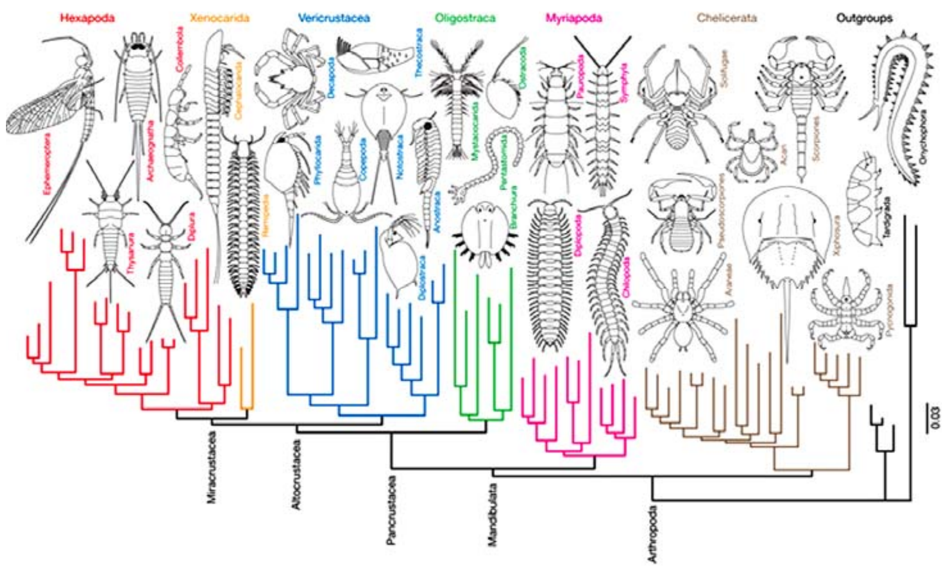
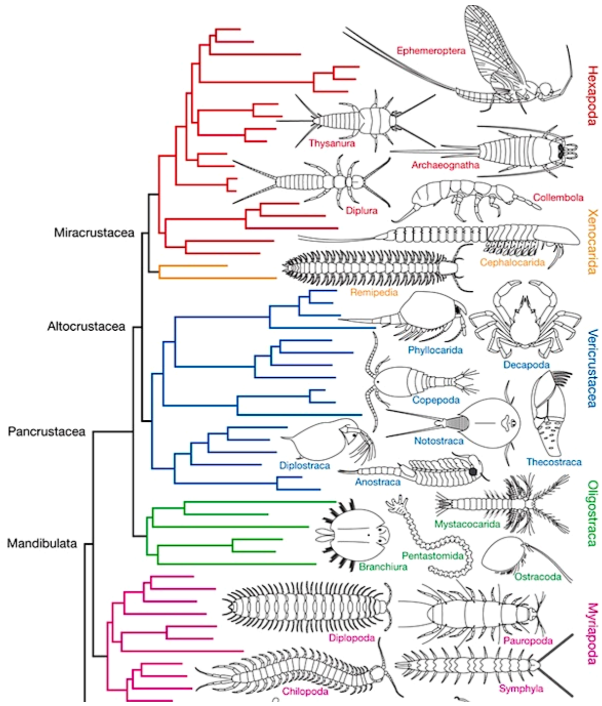
Main arthropod clades (Regier et al 2010)

- Trilobita
- Chelicerata
- Mandibulata
  - Myriapoda (Chilopoda, Diplopoda)
  - Pancrustacea
    - Oligostraca (Ostracoda, Branchiura)
    - Altocrustacea
      - Vericrustacea
        - » (Branchiopoda, Decapoda)
      - Miracrustacea
        - » Xenocarida (Remipedia, Cephalocarida)
        - » Hexapoda (including Insecta)



(Regier et al 2010, Nature)

