Taxonomy & Systematics

- These give us the background to understand the evolution of:
  - Morphology
  - Physiology
  - Ecology
  - Life History
  - Geography
  - Etc.

What are they?

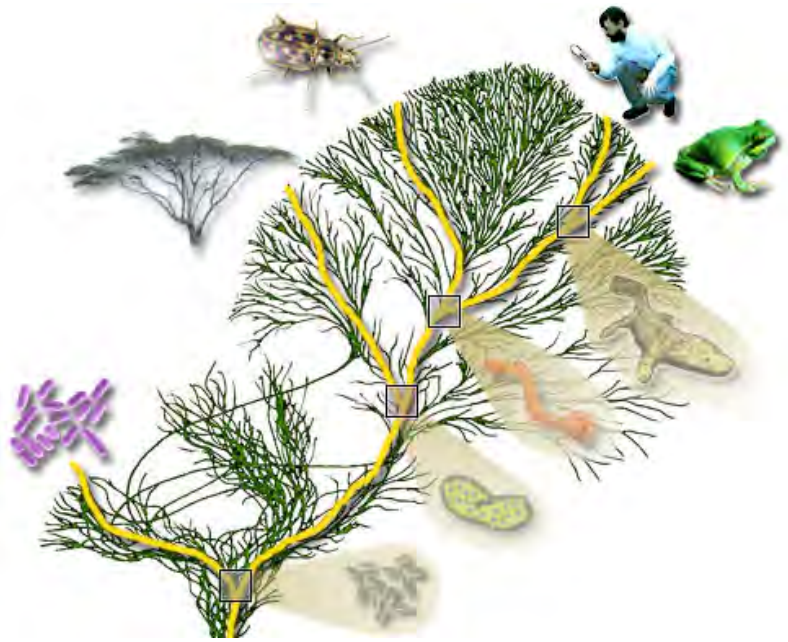
- Taxonomy?

- Systematics?

The goals of systematics…

- Determining relationships
- Understanding evolutionary history
- Describing biodiversity

- This is an incredibly challenging enterprise!

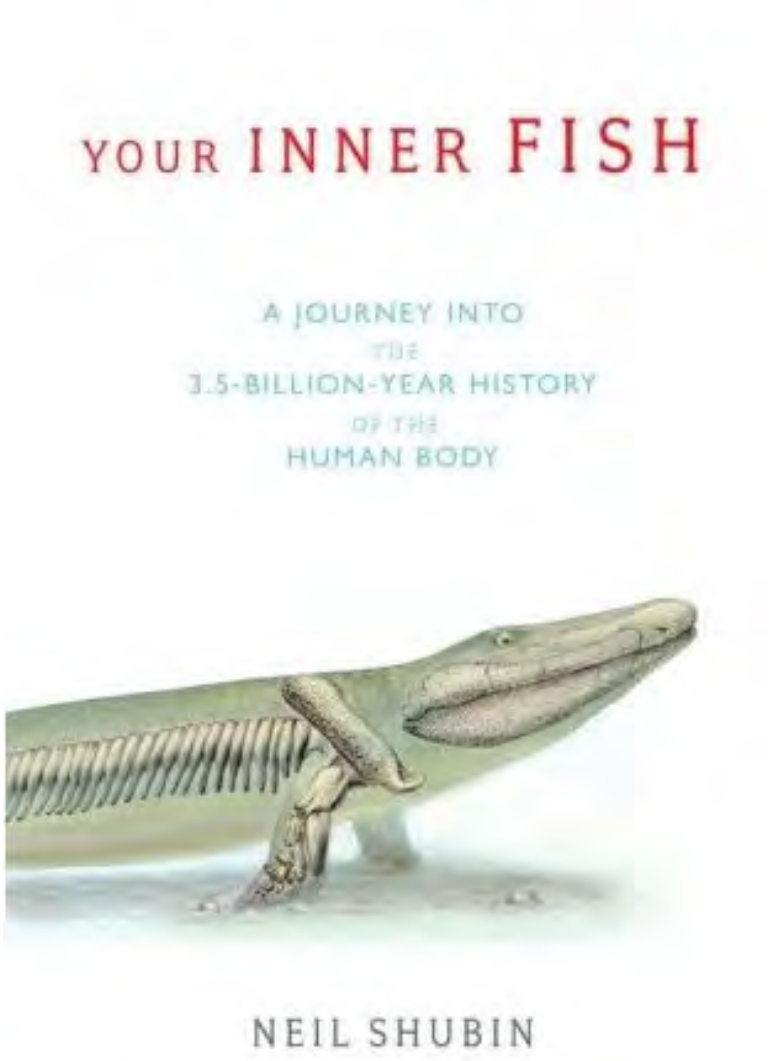


Why?

- It is primarily an **historical** and **inferential** science.
- Relationships become obscured as time passes.

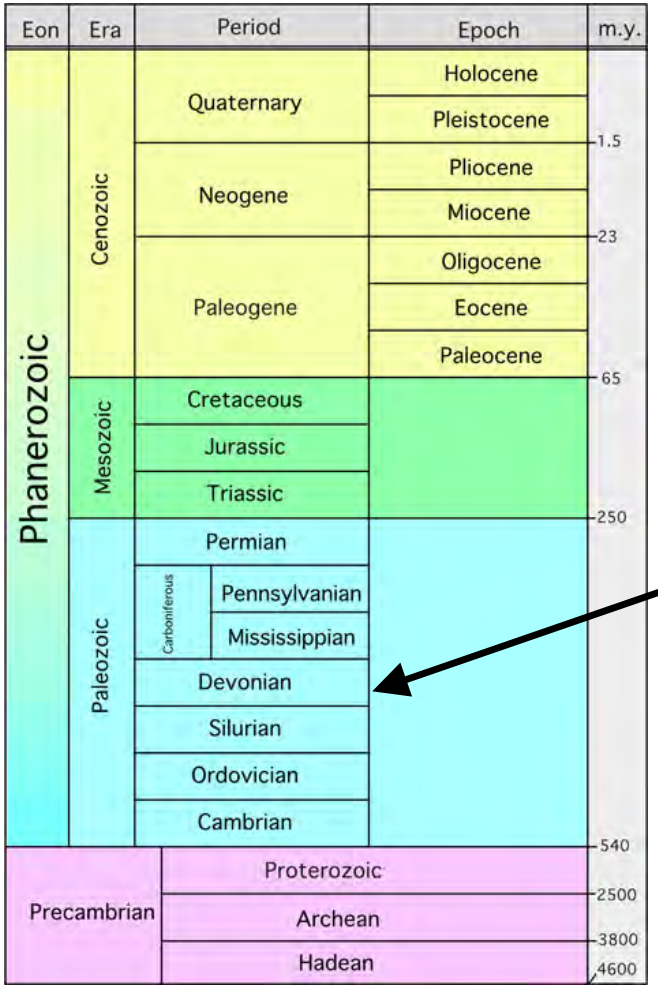
Ancestry

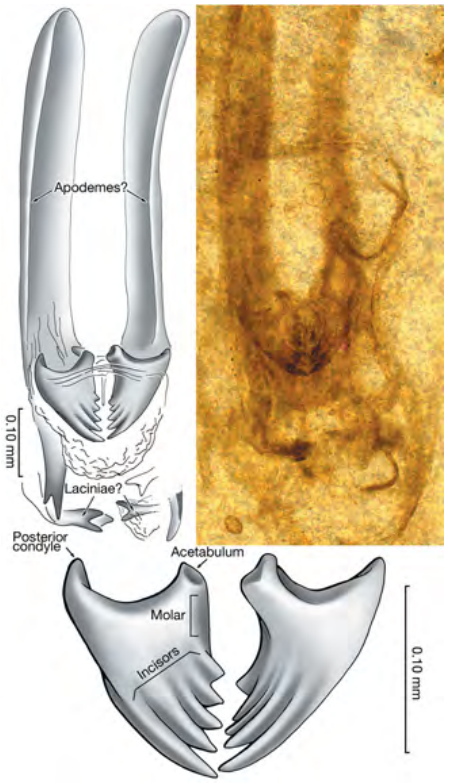
- Regardless, evolutionary history makes us what we are today.
  - 50,000 years of Homo sapiens
  - 4-6 my as homonids
  - 12-18 my as great apes
  - 85 my as primates
  - 125 my as eutherians
  - 210 my as mammals
  - 525 my as vertebrates



Arthropod Ancestry

- Insects are shaped by 400 my of history (as insects) as well.
- But now we have to sort out (who knows how many?) millions of species.

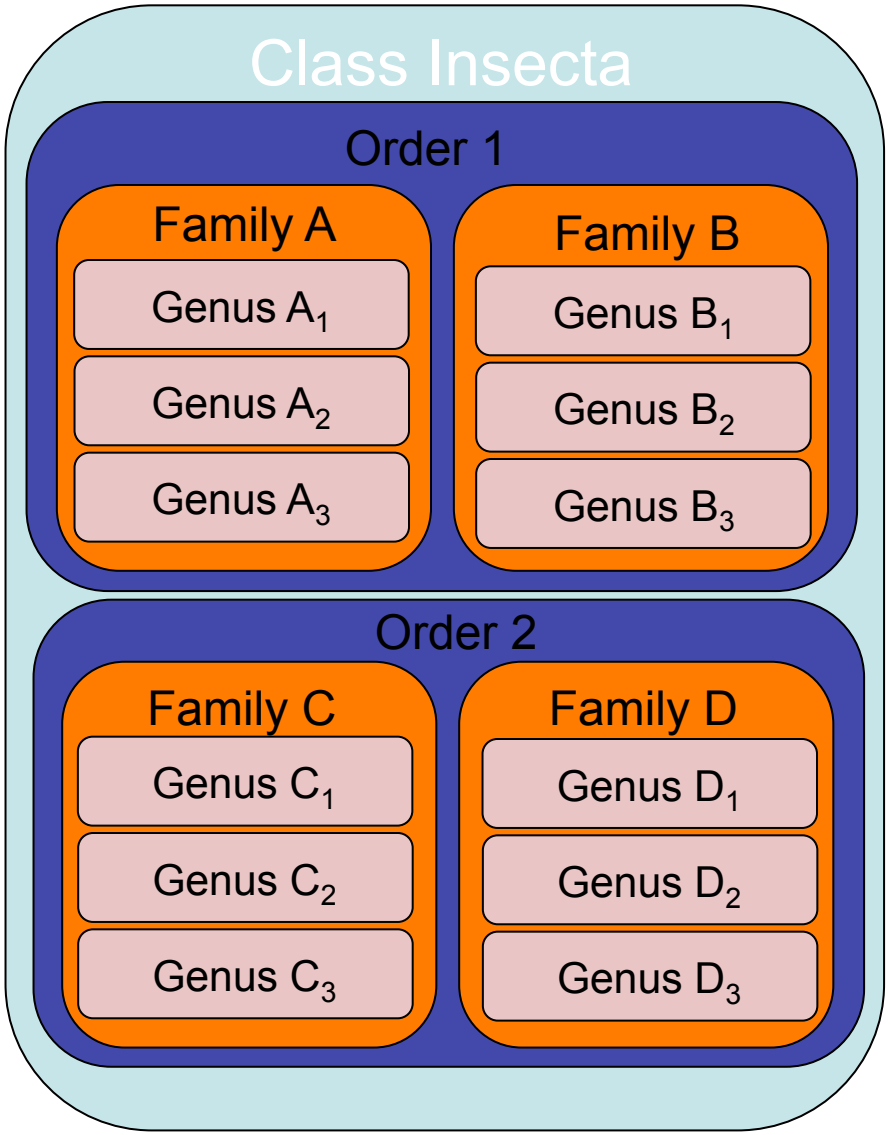




The earliest known insect fossil, *Rhyniognatha hirsti*

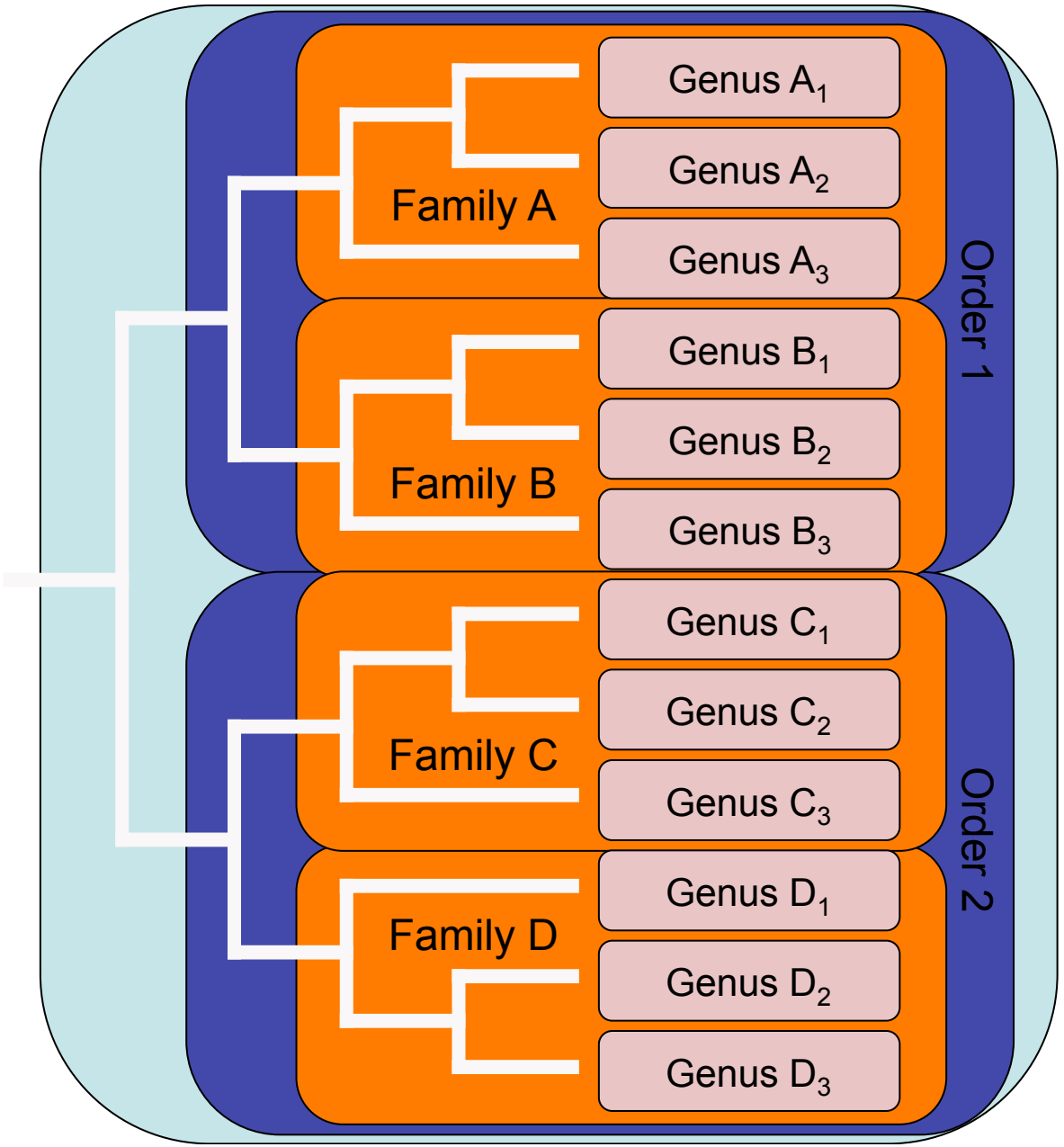
Phylogenetics

- Systematists group taxa based on the principle of *descent with modification*.
- Sort taxa into a hierarchy of Orders, Families, and Genera.



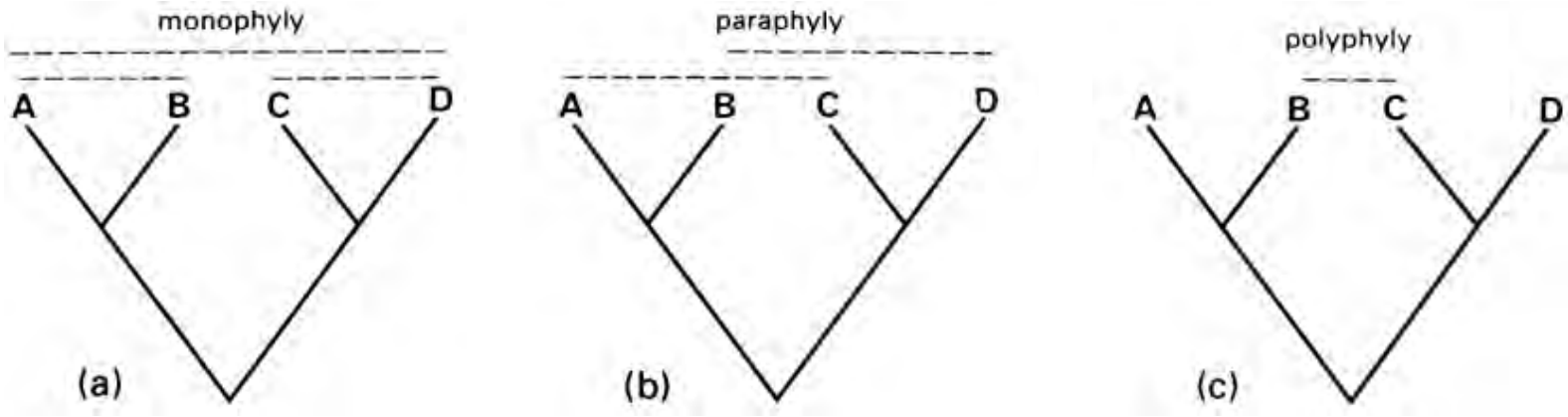
Phylogenetics

- Systematists group taxa based on the principle of *descent with modification*.
- Sort taxa into a hierarchy of Orders, Family, and Genera.
- The goal is to construct these so that this hierarchy reflects evolutionary history.



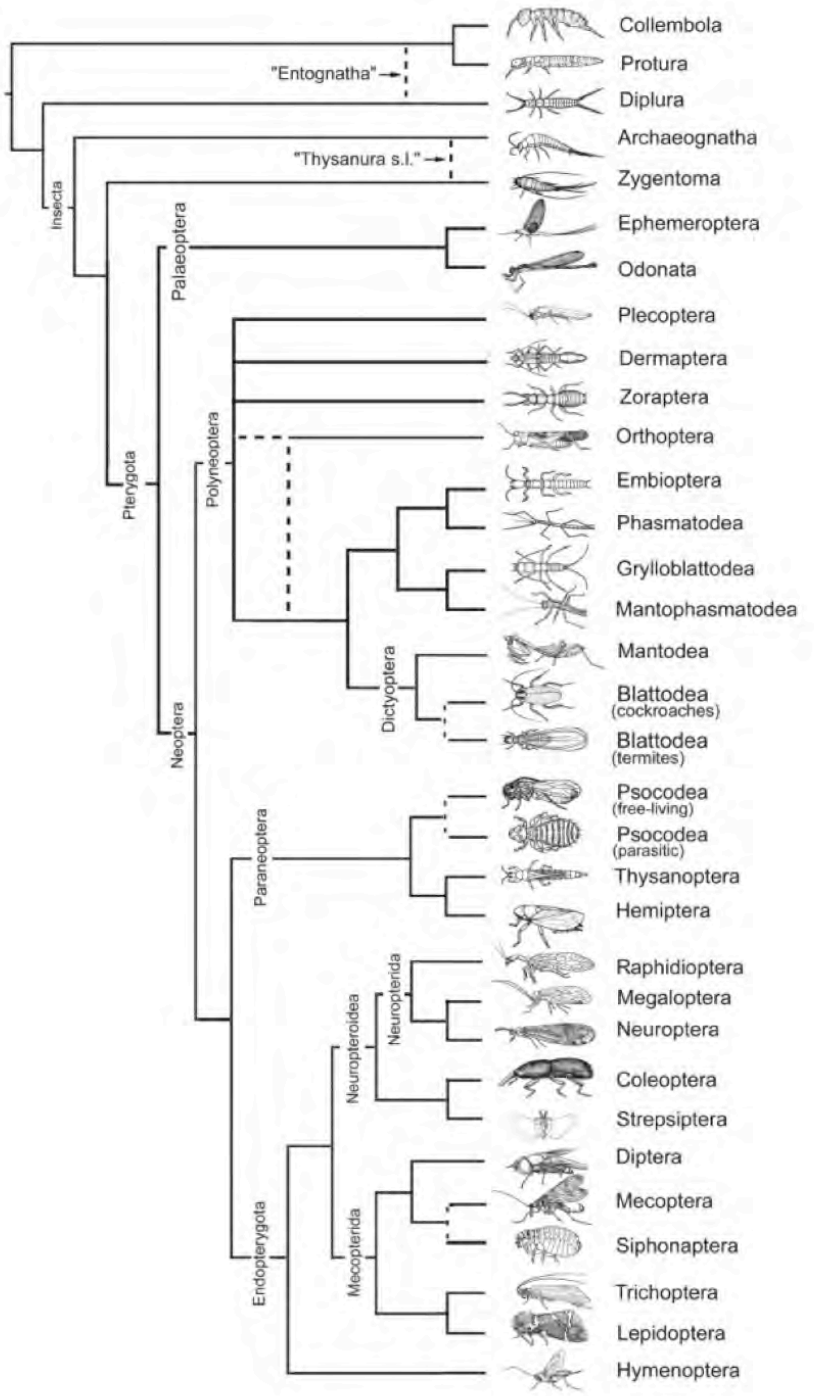
Phylogenetics

- Therefore, we want our groups to be **monophyletic**.
- Not **paraphyletic.**
- Not **polyphyletic.**



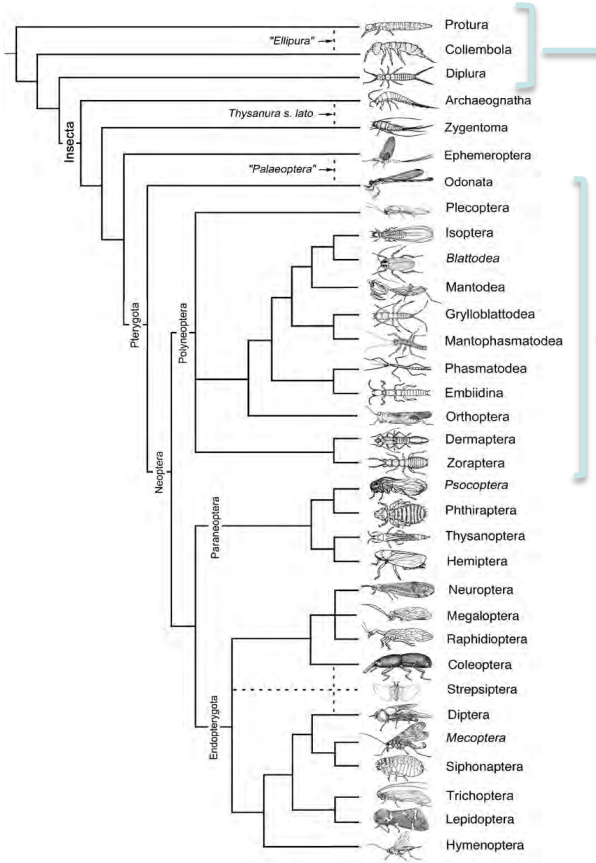
Phylogenetics

- You will have a better understanding of <u>each individual group</u> by learning about its:
  - <u>Evolutionary history</u>
  - <u>Selective pressures</u>
  - <u>Differences from close relatives</u>
- Note that Figure 7.2 in your book is the best current **working hypothesis** of the insect Tree of Life

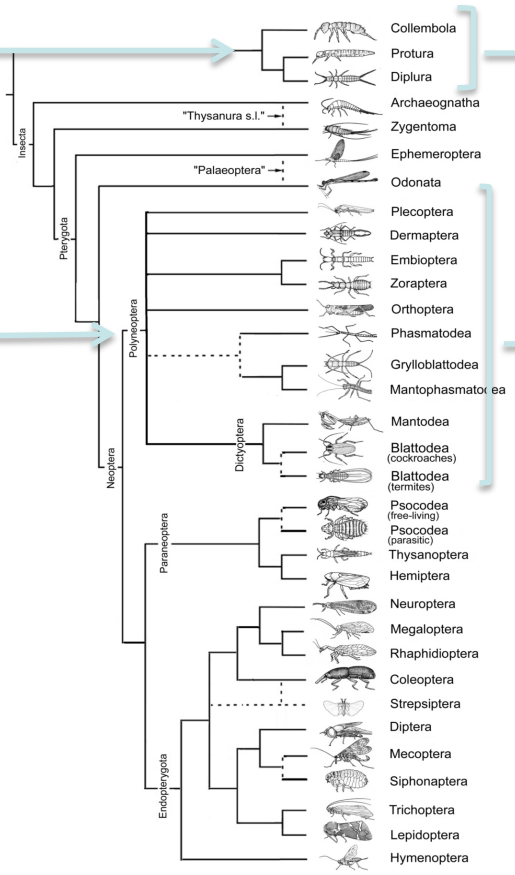


But it is an hypothesis

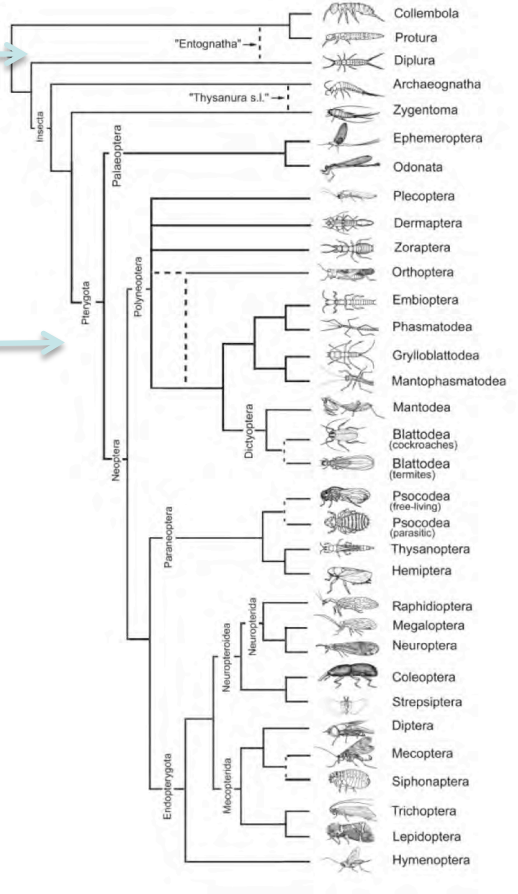
3rd Edition:



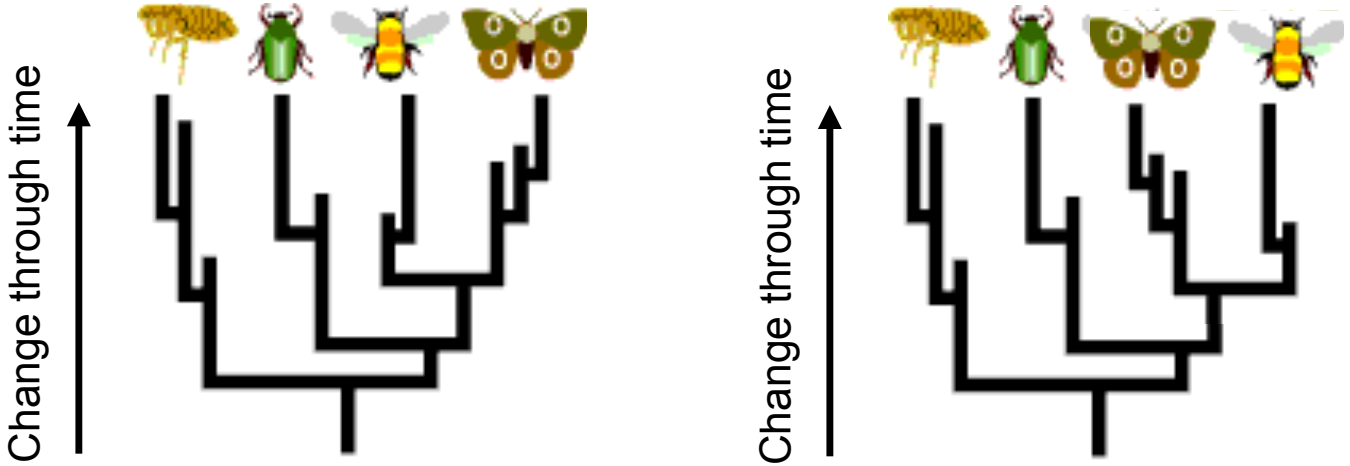
4th Edition:



5th Edition:

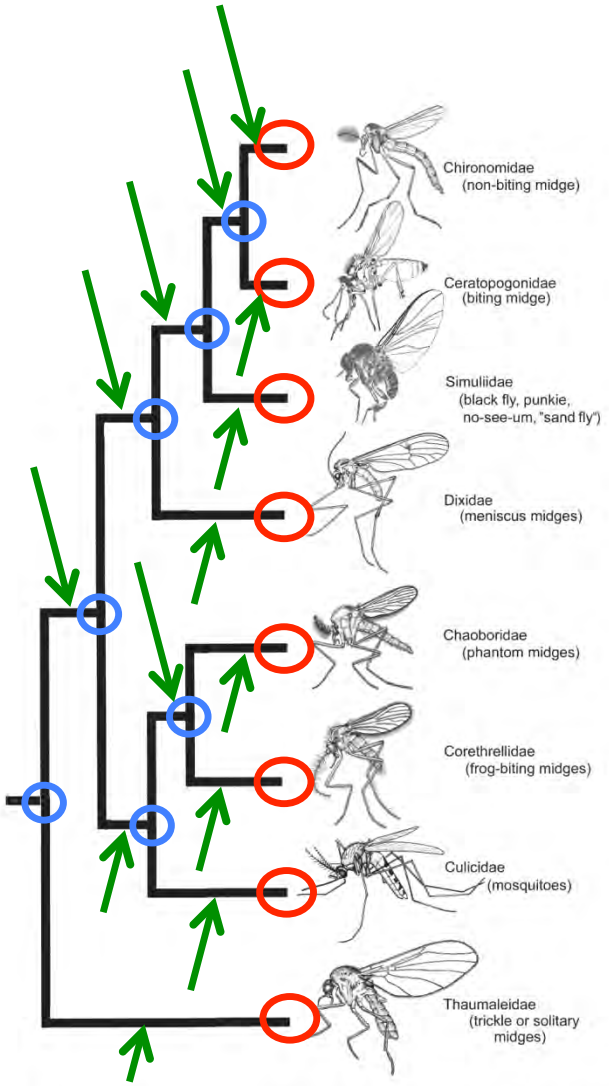


Phylogenetics Review



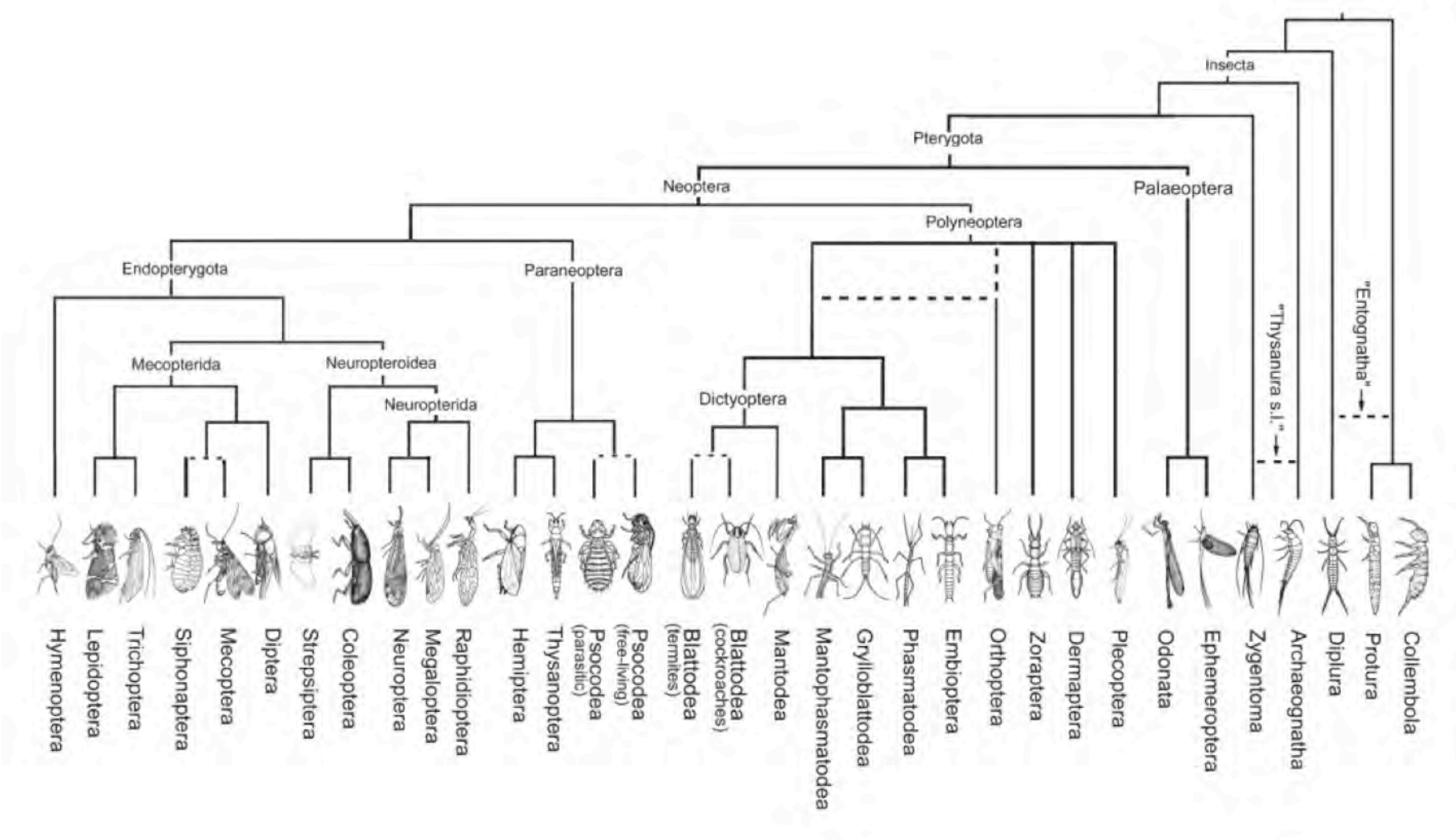
Relative position is the only thing that matters!

Nodes, Tips, Internodes

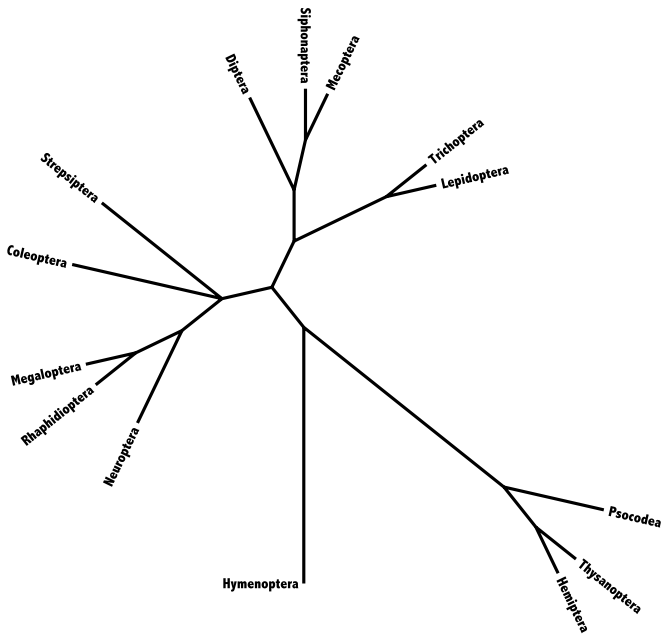


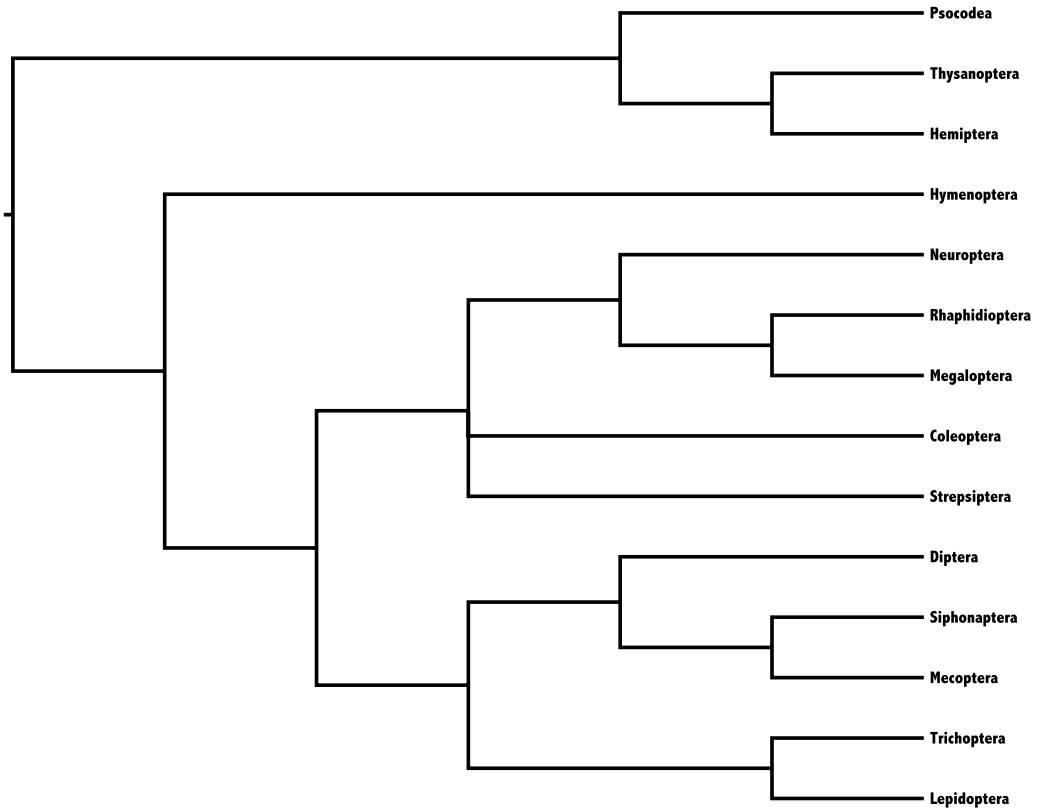
Tree showing proposed relationships between mosquitoes, midges and their relatives. (After various sources.)

Sister groups: The two taxa on either side of a split.
Polytomies: When resolution of the branching diagram is difficult.
Outgroups: Not part of the group in question, but is closely related to the group.



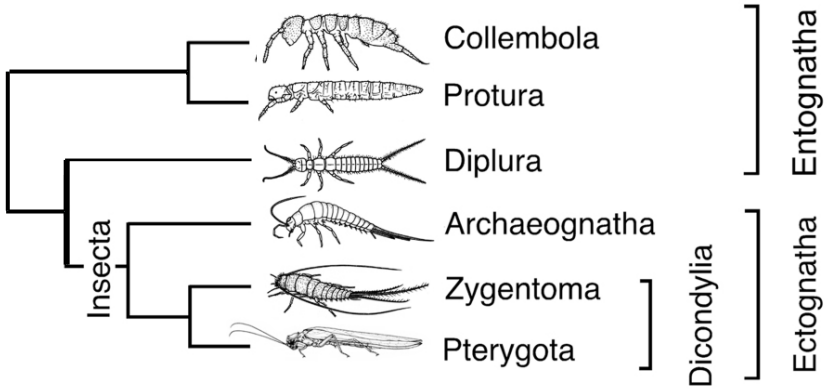
Outgroups


Diptera
Siphonaptera
Mecoptera
Trichoptera
Lepidoptera
Strepsiptera
Coleoptera
Megaloptera
Rhaphidioptera
Neuroptera
Hymenoptera
Psocodea
Thysanoptera
Hemiptera

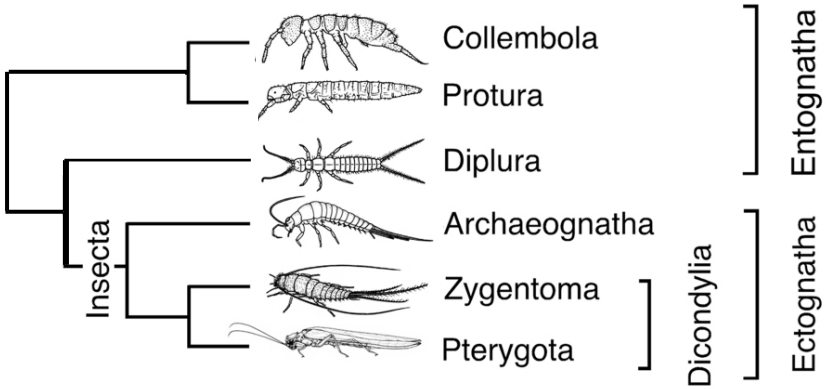

Psocodea
Thysanoptera
Hemiptera
Hymenoptera
Neuroptera
Rhaphidioptera
Megaloptera
Coleoptera
Strepsiptera
Diptera
Siphonaptera
Mecoptera
Trichoptera
Lepidoptera

Terminology.

