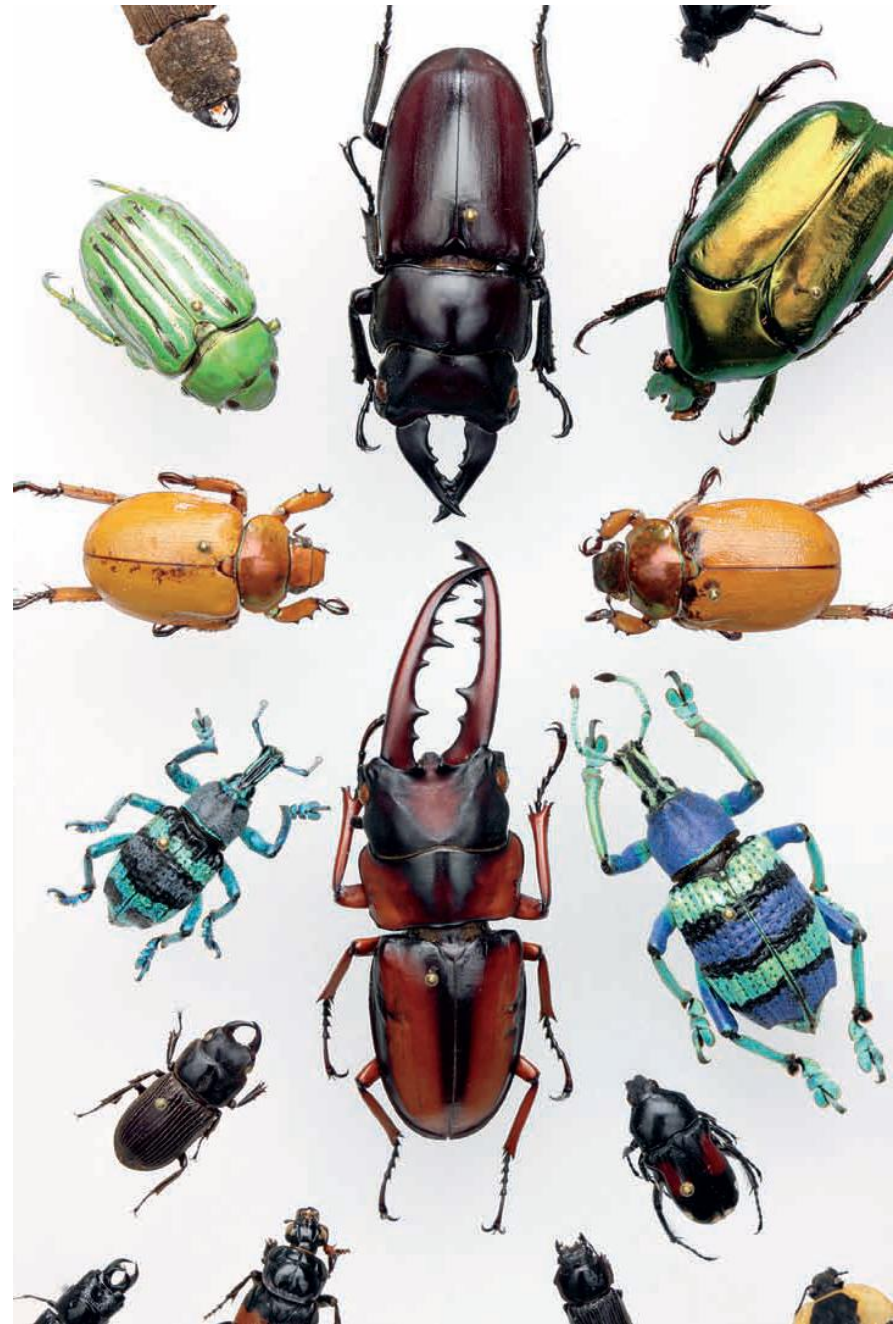


Systematics, Phylogenies, and Comparative Biology

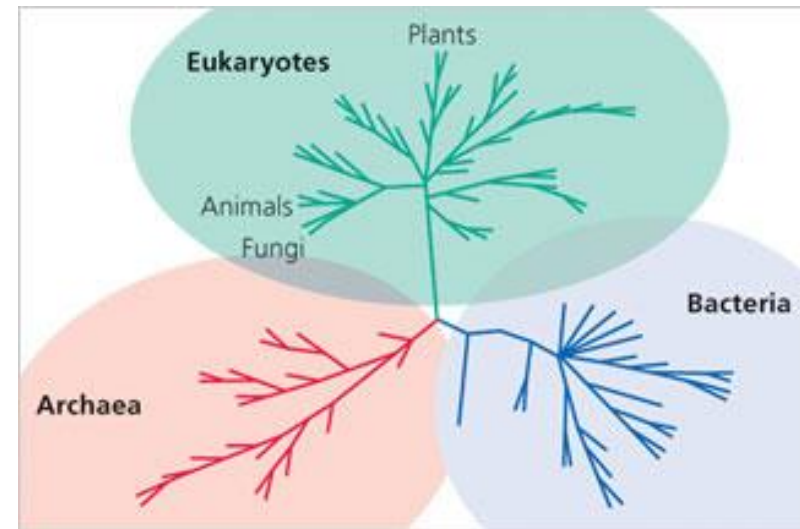
Chapter 23



Systematics

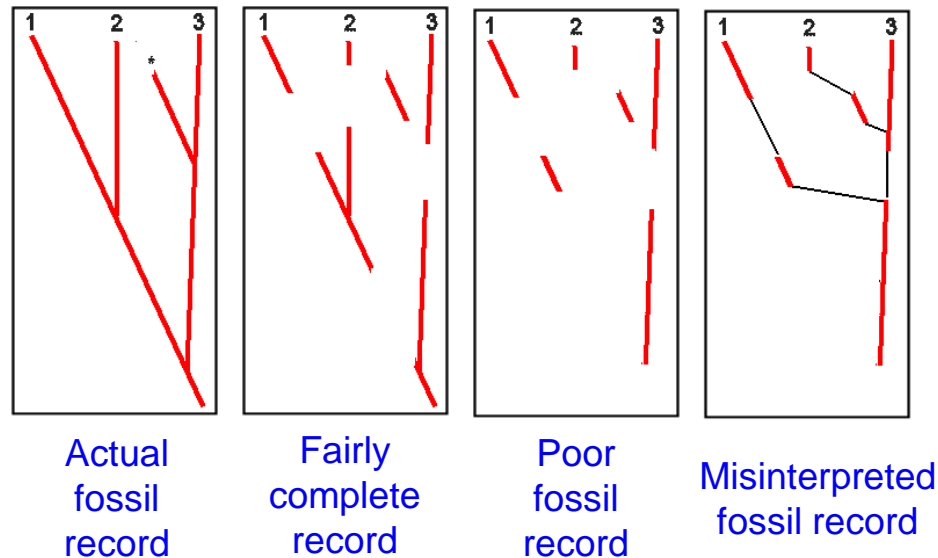
- All organisms share many characteristics:

- Composed of one or more cells
- Carry out metabolism
- Transfer energy with ATP
- Encode hereditary information in DNA



- Tremendous diversity of life
 - Bacteria, whales, sequoia trees

- Biologists group organisms based on shared characteristics and newer molecular sequence data
 - Since fossil records are not complete,...
 - Scientists rely on other types of evidence to establish the best hypothesis of evolutionary relationships

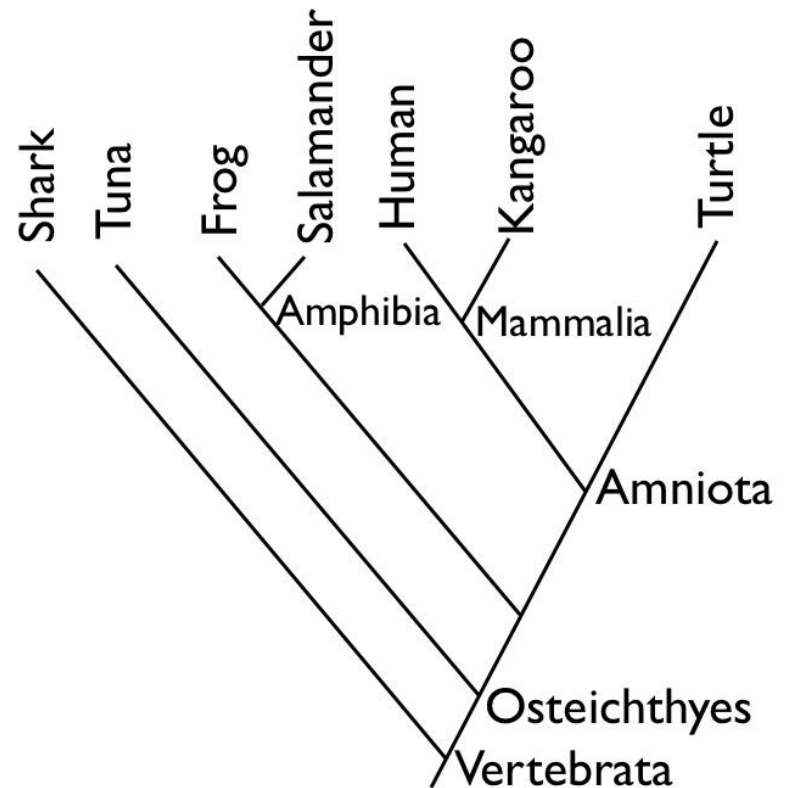


- **Systematics**

- Reconstruction and study of evolutionary relationships

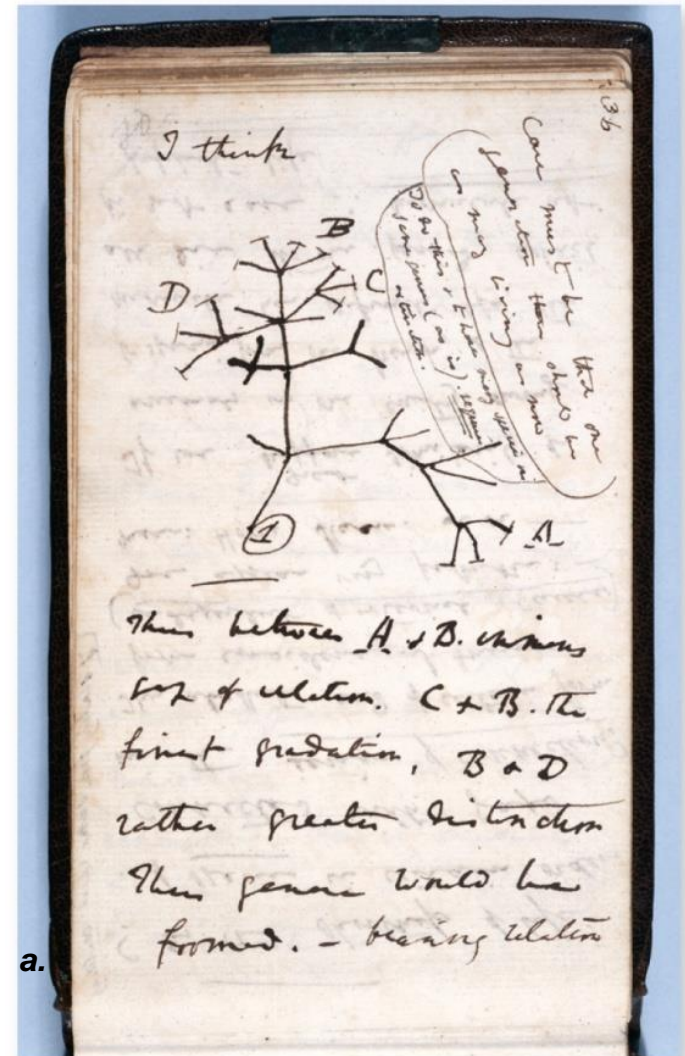
- **Phylogeny**

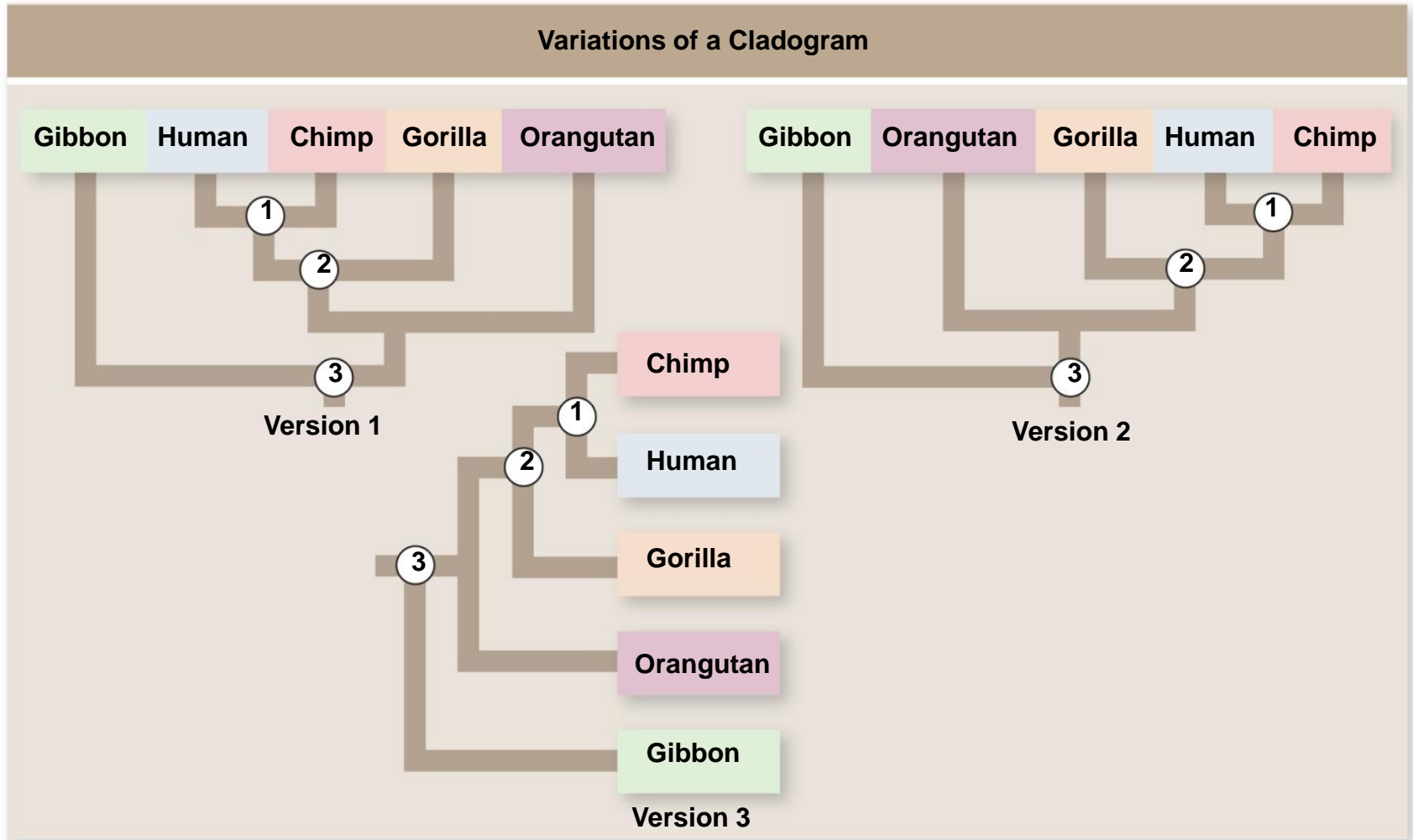
- Hypothesis about patterns of relationship among species
 - **Cladogram** or phylogenetic tree



Darwin envisioned that all species were descended from a single common ancestor

- He depicted this history of life as a branching tree
- “Descent with modification”

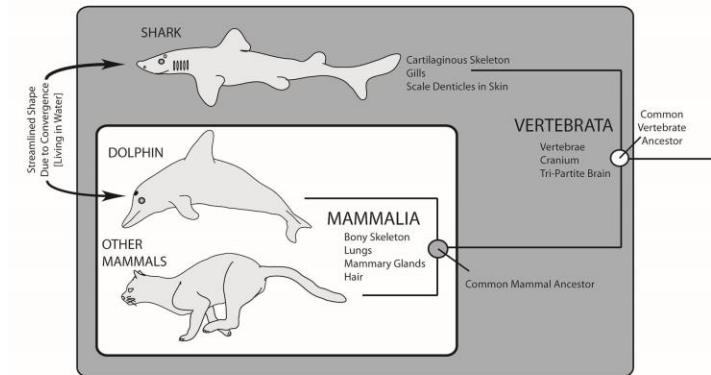




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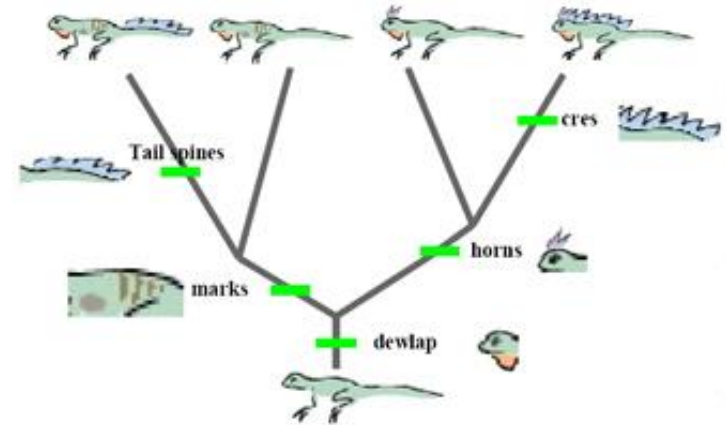
- Key to interpreting a phylogeny – *look at how recently species share a common ancestor*

- Similarity may not accurately predict evolutionary relationships
 - Early systematists relied on the expectation that the greater the time since two species diverged from a common ancestor, the more different they would be
 - Rates of evolution vary
 - Evolution may not be unidirectional
 - Evolution is not always divergent
 - **Convergent evolution** – similar characters not derived from common ancestry

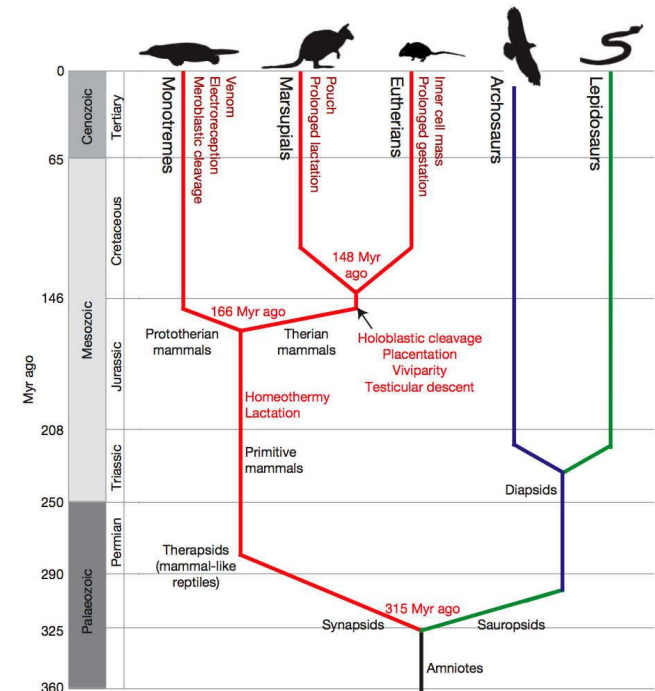


Cladistics

- **Derived characteristic**
 - Similarity that is inherited from the most recent common ancestor of an entire group
- **Ancestral characteristic**
 - Similarity that arose prior to the common ancestor of the group
- In cladistics, only ***shared derived characters*** (***synapomorphies***) are considered informative about evolutionary relationships



- Examples of ancestral versus derived characters, often dependent on context
 - Presence of hair is a shared derived feature of mammals
 - Presence of lungs in mammals is an ancestral feature; also present in amphibians and reptiles
 - Shared, derived feature of hair suggests that all mammal species share a common ancestor that existed more recently than the common ancestor of mammals, amphibians, and reptiles