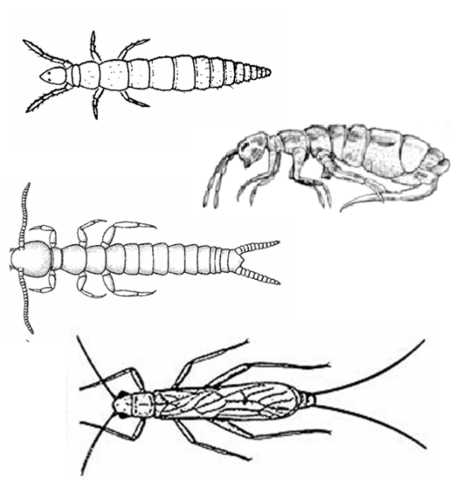


Xenocarida sister to Hexapoda:

http://blogs.discovermagazine.com/loom/2010/02/10/blind-cousins-to-the-arthropod-superstars/

Hexapoda ("six-footed)

- Protura
- Collembola
- Diplura
- Insecta



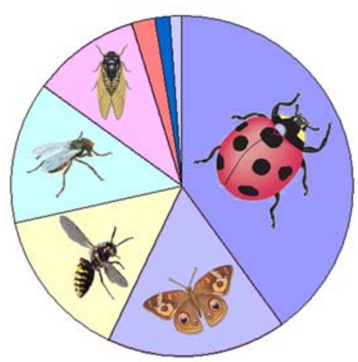
Insect diversity and significance

- More species of insects than all other animals combined- millions of species
- Entomology- the study of insects- courses, academic departments, professionals
- 8-10K professional entomologists the US, most of these in economic or applied entomology. Many more amateurs.

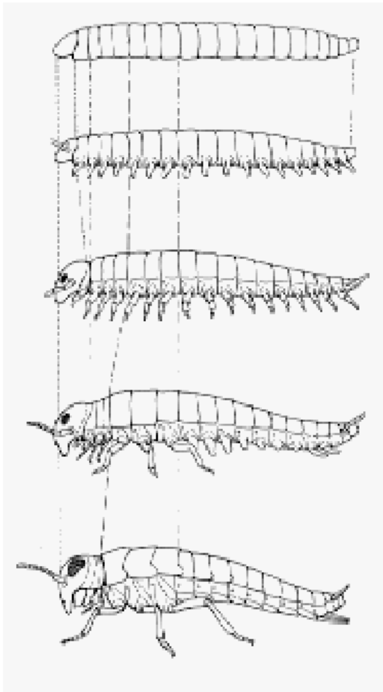
~32 Living Insect Orders

1. Coleoptera (beetles)	350,000
2. Lepidoptera	150,000
3. Hymenoptera (ants, bees)	125,000
4. Diptera (flies)	120,000
5. Hemiptera (bugs)	90,000
6. Orthoptera (crickets etc)	20,000
7. Trichoptera (caddisflies)	13,000
8. Collembola (springtails)	9,000

24 other Orders…………......53,000
Total……………………...930,000



Data from Grimaldi & Engle 2005, Evolution of the Insecta.

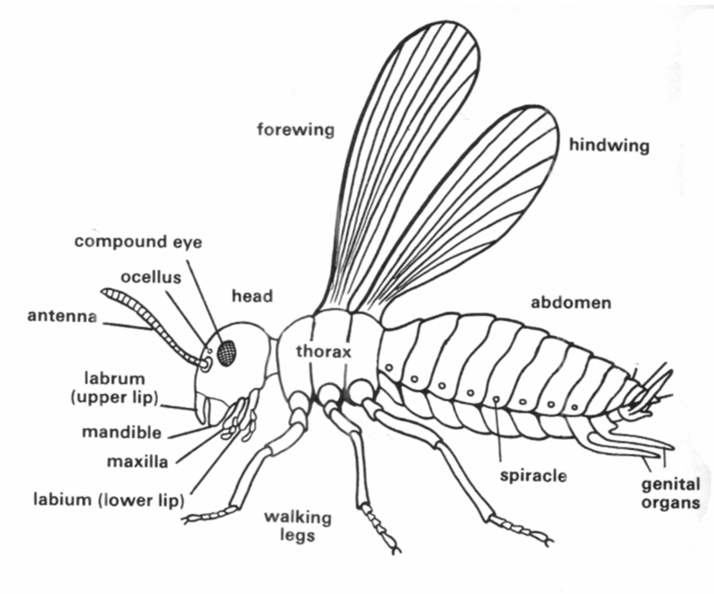


Hypothetical evolutionary transition from annelid-like ancestor with similar segments to tagmatized hexapod arthropod