- Phylogenies are based on **shared, derived (or unique) *homologous* features**. These are known as **apomorphies**.
- **Synapomorphies** are traits that are unique, derived, and indicate relationships. They denote clades.
- **Autapomorphies** are traits that are unique and derived, but do not indicate relationships. They denote tips.
- **Plesiomorphies** are traits shared by a number of groups, and are inherited from ancestors older than the last common ancestor. They do not denote clades.

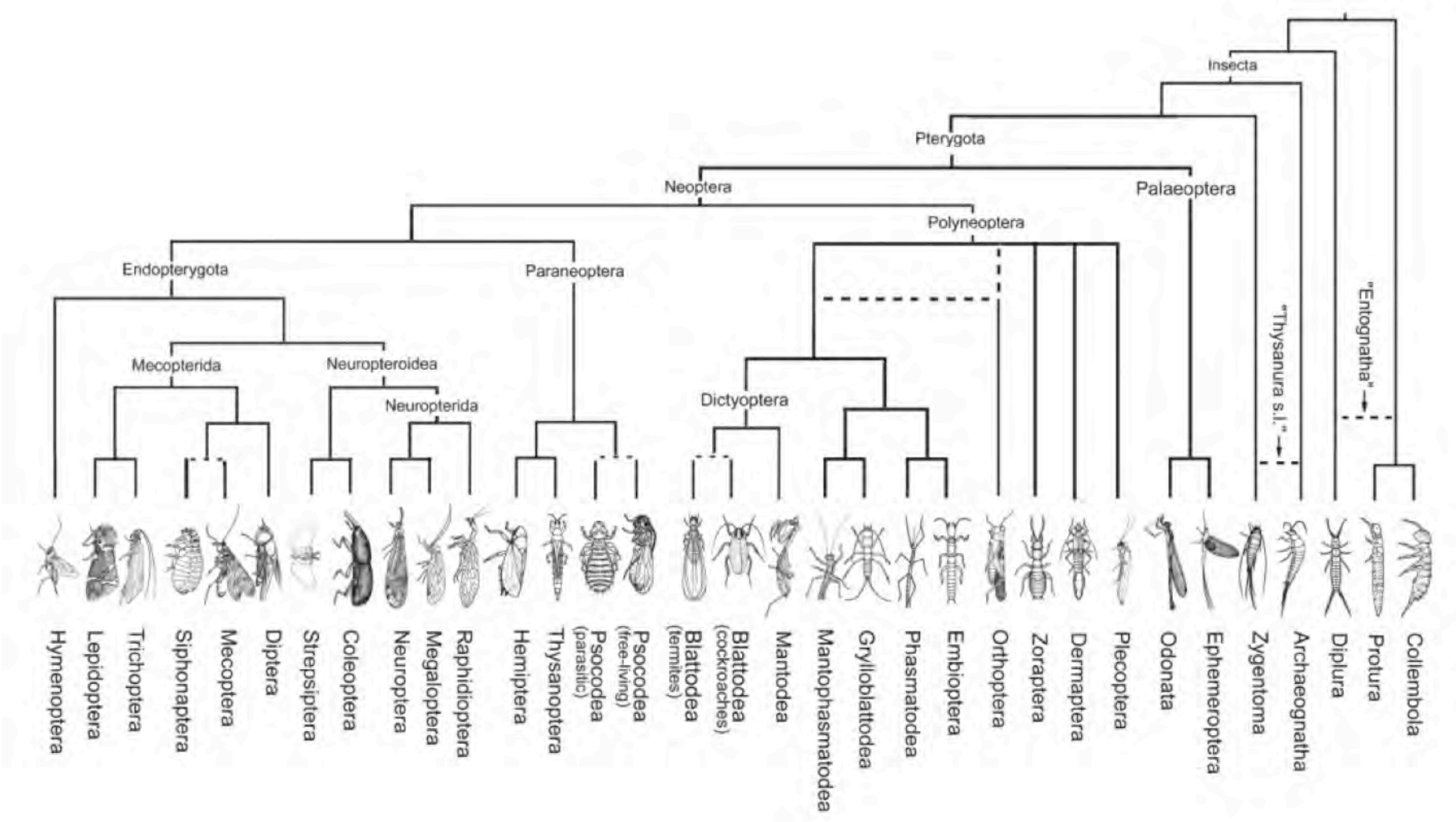


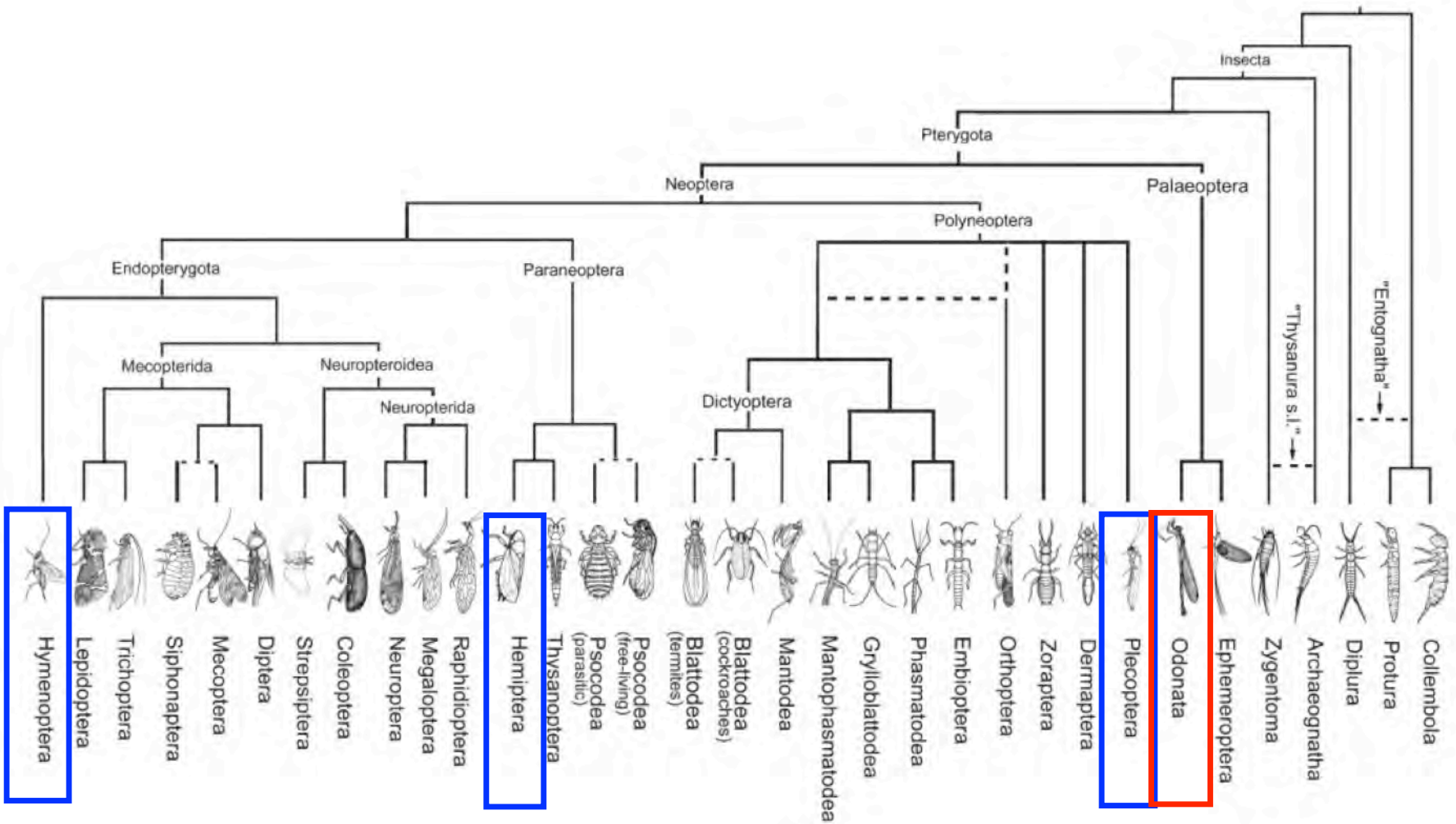
Synapomorphies, Autapomorphies, & Plesiomorphies



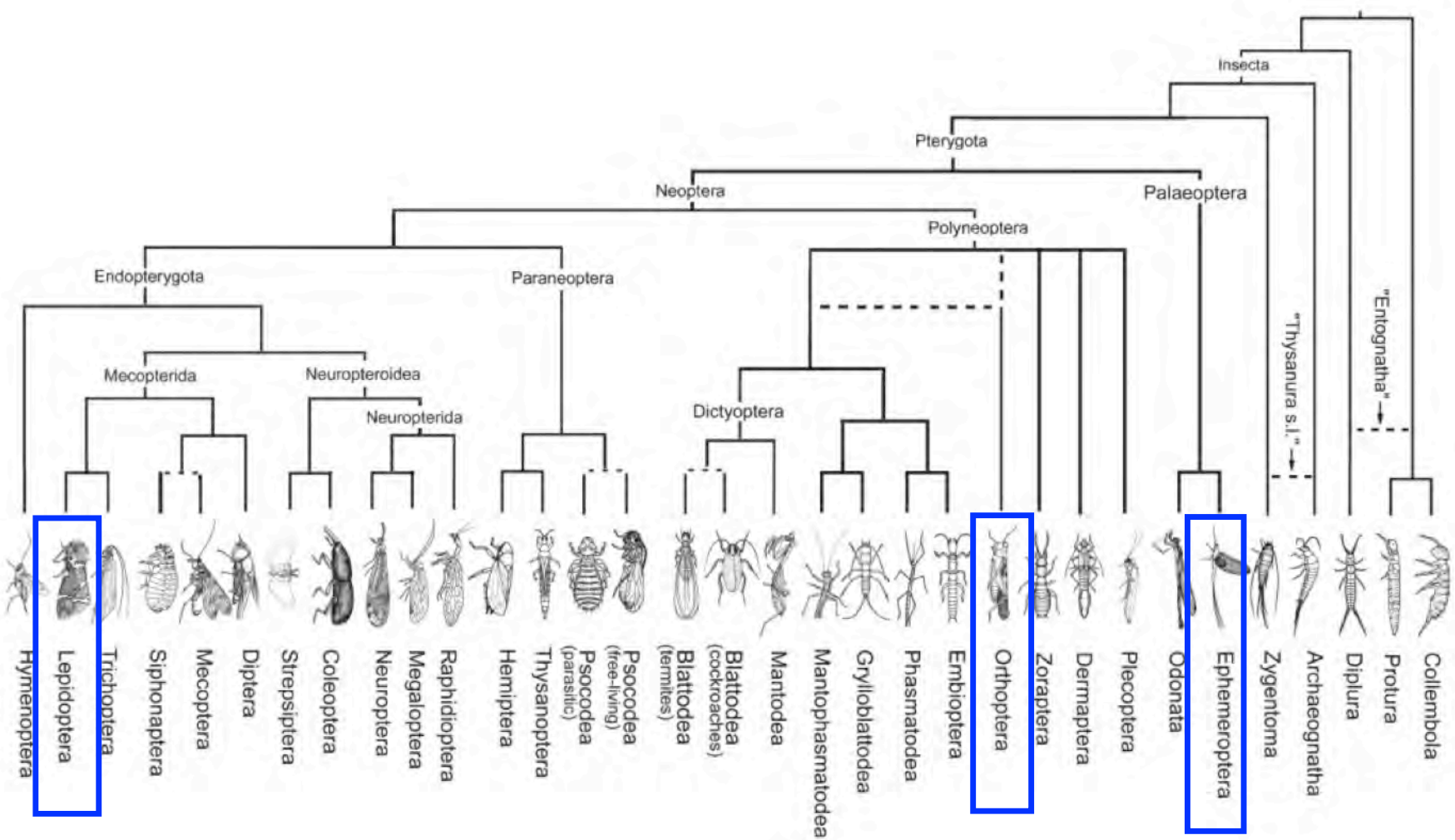
- Insects are a very well-supported monophyletic group.
- Numerous recognized synapomorphies.
- Let's consider two traits: ectognathy and wings.

How about metamorphosis?
Are three pairs of legs a defining feature of Insecta? How or how not?





Tree-thinking questions: Which is most closely related to a dragonfly: wasps, true bugs, or stoneflies?



Tree-thinking questions: Which is most evolved: Lepidoptera, Orthoptera, or Ephemeroptera?

Phylogenetic Analysis

- How do we reconstruct phylogenetic trees?
- Based on using characters to test hypotheses of phylogenetic relationships.
- Remember that the branching diagram is the hypothesis.

CHARACTERS

- A set of alternative conditions (character state) that are considered able to evolve one to another.
- For phylogenies, these are **consistent** within taxa, but vary **among** taxa.
- Must search for and evaluate **homologous** structures.
  - Must follow *Recognition Criteria of Homology*:
    1. Similarity in position
    2. Detailed resemblance
    3. Continuance through intermediate forms

CHARACTERS

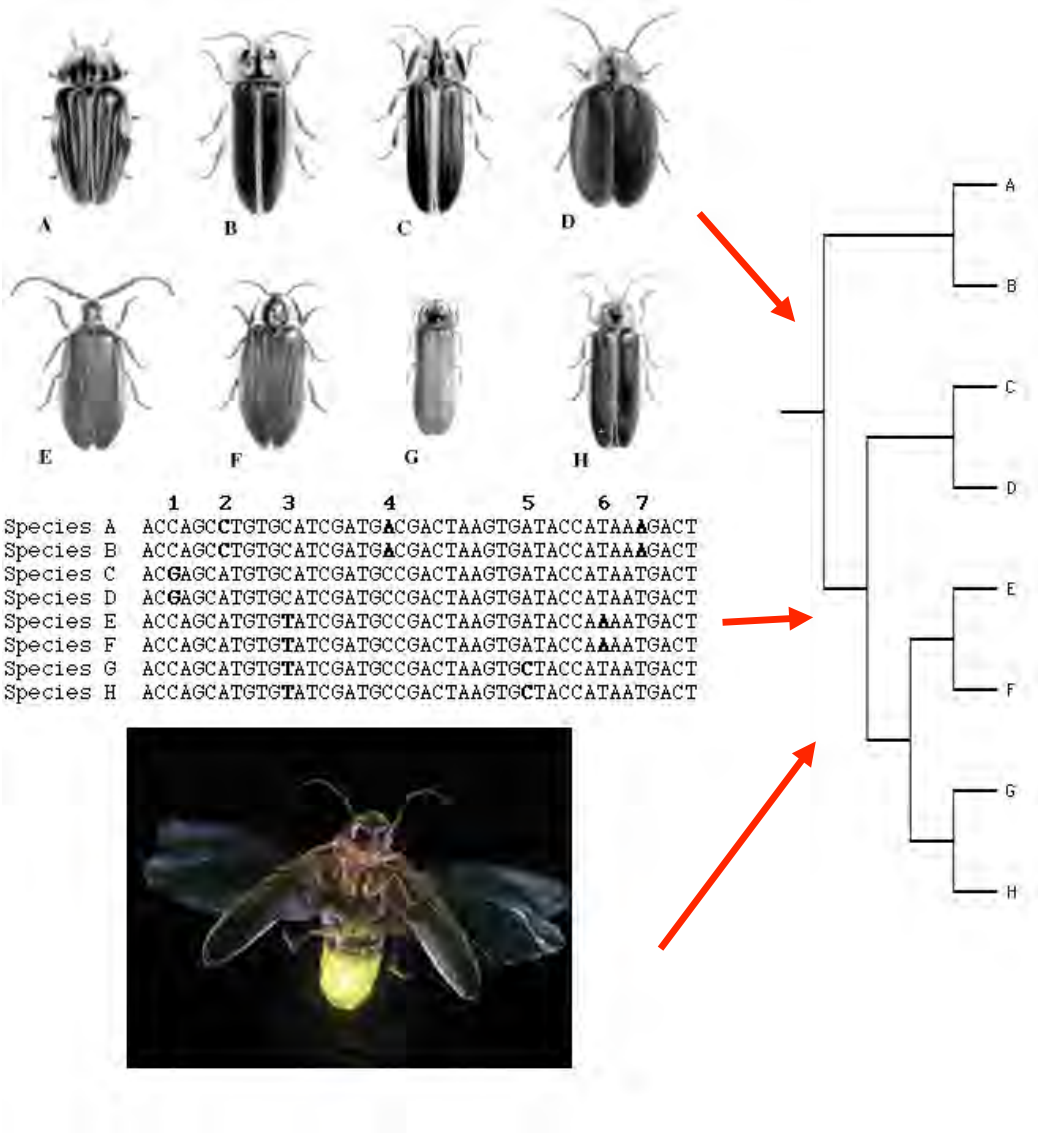
- Types of Characters:
  - Must be products of evolutionary process
  - Must be heritable
  - What kinds of things fall under this?

- **Morphological Characters**
- **Physiological characters**
- **Molecular characters**
- Behavioral characters
- Ecological characters
- Geographic characters

CHARACTERS

A simple rule for hypothesis testing

- The more data, the better!
  - This applies to testing phylogenetic relationships as well: the more characters, the better
  - Also, the more character *systems*, the better.



Phylogenetic Analysis

- How do we reconstruct phylogenetic trees?
- Based on using characters to test hypotheses of phylogenetic relationships.
- Remember that the branching diagram is the hypothesis.

Phylogenetic Analysis

1. A set of **data** (character X taxon matrix)
2. A set of possible evolutionary trees
3. A means of evaluating the alternative trees *given the data*.

Phylogenetic Analysis

1. A set of **data** (character X taxon matrix)
2. A set of possible evolutionary trees
3. A means of evaluating the alternative trees *given the data*.

- Identify homologous characters and delineate alternative character states.

Phylogenetic Analysis

1. A set of **data** (character X taxon matrix)
2. A set of possible evolutionary trees
3. A means of evaluating the alternative trees *given the data*.

- These are the alternative hypotheses.
- There are a tremendous number of alternative hypotheses (e.g. with 10 species, there are 34,459,425 possible trees)

$$\frac{n!(n-1)!}{2^{n-1}}$$

Phylogenetic Analysis

1. A set of **data** (character X taxon matrix)
2. A set of possible evolutionary trees
3. A means of evaluating the alternative trees *given the data*.

- Based on distribution of using shared derived characters (**apomorphies**) to identify **clades.**
- Evaluated based on **maximum parsimony** or **maximum likelihood** as the **optimality criterion**.

Which tree is preferred?

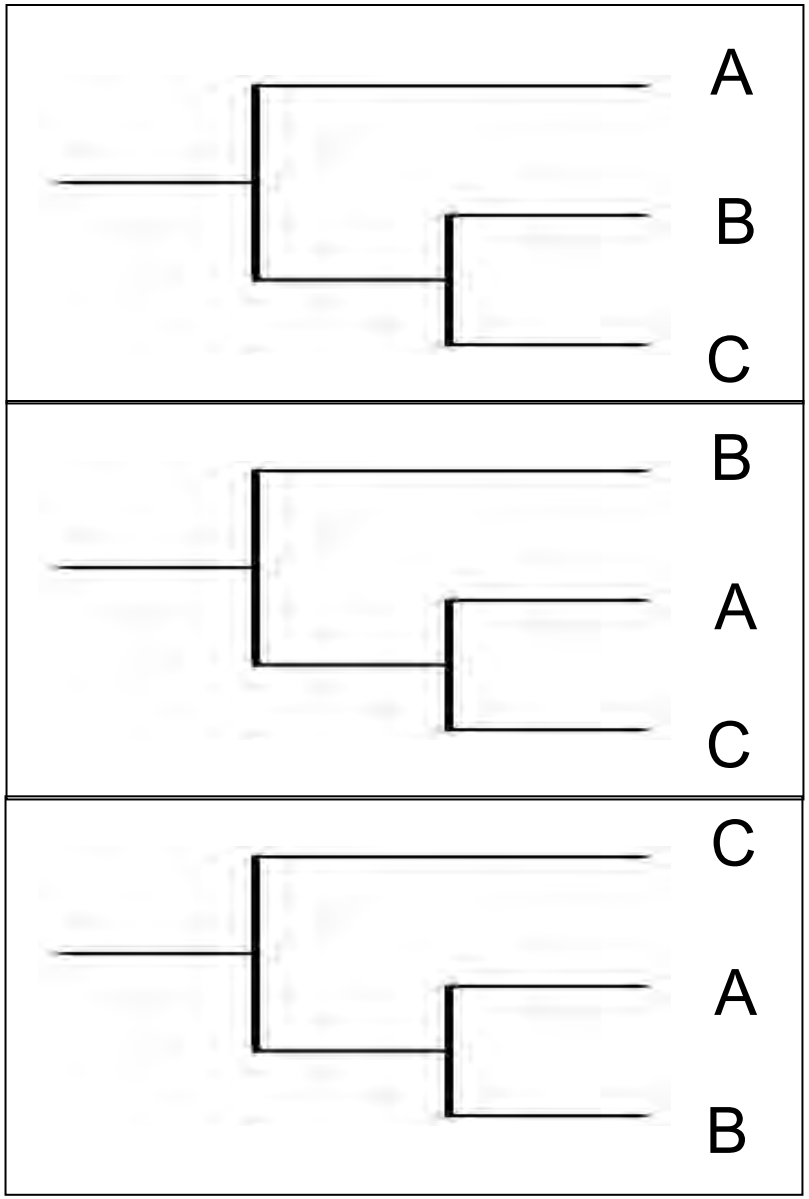
- Parsimony
- Maximum-likelihood

- We should first investigate the simplest explanation for observed character state distributions.
- Minimizes the number of evolutionary events on a tree.
- Maximizes apomorphic characters while mimizing homoplasious characters.

Which tree is preferred?

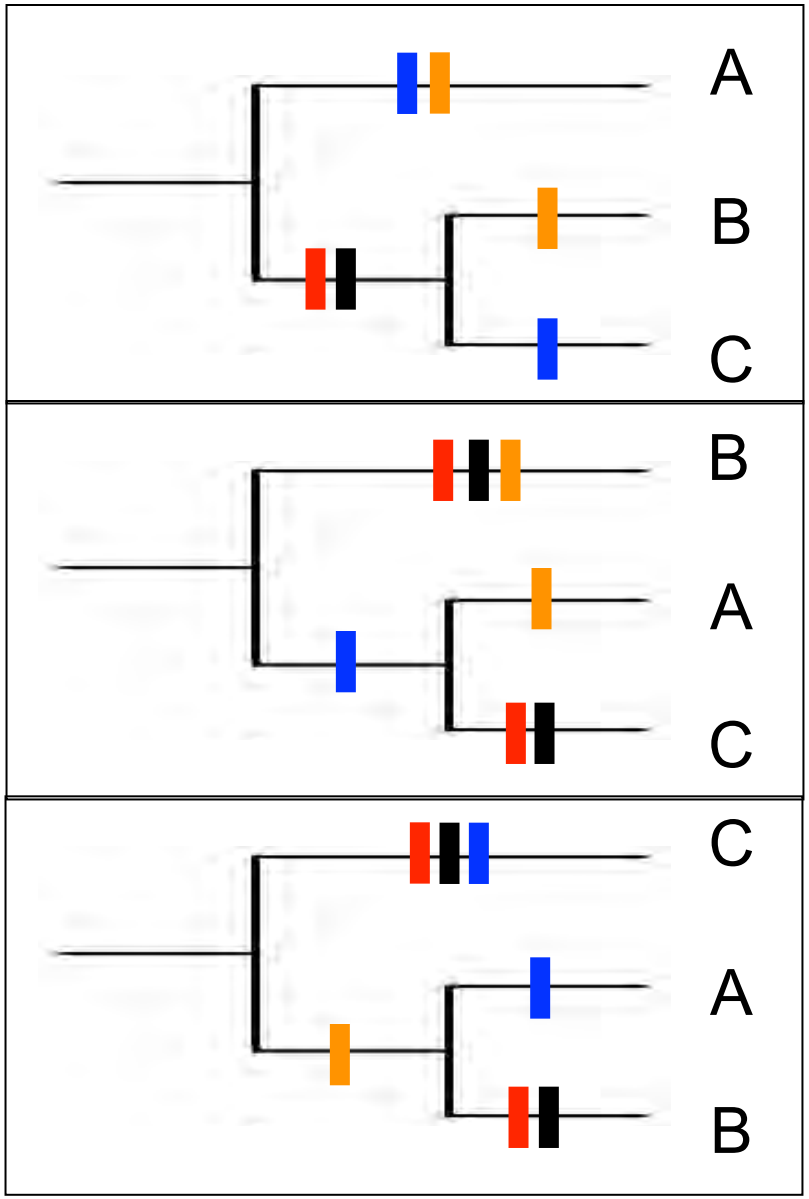
- Parsimony
  - Data matrix & alternative hypotheses.
  - Minimize character changes on the trees.

	Head black	Legs blue	Dorsum orange	Wings red
A				
B				
C				



Which tree is preferred?

- Parsimony
  - Minimize character changes on the trees.
  - Do so for every character.
  - Count the number of changes.
  - Which is *most parsimonious*?



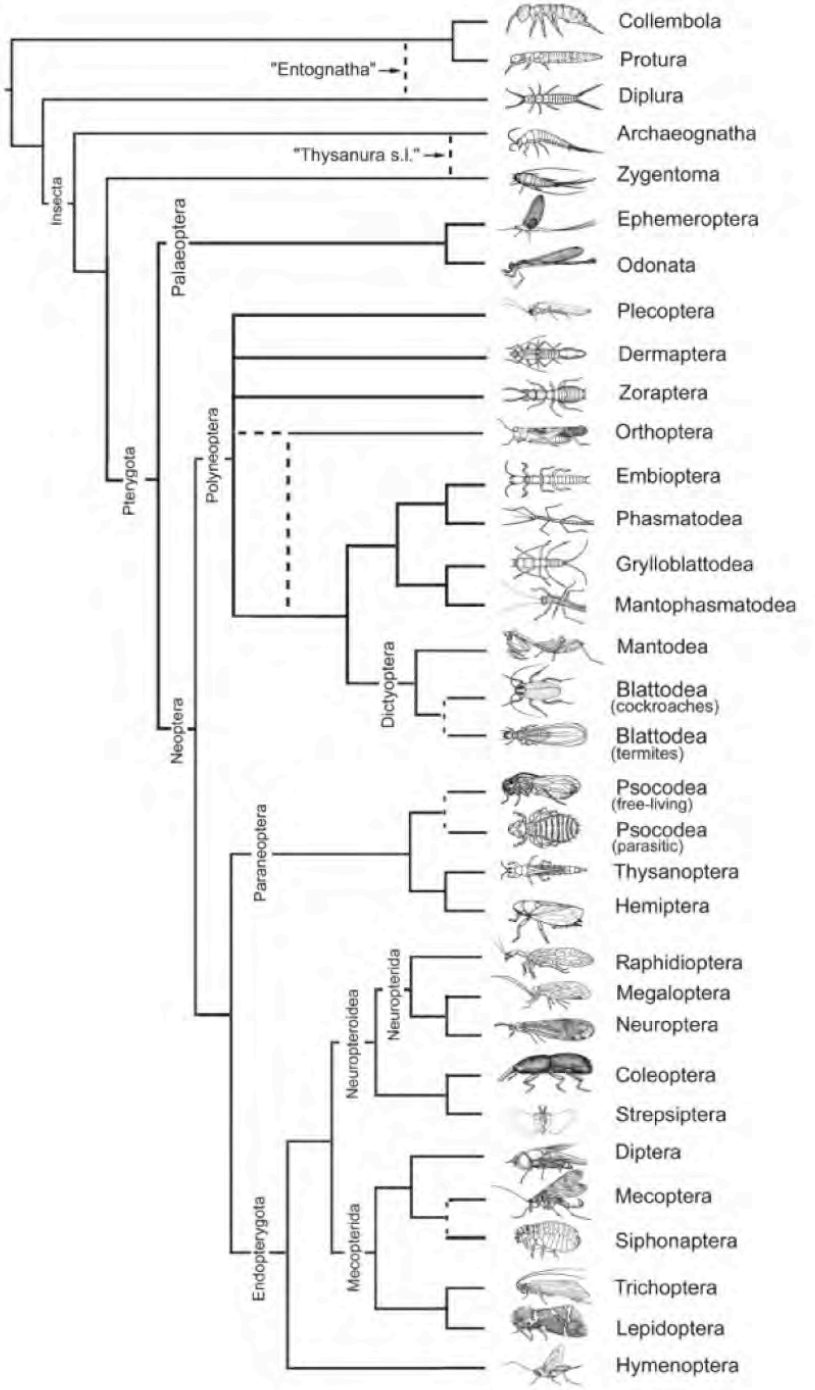
Which tree is preferred?

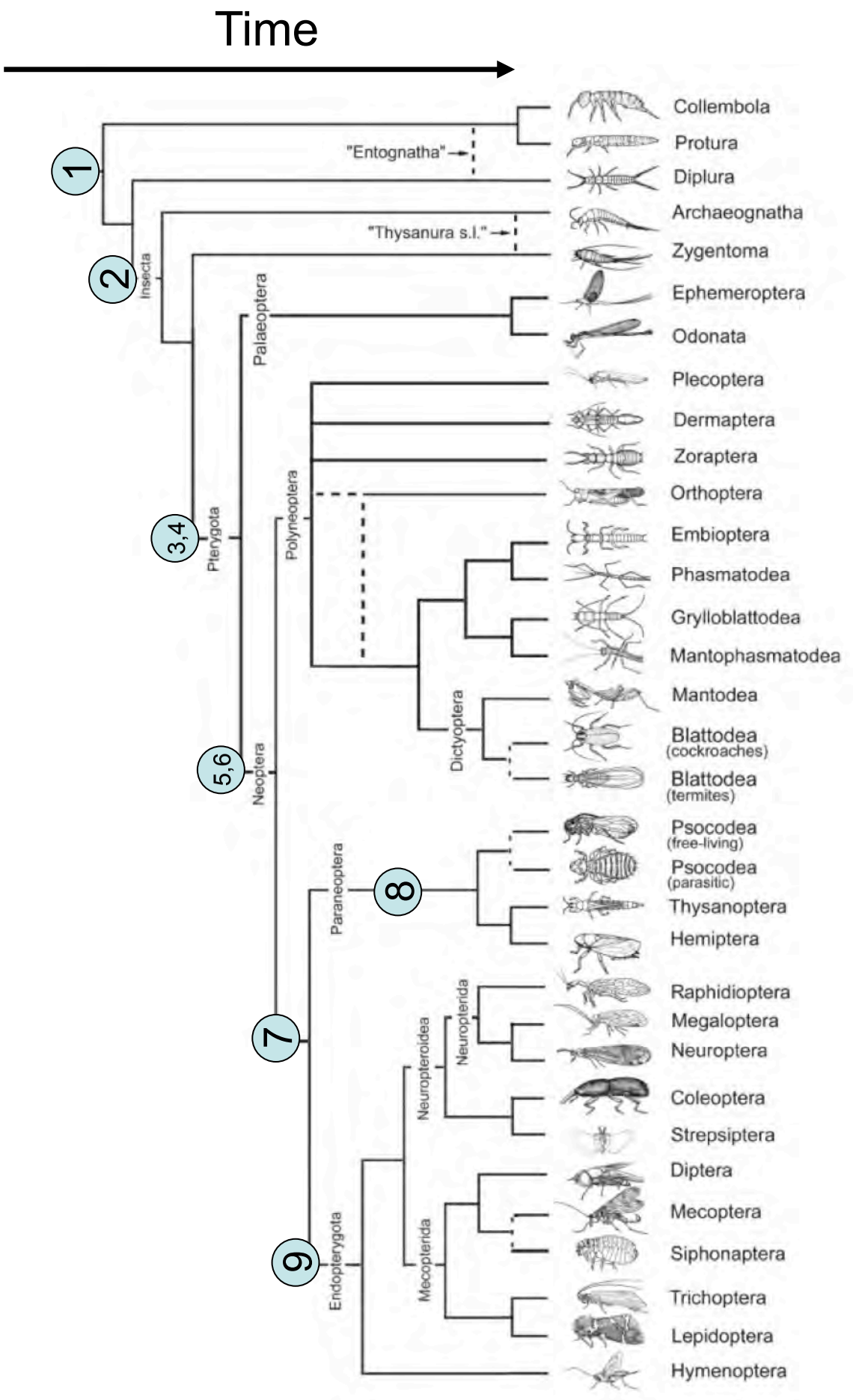
- Parsimony
- **Maximum-likelihood**

- Similar, but now optimality no longer based on principle of parsimony.
- Optimality based on specified model of evolution.
- Generally applied to molecular data.
- Uses external information.

The Insects

- For now, don't get bogged down in the details.
- Today we'll focus on the big picture and use this as a starting point for touring some of the major milestones in insect evolution.




Time
1
2
3,4
5,6
7
8
9
Insecta
Pterygota
Palaeoptera
Neoptera
Polyneoptera
Paraneoptera
Endopterygota
Dictyoptera
Neuropteroidea
Neuropterida
Mecopterida
"Entognatha"
"Thysanura s.l."
Collembola
Protura
Diplura
Archaeognatha
Zygentoma
Ephemeroptera
Odonata
Plecoptera
Dermaptera
Zoraptera
Orthoptera
Embioptera
Phasmatodea
Grylloblattodea
Mantophasmatodea
Mantodea
Blattodea (cockroaches)
Blattodea (termites)
Psocodea (free-living)
Psocodea (parasitic)
Thysanoptera
Hemiptera
Raphidioptera
Megaloptera
Neuroptera
Coleoptera
Strepsiptera
Diptera
Mecoptera
Siphonaptera
Trichoptera
Lepidoptera
Hymenoptera

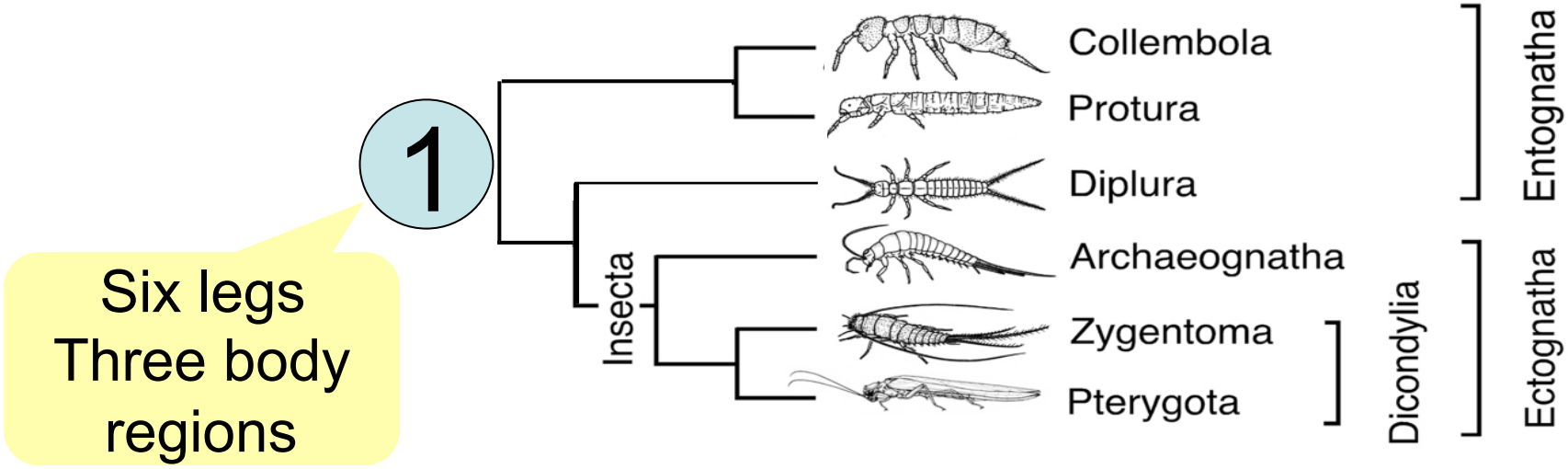
Evolutionary Milestones

- Each number corresponds to a new or improved physical characteristic (perhaps a mutation or a novel adaptation) that proved to have selective value and was passed on to succeeding generations.
- These are cumulative.

- Pre-adaptations: life on land…

1. Six legs, three body regions.
2. Ectognathous mouthparts.
3. Wings.
4. Metamorphosis.
5. Foldable wings.
6. Indirect flight muscles.
7. Concentration of ganglia.
8. Sucking mouthparts.
9. Complete metamorphosis.

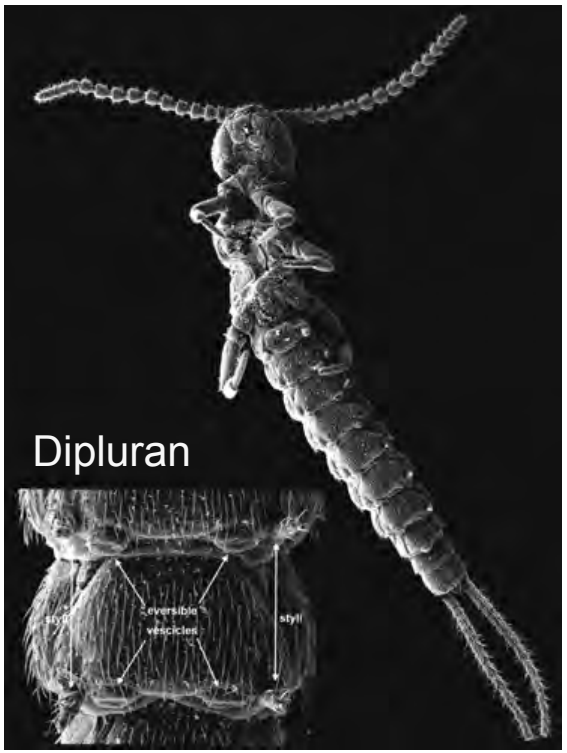
Hexapoda

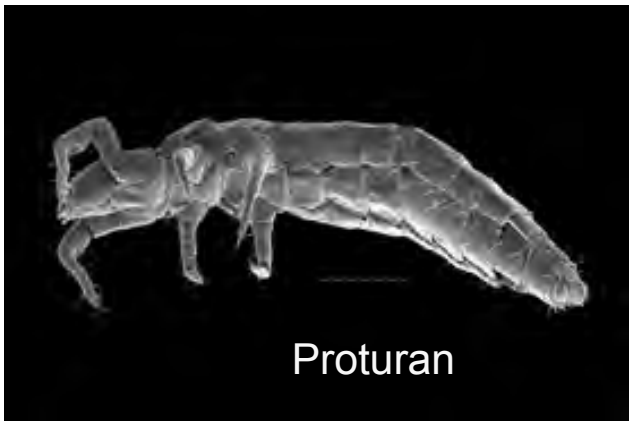


- ‘Lumpers’ put all of these into the Insecta.
- ‘Splitters’ separate into two classes: Entognatha & Insecta (a.k.a. Ectognatha).

Entognatha

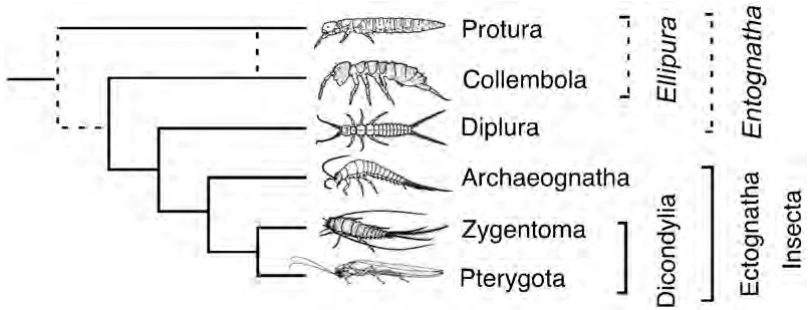
- Mouthpart appendages recessed within pouch on head.