Manual cladistic analysis

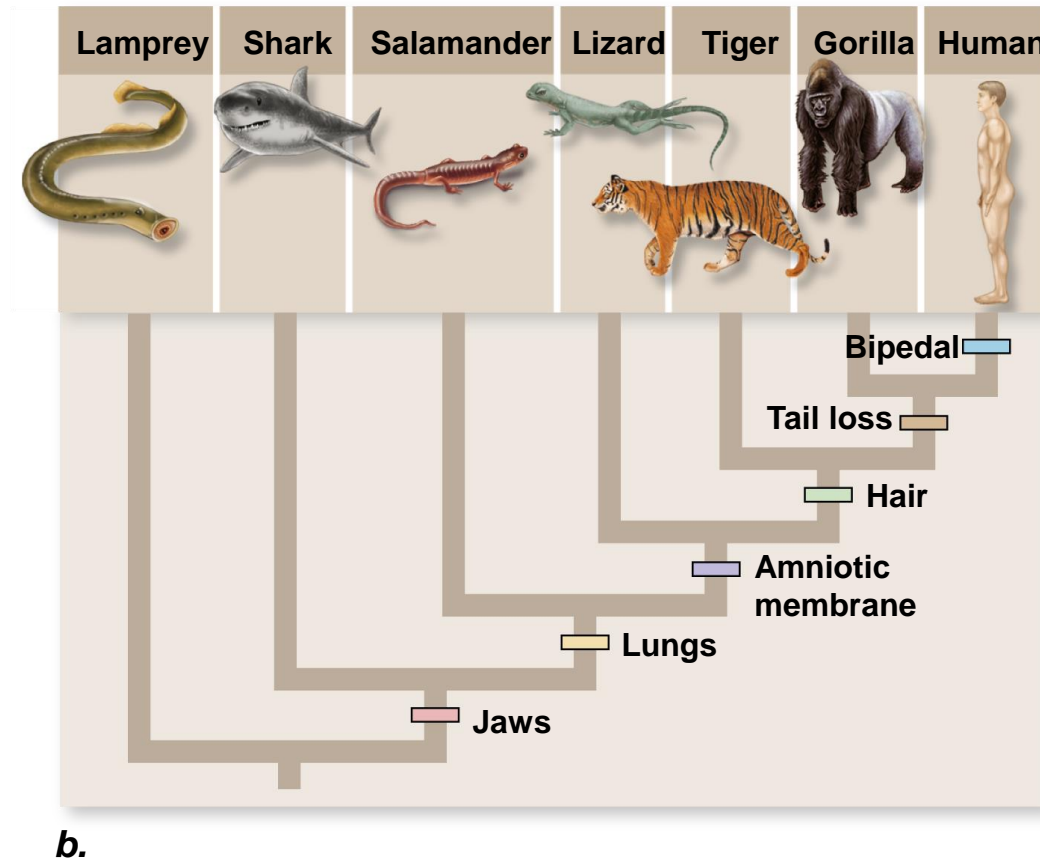
- First step is to polarize the characters (are they ancestral or derived)
 - Example: polarize “hair” means to determine presence or absence in the most recent common ancestor
 - **Outgroup comparison** used
 - Species or group of species that is closely related to, but not a member of, the group under study is designated as the **outgroup**
 - **Outgroup** species do not always exhibit the ancestral condition

Traits: Organism	Jaws	Lungs	Amniotic Membrane	Hair	No Tail	Bipedal
Lamprey	0	0	0	0	0	0
Shark	1	0	0	0	0	0
Salamander	1	1	0	0	0	0
Lizard	1	1	1	0	0	0
Tiger	1	1	1	1	0	0
Gorilla	1	1	1	1	1	0
Human	1	1	1	1	1	1

a.

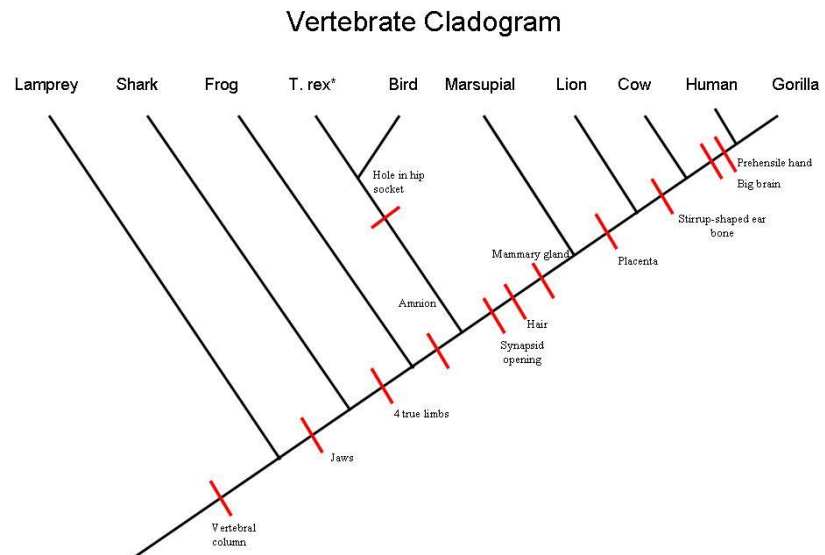
“1” = possession of derived character state

“0” = possession of ancestral character state



- Derived characters between the cladogram branch points are shared by all organisms above the branch points and are not present in any below them
- The **outgroup** (in this case, the lamprey) does not possess any of the derived characters
 - Outgroup may or may not exhibit ancestral form

- When the group under study exhibits multiple character states, and one of those states is exhibited by the outgroup, then that state is ancestral and other states are derived
 - Most reliable if character state is exhibited by several different outgroups
 - Presence of teeth in mammals and reptiles is ancestral
 - Absence of teeth in birds and turtles is derived

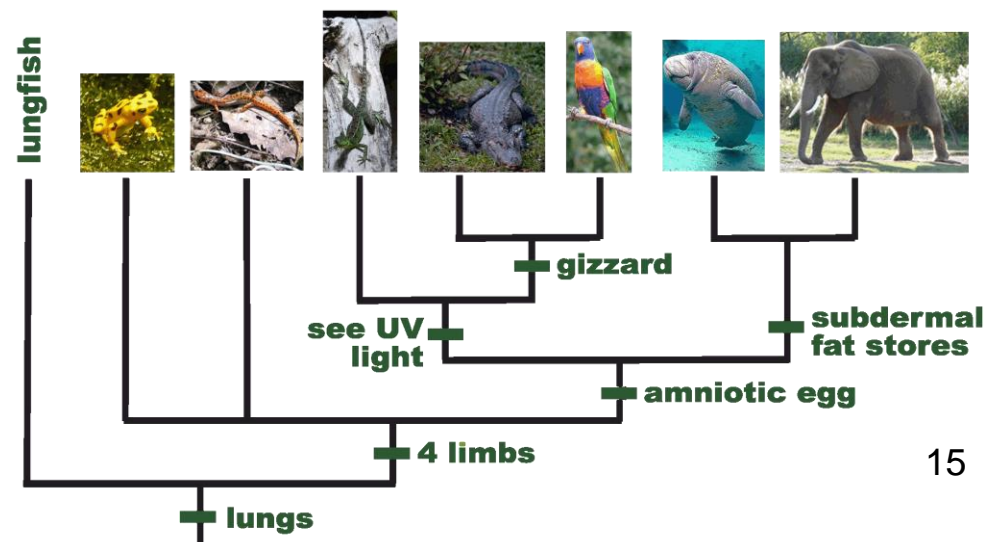


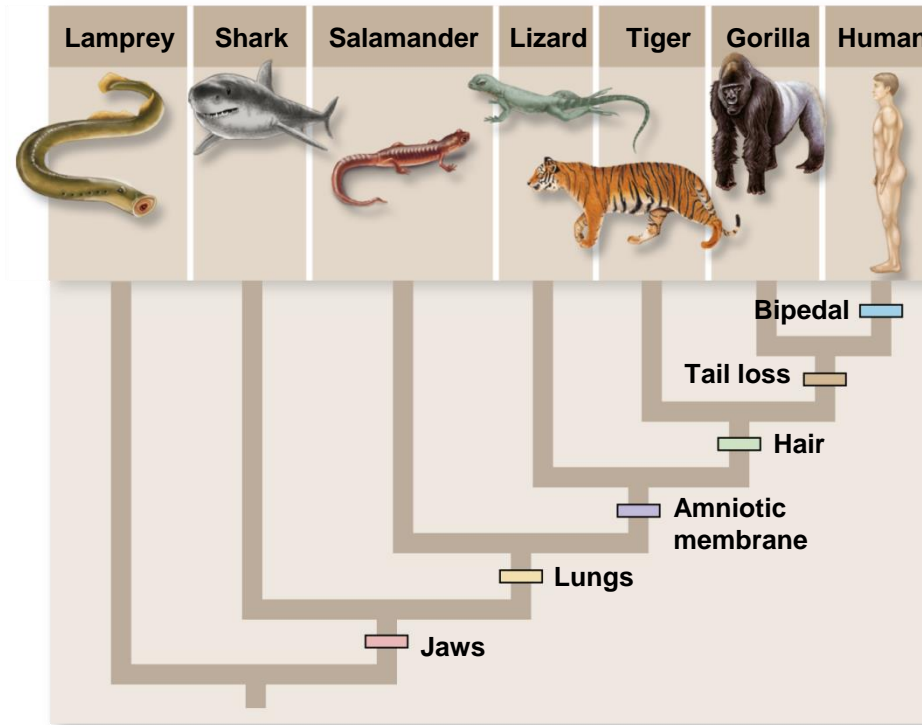
- **Cladogram**

- Depicts a hypothesis of evolutionary relationships

- **Clade**

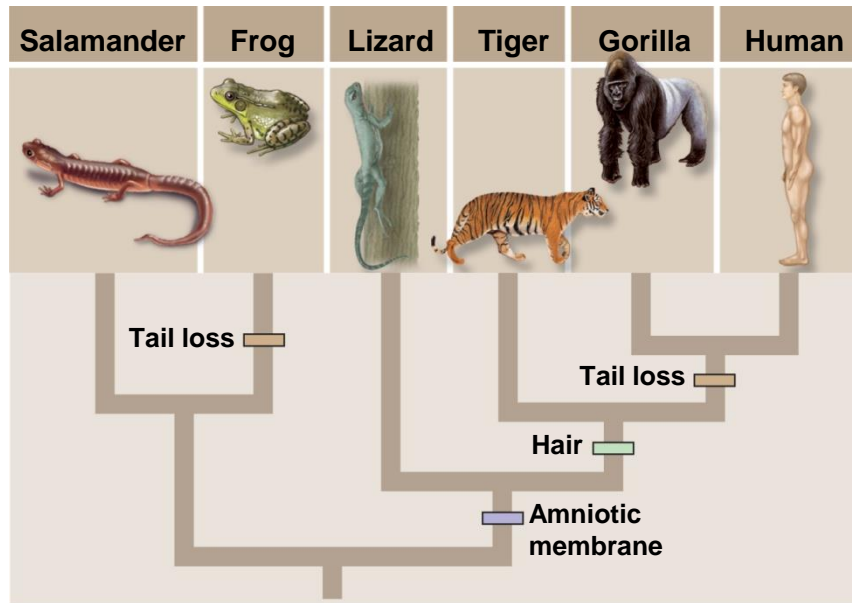
- Species that share a common ancestor as indicated by the possession of shared derived characters
 - Evolutionary units refer to a common ancestor and all descendants
 - **Synapomorphy** – derived character shared by clade members





b.

- Simple cladogram is a nested set of clades, each characterized by its own synapomorphies
 - Amniotes are a clade for which the evolution of an amniotic membrane is a synapomorphy
 - Within that clade, mammals are a clade, with hair as a synapomorphy

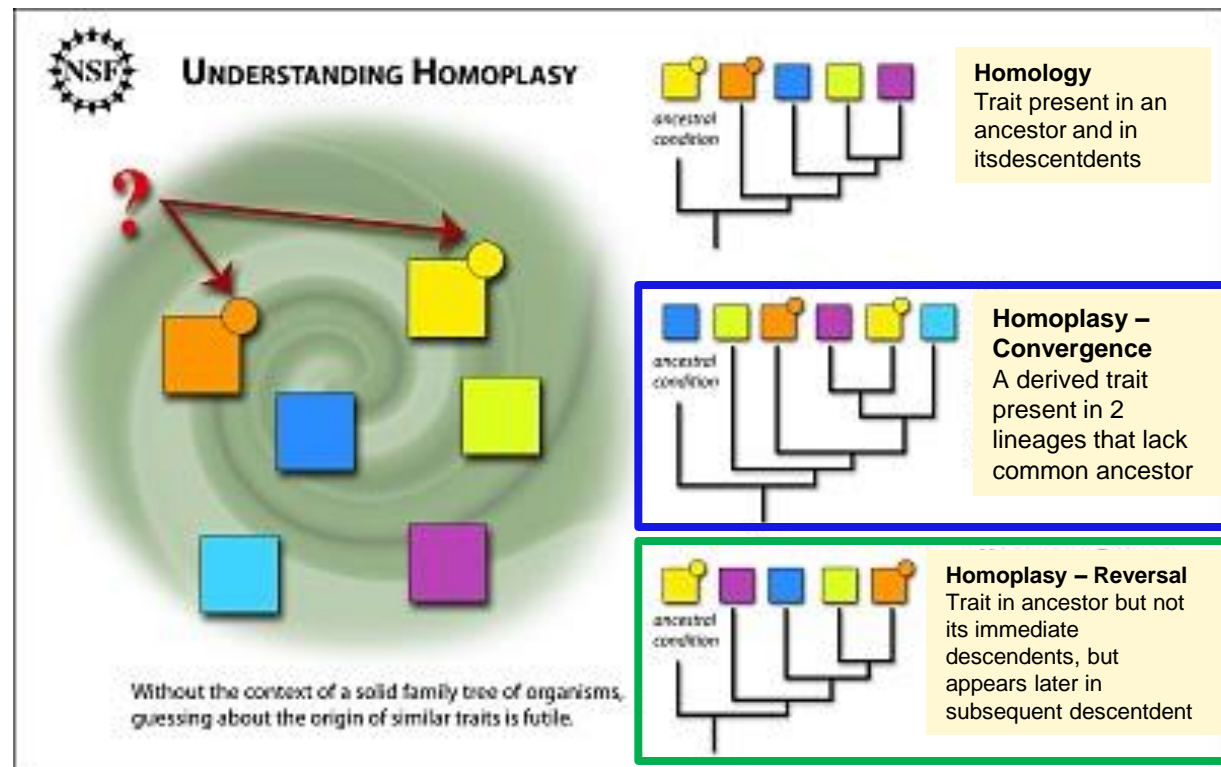


a.

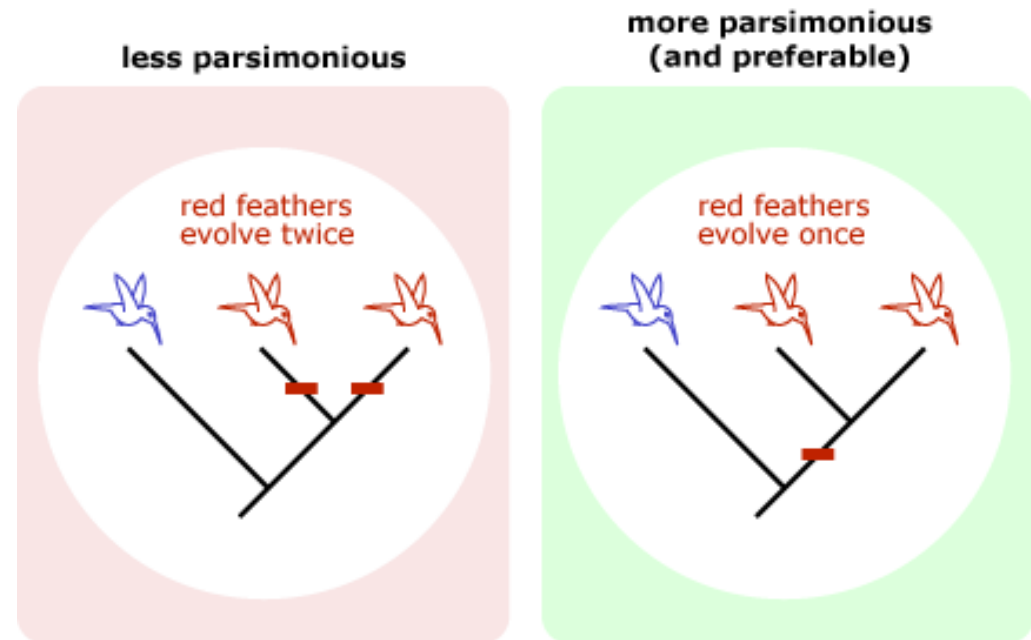
Can't just use one character...may be misleading. Must use many characters

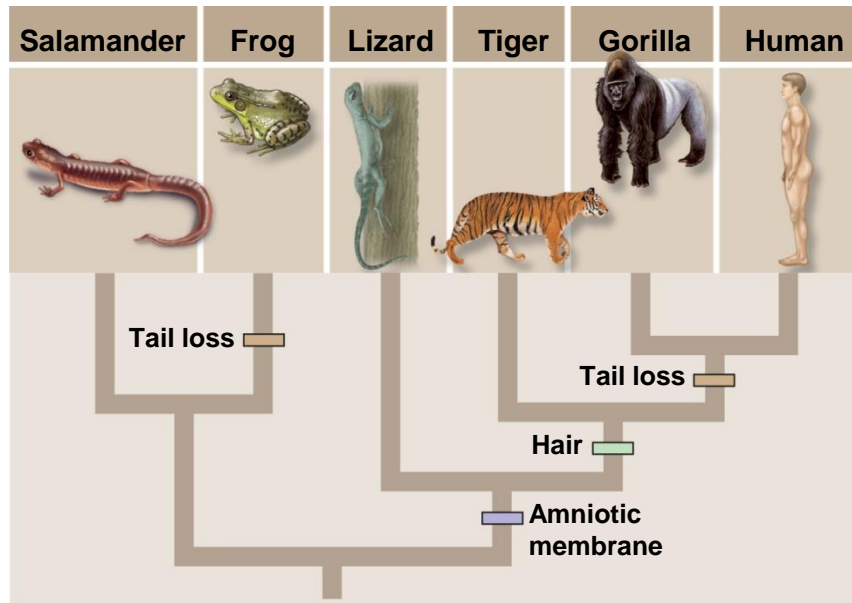
- **Plesiomorphies** – ancestral states
- **Symplesiomorphies** – shared ancestral states
- Character state “presence of a tail”
 - Exhibited by lampreys, sharks, salamanders, lizards, and tigers
 - Are tigers more closely related to lizards and sharks than apes and humans?
 - Symplesiomorphies reflect character states inherited from a distant ancestor, they do not imply that species exhibiting that state are closely related

- **Homoplasy** – a shared character state that has not been inherited from a common ancestor
 - **Convergent evolution** (*independent evolution*)
 - **Evolutionary reversal** (return to ancestral state)

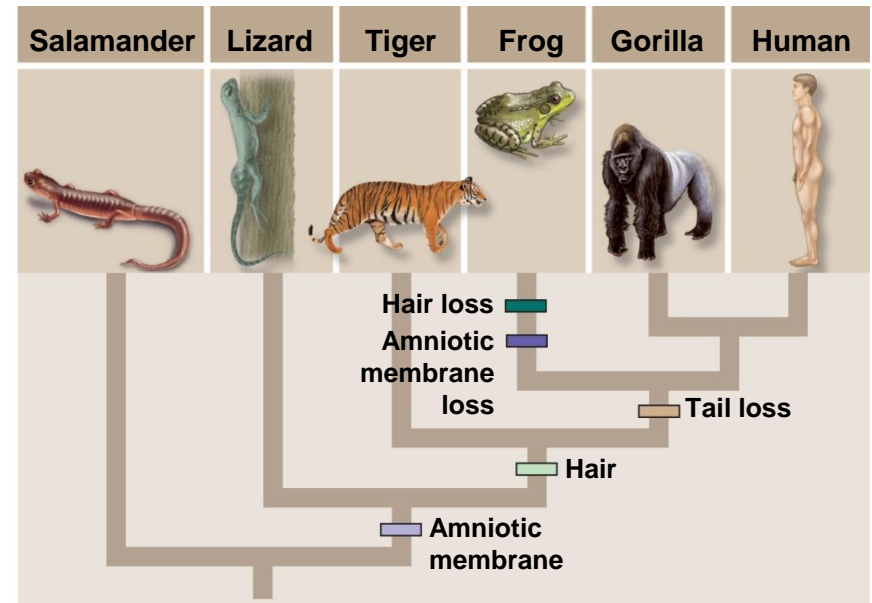


- Systematists rely on the principle of **parsimony**, which favors the hypothesis that requires the fewest assumptions





a.



b.