“Articulata’ hypothesis

Insect tagmatization

- Head – antennae, mandibles, first maxillae, second maxillae (often fused to form a flap like labium), 1 pair sessile compound eyes, plus 3 median ocelli (usually)
- Thorax- 3 segments with 1 pair legs on each 2 pair of wings, if present, not derived from legs
- Abdomen- usually 11 segments.
  No abdominal appendages except (sometimes) caudal cerci.



Why so diverse?

- Symbiosis with Anthophyta (flowering plants).
- Possess the most adaptable body plan, life history, and physiology for life on land.

Key adaptations:

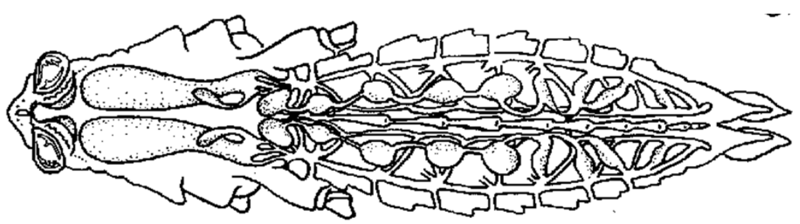
1. Waterproof exoskeleton
2. Tracheal system
3. Terrestrial egg
4. Metamorphosis
5. Flight
6. Social behavior.

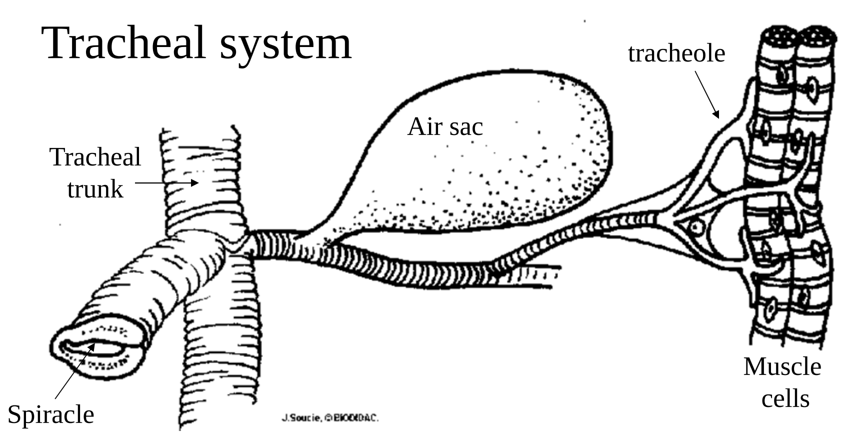
Waterproofing

- Epicuticular lipids- waxy coat to reduce water loss through the body surface
- Closeable spiracles to reduce water loss from tracheal system
- Nitrogenous waste = purines
- Recovery of water from feces
- Water vapor uptake in some insects

