

### Why this title?

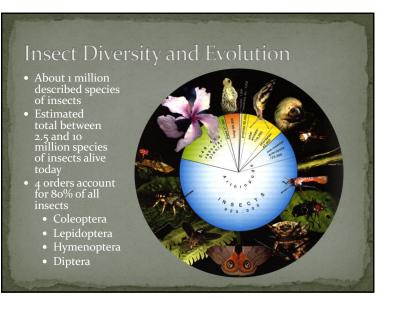
- Evolution is inherently about organisms responding to environmental change
- Insects have ruled this planet for the past 400 million years (at least in terrestrial environments)
- What is the most dangerous animal on the planet today?
  - Shark?
  - Mosquito?
  - Rat Flea?
  - Louse?

### Agenda

Review of insect diversity and major localities for insect fossils

### Discussion of Insect Origins

Overview/ evolution of major insect orders



### Reasons for success

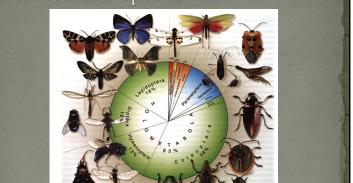
- "Big 4" orders all are holometabolous (egg > larva > pupa > adult)
- They also have wings
  - Insects, pterosaurs, birds, bats
  - Insects were first (by roughly 100 MY)
  - Permian Meganeuropsis permiana 27 inch wingspan

### What is a species?

- Consider this the fundamental unit of nature
- Mayr "group of actually or potentially interbreeding populations, which are reproductively isolated from other such groups"
  - Biological species concept
- Grimaldi "discrete group of individual organisms that can be diagnosed, or defined on the basis of certain specialized features, and that had a common ancestor and unique evolutionary history"
  - Evolutionary species concept

### Systematics

- "The first part of knowledge is getting the names right" - Chinese proverb
- Most human cultures name the organisms they encounter
- Today, we rely on a structured scheme (originally proposed by Linnaeus 1758)
- Species are grouped into genera, genera are grouped into families and so forth



### Evolution

- Change in inherited traits in a population from one generation to next
- Processes involved
  - Variation
  - Reproduction
  - Selection
- Mechanisms that drive
  - Natural selection
  - Genetic drift

### Evolution (2)

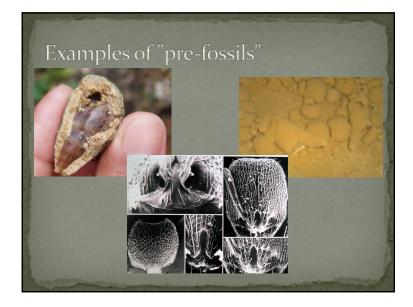
- Most unifying concept in biology
  - "Nothing makes sense in biology except in the light of evolution" Theodosius Dobzhansky (1973)
- Evolution is inherently about organisms responding to environmental change

### Paleontology

- Fossils provide information on 4 aspects of evolution
  - Documentation of extinct species (and lineages)
  - Actual and estimated ages of lineages
  - Phylogeny (relationships)
  - Biogeography (factors that contribute to present day distributions of organisms)

### Fossilization

- Majority of insects (and other life forms) die, then decay leaving little or no trace
- Common insect fossils are from lake environments
- Insects swept over the lake or deposited by a stream
- Drowned and not eaten
- Rapidly buried in lake sediments
- Many are represented by wings (or wing fragments)
   Many also have parts of body preserved (or impressions)
- There are exceptions to lake based fossils
  Some are near shore marine environments
- Taphonomy is the study of how organisms fossilize



### Types of preservation

- Impressions like a cast or mold (no color from exoskeleton)
- Compressions preserve remains of exoskeleton
- Concretions minerals precipitated around decaying organism
- Mineral replication complete (or partial) 3 dimensional replacement
- Amber/ copal inclusions preserved tree resin
- Trace fossils (fossil burrows and nests)



### Lagerstätten (age increasing down lis

- Exceptional fossil insect deposits (most specimens we examine will be from these deposits)
  - Amber (Dominican Republic) Miocene
  - Florissant Formation (Colorado) Oligocene
  - Green River Formation (Rocky Mtns) Eocene
  - Santana Formation (Brasil) Cretaceous limestone
  - Liaoning (China) early Cretaceous
  - Solnhofen (Germany) late Jurassic limestone
  - Elmo (Kansas) Permian limestone
  - Mazon Creek Francis Creek Shale (northern Illinois) late Carboniferous

### Fossil Resins

• Amber (> 2 Ma) vs. Copal (< 1.6 Ma, some very recent)





### Drop of alcohol Copal becomes sticky

Amber does not

### Amber – Dominican Republic

- Age mid-Miocene (17 20 Ma)
- Over 400 families, 1,500 species of insects known
- Distinctly tropical environment
- Caribbean landmasses have complex history of drift, submergence, and land bridges
- These fossils provide insights into origins of modern ecosystems in the area
- Although most species are found in region, there are exceptions
  - Some species of ants and termites only known from Australia today



### **Baltic Amber**

- Denmark, Sweden, Lithuania, Poland, Germany
- Formation runs about 45 m below the surface (and extends to about 5 m below sea level)
- Age roughly middle Eocene (44 MYA)
- Several thousand species of insects known
- Gathered by humans for at least 13 centuries
- Amber room (above) was made from Baltic amber
- Cockroach (Lithuania)



