

Phylogeny and the history of life

Phylogeny

The history of life

Processes of diversification

Outline

Phylogeny

- Constructing phylogenetic trees

- Example: the evolution of whales

The history of life

- The shape of the tree

- The fossil record

- Putting the timeline together

Processes of diversification

- Adaptive radiations

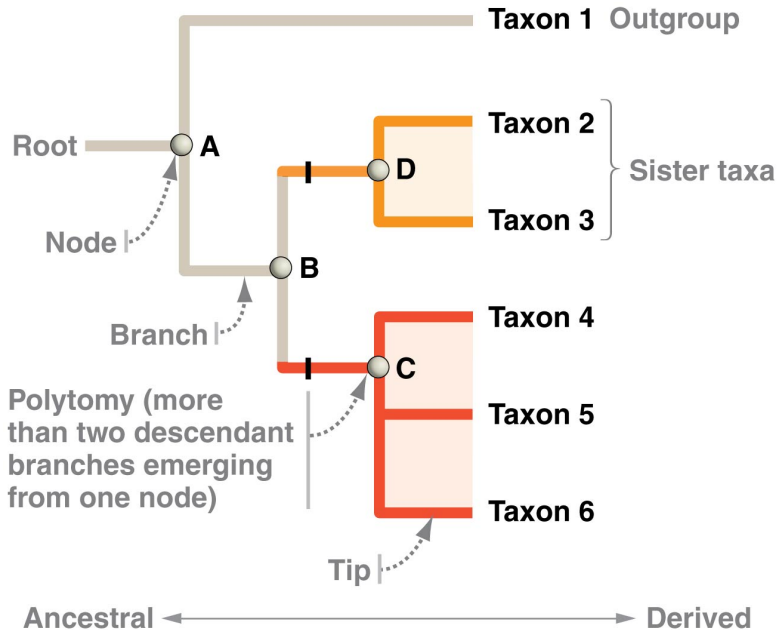
- Mass extinctions

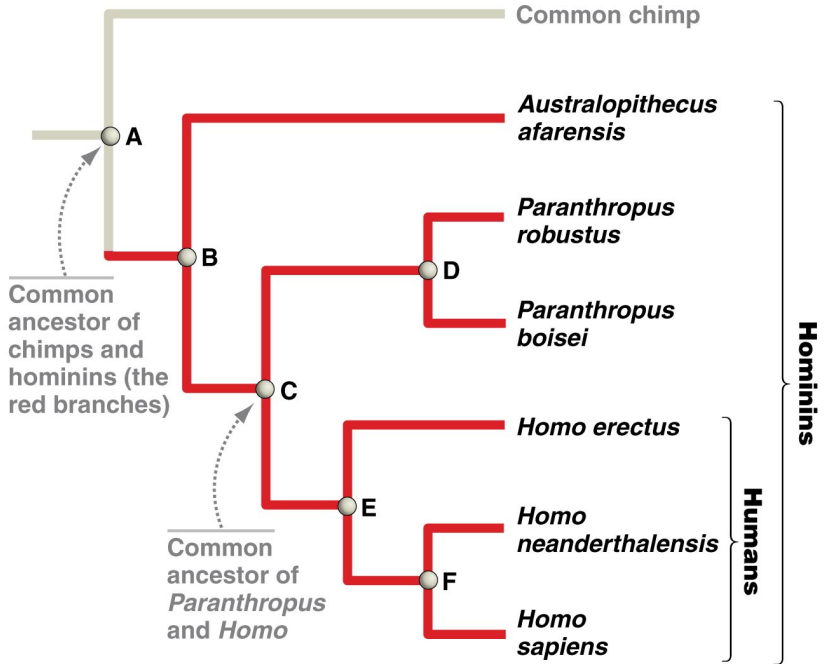
Phylogeny

- ▶ Phylogeny is the evolutionary history of a group of organisms
- ▶ Based on the idea that organisms are related by evolution
- ▶ Understanding these relationships is critical to our understanding of both evolution, and how biological processes work