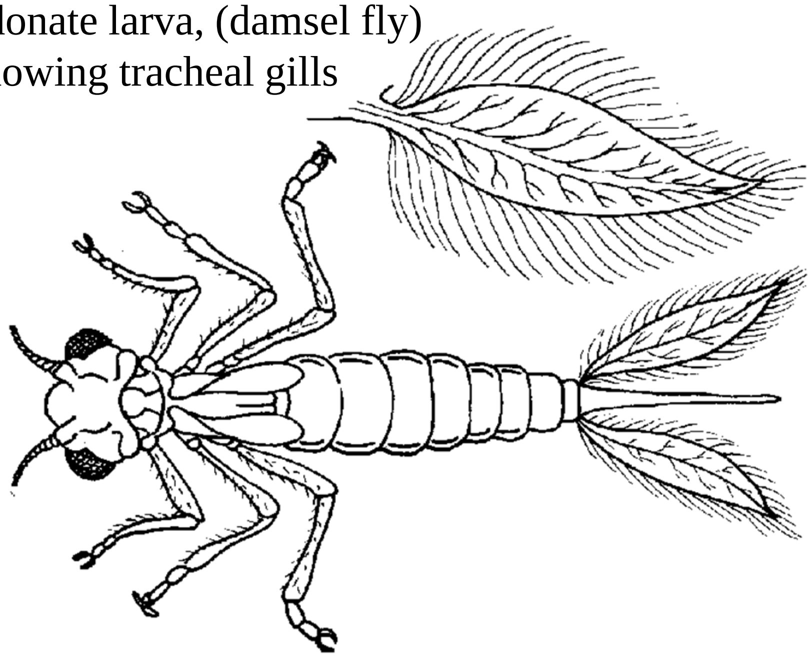
Tracheal systems

- Air-filled tubes, provide respiratory gas exchange between atmosphere and cells
- Spiracles, tracheal trunks, air sacs, tracheoles
- Trunks lined with exoskeleton, supported by spiral taenidia

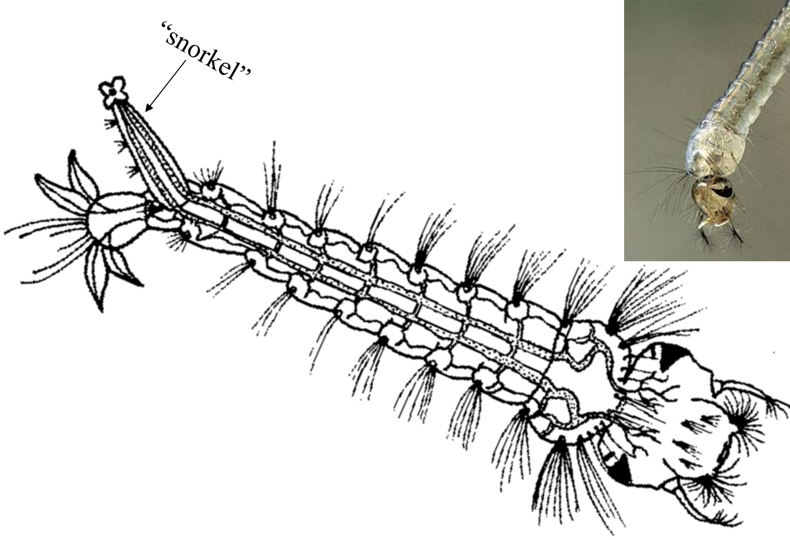




Odonate larva, (damsel fly)
showing tracheal gills



Dipteran larva, (mosquito)
showing tracheal snorkel



Tracheal tubes of *Tenebrio*

Insect flight- a key adaptation

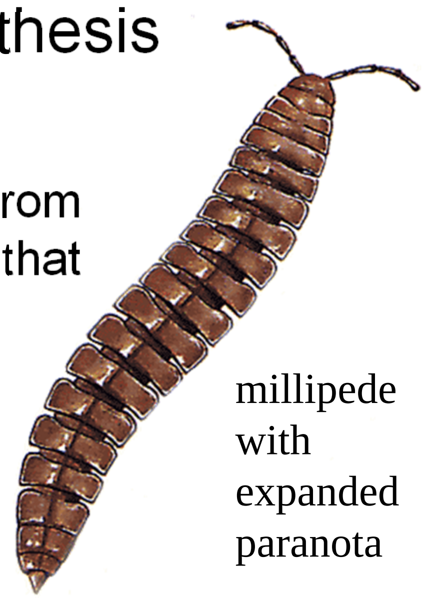
- Dispersal
- Seasonal migration
- Finding food
- Capturing prey
- Finding mates
- Escape from predators

Evolution of insect flight

- Anatomical origin of wings
  - Paranotal hypothesis
  - Gill hypothesis
- Functional evolutionary intermediates