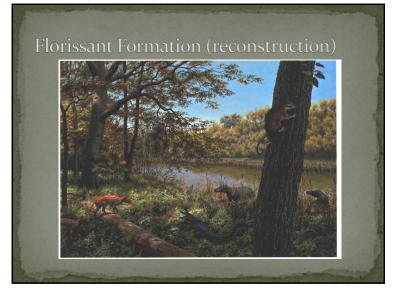
### Burmese amber – Myanmar

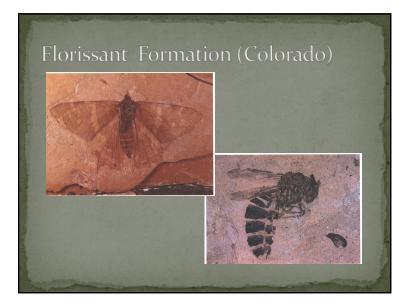
- 2017 new insect discovered Cretaceous amber (100 Ma) - New insect order - Aethiocarenodea
- Single species *Aethiocarenus burmanicus*



### Florissant Formation (Colorado)

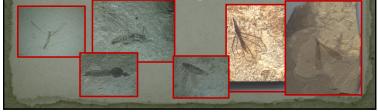
- Age Late Eocene to Lower Oligocene (45 30 Ma)
- 200 families, 1,100 species of insects known
- Ancient Lake Florissant formed by volcanic mudflows that dammed up a river valley
- Over 1 2 million years repeated volcanic eruptions blanketed area with ash
- Two insect groups no longer common in North America
- Spoon winged lacewings (mostly Africa, some in Australia, South America, Asia)
- Tsetse flies (only Africa today)
  These were 2x the size of the recent species





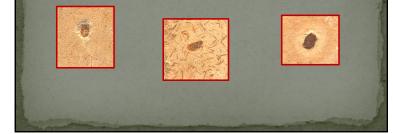
### Green River Formation

- Age Eocene (55 38 Ma)
- One of largest fossil lake systems in the world
  65,000 km<sup>2</sup>
  - Deposits roughly 600 m thick in places
- Climate warm temperate to sub-tropical
- 14 orders, 100 families, 300 species of insects known



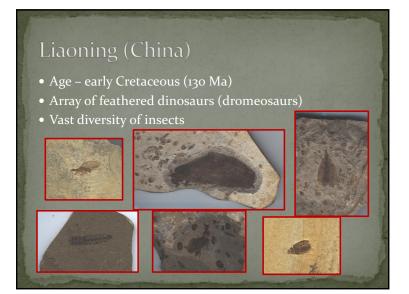
### Santana Formation (Brazil)

- Age Cretaceous (120 Ma)
- Near shore deposit
- Insects are preserved as permineralized replicas
- 18 orders, 100 families, 300 species known



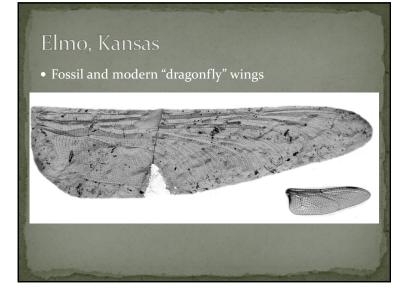
### Solnhofen (Germany)

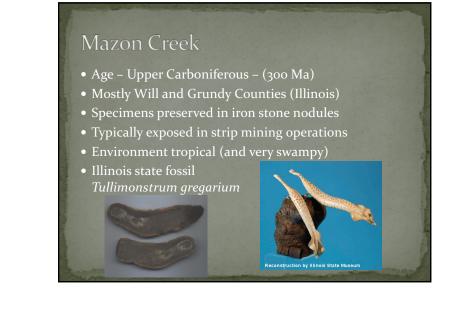
- Age Jurassic
- Most famous for *Archaeopteryx lithographica* (6 specimens)
  - Transition form between raptor dinosaurs and birds
- Fine grained layered limestone (initially quarried by Romans)
- Fossils preserved in mud of isolated lagoons
- 12 orders, 50 genera of insects known (many dragonflies)

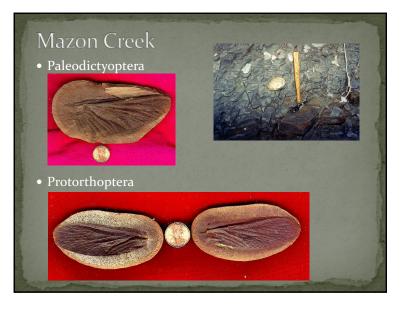


### Elmo, Kansas

- Age Permian (267 Ma)
- Most insect fossils found in lenses
- These are thought to be lakes (some fresh water, some playas)
- Coastal region tropical climate
- 15,500 specimens, 17 orders, 150 species known
- Largest insect ever is known from this formation (Wellington)
  - Roughly 27 inch wingspan







### Mazon Creek Reconstruction

- Illinois straddled the equator
- Illinois State Museum reconstruction



### Defining features of insects

- Obviously 6 legs... (but immature chiggers have 6 legs)
- Specifically...
  - Loss of musculature in the antenna beyond the scape
  - Presence of chordontal organ (Johnston's organ) in the antennal pedicel
  - Development of posterior tentorium into a transverse bar
  - Loss of articulation between coxae and sterna
  - Subsegmentation of tarsus into tarsomeres
  - Articulation of pretarsal claws with apical most tarsomere
  - Presence in females of ovipositor (formed by outgrowths of 8<sup>th</sup> and 9<sup>th</sup> abdominal segments)
  - Presence (primitively) of long terminal filament on dorsum of 11<sup>th</sup> abdominal segment

### Origins of Insects

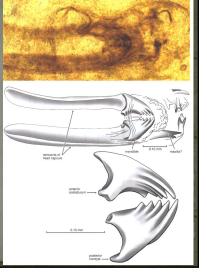
- Insects are principally terrestrial organisms
- Earliest terrestrial relatives (springtails)
  - *Rhyniella hirsti* Rhynie Chert (Scotland) Devonian (360 400 Ma)
  - Also known from Gaspé fossil beds of Quebec
- Bristletails (modern example from Tree of Life project)



