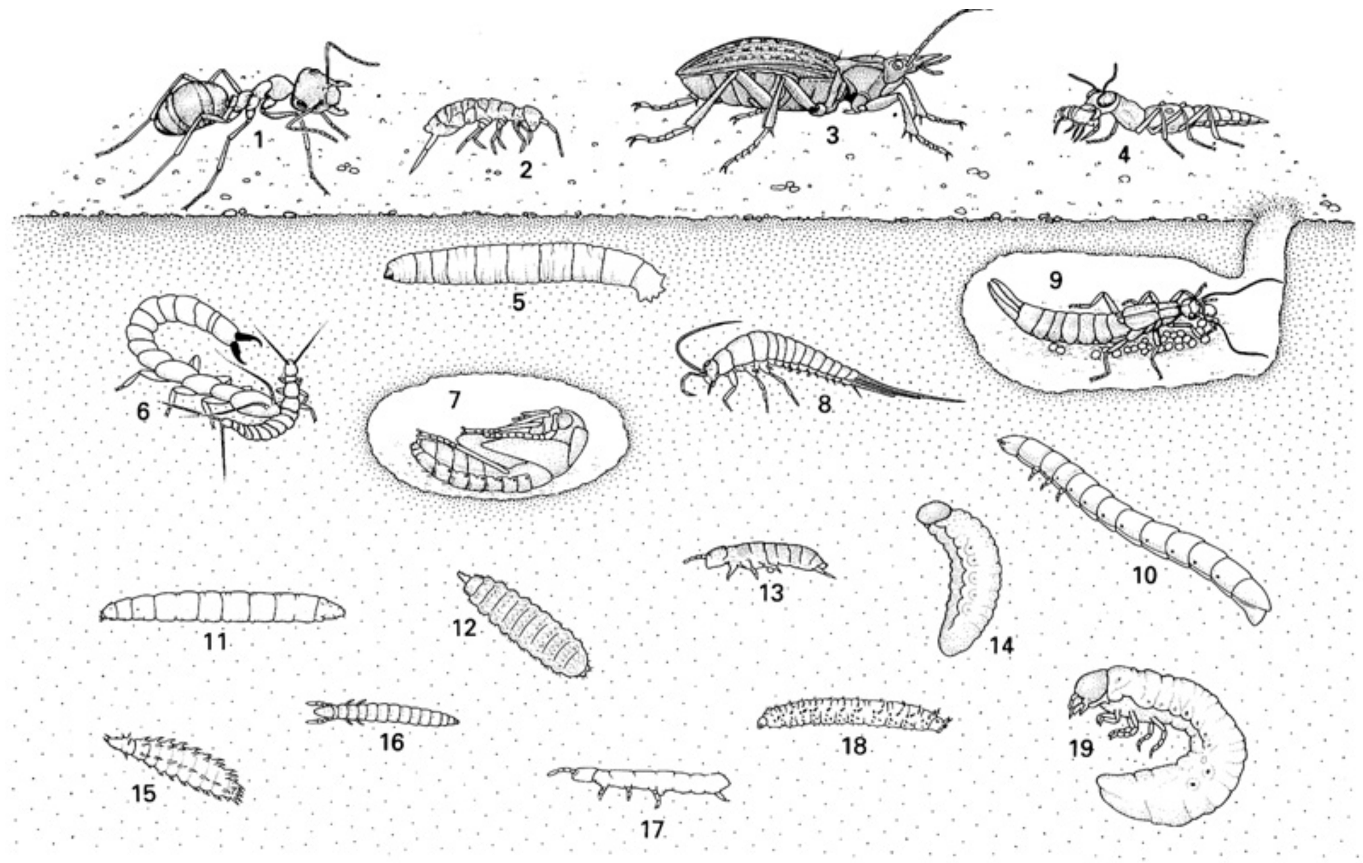
What do insects do for a living?

Insect Ecology

Ground-dwelling: Where are they found and what are they doing?



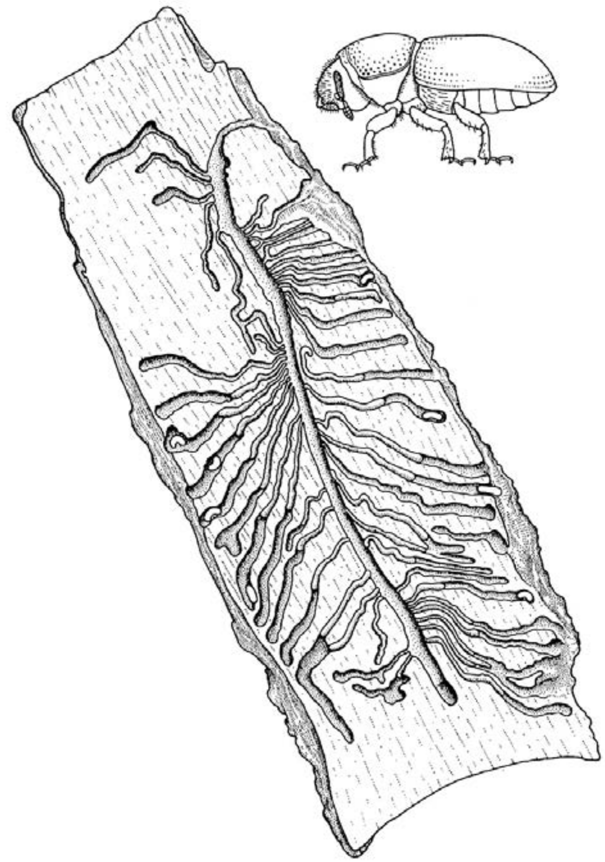
Common habits

- Detritivores and saprophages
- Rhizophagous insects
- Predators and ground-nesting insects
- Decaying wood
- Coprophages
- Necrophages
- Fungivores

Predators & Ground-nesters

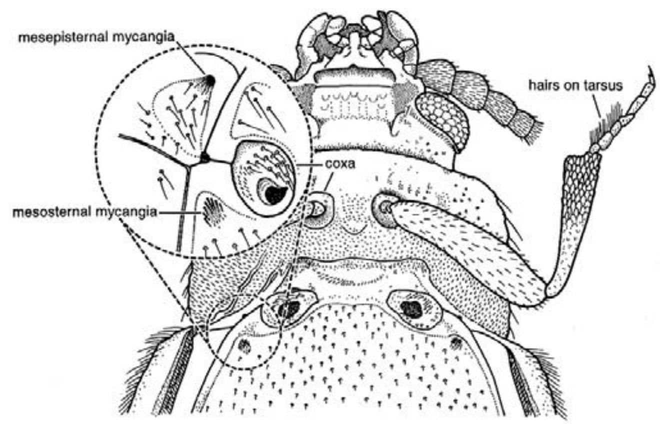
Decaying Wood

- Usually associated with fungi
  - What else is there?
- Numerous taxa
  - Wood wasps, bark beetles, ambrosia beetles, scavenger beetles, silken fungus beetles, dance flies, termites, cockroaches.



Associations with fungi

- Most have specialized structures for carrying fungal spores: **mycangia.**
- Why are most attracted to forest fires?: **pyrophilous**.

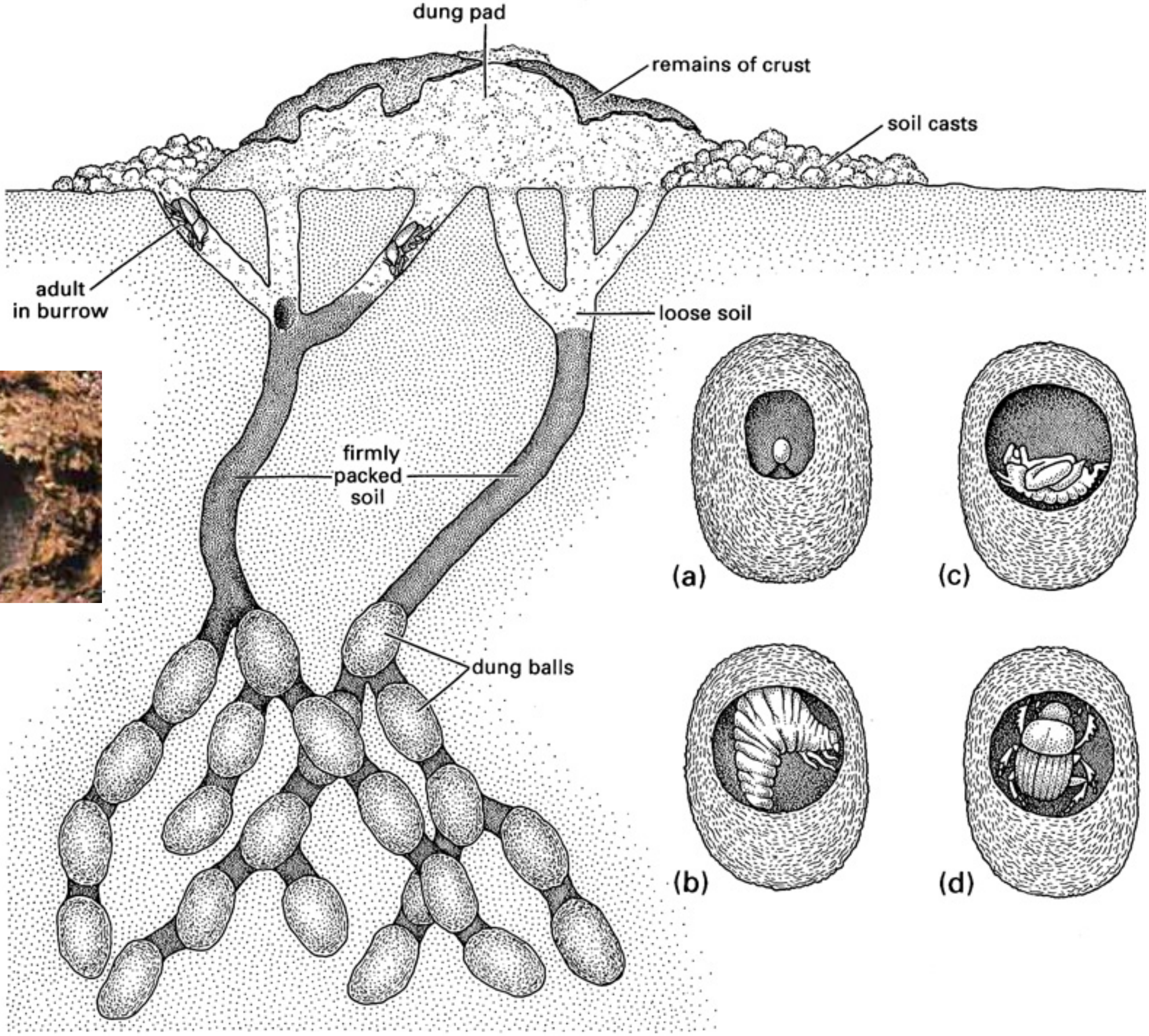


Coprophages

- What are these?
- What are they feeding on?
- Why is this such a good lifestyle?
- First colonization usually dung flies.
- ~45 independent origins of viviparity. Why?

Coprophages

- These can get to nuisance levels.
- Dung dispersers therefore provide an important ecosystem service.
- Almost always Scarabaeidae


dung pad
remains of crust
soil casts
adult in burrow
loose soil
firmly packed soil
dung balls
(a)
(c)
(b)
(d)

Necrophages

- Often a *very* similar lifestyle to coprophages.
- Often very closely related.
- Most other origins of viviparity here.

Necrophages

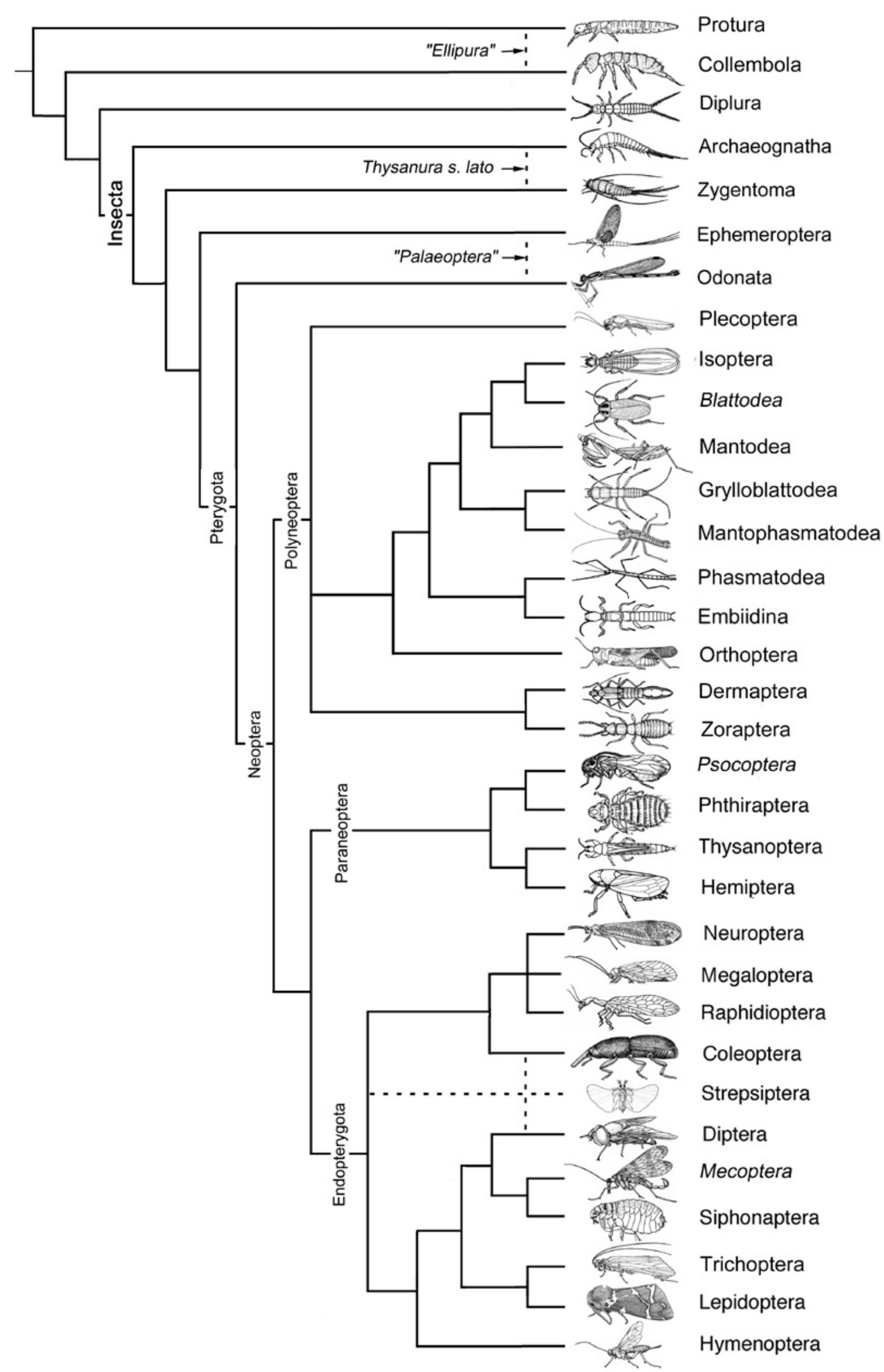
- Often distinct succession.
- Very useful for forensic entomology.
- Most initial colonizers are Diptera.
- Later are Coleoptera (e.g. Silphidae).
- Dried are more Coleoptera (e.g. Dermestidae)
- Final stages are tineid larvae (keratin)

Fungivores

- The true decomposers are fungi.
- There is a whole guild of insects that specialize on these.

Aquatic Insects

- Insecta (even Hexapoda) are plesiomorphically **terrestrial**.
- But there have been numerous colonizations of the **freshwater** aquatic environment.
- Far fewer colonizations of **marine** aquatic environment.

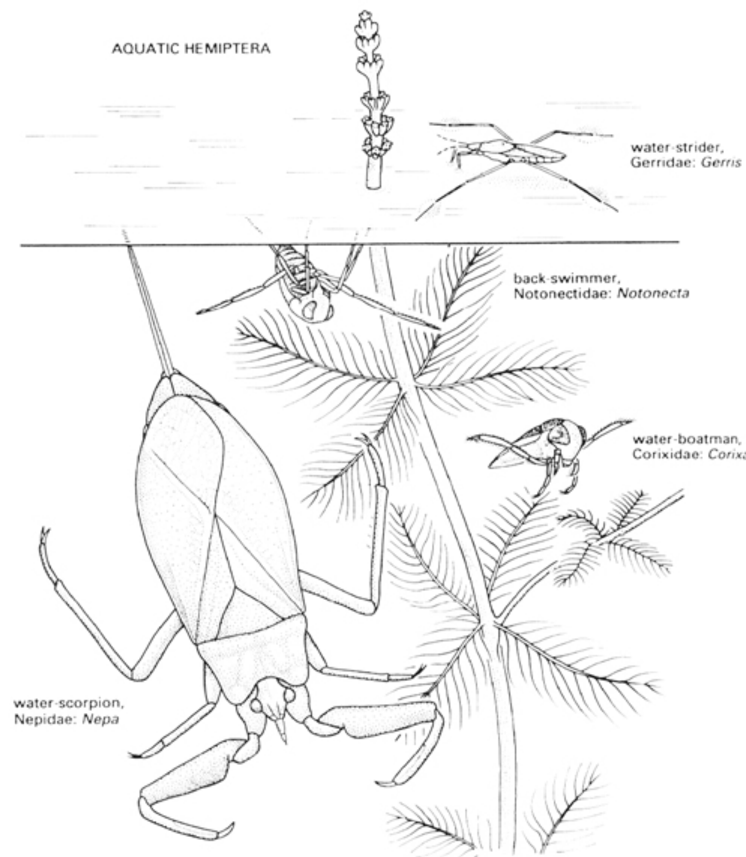


Hemimetabolous Aquatic Insects

- Some lineages have *almost** exclusively aquatic **naiads**.
  - Ephemeroptera
  - Odonata*
  - Plecoptera (the only aquatic Polyneoptera)
- All of these have terrestrial adults.

Hemimetabolous Aquatic Insects

- There are multiple colonizations of aquatic environments by Heteroptera.
- Most of these are also aquatic as adults.



Holometabolous Aquatic Insects

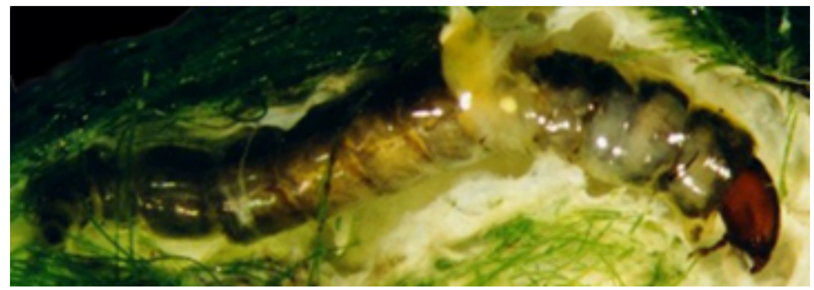
- Colonized aquatic environments much more recently.
- Numerous colonizations within numerous orders
- Only two have exclusively* aquatic larvae.
- Only some Coleoptera remain aquatic as adults.