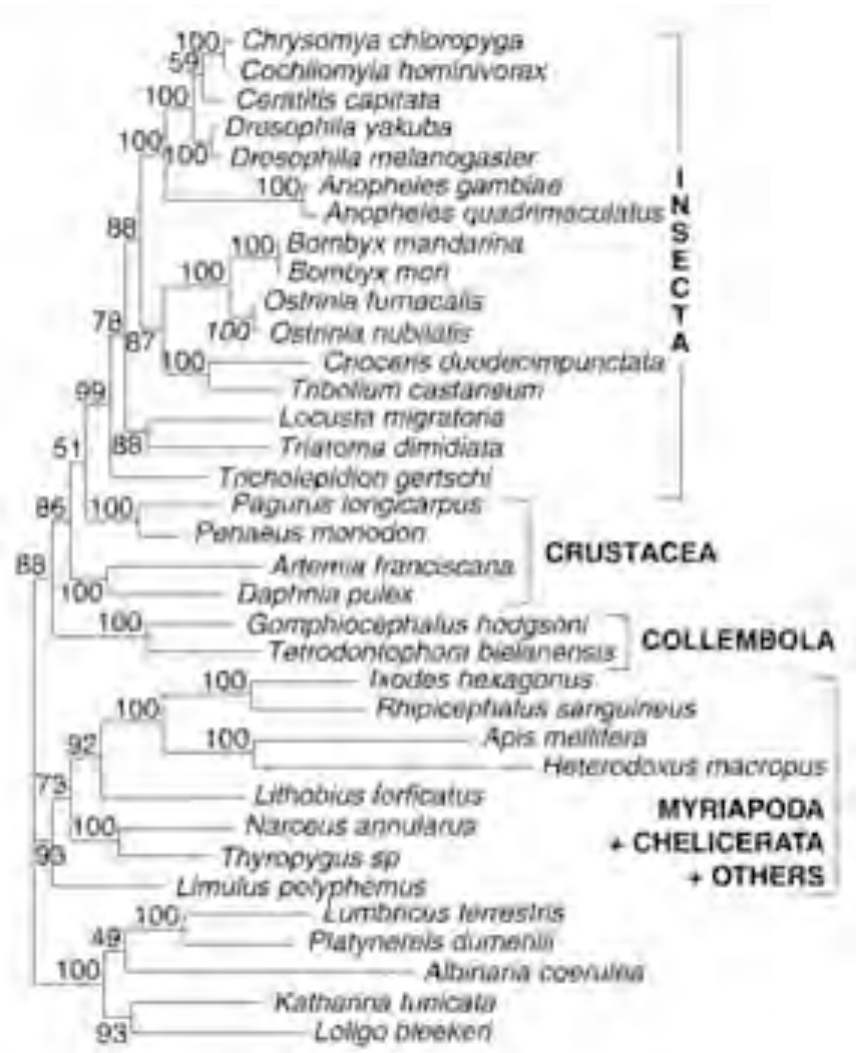


Entognatha

- Monophyly with Insecta under question.
- What features do they have in common with Insecta?



Delsuc *et al* Science 2003



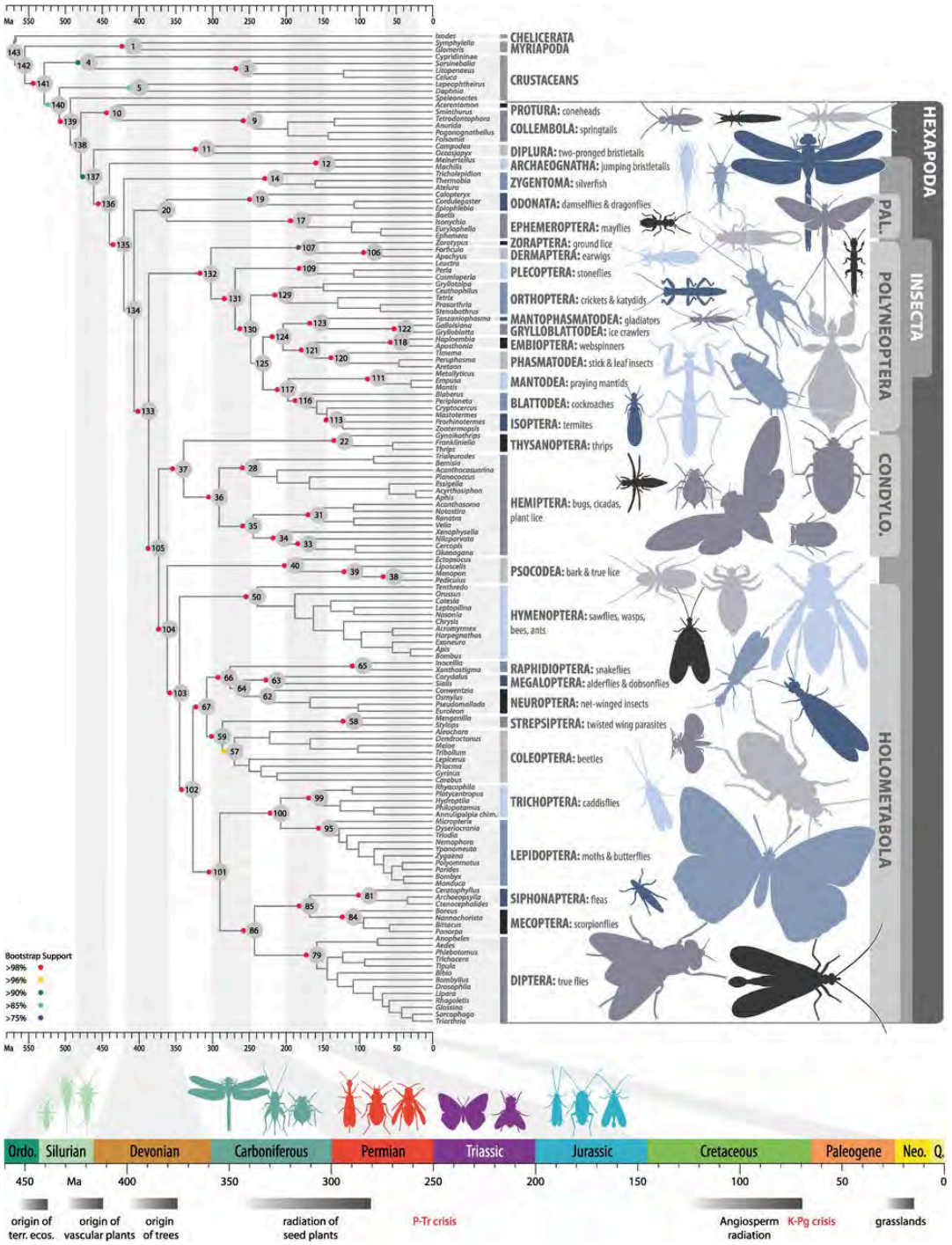
Nardi *et al* Science 2003

November 2014

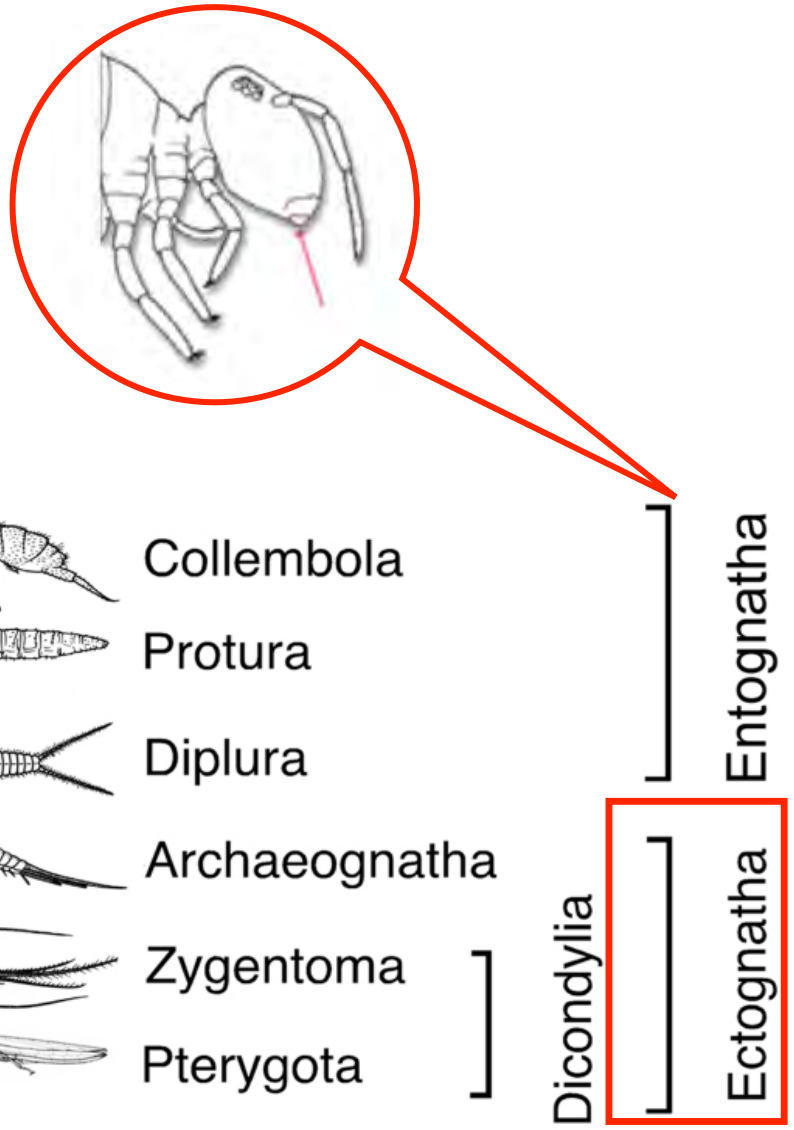
2.5 gigabases of DNA

Misof *et al.* Science

Hexapoda monophyletic but Entognatha paraphyletic

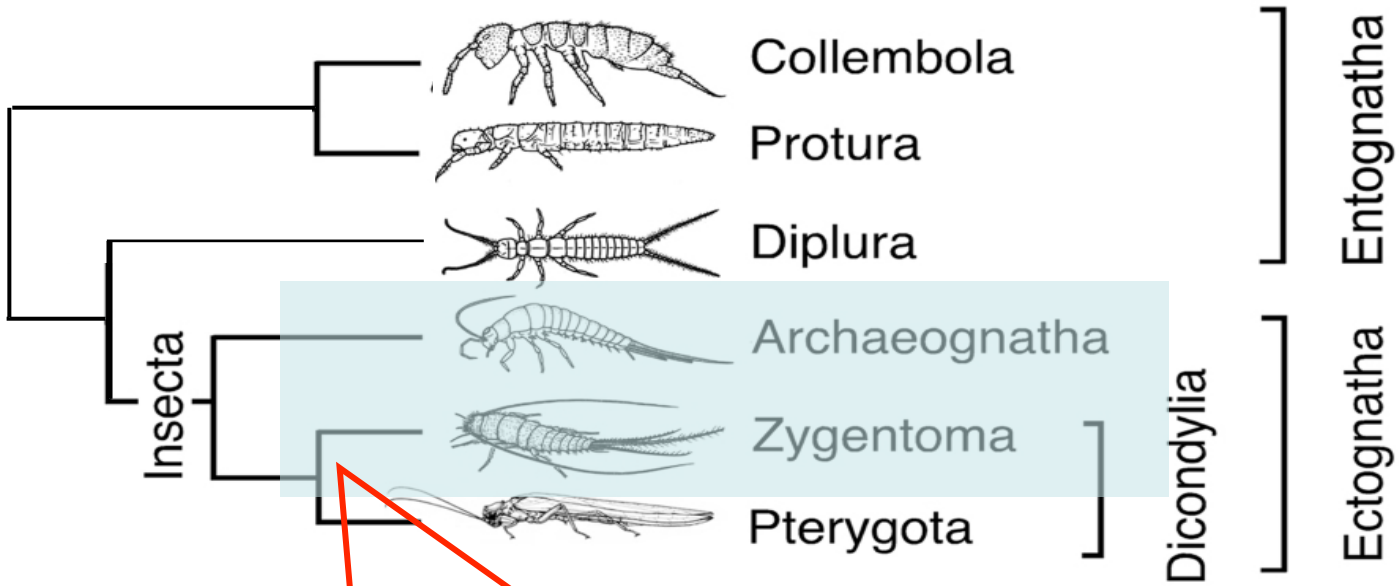


Insecta


Collembola
Protura
Diplura
Archaeognatha
Zygentoma
Pterygota
2
Insecta
Entognatha
Dicondylia
Ectognatha

‘Apterygota’

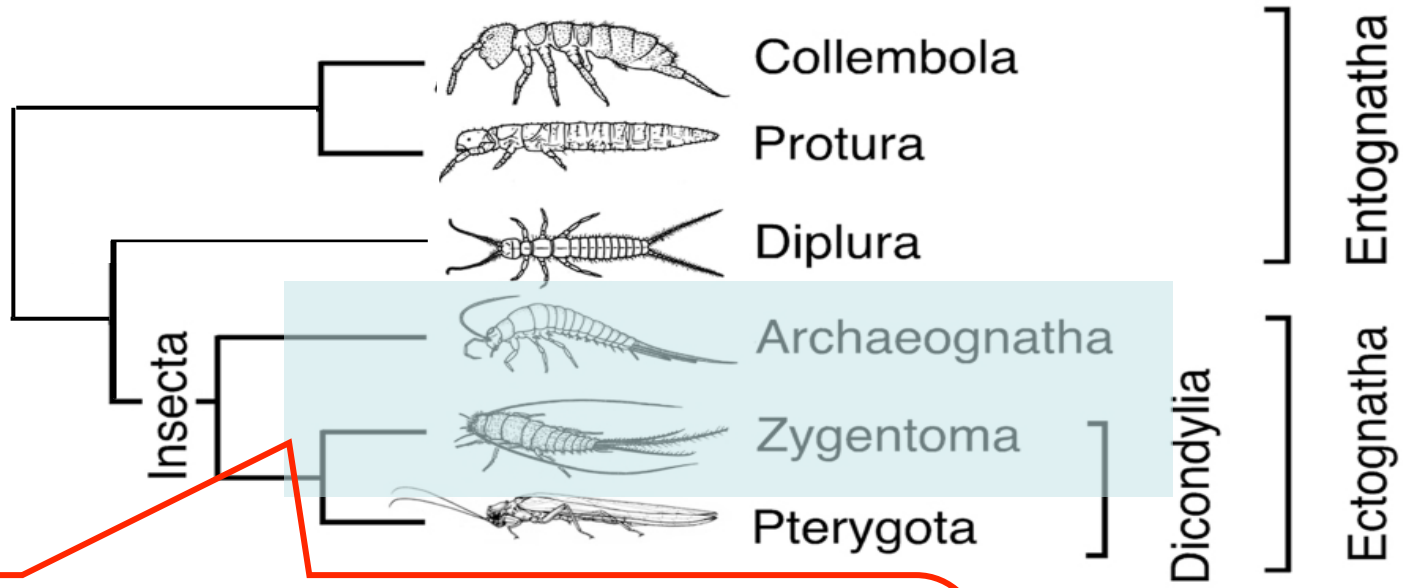

Archaeognatha: Bristletails



Paraphyletic grade of **plesiomorphically** wingless **true** insects

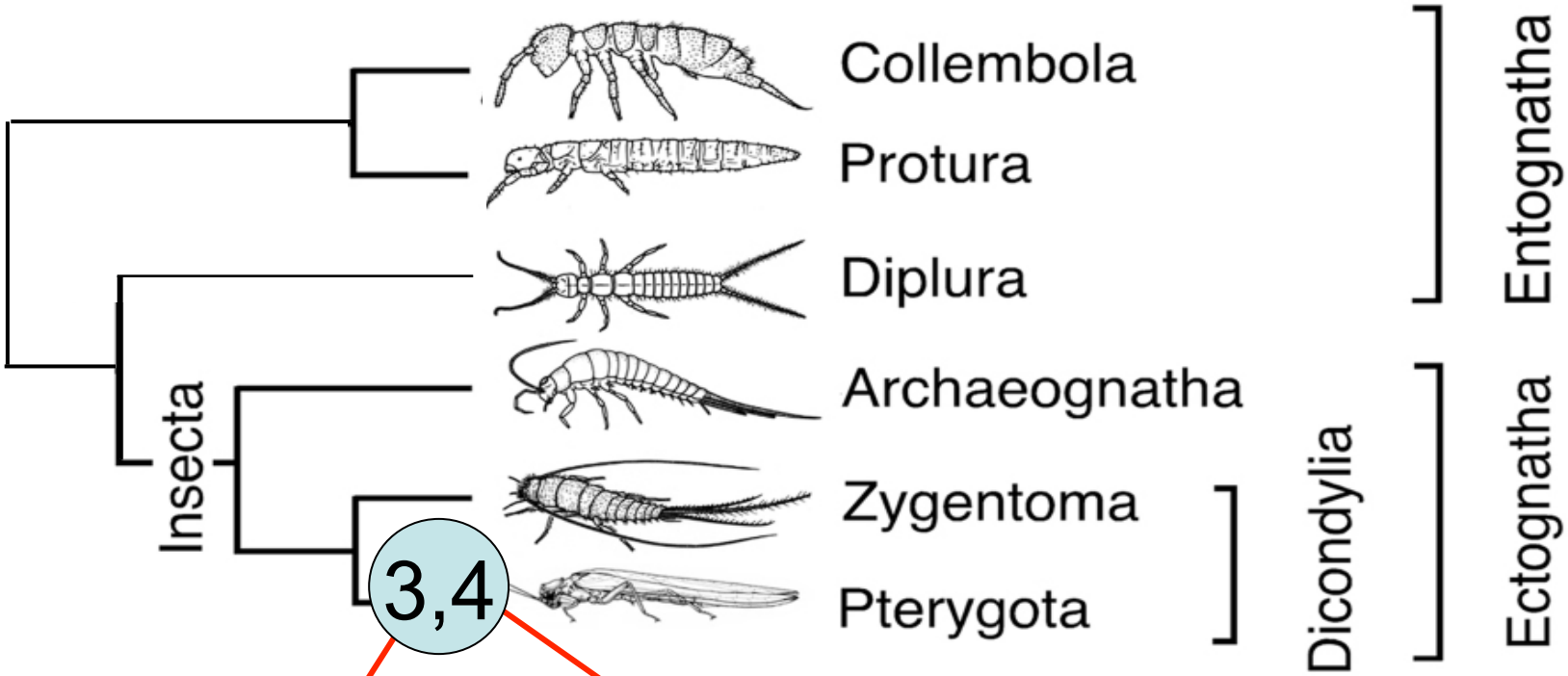

Zygentoma:Silverfish

‘Apterygota’



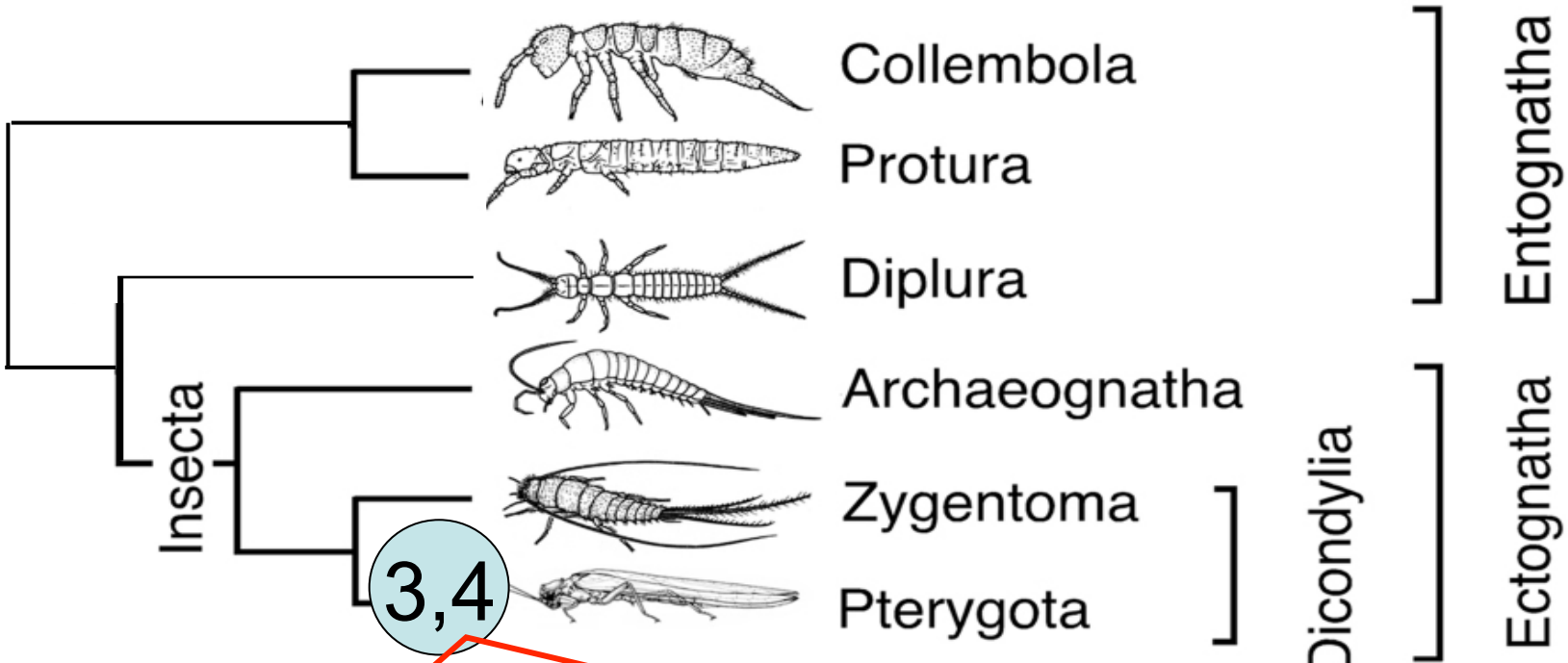
What kind of development
do they have?
With whom do they share this?
Is is plesiomorphic or derived?

Pterygota



These milestones are intimately linked.
What are they?

Pterygota



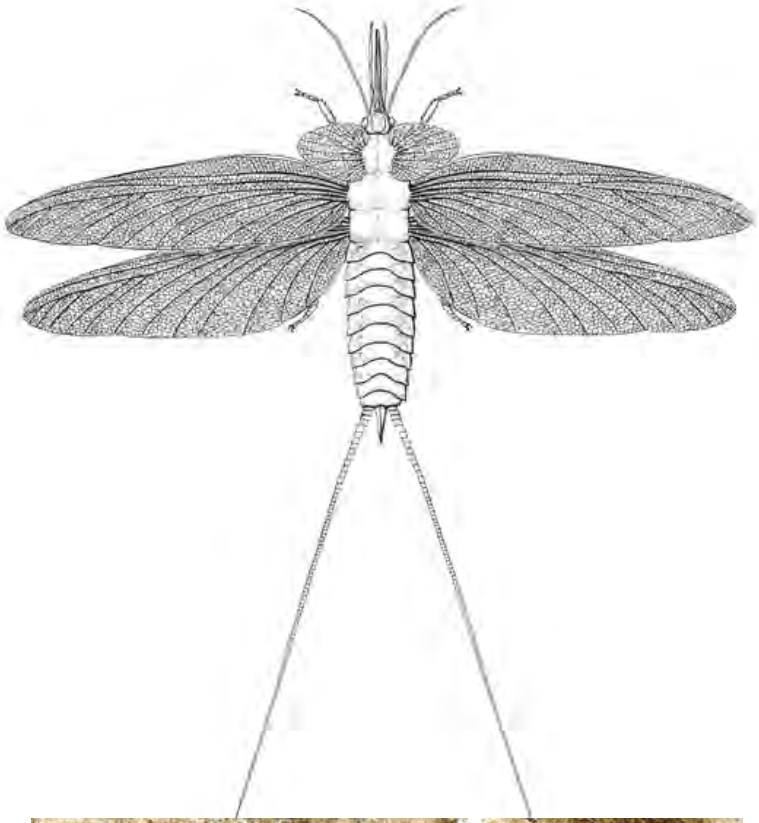
These are <u>synapomorphies</u> for Pterygota.
What is the <u>plesiomorphic</u> state for each character *within* the Pterygota?
What is the <u>derived</u> state for each character?

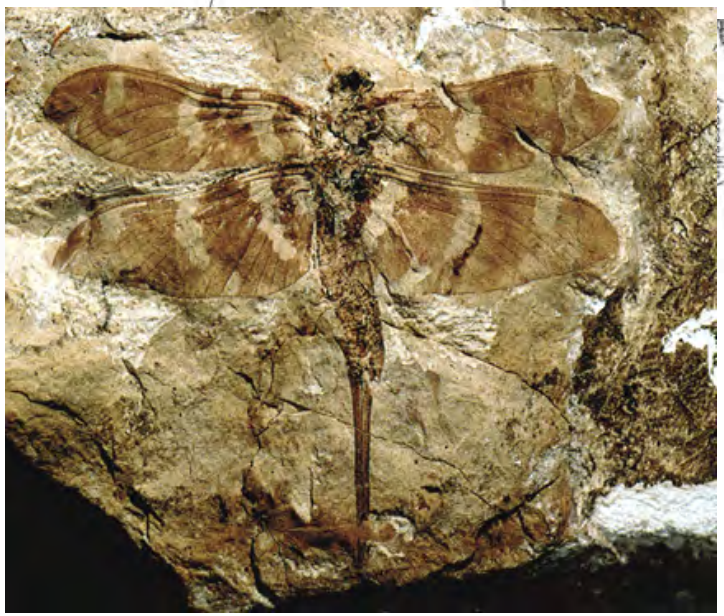
Paleoptera

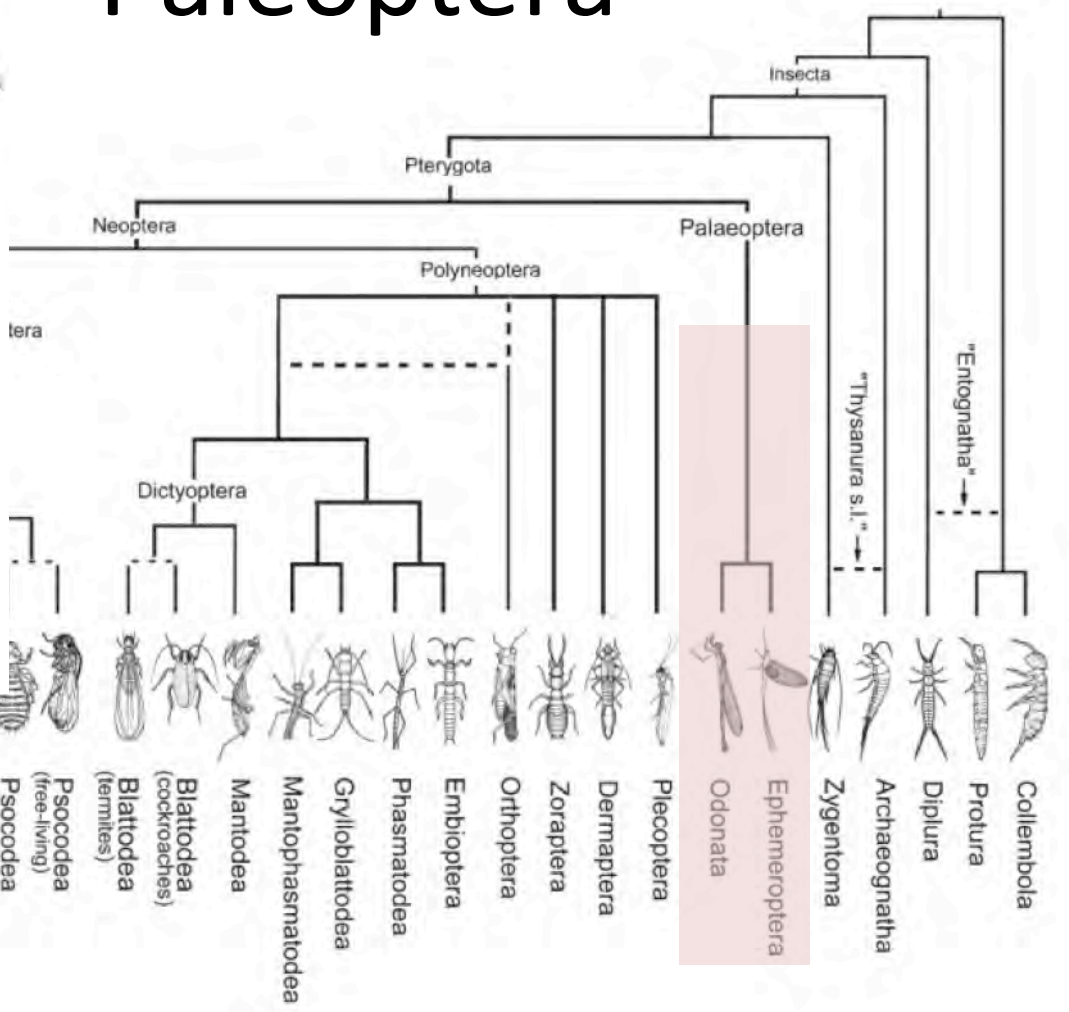
Monophyletic?

Flight? Wings?

Paleoptera

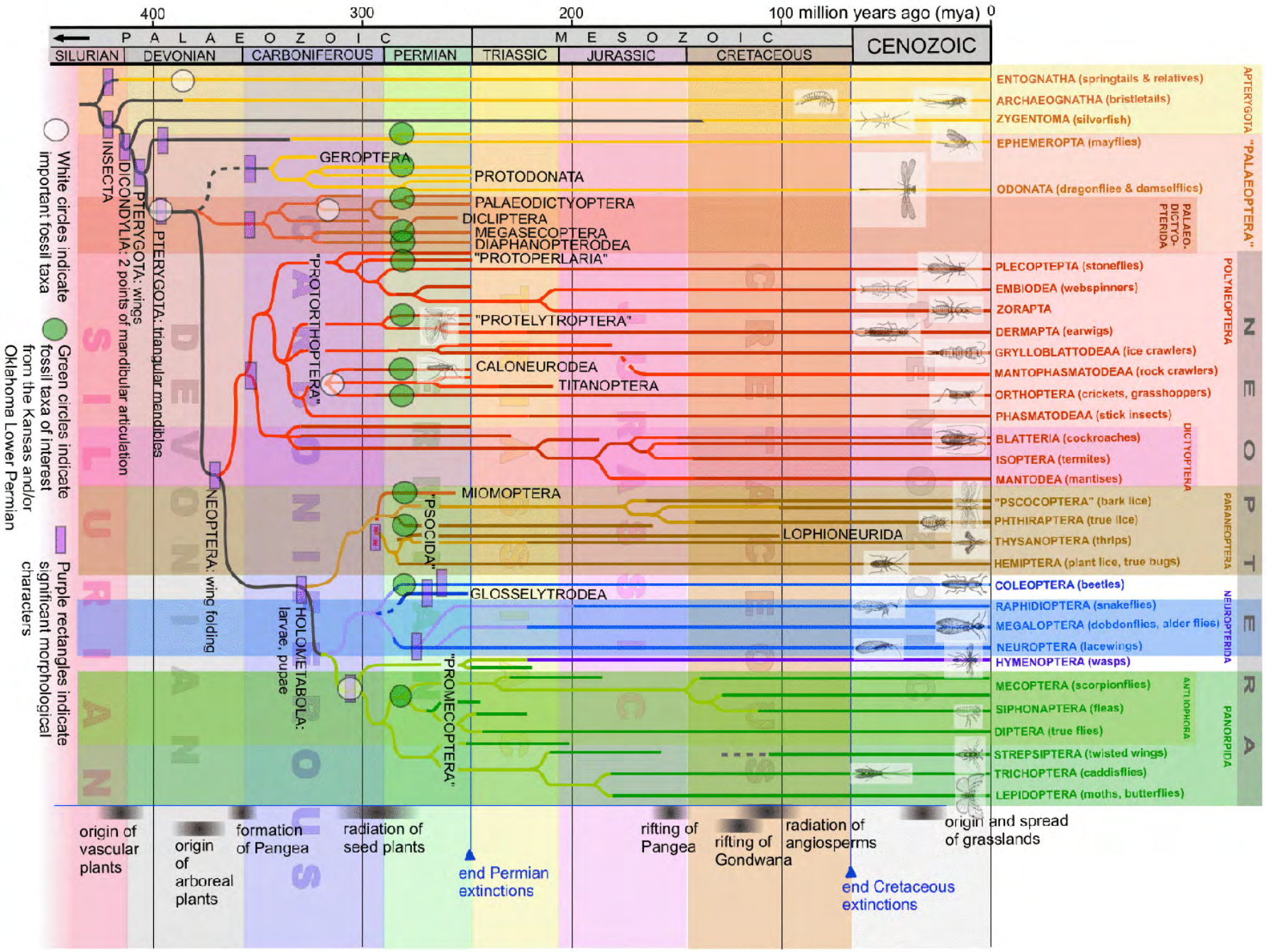




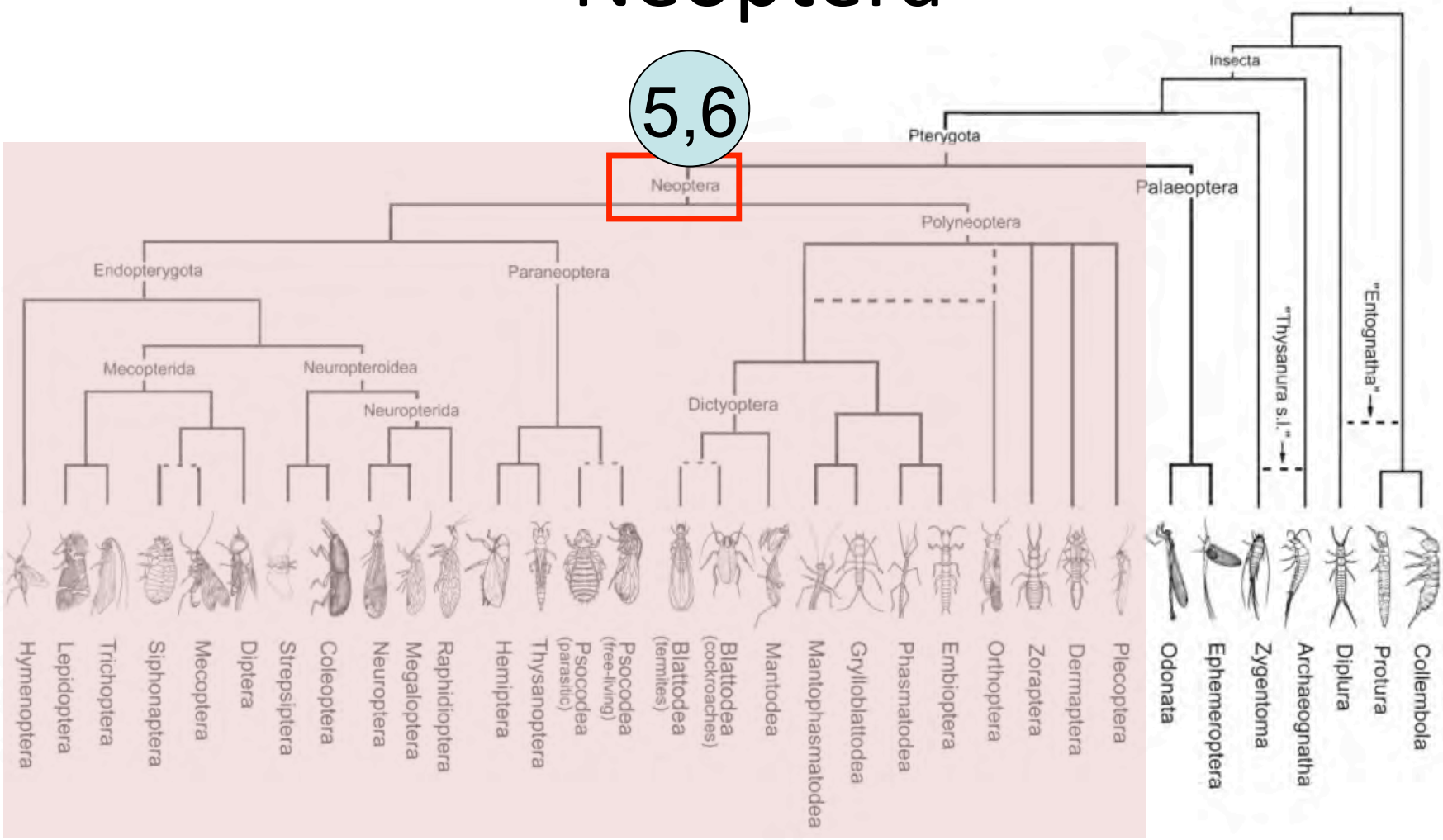


Only two lineages currently

But 6-8 lineages, numerous species from Carboniferous & Permian


400
300
200
100 million years ago (mya)
0
PALAEOZOIC
MESOZOIC
CENOZOIC
SILURIAN
DEVONIAN
CARBONIFEROUS
PERMIAN
TRIASSIC
JURASSIC
CRETACEOUS
INSECTA
DICONDYLIA: 2 points of mandibular articulation
PTERYGOTA: wings
PTERYGOTA: triangular mandibles
NEOPTERA: wing folding
HOLOMETABOLA: larvae, pupae
GEROPTERA
PROTODONATA
PALAEODICTYOPTERA
DICLIPTERA
MEGASECOPTERA
DIAPHANOPTERODEA
"PROTOPERLARIA"
"PROTORTHOPTERA"
"PROTELYTROPTERA"
CALONEURODEA
TITANOPTERA
MIOMOPTERA
"PSOCIDA"
GLOSSELYTRODEA
"PROMECOPTERA"
LOPHIONEURIDA
ENTOGNATHA (springtails & relatives)
ARCHAEOGNATHA (bristletails)
ZYGENTOMA (silverfish)
EPHEMEROPTA (mayflies)
ODONATA (dragonflies & damselflies)
PLECOPTEPTA (stoneflies)
EMBIODEA (webspinners)
ZORAPTA
DERMAPTA (earwigs)
GRYLLOBLATTODEAA (ice crawlers)
MANTOPHASMATODEAA (rock crawlers)
ORTHOPTERA (crickets, grasshoppers)
PHASMATODEAA (stick insects)
BLATTERIA (cockroaches)
ISOPTERA (termites)
MANTODEA (mantises)
"PSCOCOPTERA" (bark lice)
PHTHIRAPTERA (true lice)
THYSANOPTERA (thrips)
HEMIPTERA (plant lice, true bugs)
COLEOPTERA (beetles)
RAPHIDIOPTERA (snakeflies)
MEGALOPTERA (dobsonflies, alder flies)
NEUROPTERA (lacewings)
HYMENOPTERA (wasps)
MECOPTERA (scorpionflies)
SIPHONAPTERA (fleas)
DIPTERA (true flies)
STREPSIPTERA (twisted wings)
TRICHOPTERA (caddisflies)
LEPIDOPTERA (moths, butterflies)
APTERYGOTA
"PALAEOPTERA"
PALAEODICTYOPTERIDA
POLYNEOPTERA
DICTYOPTERA
PARANEOPTERA
NEUROPTERIDA
ANTLIOPHORA
PANORPIDA
NEOPTERA
origin of vascular plants
origin of arboreal plants
formation of Pangea
radiation of seed plants
end Permian extinctions
rifting of Pangea
rifting of Gondwana
radiation of angiosperms
end Cretaceous extinctions
origin and spread of grasslands
White circles indicate important fossil taxa
Green circles indicate fossil taxa of interest from the Kansas and/or Oklahoma Lower Permian
Purple rectangles indicate significant morphological characters

Neoptera

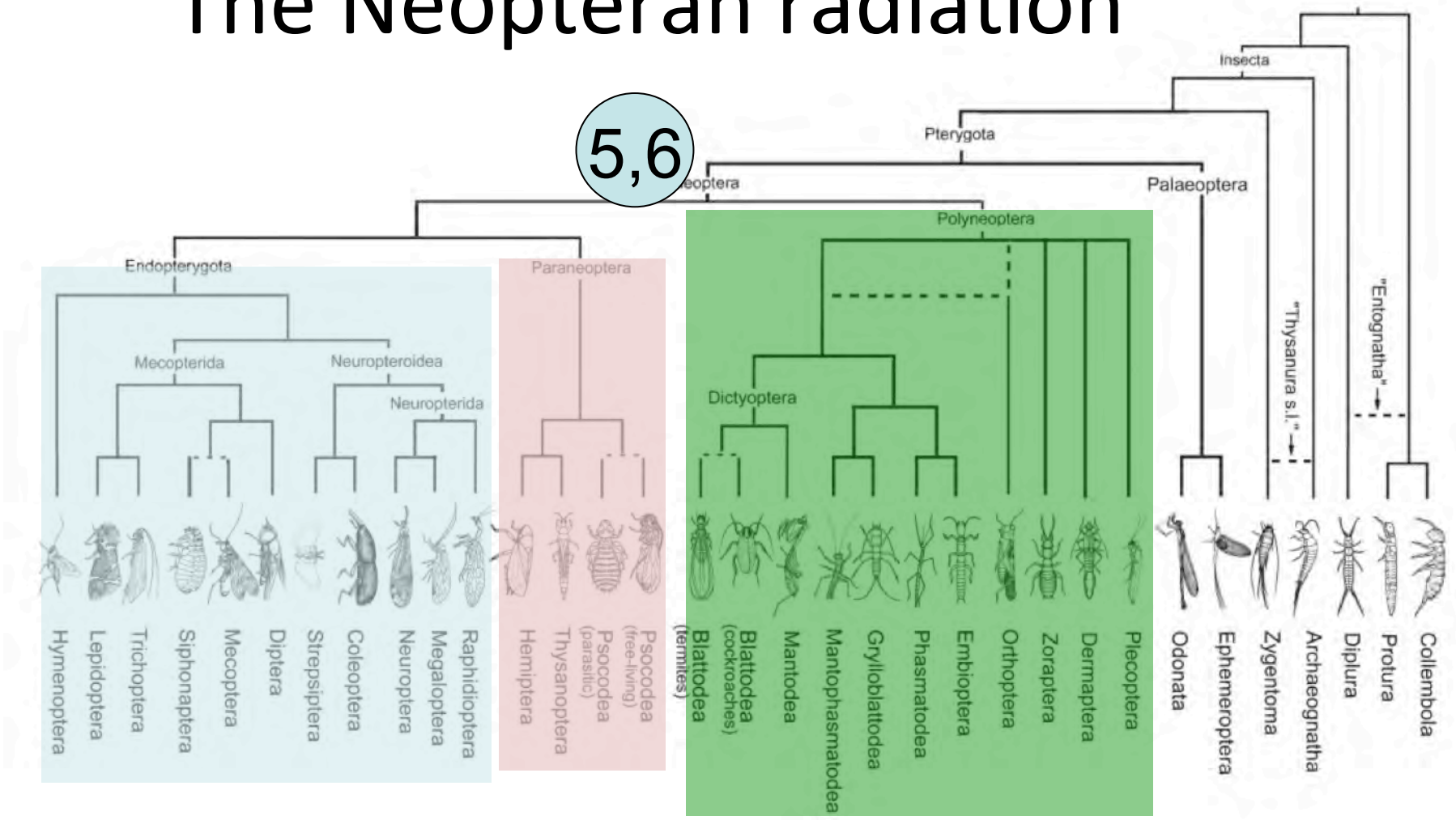


Milestones 5 & 6 are **<u>synapomorphies</u>** for the Neoptera.