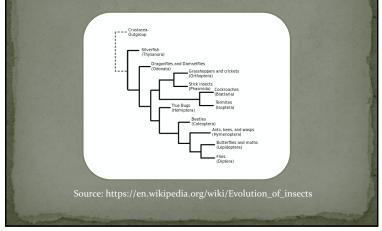
- http://tolweb.org/Archaeognatha
- Nocturnal, hide in crevices in day, loose bark or stones

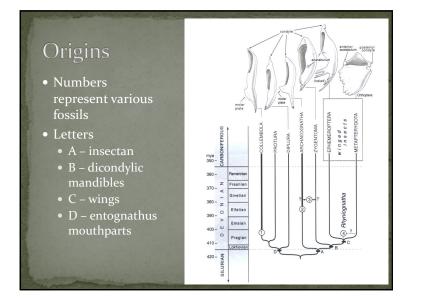
### Rhyniella

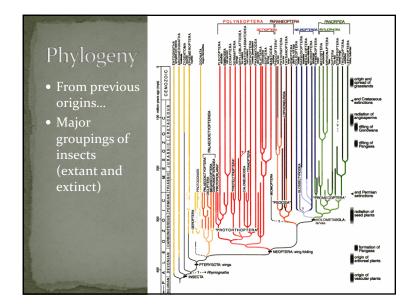
- Rhynie Chert (Scotland)
- Devonian (360 400 Ma)
- Mandibles are more representative of winged insects than primitive groups
- This has lead some to suspect origin of insects is Silurian
- Recent molecular study placed origin (of insects) in Ordovician

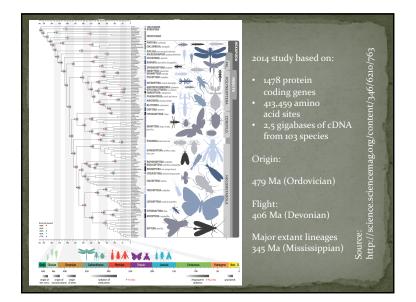












Why so many species of insects?
<ul> <li>Age – earliest known fossil insect from early Devonian</li> <li>Probably evolved in Ordovician (&gt; 479 Ma)</li> <li>As terrestrial ecosystems evolved, insects were present and readily exploited new resources</li> </ul>
<ul> <li>Design – cascade of innovations</li> <li>Exoskeleton – physical protection</li> <li>Segmentation (and repetition) allows specialization of some appendages while retaining original functions of others</li> <li>Flight – escape from predators, disperse to new areas</li> <li>Larval stage – exploit different diets from adults</li> </ul>

### Why so many species of insects? (2)

- Capacity for high rates of speciation consider
  - Lepidoptera and plant eating beetles
  - Roughly 250,000 species (majority feed on angiosperms)
  - Angiosperms have been around at best 100 million years
  - Short generation time (life span)
  - Coupled with high reproductive rates
  - Consider *Drosophila melanogaster* (fruit fly)
    - Suppose 1 female lays 100 viable eggs
    - Half of these produce viable females that do the same
    - At the end of 25 generations mass would be larger than the earth itself

### Why so many species of insects? (3)

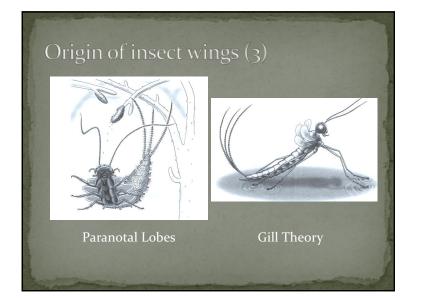
- Low rates of natural extinction
- Consider Cretaceous extinctions
- Dinosaurs, many oceanic organisms when extinct
- Negligible effect on insects
- Permian extinctions only 3 major groups went extinct
- Paleodictyopterida, Caloneurodea, Miomoptera
- Yet roughly 95% of life vanished (trilobites and a whole lot more)
- Today experiencing another great extinction spasms
  - Likely insects will remain long after humans

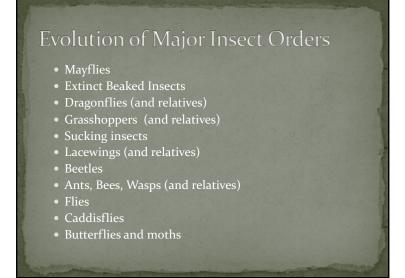
### Origin of insect wings

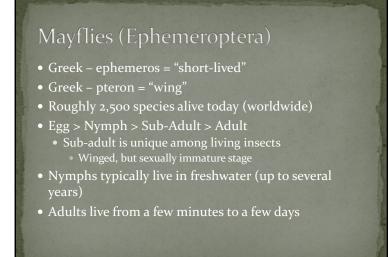
- Insects the only group of invertebrates to achieve powered flight (at least 90 MY before winged vertebrates) [Most recent estimate early Devonian 406 Ma]
  - Improved dispersal capabilities
  - Quick retreat from predators
  - Improved capabilities of finding a mate
- Function of insect wings
  - For most lower pressure on upper surface creates lift (Bernoulli's principle)
  - Indirect (up to 1,000 cycles per second) or direct flight muscles
  - For some (minute species) flight is like swimming through a vat of melted chocolate

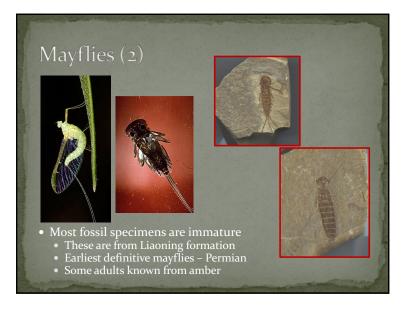
### Origin of insect wings (2)