Holometabolous Aquatic Insects

- Neuroptera: One lineage (Sisyridae, spongillaflies).
  - Osmylidae amphibious
- Coleoptera: Numerous colonizations throughout.
- Diptera: Numerous colonizations, especially in Nematocera.
- Lepidoptera: Numerous origins, but NOT common

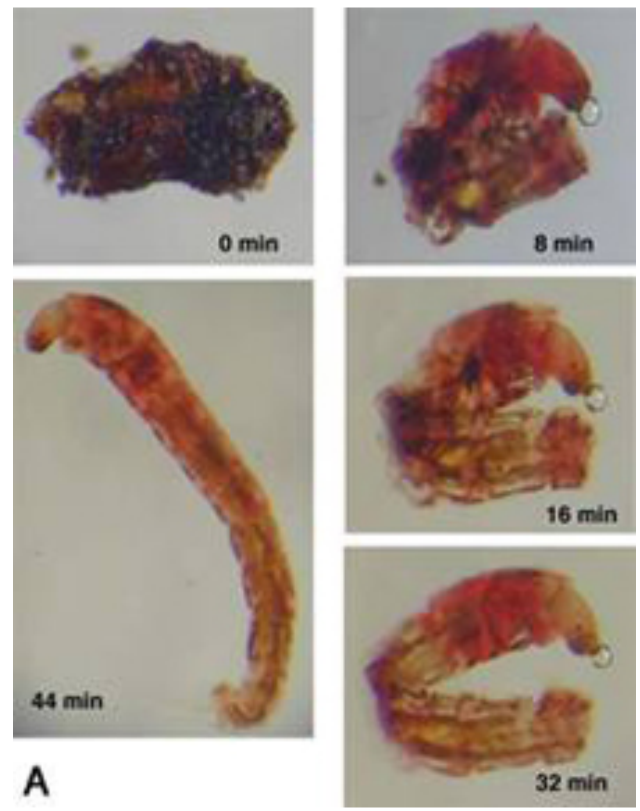
Unusual Aquatic Habitats

- Marine environments
  - Intertidal habitats
    - Between high and low tide
    - biting flies, plant feeding insects, detritivores
  - Littoral habitats
    - Coastal regions with shallow water
    - Some midges and beetles
  - Open ocean: water striders feeding on food of terrestrial origin
- RARE! WHY???

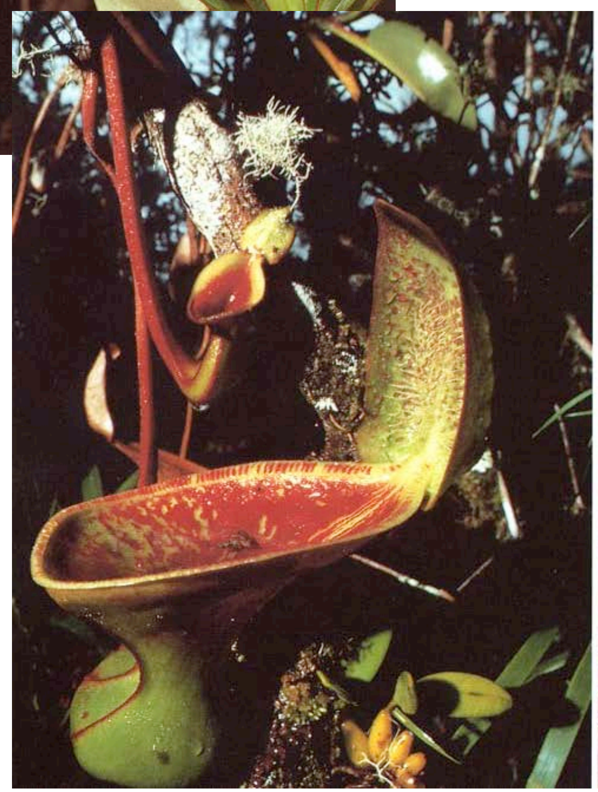
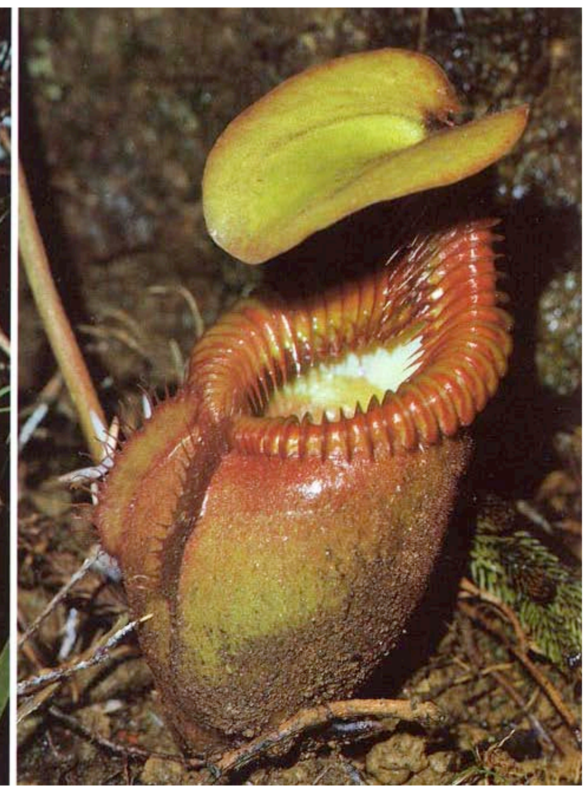


Unusual Habitats

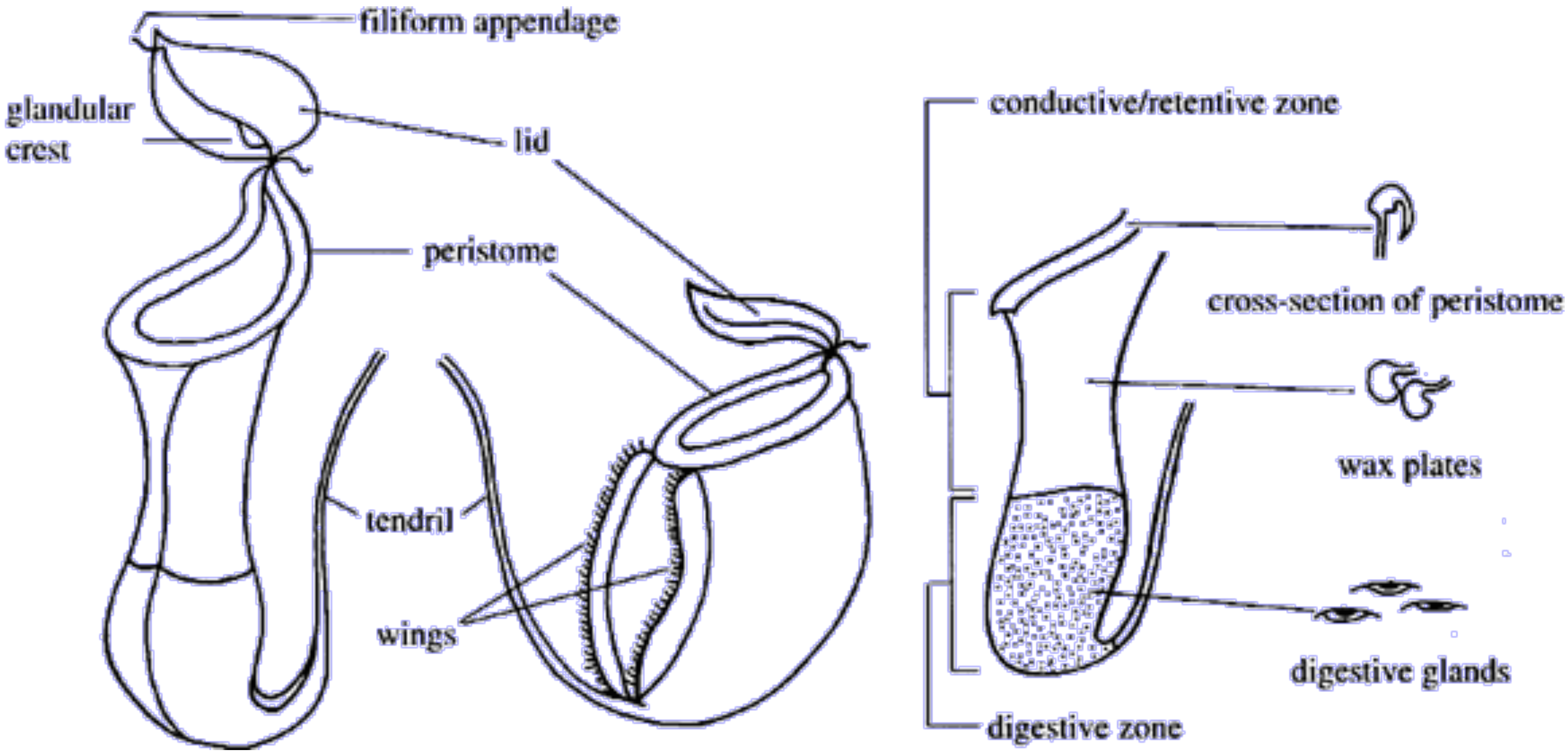
- Temporal water bodies (e.g. vernal pools)
  - Common in areas with seasonal rainfalls
- Numerous adaptations
  - Ability to find ephemeral pools (meteorological cues?)
  - Desiccation resistant diapause
    - Very common as eggs
    - Some with ability to undergo numerous dehydrate/rehydrate cycles: **anhydrobiosis**
- Plant container habitats: Phytotelmata




Nepenthes pitcher plants

Nepenthes anatomy



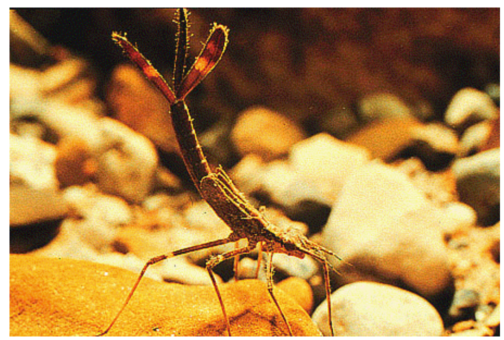
Nepenthes are carnivorous plants

But they rely on
DECOMPOSERS

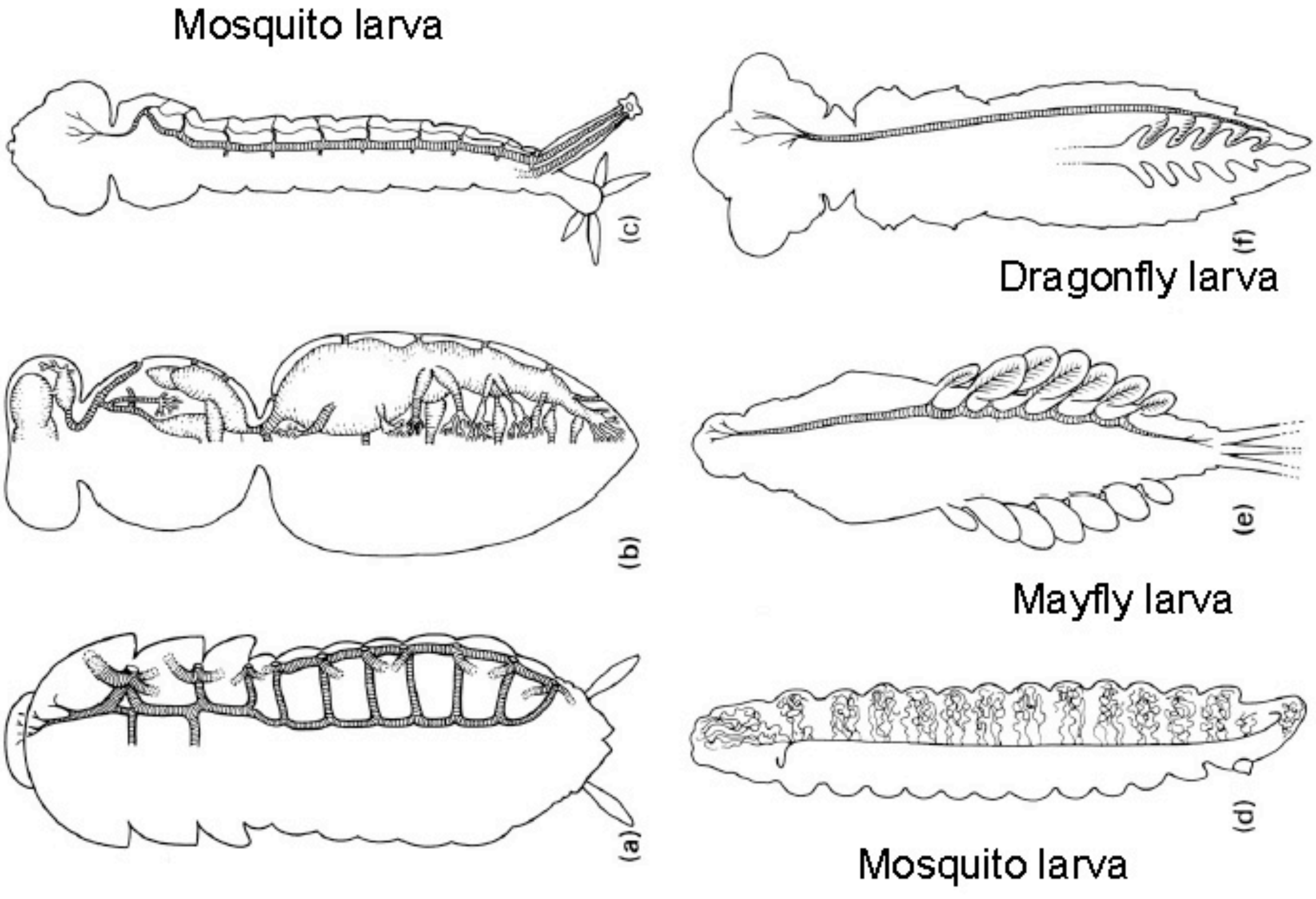
How do aquatic insects obtain oxygen?

- Atmospheric oxygen
  - Keep part of body out of water
  - Carry oxygen into water
- Aqueous oxygen
  - Use of open tracheal system
    - Adult insects
    - Immature forms
  - Use of closed tracheal system
    - Specialized structures for gas exchange in water
    - Often adults have open tracheal system



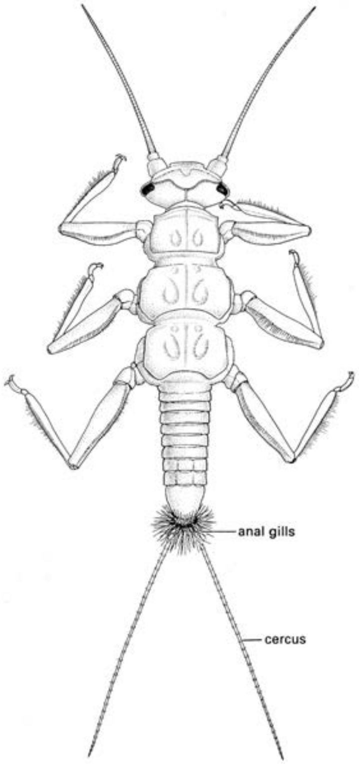



Tracheal System



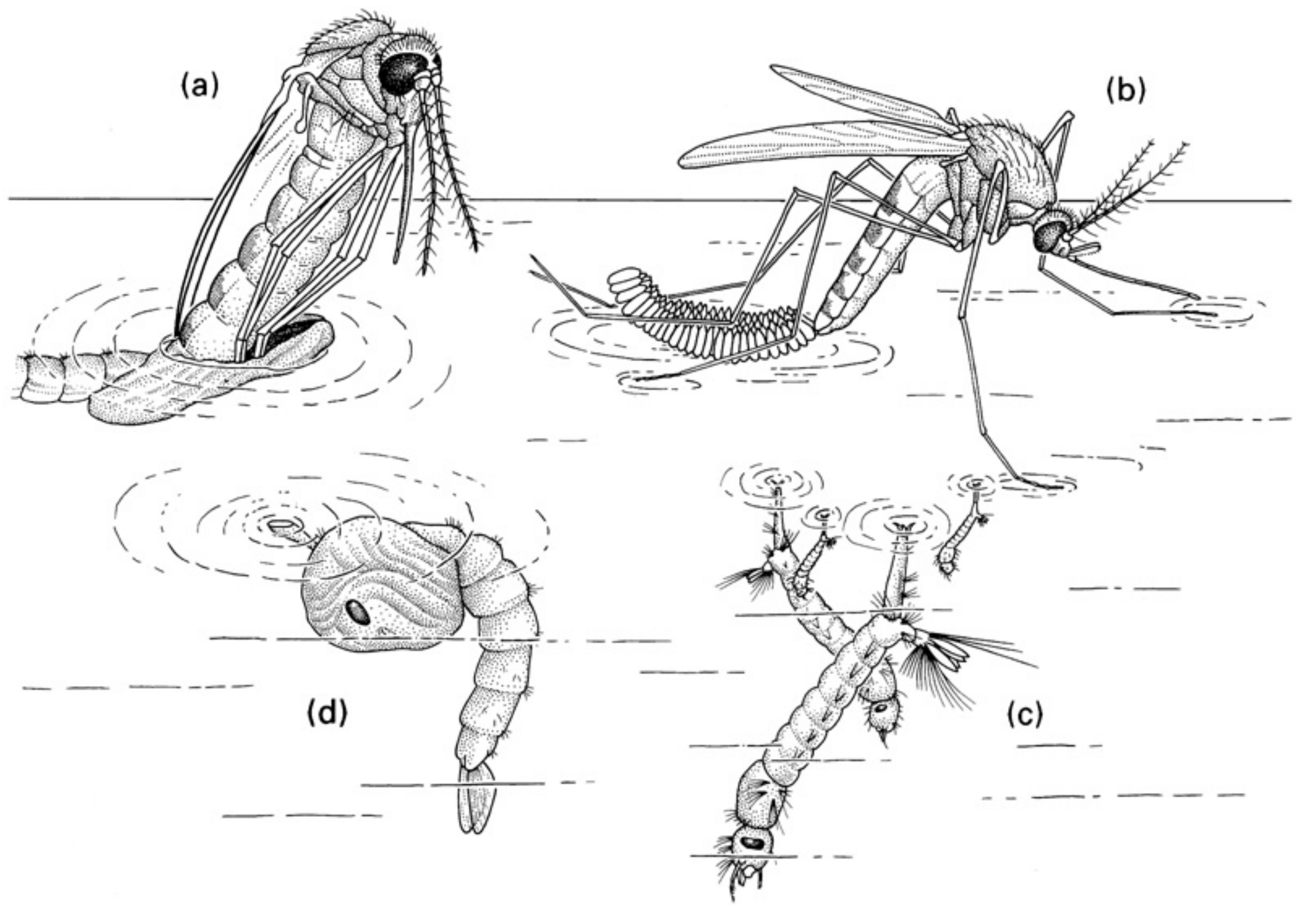
Closed Tracheal System

- Gills- lamellar extensions of tracheal system
- Found in many insect orders
- Gills may be in many places
  - Base of legs
  - Abdomen
  - End of abdomen
  - How is this analogous to insect ears?