Based on the **principle of parsimony**, the cladogram that requires the fewest number of evolutionary changes is favored

- The cladogram in (a) requires four changes, whereas...
- (b) requires five

Systematists increasingly use DNA sequence data to construct phylogenies

- Large number of characters that can be obtained through sequencing
- Character states are polarized by reference to the sequence of an outgroup
- Cladogram is constructed that minimizes the amount of character evolution required

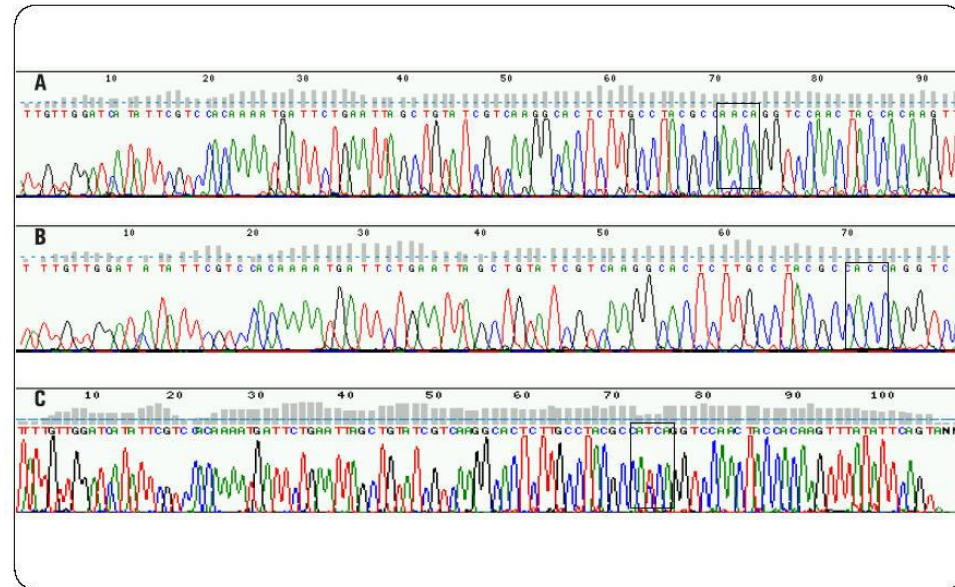





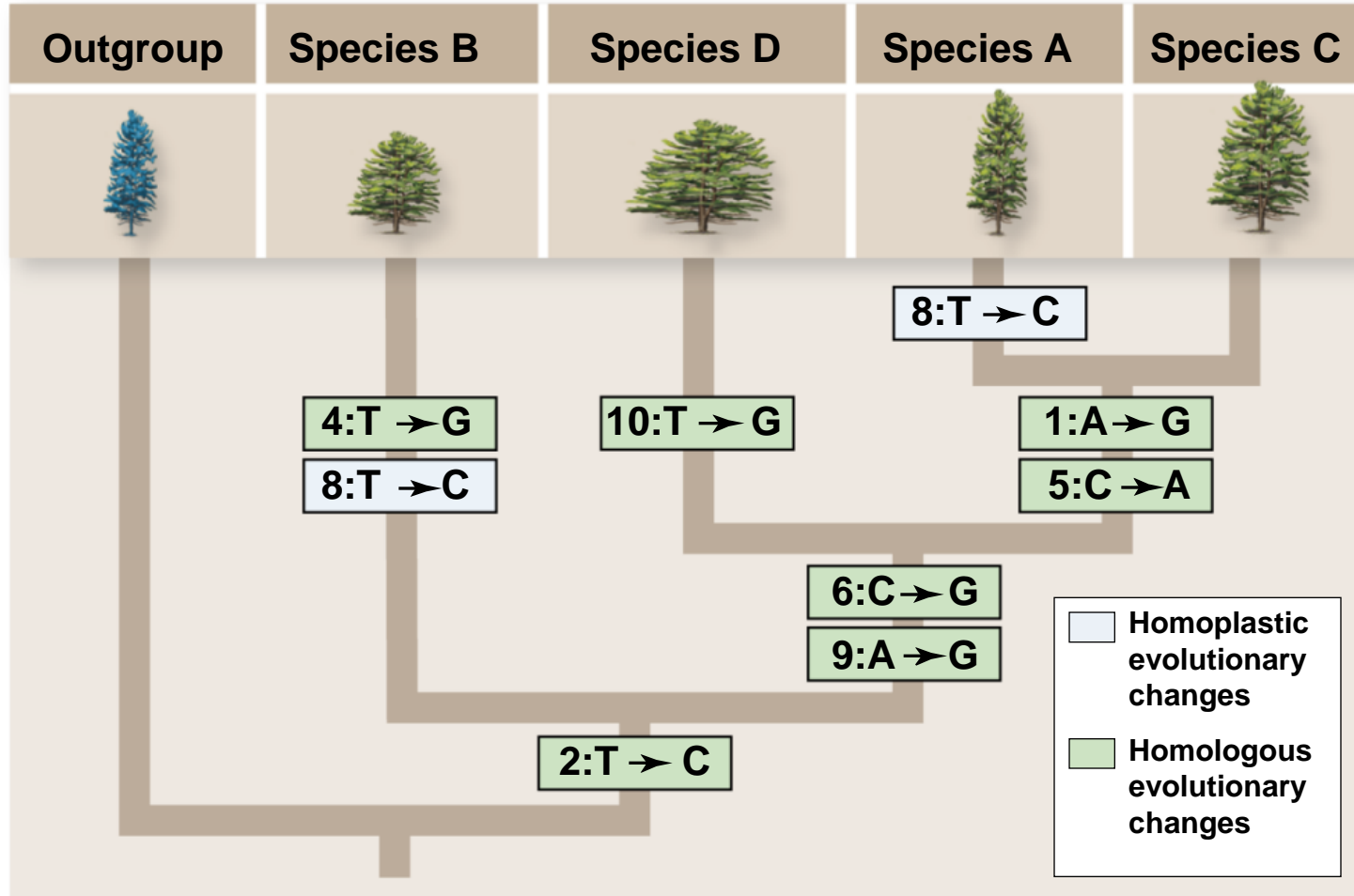


Figure 2
DNA sequence chromatograms from K-ras codon 12 PCR's.
A) AAC reverse sequence is GTT forward sequence=valine mutant at codon 12.
B) ACC reverse sequence is GGT forward sequence=glycine normal at codon 12.
C) ATC/ACC reverse sequence is GAT/GGT forward sequence= aspartic acid mutant and glycine normal at codon 12.

	DNA Sequence									
Site	1	2	3	4	5	6	7	8	9	10
Species A 	G	C	A	T	A	G	G	C	G	T
Species B 	A	C	A	G	C	C	G	C	A	T
Species C 	G	C	A	T	A	G	G	T	G	T
Species D 	A	C	A	T	C	G	G	T	G	G
Outgroup 	A	T	A	T	C	C	G	T	A	T

Parsimony also attempts to minimize homoplasies

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Other Phylogenetic Methods

Potential problems with DNA sequences...

- Some characters evolve rapidly, so using parsimony principle may be misleading
- Stretches of DNA with no function have high rates of evolution of new character states due to genetic drift
- Only 4 character states are possible (A, T, G, C) so there is a high probability that two species will independently evolve the same derived character state at any particular base position... appear homologous when they are not

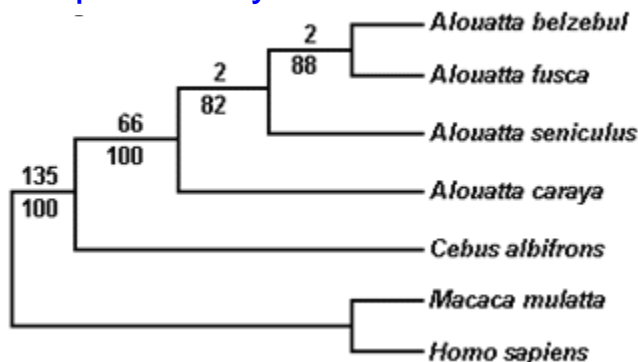
Other Phylogenetic Methods

- **Statistical (maximum likelihood) approach**

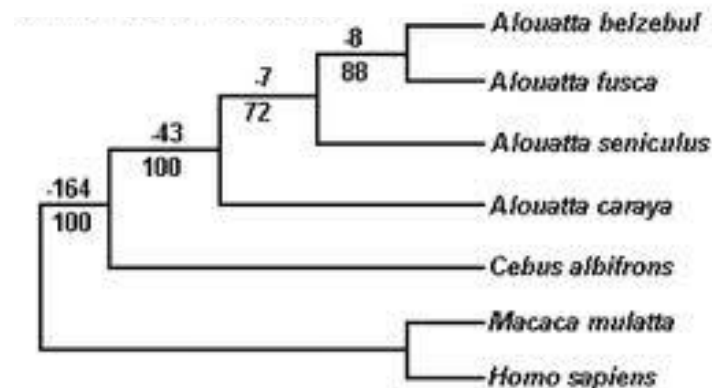
- Start with an assumption about the rate at which characters evolve (change)
- Fit the data to these models to derive the phylogeny that best follows (i.e., “maximally likely”) these assumptions
- Narrows down possible cladograms to “most likely”
- Usually compared with parsimony model

Optional

Maximum parsimony tree



Maximum likelihood tree

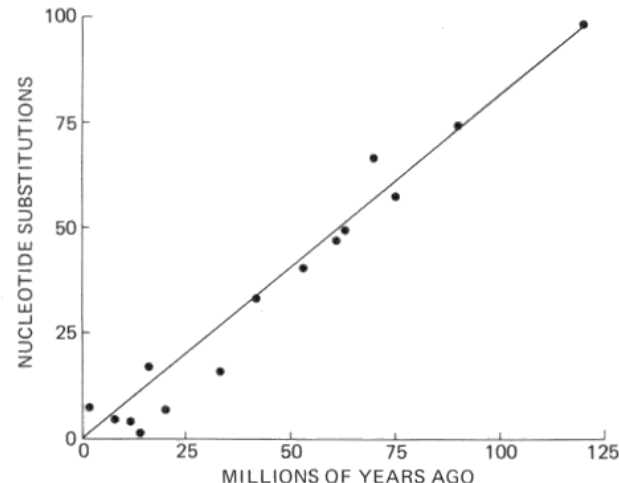


Other Phylogenetic Methods

Optional

- **Molecular clock**

- Assumes rate of evolution of a molecule is constant through time (see figure)
- Divergence in DNA can be used to calculate the times at which branching events have occurred
- Mutation rates may not be constant, depending on selection pressures on traits



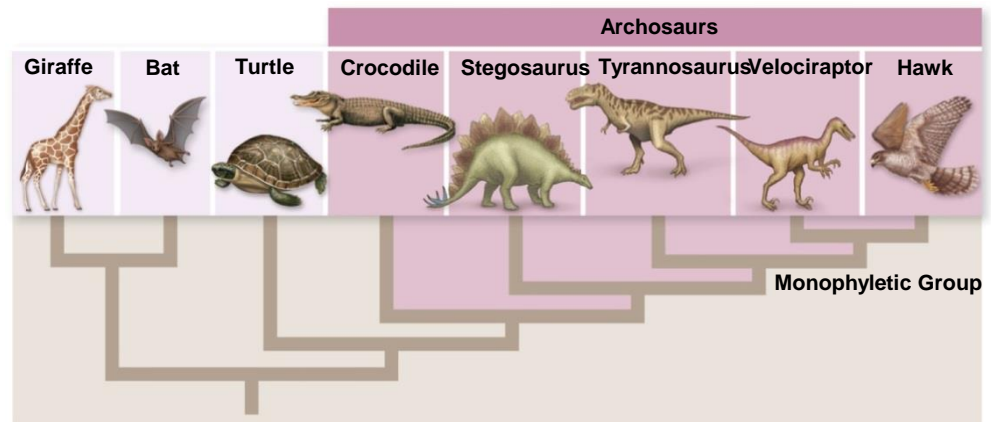
Systematics and Classification

- **Classification**

- How we place species and higher groups into the taxonomic hierarchy – should follow evolutionary history
- Genus, family, order, class, phylum, kingdom, domain

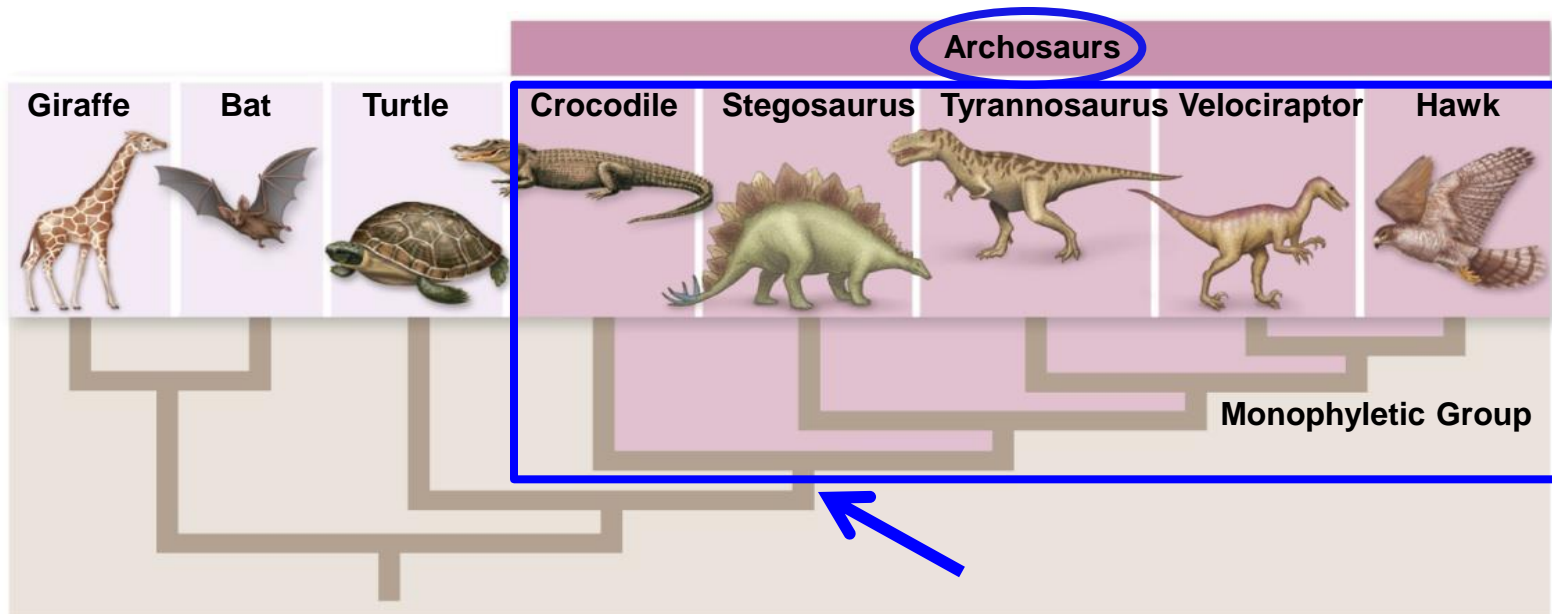
- **Monophyletic** group (the “goal”)

- Includes the *most recent common ancestor* of the group *and all of its descendants* (clade)

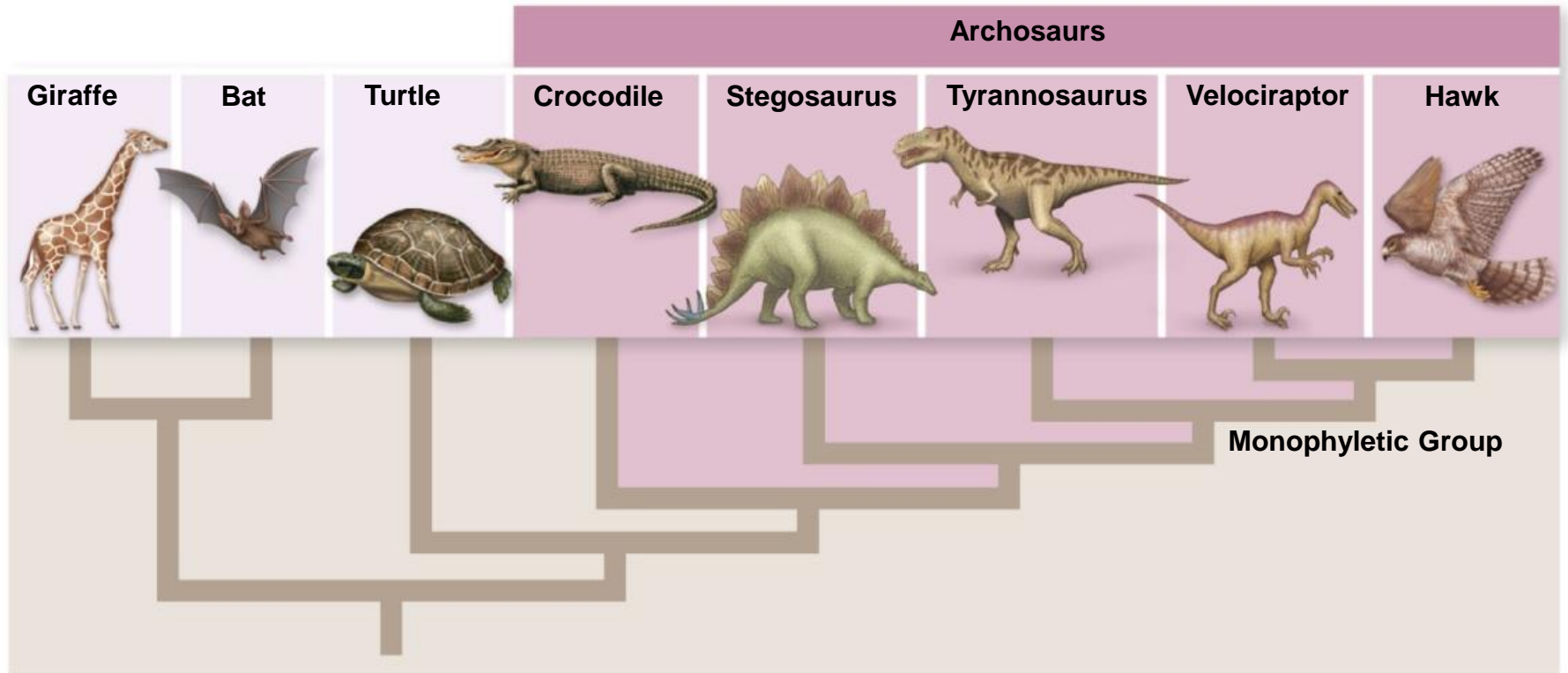


Systematics and Classification

- **Monophyletic group**
 - Includes the *most recent common ancestor* of the group *and all of its descendants* (clade)
 - “*Single cut*” of cladogram
 - The goal of “good” phylogeny