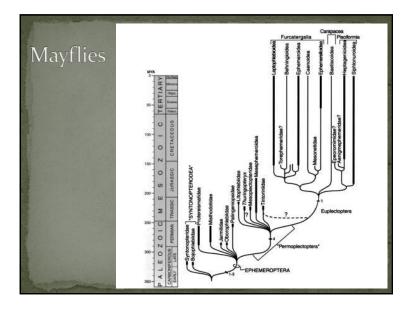
- Single origin for all insects now accepted (Pterygota)
  - Ephemeroptera (mayflies)
  - Paleodictyopterida (extinct beaked insects)
  - Odonatoptera (dragonflies, damselflies and extinct relatives)
  - Neoptera (all remaining winged insects) flex wings over abdomen while at rest
- 2 current/ contrasting theories about origin of insect wings
  - Paranotal lobes fixed extensions of thorax initially gliding
  - Gill theory arose from modified gills on thorax
- Estimated origin in Devonian
  - Paranotal lobes theory has more supporters
  - Still lacking an insect equivalent of *Archaeopteryx*







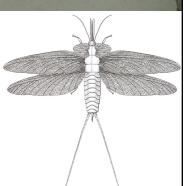


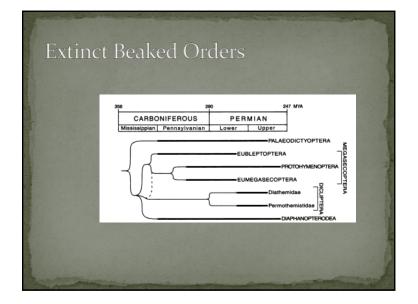




### Extinct Beaked Orders

- Paleodictyoptera (this one reconstructed from Carboniferous of France)
- Most common insects of Paleozoic
- Note prothoracic paranotal lobes
- Mouthparts designed for piercing/ sucking
- Some quite large (up to 22 inches)
- Most likely herbivorous





### Extinct Beaked Orders

- Key fossils
  - Dunbaria fascipennis
  - Permian
  - Elmo, KS
  - Note striking patterns on this paleodictyopteran

### ris

### Extinct Beaked Orders (2)

- Key fossils
- Moravia grandis
- Permian
- Midco, OK
- Some paleodictyopteran were large
   This hindwing measures 73 mm wide



### Extinct Beaked Orders (3)

- Key fossils
  - Lithomantis carbonarius
  - Late Carboniferous
  - Scotland
  - Note large paranotal lobes on first thoracic segment

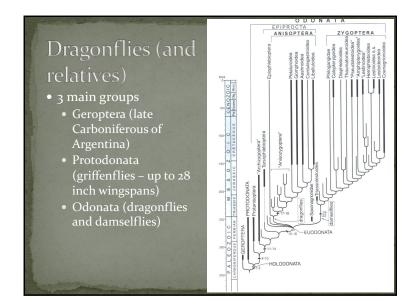




### Dragonflies (and damselflies and griffenflies)

- Greek odon = "tooth"
- Roughly 6,500 species alive today (worldwide)
- Egg > Nymph > Adult
- Nymphs typically live in freshwater (up to several years) and are predators
  - Some species in Hawaii live in moist leaf litter
- Adults are predators
- Common names include: "mosquito hawks," "devil's darning needles," and "snake doctors"
- Some species are estimated to fly at over 55 kph







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### Dragonflies (and relatives) (3) Key fossils *Eoprotoneura hyperstigma*Early Cretaceous

- Santana Formation, Brazil
- Damselfly



### Dragonflies (and relatives) (4)

- Key fossils
  - Pseudomacromia sensibilis
  - Early Cretaceous
  - Santana Formation, Brazil
  - Dragonfly nymph
     Long antenna may have helped detect prey in dense aquatic vegetation



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### Mark DuBois - Insect Evolution - PRM Talk

### Grasshoppers (and relatives)

- Greek orthos = "straight"
- Greek pteron = "wing"
- Roughly 37,000 species alive today (worldwide)
- Egg > Nymph > Adult
- Grasshoppers, crickets and locusts
- Several smaller orders
- Many produce sound (via stridulation)

### Grasshoppers (and relatives) Embioptera Zoraptera Plecoptera Grylloblattodea Mantophasmatodea Dermaptera Isoptera

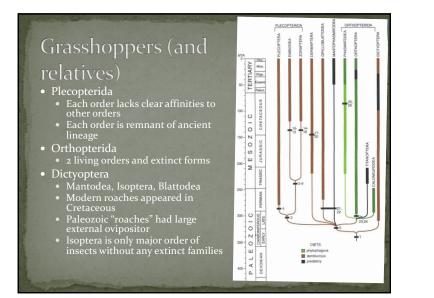












### Termite origins

- "Some primal termite knocked on wood And tasted it and found it good And that is why your cousin May Fell through the parlor floor today."
  - Ogden Nash
- Most termite radiation occurred within a 50 million year span in the early Cretaceous
- Roach *Cryptocercus* (Appalachian Mountains) also contains similar Protozoa

### Grasshoppers (and relatives)

- Key fossils
  - Chresmoda aquatica
  - Early Cretaceous
  - Spain
  - Resemble modern water striders (Heteroptera: Gerridae), but these were relatives of Orthoptera and Phasmatodea



### Grasshoppers (and relatives) (2)

- Key fossils
- Lemmatophora typa
- Early PermianElmo, KS
- Primitive relative of modern stoneflies





### Grasshoppers (and relatives) (4)

- Key fossils
- Zorotypus
- nascimbenei
- Cretaceous amber
- Burma
- Resembles modern
   species