Paranotal hypothesis

- Paranota are rigid lateral extensions from thoracic segments that protect the limbs in many arthropods



millipede with expanded paranota

Possible intermediate functions of ‘wing’ precursors

- Perhaps elongated paranota stabilized jumping or falling insect

- Solar panels for thermoregulation (true in some modern insects)

Problems with paranotal hypothesis

- Tests suggest that aerodynamic stabilization requires very long extensions for small bodies.
- Paranota are immobile in extant arthropods- no clear advantage to development of flapping musculature

Gill (pleural) hypothesis

- Wings developed from respiratory exites of biramous appendage
- Upper portion of the leg with exite fused with body wall (supported by anatomical details).
- Exite flapping could have served initially for ventilation and/or swimming

Support for gill hypothesis

- Mobile abdominal gills are present in living Trichoptera (mayflies) and Plecoptera (stoneflies)

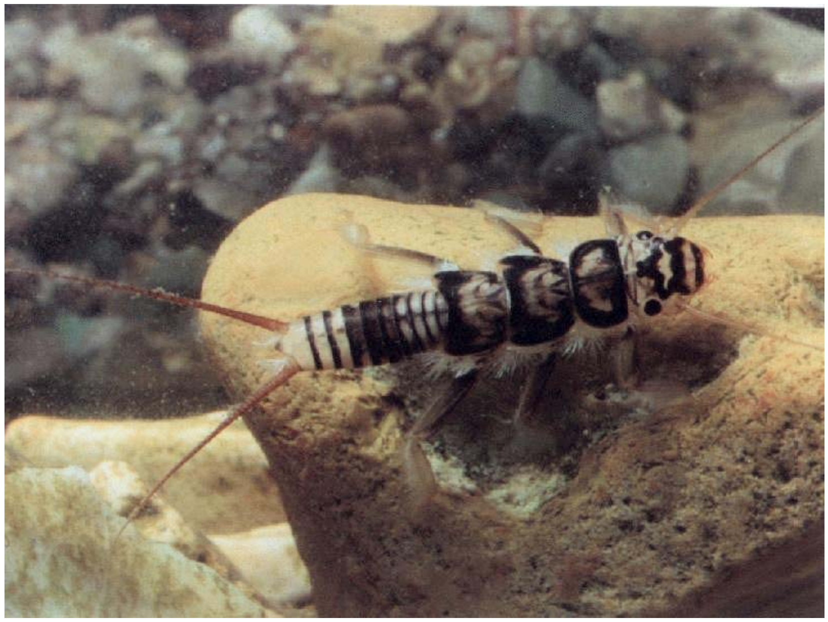
- (Quick-Time video of gill movements of Ephemeroptera and Plecoptera)

Support for gill hypothesis, continued

- Abdominal neurons fire synchronously with flight neurons in locust- possible vestigial remnant of abdominal gills/winglets
- Functional transitional stages to flight are observed in modern aquatic insects

Skimming- transition to flight

- Investigated by Jim Marden at Penn State
- Living stoneflies and mayflies use sailing or wing flapping to locomote on water surface
- Allows adult to reach shore after metamorphosis of aquatic nymph
- Possible transitional function from gill flapping to flight.