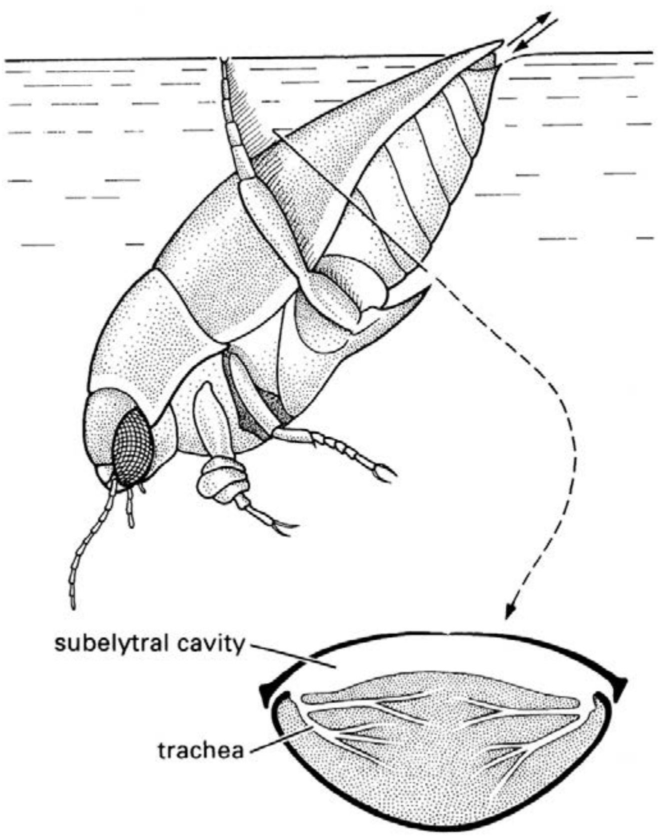
Open tracheal system in flies

- Respiratory siphons near abdomen or thorax
- Different location in mosquito pupa than larva



Open tracheal system in diving beetles

- Bubble stored beneath elytra
- Gas exchange can occur in water



Does the bubble decrease linearly with oxygen consumption?

What happens to the exhalation product?

Other air bubble gills

- Water kept away from body through ‘hairs’ or ‘mesh’
- Oxygen diffuses from water to air against body
- Usually slow moving insects with low oxygen demand

Adaptations to nearly anoxic environments

- Hemoglobins
  - Many larval chironomid midges (Diptera) = bloodworms
  - Some notonectid bugs (Heteroptera) = backswimmers
  - Very, very high affinity for oxygen (unlike us)
  - Only downloads when oxygen concentrations in tissues decrease, not when tissues become acidic

Plant Insect Interactions

- Herbivory
- Plant reproduction
- Domatia

Evolution of Insect Herbivory

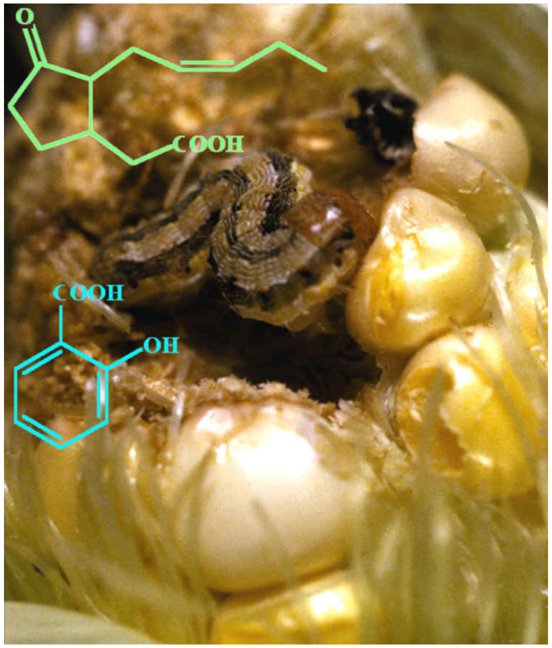
- Early hexapods contact plant parts in soil
- Vascular plants diversfied 300 MYA
- Fossil traces of insect eating appear shortly thereafter
- Early herbivores often beetles

Cretaceous

- What major plant radiation occurred in the Cretaceous,145 – 65 mya?
- Radiations

Challenges of phytophagy

- Clinging to vegetation
- Subject to desiccation
- Inferior diet
- Plant defenses



Diet Breadth

- Monophagous
  - Feeds on one plant taxon
- Oligophagous
  - Feeds on only a few plant taxa
- Polyphagous
  - Feeds on many plant taxa

How Insects Feed on Plants

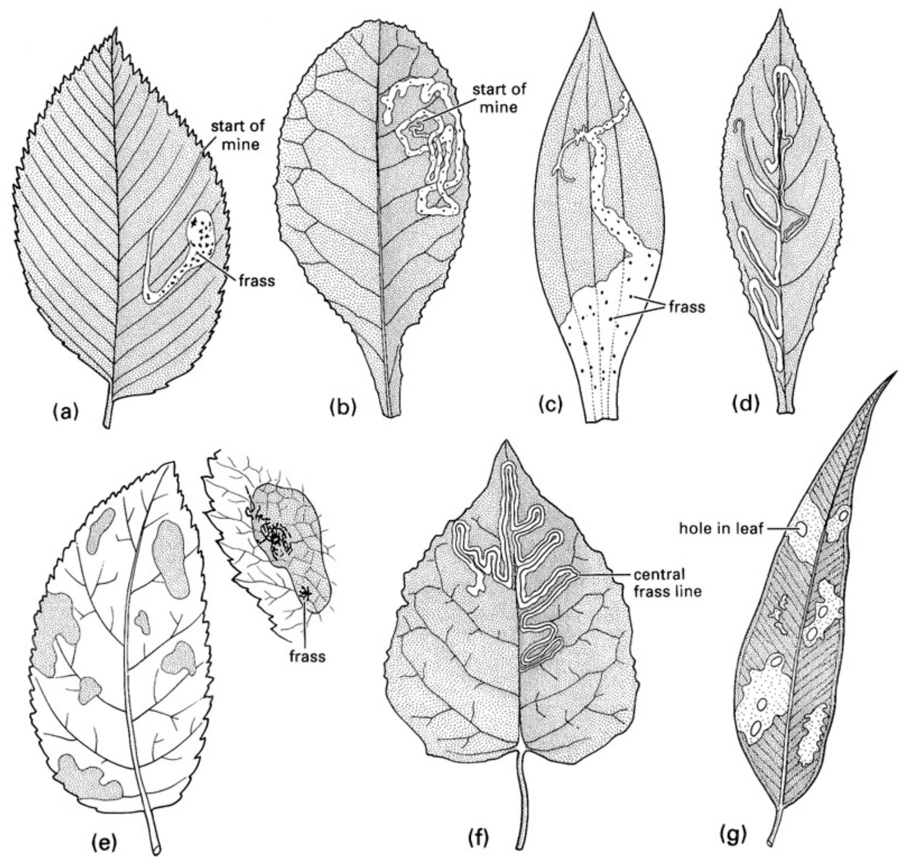
- Chewing
- Sap sucking
- Flower feeding
- Root or shoot feeding Mining
- Boring
- Gall induction
- Seed predation

Chewing & Leaf rolling

- 20-45% of foliage may be normally lost in some plant taxa
- Up to 100% in outbreak conditions
- What risks does leaf chewing have?
- How might leaf rolling combat these?

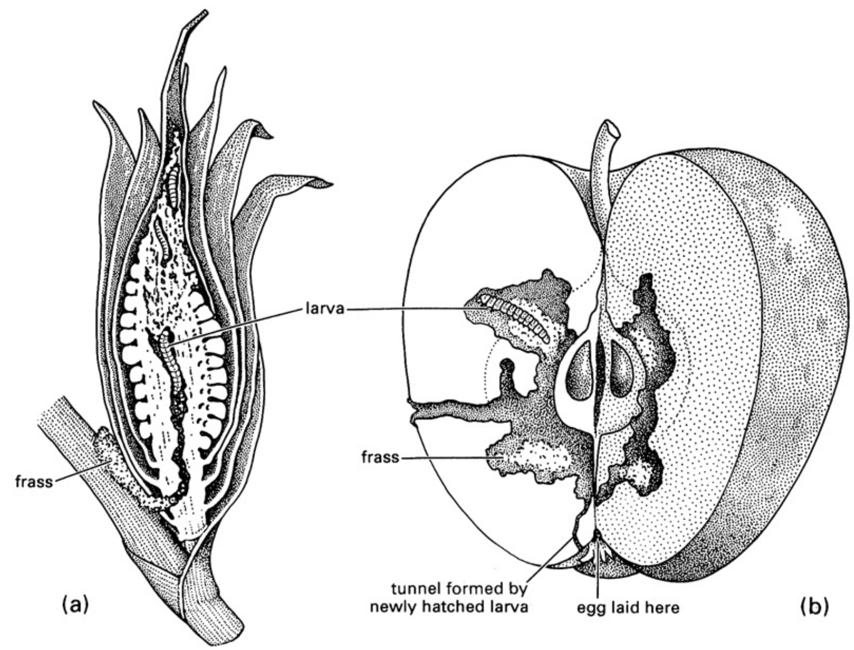
Mining

Living leaves, consumes parenchyma



Boring

Deep tissue
Living or decaying/dead tissue
    What do they consume?

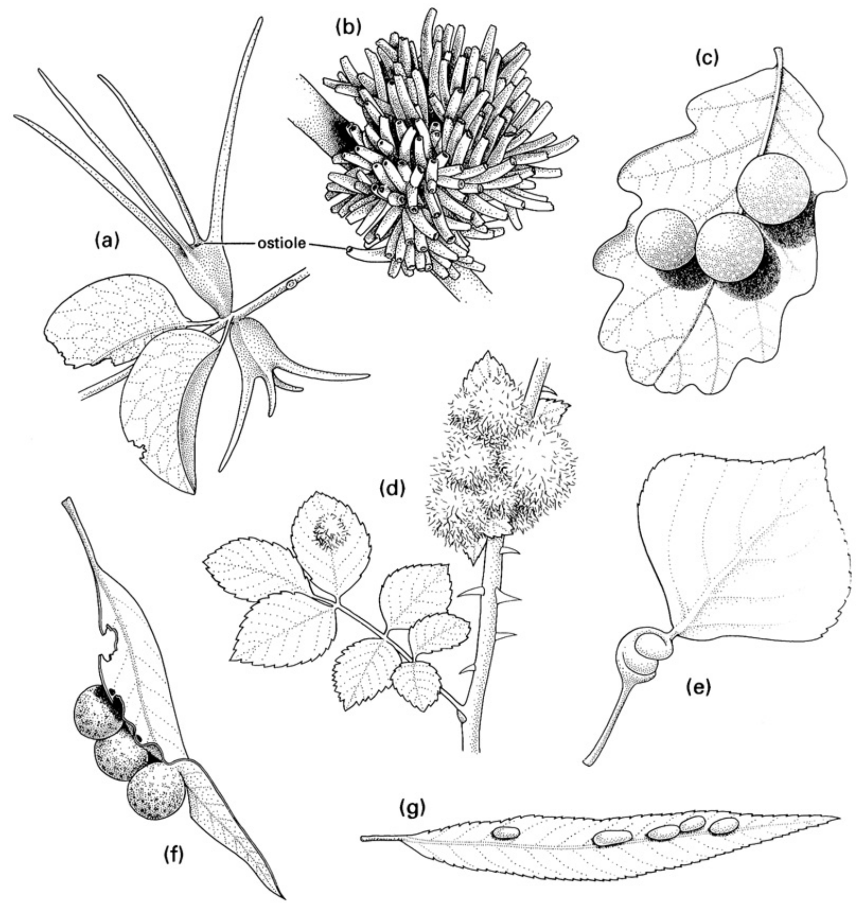


Sap-sucking

- Almost exclusively Hemiptera.
- What structures do they feed from?
- Very low quality food source (especially xylem).
- How do they deal with this?

Gall induction

- Kinds of galls
  - Covering galls
  - Filz galls
  - Pouch galls
  - Mark galls
  - Pit galls
  - Bud and rosette galls



Process

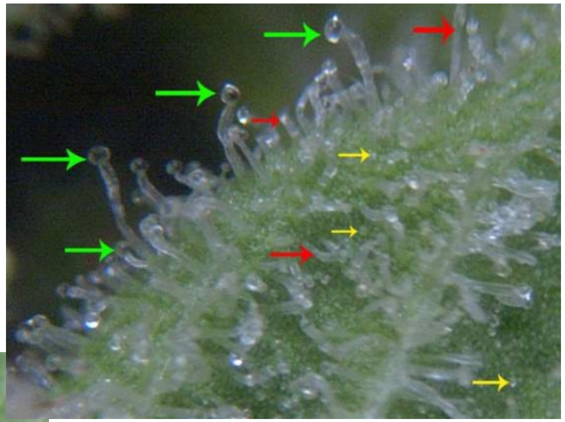
- initiation
- growth
- insects alter plant growth patterns in some way

Seed predation

- Most extreme phytophagy
  - Kills entire plant
  - Converts material intended for plant offspring into insect offspring
- Seed harvesting and external consumption
  - How could this be a mutualism?
- Development inside the seeds

Plant defenses

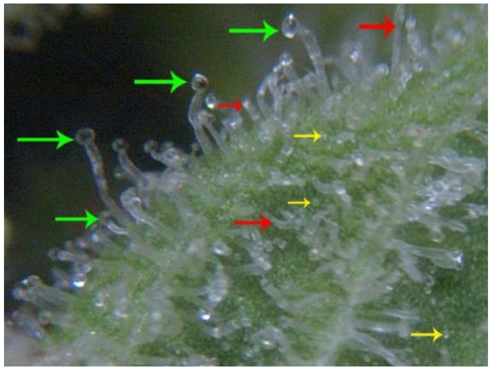
- Physical
- Chemical
- Mutualisms
- Life history traits



Physical defenses

- What are some that you can think of?

- Physical defenses against insects more subtle
  - Glandular trichones
  - Stellate hairs
  - Thick wax
  - Silica crystals
  - Sclereids



Chemical defenses

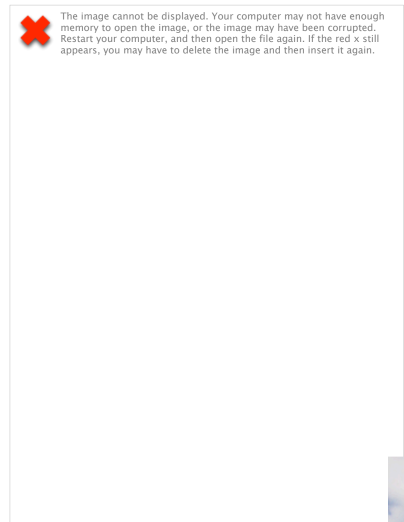
- Secondary plant compounds
  - Defensive chemicals
  - Not principally metabolic (although might be derived from these)
- Effects:
  - Repellant or inhibit oviposition or feeding
  - Toxic

Why is mustard pungent?

L-canavanine Inhibits growth in most insects

Plant apparency

- Plants are *apparent* if they are easy to find (do not require unique neural searching mechanisms by enemies).

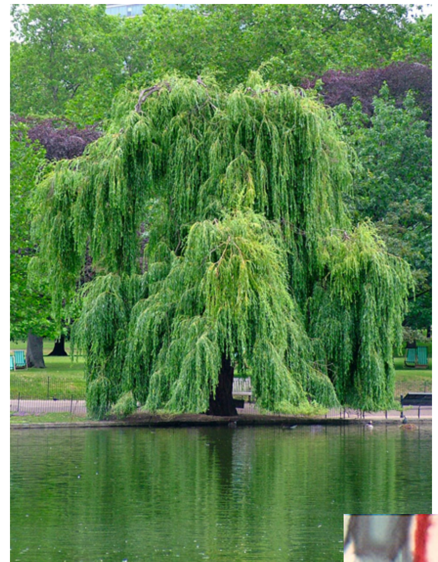


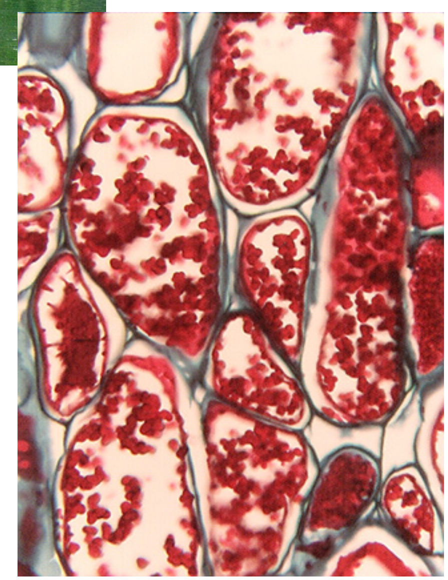
Plant apparency

- Plants are *unapparent* if they are difficult to find (require unique neural searching mechanisms by enemies).

Plant apparency

- **Quantitative defenses:**
  - Quantitative defenses: dose-dependent, defend against *generalist* enemies
  - Which types of plants will have these?





Plant apparency

- **Qualitative defenses:**
  - Qualitative defenses: lethal in small doses, defend against *specialized* enemies.
  - What kinds of plants will have these? Why?

Mutualisms

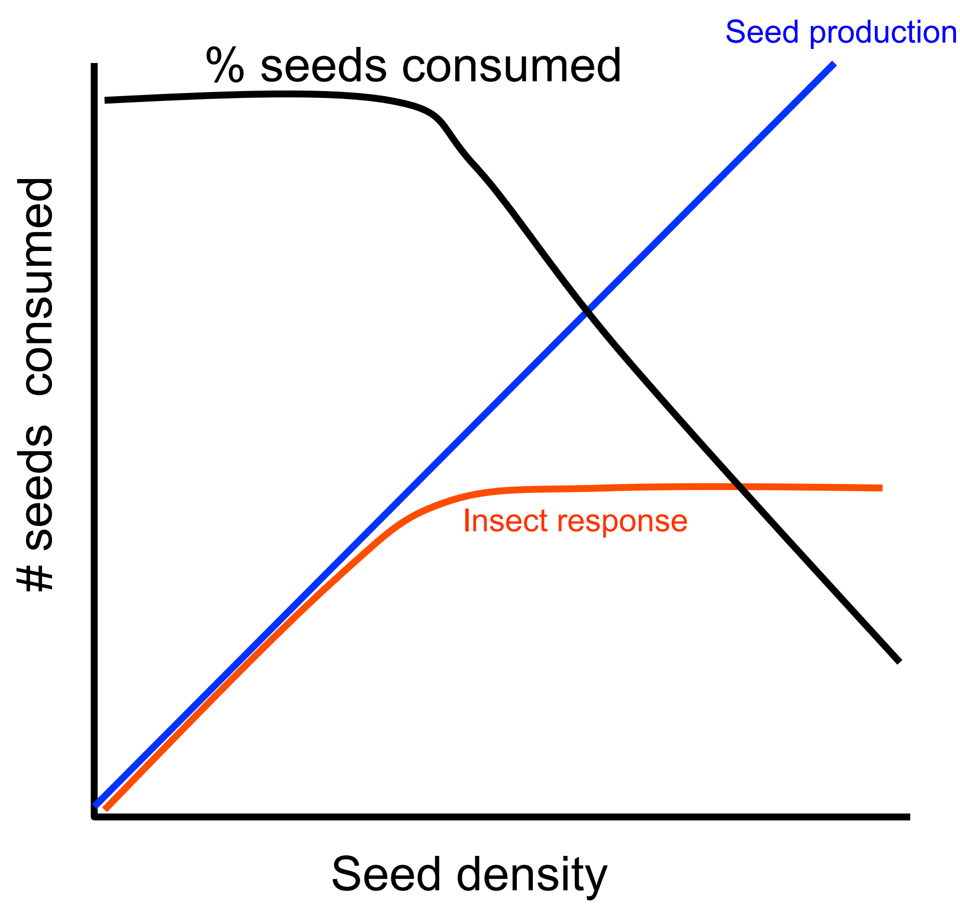
- Almost all plant defense mutualisms involve ants
  - *E.g. Cecropia* and *Acacia*
- Generally provide some **domatia** for the colony
- What is the mutualism?