Phylogenetic trees

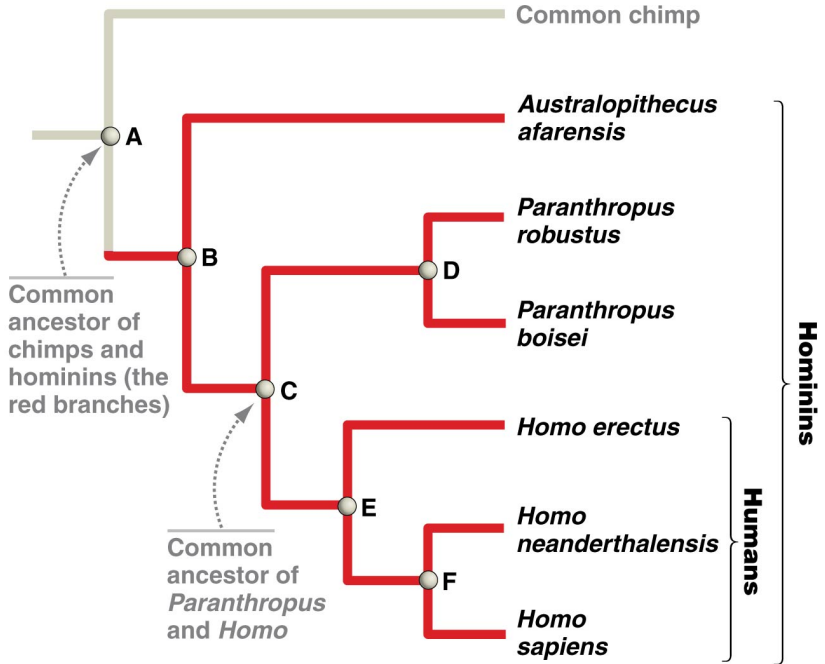
- ▶ A **phylogenetic tree** is a model of how a group of organisms descended from a common ancestor
- ▶ The model consists of **nodes**, where groups split, **branches** where evolution occurs, and **tips** representing observed **taxa** which are the endpoints of the process we are trying to model.
- ▶ A point where more than two branches diverge is called a *polytomy*.
 - ▶ Polytomies mean we don't know which event happened first.





Monophyletic group

- ▶ A **monophyletic group** is a group *defined by* a single common ancestor
 - ▶ All descendants of the ancestor must be in the group
- ▶ Monophyletic groups can also be called **clades** or **taxa**.
- ▶ As biologists, we should try to think in terms of clades
 - ▶ Are flying vertebrates a clade?
 - ▶ What are some prominent groups that are not clades?
 - ▶ * apes, reptiles, trees

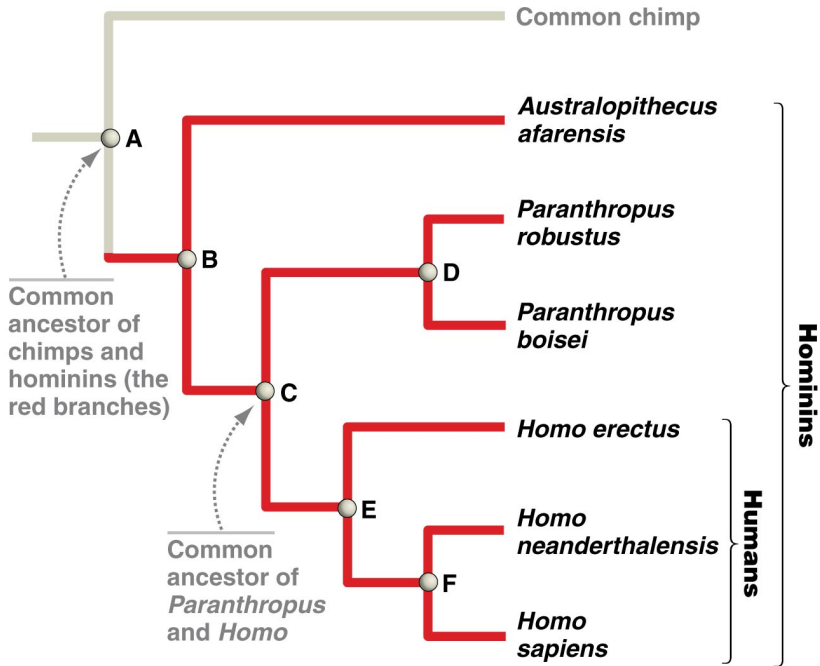


Sister taxa

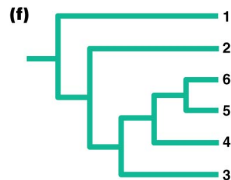
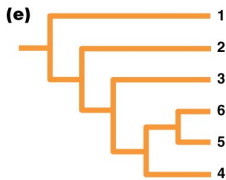
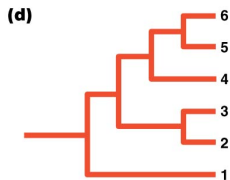
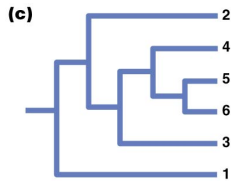
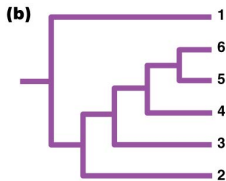
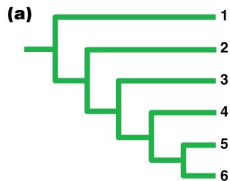
- ▶ Sister taxa can be a useful way of thinking about trees
 - ▶ two taxa that share a common node
 - ▶ You need to take the whole taxon
- ▶ E.g., sisters of: *Homo sapiens*; *Homo erectus*; humans?
 - ▶ * *Homo neanderthalensis*; *Hn* and *Hs*; *Paranthropus*