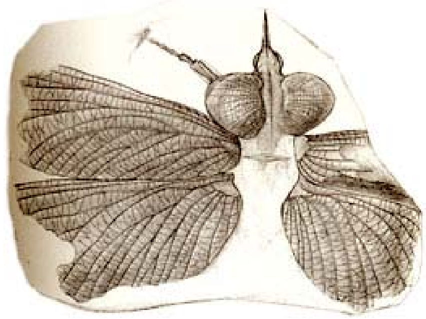


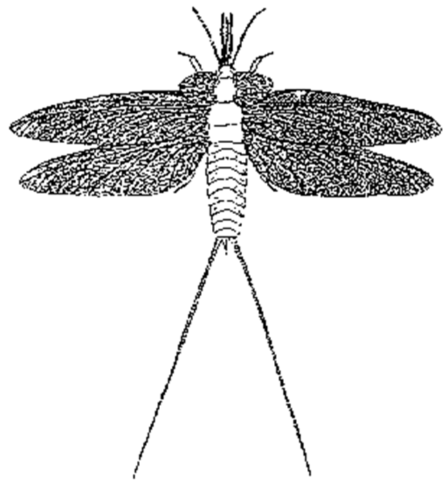
Paleodictyoptera

-Extinct Carboniferous order

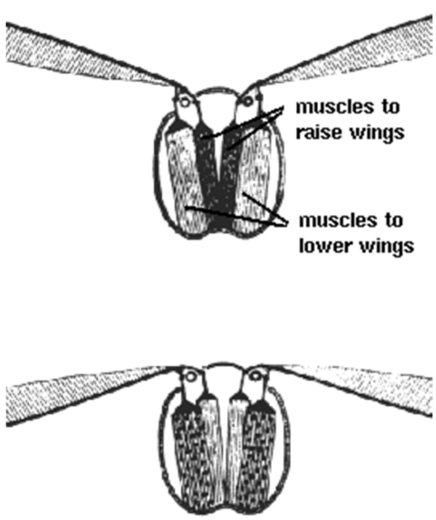
-most primitive known flying insects

-note third pair of wings

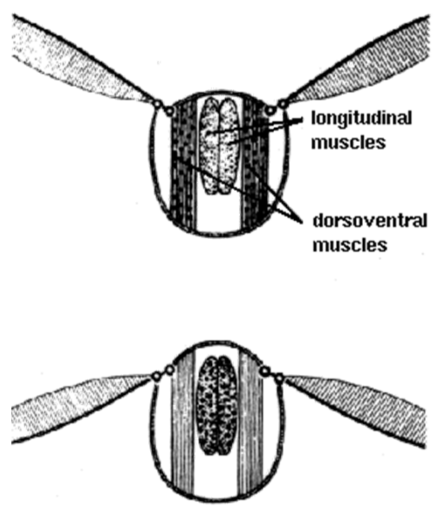




Direct flight muscles, e.g. Orthoptera



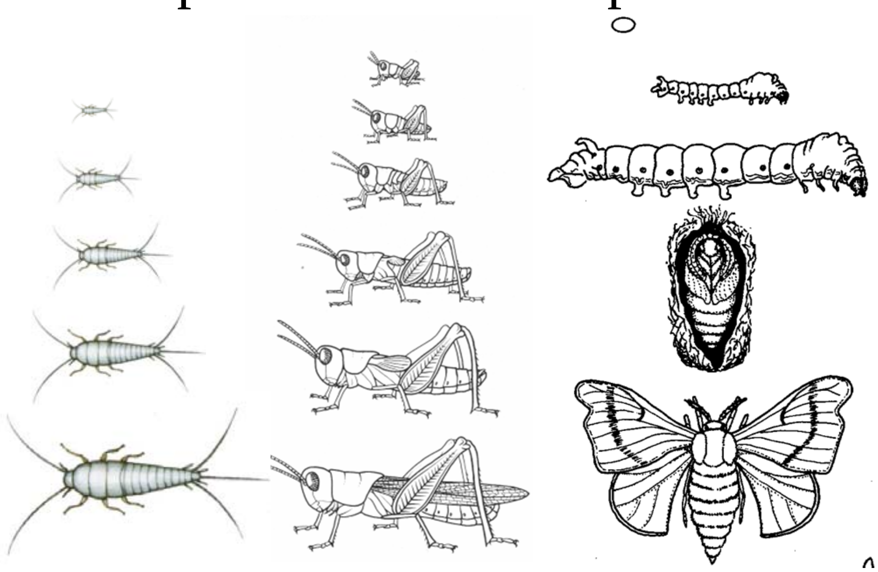
Indirect flight muscles, e.g. Diptera



Two types of flight muscle

- Synchronous flight muscle – each contraction is triggered by a separate nerve impulse (similar to vertebrate muscle fibers) up to ~100 Hz
- Asynchronous flight muscle- each impulse triggers a series of contractions at high frequency, in excess of the frequency of nerve transmission up to ~1000 Hz

