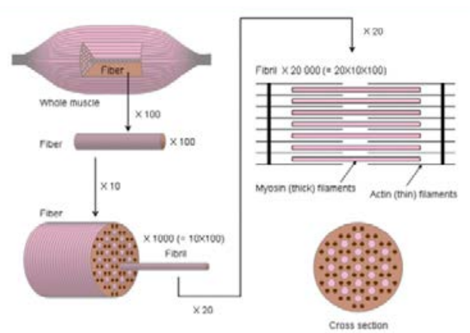


Insect vs. human muscular system

- Types of muscles
- What types are present in humans?
- Only one type of these is present in insects.



Insect Muscle

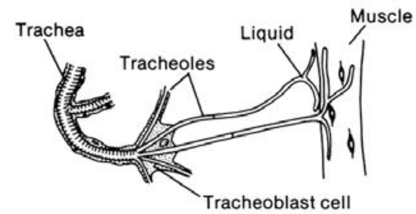


Types of Insect Muscles

- **Synchronous muscle**
  - Synchronized with neural impulse
  - One contraction and relaxation per 1 neural impulse.
- **Asynchronous muscle**
  - More than 1 contraction and relaxation per 1 neural impulse.
  - When might this be useful?

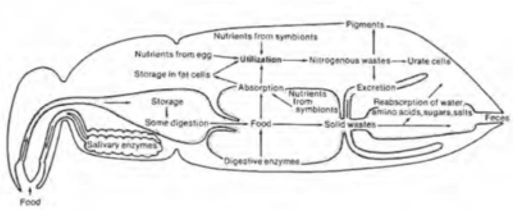
Oxygen and energy source

- How can insect muscles get oxygen?



Oxygen and energy source

- How can insect muscles get energy?

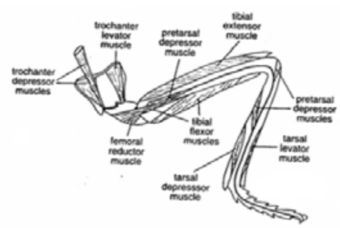


Insect Locomotion

- Why do insects have six legs?

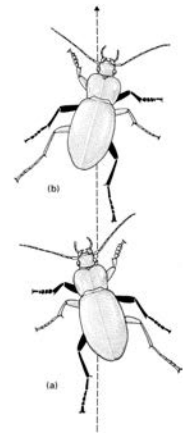
Insect Locomotion

- Muscles for insect locomotion
  - Levator vs. depressor muscles.
  - Flexor vs extensor muscles.



Insect Locomotion

- Generally, always three legs on the ground (how do they grip the ground?).
- What other non-flying means of locomotion do we see?

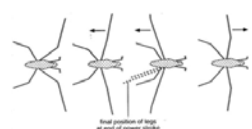


Jumping

- Generally, accomplished by storing energy through compression of resilin.
- Release of compression yields instantaneous spring.
- Sometimes, compression is stored in other locations…

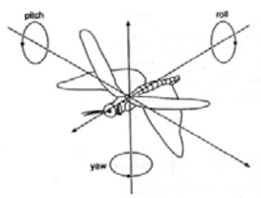
Sliding

- Water striders have hydrofuge cuticles or hair fringes
- Move by rowing with hair fringed legs.



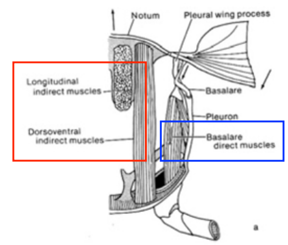
Insect Flight Mechanism

- Wings not true appendages, extensions of **exoskeleton**
- No appendages given over to flight (compare to other winged animals)
- Powered flight is only found in **adult** insects.
- Air ahead must be thrown downward and backward, giving **lift** and **thrust**.
- Modifications in left versus right permit turning.