Both involved in flight.

Likely provided significant advantages.

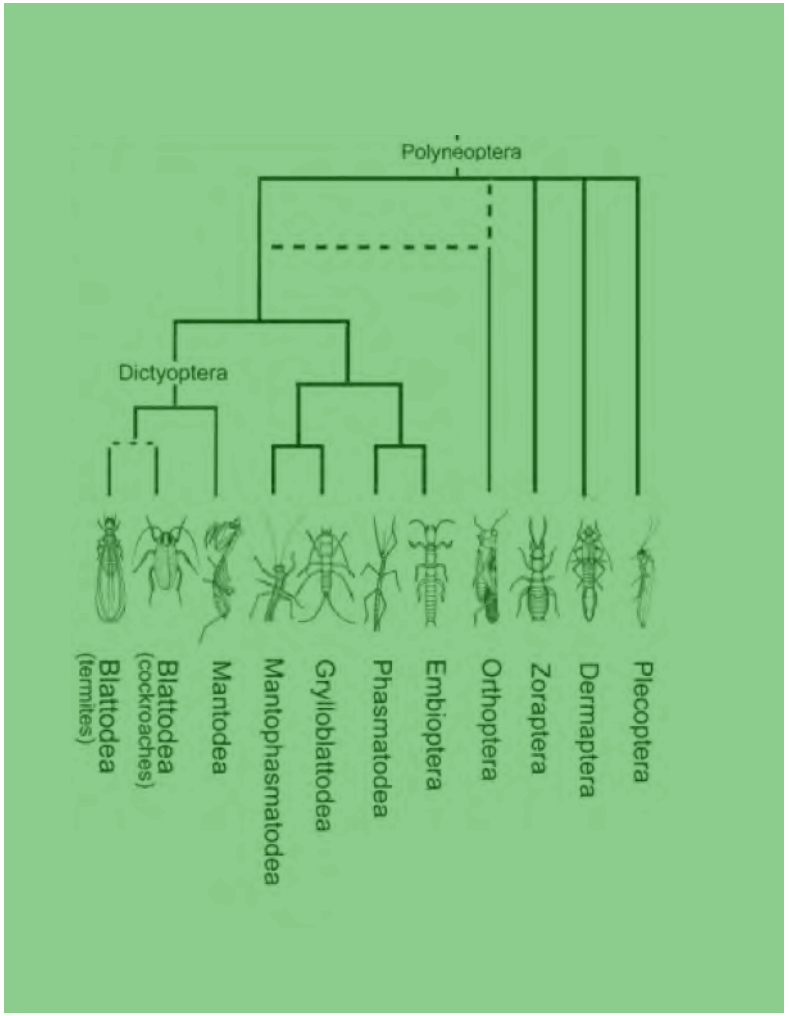
The Neopteran radiation



- Diversified and dominated in the Carboniferous.
- With evolution of conifers, boomed into three main clades: **Polyneoptera**, **Paraneoptera**, **Endopterygota**

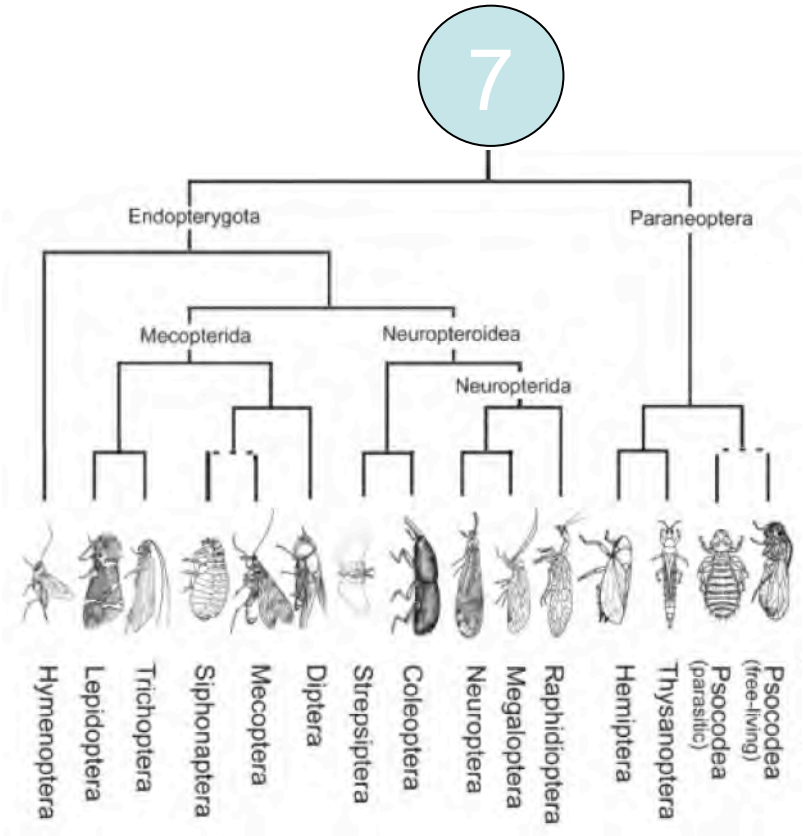
Polyneoptera

- 10 insect orders that have remained largely unspecialized.
- Mostly scavengers and herbivores.
- Plesiomorphic mouthparts with mandibles for chewing or grinding solid food.



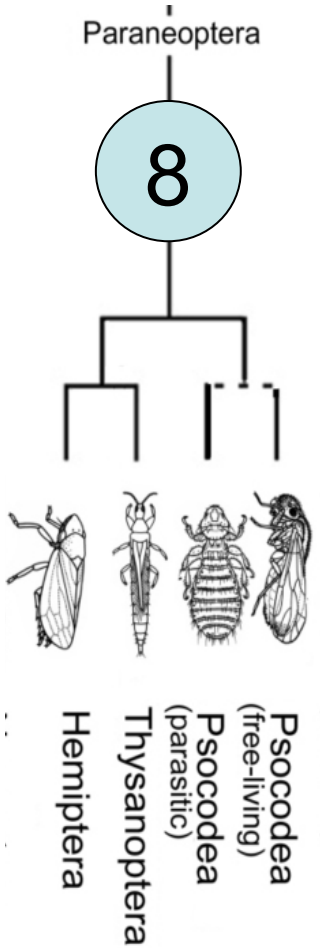
Milestone 7

- Associated with a reduction in the number of abdominal segments and the concentration of neural tissue into a single abdominal ganglion
- Both of these represent a departure from the primitive body form of Polyneoptera in which each segment of the body was innervated by a separate pair of ganglia.
- Synapomorphy for Paraneoptera + Endopterygota = the **Phalloneoptera**



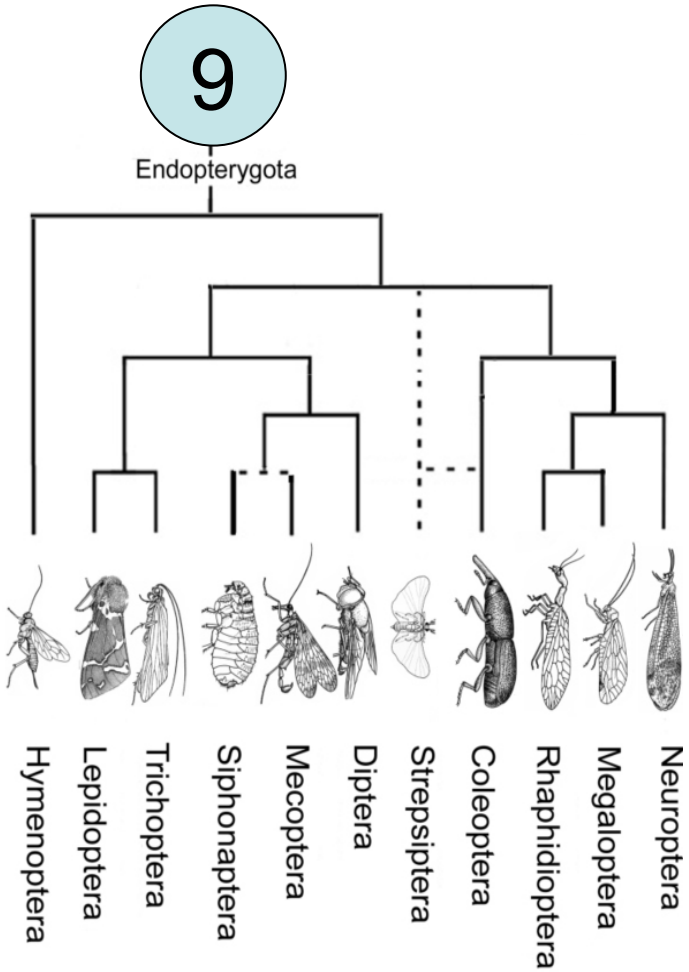
Milestone 8

- Paraneopteran lineage is distinguished by adaptations of the mouthparts for consuming liquid food by rasping and sucking or by piercing and sucking.
- These insects are grouped into four orders: Hemiptera, Thysanoptera, ‘Psocoptera’, and Phthiraptera.

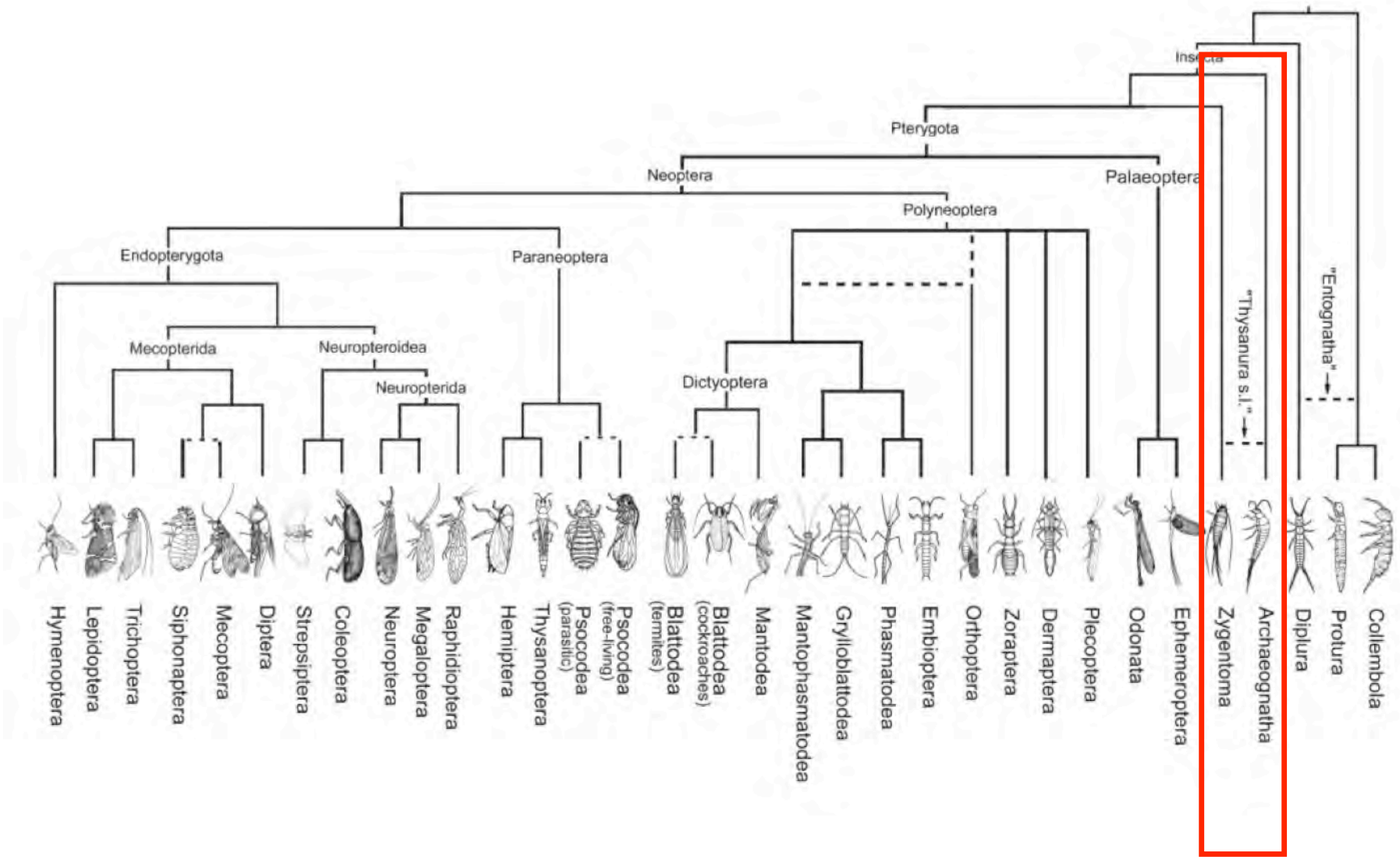


Milestone 9: Endopterygota

- Includes all insects that undergo complete metamorphosis (**holometabolous** development).
- This is Milestone #9, the pinnacle of insect evolution.
- How many stages make up this life cycle?
- Larvae are quite different in appearance from adults.
- How do wings form?
- The eleven holometabolous orders include about 4/5 of all living insect species.



The ‘Apterygote’ Orders

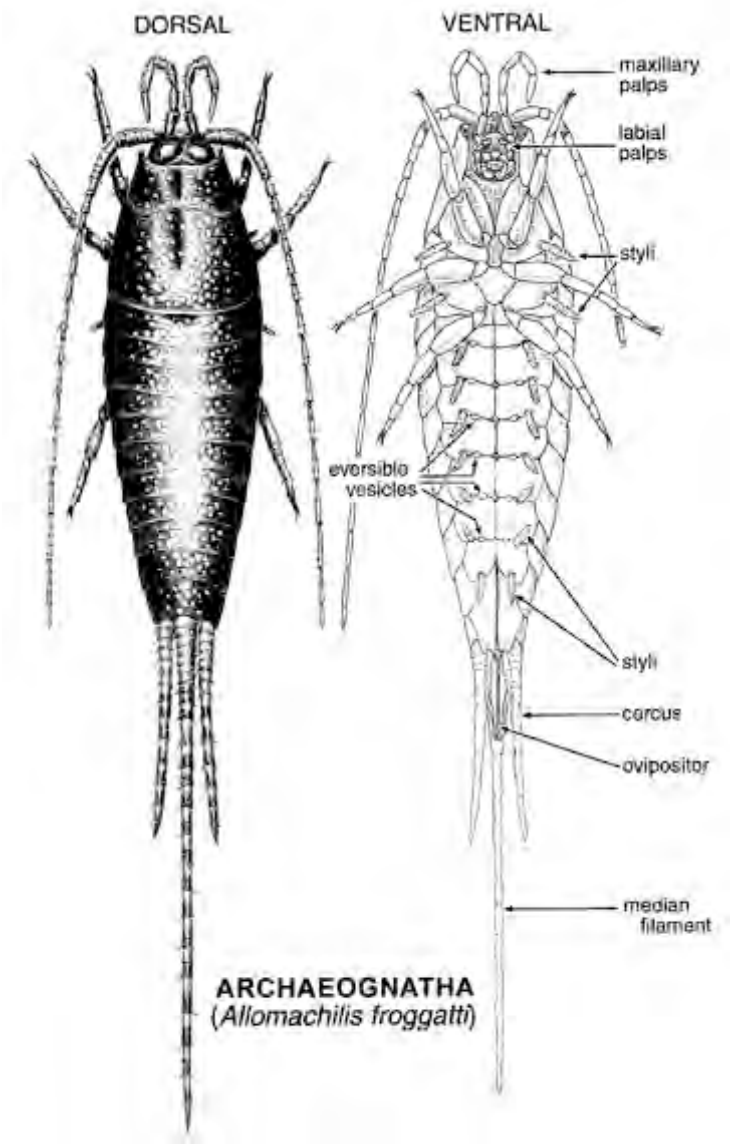


Archaeognatha: Bristletails

- Persisted largely unchanged since mid-Devonian.
- Sister taxon to Dicondylia (Zygentoma + Pterygota).
- Monocondylic jaw articulation.
- Cryptic, nocturnal, scavengers.
- ~500 species worldwide.

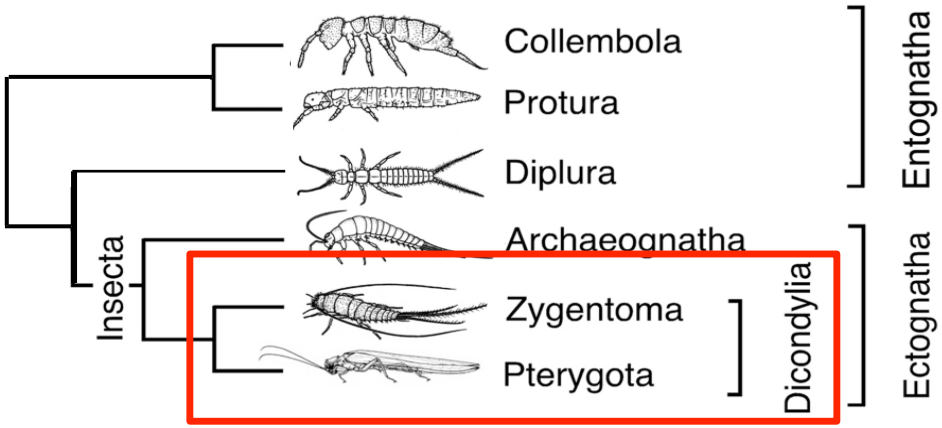
Archaeognatha: Bristletails

- Muscularized styli on abdominal segments.
  - What are these?
- Eversible vesicles
  - Water absorption organs.
- Large, well-developed eyes that meet at the top of the head



Zygentoma: Silverfish

- Sister taxon to Pterygota.
- ~370 species worldwide.
- Primitively wingless, flattened, reduced eyes, no ocelli.
- Abdominal styli present.

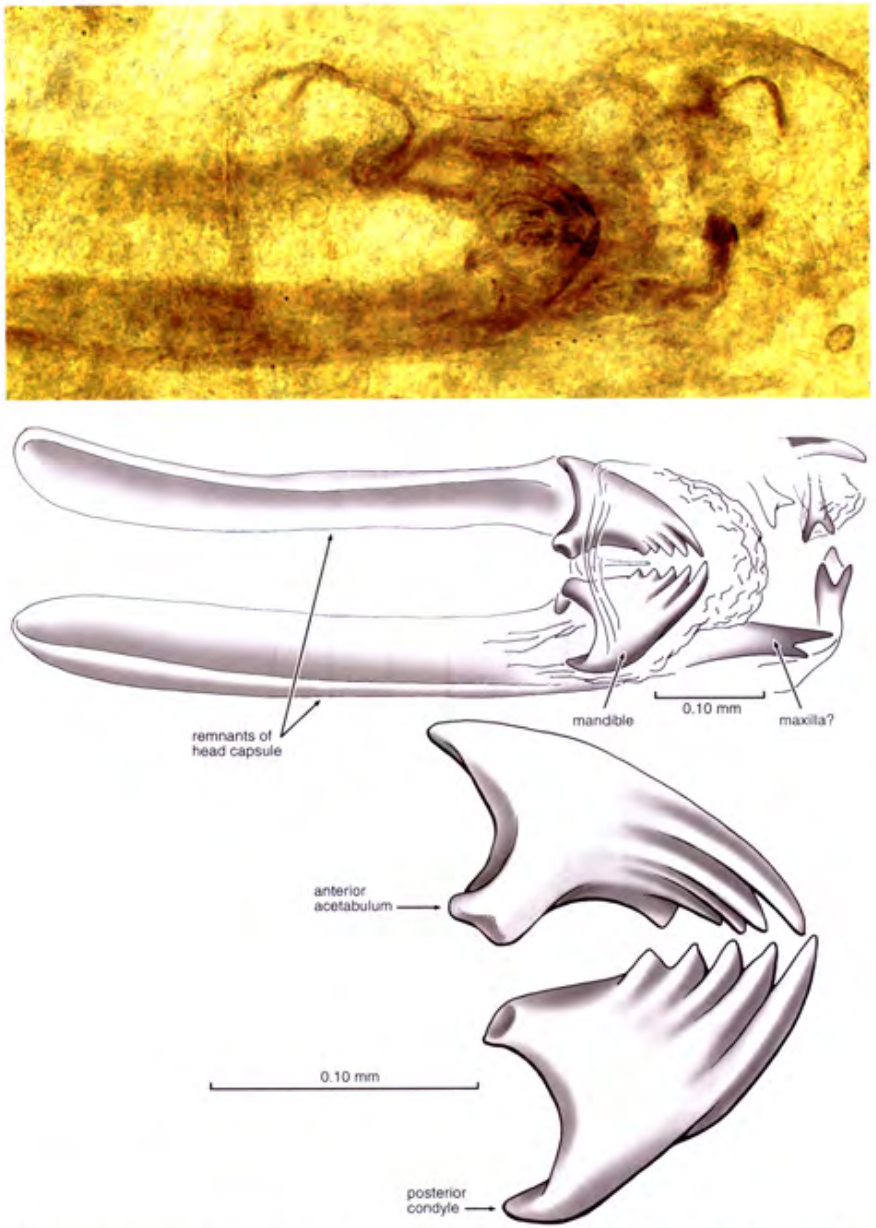


Zygentoma: Silverfish

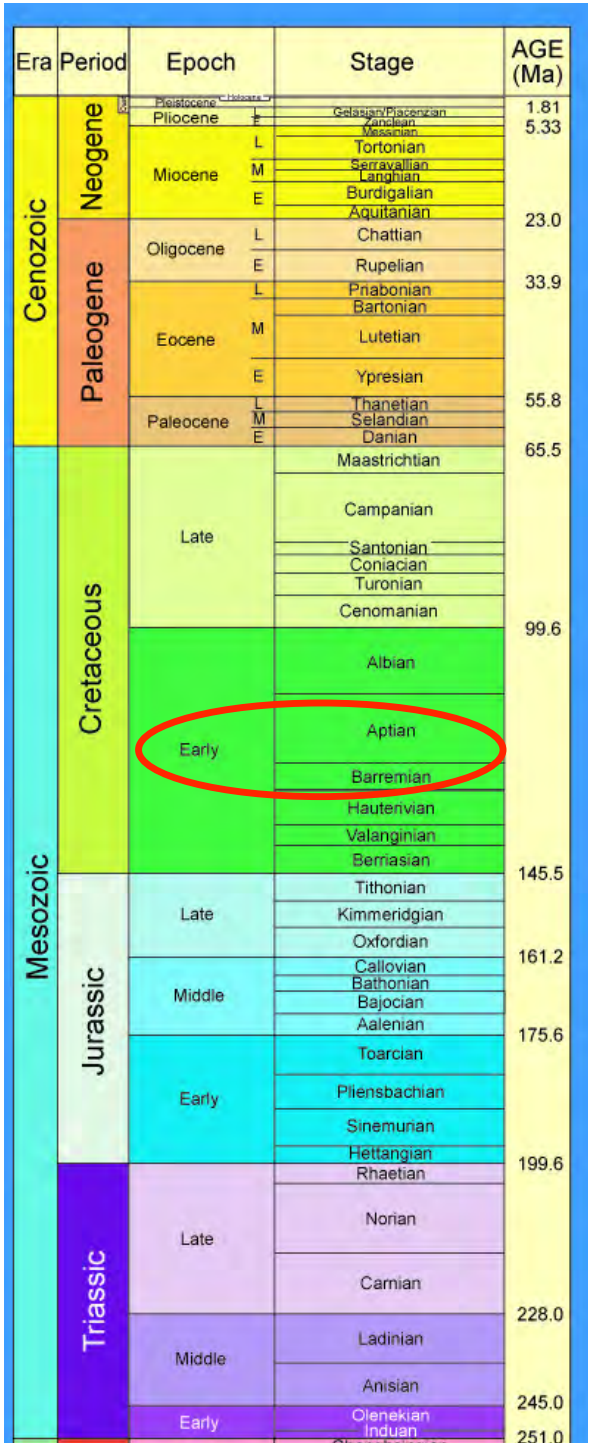
- Scarce in the fossil record
- First fossils from Cretaceous.
- Why would we expect fossils from much earlier?

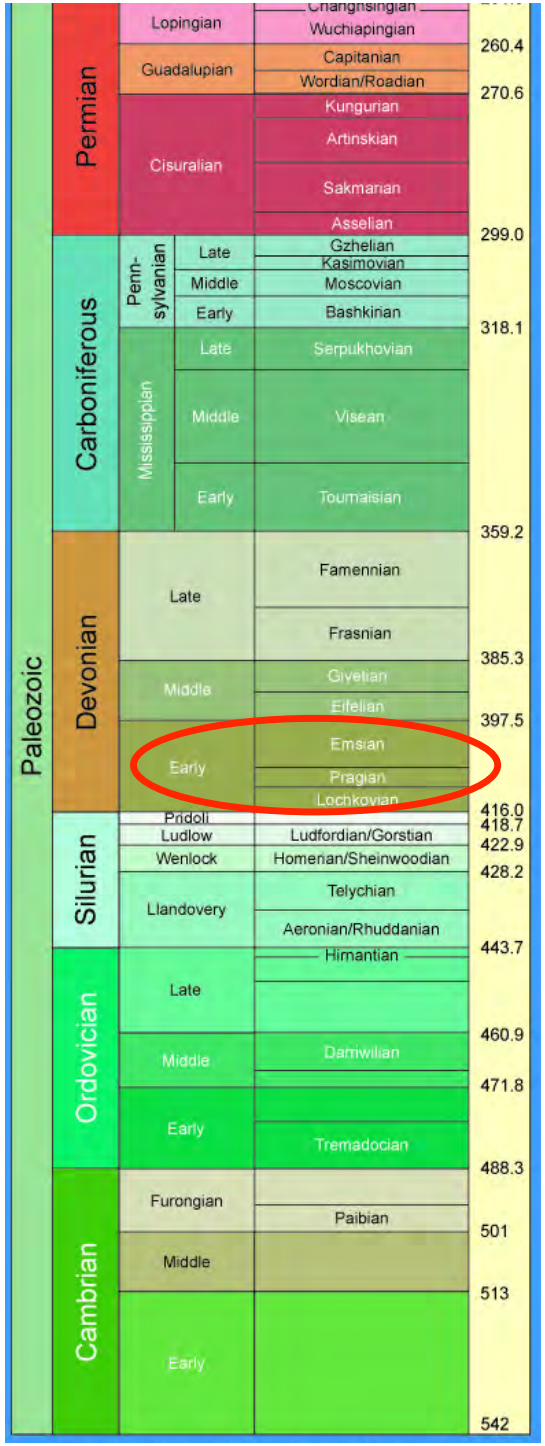
Dicondylia

- First demonstrable dicondylic insect (*Rhyniognatha*) present in Devonian chert.



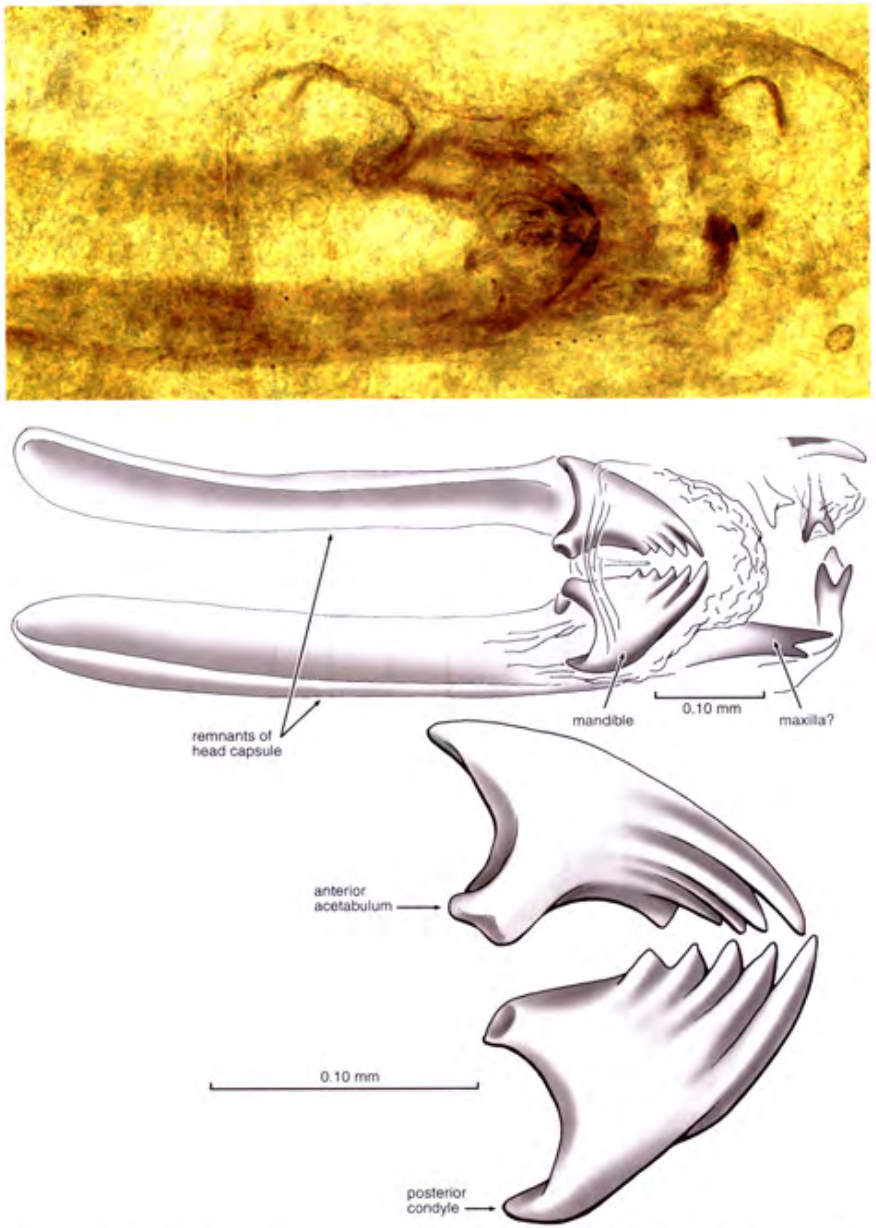
5.8. The oldest insect, *Rhyniognatha hirsti*, from the Early Devonian chert near Rhynie, Scotland. Only portions of the head are preserved, but the dicondylic mandibles indicate it was an insect; their triangular shapes indicate it may even have been a winged insect. NHML In. 38234.


Era
Period
Epoch
Stage
AGE (Ma)
Cenozoic
Neogene
Paleogene
Mesozoic
Cretaceous
Jurassic
Triassic
Pleistocene
Pliocene
Miocene
Oligocene
Eocene
Paleocene
Late
Early
Middle
Gelasian/Piacenzian
Zanclean
Messinian
Tortonian
Serravallian
Langhian
Burdigalian
Aquitanian
Chattian
Rupelian
Priabonian
Bartonian
Lutetian
Ypresian
Thanetian
Selandian
Danian
Maastrichtian
Campanian
Santonian
Coniacian
Turonian
Cenomanian
Albian
Aptian
Barremian
Hauterivian
Valanginian
Berriasian
Tithonian
Kimmeridgian
Oxfordian
Callovian
Bathonian
Bajocian
Aalenian
Toarcian
Pliensbachian
Sinemurian
Hettangian
Rhaetian
Norian
Carnian
Ladinian
Anisian
Olenekian
Induan
1.81
5.33
23.0
33.9
55.8
65.5
99.6
145.5
161.2
175.6
199.6
228.0
245.0
251.0


Paleozoic
Permian
Carboniferous
Devonian
Silurian
Ordovician
Cambrian
Lopingian
Guadalupian
Cisuralian
Pennsylvanian
Mississippian
Late
Middle
Early
Changhsingian
Wuchiapingian
Capitanian
Wordian/Roadian
Kungurian
Artinskian
Sakmarian
Asselian
Gzhelian
Kasimovian
Moscovian
Bashkirian
Serpukhovian
Visean
Tournaisian
Famennian
Frasnian
Givetian
Eifelian
Emsian
Pragian
Lochkovian
Pridoli
Ludlow
Wenlock
Llandovery
Ludfordian/Gorstian
Homerian/Sheinwoodian
Telychian
Aeronian/Rhuddanian
Himantian
Darriwilian
Tremadocian
Furongian
Paibian
260.4
270.6
299.0
318.1
359.2
385.3
397.5
416.0
418.7
422.9
428.2
443.7
460.9
471.8
488.3
501
513
542

Dicondylia

- First demonstrable dicondylic insect (*Rhyniognatha*) present in Devonian chert.
- Mandibles characteristic of a *winged* group.
- By definition, sister groups are the same age, therefore wingless dicondylic insects should be present before winged dicondylic insects.



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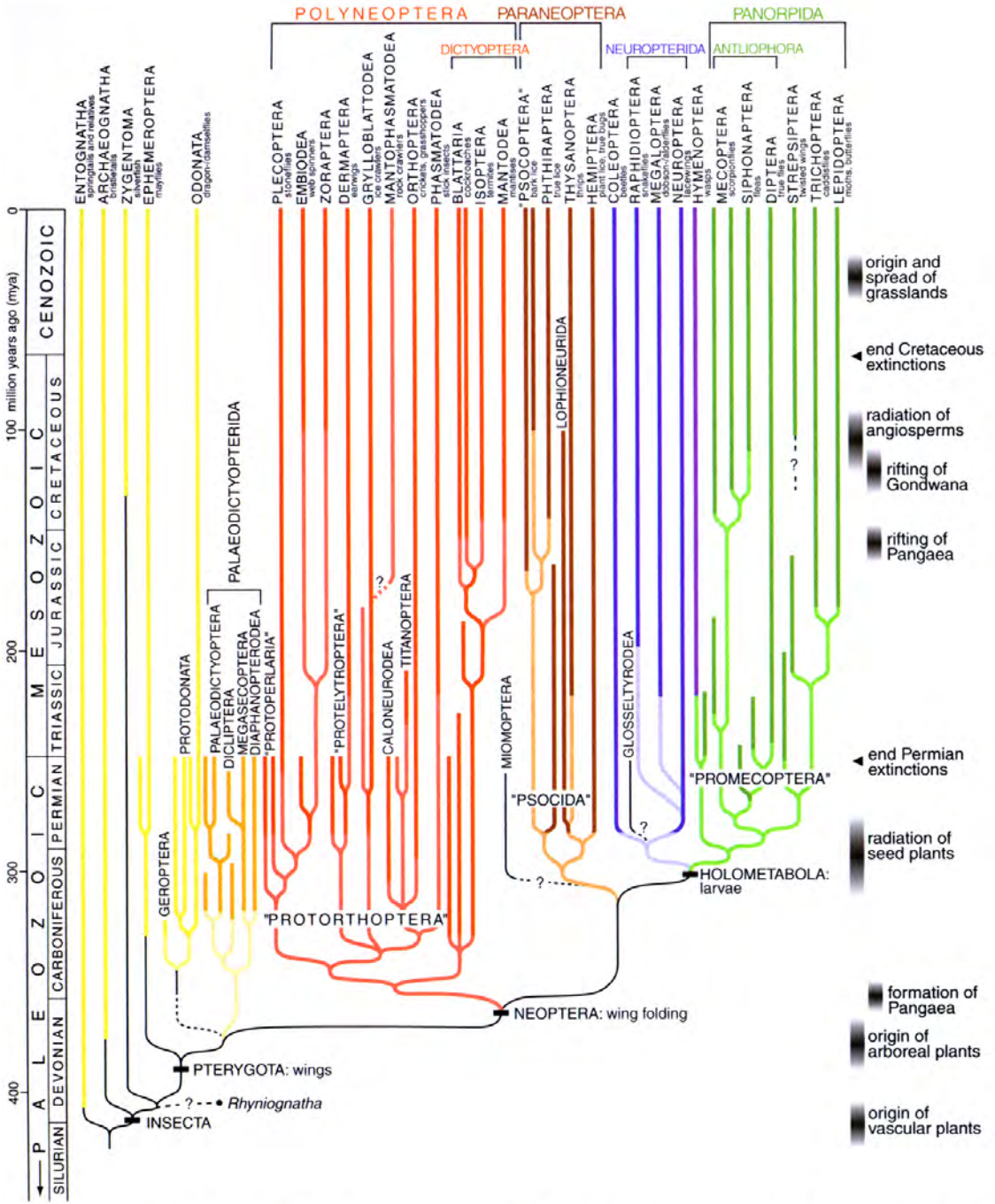
Pterygota and the evolution of wings

Devonian

Wings are a _____ of Pterygota.

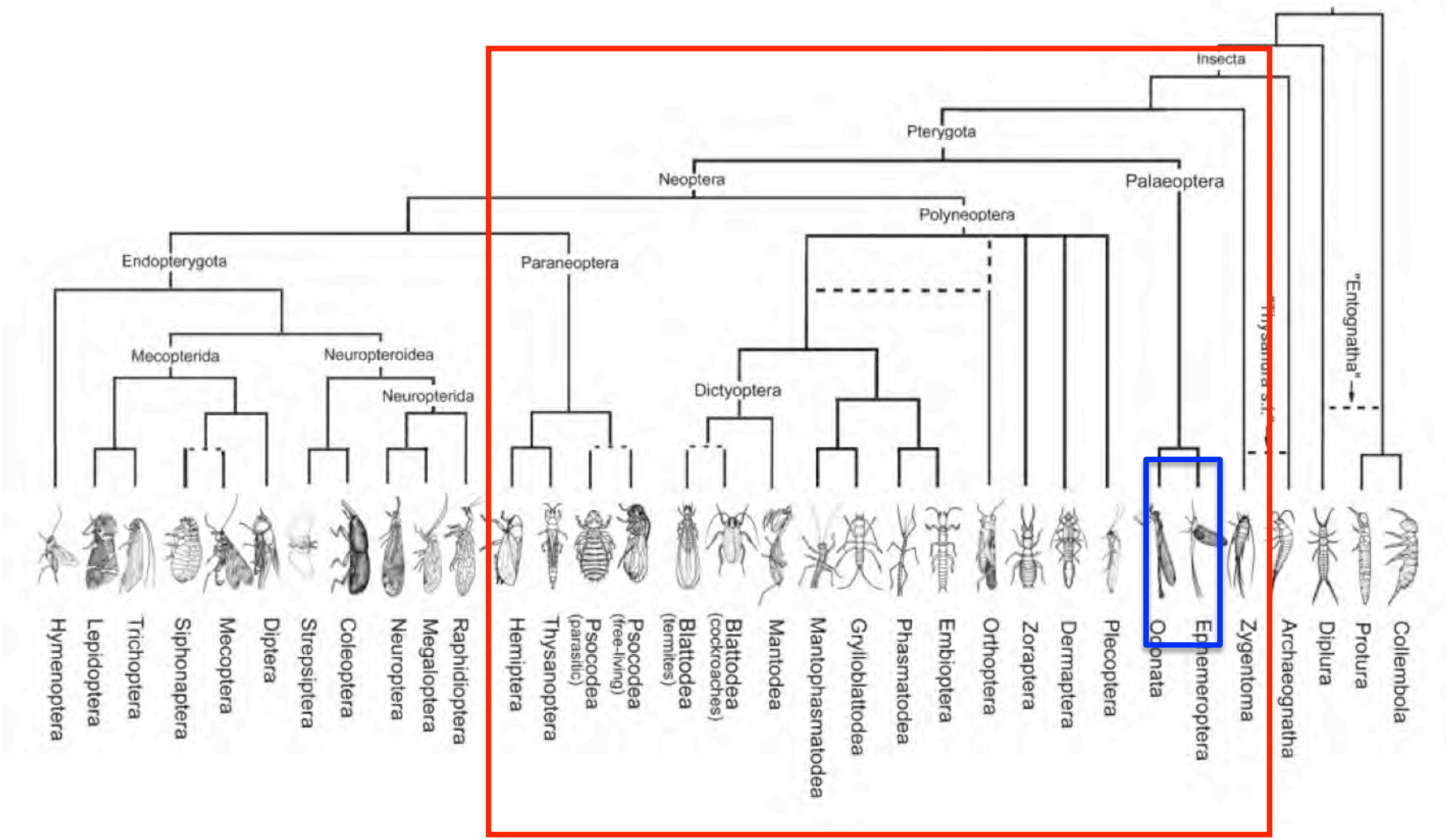
_____ flight/ wings is/are the plesiomorphic condition for Pterygota

Ephemeroptera is sister to remaining Pterygota



4.24. The phylogeny of living and extinct insect orders of insects used in this book, based on various sources (see text). Colors denote most major lineages; darker colors indicate the known extent of fossils.