Life history: Masting

- Predator saturation
- Reproduction by plant populations occurs simultaneously and in massive numbers
- Produce more seeds than intrinsic reproductive capacity of insects can keep up with
- Some seeds will escape insect predation

Predator satiation and Masting

- Seed production by plant is numerical (or linear).
- Predator satiation is the result a functional response.
- Results in decreasing % of prey population being consumed at high density.



Insect-Plant Interactions

- Evolution
  - 50% of all insects feed on plants
  - This great diversification of insects occurred mostly only within last 60 million yrs.
  - Why?

Coevolution

- Evolutionary change (genetic change) in one species causes evolutionary change in another
  - Hot topic in evolutionary biology
  - Predators vs prey- insect-insect interactions
  - Hosts vs parasites
  - Parasitoids and host insects
  - Bacteria versus host insect
  - Mimicry- Batesian and Mullerian
  - Mutualisms- plants and pollinators

Coevolution

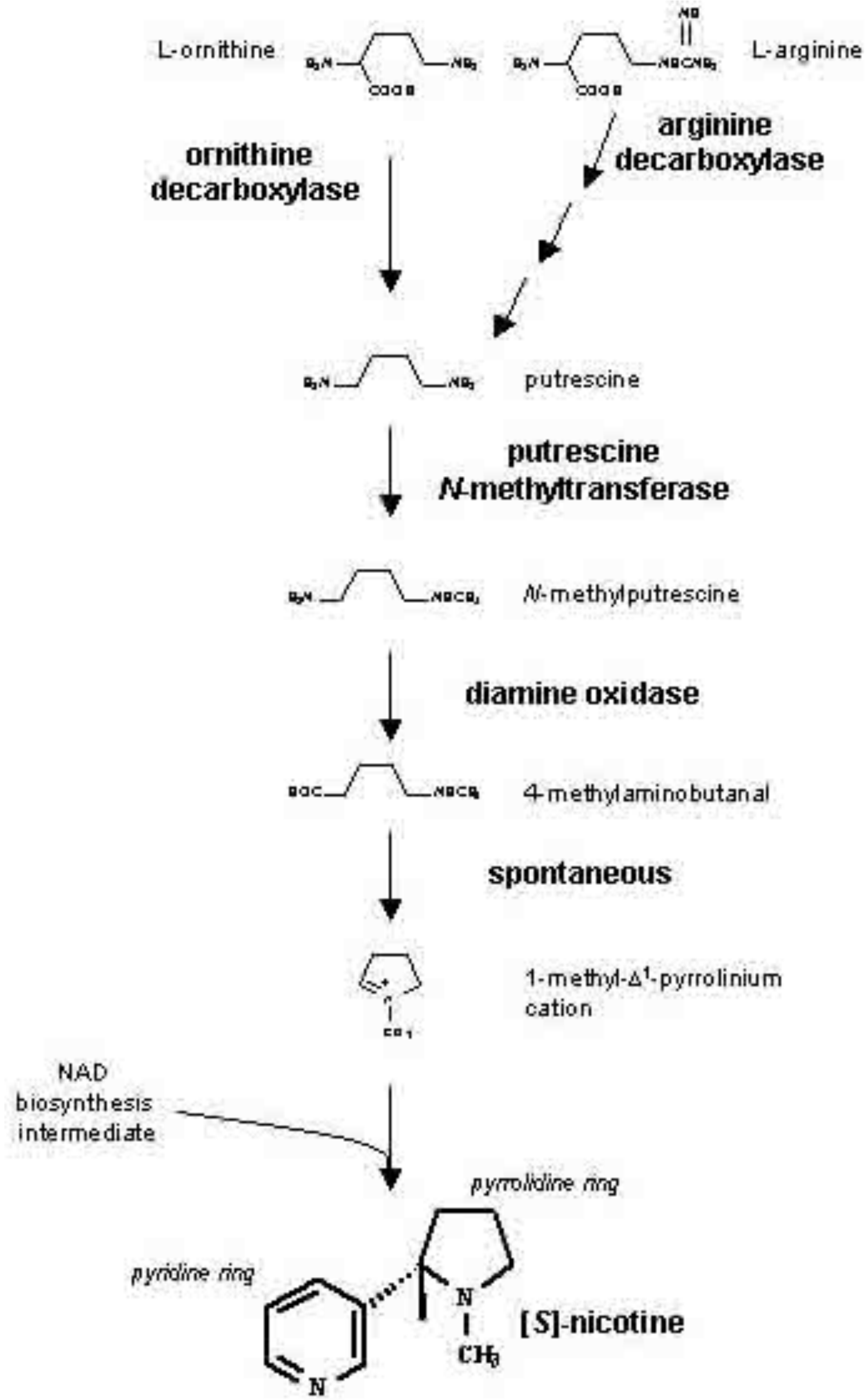
- Pairwise coevolution
  - Evolution of traits in **one** species cause changes in another
  - These changes in the other species cause changes in the first
  - <u>Reciprocal interactions proposed</u>
  - <u>May cause speciation</u>

Coevolution

- Diffuse coevolution
  - Reciprocal evolutionary change among groups of species rather than specific pairs
  - Specificity of response not as important

Role of Plant Chemicals

- Plants possess many compounds not needed for primary metabolism (secondary metabolites)
- These are often repellent or toxic to herbivores
- Perhaps they evolved in response to insect herbivory



Cost of Secondary Metabolite Production

- Example of nicotine biosynthesis
  - Requires several biosynthetic steps
  - Requires nitrogen
  - Nicotine concentration increases after herbivore damage (induced)
- Benefit: reduces herbivory
- Cost: Flower production reduced by nicotine induction

The Ehrlich & Raven Hypothesis

BUTTERFLIES AND PLANTS: A STUDY IN COEVOLUTION[1]

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Accepted June 15, 1964

One of the least understood aspects of population biology is community evolution—the evolutionary interactions found among different kinds or organisms where exchange of genetic information among the kinds is assumed to be minimal or absent. Studies of community evolution have, in general, tended to be narrow in scope and to ignore the reciprocal aspects of these interactions. Indeed, one group of organisms is all too often viewed as a kind of physical constant. In an extreme example a parasitologist might not consider the evolutionary history and responses of hosts, while a specialist in vertebrates might assume species of vertebrate parasites to be invariate entities. This viewpoint is one factor in the general lack of progress toward the understanding of organic diversification.

One approach to what we would like to call coevolution is the examination of patterns of interaction between two major groups of organisms with a close and evident ecological relationship, such as plants and herbivores. The considerable amount of information available about butterflies and their food plants make them particularly suitable for these investigations. Further, recent detailed investigations have provided a relatively firm basis for statements about the phenetic relationships of the various higher groups of Papilionoidea (Ehrlich, 1958, and unpubl.). It should, however, be remembered that we are considering the butterflies as a model. They are only one of the many groups of herbivorous organisms coevolving with plants. In this paper, we shall investigate the relationship between butterflies and their food plants with the hope of answering the following general questions:

1. Without recourse to long-term experimentation on single systems, what can be learned about the coevolutionary responses of ecologically intimate organisms?

2. Are predictive generalities about community evolution attainable?

3. In the absence of a fossil record can the patterns discovered aid in separating the rate and time components of evolutionary change in either or both groups?

4. Do studies of coevolution provide a reasonable starting point for the understanding of community evolution in general?

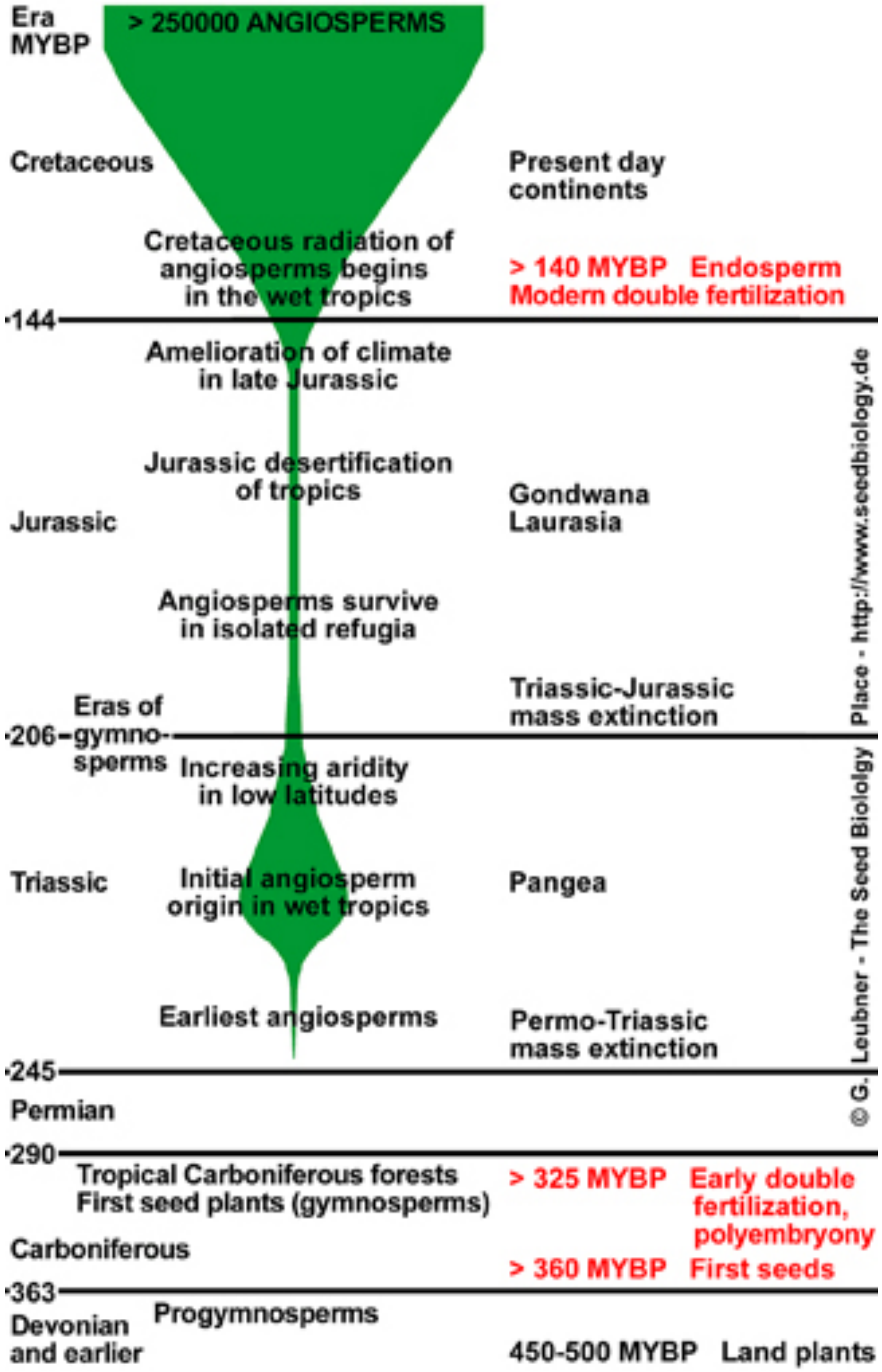
FACTORS DETERMINING FOOD CHOICE

Before proceeding to a consideration of the relationships between butterfly groups and their food plants throughout the world, it is necessary briefly to consider some of the factors that determine the choice of food plants in this group and in phytophagous insects in general. Any group of phytophagous animals must draw its food supply from those plants that are available in its geographical and ecological range (Dethier, 1954). For instance, the butterflies are primarily a tropical group, and therefore there is a relatively greater utilization of primarily tropical than of temperate families of plants. The choice of oviposition site by the imago is also important. Many adult butterflies and moths lay their eggs on certain food plants with great precision as stressed by Merz (1959), but on the other hand, numerous "mistakes" have been recorded (e.g., Remington, 1952; Dethier, 1959). In such cases, larvae have either to find an appropriate plant or perish. There is an obvious selective advantage in oviposition on suitable

[1] This work has been supported in part by National Science Foundation Grants GB-123 (Ehrlich) and GB-141 (Raven).

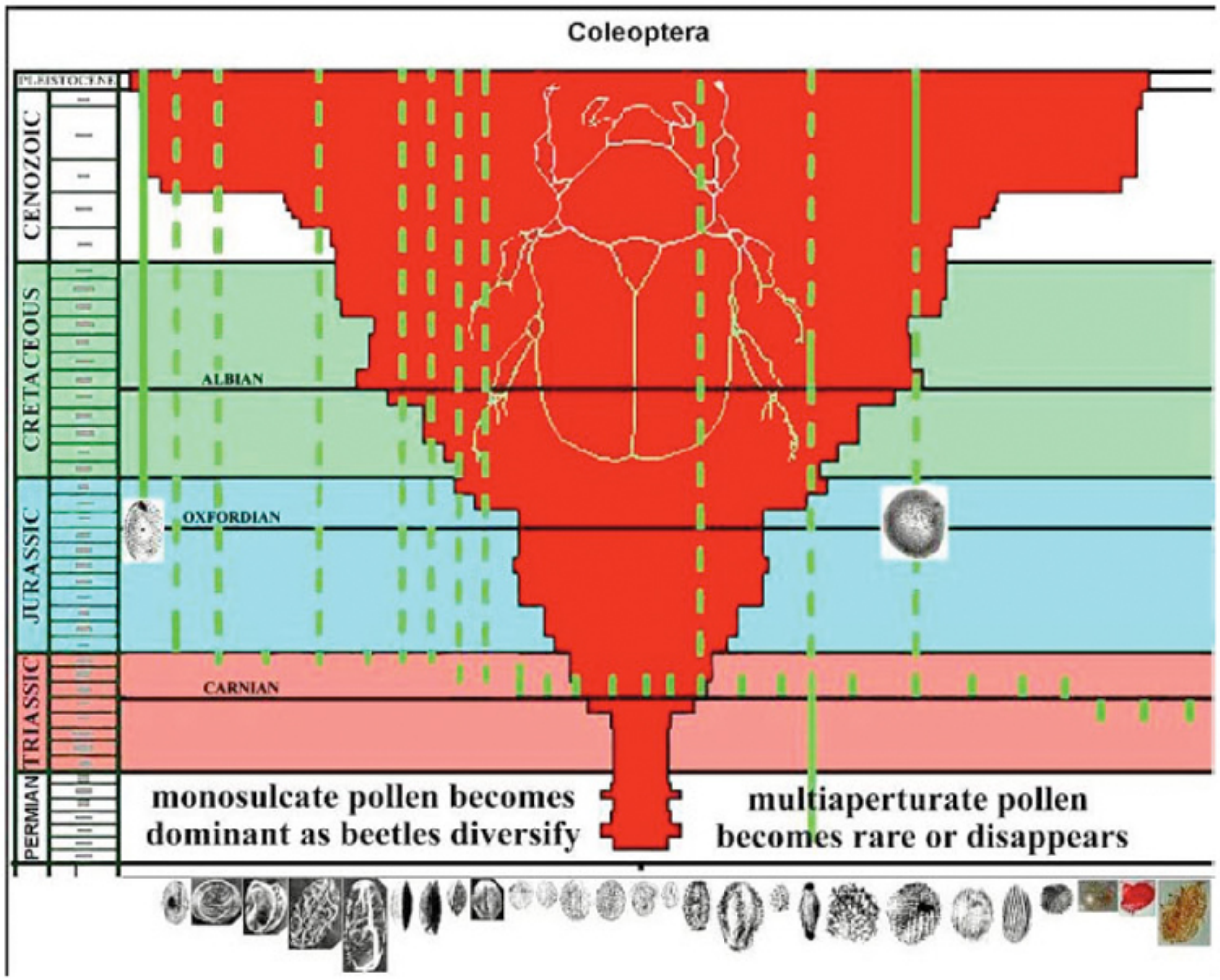
The Ehrlich & Raven Hypothesis

- Plants evolve new secondary metabolites in response to herbivores
- Plants diversify because herbivore pressure temporarily reduced
- Herbivores evolve resistance to toxic plant compounds
- Herbivores speciate onto formerly toxic plants
- Repeat first step- again and again