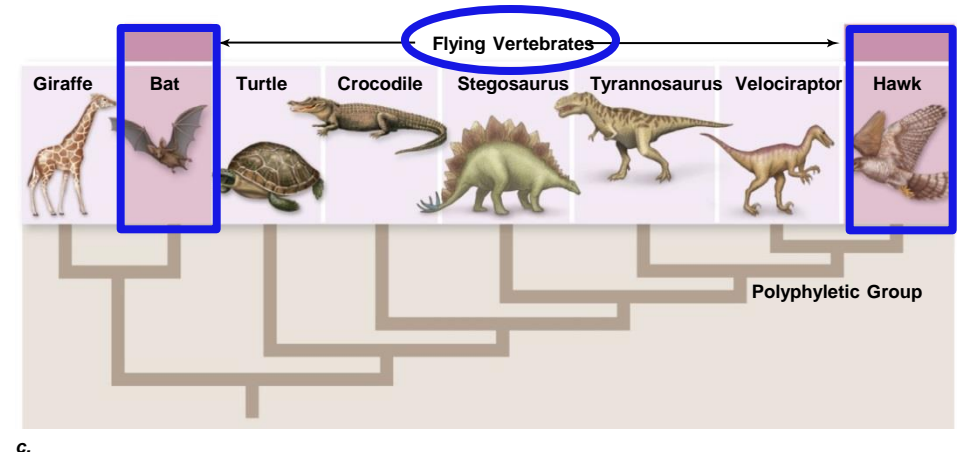
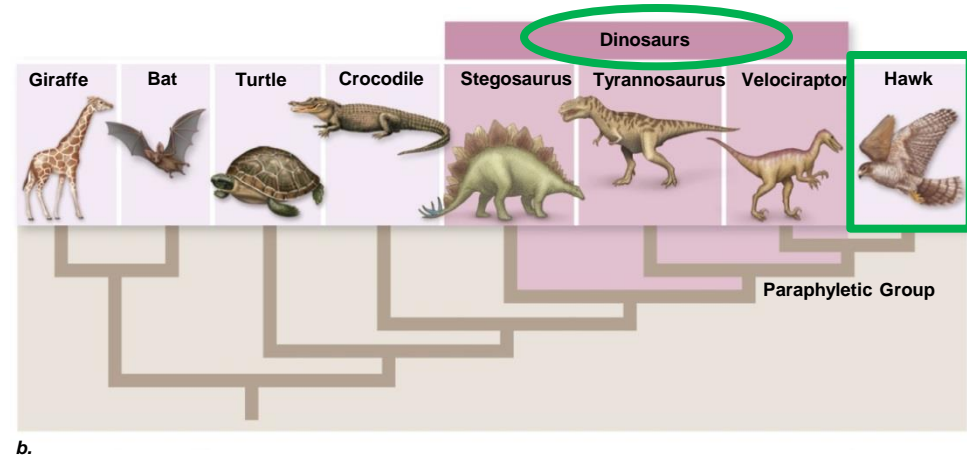
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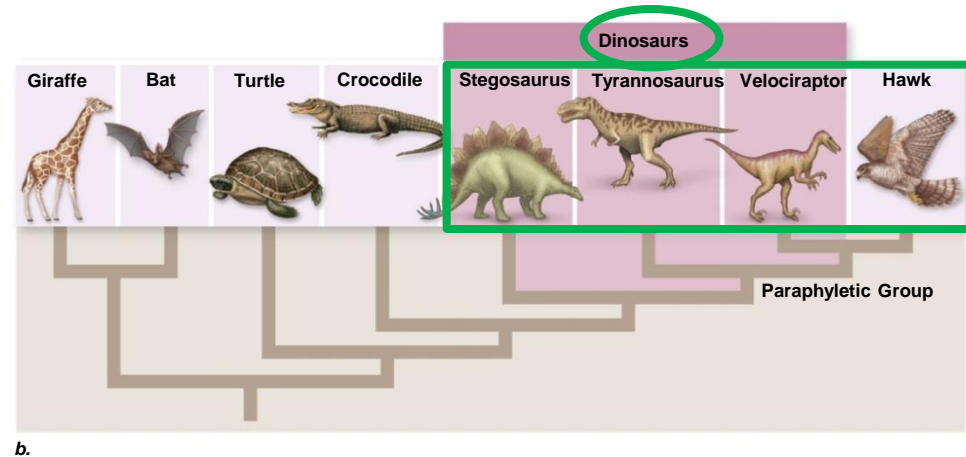
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Systematics and Classification

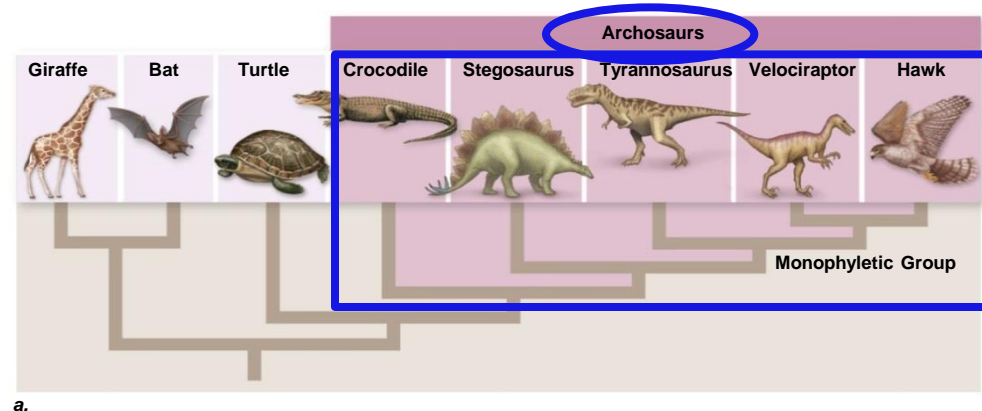
- **Paraphyletic group**
 - Includes the most recent common ancestor of the group, but *not all its descendants*
- **Polyphyletic group**
 - Does *not include the most recent common ancestor* of all members of the group



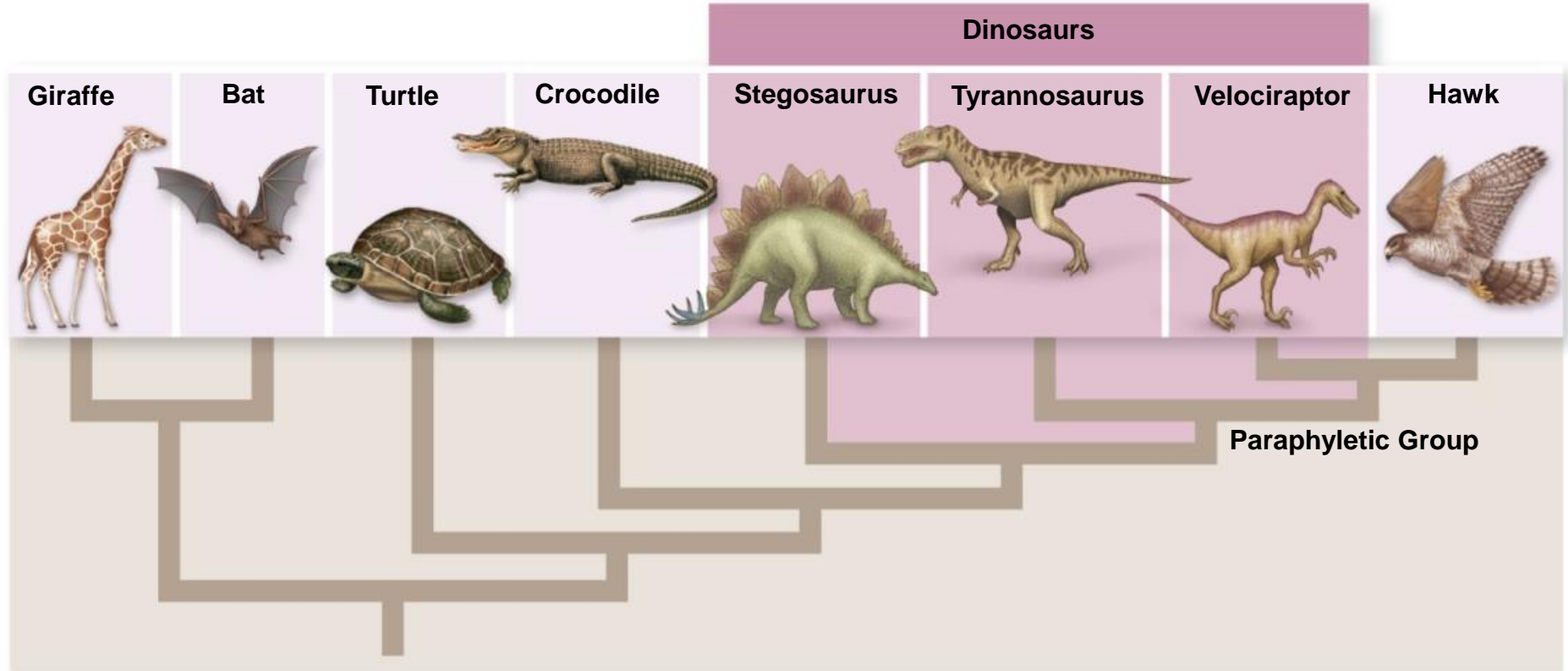
- Taxonomic hierarchies are based on shared traits, should reflect evolutionary relationships, i.e. **be monophyletic**



- Birds as an example
 - Must be included in dinosaurs to be monophyletic

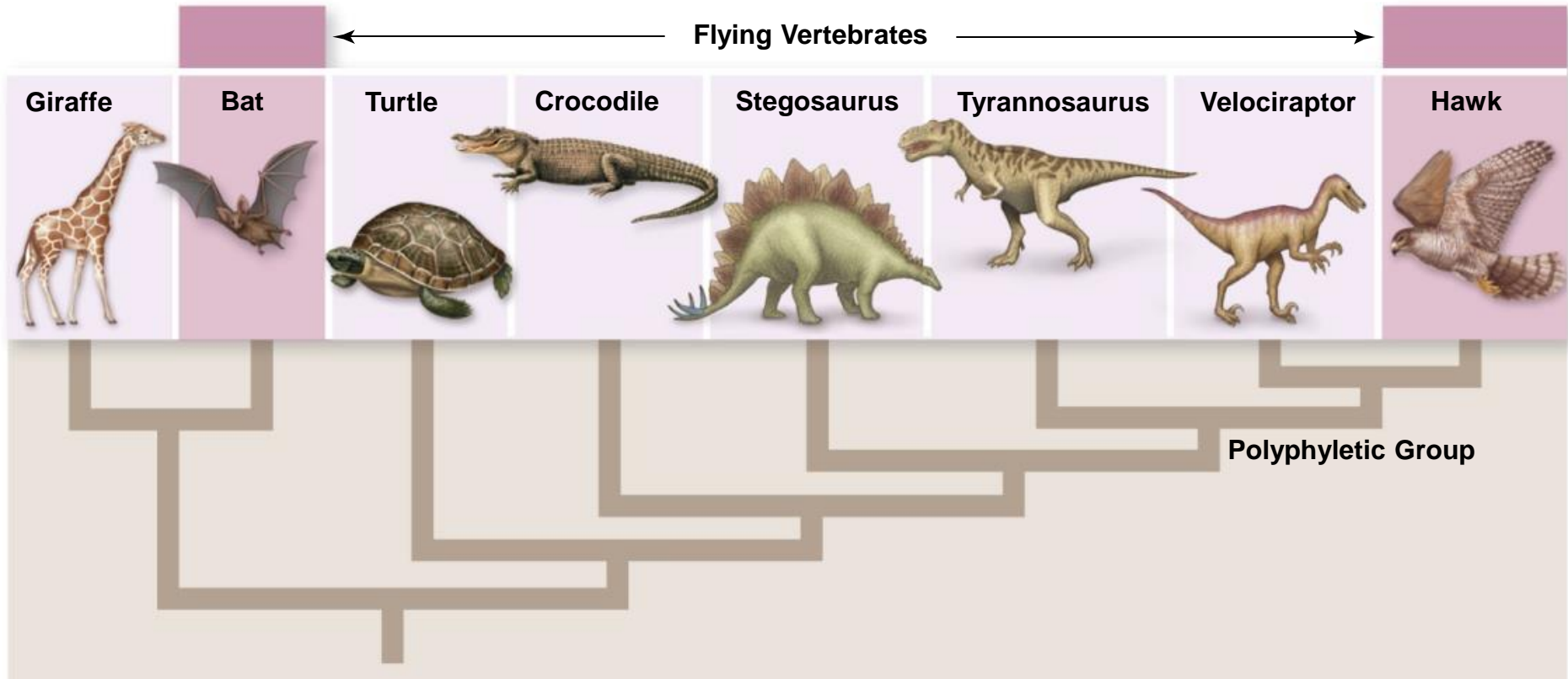


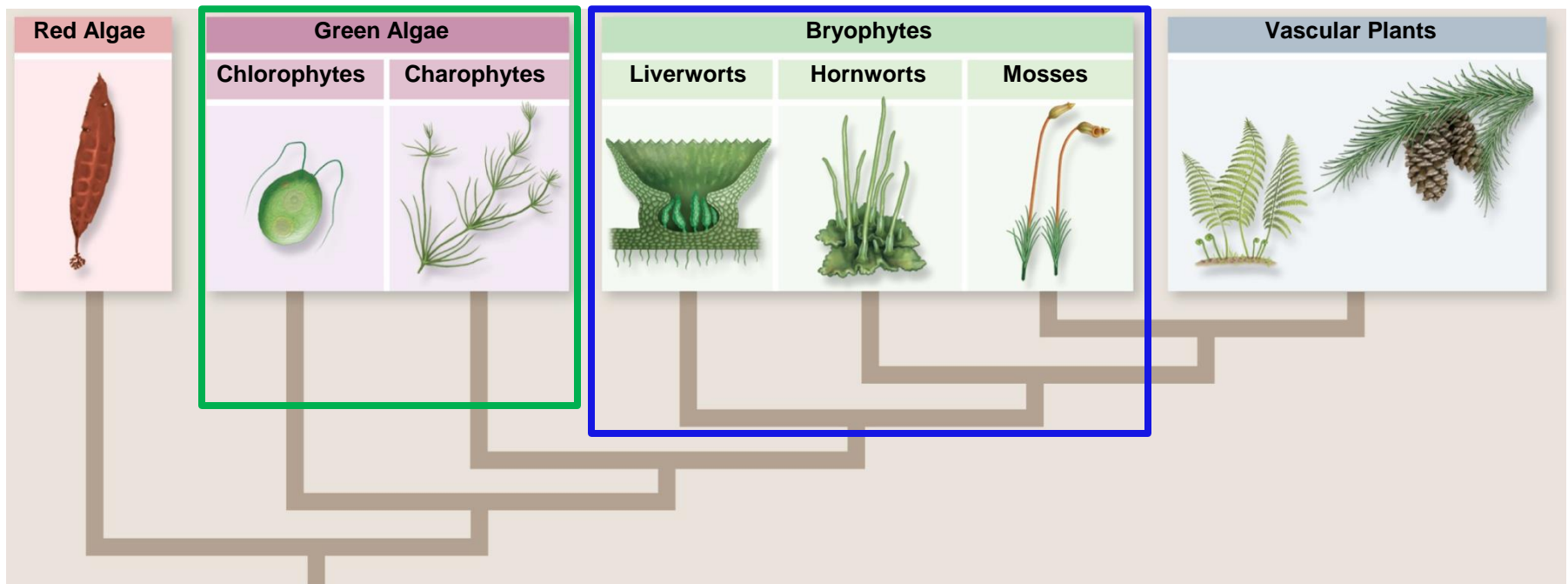
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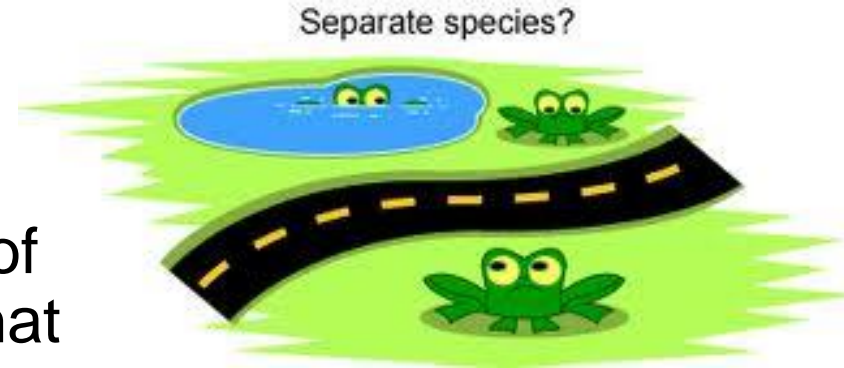


- The traditional classification included two groups that we now realize are not monophyletic: the **green algae** and **bryophytes**
 - New classification of plants does not include these groups

Species concepts

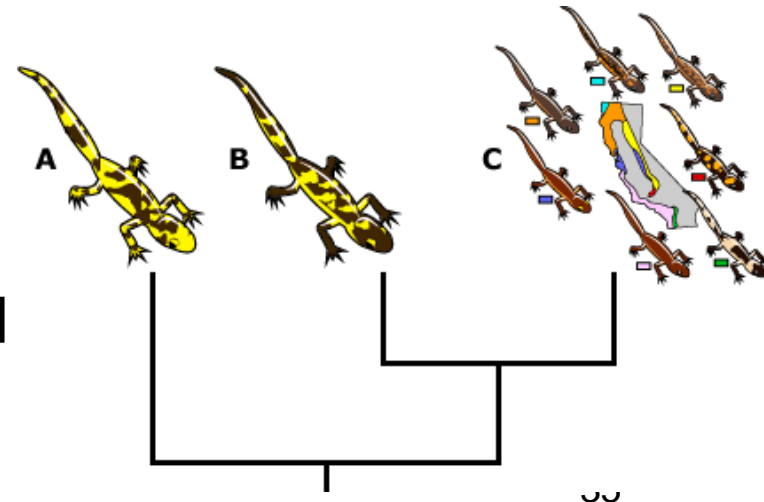
- **Biological species concept (BSC)**

- Defines species as groups of interbreeding populations that are reproductively isolated

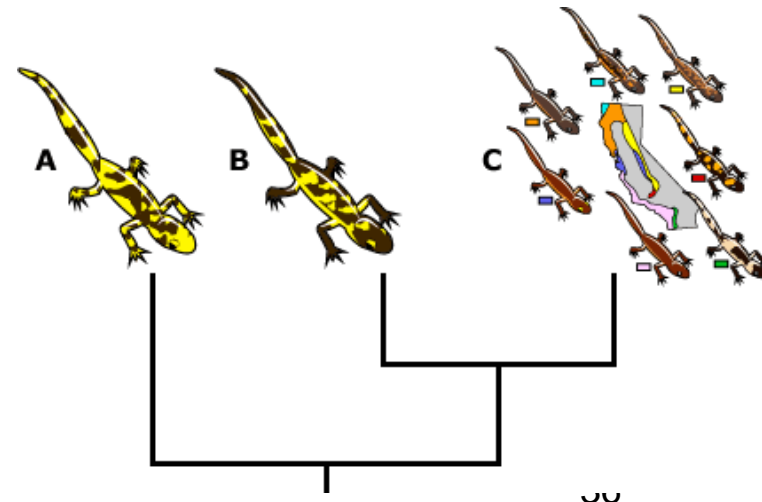
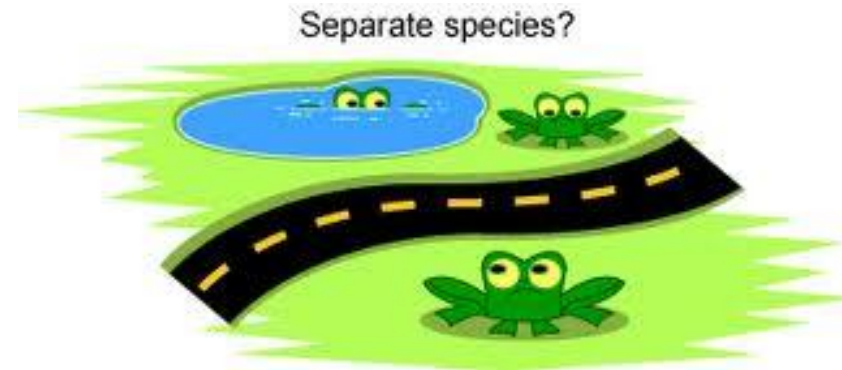