The Hemimetabolous Orders



Ephemeroptera: Mayflies

- Naiads are proteinaceous base of freshwater food chain.
- Immatures entirely aquatic.
  - How do they breathe?
- Used as environmental indicators.

Ephemeroptera: Mayflies

- Retain plesiomorphic characters:
  - Retains caudal, median filament
  - Subimaginal molt
  - Naiads retain abdominal styli as modified gills
- Distinctive characters
  - Adults with vestigial mouthparts
  - **Aristate** antennae
- Fossil record from Carboniferous

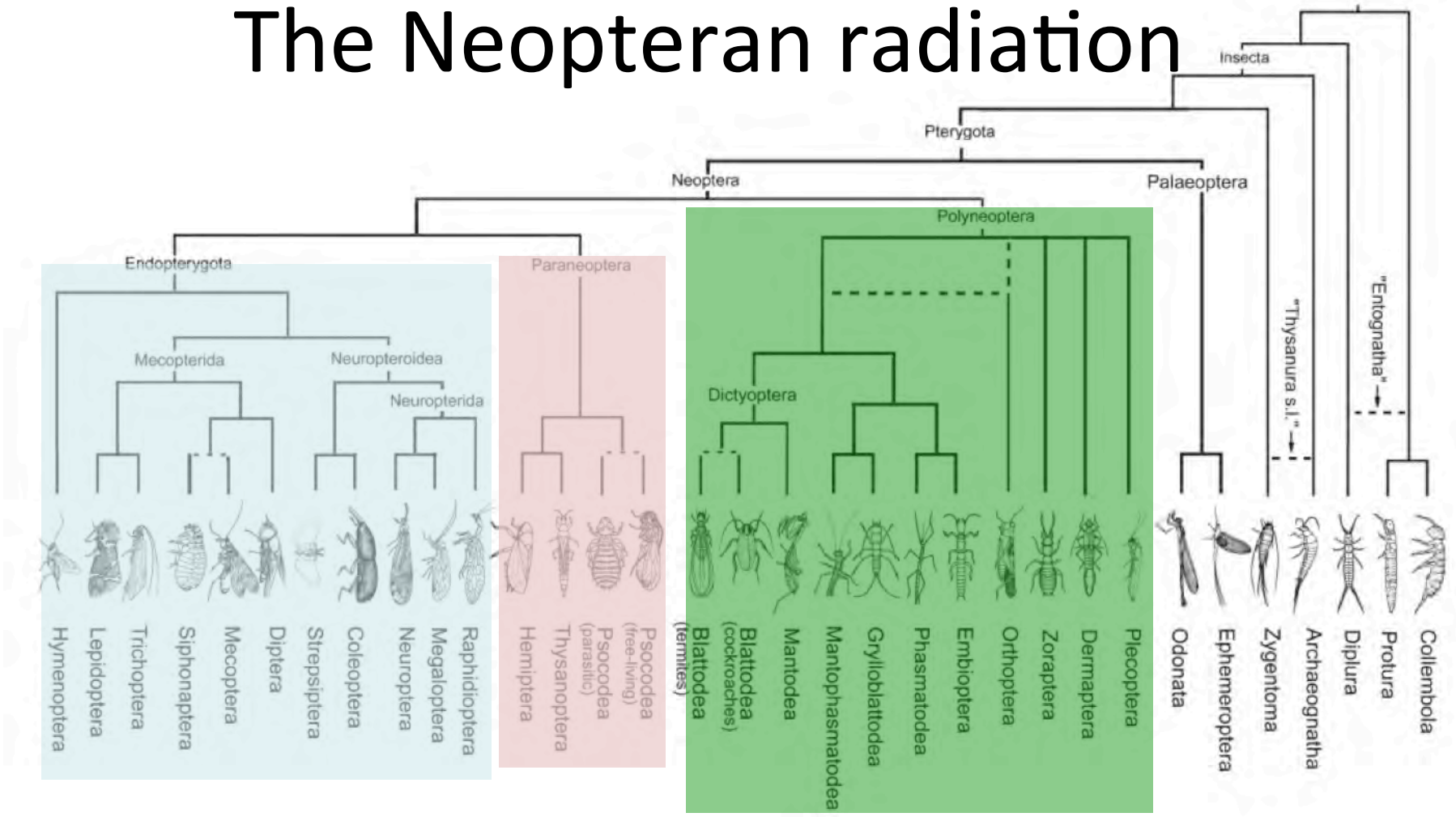
Odonata: Dragonflies & Damselflies

- No winged molts.
- 6000 species worldwide
- Aquatic naiads
- Predaceous adults

Odonata: Tandem wheel

- Distinctive copulatory behavior
- Secondary copulatory apparatus on ventral segments 2-3 of the male

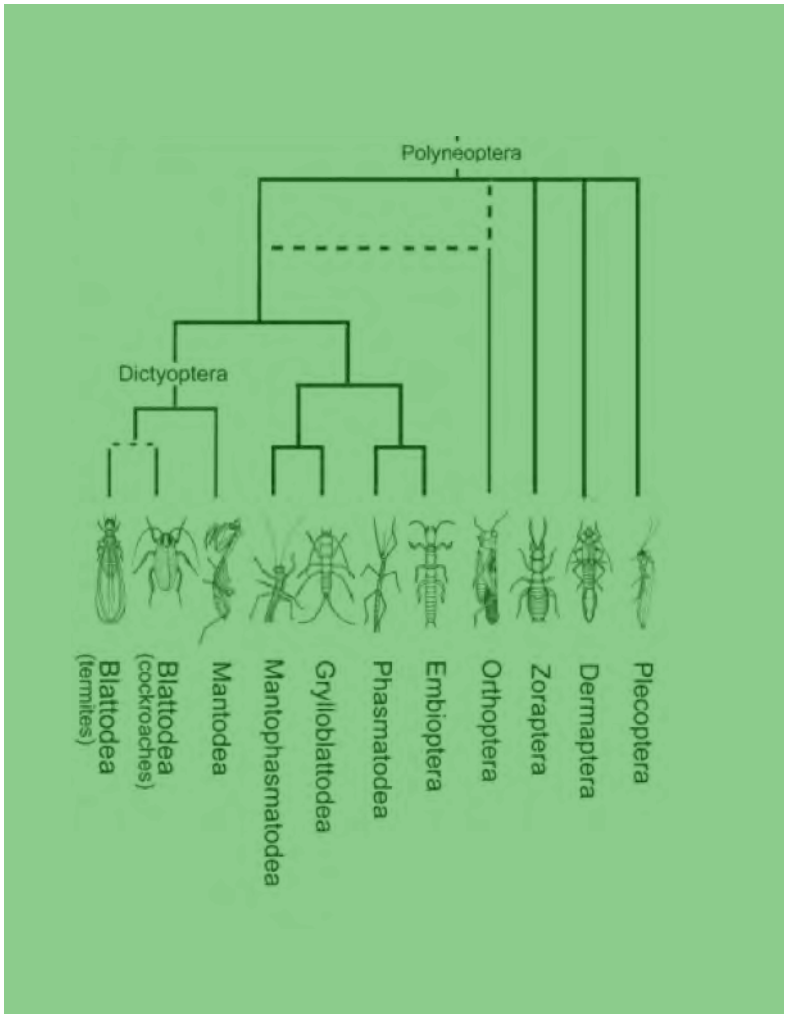
The Neopteran radiation



- Diversified and dominated in the Carboniferous.
- With evolution of conifers, boomed into three main clades: **Polyneoptera**, **Paraneoptera**, **Endopterygota**

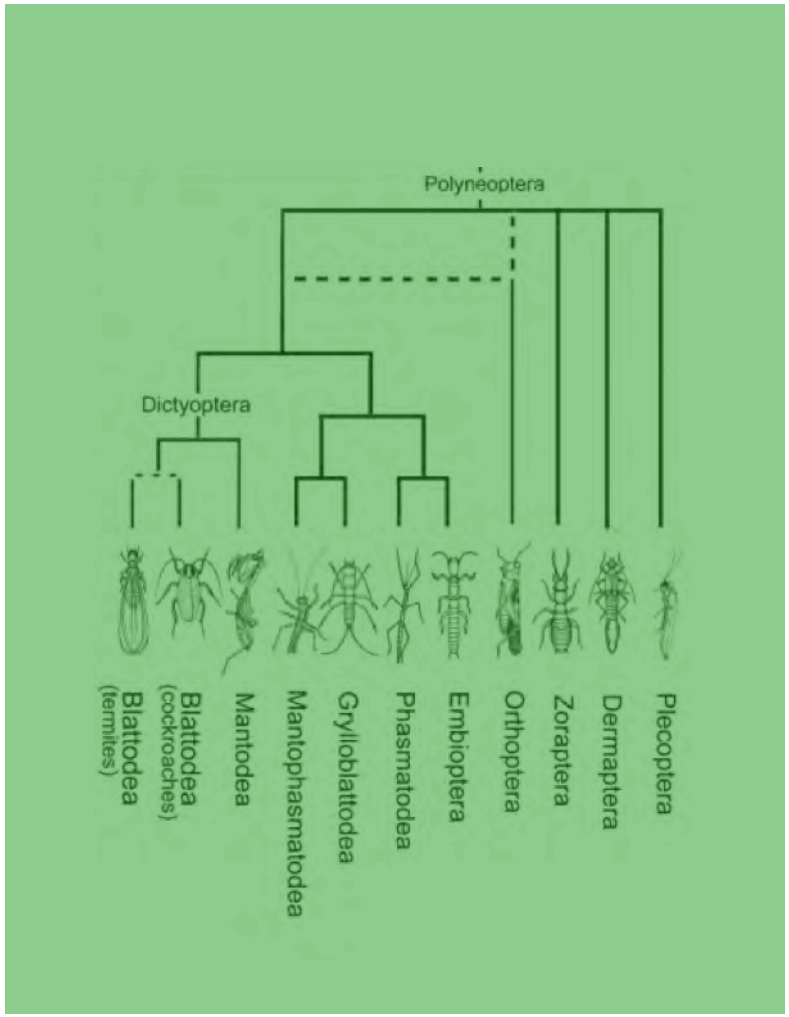
Polyneoptera

- Diversified early and rapidly into major lineages (orders).
- Difficult to resolve phylogeny because of ancient, rapid diversification.
- Perhaps best understood as a **polytomy**



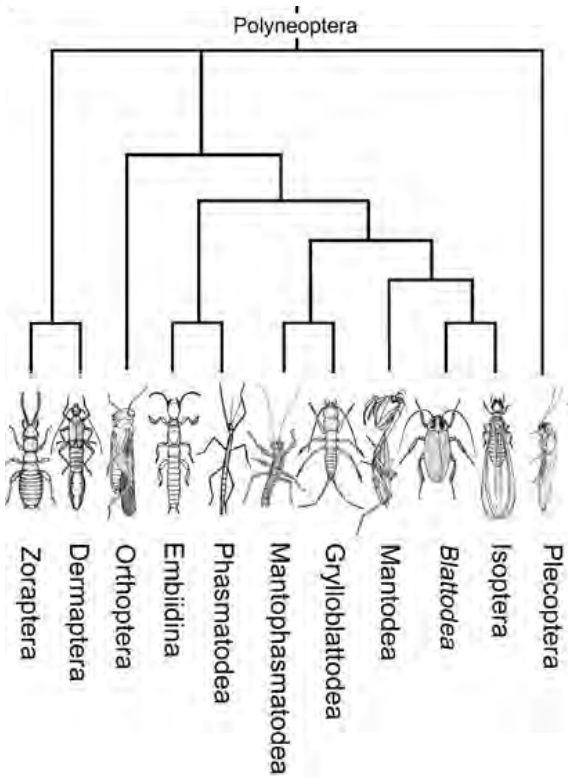
Polyneoptera

- We'll use this one as our working hypothesis.
- But recent work has fluctuated quite a bit on these relationships…

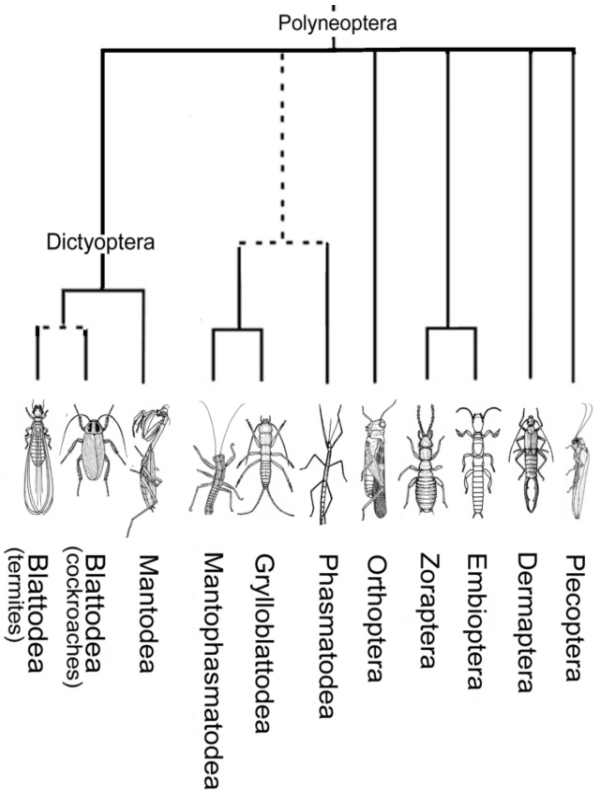


Polyneoptera

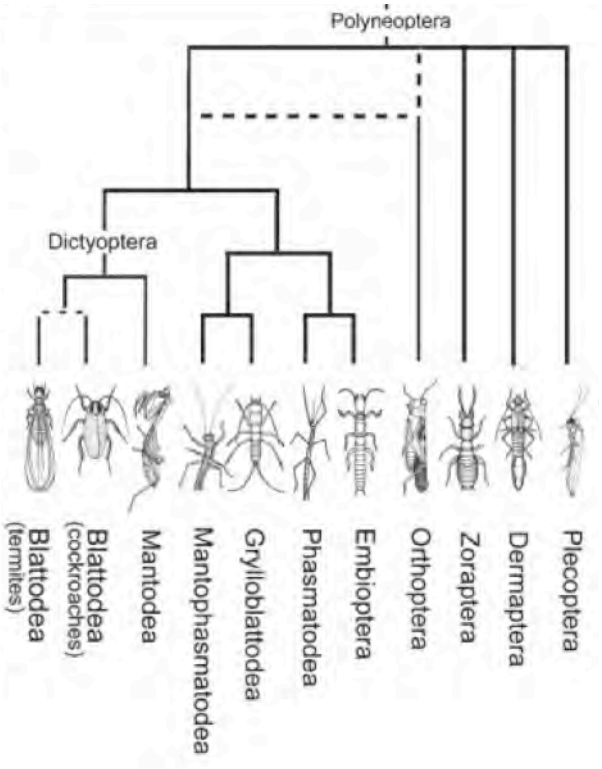
3rd Edition:



4th Edition:



5th Edition:

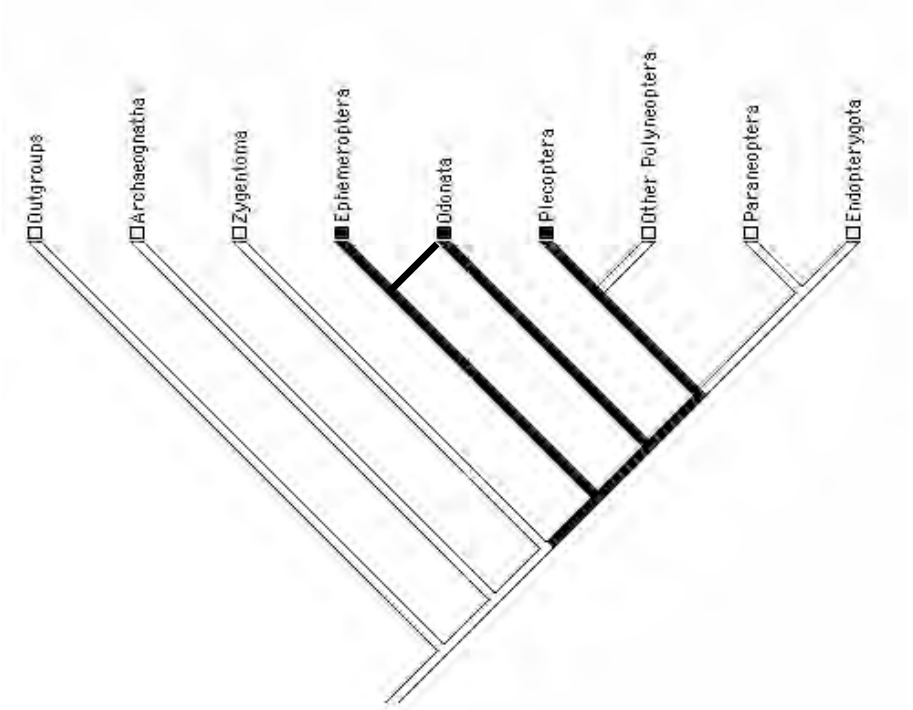


Plecoptera

- Unique amongst Polyneoptera: Naiads strictly aquatic.
- Mostly detritivores or omnivores, few predators.
- ~2000 species in 16 families.
  - Gondwanan & Laurasian lineages

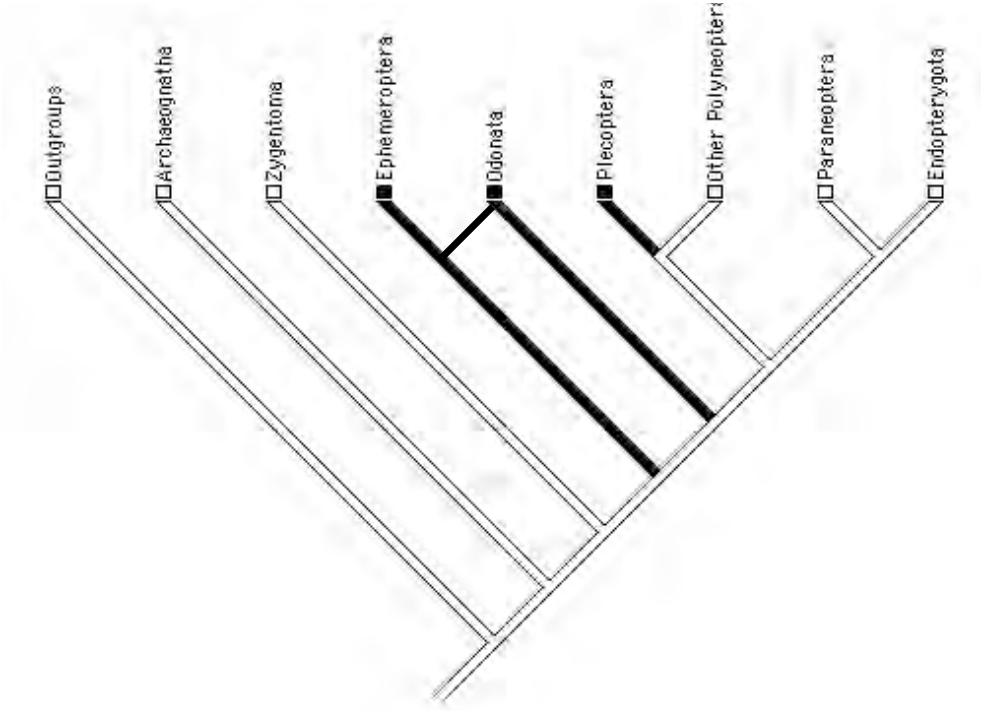
Plecoptera

- Traditionally treated as sister to rest of Polyneoptera
  - Aquatic larvae presumed to be homologous and **plesiomorphic** with Odonata & Ephemeroptera

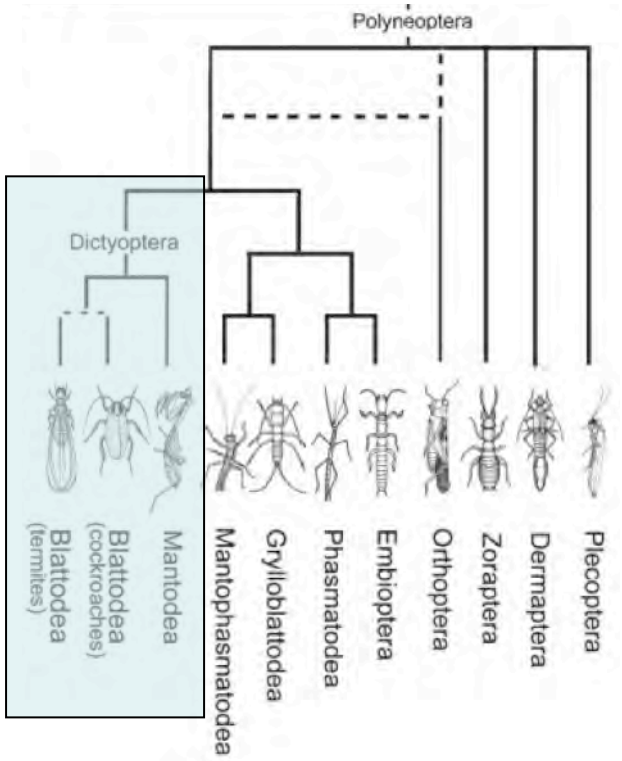


Plecoptera

- Traditionally treated as sister to rest of Polyneoptera
  - Aquatic larvae presumed to be homologous and **plesiomorphic** with Odonata & Ephemeroptera
- Fine morphology of aquatic adaptations, DNA sequence data, and fossils all support three independent colonizations of aquatic environments.

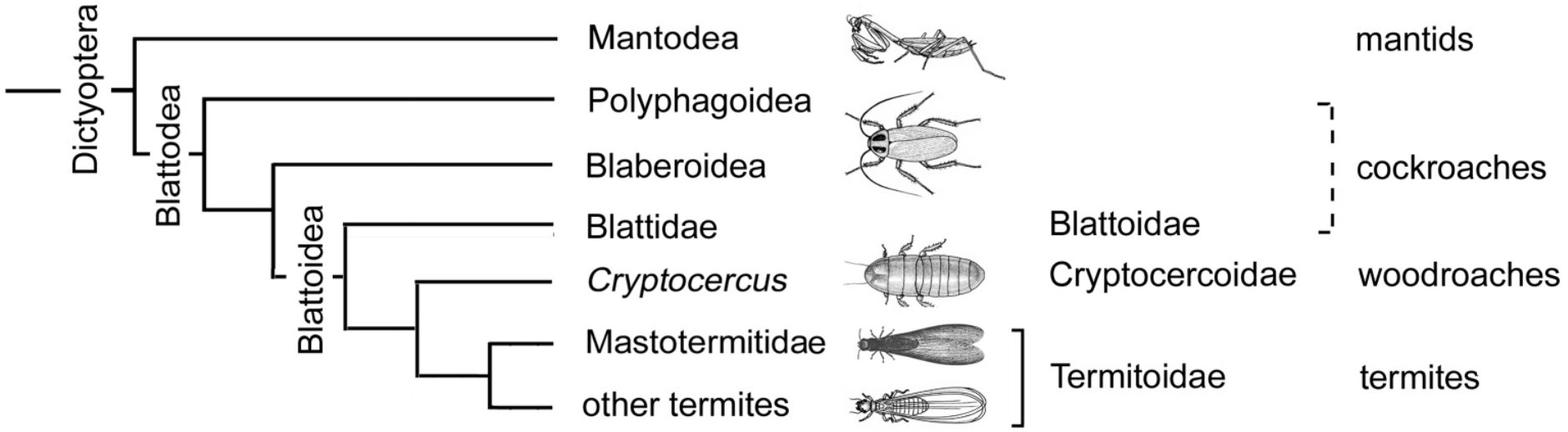


Dictyoptera



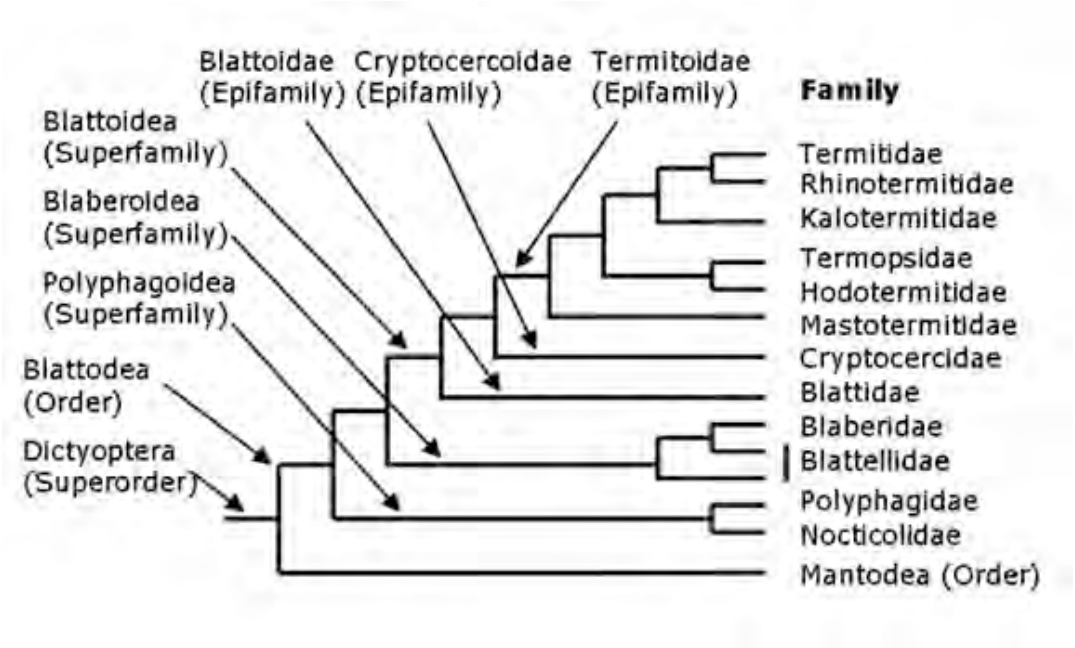
- Mantodea (mantises) + Blattodea (cockroaches) + Termitoidae (termites).

Dictyoptera



- Perhaps best understood as cockroaches, with some lineages having gone predaceous and some eusocial.

Dictyoptera



Combined DNA and morphology supports this (Eggleton *et al*, PNAS, 2007).

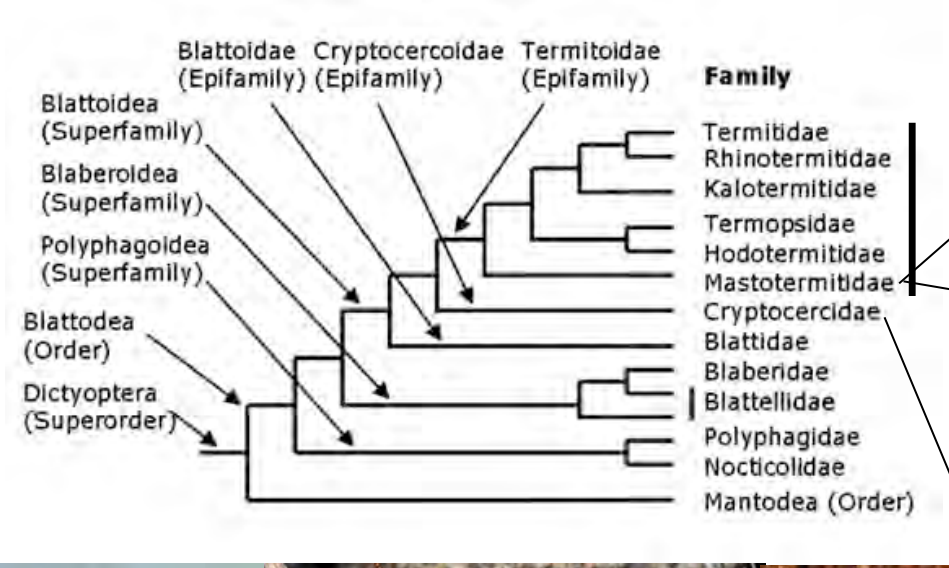
- Perhaps best understood as cockroaches, with some lineages having gone predaceous and some eusocial.

Mantodea form monophyletic group.

Different feeding strategies evolve in **conservative** manner.

Fig. 3. Direct optimization topology with predatory strategy indicated on the topology and mapped on the nodes. The ancestral condition in mantids is generalist, with two shifts to cursorial strategy in clade 1 and one shift in clade 2. This topology supports a single origin of the ambush strategy. The strategy of *Mantoida schraderi* is unknown.

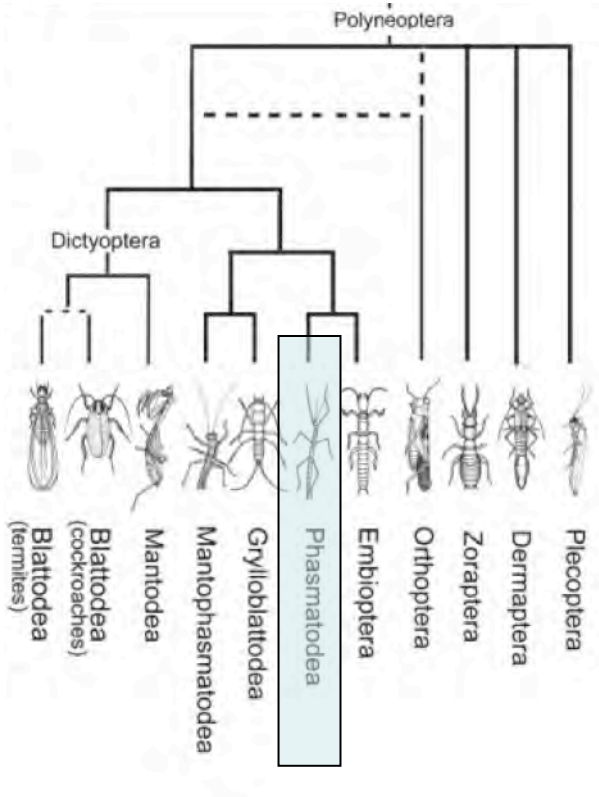
Termites are essentially eusocial cockroaches



American woodroaches are subsocial

Phasmatodea: Walkingsticks

- Relationships quite challenging.
- Different, poorly resolved results from morphology, DNA.
- Long considered sister to Orthoptera.
- Now considered to be related to Embioptera.
- Currently best hypothesis is sister to Notoptera.



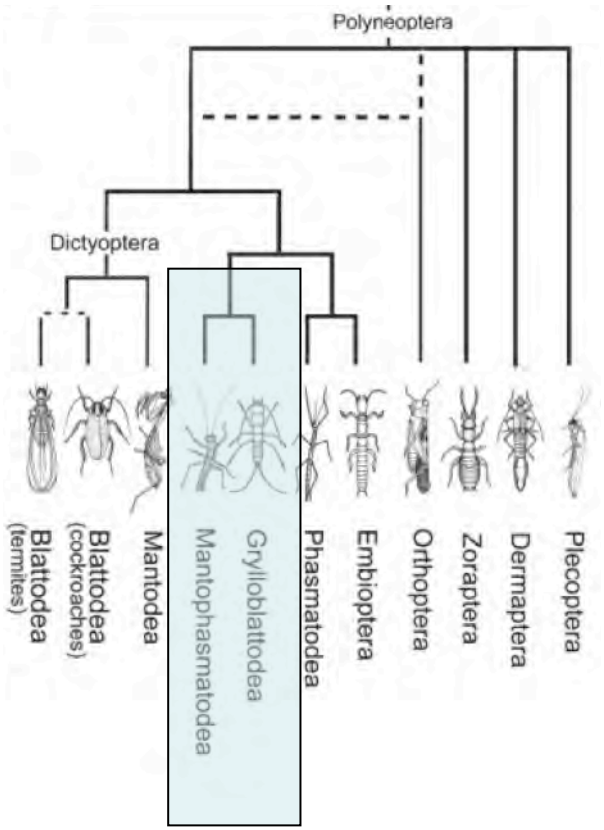
Phasmatodea: Walkingsticks

- Greatly elongate, either cylindrical and resembling twigs or flattened and resembling leaves.
- Incredibly cryptic.
- Parthenogenesis common.
- Unique amongst insects: nymphs can regenerate limbs.

Embioptera: Webspinners

- ~300 species
- Well-supported monophyletic group
- Produce silk from unicellular glands in the foretarsus.
- Other features include swollen hind femora, two-segmented cerci.
- Females ALWAYS wingless.
- Live in colonies with considerable parental care.
- Feed on decaying plant material.

Grylloblattodea & Mantophasmatodea = Notoptera



Grylloblattodea & Mantophasmatodea

- Grylloblattodea: ice crawlers & rock crawlers.
  - All associated with montane ice fields 1000-3000 masl.
  - Scavengers of insect carcasses.
  - 20 species in western North American and northeast Asia
- Mantophasmatodea: heelwalkers or gladiators.
  - Previously only known from fossil record
  - All apterous, all carnivores.
  - Newest insect order (2002)
  - 13 African species
- Sister relationship confirmed by morphology and molecules (including whole mitochondrial genomes).

Mantophasmatodea: A New Insect Order with Extant Members in the Afrotropics

Klaus-D. Klass,[1,3]* Oliver Zompro,[2]* Niels P. Kristensen,[1] Joachim Adis[2]

A new insect order, Mantophasmatodea, is described on the basis of museum specimens of a new genus with two species: *Mantophasma zephyra* gen. et sp. nov. (one female from Namibia) and *M. subsolana* sp. nov. (one male from Tanzania). This is the first time since 1914 that a newly described extant insect taxon has proved unplaceable within a recognized order. Mantophasmatodeans are apterous carnivores. Their closest phylogenetic relationships may be to Grylloblattodea (ice-crawlers) and/or Phasmatodea (stick insects), but the morphological evidence is ambiguous. *Raptophasma* Zompro from Baltic amber is assigned to the Mantophasmatodea, revealing a wider previous range for the lineage.

All of the currently recognized orders of extant insects have been known throughout most of the 20th century. While several high-rank clades of marine animals have been discovered during the past 50 years, the numerous new insects described in that period have all been referable to known orders [with the possible exception of the apterygote *Tricholepidion gertschi* Wygodzinsky, 1961, whose assignment to the Zygentoma remains disputable (*1*–*3*)]. The recognized insect order based on the most recently discovered extant taxon is the Grylloblattodea (= Notoptera, "ice-crawlers"), the first of whose 26 currently known species was described in 1914. We here report the finding (*4*) of a new Afrotropical insect genus that cannot be placed within any recognized extant order, and whose phylogenetic relationships to extant or extinct orders remain unclarified. A new order is therefore established to accommodate these insects as well as *Raptophasma kerneggeri* Zompro, 2001, from Baltic amber, hitherto classified as "Orthoptera incertae sedis."

Classification (*5*): Order Mantophasmatodea Zompro, Klass, Kristensen et Adis, ord. nov. Family Mantophasmatidae Zompro, Klass, Kristensen et Adis, fam. nov. Type genus: *Mantophasma* Zompro, Klass, Kristensen et Adis, gen. nov., with two species (extant), known from one ethanol-preserved female specimen (Fig. 1, B and C) and one dried, shriveled, teneral adult male specimen (Fig. 1A), respectively. Other included genus: *Raptophasma* Zompro, 2001, with one species (from Baltic amber).

Etymology: *Mantis* was the Linnaean name for mantises (including stick insects), and *Phasma* is a classical generic name for stick insects; the name alludes to the superficial similarity of all the insects in question.

Order and family description (*6*): Development of the external genitalia indicates that both available specimens of *Mantophasma* are adults. Head hypognathous (Fig. 1, D to F) with generalized mouthparts. Mandibles only with three small teeth in molar area. Palps five-segmented (maxillae) or three-segmented (labium). Antennae long, filiform, multisegmented. Ocelli absent. Tentorium without perforation, anterior pit far above anterior mandibular articulation. Epistomal sulcus lacking. Subgenal sulcus with unusual course, extending from posterior mandibular articulation directly to anterior tentorial pit and thence downward/backward to anterior mandibular articulation (Fig. 1E). Head capsule posteroventrally closed by weak submentum (no gula).

Thorax with each tergum narrowly overlapping the following. Prothoracic pleuron large, fully exposed (Fig. 1F). Wings entirely lacking. Metathorax without spinal apodeme. Coxae elongate. Tarsi (Fig. 1, G and H) with five tarsomeres, four basal with euplantulae. Three basal tarsomeres syncleritous, borders distinctly indicated by grooves. Dorsal membrane beyond third tarsomere with triangular process (Fig. 1I). Pretarsal arolium very large, with row of long setae (Fig. 1J).

In abdomen, tergum I and coxosternum I distinct but short, both free from metathorax; coxosternum without midventral sac. Small spiracles I to VIII located in pleural membrane, with intrinsic occlusor and extrinsic (coxosternal) dilator muscle. Male: Coxosternum IX (Fig. 2A) not subdivided, forming subgenital lobe with median spatulate process; styli absent. Phallic region (Fig. 2, B and C) with membranous lobes around gonopore and transverse, medially asymmetrically produced sclerite articulating with anterolateral corners of tergum X. Cerci one-segmented, prominent, clasping, not forming differentiated articulation with tergum X. Female: Ovipositor projecting markedly beyond short subgenital lobe formed by coxosternum VIII (Fig. 2D). Gonoplacs short, strongly sclerotized. Gonapophyses VIII markedly blunt distally. Gonapophyses IX largely fused with gonoplacs; composite formation with ventral keel interlocking with dorsal groove on gonapophyses VIII. Gonangulum with usual three articulations. One-segmented cerci much shorter than in male.

Foregut with large proventricle (Fig. 2, E and F) armed with weak, papillose (Fig. 2, G and H) sclerites that terminate in three successive whorls of weakly sclerotized lobes. Midgut caeca a pair of short and wide lateral pouches; no pyriform appendices detected. Heart lacking lateral arteries in mid-abdomen. Abdomen with ventral diaphragm. Abdominal ganglion VII free from terminal ganglion (VIIIff). Egg lacking micropylar plate and (defined) operculum, but with circular ridge (Fig. 2, I and J); chorion with hexagonal pattern of grooves traversed by delicate bars (Fig. 2, K and L).

Genus and species descriptions: *Mantophasma* Zompro, Klass, Kristensen et Adis, gen. nov. Eyes moderately sized, less high than gena. Fore-femora distinctly thickened; mid- and (particularly) hind-femora more slender. Fore- and mid-femora with ventral rows of short spines. Type species by present designation: *Mantophasma zephyra* Zompro, Klass, Kristensen et Adis, sp. nov. Etymology: Latin for west wind. Holotype: Female (Fig. 1, B and C). Label data: D. S. W. Afr. [Namibia] S. G. Seewald "JR. No. 827/09" [possibly meaning specimen 827 from 1909]. Museum für Naturkunde, Humboldt University, Berlin, Germany. Length (frons to epiproct apex), 22.5 mm. Color (as preserved), uniformly light brown. Head (Fig. 1E) rounded, three low tubercles between antennae, no tubercle behind antennae, eyes weakly convex. Other included species: *Mantophasma subsolana* Zompro, Klass, Kristensen et Adis, sp. nov. Etymology: Latin for east wind. Holotype: Male (Fig. 1A). Label data: Tanganyika [Tanzania] Ufipa Dish, L. Kwela, 22.iii.1950, H. O. Backlund. Zoological Museum, University of Lund, Sweden. Length (frons to epiproct apex, specimen shriveled), 17.5 mm. Color, light reddish brown with red spots. Head (Fig. 1D) distinctly angular in anterior view, three

[1]Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark. [2]Max-Planck-Institut für Limnologie, AG Tropenökologie, August-Thienemann-Strasse 2, D-24306 Plön, Germany. [3]Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde, Königsbrücker Landstrasse 159, A.B. Meyer Bau, D-01109 Dresden, Germany.