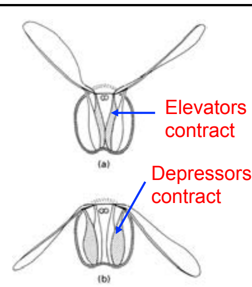
Insect Flight Muscles

- Two types:
- Direct muscles
  - Only type found in **Paleoptera**
- Indirect muscles
  - Found in **Neoptera**
- **Neoptera** have both…



Direct flight

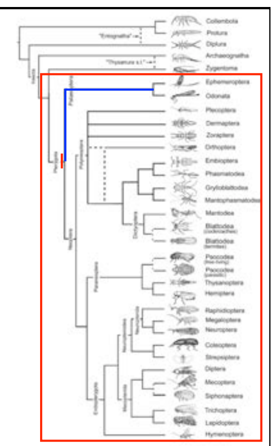
- Muscles directly attached to wings
- Very fine control
- One nerve impulse = one muscle contraction = one wing beat (what kind of muscles are these?)
- Ancestral form, found in **Paleoptera**: Dragonflies & Mayflies



Insect Evolution

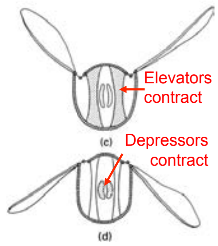
Wings & Flight
Pterygota

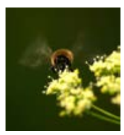
Ancestral:
Direct Flight
Paleoptera



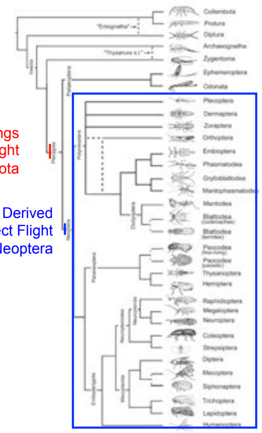
Indirect flight

- Flight muscles attached to interior of thorax (NOT directly to wings)
- Energy is conserved because the elasticity of the thorax restores its shape
- Single nerve impulse required to initiate muscle contraction, single impulse to cease (what kind of muscles are these?).
  - Reduces number of nerve impulses to muscle contractions immensely.
  - Results in much more rapid wing beats (up to 1,000 times per second in some gnats)
- Derived form found in **Neoptera**



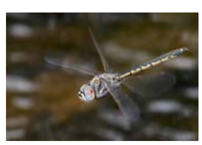


Insect Evolution



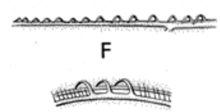
General trend in insect flight

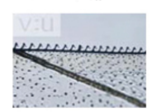
- **Harmonization of wing beat.**
- Direct to indirect an obvious transition.
  - Direct can move *each wing* individually.
  - Sides are coordinated by contortion of thorax.
  - Permits evolution of asynchronous muscles.

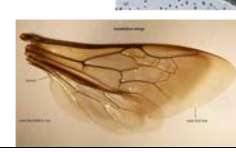


General trend in insect flight

- **Harmonization of wing beat.**
- Carried further in other insects.
- Fore and hindwings coupled.
  - Hamuli lock forewing and hindwing together in Hymenoptera

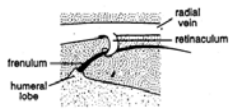






General trend in insect flight

- **Harmonization of wing beat.**
- Carried further in other insects.
- Fore and hindwings coupled.
  - Frenula lock them together in Lepidoptera.
  - Similar structures found in Orthoptera, Hemiptera.



General trend in insect flight

- **Harmonization of wing beat.**
- OR, powered flight eliminated in one pair of wings.
- **Sclerotized forewings:**
- **Elytra** of Coleoptera
- **Tegmina** of Orthoptera & Dermaptera

General trend in insect flight

- **Harmonization of wing beat.**
- OR, powered flight eliminated in one pair of wings.
- **Sclerotized forewings:**
- **Elytra** of Coleoptera
- **Tegmina** of Orthoptera & Dermaptera

- **Wing reduction**
- **Halteres** of Diptera
- **Halteres** of Strepsiptera