- **Phylogenetic species concept (PSC)**

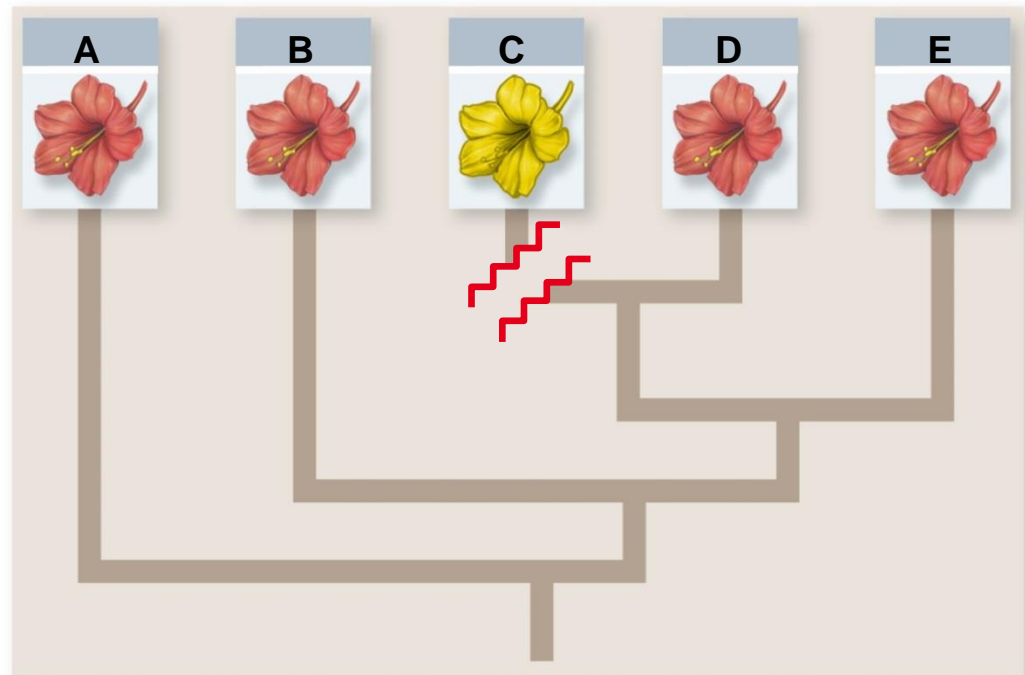
- Species is a population or set of populations characterized by one or more shared derived characters



- **PSC solves 2 BSC problems**
 - BSC cannot be applied to allopatric (separate) populations – would they interbreed?
 - PSC looks to the past to see if they have been separated long enough to develop their own derived characters
 - BSC can be applied only to sexual species
 - PSC can be applied to both sexual and asexual species

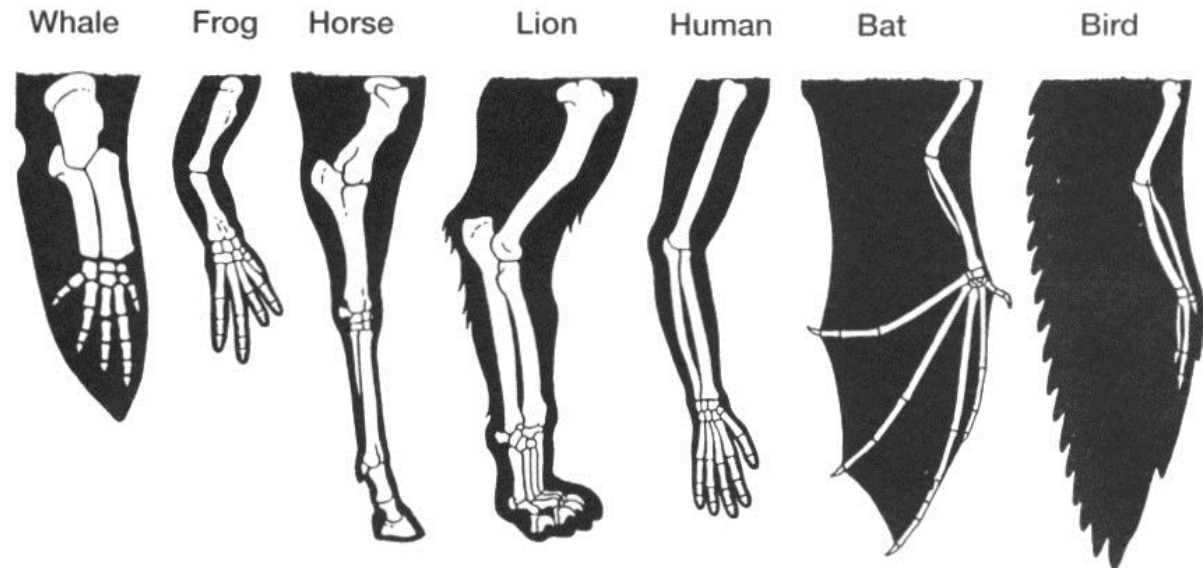


- **PSC still controversial**
 - Critics contend it will lead to the recognition of even slightly different populations as distinct species – “splitting”
 - **Paraphyly problem** – if species C evolved apart from other genetically connected “species” A,B, D & E



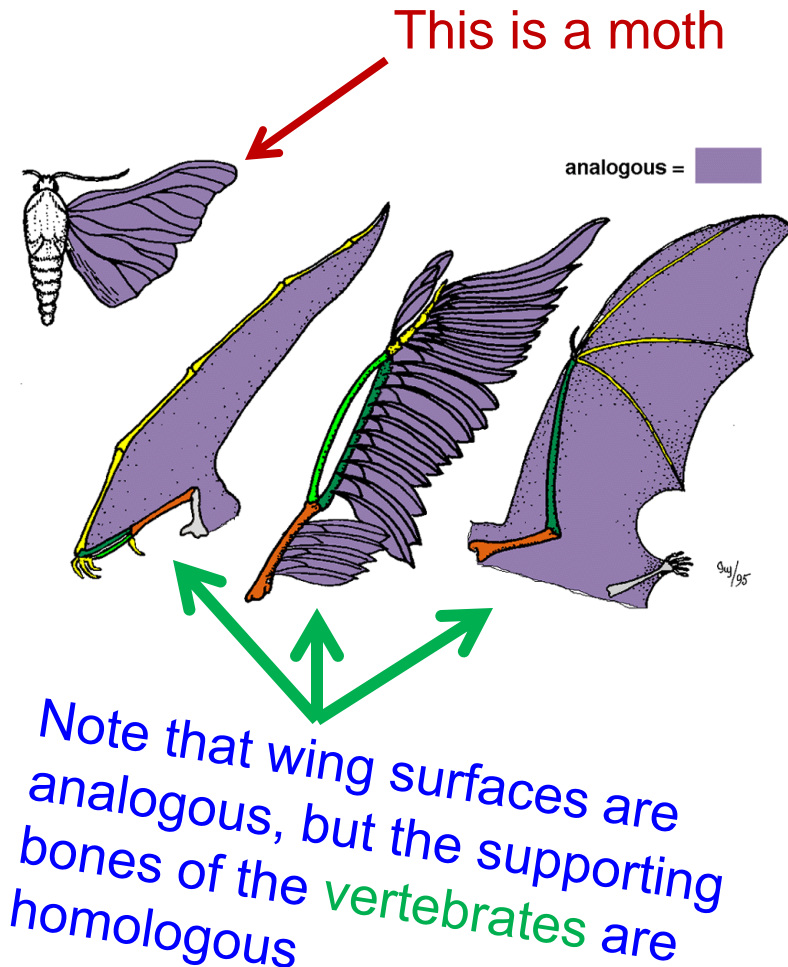
Phylogenetics

- Basis for all comparative biology
- **Homologous** structures
 - Derived from the same ancestral source
 - Dolphin flipper and horse leg

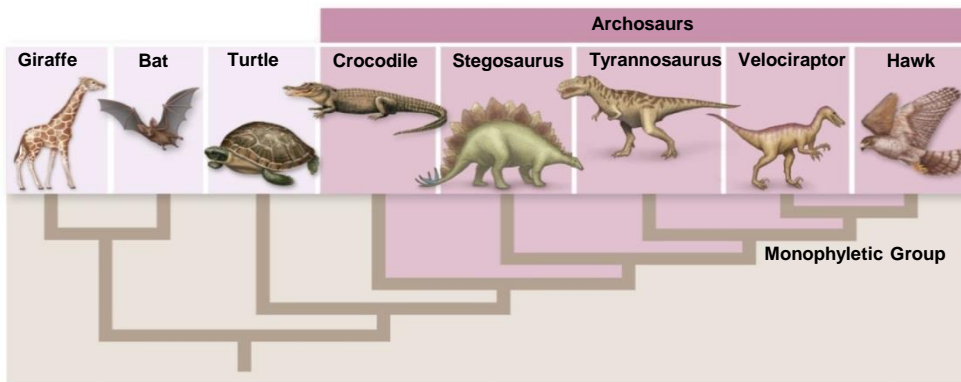


Phylogenetics

- **Homoplastic** structures are not
 - **Analogous** – similar function due to similar selection pressures
 - Wings of birds and dragonflies
- Phylogenetic analysis can help determine which structures are homologous vs. analogous



- Parental care in dinosaurs initially treated as unexpected
 - Examination of phylogenetic comparison of dinosaurs indicates they are most closely related to crocodiles and birds – both show parental care



a.

- Parental care in three groups not **convergent** (or **analogous**) but homologous behaviors

Fossil dinosaur incubating eggs



a.

a: Image #5789, photo by D. Finnin/American Museum of Natural History

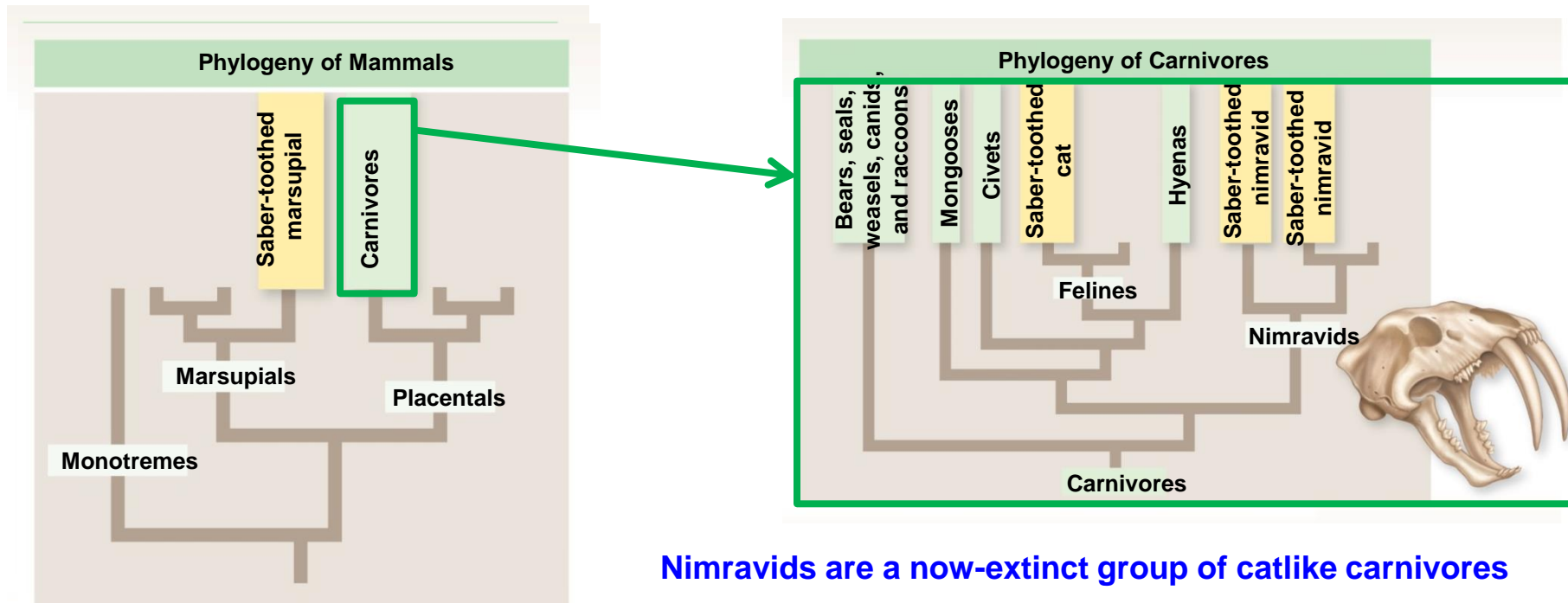


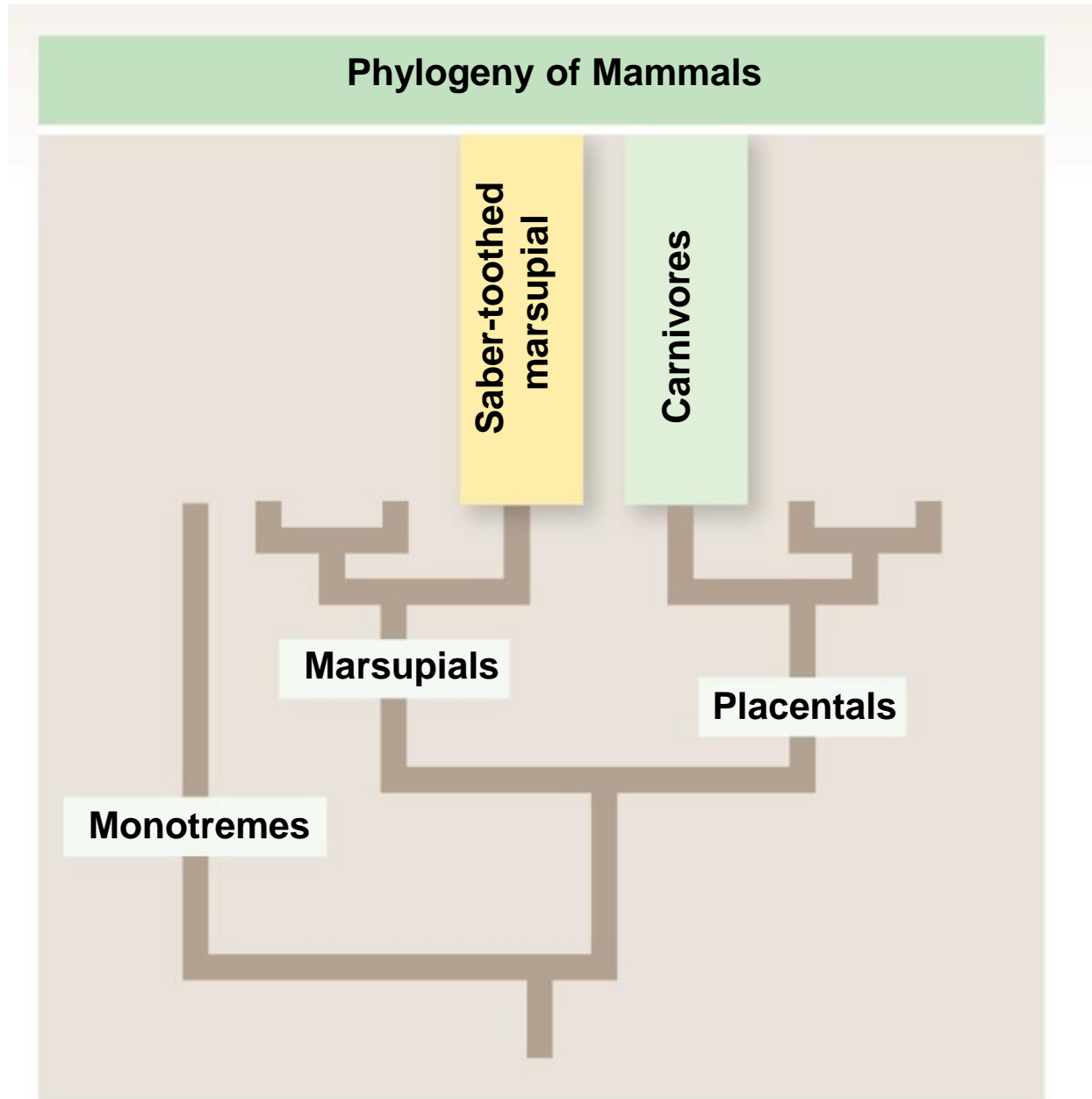
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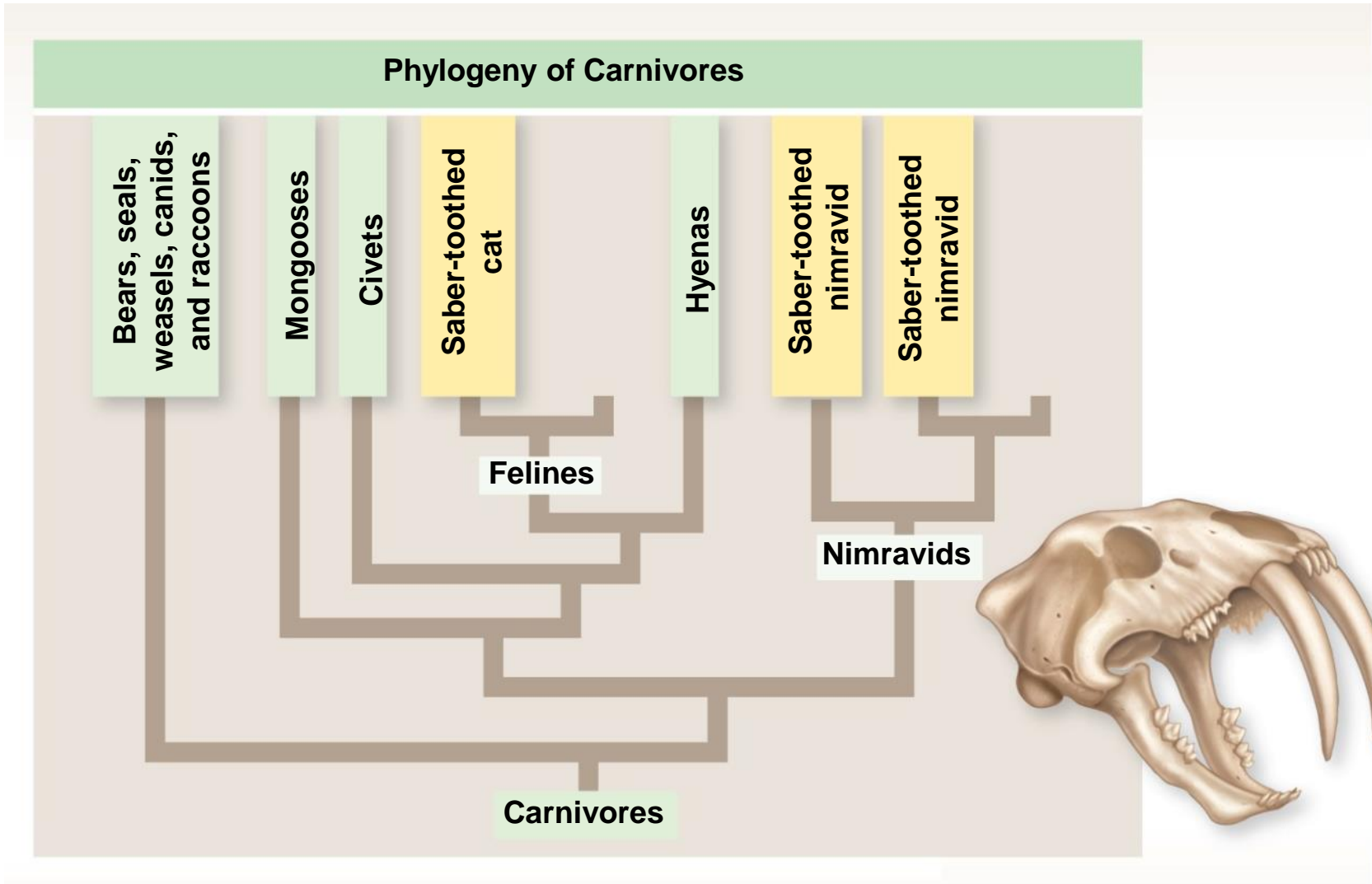
b: © Roger De La Harpe/Animals Animals

Homoplastic convergence

- Ex: *saber teeth*
 - Evolved independently in different clades of extinct carnivores
 - Similar body proportions (cat) & predatory lifestyle
 - Most likely evolved independently at least 3 times