### Grasshoppers (and relatives) (5)

- Key fossils
  - Katydid like
  - Early Cretaceous
  - Brazil
  - Resembles modern species
  - Note long, thin ovipositor





### Grasshoppers (and relatives) (7)

- Key fossils
  - Earwig
  - Miocene amber
  - Dominican Republic
  - Resembles modern species

## <section-header> Grasshoppers (and relatives) (8) Key fossils Tillyardembia antennaeplana Permian Russia Early relative of Grylloblatodea (rock crawlers)

### Grasshoppers (and relatives) (9)

- Key fossils
  - Phylloblatta gallica
  - Late Carboniferous
  - France
  - Closely resemble modern roaches, but have large ovipositor



### Grasshoppers (and relatives) (10)

- Key fossils
  - Karataublatta longicaudata
  - Late Jurassic
  - Kazakhstan
  - Closely resemble modern roaches, but have large ovipositor
  - One of last times "roachoids" appear in fossil record



### Grasshoppers (and relatives) (II)

### • Key fossils

- Blatellidae
- Early Cretaceous
- Brazil
- Ootheca (egg case) still lodged in terminalia



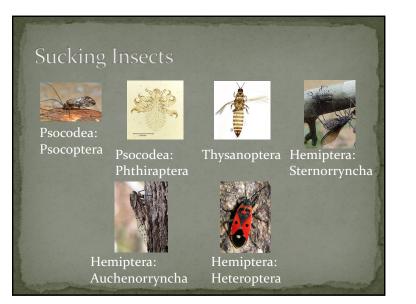
### Grasshoppers (and relatives) (12)

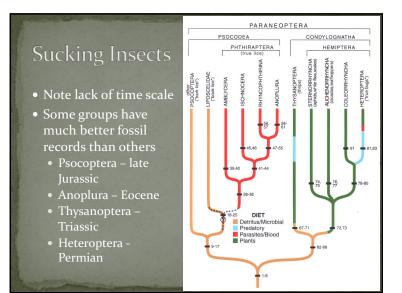
- Key fossils
  - Santanmant
  - axelrodi
  - Cretaceous
  - Brazil
- Primitive mantis



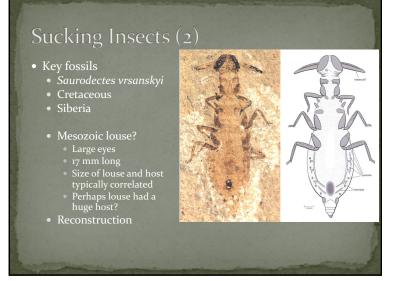
### Sucking insects

- Roughly 102,000 species alive today (worldwide)
- Egg > Nymph > Adult
- Bark lice, true lice, thrips, aphids, cicadas, true bugs
- Some produce ultrasound (communicate via plant sap)
- Some produce sound (cicadas)
- Many species are easily overlooked (small in size, secretive)

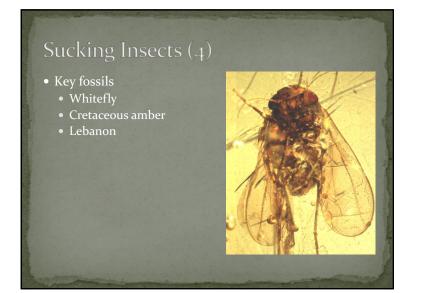


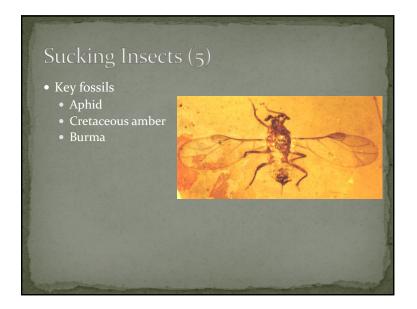










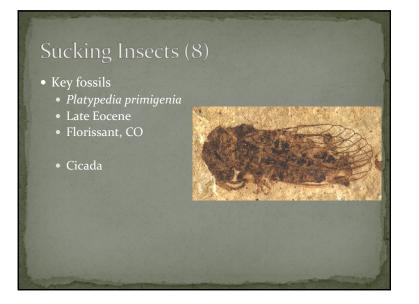


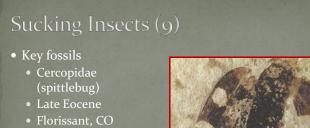
### Sucking Insects (6)

- Key fossils
  - Scale insect
  - Miocene amber
  - Dominican Republic
  - Acropyga queen ant carrying scale insect (she takes one or more when founding a new ant colony)







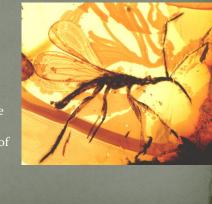


 Nymphs of living species typically live in protective mass of spittle



### Sucking Insects (10)

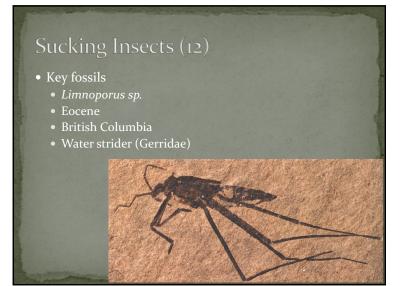
- Key fossils
  - Enicocephalidae
  - Early Cretace
     amber
  - Lebanor
  - Most primitive "true bugs"
  - Sister group to rest of <u>Het</u>eroptera



### Sucking Insects (11)

- Key fossils
  - Duncanovelia extensa
  - Early Cretaceous
- Australia
- Example of fossil Heteroptera