Development & metamorphosis



Ametabolous Hemimetabolous Holometabolous

Advantages of metamorphosis

- Division of labor
- Growth takes place in larval stage specialized for feeding
- Winged adult specialized for reproduction and dispersal

Endothermy & flight

- Flight demands high power output = heat production
- Speed & power enhanced by high temperature
- In many flying insects the power output is sufficient to maintain high body temperature

Insect endothermy, continued

- Pre-flight warm-up (shivering)
- Heat retention aided by insulation (air sacs, pelage) and controlled by blood circulation to abdomen
- Dung beetle terrestrial endothermy and intraspecific competition

Origin of complexity

- Duplication of functional units (cells, segments, individuals)
- Specialization & cooperation among units
- Multicellularity, metamerism & tagmatization, sociality

Social behavior

- Broadly defined= cooperation among individuals
- Range from simple parental care to complex colonies of multiple generations
- Occurs in many animal taxa but most dramatically in certain insects and tetrapod vertebrates

Eusociality

- Individuals cooperate in caring for young.
- Overlap of two or more generations in a colony…young assist parents in caring for siblings
- Sterile individuals (worker caste) work to care for offspring of reproductive individual(s)

Eusocial taxa

- Hymenoptera (wasps, bees, and ants). Eusociality evolved several times in this order
- Isoptera (termites)…wood-eating insects that depend on intestinal symbiotes, passed from parents to offspring.
  All termites are eusocial- primitive character of the order.

Leaf-cutter ants, genus *Atta*, are dominant herbivores in subtropical and tropical forests- fungus gardeners

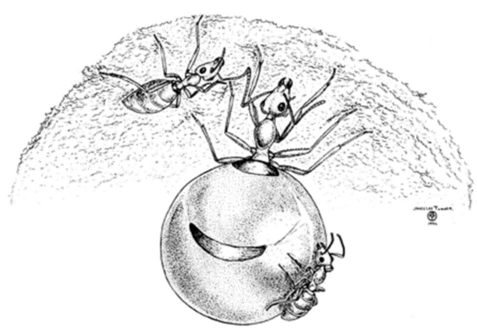
Life cycle of typical ant colony

- Colony is founded by a lone female (queen)
- First broods are sterile females (workers) who forage, care for brood etc.
- When colony reaches sufficient size, it produces reproductives (alates) annually
- Lifespan of colony may be many years- limited by lifespan of queen- or may adopt new queen from brood

Paper wasps- *Polistes*

Developmental castes in eusocial Hymenoptera

- Queen = reproductive female (diploid)
- Workers =sterile females
  - Major
  - Minor
  - Soldier
  - others
- Drone = reproductive male (haploid)



Hymenopteran castes can be highly modified for specific functions-

Replete workers of the ant genus *Myrmecocystus* are living storage containers for sugars

Haplodiploidy

- Unfertilized eggs develop into males
- Allows the female parent to control the sex of offspring, by controlling fertilization of the eggs.
- Functionally important in social insects
- May also predispose Hymenoptera to evolution of sociality

Haplodiploidy, altruism, and eusociality

- How can sterile worker castes evolve when evolution optimizes reproduction?
- Extreme example of *altruism*- loss of reproductive fitness to benefit another
- W.D. Hamilton (1964) inclusive fitness: for an altruistic trait to evolve, loss of fitness of individual must be compensated by increased fitness of close relatives.