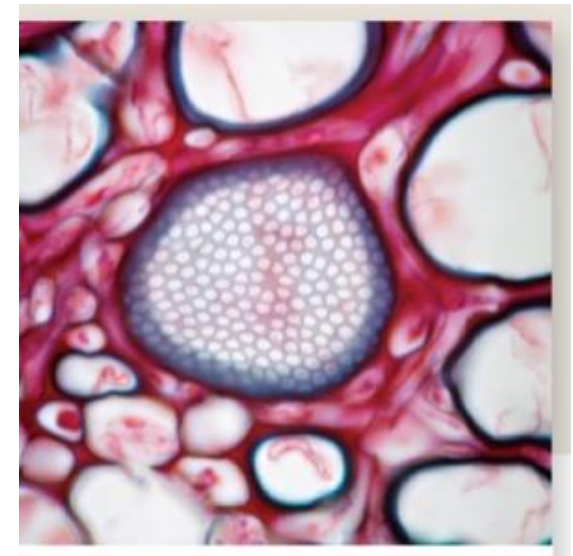
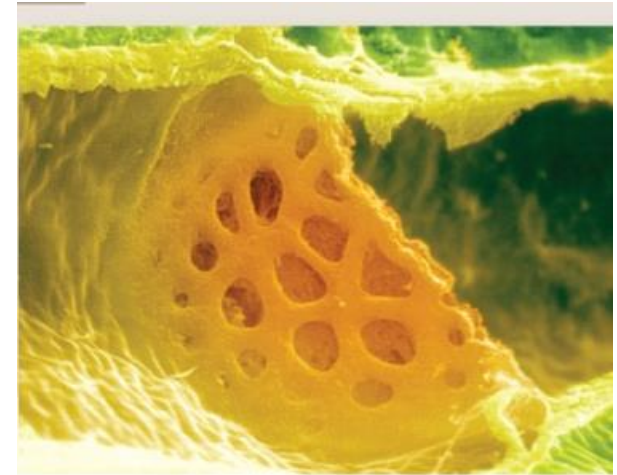




Nimravids are a now-extinct group of catlike carnivores

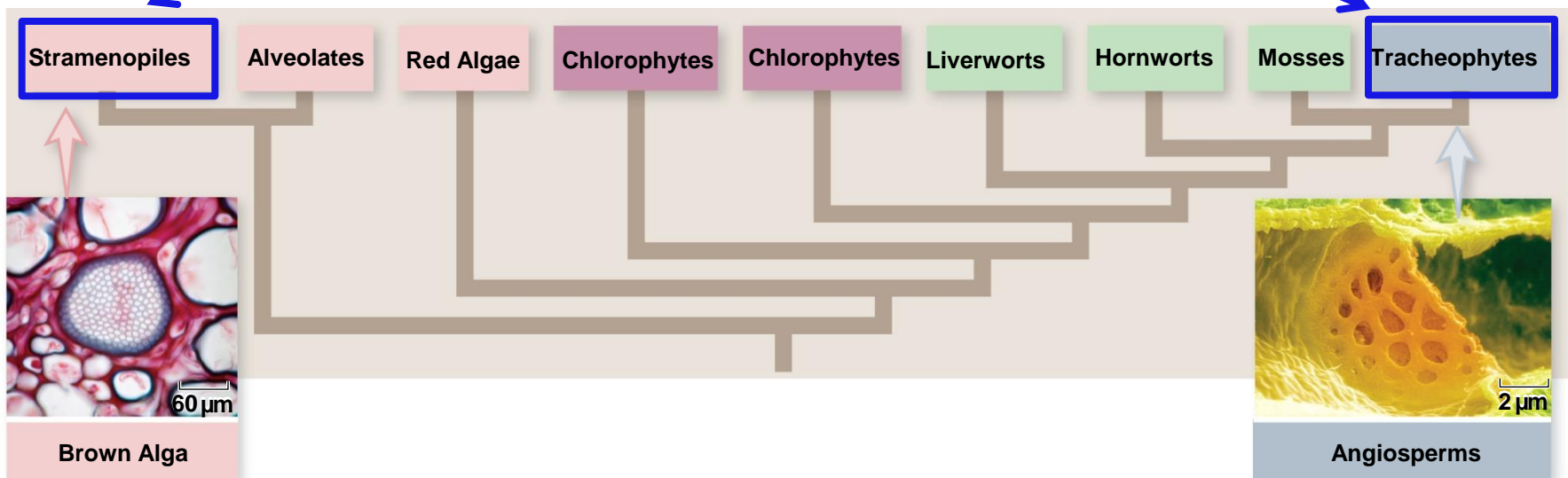
Homoplastic convergence

- Ex: plant conducting tubes
 - Sieve tubes facilitate long-distance transport of food and other substances in vascular plants
 - Essential to the survival of tall plants on land
 - Brown algae also have **sieve elements**
 - Closest ancestor of these two taxa is a single-celled organism that could not have had a multicellular transport system...



- Closest ancestor of these two taxa is a single-celled organism that could not have had a multicellular transport system

No way these two traits are homologous,
they must be independently derived!!

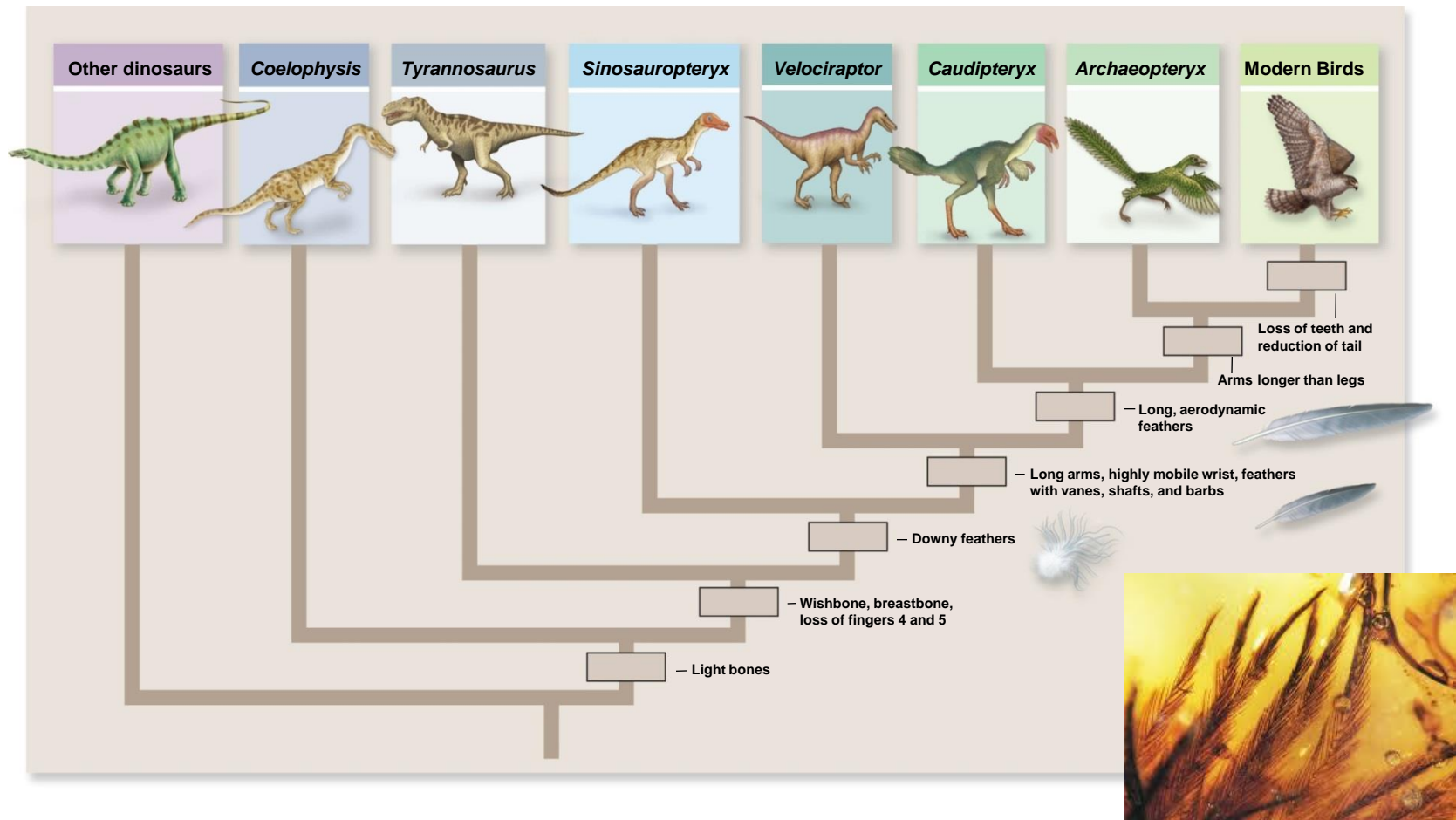


Comparative Biology

Most complex characters do not evolve in one step

- Evolve through a sequence of evolutionary changes
- Initial stages of a character evolved as an adaptation to some environmental selective pressure
- Modern-day birds are exquisite flying machines
 - Wings, feathers, light bones, breastbone



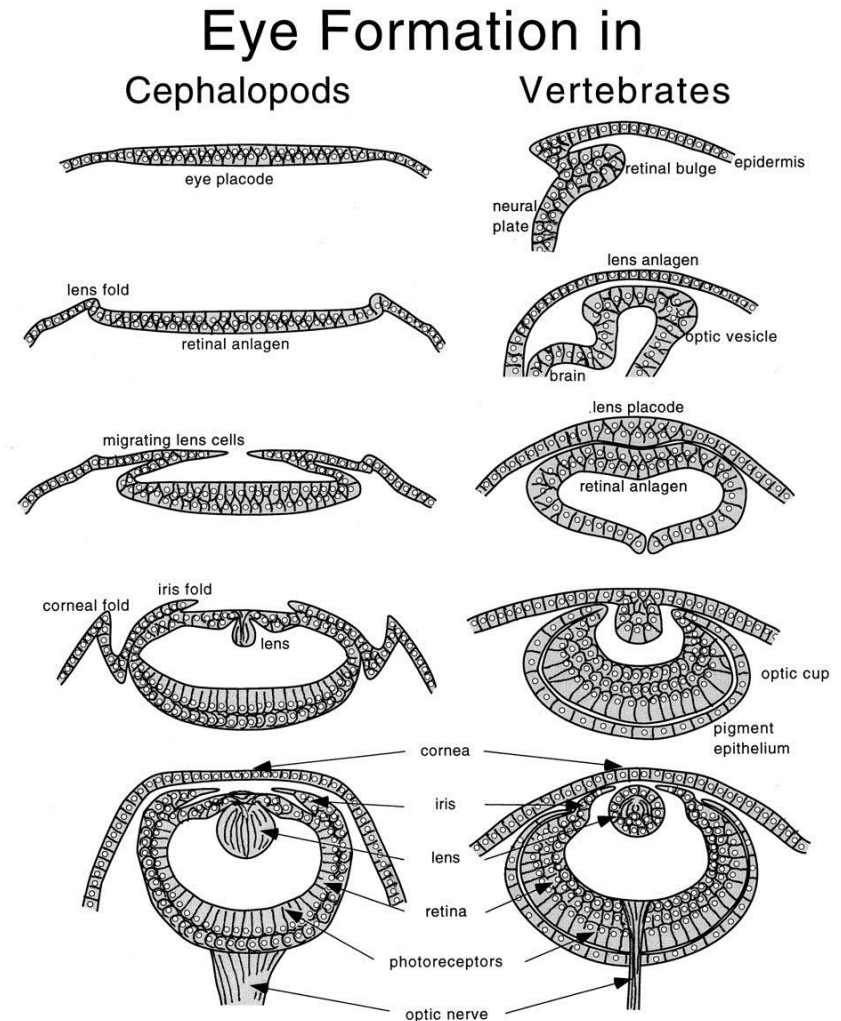


- First featherlike structure evolved in theropod phylogeny
 - For insulation or perhaps decoration
 - Selection works with what is present

70-85 my old
feathers trapped
in amber

Comparative Biology

- Ex: Vertebrate eye vs. cephalopod eye
 - Both “camera” eyes, look similar
 - Developmental process is very different
 - Highly complex structures, independently derived (convergence)



Phylogenetic Analysis

Phylogenetic methods can be used to distinguish between competing hypotheses

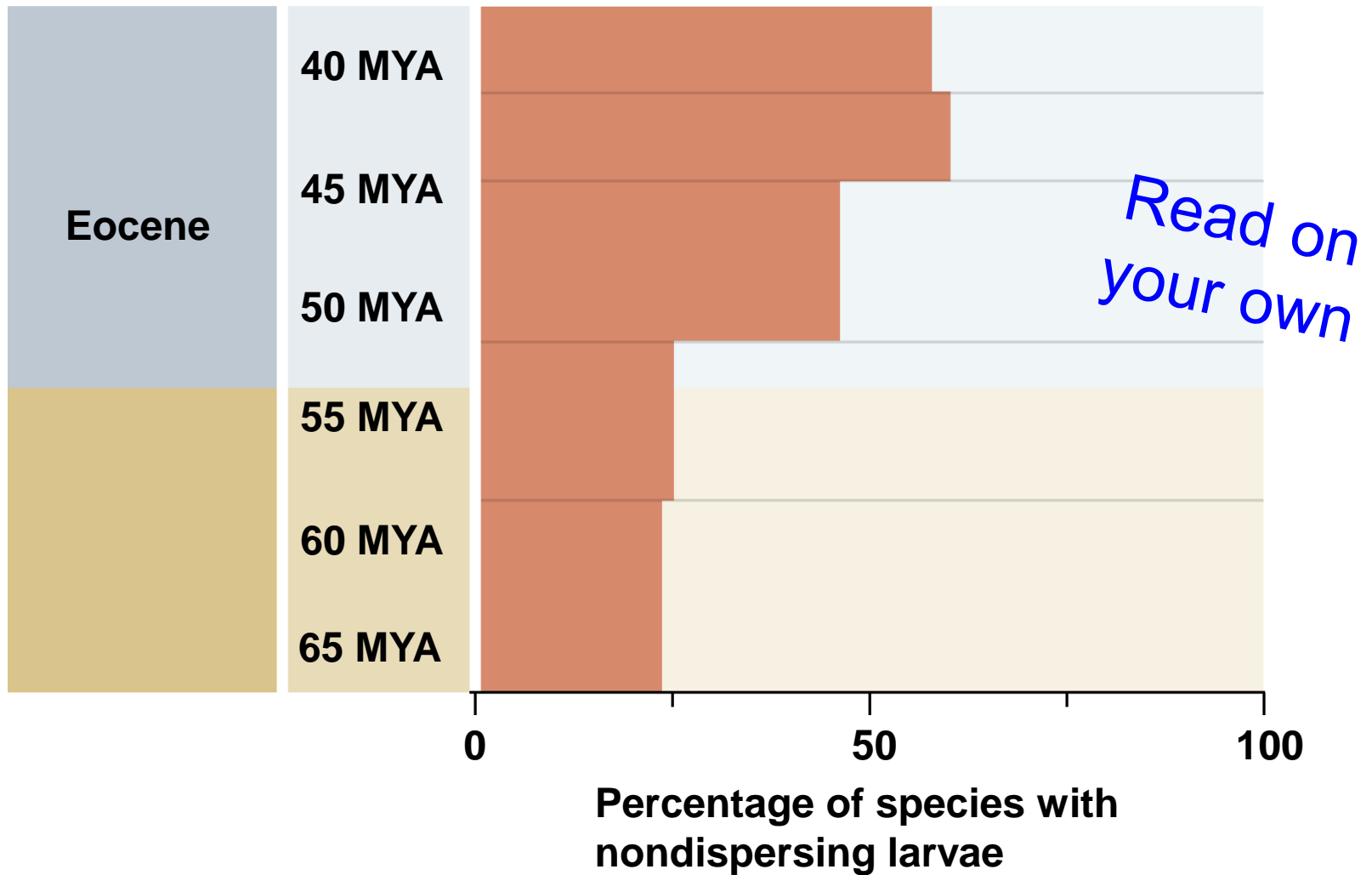
- Larval dispersal in marine snails
 - Some snails produce microscopic larvae that drift in the ocean currents
 - Some species have larvae that settle to the ocean bottom and do not disperse

Veliger larvae
dispersal stage



[Jump to
Slide #59](#)