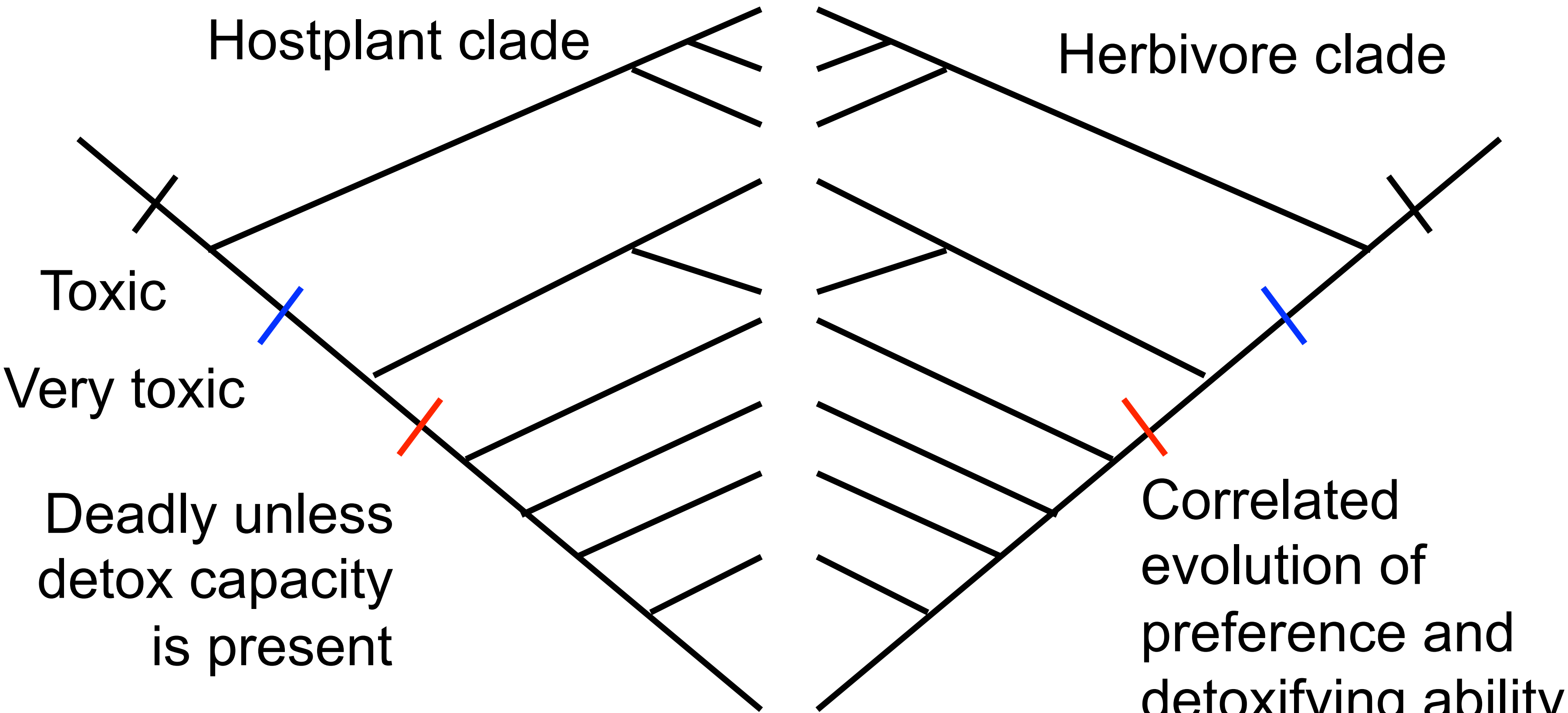


Diversification of Angiosperms

Herbivorous insect diversification at same time…



Parallel phylogenies under coevolution



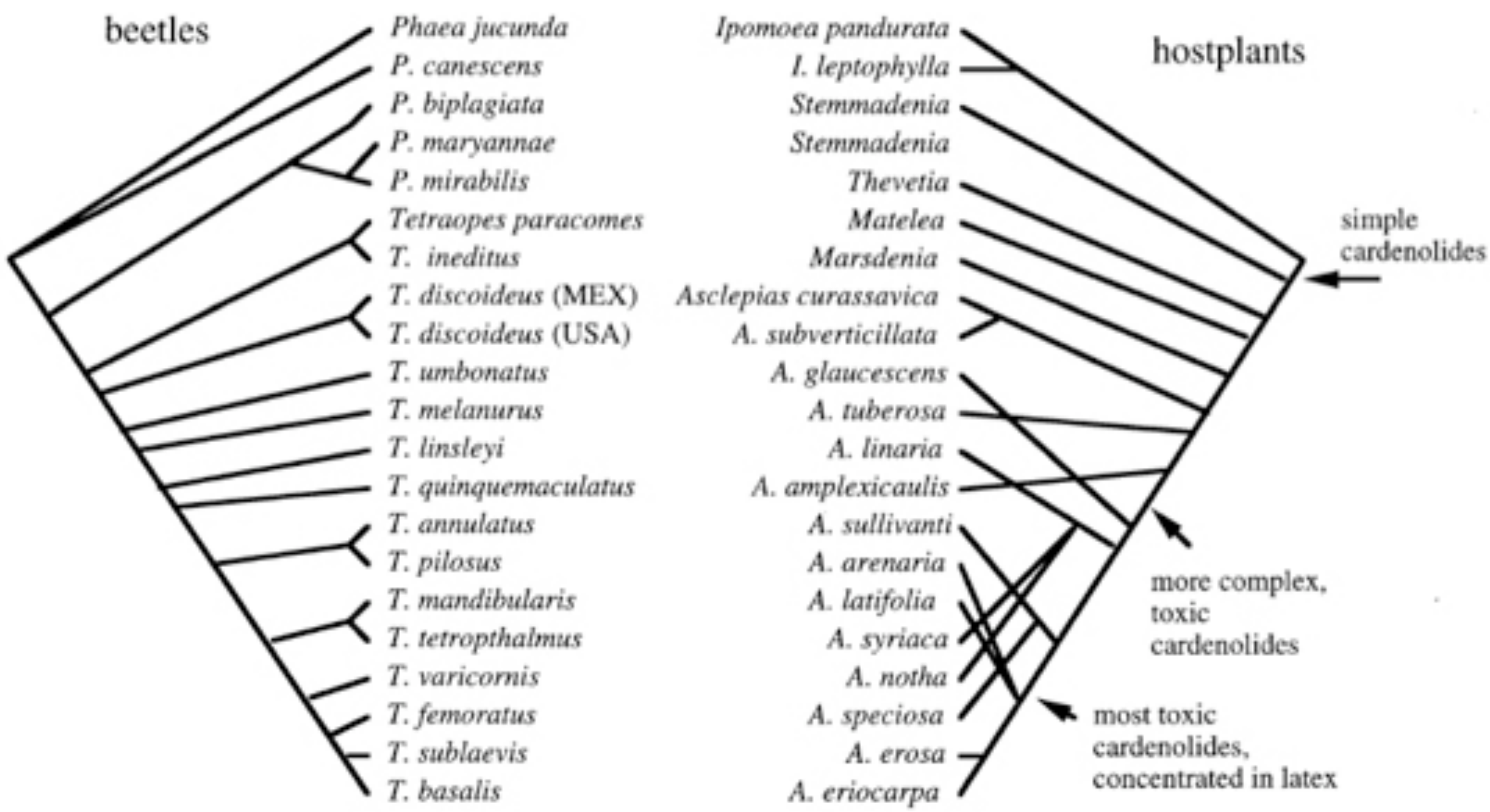
Example of pairwise coevolution

- *Asclepias* milkweeds live in the same area as *Tetraopes* longhorn beetles.
- Plants produce spectacular toxins that kill potential herbivores.

Asclepias / Tetraopes

- Longhorn beetles specialized on milkweed
- Derived beetles have specific methods to circumvent plant defense

Asclepias / Tetraopes



Kinds of plant insect interactions

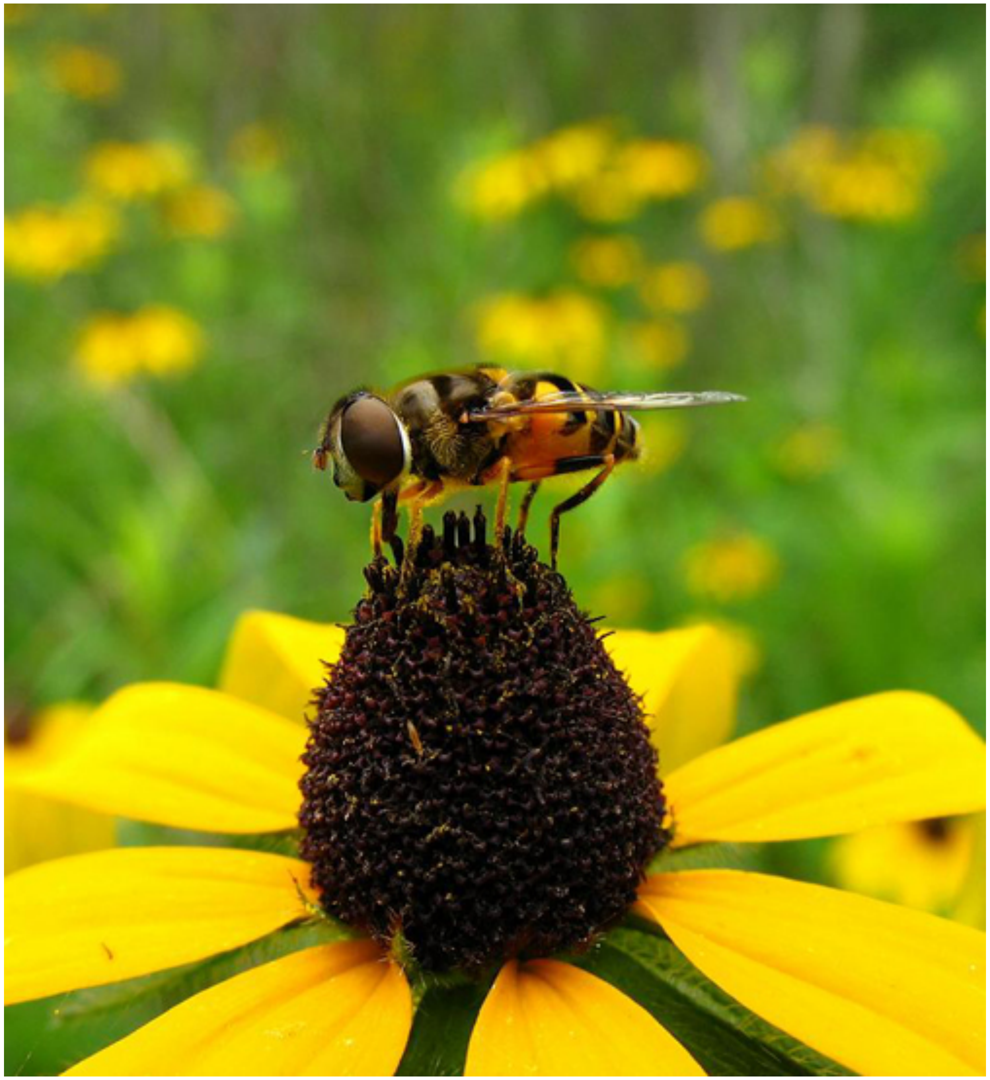
- Plant herbivore interactions
- Plant pollinator interactions
- Insects protecting plants from herbivory (domatia)
- Insects as seed dispersers

Insects as Pollinators

- Plant evolves reward for insect visitor
- Insect evolves behavior and/or structure to enhance pollination
- Benefits to plant
  - More reliable pollination
  - Less energy allocated to pollen production
  - Less pollen mixing
- Costs to plant
  - Dependence on insect
  - Cost of reward
- Cheating
  - Plant doesn't offer reward (orchids)
  - Insect consumes seeds (yucca moth) or reward without pollinating

Types of Insect Pollinators

- Beetles
  - Oldest pollinators (e.g. cycads)
  - Often attracted to flowers near ground, smell like fermented fruit
- Flies
  - Some attracted to carrion or dung smell
  - Others feed on pollen
- Hymenoptera
  - Sweet nectar
  - Mouthparts match flower
- Butterflies and moths

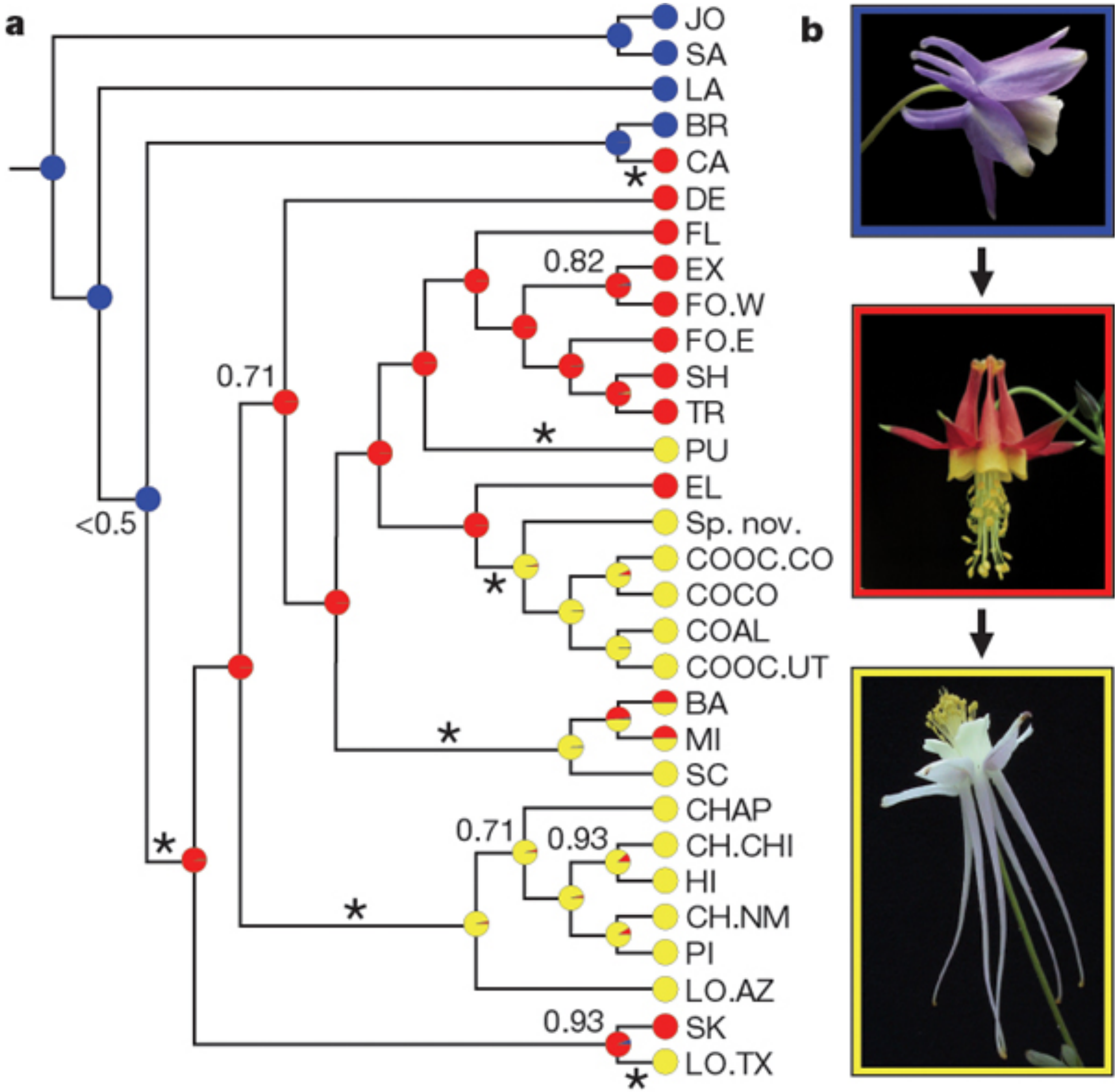



Columbine Coevolution

Nectar is at end of tubes

Pollen is at end of stamens

- Shortest spurs: Bees
- Next: Long-tongued bees
- Next: Bumblebees
- Longest: Hummingbirds.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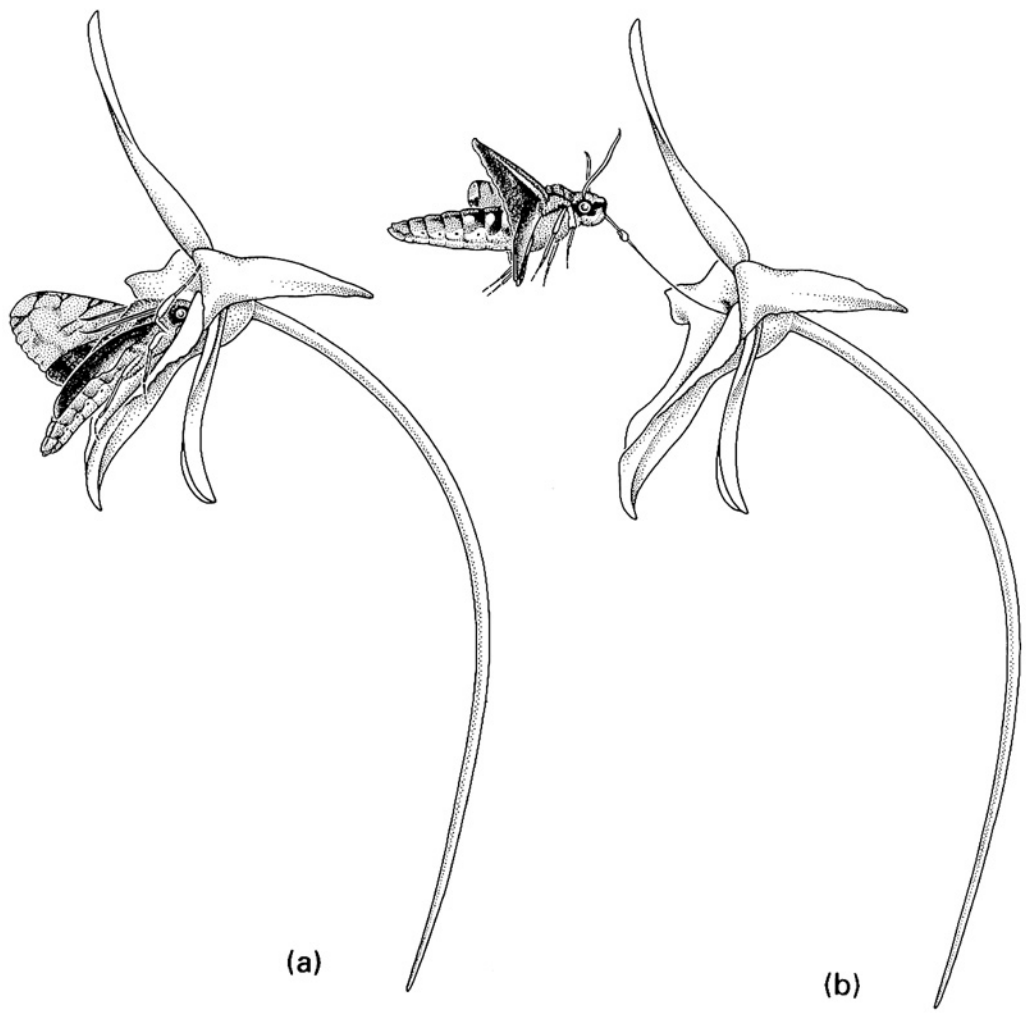
Hawkmoths



Cheating by plants for pollination

- Orchid mimics female wasp
- Produces pheromones to attract male

Cheating by Insects

- Nectar robbing by bumblebees
- Why?

Coevolution: Figs & Fig Wasps

- Species-specific
- Both species depend on each other
- Figs?
- Wasps?