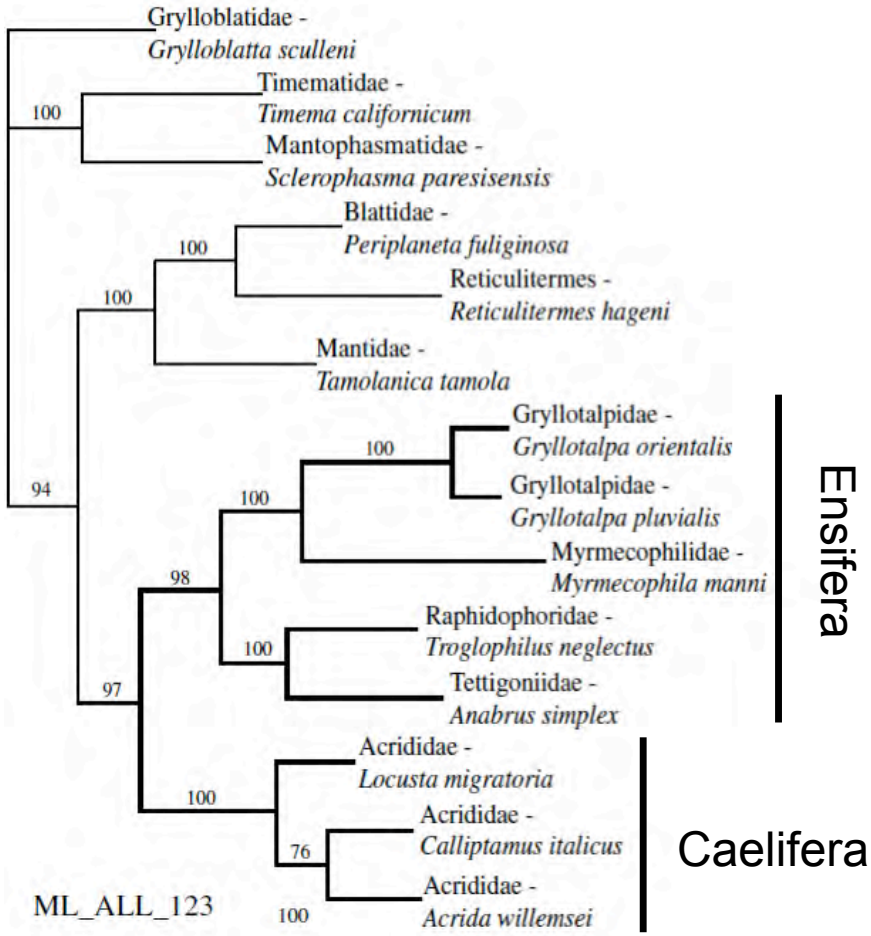
*To whom correspondence should be addressed. E-mail: klass@snsd.de, zompro@mpil-ploen.mpg.de

ORTHOPTERA:
Grasshoppers, locusts, katydids, crickets

- Largest clade of Polyneoptera: 20,000 species worldwide.
- Distinguishing characters?
- Distinctive saltatory (jumping) hindlegs.
- Prothorax large and shield-like.
- Two monophyletic suborders: Caelifera and Ensifera.

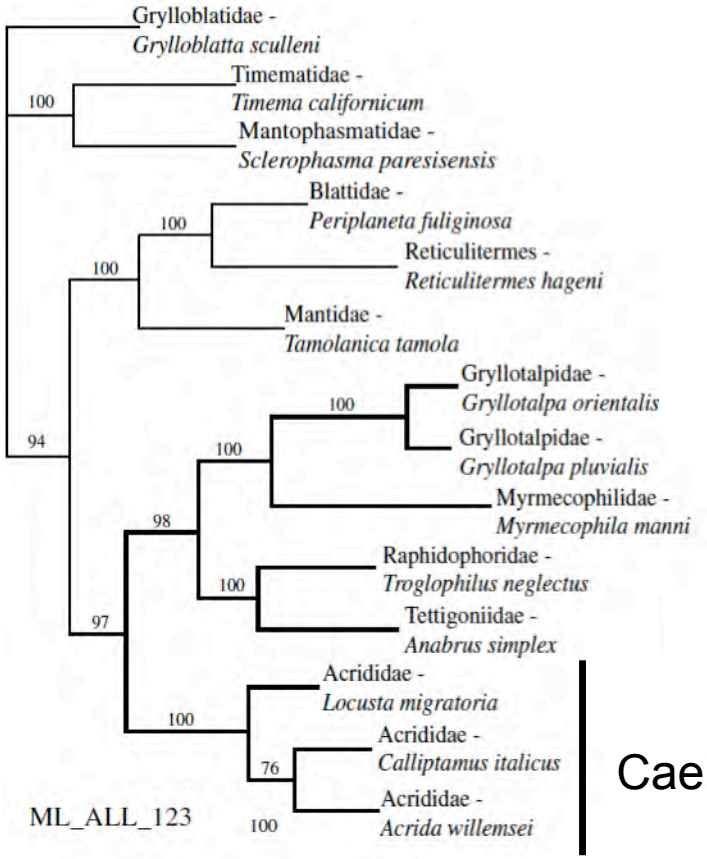
Caelifera & Ensifera

- Monophyly supported by just about everything…
  - Morphology
  - Every genetic source looked at.



Caelifera

Split at Permo-Triassic Boundary (~250mya)



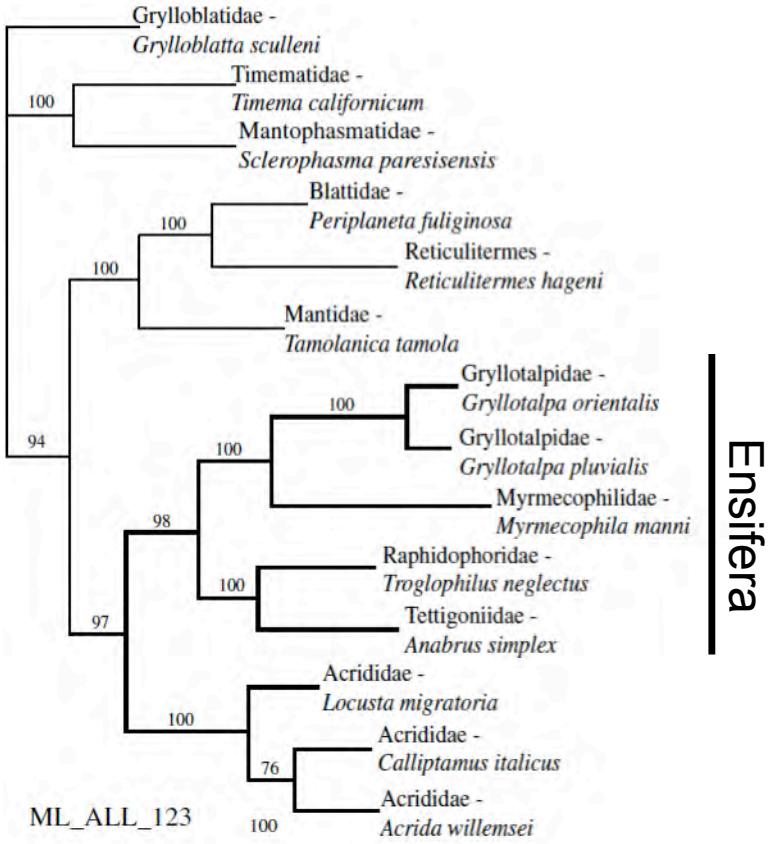
Caelifera

Caelifera

- Grasshoppers and locusts
- Day-active, fast-moving, visually acute, terrestrial herbivores
- Short antennae, short ovipositors

Ensifera

When did they originate?



Ensifera

- Katydids
- Crickets
- Mormon crickets,
- Jerusalem crickets
- wetas
- Cooloola monsters.
- Often night-active, camouflaged or mimetic, predators, omnivores, or phytophages.





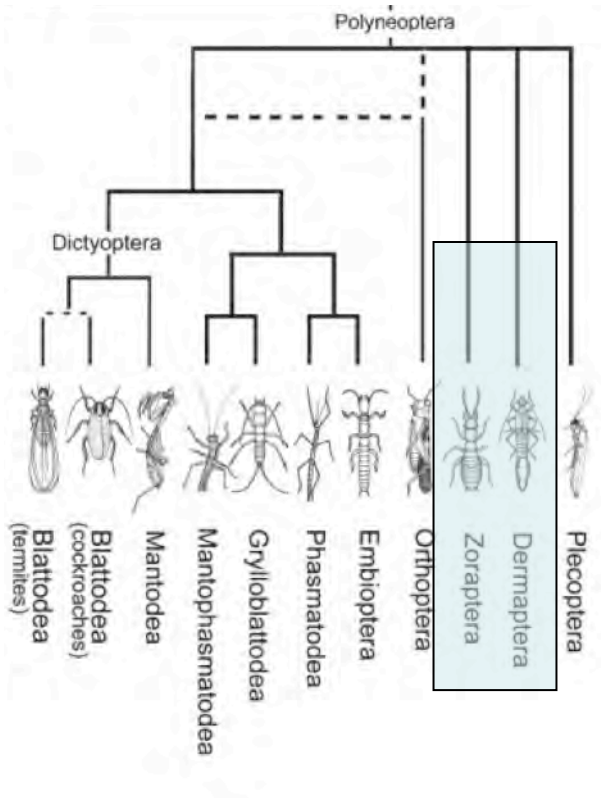

Ensifera

- Long antennae
- Long ovipositors

Dermaptera & Zoraptera

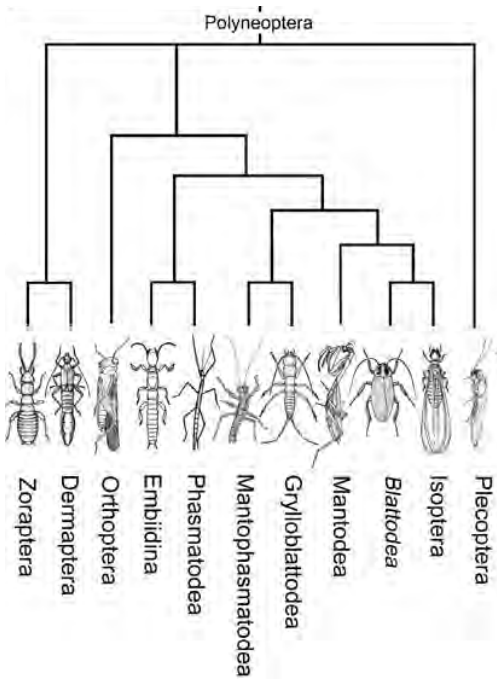
Group based on morphology, behavior, and ecology.

Odd DNA sequence evolution made this problematic for a very long time.

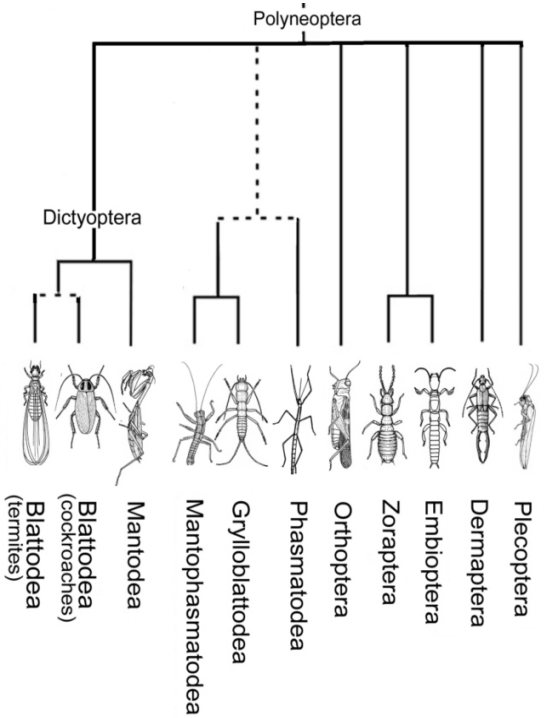


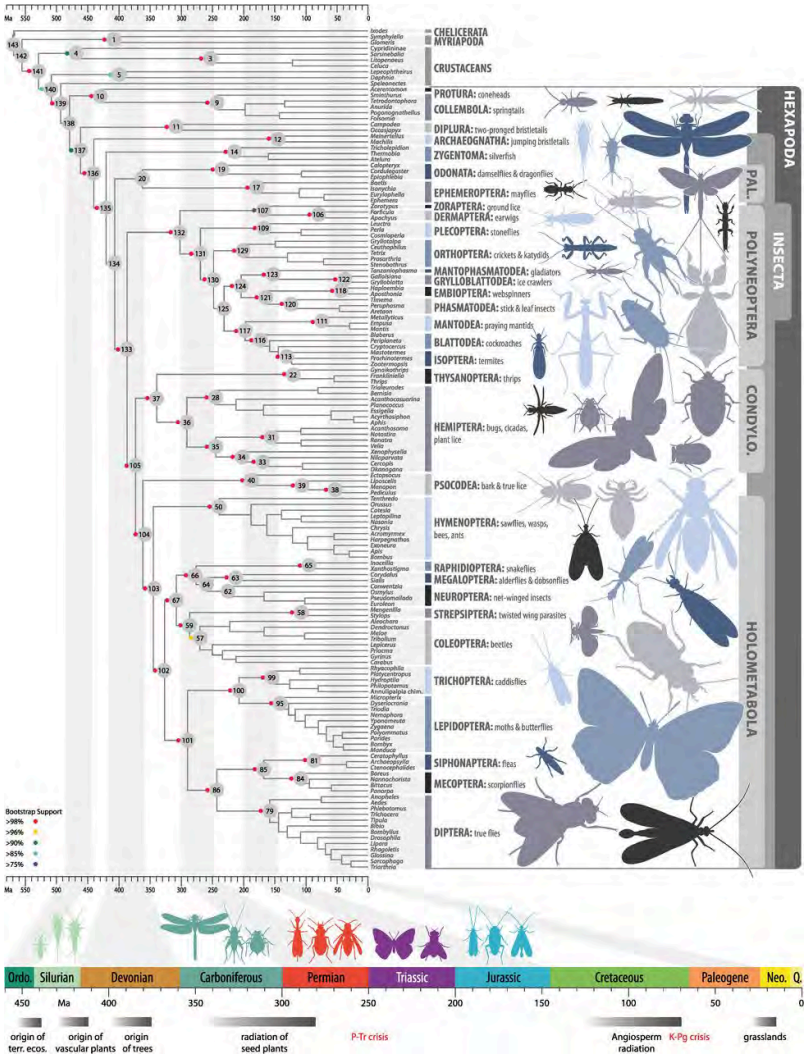
Polyneoptera

3rd Edition:



4th Edition:



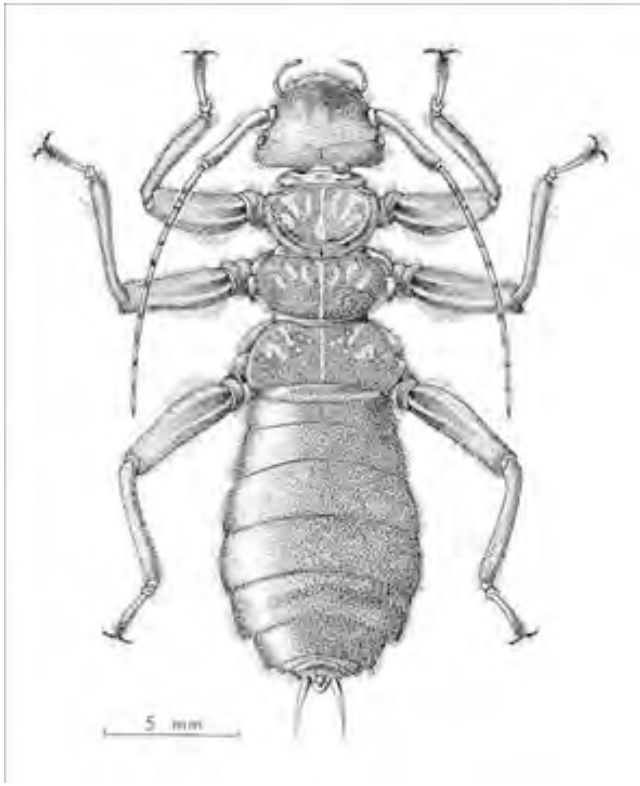


Zoraptera: Angel Insects

- Least known insect order.
- Primarily circumtropical except Australia.
- Subsocial, live in rotting logs, considerable parental care.
- Feed on fungi and spores.
- 30 species total.

Dermaptera: Earwings

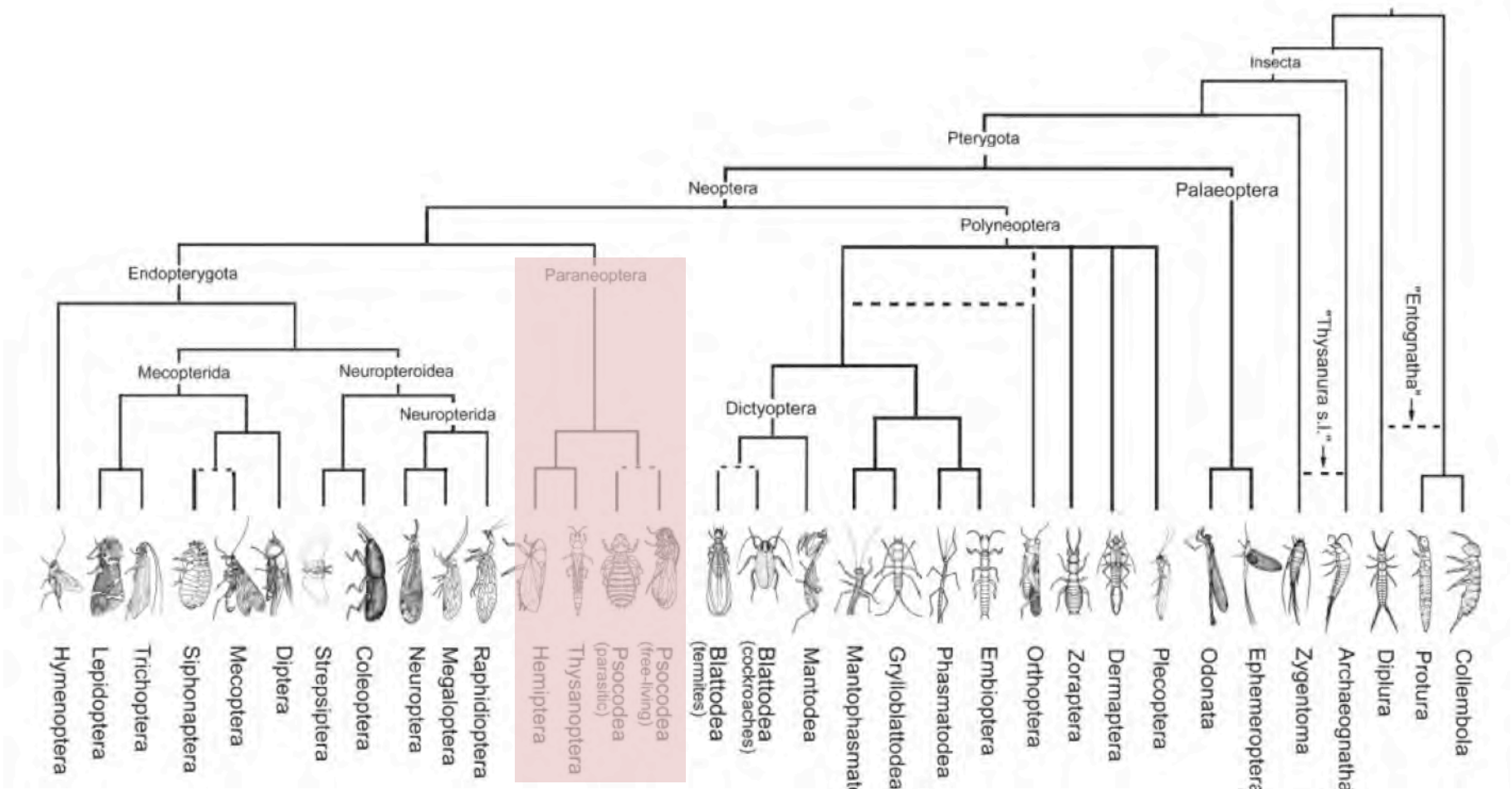
- Distinctive pincer-like cerci.
- Short fore wings (elytra), hind wings fold underneath.
- Omnivorous.
  - Some parasites
  - Some predators
- Considerable parental care.



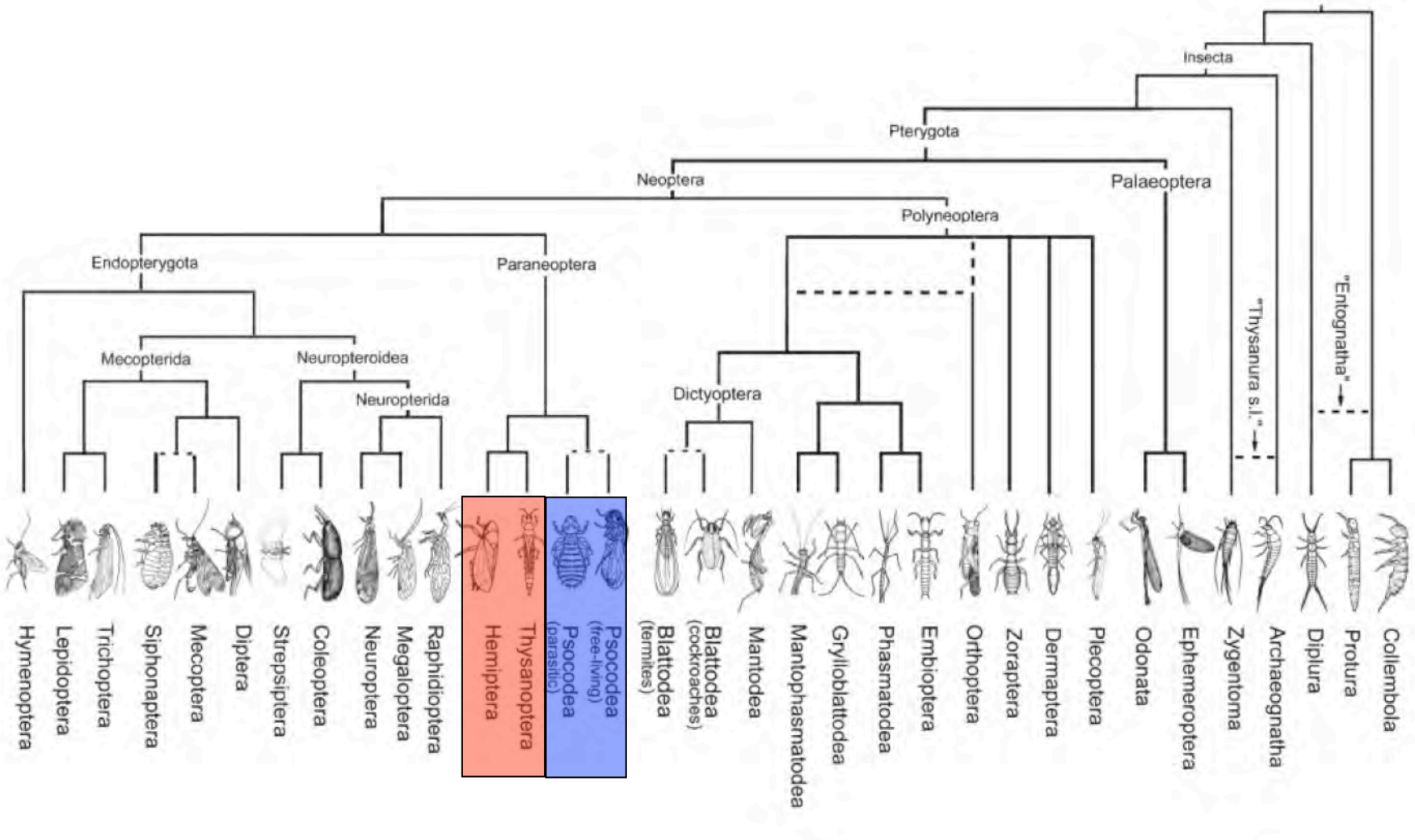
Some evidence groups Zoraptera + Dermaptera with Embioptera

What trait might be a synapomorphy for these orders?

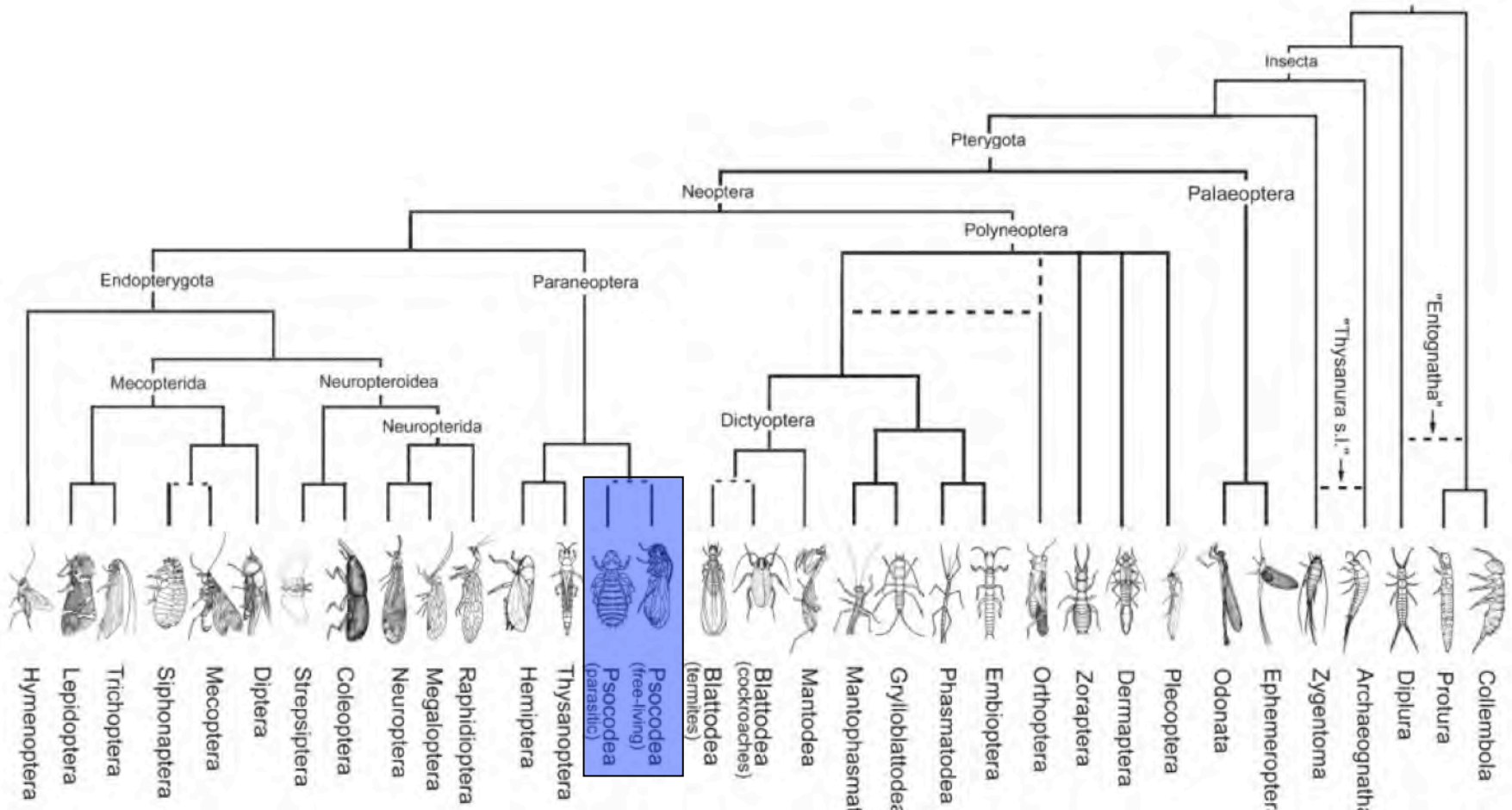
Paraneoptera: What major landmark in the roadmap of insect evolution distinguishes them?



Two major clades: Psocodea & Condylognatha

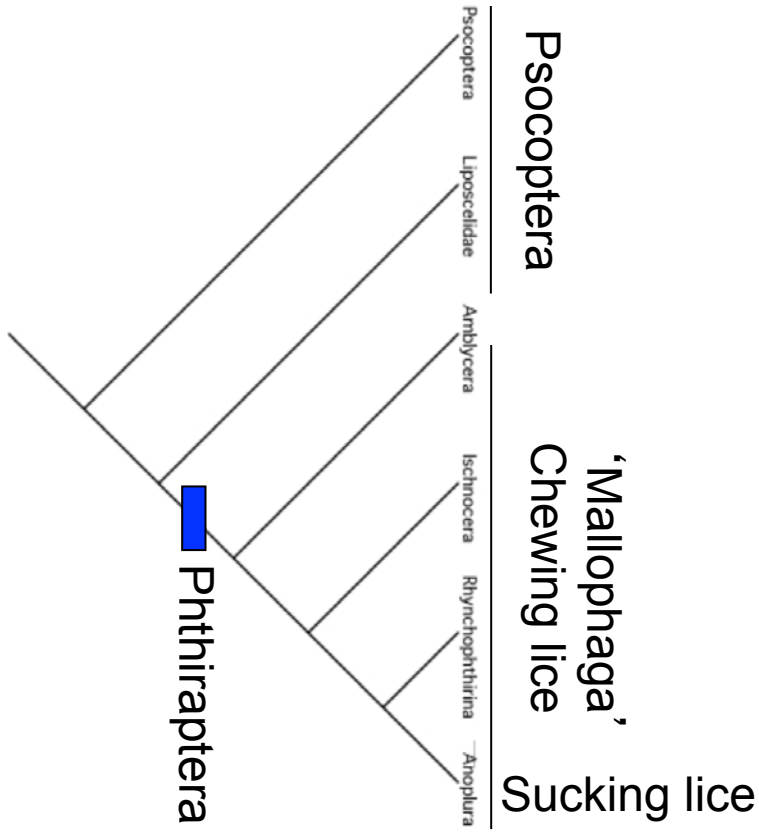


Psocodea: ‘Psocoptera’ + Phthiraptera



Psocodea

- ‘Psocoptera’ is paraphyletic with respect to monophyletic Phthiraptera.
- ‘Psocoptera’: Booklice & Barklice
- Phthiraptera: Parasitic lice



Data from morphology & mtDNA

‘Psocoptera’: Book & Bark Lice

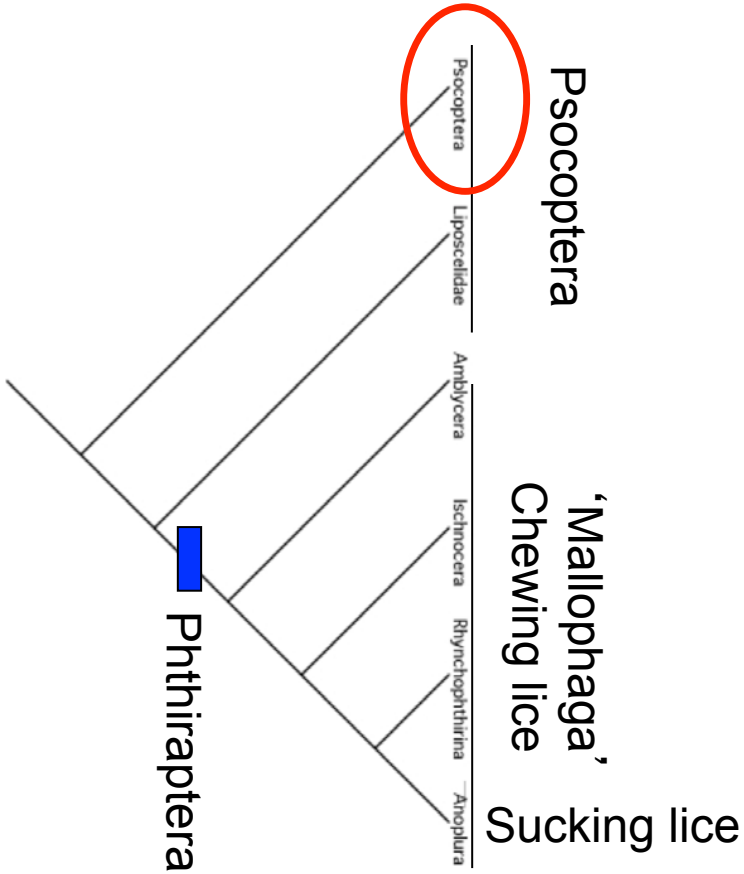
- 5,500 species.
- Detritivores, algivores, lichenivores.

Psocoptera

- Often regarded as the most primitive Paraneoptera alive today because their mouthparts show the least modification from the primitive mandibulate condition
- Only the lacinia (a subdivision of the maxilla) has become a separate, rod-like structure that is pushed against the substrate as a brace while the mandibles scrape off surrounding food particles

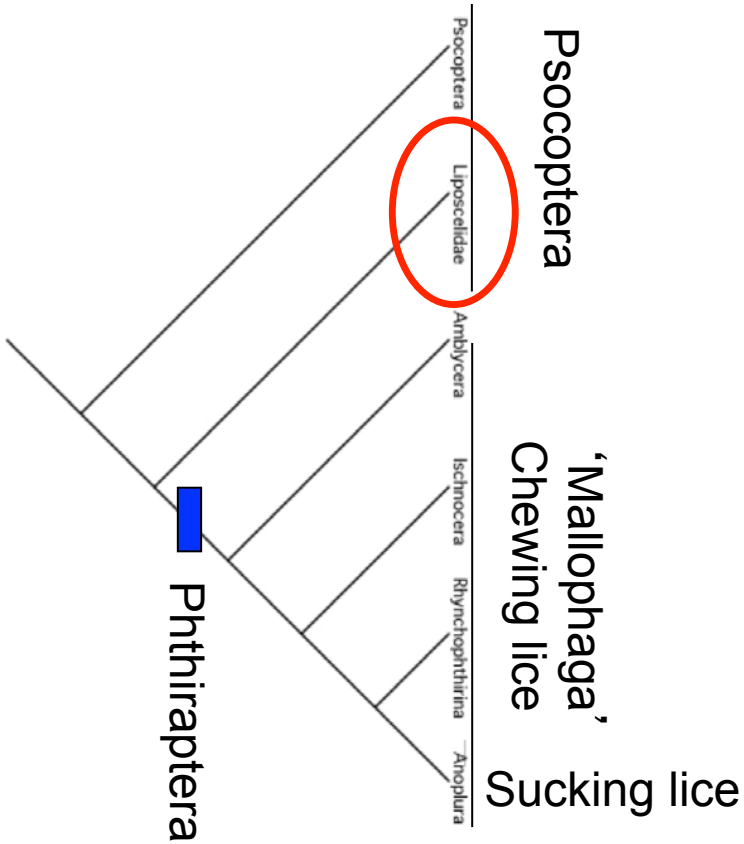
Traditional Psocoptera

- Secretive generalists that forage on algae, lichens, fungi, and a variety of plant products.
- Why is the order Psocoptera paraphyletic?



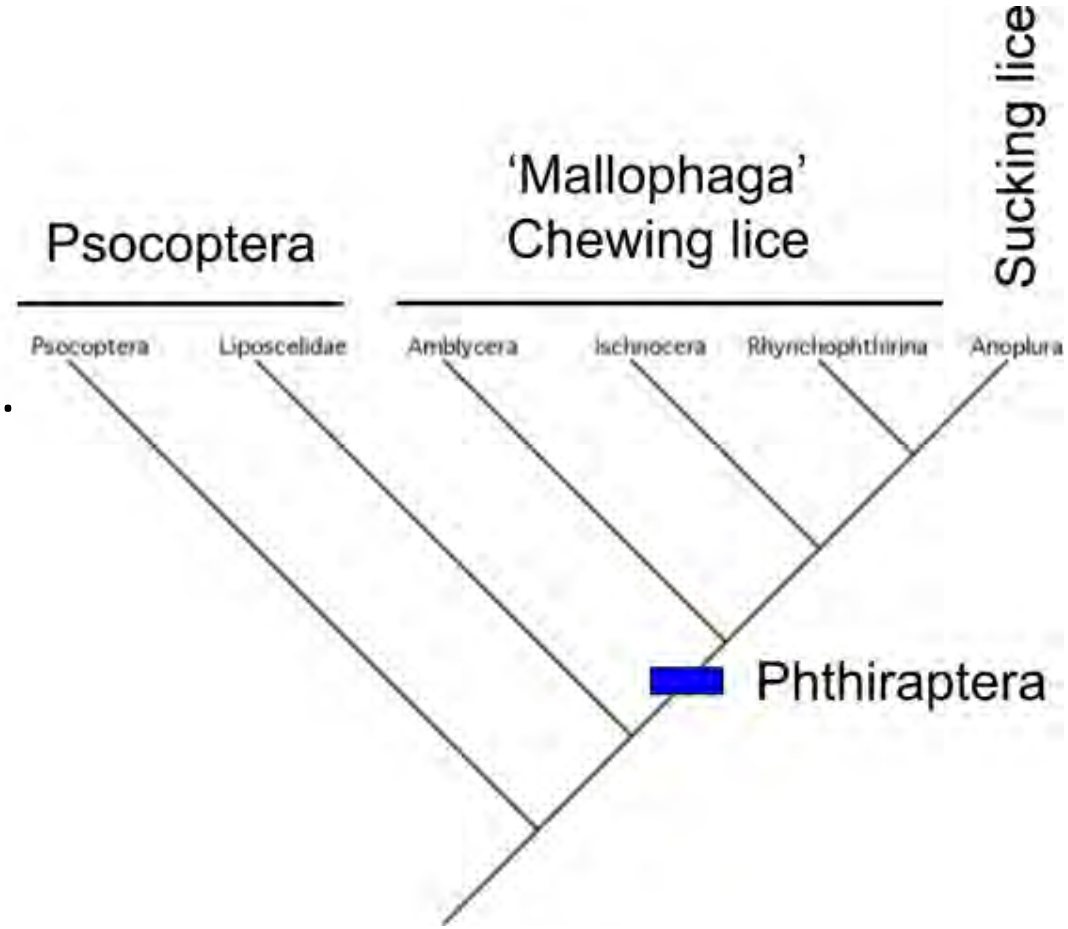
Liposcelidae

- Commensal detritivores in bird nests.
- What is their sister taxon?
- Any thoughts as to what first lineages of parasitic Mallophaga feed on?



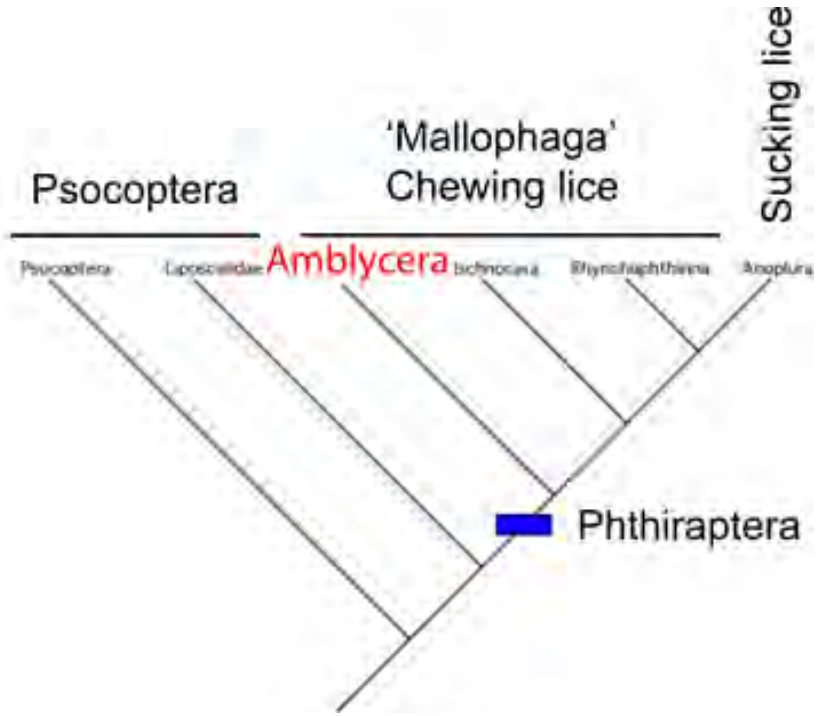
PHTHIRAPTERA: True lice

- Derived within Psocoptera.
- Plesiomorphic condition with functional mandibles (chewing lice).
- Derived condition without functional mandibles (sucking lice).



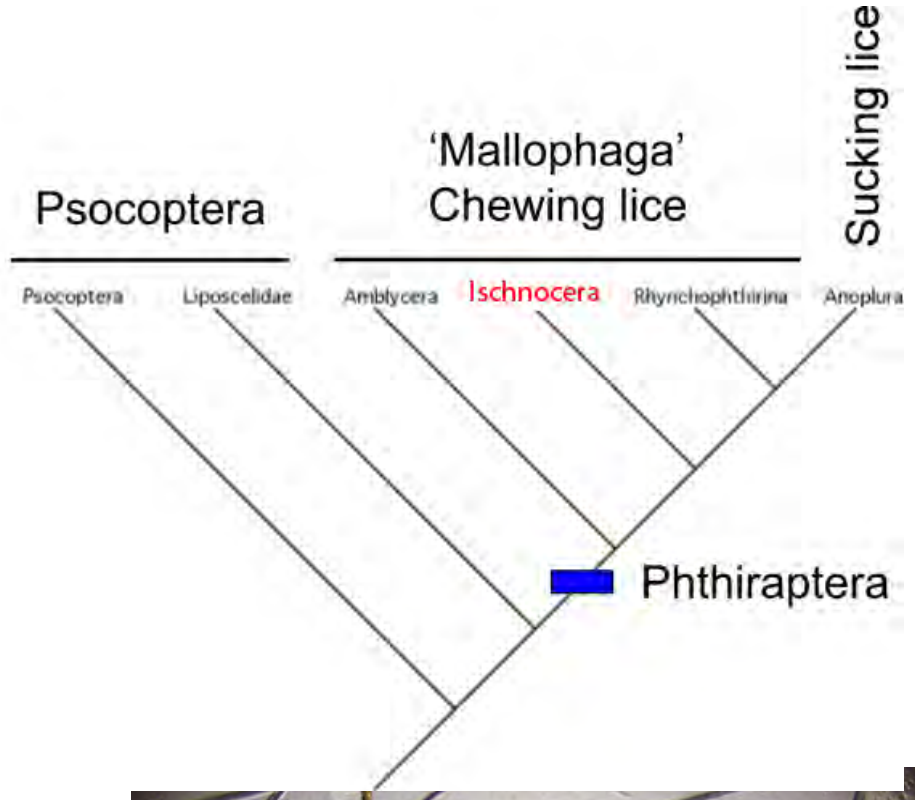
Phthiraptera

- All *wingless* external parasites of birds and mammals.
- Cannot survive long if separated from host.
- First lineages all parasites on birds (feathers & dead skin).