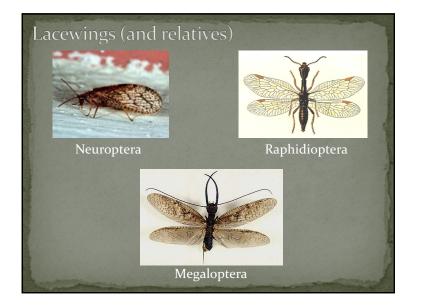
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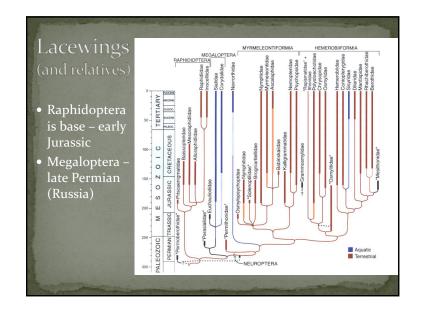
### Origins of "complete" metamorphosis

- All groups discussed to this point have similar development
  - Egg > Nymph > Adult
- Groups we will cover next have a different development
  - Egg > Larva > Pupa > Adult
- Two theories
  - Pupa developed as intermediate form as young and adults increasingly differed
  - Preferred larvae are essentially free living embryos
     Most hemimatabolous insects have a brief pronymph stage (between hatching from egg and first instar)

### Lacewings (and relatives)

- Roughly 25,000 species alive today (worldwide)
- Egg > Larva > Pupa > Adult
- Neuroptera, Megaloptera, Raphidioptera
- These three are a sister group of the beetles

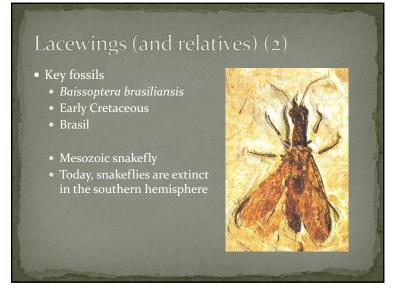




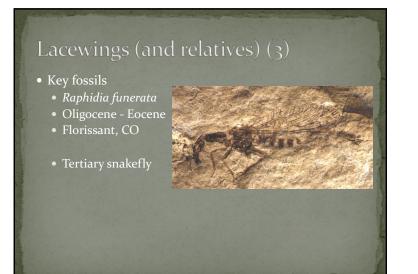


- Key fossils
  - Mesoraphidia pterostigmalis
  - Late Jurassic
  - Kazakhstan
  - Mesozoic snakefly

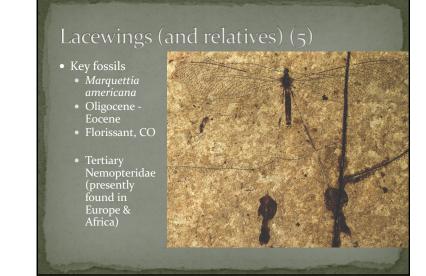




### Mark DuBois - Insect Evolution - PRM Talk









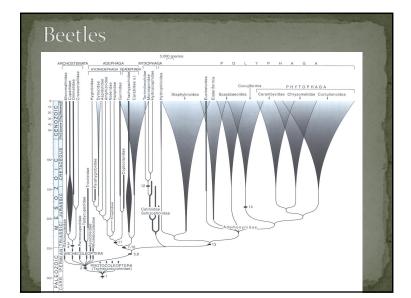


### Beetles (Coleoptera) Greek - koleos= "sheath" Greek - pteron = "wing" Roughly 350,000 species alive today (worldwide) Every one in four animals is a beetle Most of diversity achieved by late Jurassic Egg > Larva > Pupa > Adult Strepsiptera is a sister group (small, parasitic)

### Beetles

- Examples of some diversity
- Major groups
- Archostemata (35 extant species most ancient)
- Myxophaga (65 extant species)
- Adephaga (10% of all beetle species – ground and aquation beetles)
   Mostly predators
- Polyphaga (90% of all beetle species)
  Highly varied diets





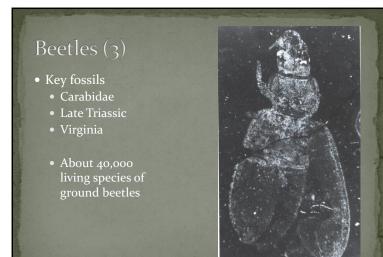
### Beetles

- Key fossils
- Cupedidae
- Early Cretaceous
- Spain

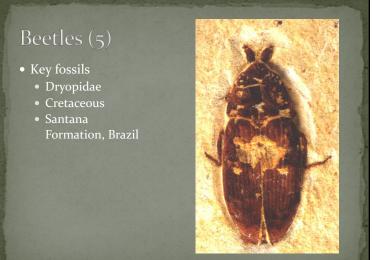
### Group was diverse throughout early Mesozoic, but declined in Cretaceous