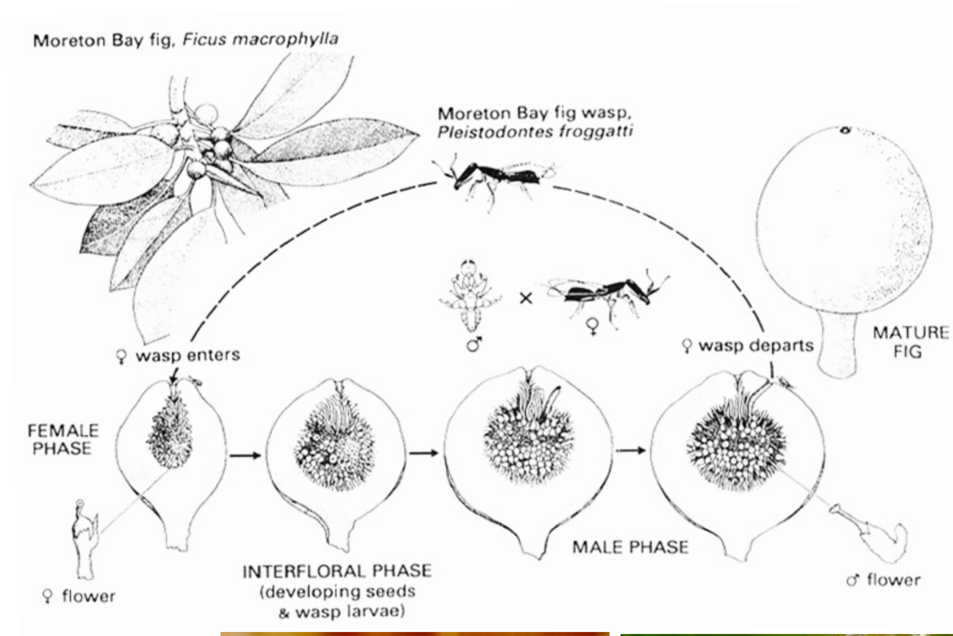
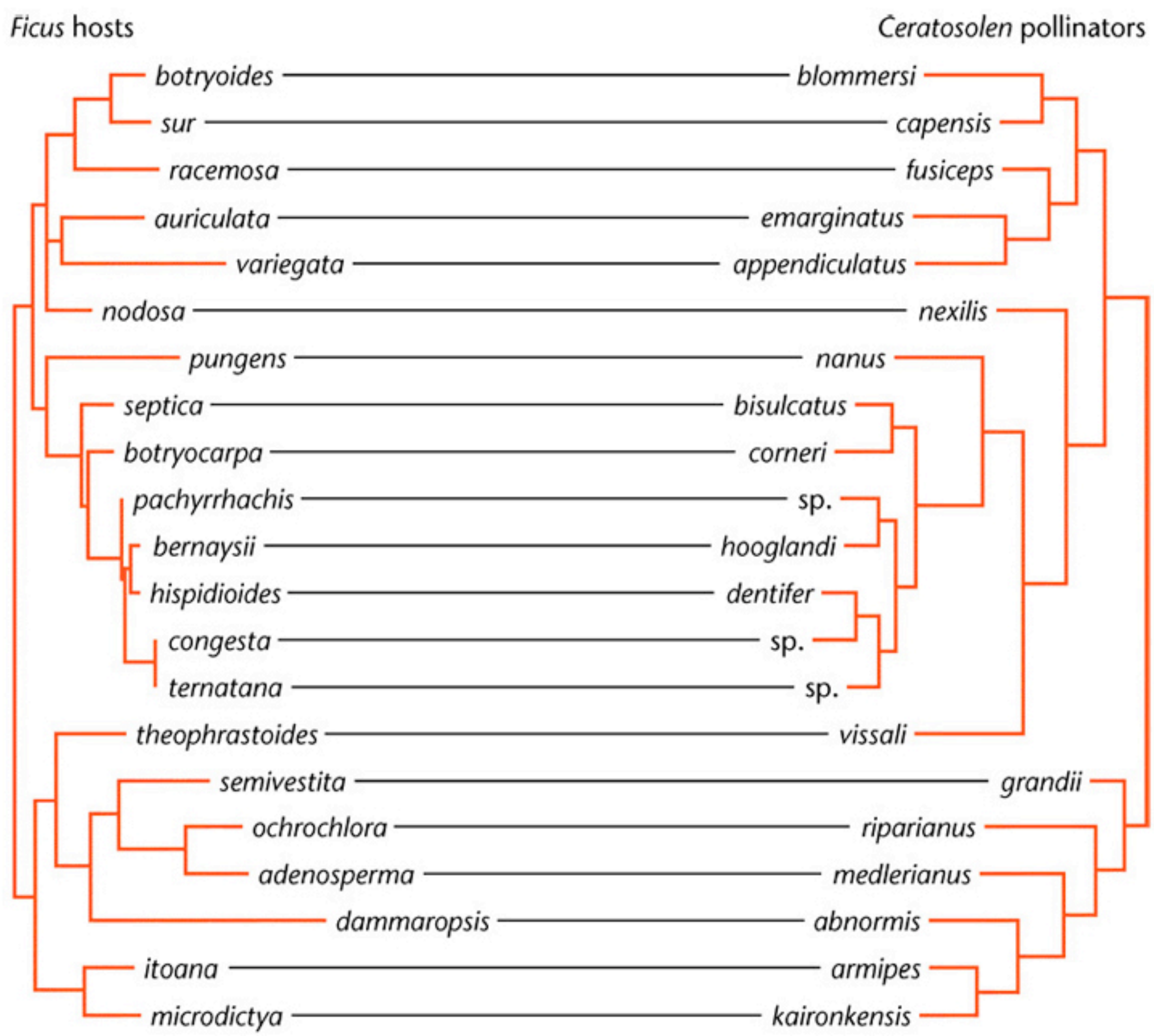


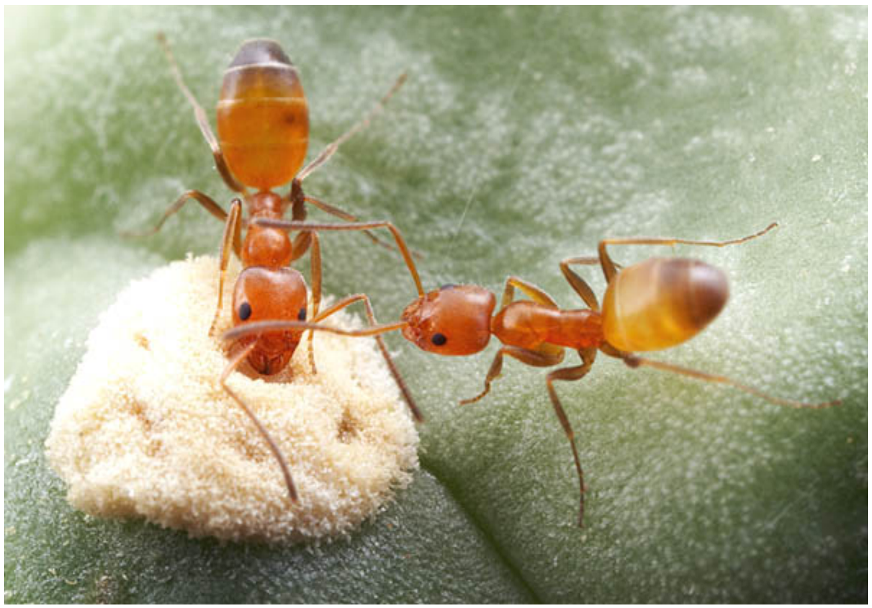
Fig & Fig Wasp Cospeciation



Plant associations with ants

- Ants may tend aphids or butterfly larvae (negative)
- Ants may gather leaves or seeds (negative)
- Ants may tend extrafloral nectaries of plants (positive)
- Ants may disperse seeds (myrmechory, positive)
- Ants may live in plant domatia and protect plant from herbivory (positive)

Extrafloral Nectaries



- Found in many plants from ferns to Acacias
- Attract ants
- Ants eat caterpillars found on plants

Seed Dispersal by Ants: Myrmecochory

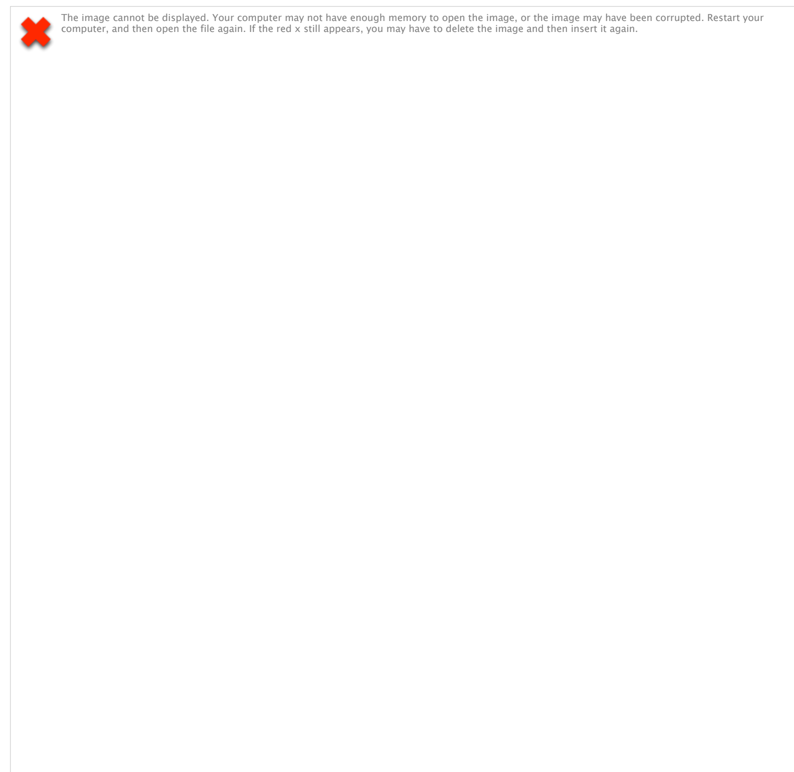
- Example: Elaiosome production by bloodroots (*Sanguinaria*)
  - Member of poppy family (Papavaraceae)
  - One of the earliest ephemeral spring flowers
  - Blooms before trees leaf out
  - Blooms only last a few days

Seed Dispersal by Ants: Myrmecochory

- Seeds grow on a separate stalk
- Once ripe, seed capsules open
- Seeds have external white fatty tissue (elaiosome) that is attractive to ants
- Ants carry seeds to their nests

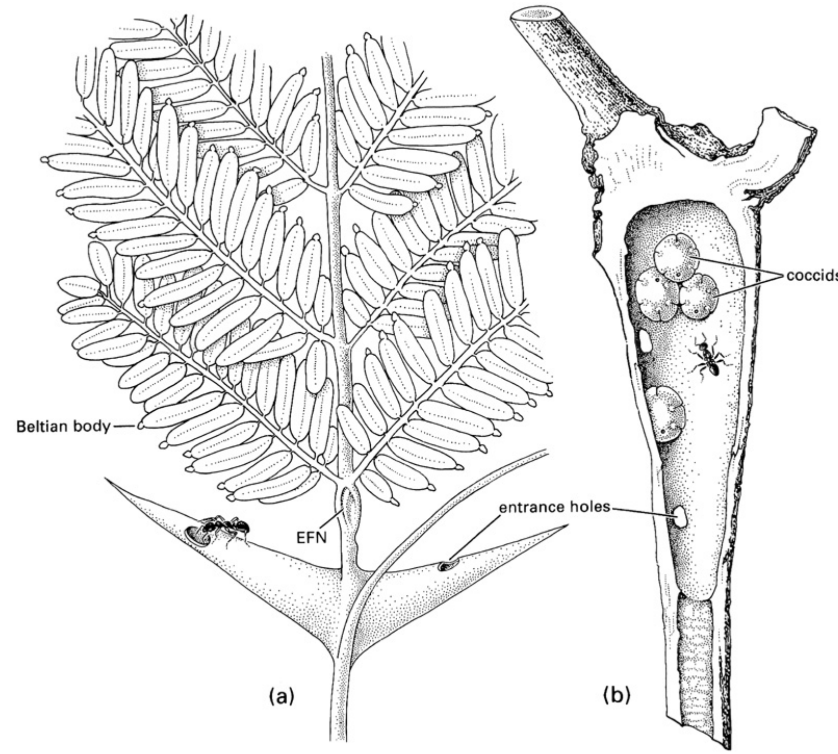
Seed Dispersal by Ants: Myrmecochory

- Elaiosomes are eaten, but seeds remain viable
- The seeds are discarded with other nest waste
- Thus, this interaction is considered a mutualism because…



Ant/Acacia system

- Acacias provide food and housing (domatia) for ants
- Ants protect plant from
  - Insect herbivores
  - Grazers
  - Plant competitors



Beltian bodies provide food for ant associates

Plants provide domatia

Ants aggressively defend plant

Mutualism and Experimental Analysis

- Why might something that we think is a mutualism not actually be one?
- What do you need to show in order to support the hypothesis that an interaction is mutualistic?

Example: *Jalmenus* butterflies and *Iridomyrmex* ants.

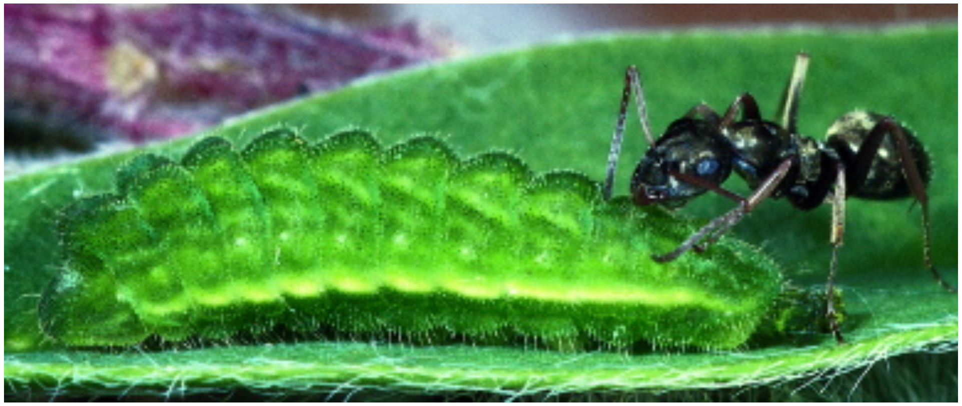
- Imperial Blue butterflies from eastern Australia are tended by ants in the genus *Iridomyrmex*.
- Ants guard the caterpillars and escort them into and out of their nests at dusk and dawn.

Is this a mutualism?

- For it to be a mutualism, there must be benefits to both the ants and the butterflies.
- If there is no benefit to one, it is a ____________.
- If there is a cost to one, it is a ______________.

Observations

- Ants tend caterpillars, provide shelter at night and actively attack parasitoid wasps.
- Ants gather secretions from specialized glands on caterpillars.



Are observations enough?

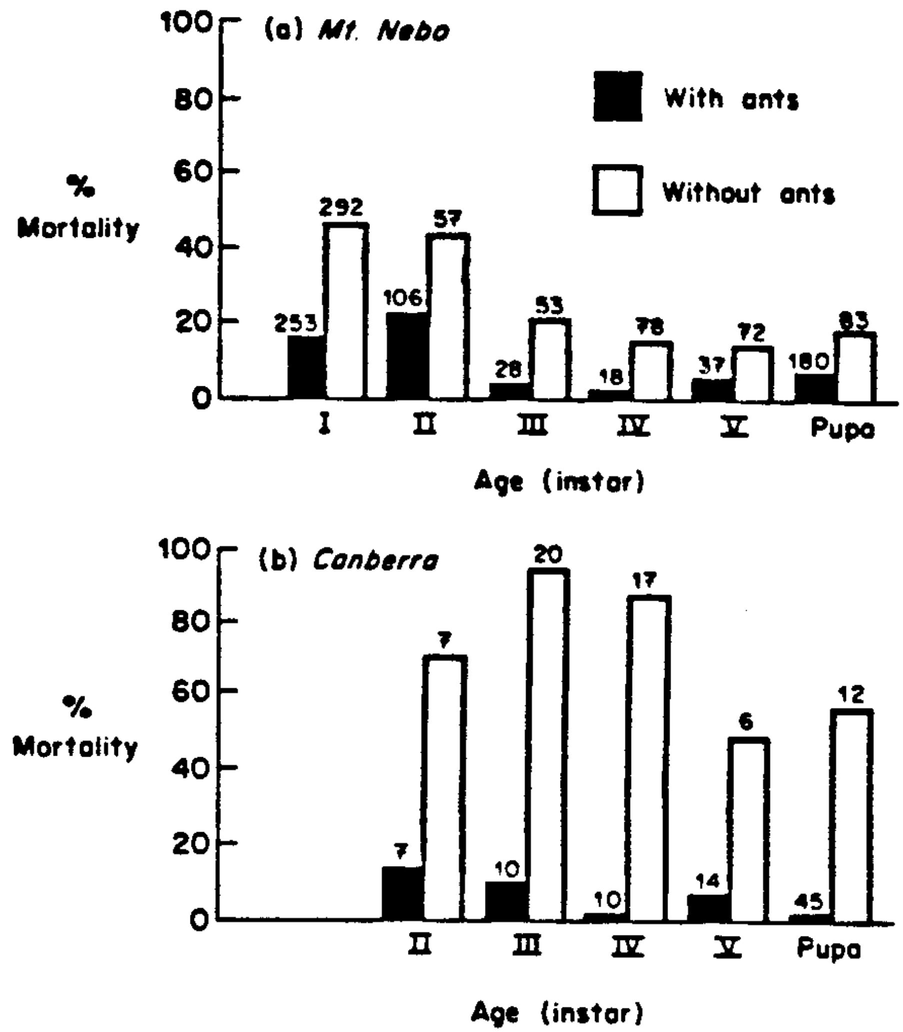
- Mutualism can be thought of as mutual exploitation.
- Each participant always wants to get more from the other (maximize benefits) while giving less (minimizing costs).

Are observations enough?

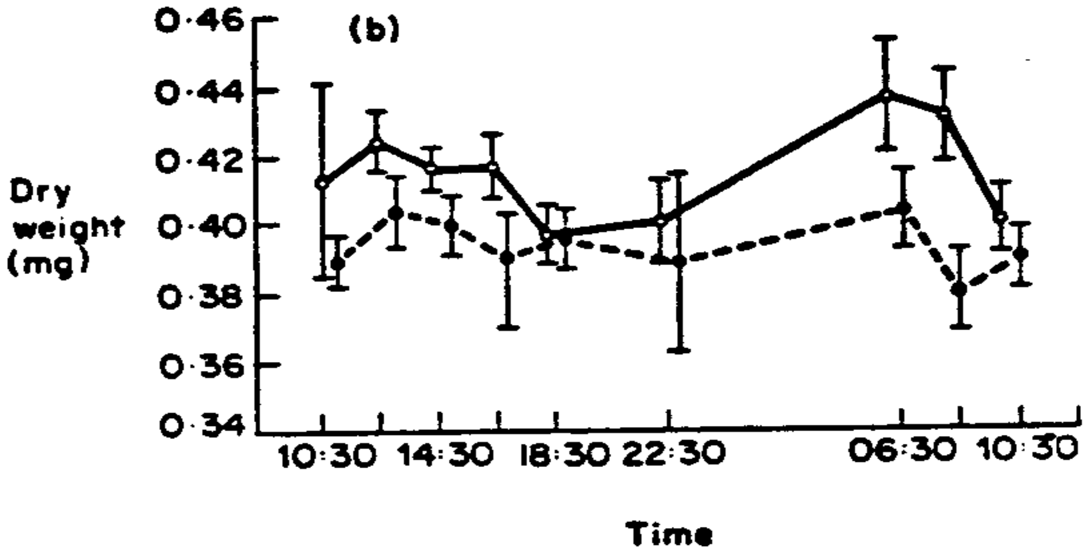
- Therefore, the evolution of parasitism from mutualism is quite common.
- Researchers must show *experimentally* that both participants benefit.