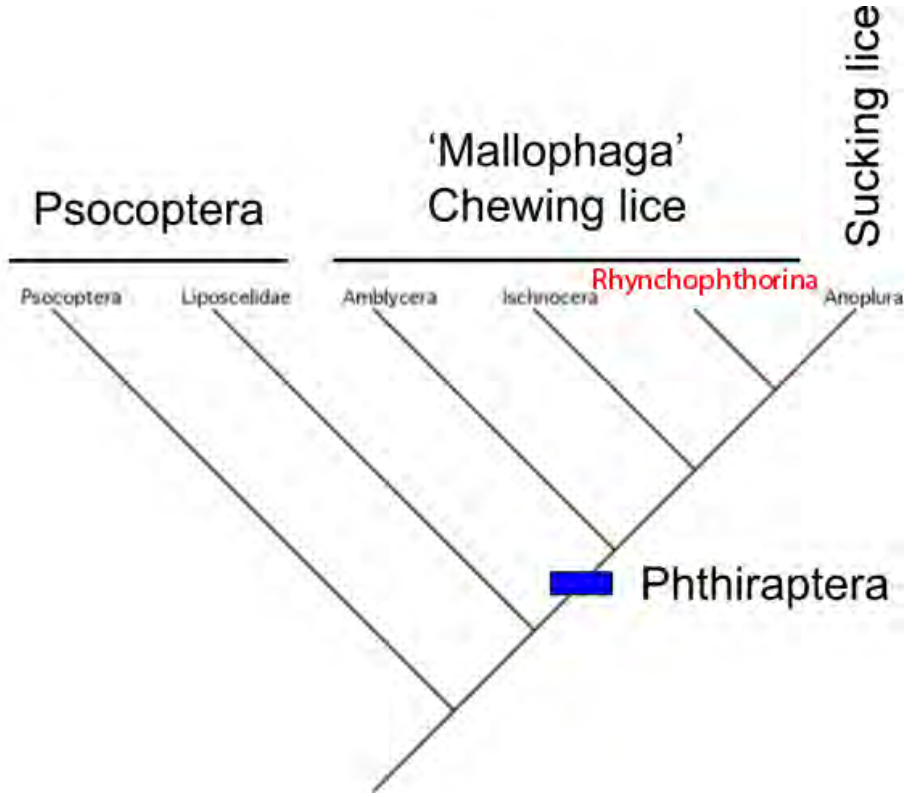
Phthiraptera

- About 135 million years ago shifted to mammals
- Ischnocera
- Hair and dead skin cells.



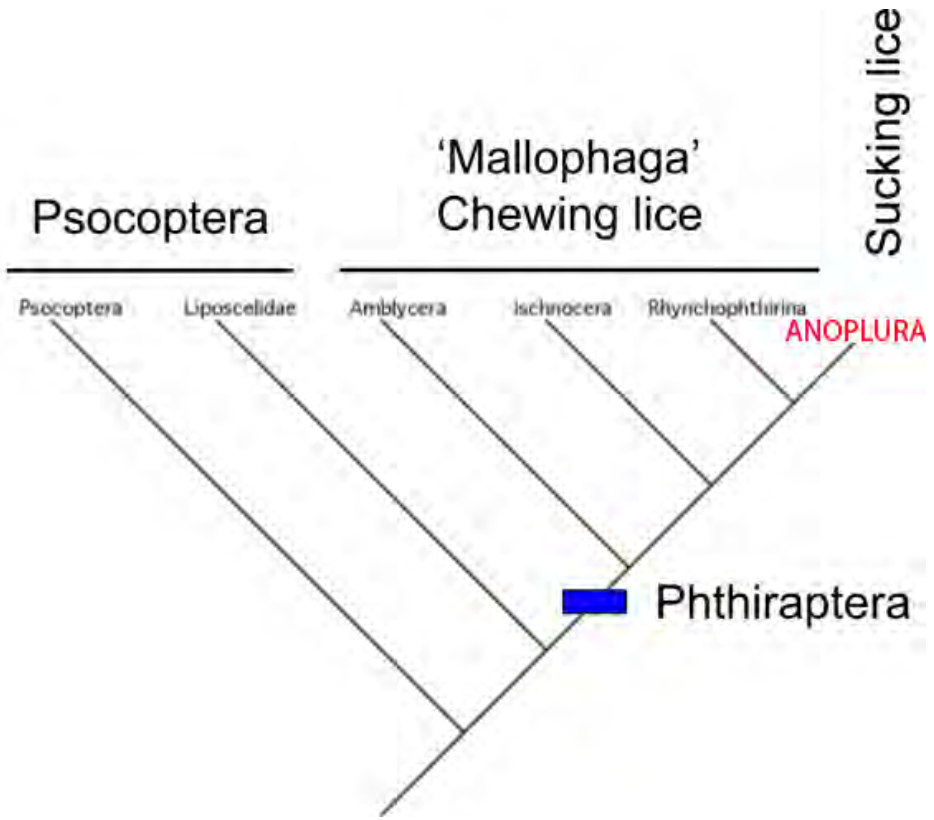
Phthiraptera

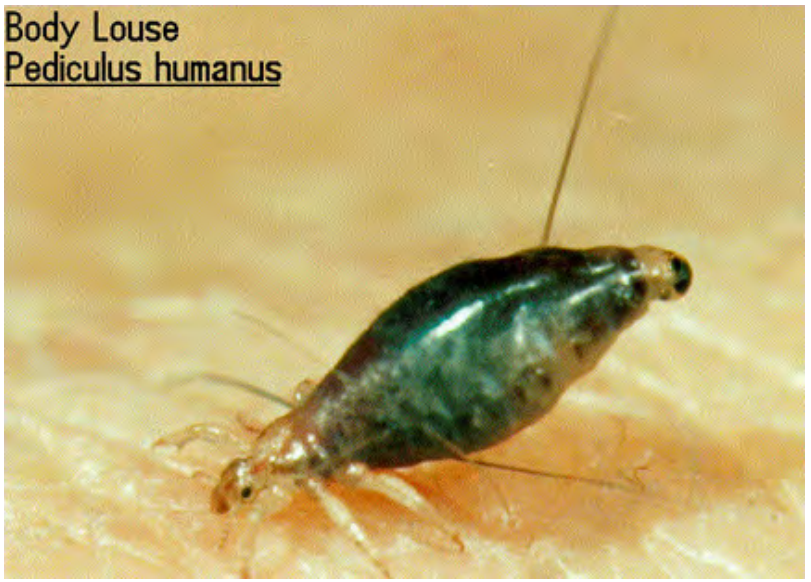
- A few of these lice (Rhynchophthirina) developed the habit of breaking their host's skin and feeding on its blood.



Phthiraptera

- This lineage presumably gave rise to sucking lice (suborder Anoplura), all of which are blood-feeding ectoparasites of placental mammals.



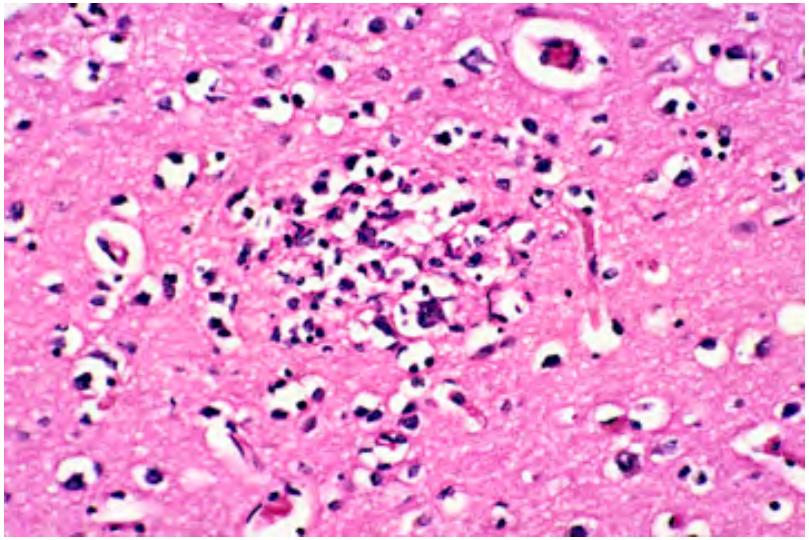


ANOPLURA: Sucking Lice

- Responsible for the spread of disease in humans and domestic animals.
- Pediculosis is an infestation of lice anywhere on the human body.

ANOPLURA: Sucking Lice

- Human body louse is responsible for…
- …the spread of relapsing fever (*Borellia recurrentis*)
- …epidemic typhus (*Rickettsia prowazeki*)
- …and trench fever (*Rickettsia quintana*).



Sucking lice and the origin of clothing.

- There are two subspecies of human louse:
  - Head louse *Pediculus humanus capitis*
  - Body louse *P. h. humanus*
- Mammalian sucking lice all live in association with hair because they can not live in exposed areas.

Sucking lice and the origin of clothing.

- Which subspecies would you expect to be ancestral?
- Should not observe the morphological shift until clothing are present.
- Molecular research suggests this took place 72,000 ± 42,000 years ago.

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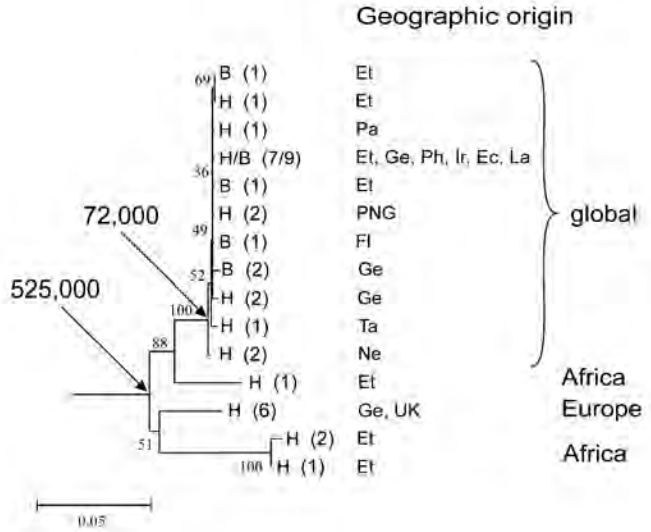
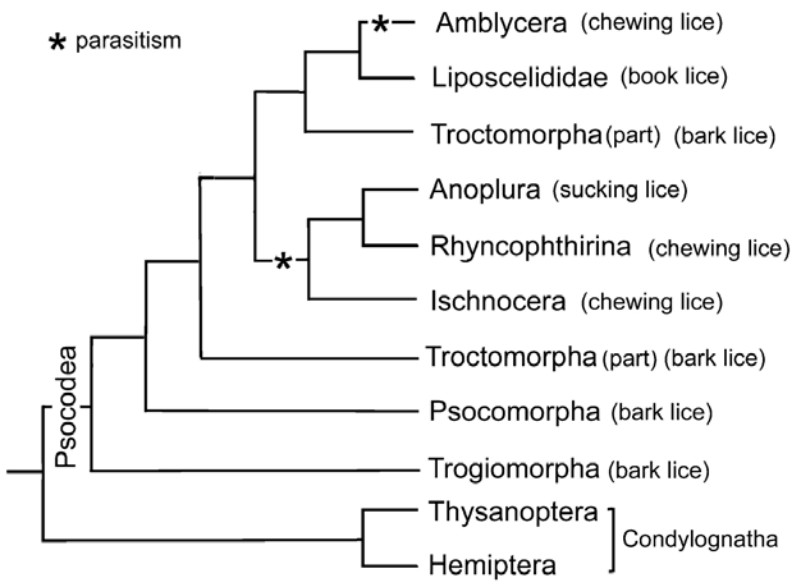
Molecular Evolution of *Pediculus humanus* and the Origin of Clothing

Ralf Kittler,[1] Manfred Kayser, and Mark Stoneking*
Max Planck Institute for Evolutionary Anthropology
Deutscher Platz 6
D-04103 Leipzig
Germany

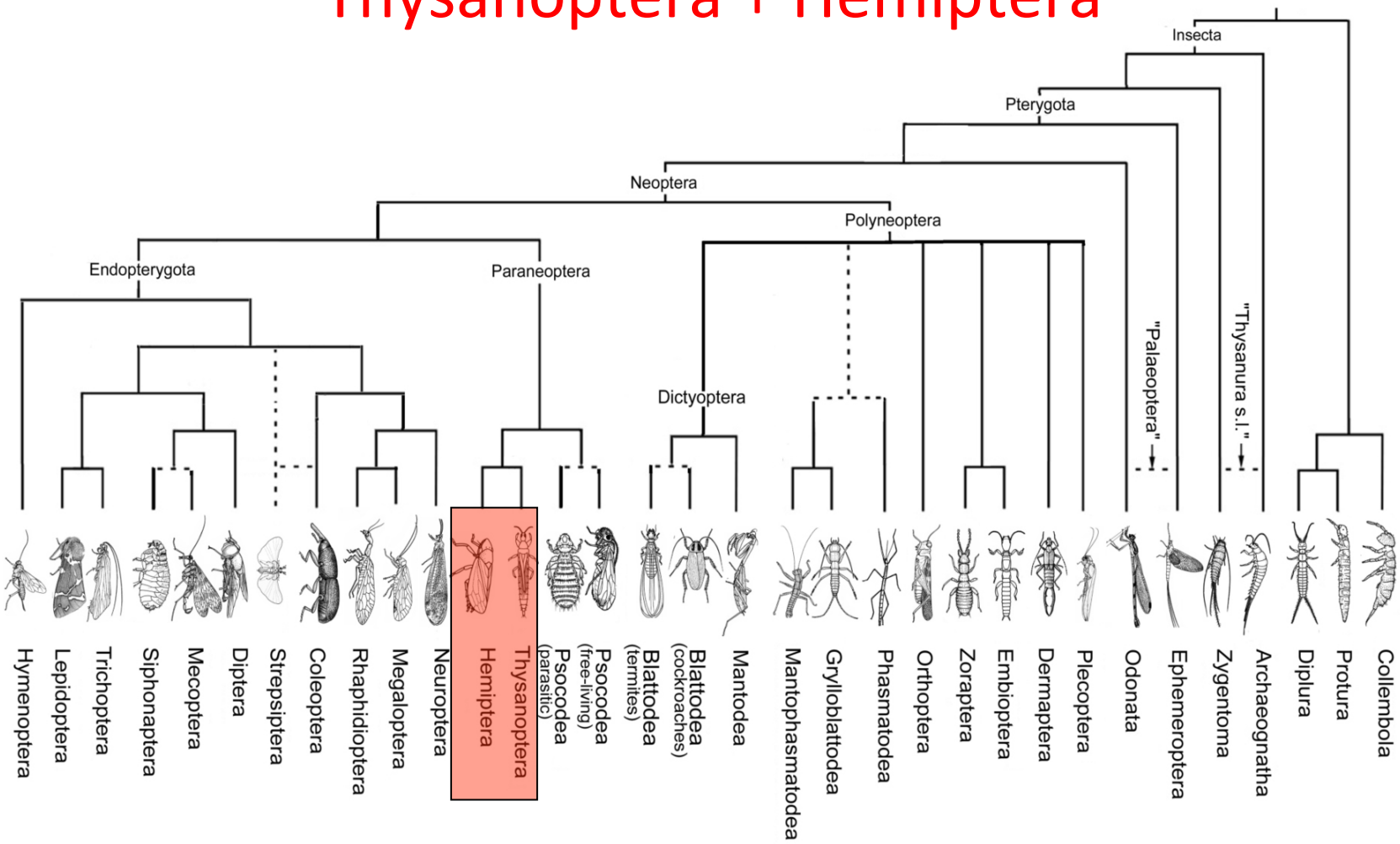


Alternative hypothesis

- Your textbook (Fig. 7.5) presents an alternative phylogeny based on ribosomal gene data.
- What does this say about the origins of parasitism that is different from previous?
- Note that this is now viewed rather skeptically…



Condylognatha:
Thysanoptera + Hemiptera



Thysanoptera: Thrips

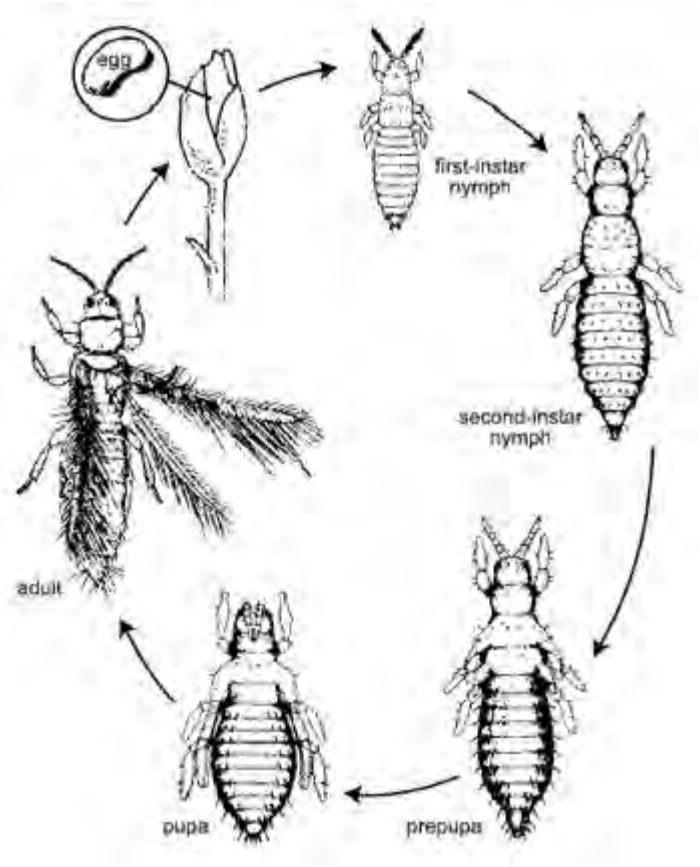
- ~4500 species
- Generally small (< 3mm).
- Most feed on plant tissues
- Some are predators of mites or other small insects
- Sexual all haplodiploid.
- Parthenogenesis common

Thysanoptera: Thrips

- Front and hind wings slender, rod-like, with a dense fringe of long hairs. Many species are secondarily wingless.
- Head narrow anteriorly forming a conical mouth opening
- Tarsi 1-2 segmented, with eversible adhesive bladders apically

Thysanoptera: Thrips

- Development is convergently ‘holometabolous’
- Quiescent pupal stage
- Not homologous with endopterygota, not with physiological restructuring.

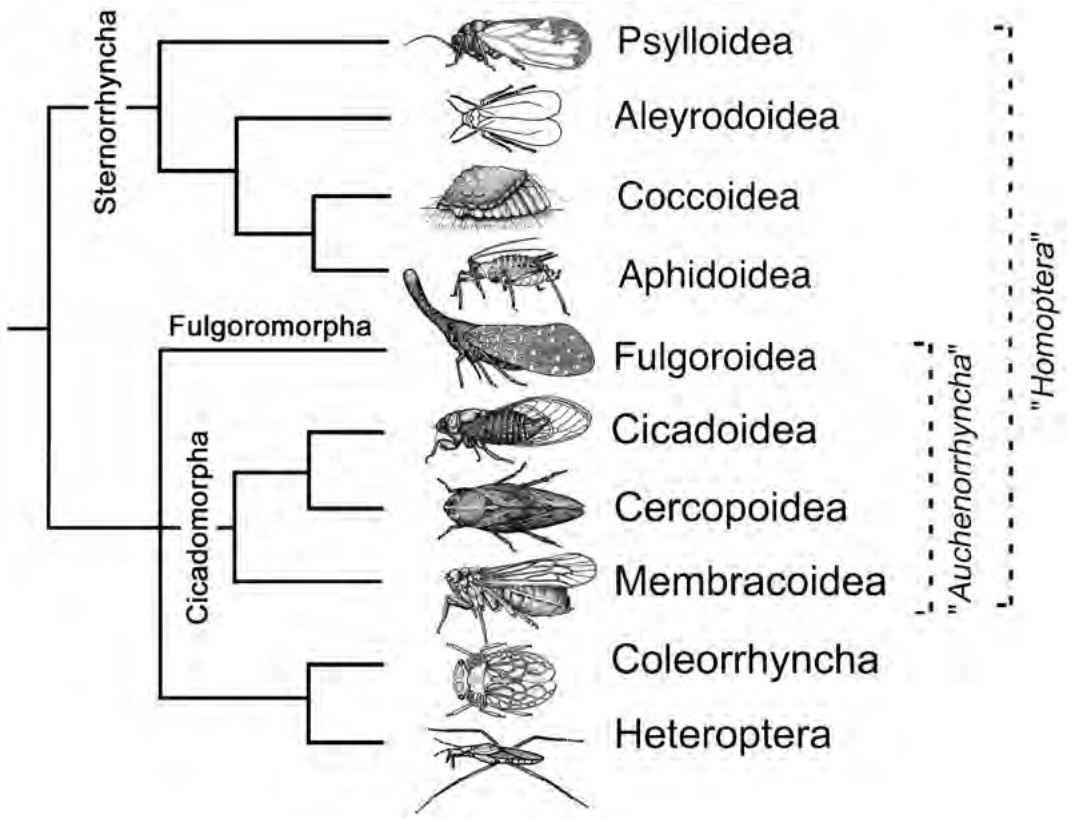


Thysanoptera: Thrips

- Eusociality?
- We will revisit these when we get to the evolution of sociality.
- So remember them!

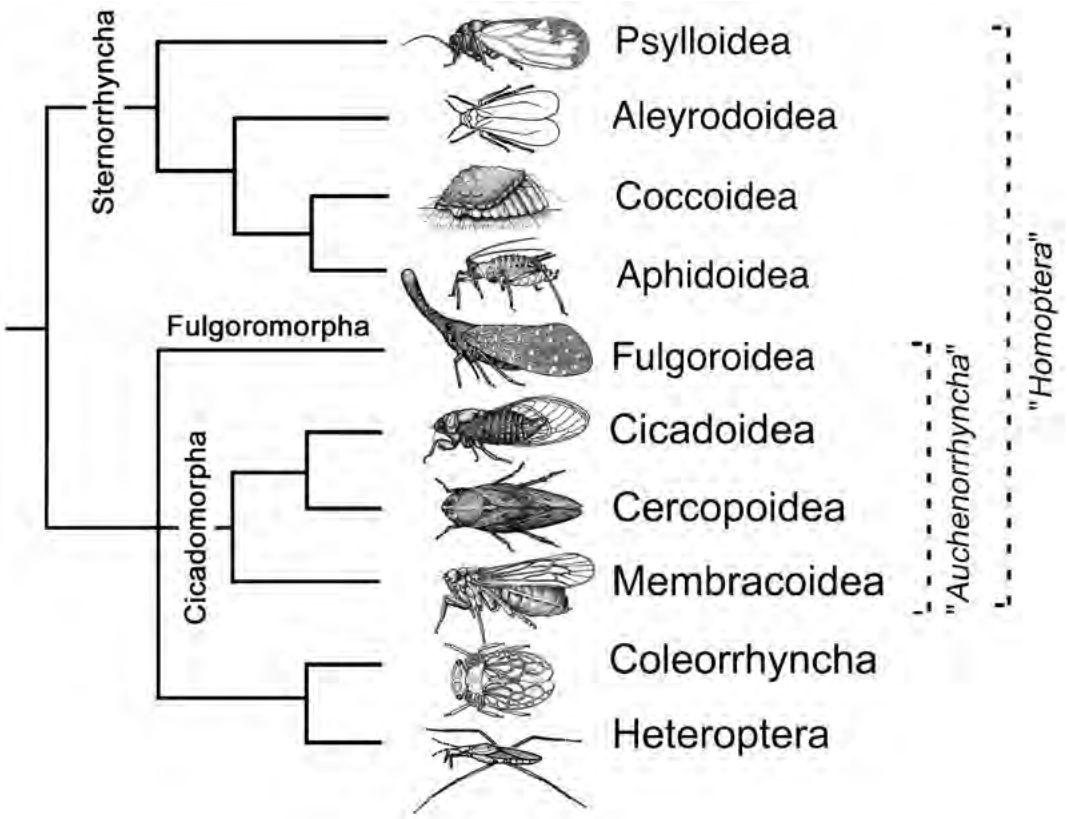
Hemiptera

- Incredibly diverse order.
- Bugs, cicadas, leafhoppers, planthoppers, spittle bugs, aphids, jumping plant lice, scale insects, whiteflies, mossbugs.
- Largest non-endopterygote order.
- ~85,000 species described.
- All with distinctive, well-developed piercing-sucking mouthparts



Hemiptera

- Haplodiploidy has evolved at least four times within the Sternorrhyncha:
- Aphids
- Whiteflies
- Twice within the scale insects



Coevolution with endosymbiotic bacteria extensive. Why?

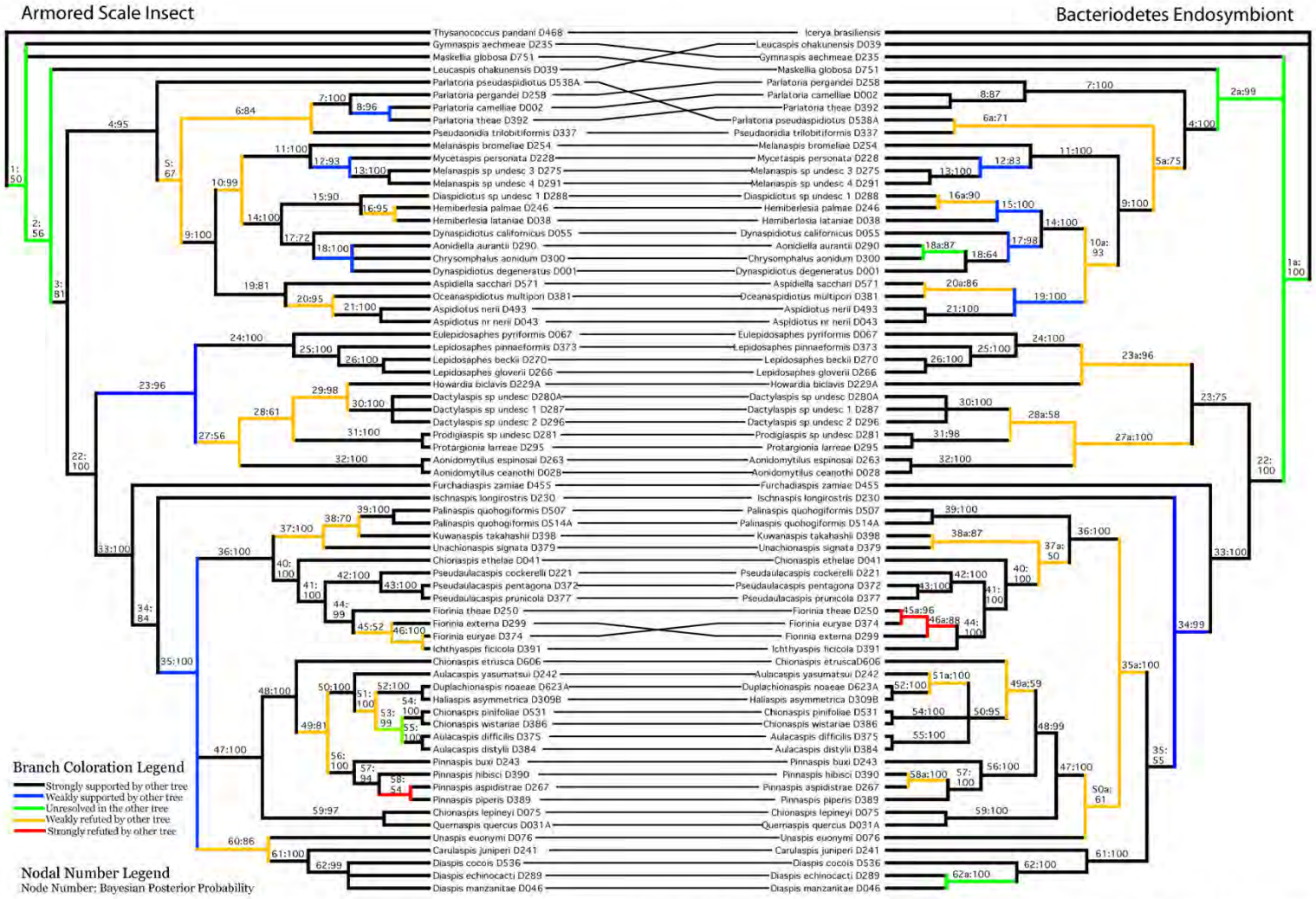


Fig. 1. Tanglegram comparing Bayesian topologies of the hosts (left) and bacteria (right). The colors of the internal branches reflect the degree of congruence with opposite tree. Strongly supported, same clade appears on opposite tree with strong support (Bayesian posterior probability $\geqslant 95$ and parsimony bootstrap support $\geqslant 80$). Weakly supported, same clade appears on opposite tree, but without strong support according to limits set above. Unresolved, clade unresolved on opposite tree. Weakly refuted, a conflicting clade occurs on the opposite tree but without strong support. Strongly refuted, strong support for a conflicting clade on the opposite tree.

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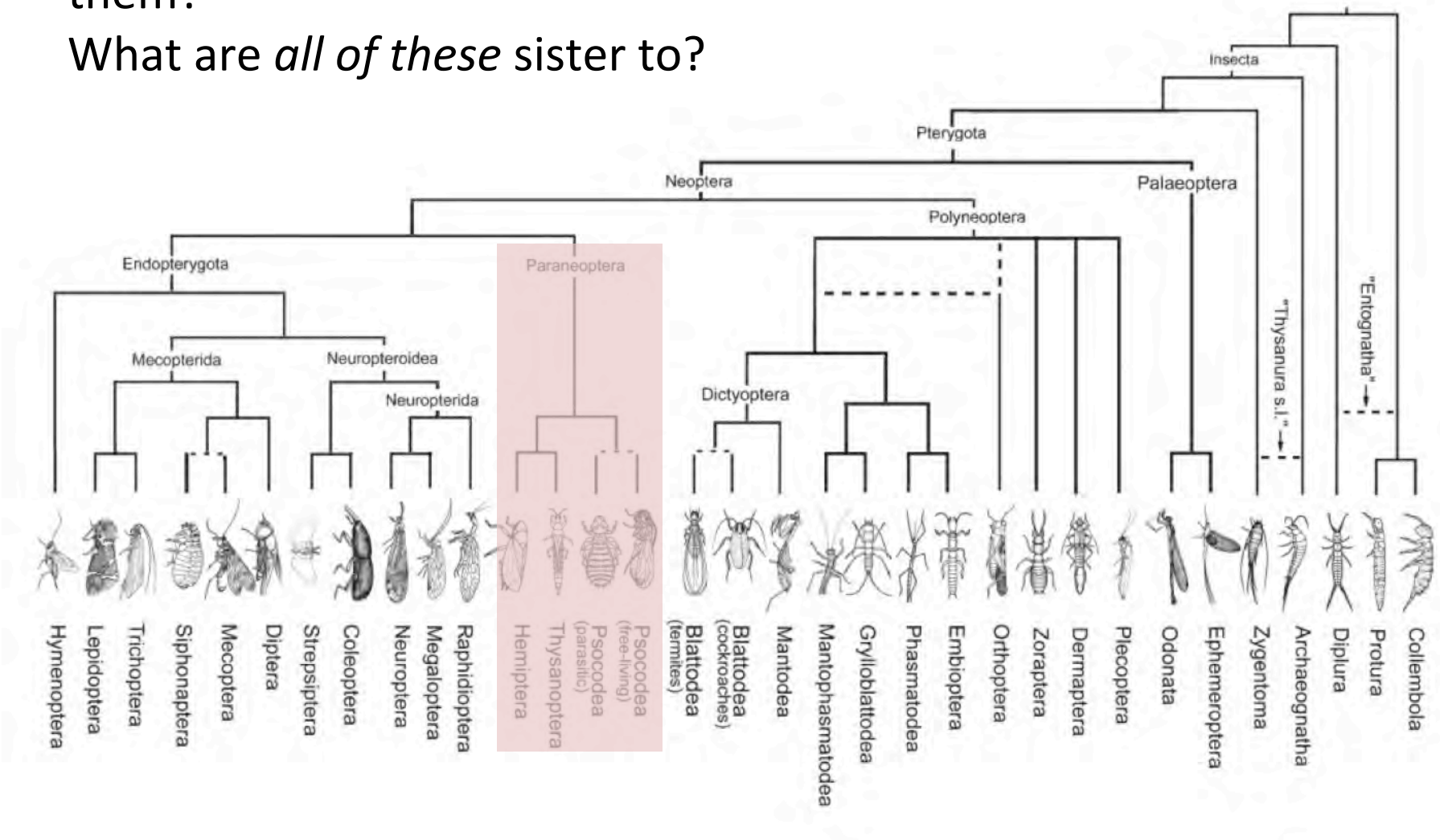
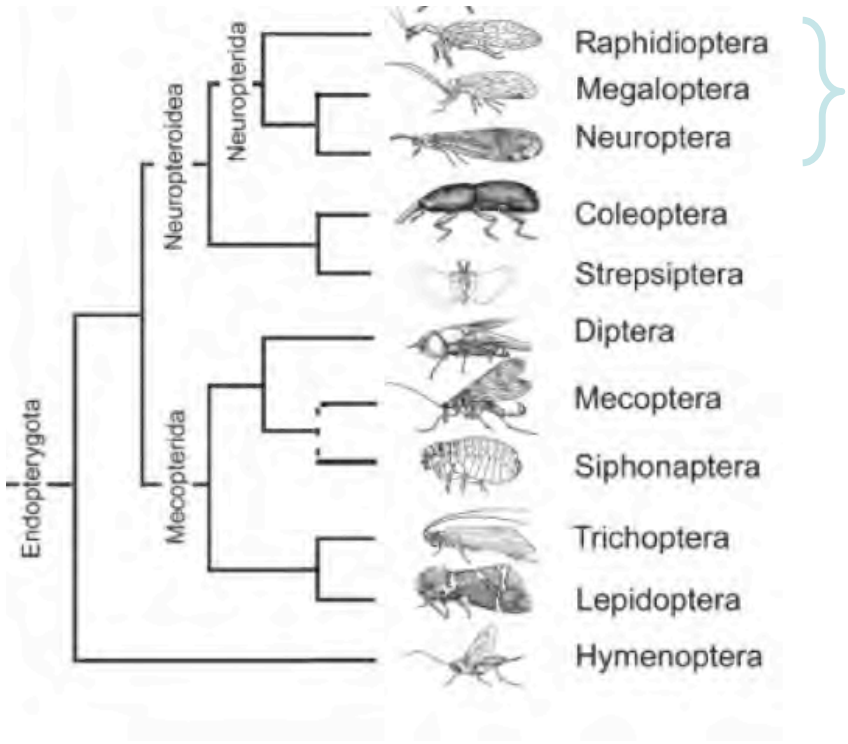
What is the sister taxon to the Paraneoptera?

What roadmap synapomorphy unites them?

What are *all of these* sister to?





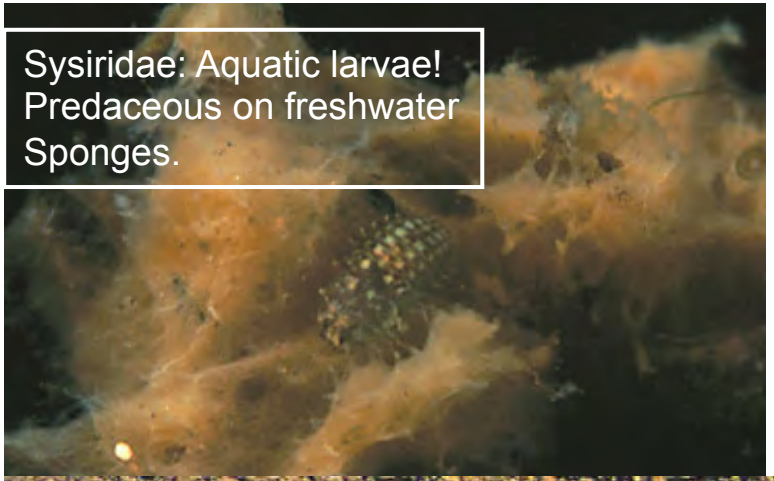
Grouping (that is sister to Coleoptera) can be called:
Neuropterida (best) or Neuroptera (in widest sense)
We prefer to treat 3 orders.

Neuroptera
Lacwings & Antlions

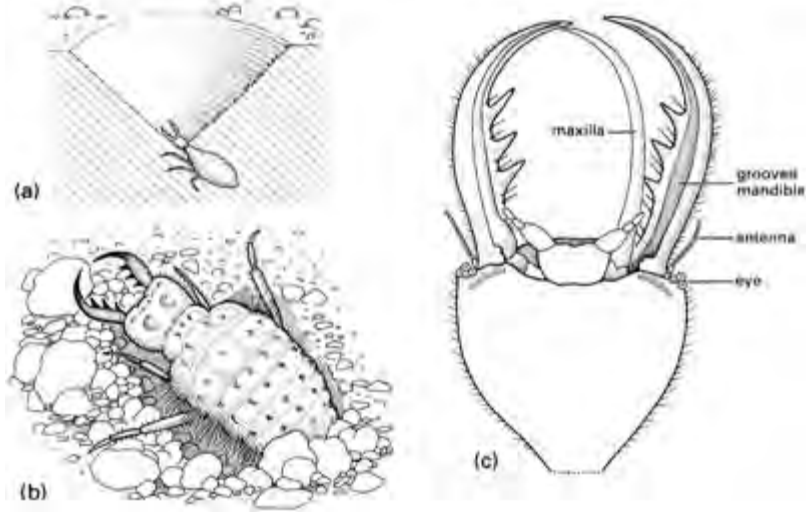
- Wings held roof-like over abdomen at rest.
- Fore & hind wings subequal with numerous cross-veins and distal “twigging” of veins.
- Immatures predominantly terrestrial, prognathous, with slender mandibles and maxillae usually forming piercing/sucking mouthparts.

Chrysopidae: Green lacewings

Hemerobiidae: Brown Lacewing

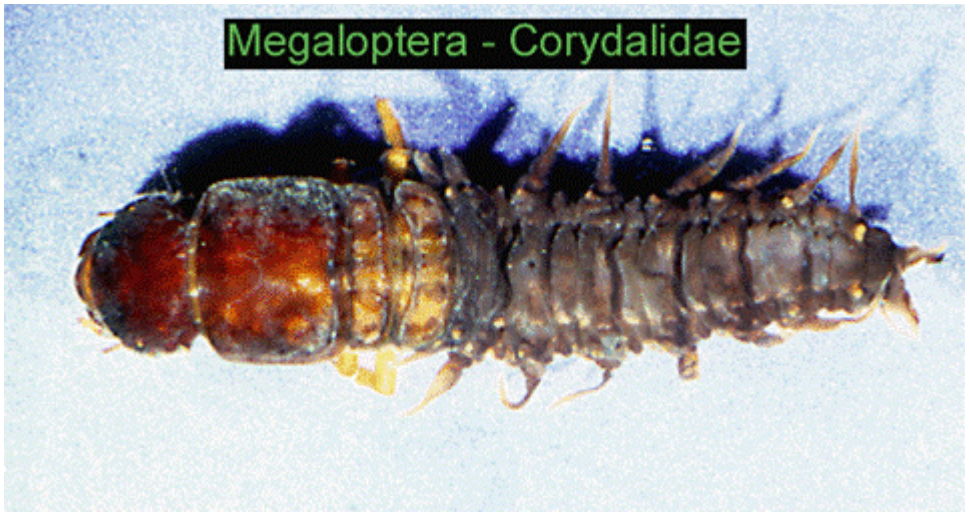


Mantispidae: Australia



MEGALOPTERA:
Alderflies, Dobsonflies, Fishflies

Aquatic predaceous larvae.
Anal gills in larvae.