Coefficient of relatedness = C_r

- Mother-daughter $C_r = 0.5$
- Sister-sister $C_r = 0.5$ in most diploid sexual organisms…share ¼ of genes from mother and ¼ of genes from father
- A trait that negates individual's own reproduction must double the total reproductive output of sisters (or quadruple that of first cousins, etc)

Hymenopteran sisters are more closely related to each other than to their own daughters

½ * ½ = ¼ genes from mother (diploid)

+

½ * 1 = ½ genes from father (haploid)

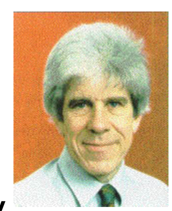
Sister-sister C_r = ¾

Mother-daughter C_r = ½

Multiple origins of eusociality in Hymenoptera

- Eusociality evolved at least 11 times in Hymenoptera: twice in wasps, 8 times in bees, once in ants
- Hamilton argued that haplodiploidy and the resulting asymmetry of inclusive fitness tip the balance in favor of eusociality in this order.

W.D. Hamilton 1936-2000



- "The most influential evolutionary biologist of the last half of the 20th century"
- Kin selection
- Red Queen hypothesis-evolution of sex
- OPV-AIDS hypothesis

Termites are not haplodiploid

- The inclusive fitness argument cannot be applied in this case
- All termites are eusocial, so it may have evolved in this group only once
- Cloistered, long-lived colonies, parental care, inbreeding resulting in high Cr among colony-mates…

Class Insecta

- Diversity- overwhelming!
  There are ~32 living orders, plus 10 extinct

- Subclass Apterygota (wingless insects)
  probably polyphyletic
- Subclass Pterygota (winged insects)
  probably monophyletic

Apterygota - wingless

- Ametabolous development.
- Collembola (springtails)
- Thysanura (silverfish, firebrats) and Archeognatha (bristletails)

Pterygota – winged

- Paleoptera
- Neoptera

O. Collembola: springtails

- Wingless, tiny
- Furcula & tenaculum.
- Collophore
- ametabolous

O. Thysanura ("fringed tail")

- Silverfish, firebrats, bristletails
- Wingless
- Epidermal scales similar to Lepidoptera
- Water vapor uptake from air
- Simple metamorphosis

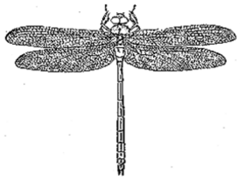
O. Thysanura (or Archaeognatha): bristletail

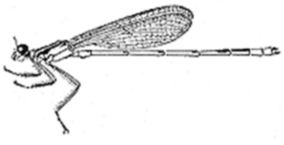
O. Thysanura: silverfish

O. Thysanura: silverfish

Paleoptera (ancient wings)

- hemimetabolous development – gradual growth of wings
- wings cannot be folded down against the body
- Includes orders Odonata (dragonflies) and Ephemeroptera (damselflies)

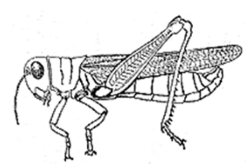




Neoptera (new wings)

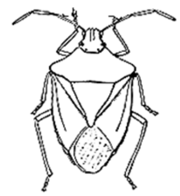
- wings can be folded against the body when at rest.
- three major clades:
  - Orthopteroid
  - Hemipteroid
  - Endopterygota

Orthopteroid orders



- at least nine hemimetabolous orders with relatively unspecialized mouthparts.
- Blattodea (cockroaches), Isoptera (termites), Mantodea (mantids), Orthoptera, (grasshoppers and crickets), Dermaptera (earwigs), Phasmatodea, (walking sticks), Plecoptera (stoneflies), Embiopteroidea (webspinners) Grylloblattodea, Mantophasmatodea, Zoraptera

Hemipteroid orders



- includes four hemimetabolous orders with mouthparts specialized for rasping or piercing/sucking.
- Hemiptera (suborder Heteroptera: true bugs, and suborder Homoptera: cicadas, leafhoppers, aphids), Psocoptera (booklice and barklice). Thysanoptera (thrips), Phthiraptera (parasitic lice),

Endopterygota

- nine holometabolous orders including about 4/5 of all insect species.
- Coleoptera (beetles), Hymenoptera (ants, bees, wasps, and sawflies), Lepidoptera (butterflies and moths), Diptera (true flies), Mecoptera (scorpionflies), Siphonaptera (fleas), Trichoptera (caddisflies), Neuroptera (netwings), Strepsiptera (twisted-wings).