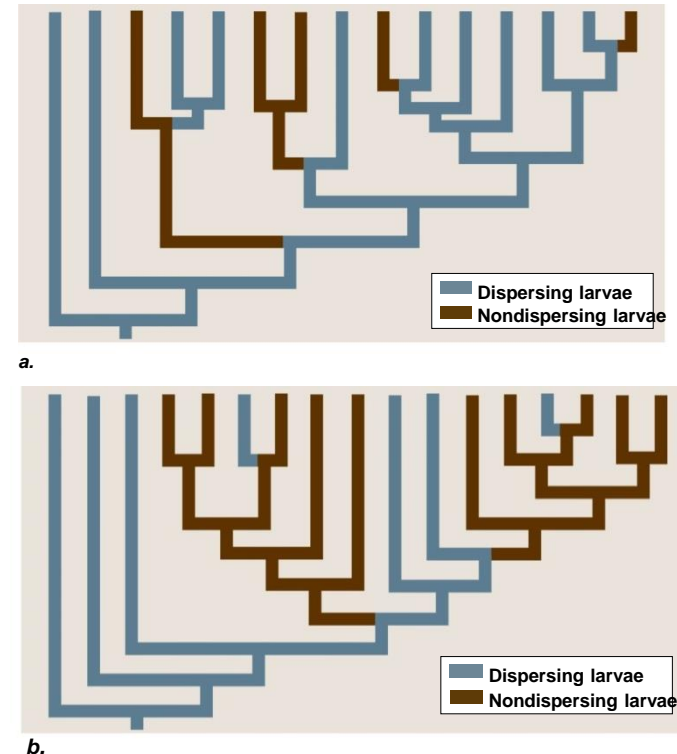
*Read on
your own*

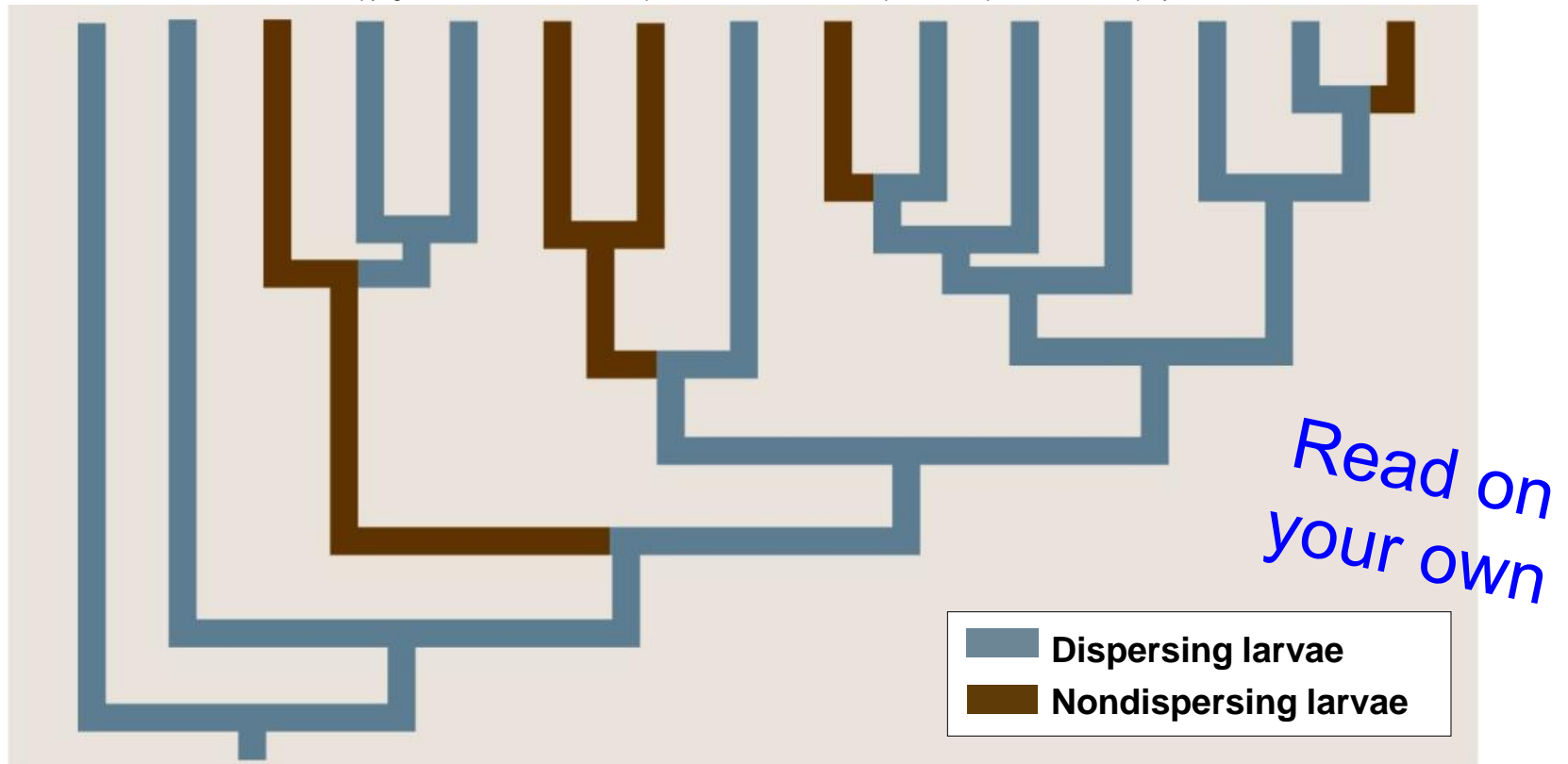


- Fossil record shows an increase in non-dispersing snails

*Read on
your own*

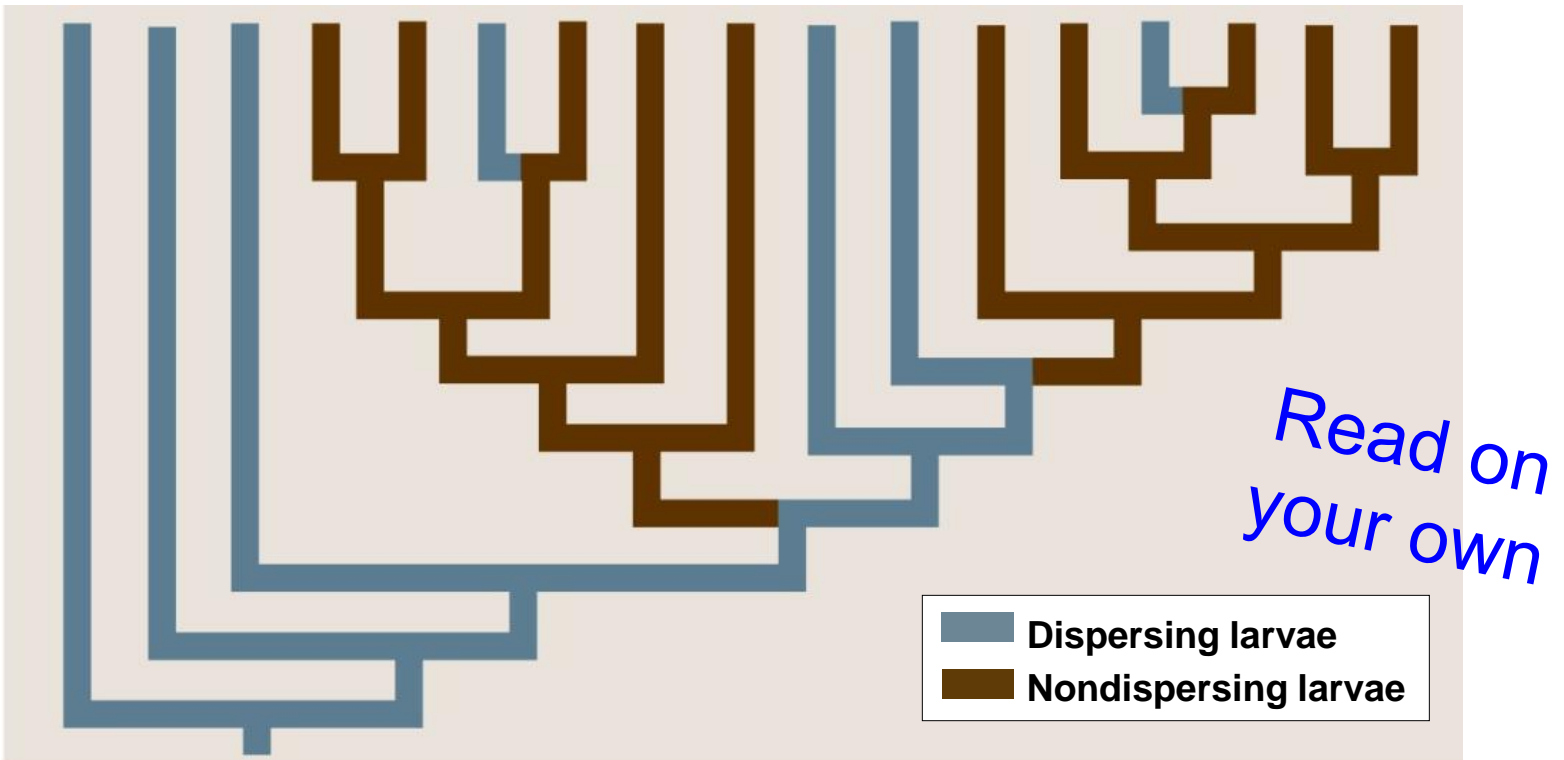
- Two processes could produce an increase in non-dispersing larvae
 - Evolutionary change from dispersing to non-dispersing occurs more often than change in the opposite direction
 - Species that are non-dispersing speciate more frequently, and/or become extinct less frequently than dispersing species
- The two processes would result in different phylogenetic patterns





a.

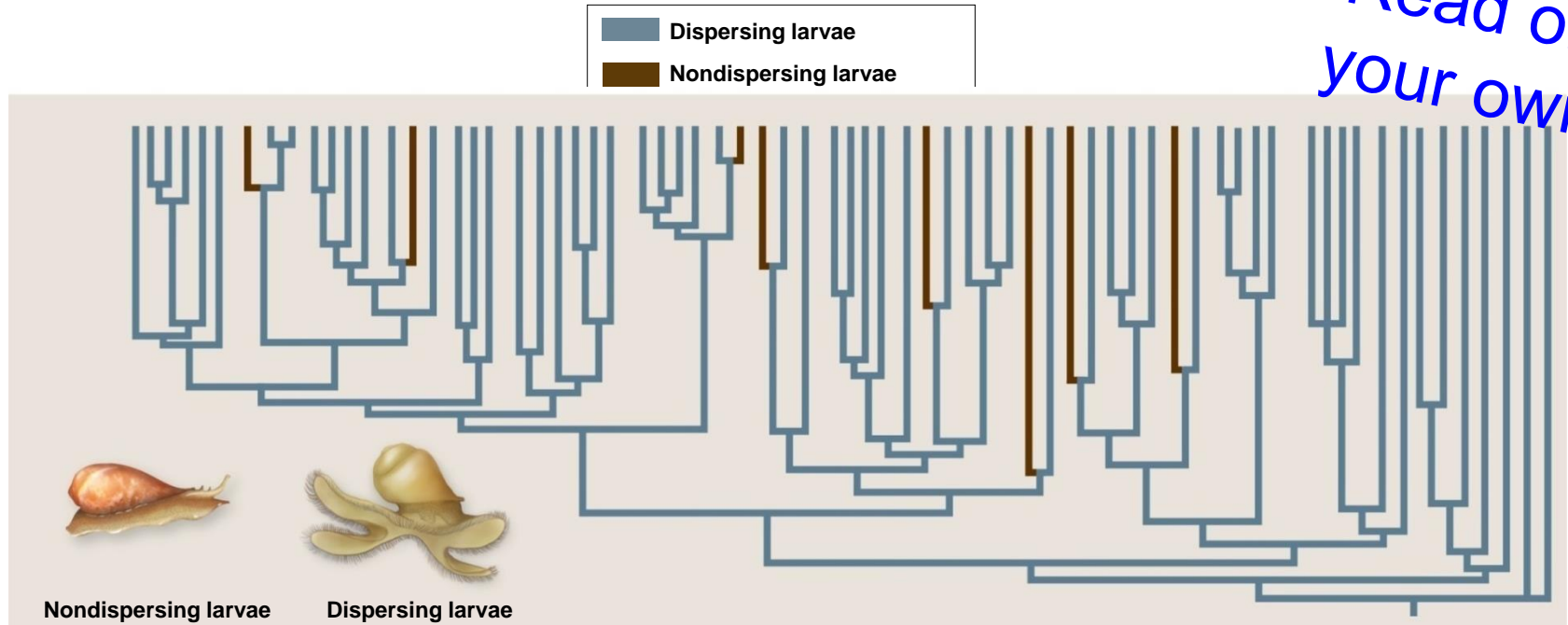
- In this hypothetical example, the evolutionary transition from dispersing to nondispersing larvae occurs more frequently (four times) than the converse (once)



b.

- By contrast, clades that have nondispersing larvae diversify to a greater extent due to higher rates of speciation or lower rates of extinction (assuming that extinct forms are not shown)

Read on
your own

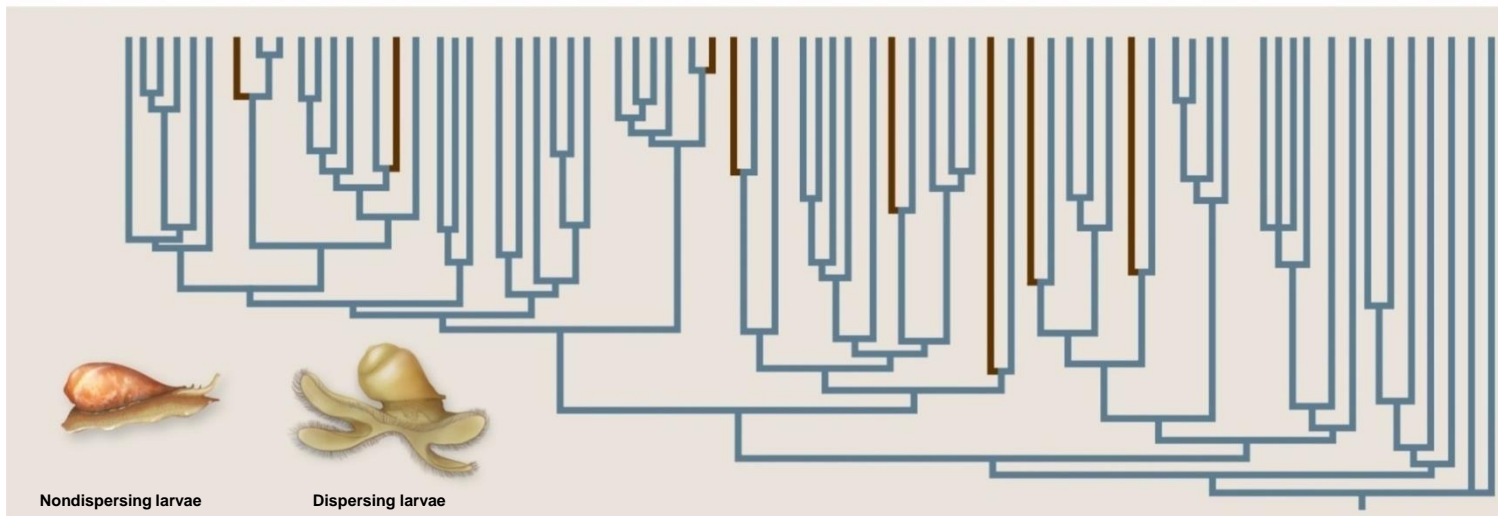


c.

- Phylogeny for *Conus*, a genus of marine snails.
 - Nondispersing larvae have evolved eight separate times from dispersing larvae, with no instances of evolution in the reverse direction.
 - This phylogeny does not show all species, however; nondispersing clades contain on average 3.5 times as many species as dispersing clades.

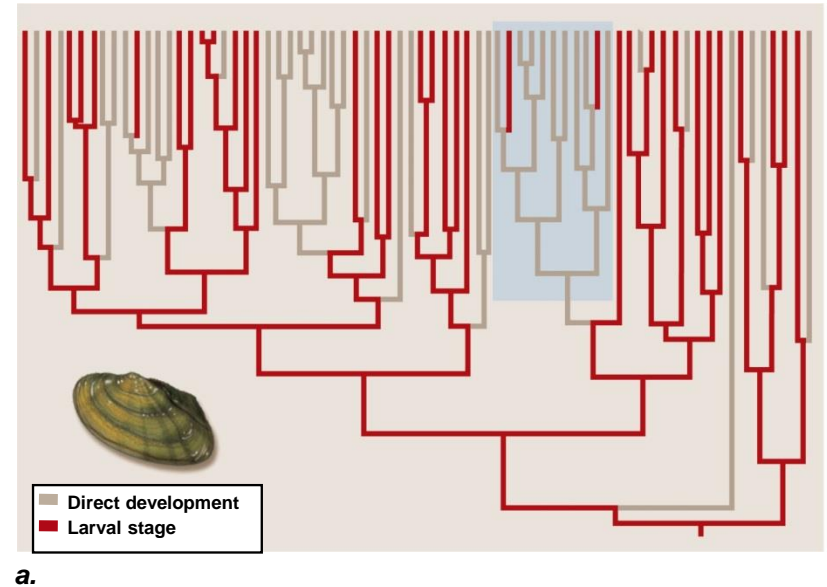
Read on
your own

- Analysis indicates:
 - Evolutionary increase in non-dispersing larvae through time may be a result of both as a bias in the evolutionary direction and an increase in rate of diversification (more likely to be isolated → higher speciation rate)
 - Lack of evolutionary reversals not surprising... evolution of non-dispersing larvae a one-way street

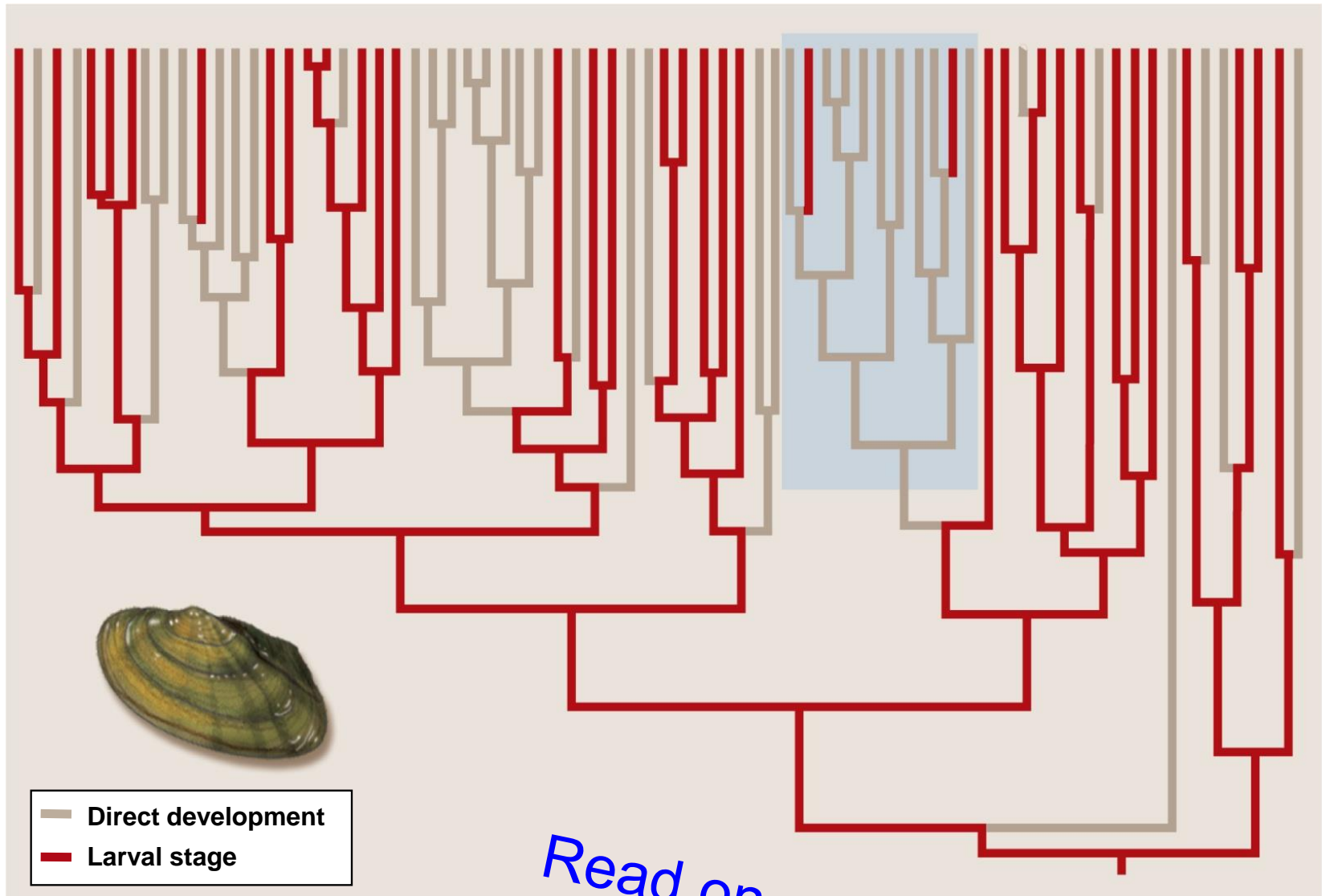


- Loss of larval stage in marine invertebrates

- Eggs develop directly into adults
- Nonreversible evolutionary change
- Marine limpets: show direct development has evolved many times
- Three cases where evolution reversed and larval stage re-evolved
- Evidence in second species supports hypotheses



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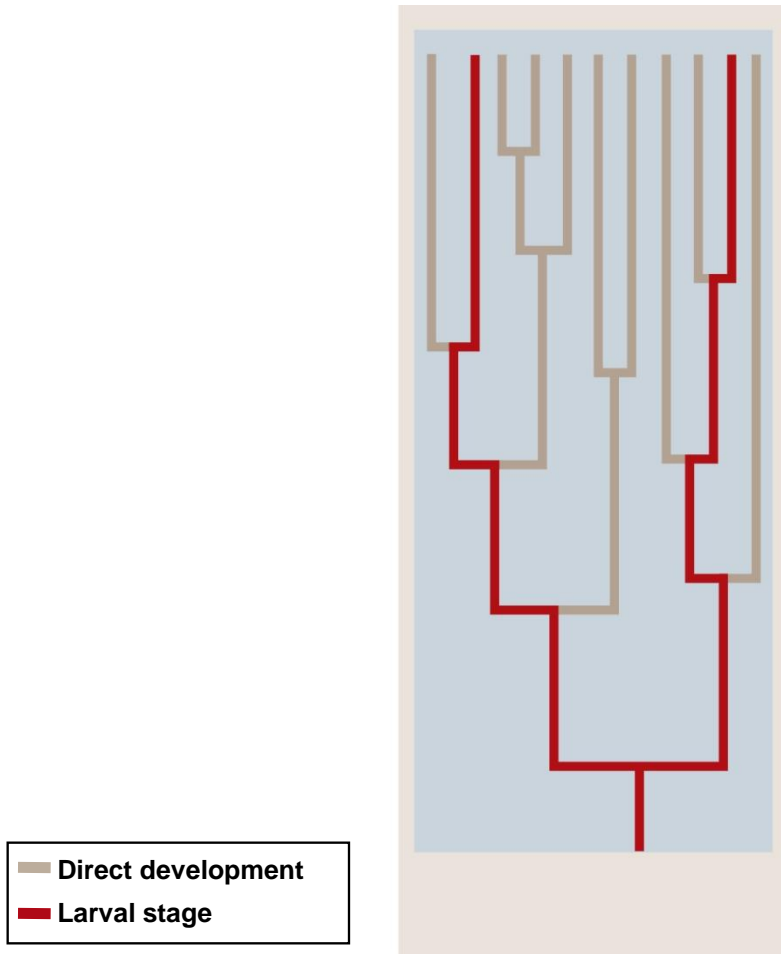


a.

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b.