Experimental manipulation: Exclusion experiments.

- Pierce (1987) removed and then excluded *Iridomyrmex* ants using Tanglefoot®.
- Then tracked mortality in treatments with and without ants.
- Showed mortality much higher in treatments without ants.



Experimental manipulation: Exclusion experiments.



- Unable to examine effects of caterpillar removal because ants abandon trees without caterpillars.
- Looked at ants going up tree (dotted line) vs those going down (solid line).
- Ants going down had food rewards from caterpillars.
- Gains in weight translate to an estimated 100 new worker ants per day per 62 caterpillars tended.

Mutualism?

- Evolution of parasitism a common result of mutualism.
- Suggests that mutualism may be unstable.
- The result of reciprocal exploitation, not altruism.
- Suggests that mutualism may often be a tug-of-war of interactors.

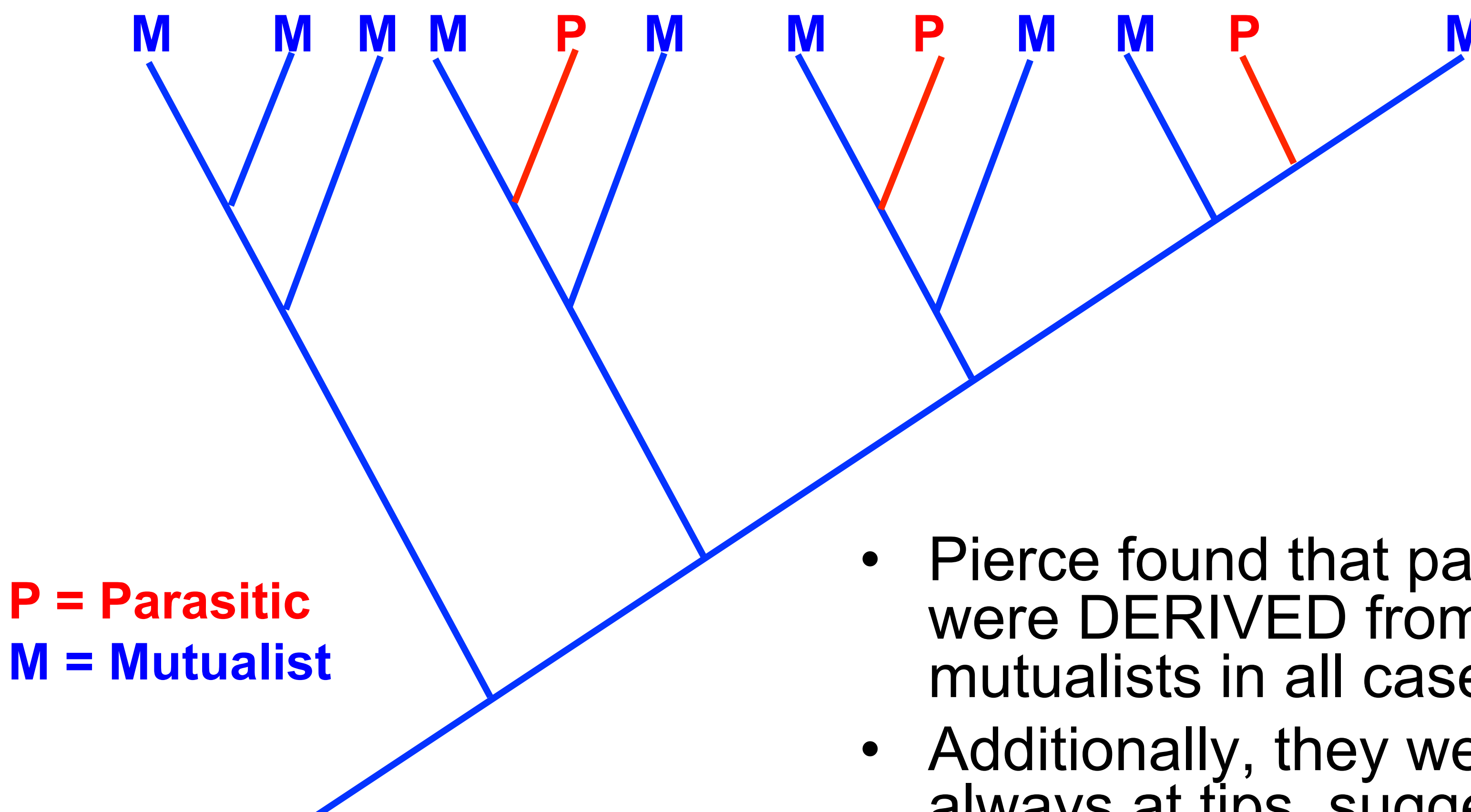
Example: A return to ants and butterflies

- About ½ of butterflies in the Lycaenidae associate with ants.
- About ½ of these are mutualistic with their ants.
- The other ½ are parasitic: they either eat the ant larvae, are fed by ants, or secrete sugar-water.

A comparative approach to the evolution of mutualism

- Comparative analysis uses the BRANCHING RELATIONSHIPS BETWEEN SPECIES to examine evolutionary history of ecological traits.
- Can assess the TRAJECTORY of evolution and the ANCESTRAL STATES of ecological traits based on current observations.
- Generally use the principle of PARSIMONY in analysis.
- PARSIMONY: the fewest number of hypotheses of change to explain the evolution of a given feature.

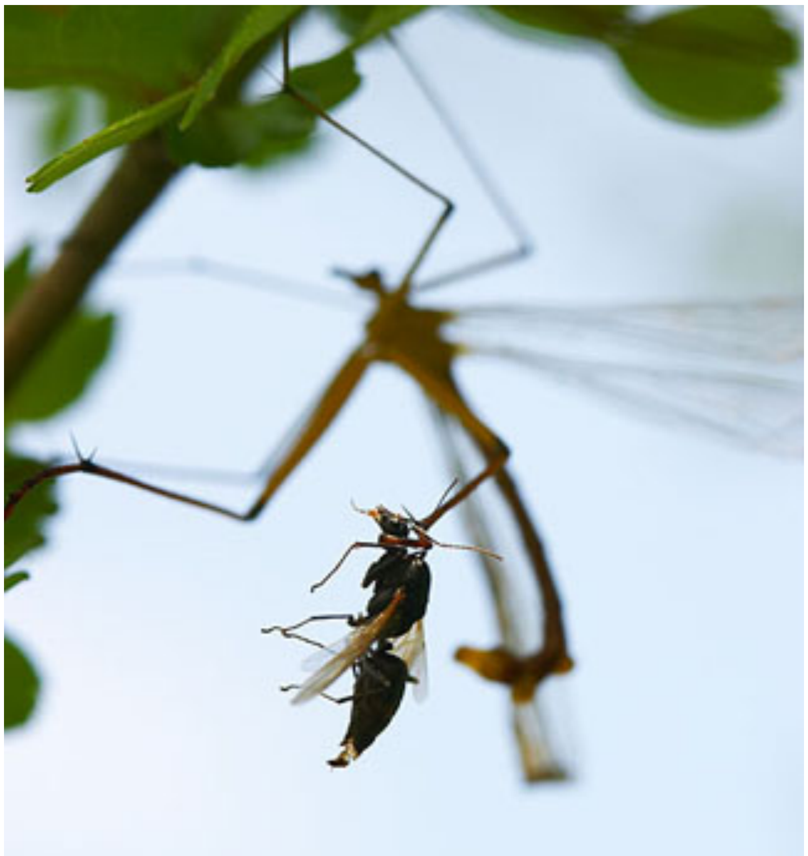
A comparative approach to the evolution of mutualism



- Pierce found that parasites were DERIVED from mutualists in all cases.
- Additionally, they were always at tips, suggesting that they go extinct after time.

Through time, some insects evolved into shapes which would make them unattractive to predators.

Insect Predators & Parasites

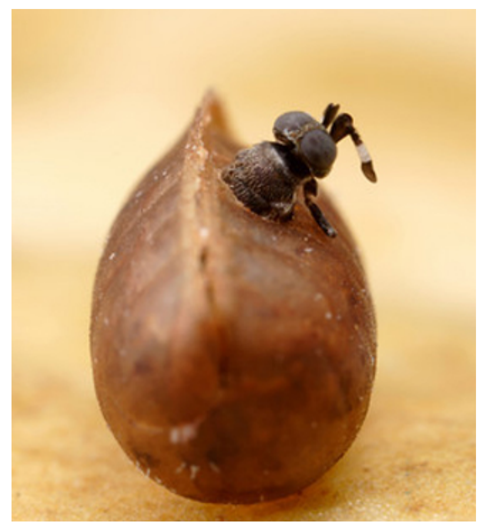


- Up to 25% of insects predators or parasitic at some stage
- Some predators eat a broad range of prey species
- Importance of specialists may be underestimated

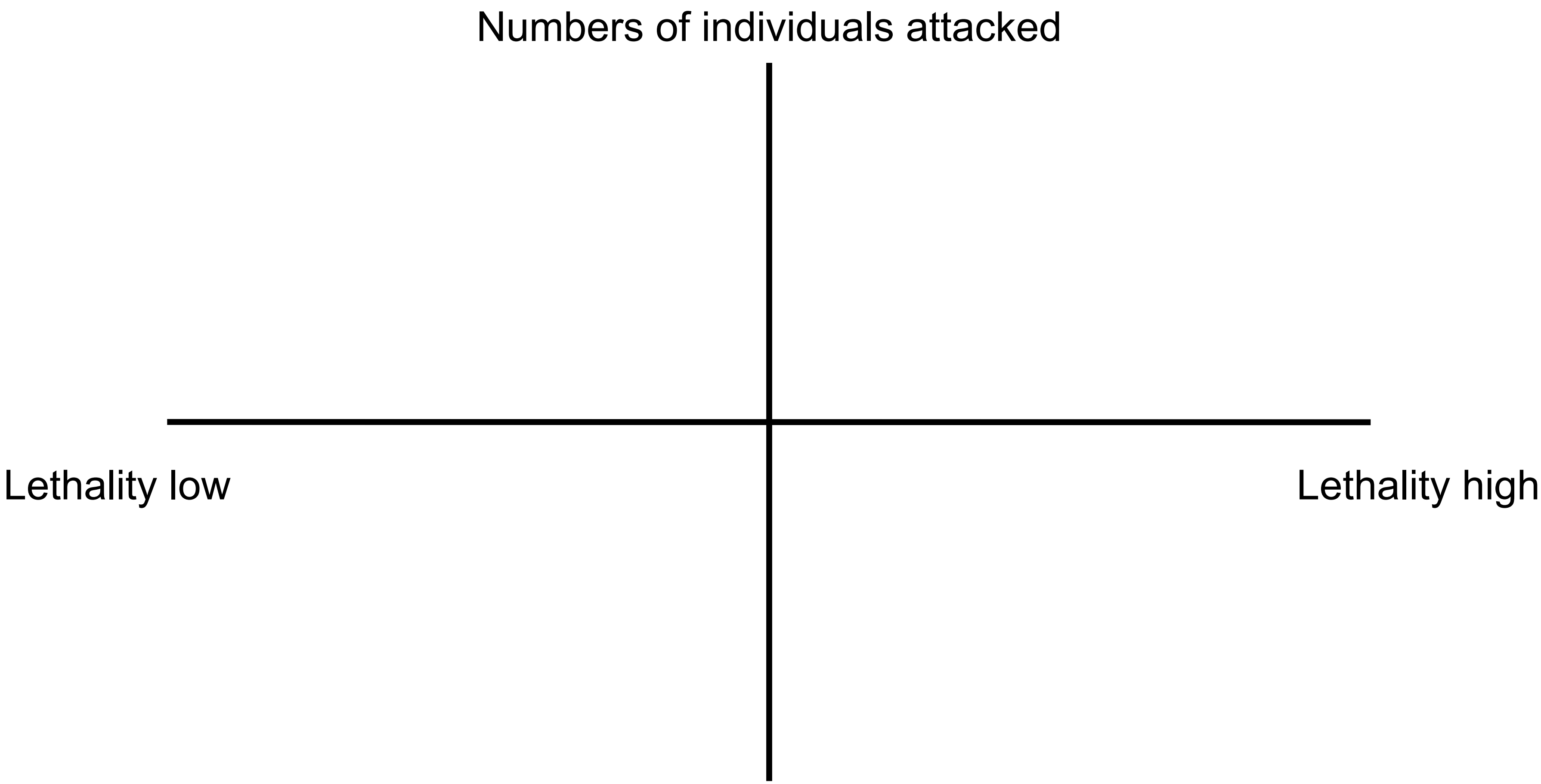
Exploitation: Predators, Parasites, Grazers, Parasitoids

- In this context, we mean the consumption of an animal by another animal when the exploited individual is alive when the exploiter first attacks it.
- Enhances fitness of one individual at the expense of the exploited individual.

- How might these differ?
  - Lethality of interaction
  - Number of individuals attacked by exploiter during its lifetime



Types of exploitation



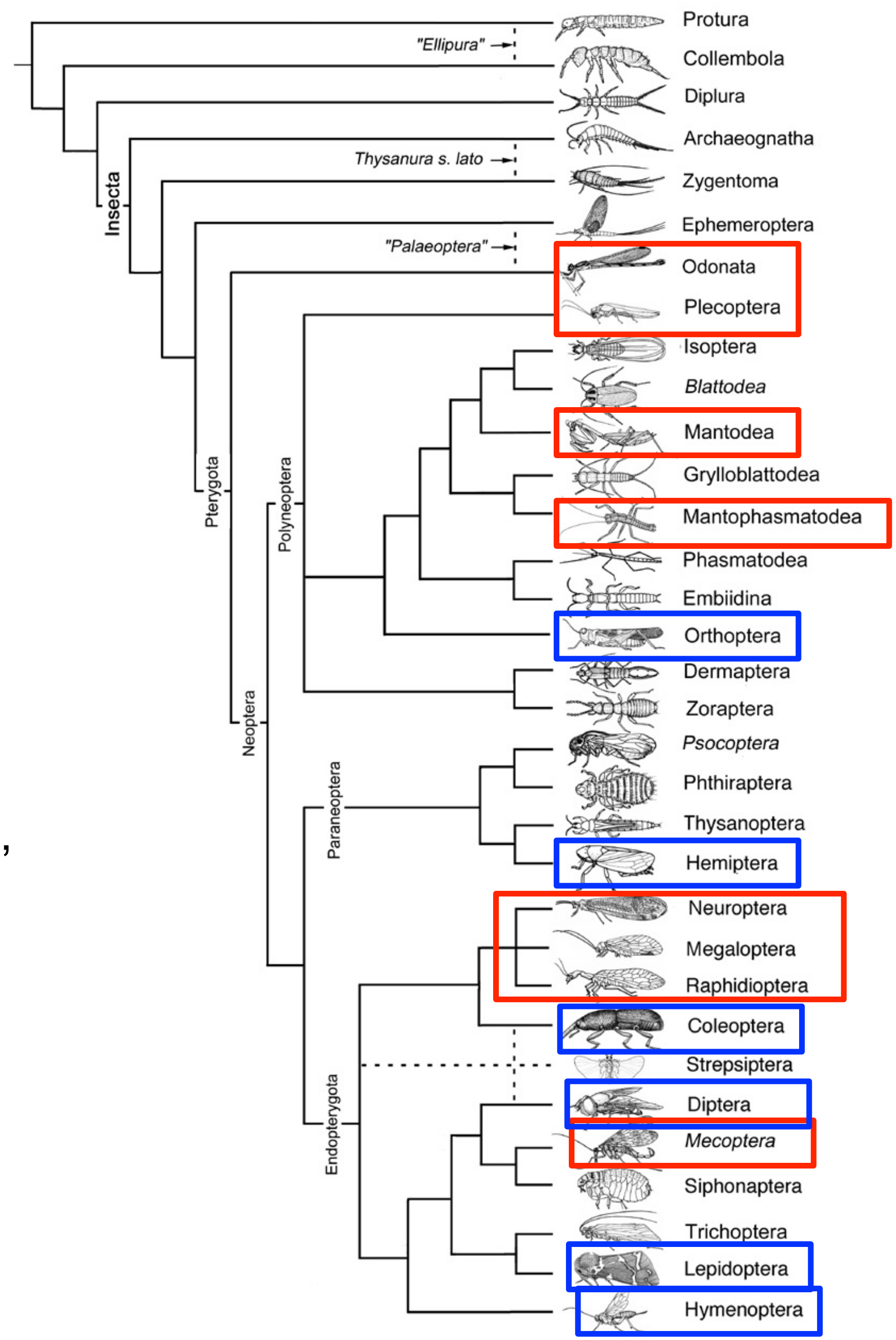
Predators

- Attacks multiple individuals in lifetime, lethal.




Taxonomic Distribution

- Widespread, numerous origins from primitively detritivorous or even phytophagous
  - Completely:
    - Odonates, Plecopterans, Mantodea, Mantophasmatodea, Raphidioptera, Megaloptera, Mecoptera
  - Partially:
    - Hemiptera (Heteroptera), Neuroptera, Coleoptera, Diptera, Hymenoptera, Orthoptera, very rare in Lepidoptera

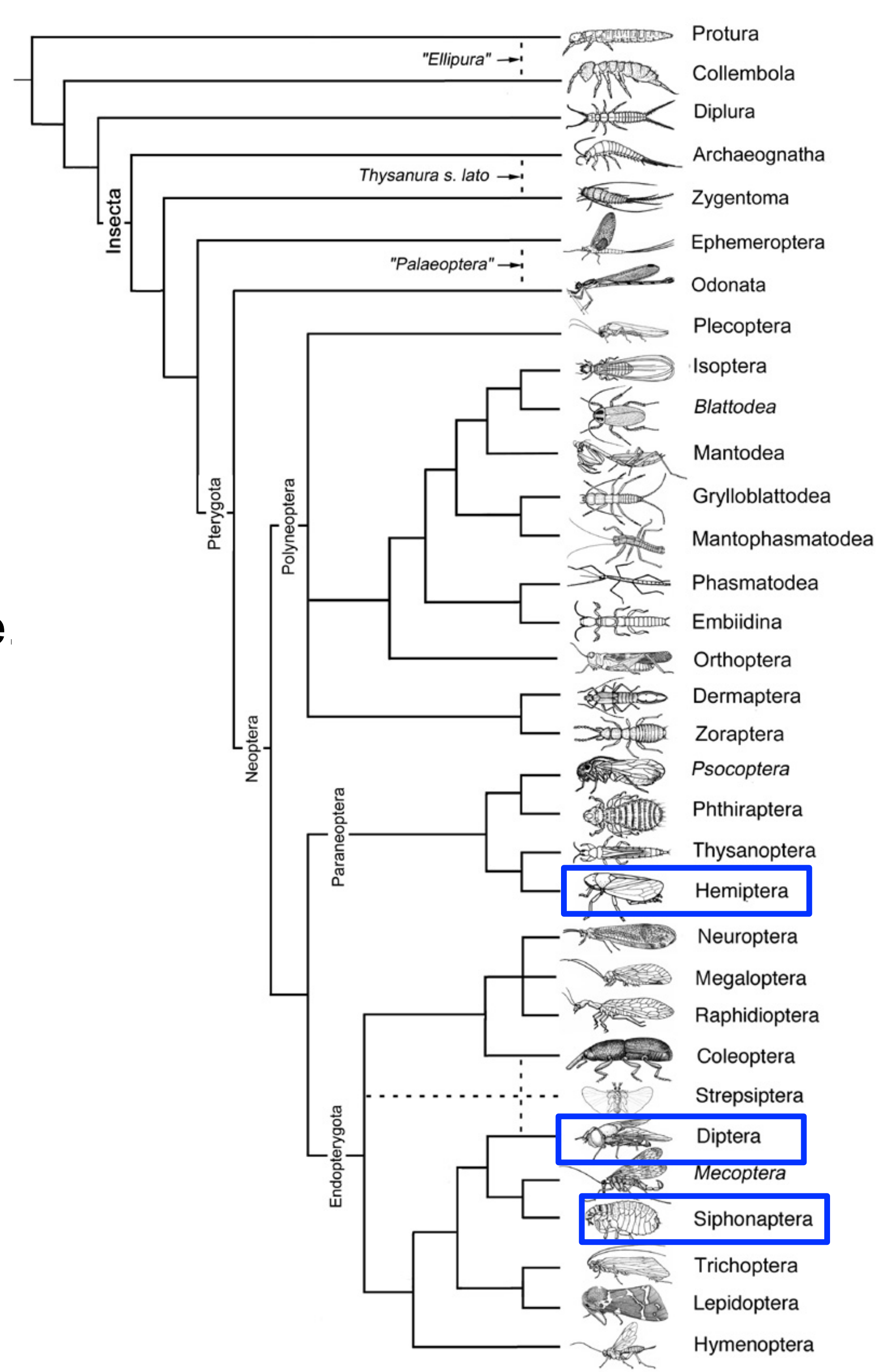


Grazers

- Attack multiple individuals in lifetime, not lethal.