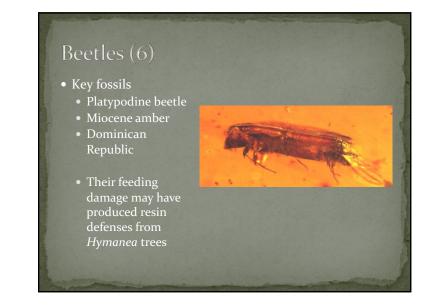




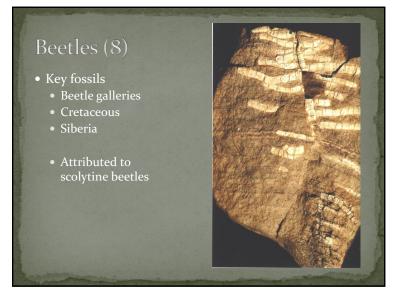






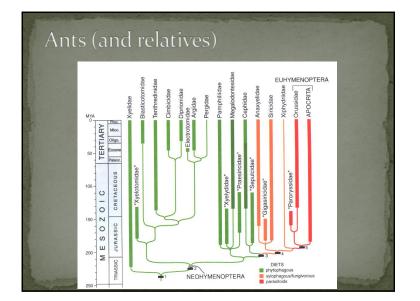


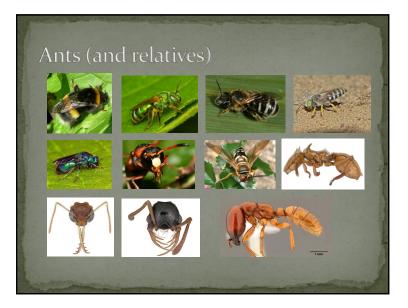


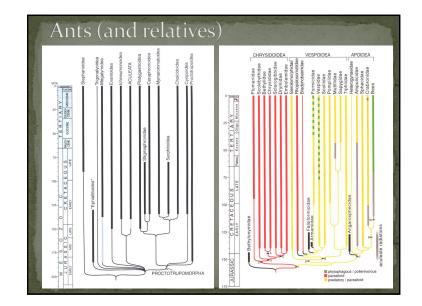


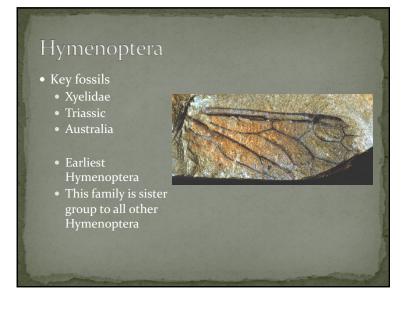
### Ants (and relatives)

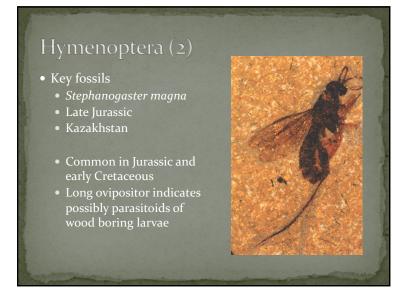
- Greek hymen = "membrane"
- Greek pteron = "wing"
- Roughly 125,000 species alive today (worldwide)
- Estimated there may be up to 1,200,000 species when fully studied
- Egg > Larva > Pupa > Adult
- Outside of termites, most of the social insects belong to this group (ants, bees, wasps)

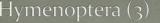












- Key fossils
  - Ensign wasp
  - Miocene amber
  - Dominican Republic
  - Modern members of Evaniidae are parasitoids of cockroach ootheca





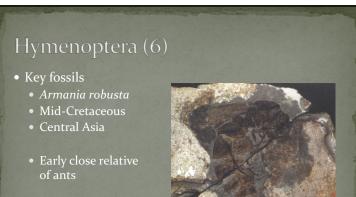
### Hymenoptera (5)

### • Key fossils

- Zacryptocerus sp.
- Miocene amber
- Dominican Republic

### Many ants are known from amber inclusions





### Hymenoptera (7)

- Key fossils
  - Cariridris bipetiolata
  - Early Cretaceous
  - Santana Formation Brazil
  - Possible ant (also attributed to Ampulicidae)



### Hymenoptera (8)

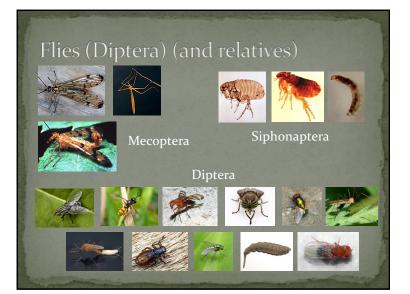
- Key fossils Brownimecia
- clavata
- Cretaceous amber
- New Jersey
- Early ant (90 Ma)

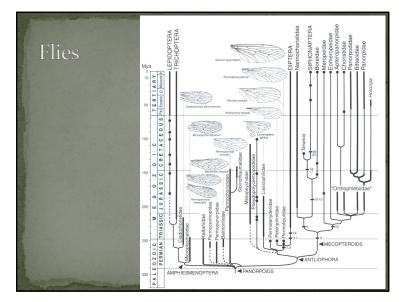




### Flies (Diptera)

- Greek di= "two"
- Greek pteron = "wing"
- Roughly 120,000 species alive today (worldwide)
- Estimated at least that many more species waiting to be described
- Egg > Larva > Pupa > Adult
- Group contains most dangerous animals on earth
- Vectors of malaria, plague, yellow fever, dengue fever, encephalitis, West Nile virus (and a host of other diseases)





### Flies (and relatives)

### • Key fossils

- Mecopteroid insects
- Early Cretaceous
- Yixian Formation, China
- Examples of scorpionflies





### Flies (and relatives) (2) Key fossils Strashila incredibilis Late Jurassic Siberia Apparently

- ectoparasitic mecopteroid • Hind legs probably
- used for grasping host
- Function of abdominal lobes unknown





### Flies (and relatives) (3)

• Key fossils

- Holcorpa maculosa
- Oligocene
- Florissant, CO
- Note genitalia at end of very long folded stalk



### Flies (and relatives) (4) Key fossils Rhopalopsyllidae Miocene amber

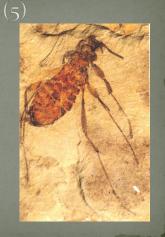
- Dominican Republic
- Modern members of this family feed on rodents



### Flies (and relatives) (5) • Key fossils

- Tarwinia australis
- Early Cretaceous
- Australia

### Likely an early relative of fleas (has some, but not all features of modern fleas)



### Flies (and relatives) (6)

- Key fossils
- Tipuloidae: Limoniidae
- Early Cretaceous
- Brazil
- Tipulids are considered to be most "primitive" of living flies