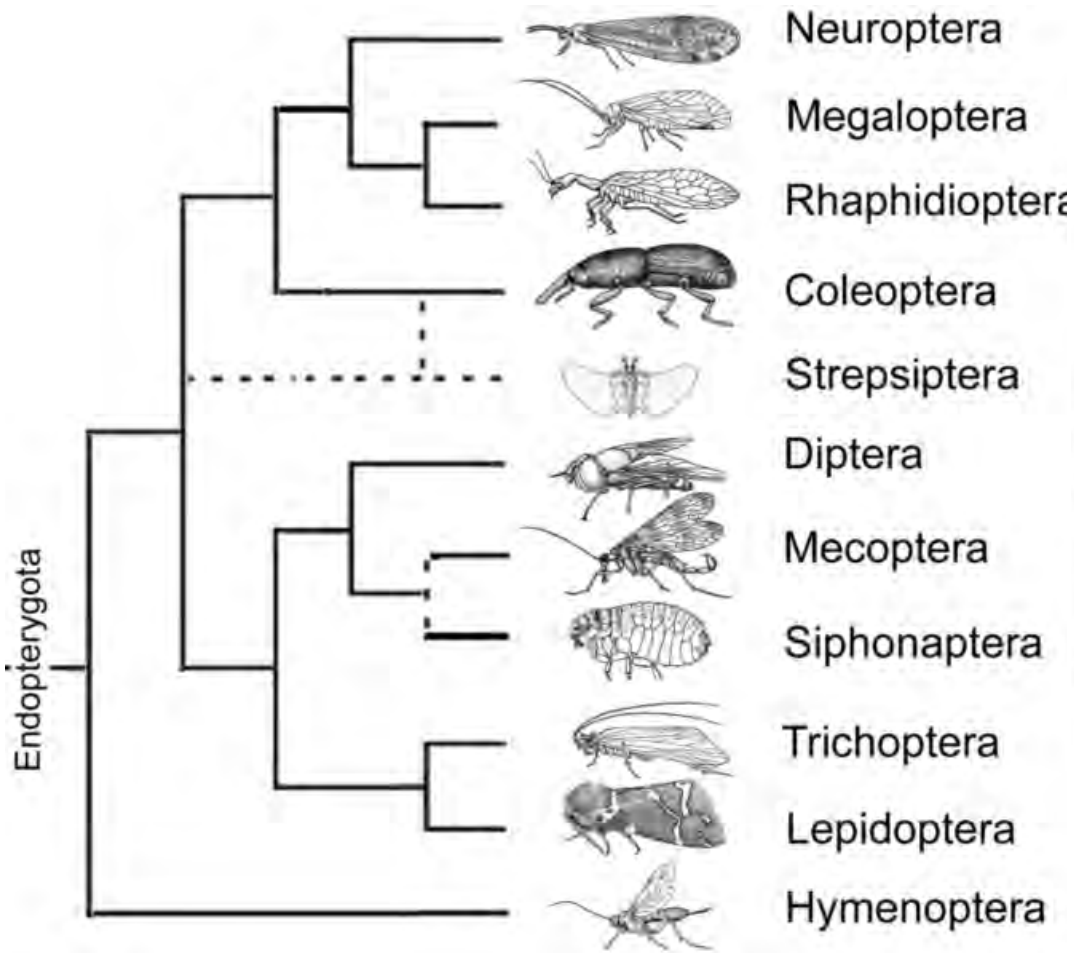


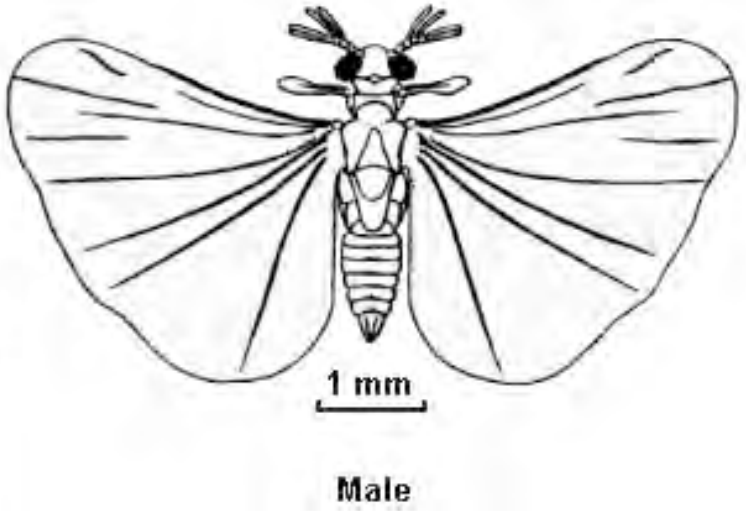
Raphidioptera: Snakeflies

Prothorax very long, appearing necklike & flexible. Completely terrestrial.

snakeflies

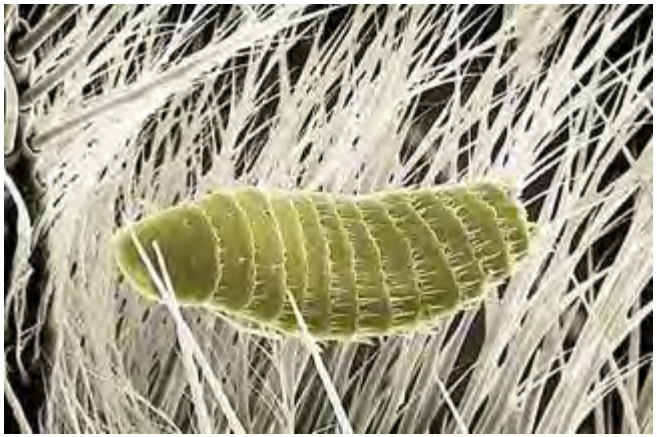
The Strepsiptera problem…





Strepsiptera: Twisted-wing parasites

Small endoparasites of insects. Defined by loss/ reductions. Female **larviform**, wingless, retained in host. Larvae undergo hypermetamorphosis.



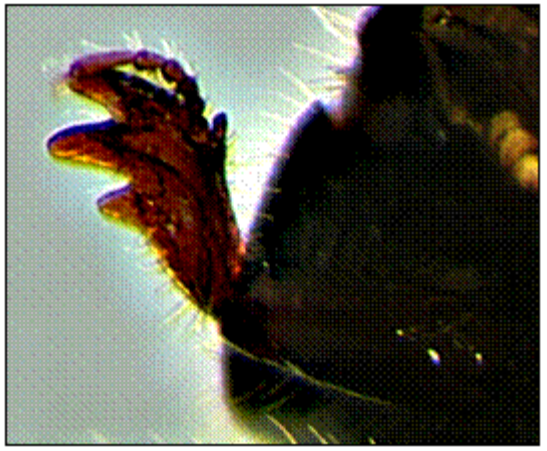
First instar (triungulin)

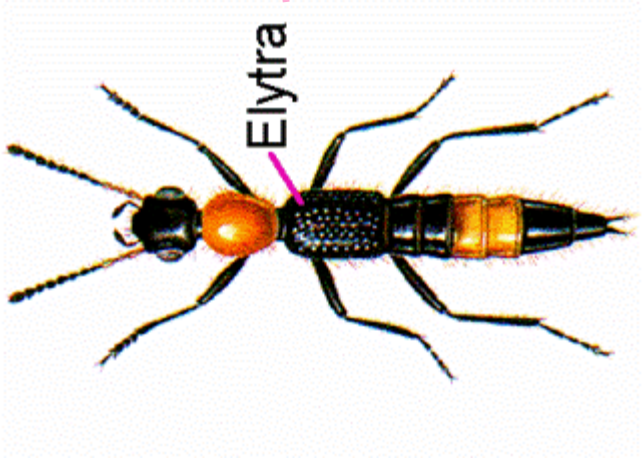
female

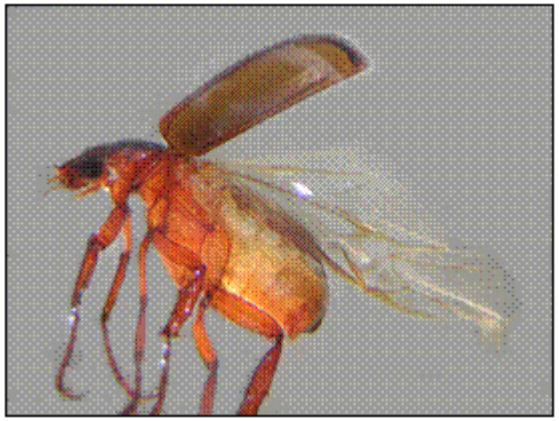
http://www.strepsiptera.uni-rostock.de/

Coleoptera: Beetles

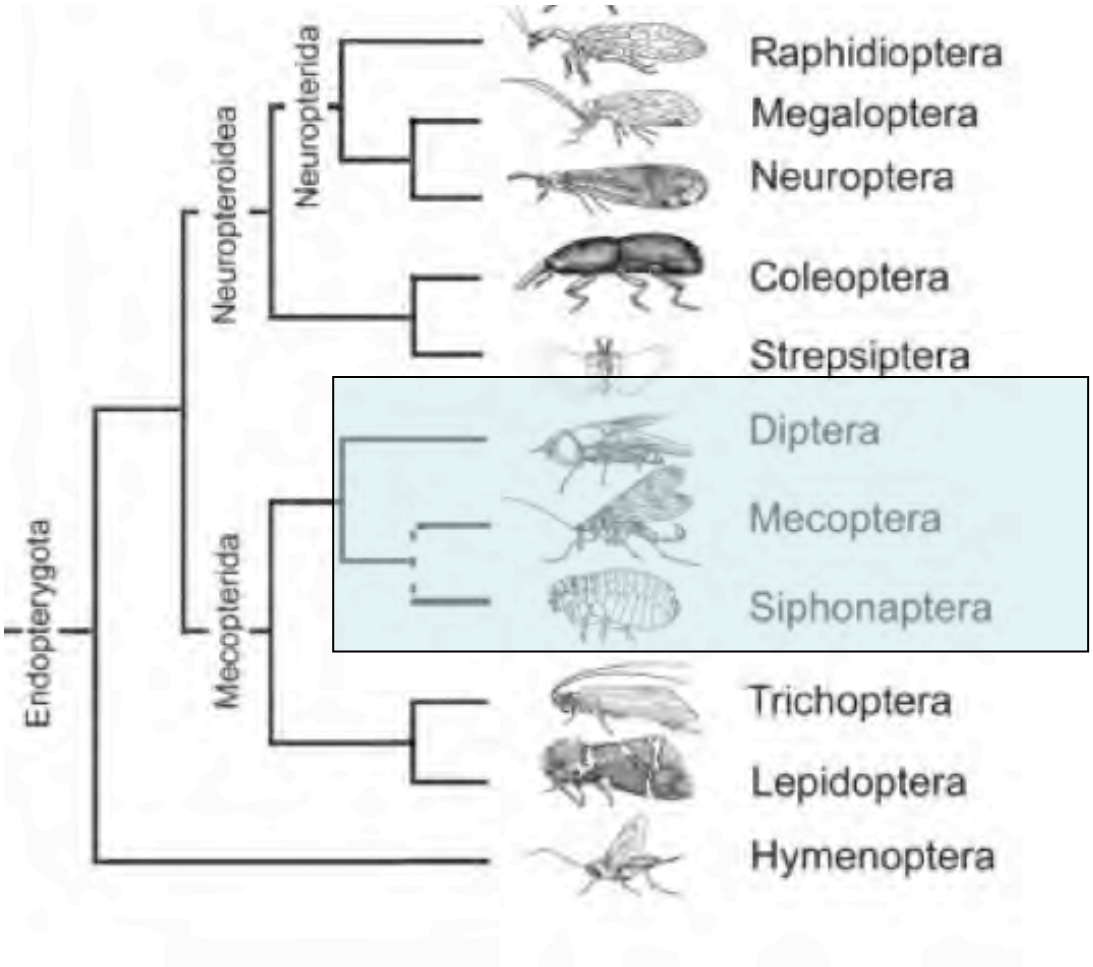
Incredibly diverse yet with very consistent morphology. What is the defining feature?





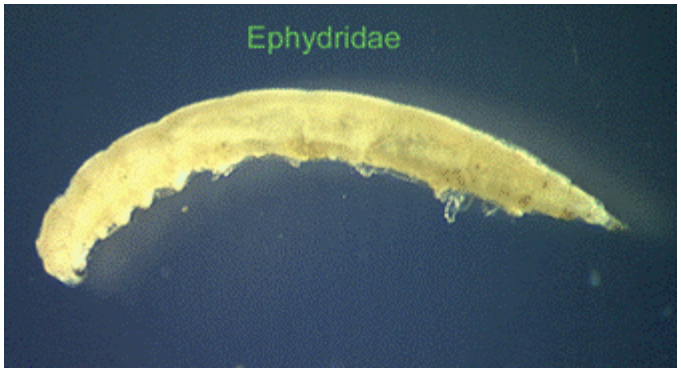


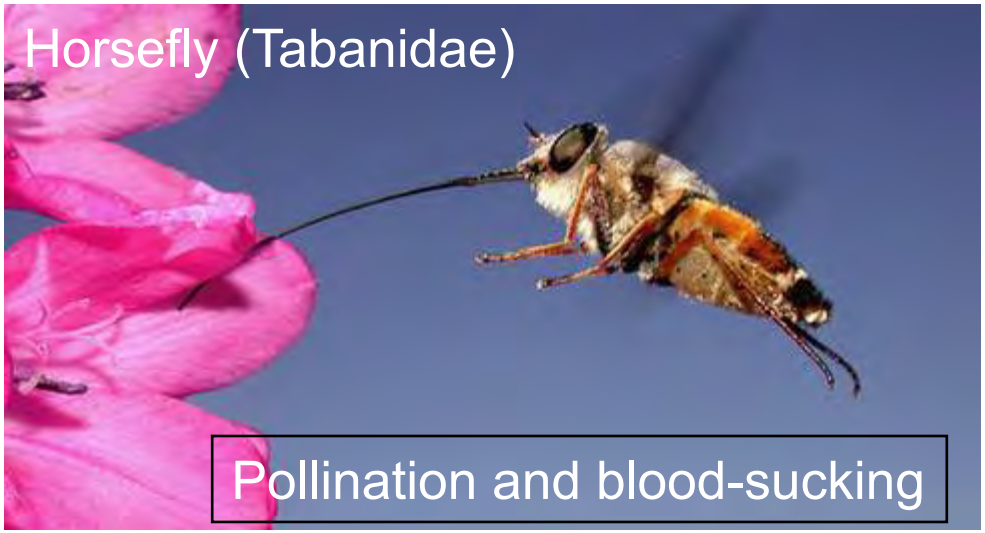
Antliophora: Diptera + Mecoptera + Siphonoptera

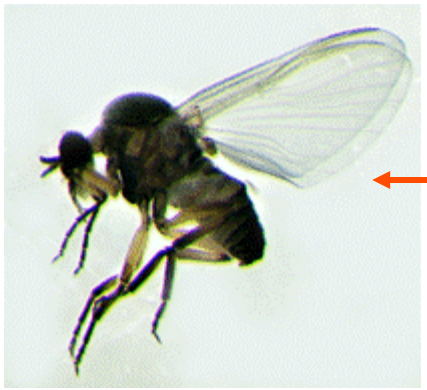


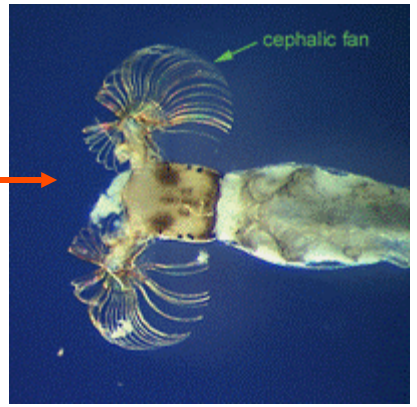
Diptera: True flies

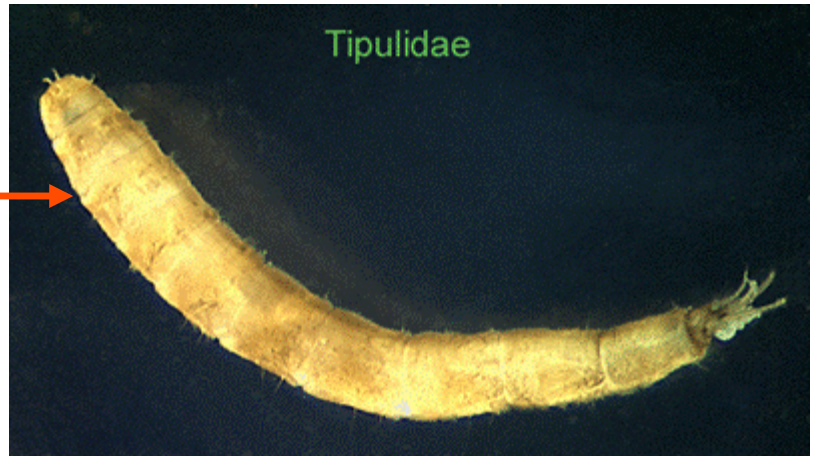
Also very diverse, highly variable morphology, ecology, and life styles. What is the defining and constant feature?











Mecoptera: Scorpionflies, hangingflies

Hypognathous, elongate rostrum formed from slender, serrate mandibles and maxillae and elongate labium. Legs raptorial. Mostly terrestrial.

Nuptial gift

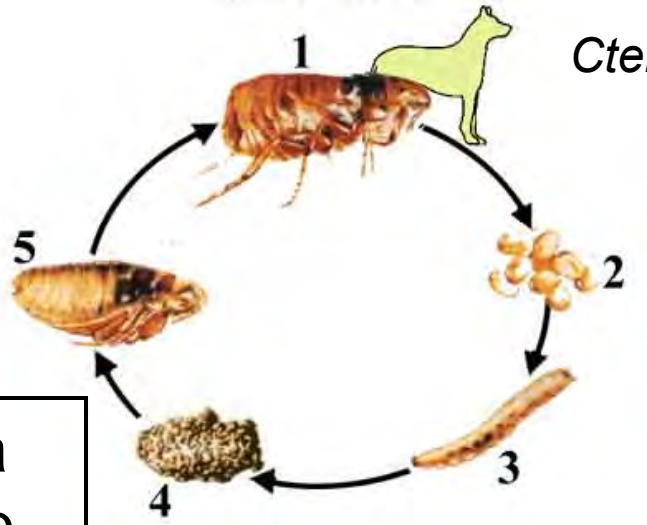
Boreus – the snow ‘flea’

Siphonaptera: Fleas

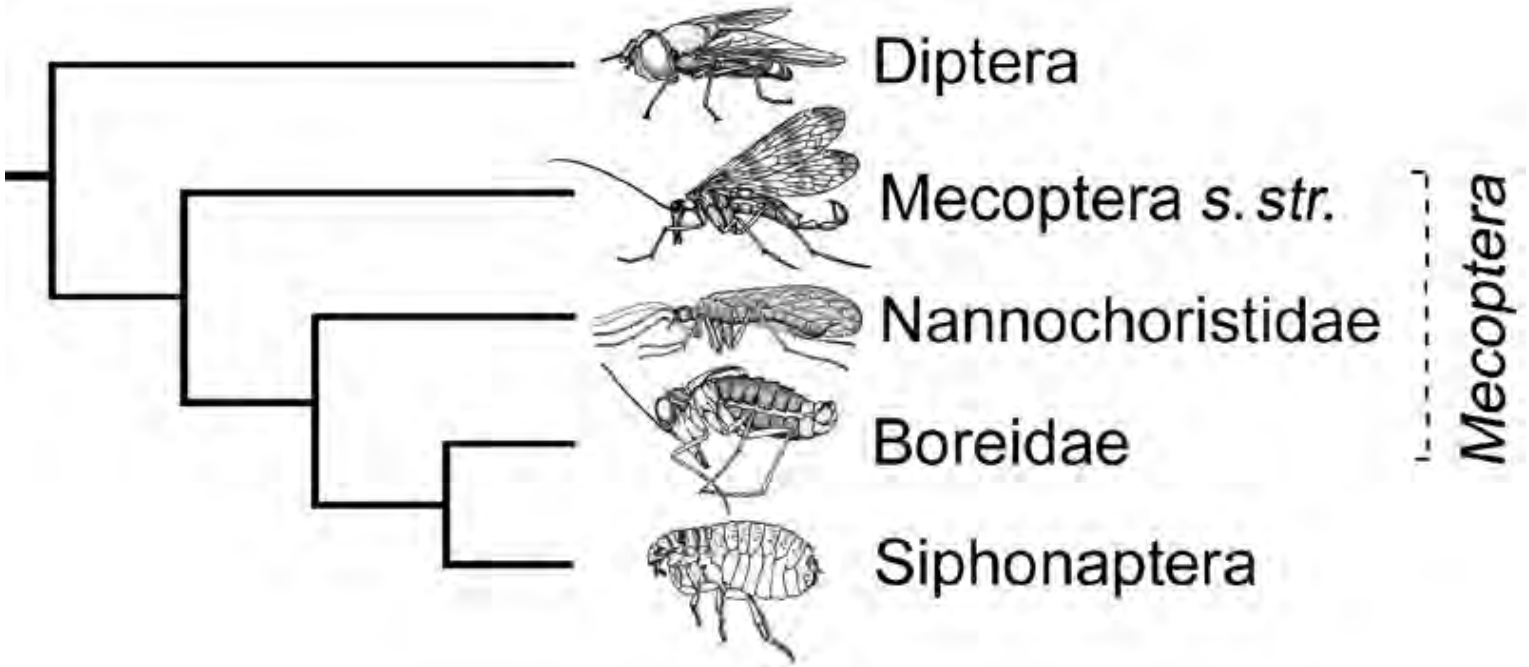
Highly modified **ectoparasites**, piercing/sucking mouthparts (no mandibles), adapted for grasping hosts

Ctenocephalides canis

Cat flea larvae



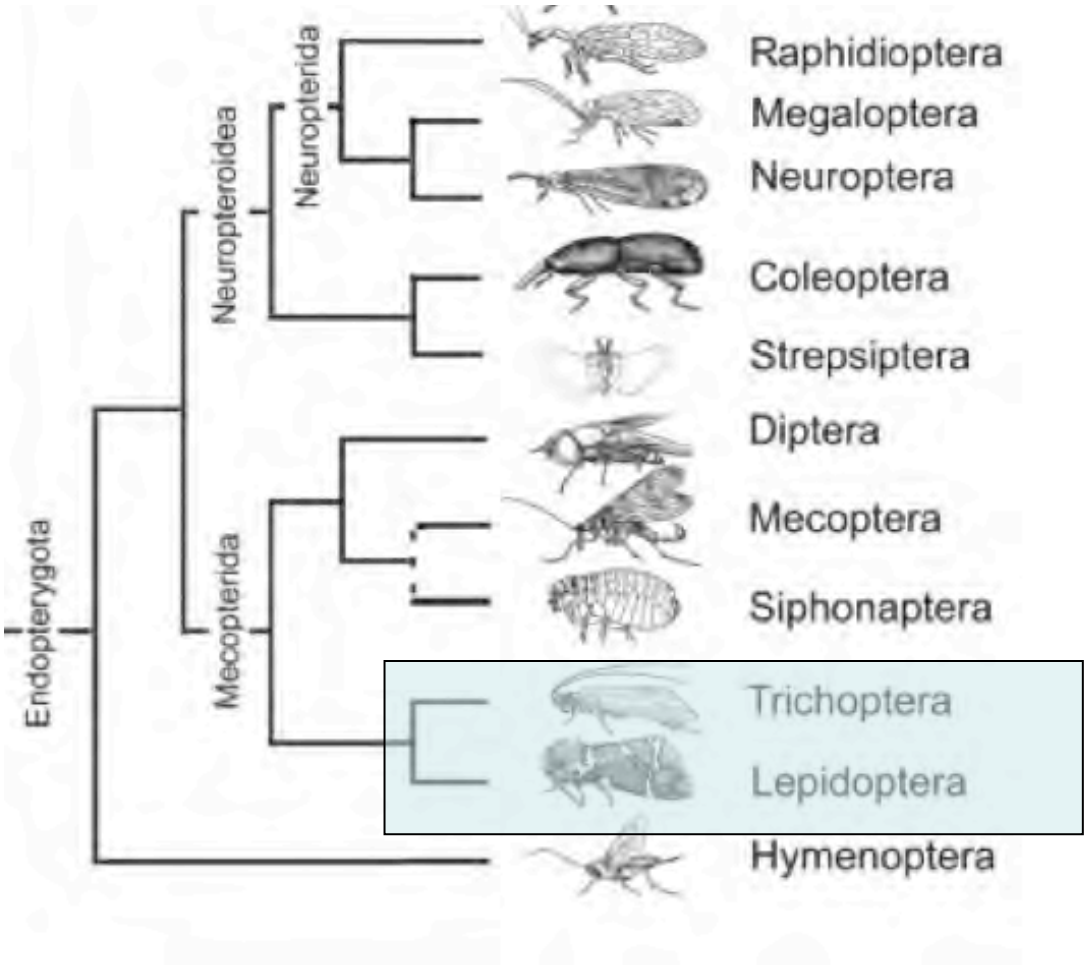
Dog flea life cycle



Boreidae – snow flea

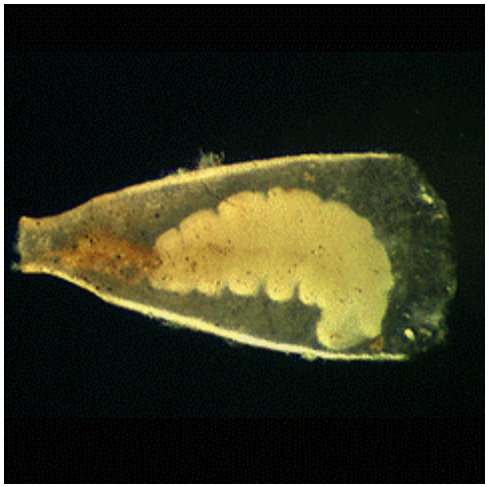
Nannochoristidae (larva)

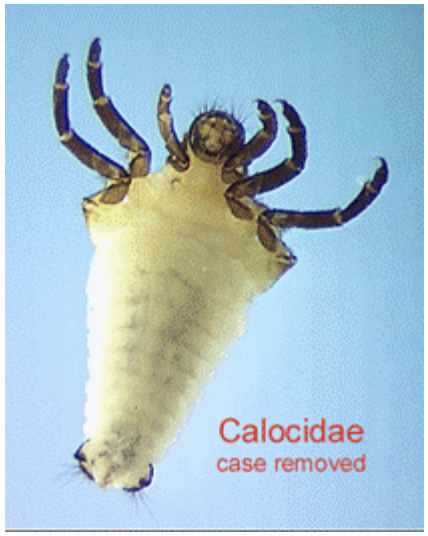
Amphiesmenoptera: Lepidoptera + Trichoptera

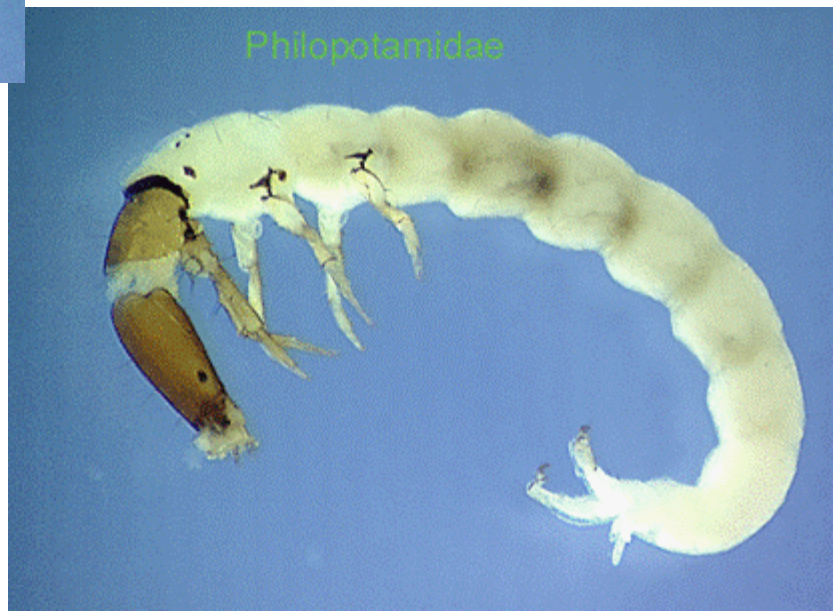


Trichoptera: Caddisflies

Hairy wings (note—sister to Lepidoptera); aquatic immatures, many of which are case-bearing.





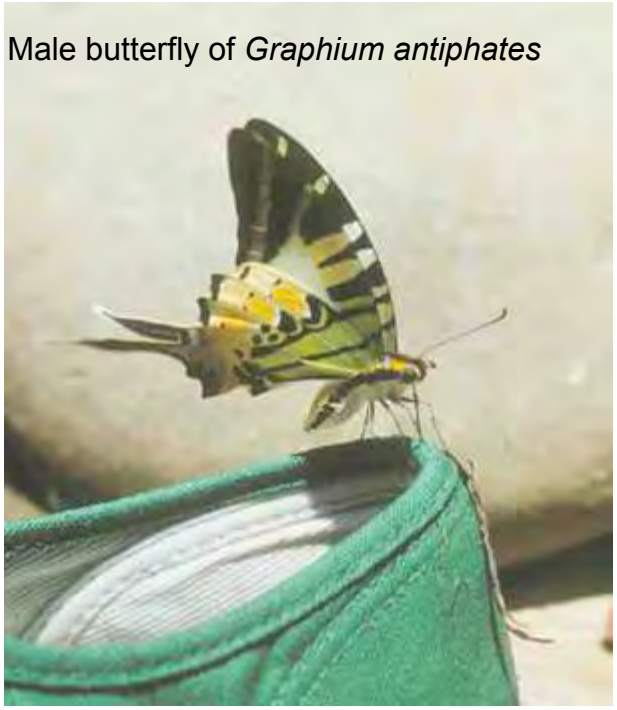


Adult Trichoptera:
Moth-like BUT:
Wings roof-like
Mouthparts reduced, palps setae, not scales

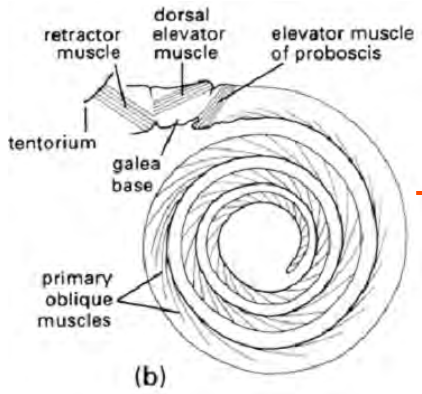
Caddisfly Cases

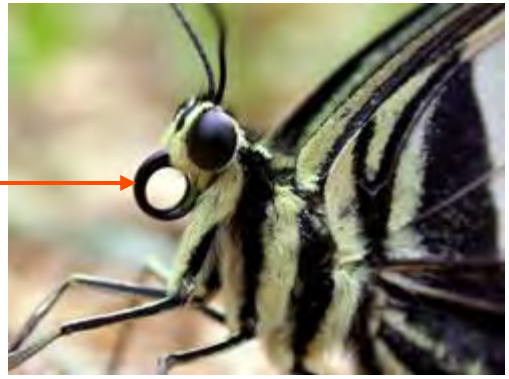
Lepidoptera: Moths & Butterflies

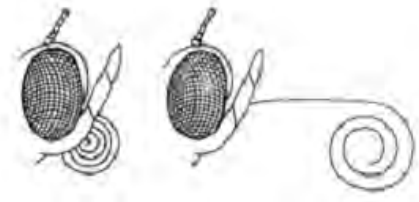
Long, coiled proboscis, wings with double layer of scales. Immatures usually terrestrial with sclerotized heads; polypodous; labial spinnerets produce silk.

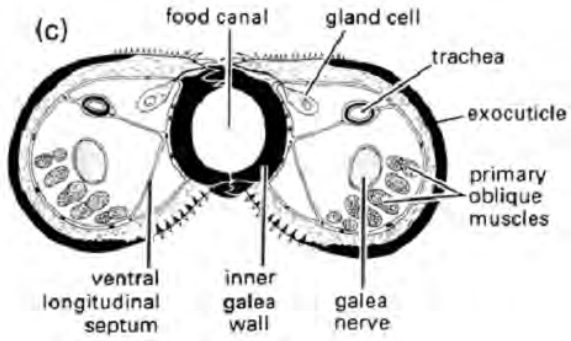


Male butterfly of *Graphium antiphates*





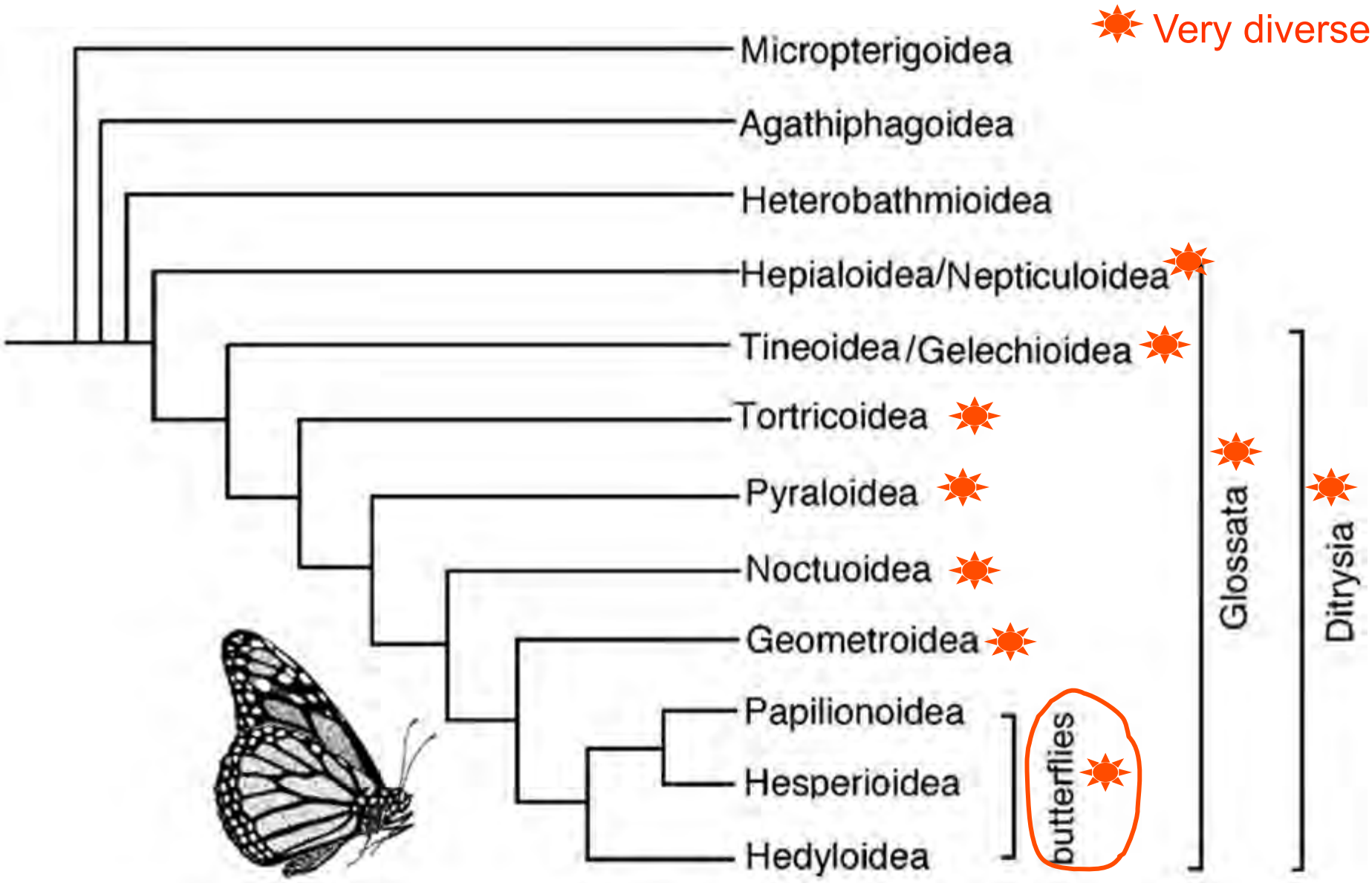




obtaining salts …

The Monarch butterfly

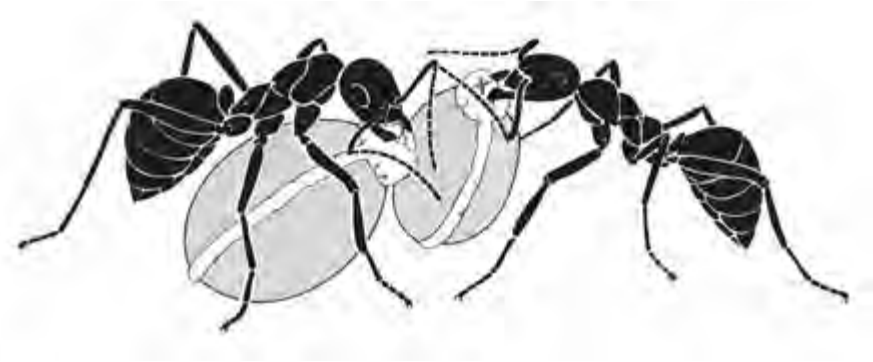
The butterflies – with respect to the rest of the Lepidoptera



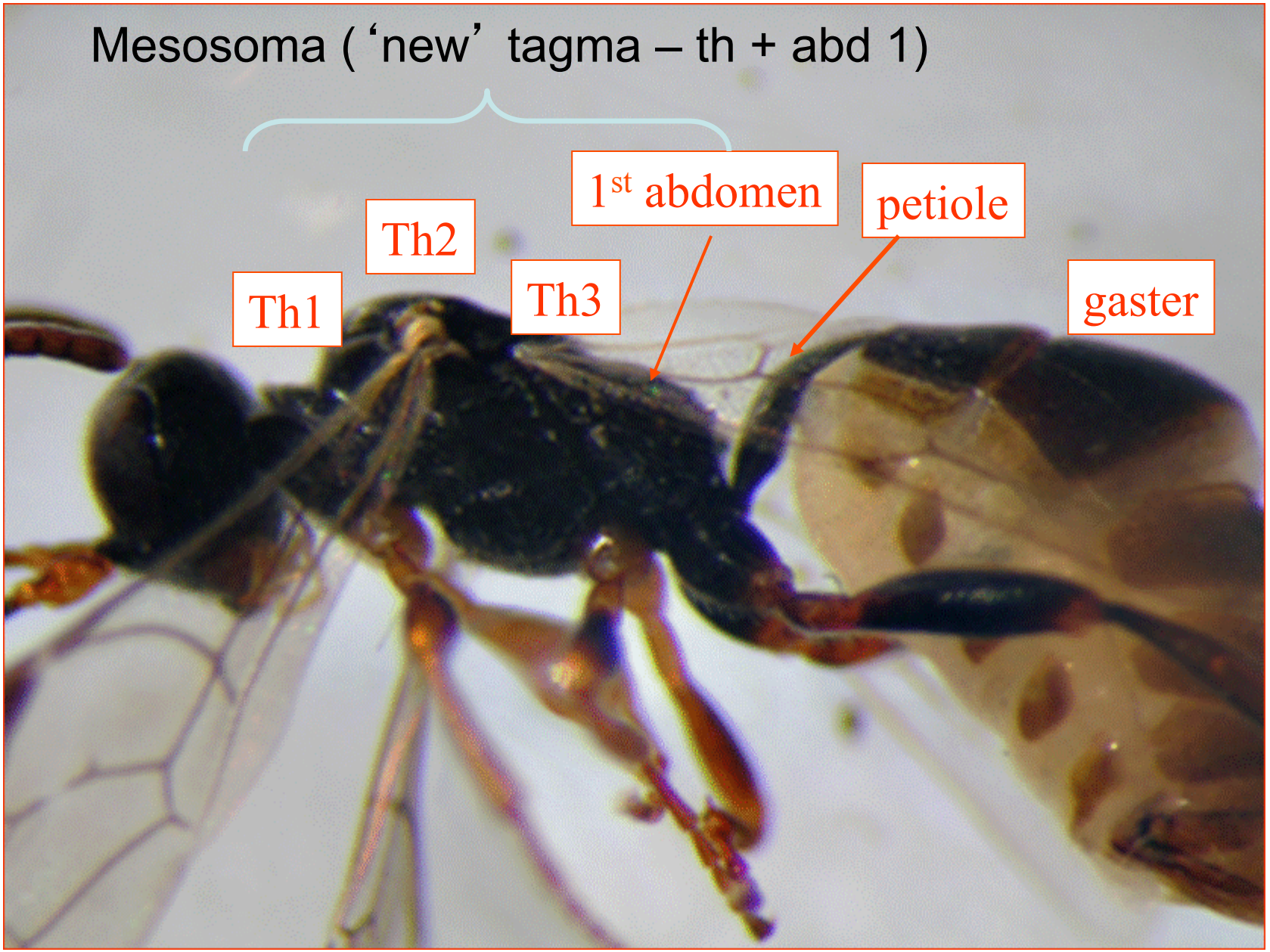
Hymenoptera: Sawflies, wasps, ants, bees

Propodeum creates mesosoma: incorporation of first abdominal segment into thorax. Abdomen often petiolate (waisted); wings with distinct coupling mechanism —hamuli. Larval stages variable: from polypodous sawflies to apodous parasitoids and nesting species. Vast majority of **eusociality** evolved here.

Pollination of an orchid by a male wasp



Myrmecochory: dispersal of seeds by ants that use seed appendages called elaiosomes


Mesosoma (‘new’ tagma – th + abd 1)
Th1
Th2
Th3
1st abdomen
petiole
gaster

Ants have slightly different terminology …..