Taxonomic Distribution

- Distribution more restricted
- Siphonaptera only order that is strictly a grazer.
  - And this grades uncomfortably into a parasite.
- Heteroptera
- Diptera
- Difficult to distinguish this from a parasite.



Parasites

- Attacks (usually) one individual in lifetime, (usually) not lethal.

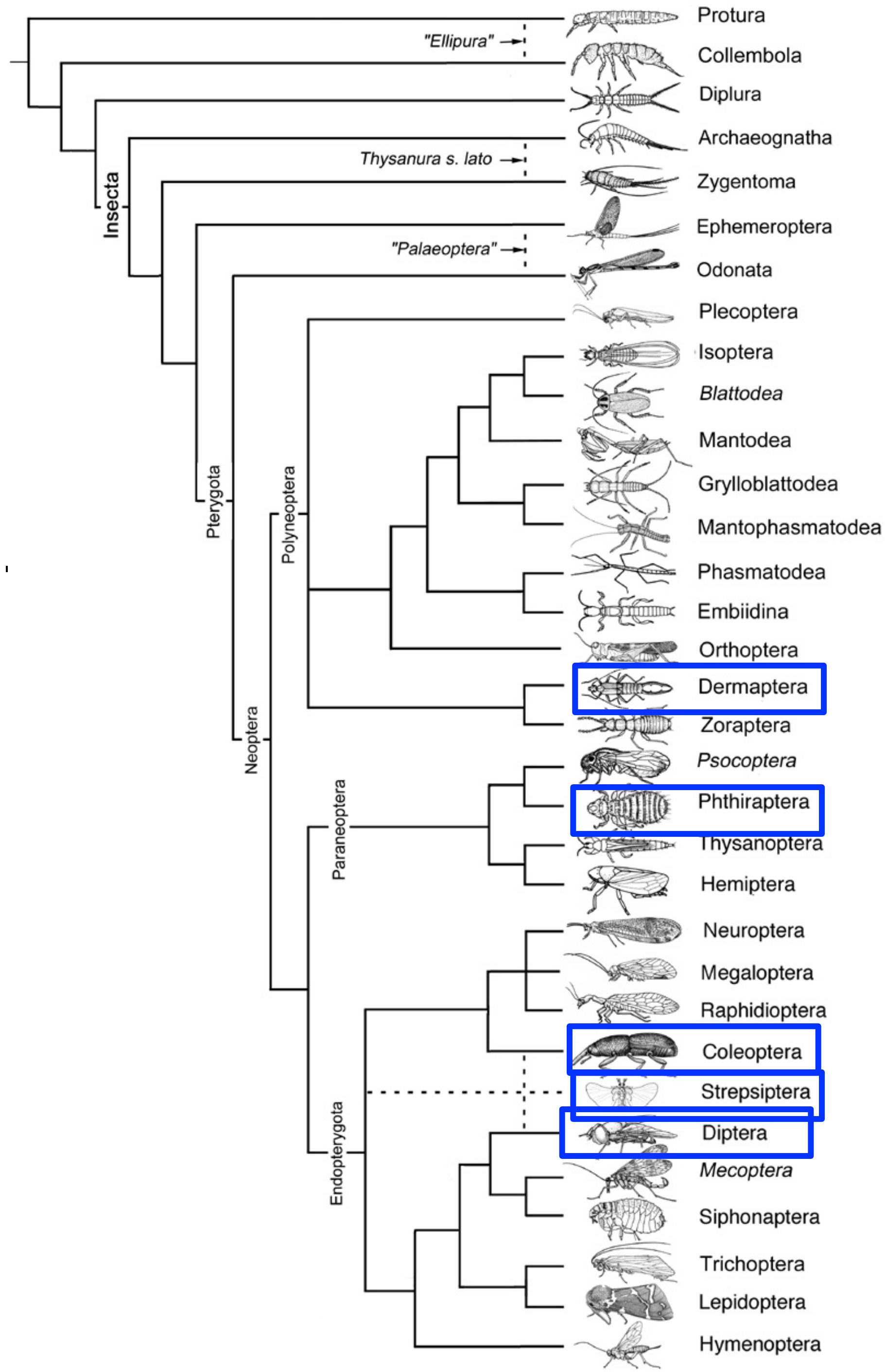
Parasites

- Attacks (usually) one individual in lifetime, (usually) not lethal.




Taxonomic Distribution

- Evolved multiple times, mostly as **ectoparasites**.
- **Strepsiptera** might be considered **endoparasites**.
- Only Strepsiptera and Phthiraptera are strictly parasites.
- Other parasites found in Dermaptera, Coleoptera, Diptera



Parasitoids

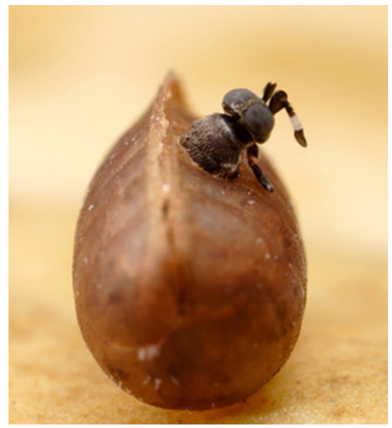
- Attack (usually) one individual in lifetime, lethal.





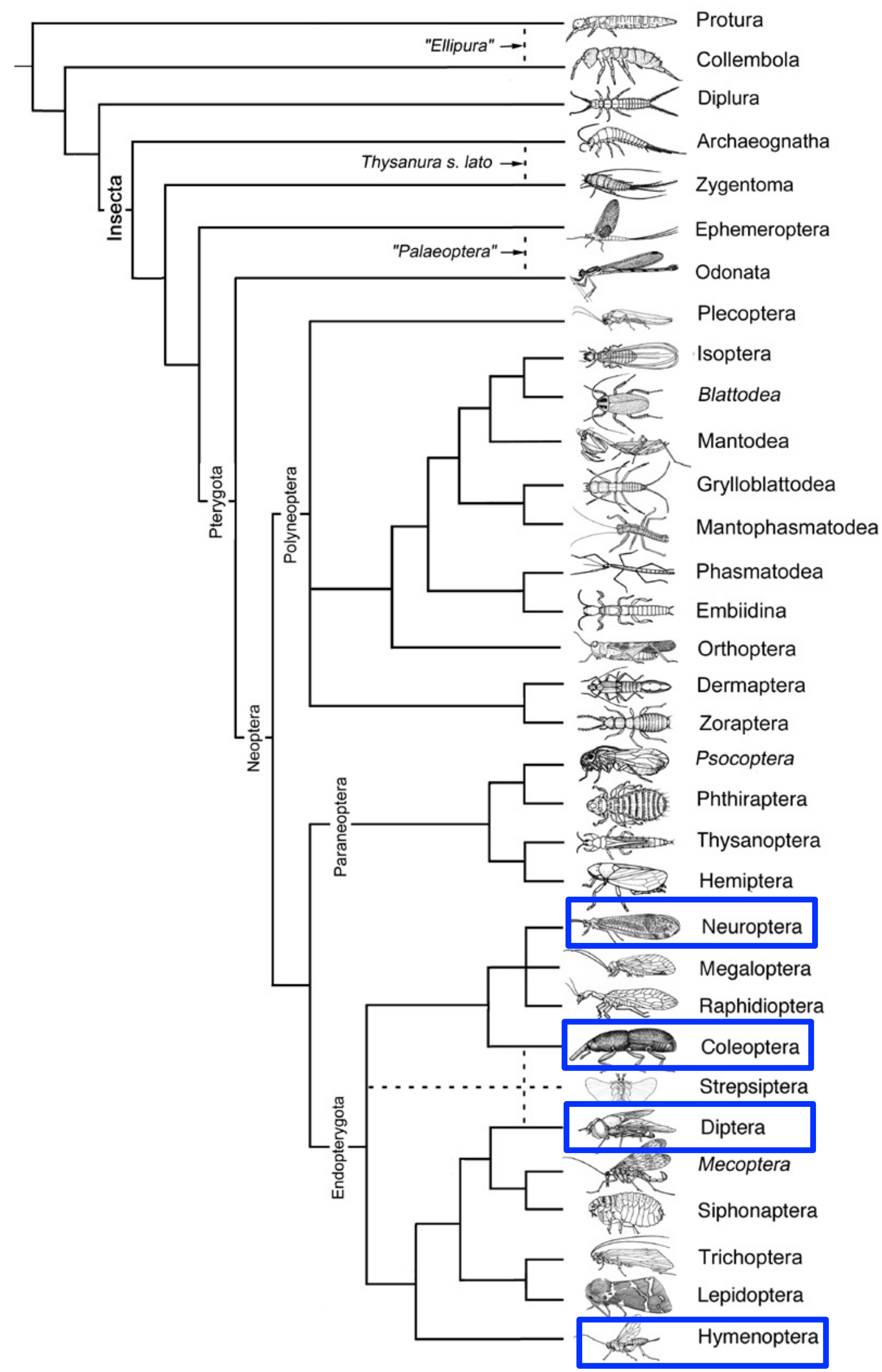
Parasitoids

- Attack (usually) one individual in lifetime, lethal.


Taxonomic Distribution

- Evolved multiple times as **endoparasites**.
- Parasitic Hymenoptera extraordinarily successful.
  - Egg, larval, pupal, adult
  - Hyperparasitoids.
- Some successful groups of Diptera, mostly on social Hymenoptera.
- Rare in Coleoptera and Neuroptera.
  - Often undergo hypermetamorphosis.
- No orders strictly parasitoids.



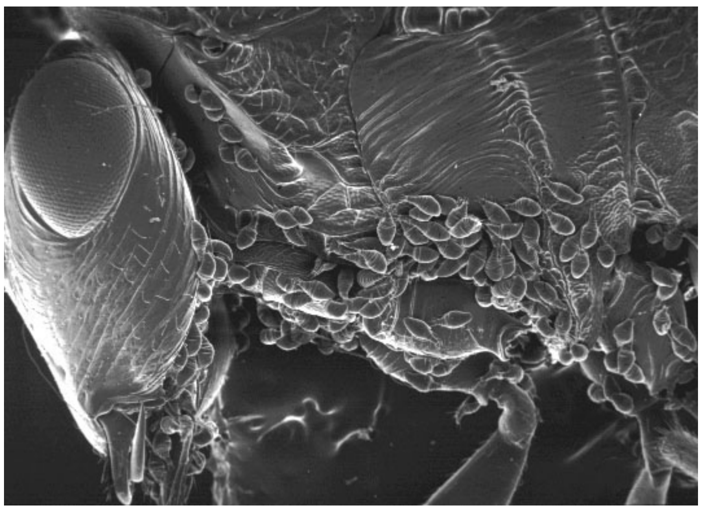
Other Origins?

Parasitoids

- Predominantly Hymenoptera and Diptera.

1. Hymenoptera
   - Adult seeks out host.
   - Antennae and ovipositor have specialized sensillae to determine appropriate host and oviposition site.
   - Modified sting in Aculeata permits nest provisioning.

Parasitoids



(also present in parasitoid Coleoptera, Strepsiptera, and some Hymenoptera)

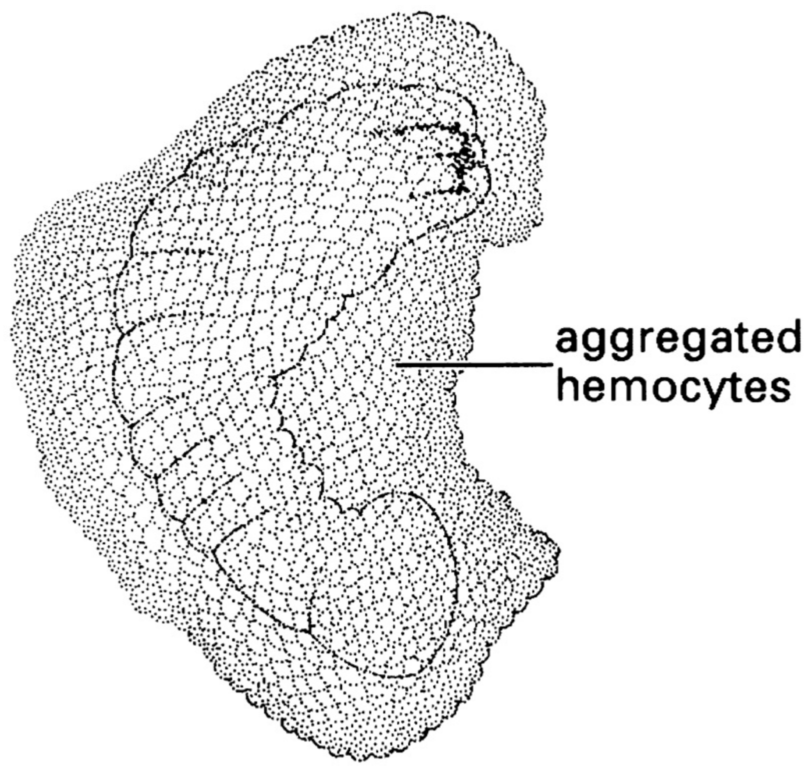
2. Diptera
   - Adult seeks out vicinity of host, lays eggs (or larvae).
   - Larvae are **planidia**
     - Flattened, highly sclerotized, highly mobile.
   - Larvae find hosts or are **phoretic**
   - Once host is found, they enter and become sessile (lose eggs, eyes, etc.): **hypermetamorphosis**

Parasitoids

- **Idiobiont**:
  - Parasitization kills or paralyzes host, development is very rapid.
  - Common in aculeate Hymenoptera
- **Konobiont**:
  - Parasitized host continues to feed and grow.
  - More complex, more traditionally considered form of parasitoidism.
  - Parasitoid uses host hormones as cues for its development.
  - Parasitoid manipulates host hormones to cause developmental arrest, or accelerated or retarded metamorphosis.
  - Why would this be good for the parasitoid?

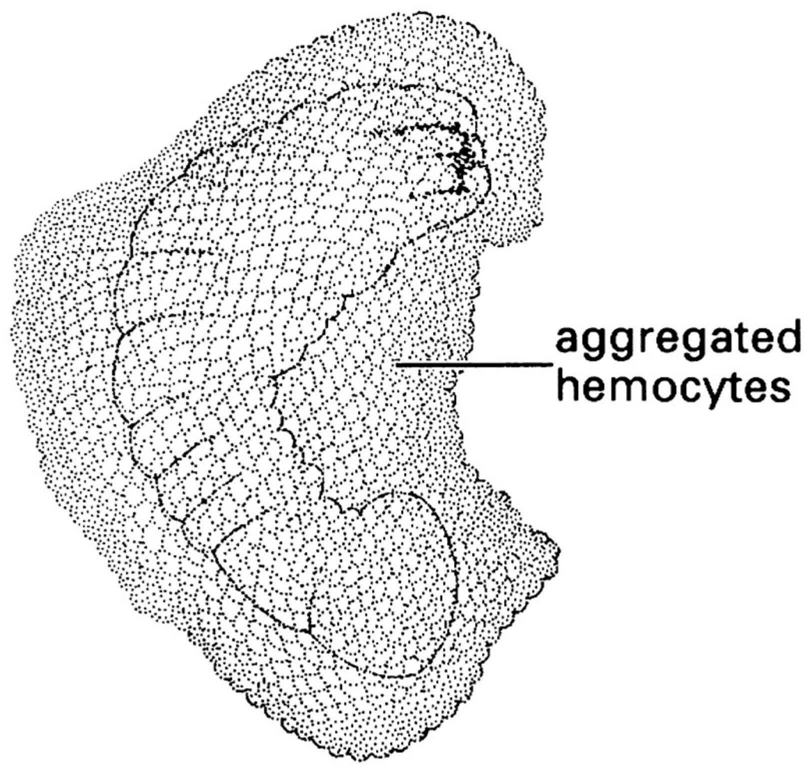
Host defenses against parasitoids

- These are often highly coevolved
  - Selecting the wrong host is fatal to the parasitoid
  - Encapsulation



Host defenses against parasitoids

- Successful attack requires specific adaptations
  - Evasion: Molecular mimicry, host does not recognize as non-self
  - Destruction: Host's immune system is destroyed
  - Suppression: Host's immune system suppressed by viruses carried by parasitoid
  - Subversion via physical resistance or teratocytes.



Host use by parasitoids

- Can **host discriminate** to find a species that they or their offspring can develop in.
- Often specialized because of tight life history association and subsequent coevolution.
- Under ideal conditions are generally **solitary** (one female lays egg or eggs on one individual)
  – Can discriminate previously parasitized individuals.

Superparasitism

- More than one egg injected into host.
- Dependent upon size and quality of the host, the size of the parasitoid, and the postinfection longevity of the host.

- Female can lay multiple eggs or can produce multiple offspring via **polyembryony**.

- What benefits might there be to superparasitism?

Multiparasitism

- Host infected by more than one species of parasitoid.
- Much more common between distantly related species. Why?

Hyperparasitism

- Likely evolved from multiparasitism.
- Has evolved numerous times.
- Secondary parasites make use of primary parasites' marking pheromones.
- Can be internal or external on primary parasitoid.