### Flies (and relatives) (7

- Key fossils
  - Procramptonomyiidae
  - Jurassi
  - Kazakhstan
  - Extinct close relative of Bibionid flies



### Flies (and relatives) (8)

- Key fossils
- Araripogon axelrodi
- Early CretaceousBrazil
- Robber fly (Asilidae)
- Modern family contains over 5,000 species
- Adults are all predators



### Flies (and relatives) (9)

### • Key fossils

- Horsefly (Tabanidae)
- Oligocene
- Florissant, CO
- Note well preserved large proboscis

### Flies (and relatives) (10)

- Key fossils
  - Glossina oligocena
  - Oligocene
  - Florissant, CO
  - Tsetse flies now restricted to sub-Saharan Africa
- This species was twice as large as modern forms



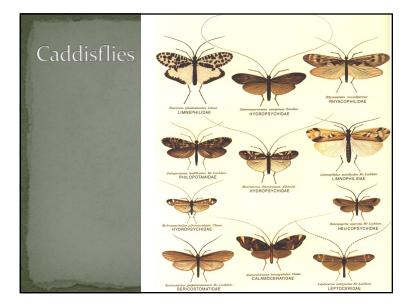
### Flies (and relatives) (11)

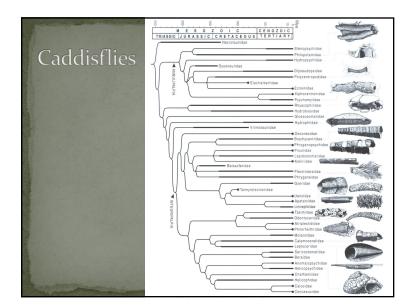
- Key fossils
  - Prosphyracephala sp.
  - Eocene
  - Baltic amber
  - Similar to modern species of stalk eyed flies



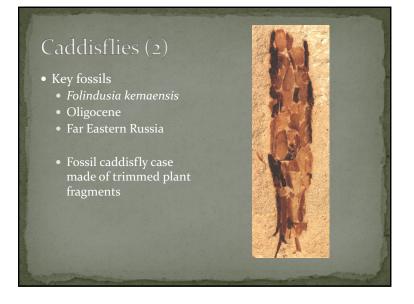
### Caddisflies (Trichoptera)

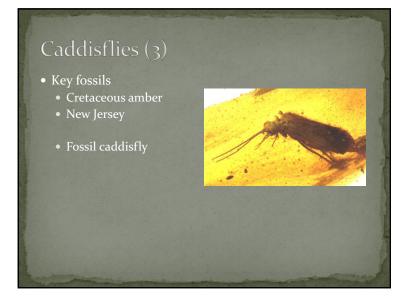
- Greek trich = "hair"
- Greek pteron = "wing"
- Roughly 11,500 species alive today (worldwide)
- Egg > Larva > Pupa > Adult
- Larvae are aquatic (many live in cases they build)
- Only group (besides midges) where some larvae develop in seawater - Chathamiidae - Australia and New Zealand)
- Oldest definitive Trichoptera Early Jurassic (Germany)







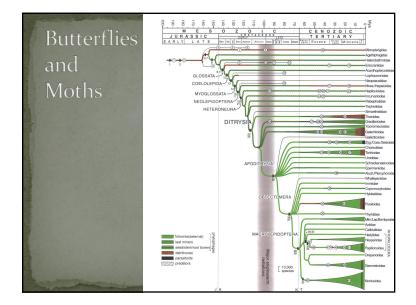






### Butterflies and Moths (Lepidoptera)

- Greek lepidos = "scale"
- Greek pteron = "wing"
- Roughly 180,000 species alive today (worldwide)
- Egg > Larva > Pupa > Adult
- Some larvae are economic pests
- Largest lineage of plant feeding organisms
- Fossil record is rather sparse
- Likely arose in Jurassic and diversified significantly in Cretaceous and early Tertiary



### Butterflies and Moths

- Key fossils
  - Protodryas persephone
  - Eocene
  - Florissant, CO
  - Butterfly shown to Frank Carpenter by Samuel Scudder
    - Inspired Frank
       Carpenter to spend 70
       years studying fossil
       insects at Harvard

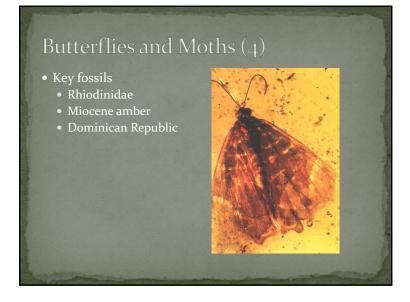


### Butterflies and Moths (3)

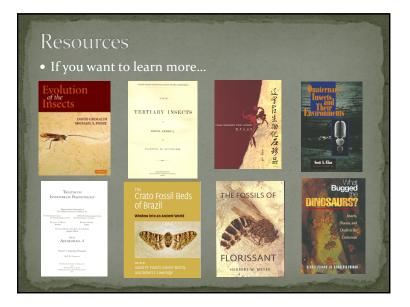
• Key fossils

- Chlorippe wilmattae
- Eocene
- Florissant, CO

### nattae







### More Resources

- Websites
  - http://tolweb.org/tree/
  - http://tolweb.org/Insecta
  - http://www.yale.edu/ypmip/locations/florissant/index.html
     http://www.nps.gov/archive/flfo/online\_museum/index.html
  - http://www.3dotstudio.com/amberhome.html
  - http://www.espd.com/amber/index.htm
- Many other resources use your favorite search engine