- Less parsimonious interpretation of evolution in the clade in the light blue box is that, rather than two evolutionary reversals, six instances of the evolution of development occurred without any evolutionary reversal

Phylogenetic Analysis

Phylogenetics helps explain species diversification

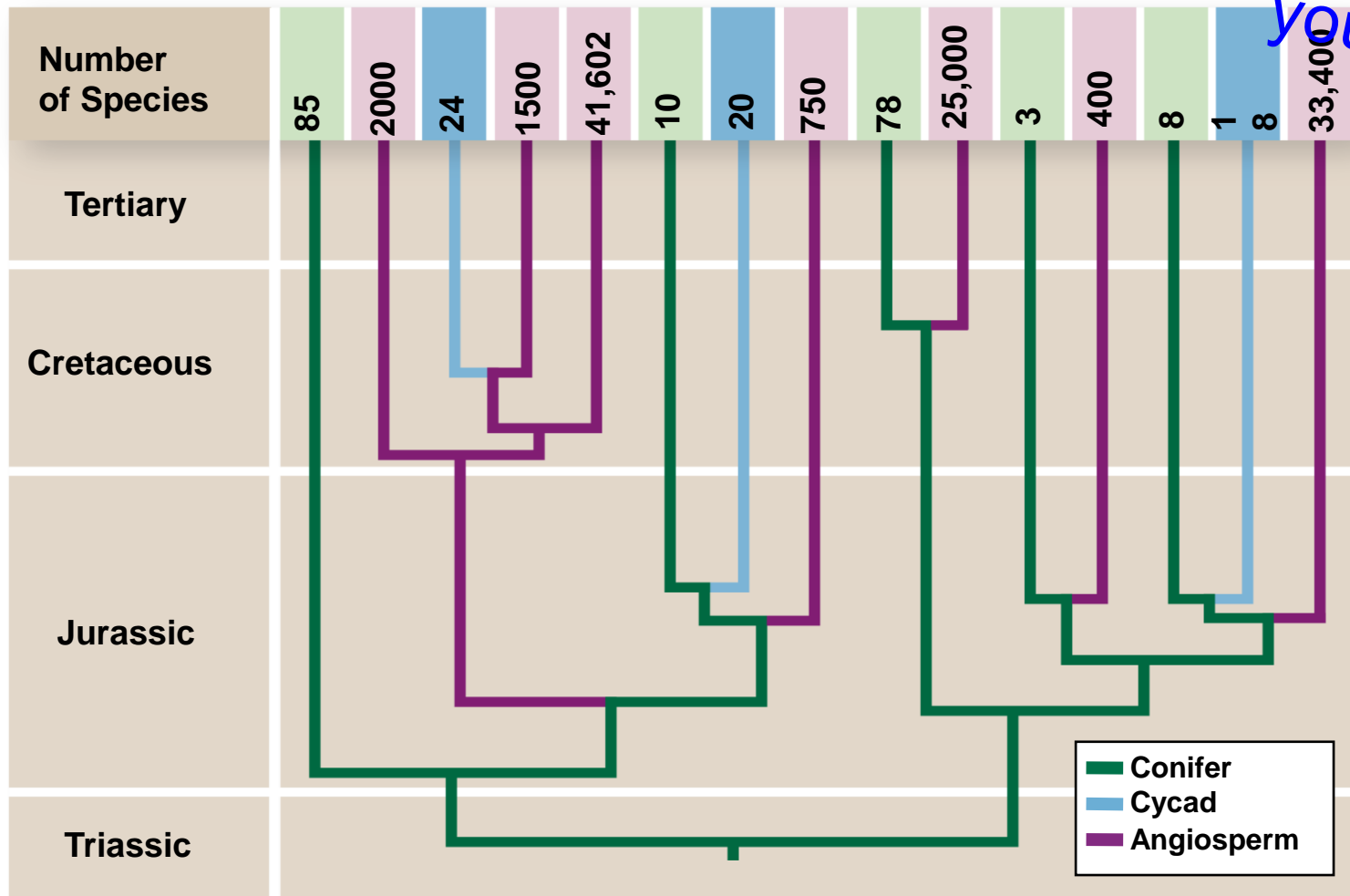
- Use phylogenetic analysis to suggest and test hypotheses
- Insight into beetle diversification
 - Correspondence between phylogenetic position and timing of plant origins suggests beetles are remarkably conservative in their diet



Beetle box: 102 species of beetles from Madagascar, representing ~0.025% of all described beetle species

- Beetle families that specialize on conifers have the **deepest branches**
- Beetles that specialize on Angiosperms have **shorter branches**

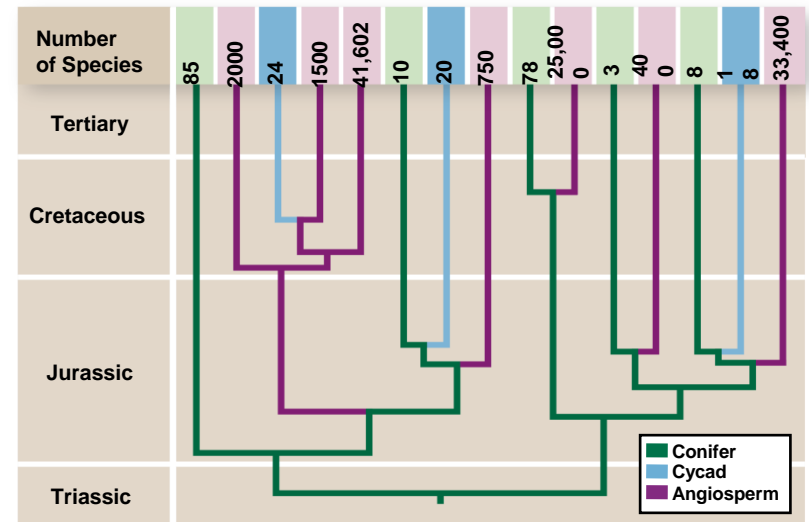
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- Phylogenetic explanations for beetle diversification

- It is not the evolution of herbivory itself
- Specialization on angiosperms was prerequisite for diversification
- Specialization has arisen five times independently within herbivorous beetles
- Angiosperm-specializing clade is more species-rich than the clade most closely related

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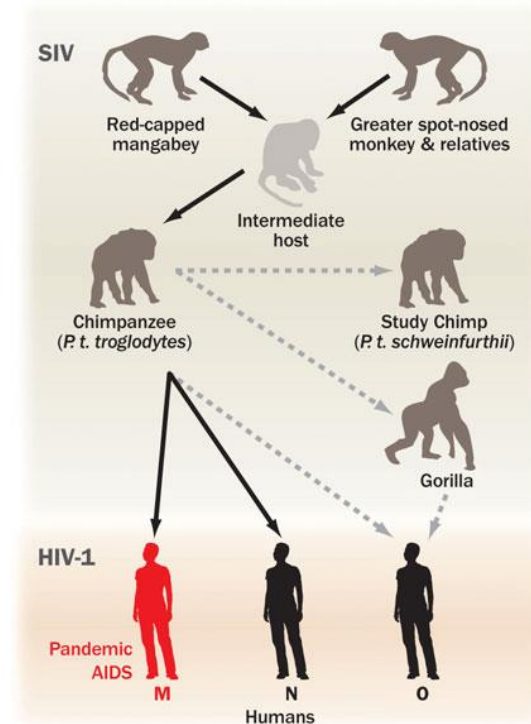


Disease Evolution

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AIDS first recognized in 1980s

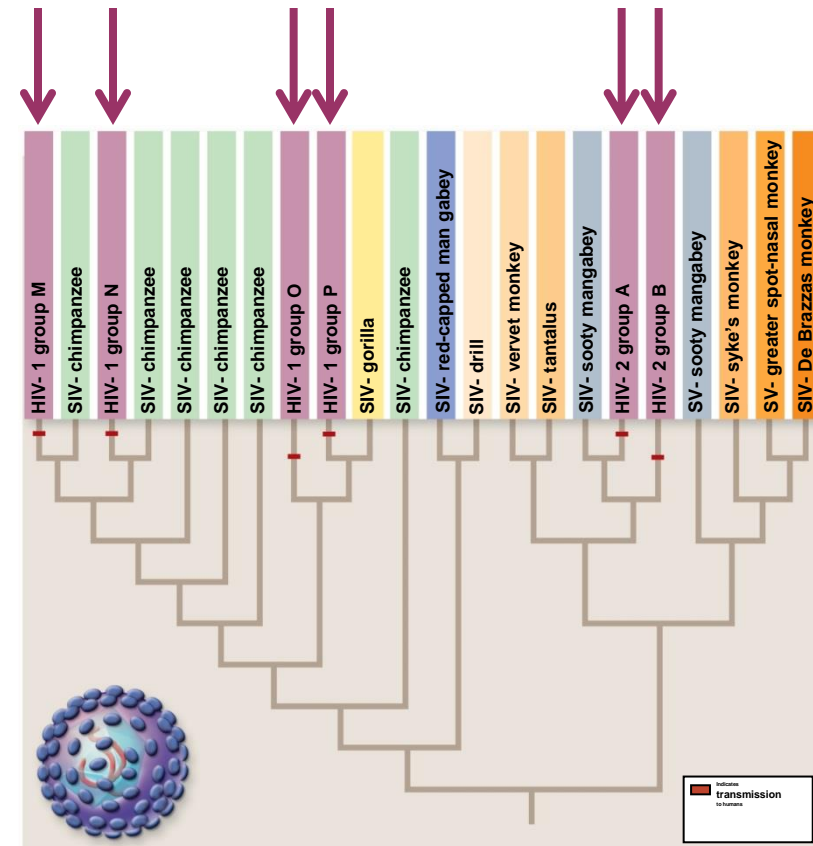
- Current estimate: > 33 million people infected with **human immunodeficiency virus (HIV)**; > 2 million die each year
- **Simian immunodeficiency virus (SIV)** found in 36 species of primates
 - Does not usually cause illness in monkeys
 - Around for more than a million years as SIV in primates



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Phylogenetic analysis of HIV and SIV

1. HIV descended from SIV
 - All strains of HIV are nested within clades of SIV
2. Several different strains of HIV exist
 - *Independent transfers from different primate species*
 - Each human strain is more closely related to a strain of SIV than to other HIV strains
 - *Separate origins for HIV strains*

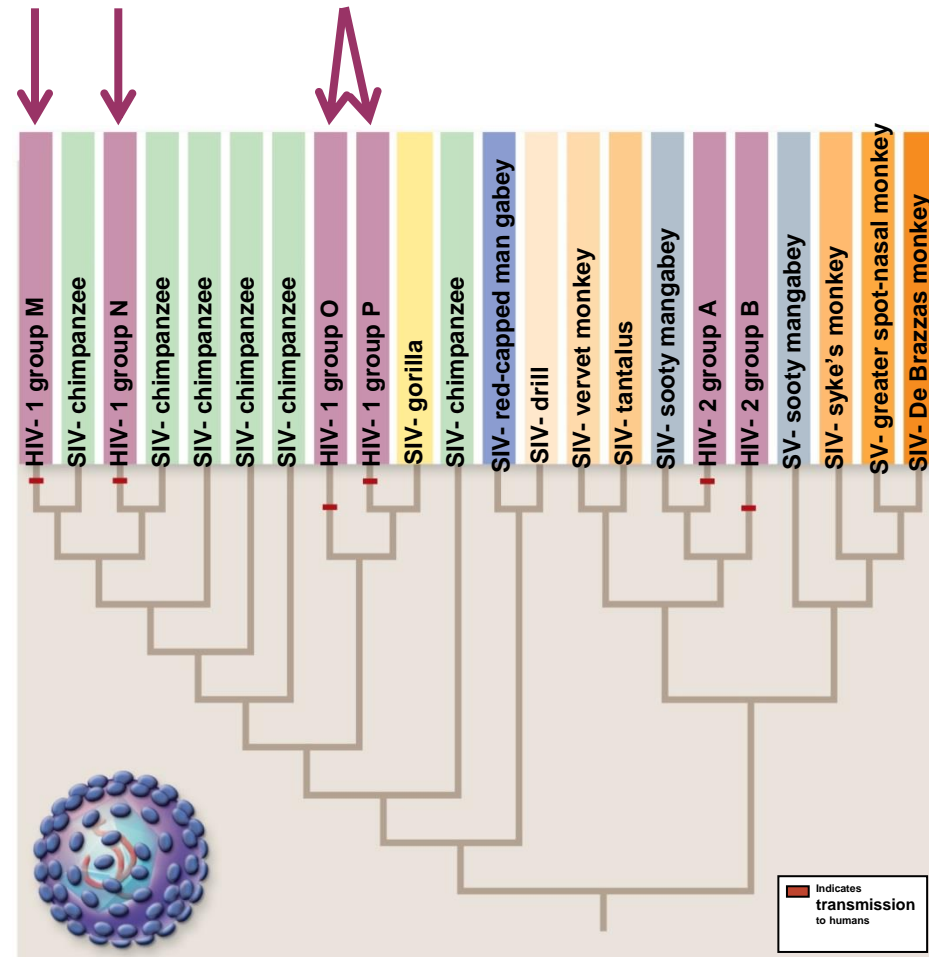


3. Humans have acquired HIV from different host species

- HIV-1, which is the virus responsible for the global epidemic, has three subtypes

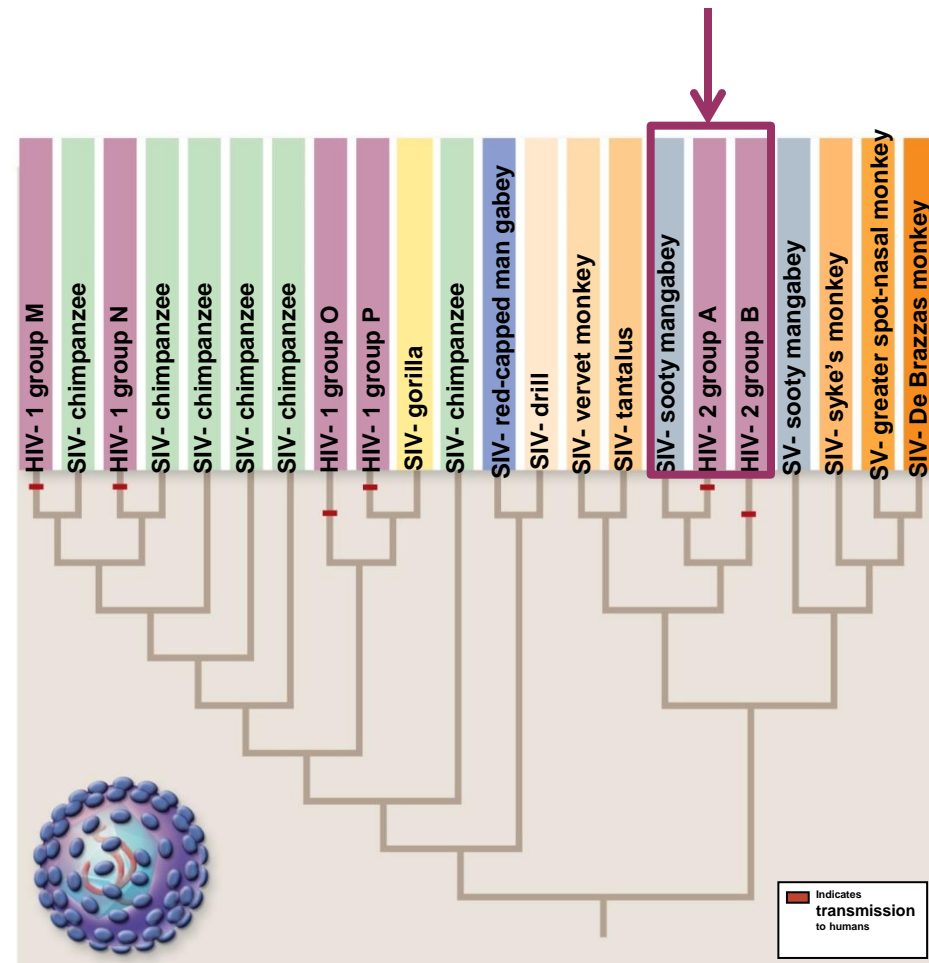
- Each subtype is most closely related to a different strain of chimpanzee SIV, indicating that the transfer occurred from chimps to humans

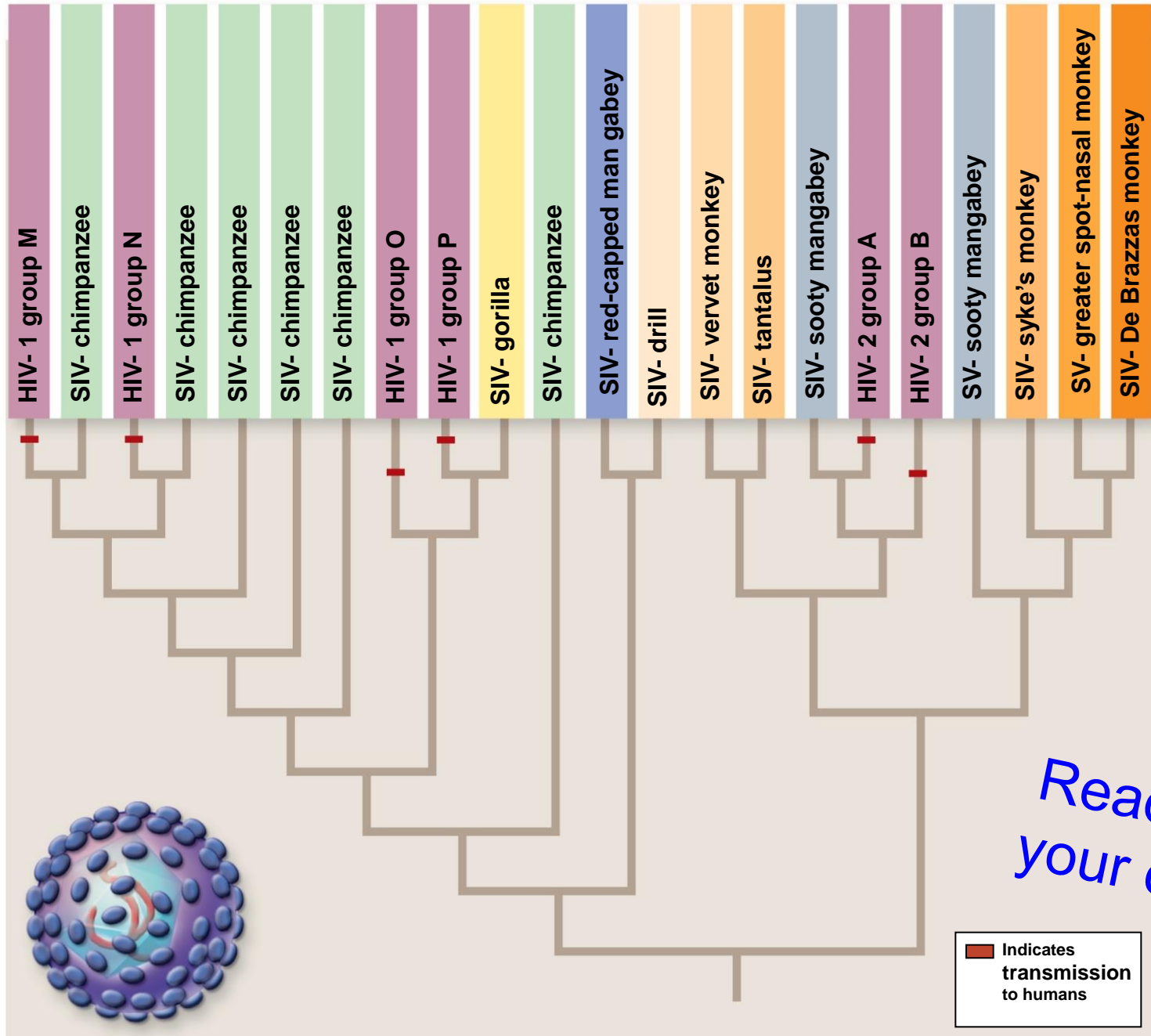
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- Subtypes of HIV-2, which is much less widespread, are related to SIV found in West African monkeys, primarily the sooty mangabey (*Cercocebus atys*)

- Moreover, the subtypes of HIV-2 also appear to represent several independent cross-species transmissions to humans





- HIV mutates so rapidly that a *single HIV-infected individual often contains multiple genotypes in a patient's body*
- As a result, it is possible to create a phylogeny of HIV strains and to identify the source of infection of a particular individual
- In this case, the HIV strains of the *victim (V)* clearly are derived from strains in the body of another individual, the patient

So they can track infectious patients and their victims to the source