Reading phylogenetic trees

- ▶ The tree indicates the pattern of branching of **lineages** (evolving lines)
- ▶ Tips are *assumed* by the model to be monophyletic
- ▶ A tree is a model of how evolution occurred
 - ▶ Trees that correspond to the same model are considered equivalent



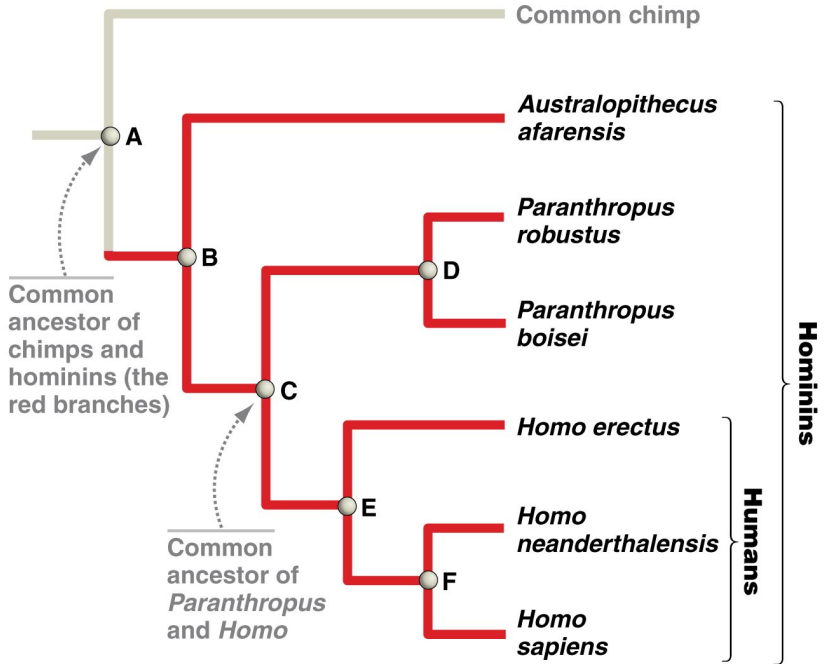
*Activity: which of these things is not like the others?
(present)*



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Order of species

- ▶ Except for the branching pattern, we don't interpret anything about the order of a tree
 - ▶ No species are higher or lower than others, according to the tree
 - ▶ We've all been evolving for the same amount of time
- ▶ How do we judge how closely related two organisms are, according to a tree?
 - ▶ * By looking for their common ancestor



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- Adaptive radiations

- Mass extinctions

Constructing phylogenetic trees

- ▶ First, measure **characteristics** (or **characters**) of the taxa of interest – i.e., anything that seems useful to measure
 - ▶ Can be **morphological** (i.e., physical) or genetic
- ▶ Then infer (make an educated guess about) the phylogenetic relationships.
 - ▶ **Phenetic** approaches use measures of distance between organisms
 - ▶ **Cladistic** approaches are based on modeling how evolution occurs on the tree

Morphological vs. genetic characteristics

- ▶ Should we use morphological or genetic characteristics to infer phylogenies?
 - ▶ We usually have more information from genetic characteristics, and this information is easier to measure precisely
- ▶ When should we use morphological characteristics?
 - ▶ * When genetic information is not available
 - ▶ * Most fossil organisms
 - ▶ *Some viruses evolve so fast that morphological characteristics can be more stable than genetic characteristics*

Phenetic vs. cladistic analysis

- ▶ Cladistic analysis makes use of the phylogenetic model of organisms evolving from each other to infer phylogenies
- ▶ Phenetic analysis ignores the phylogenetic model of organisms evolving from each other while inferring phylogenies
- ▶ Which is better?
 - ▶ * Cladistic analysis
- ▶ When should we use the other one?
 - ▶ * When our data are only distances, with no characters available – e.g., certain molecular techniques
 - ▶ * When we don't have enough baseline information

Synapomorphies

- ▶ Classical cladistic analysis is based on **synapomorphies** – shared, **derived** characters – as evidence that two taxa are related
- ▶ Why do we focus on derived characters?
 - ▶ * These are things that evolved in the relevant context
 - ▶ * So they are the things our model (the phylogenies) must explain

Flight as evidence

- ▶ Oaks and fish don't fly, but birds do
 - ▶ * We're pretty sure that the common ancestor didn't fly
 - ▶ * No evidence (any model will have flight evolve once)
 - ▶ * Flight evolved once in either case
- ▶ Mosquitoes and birds fly, but fish don't
 - ▶ * Evidence (flight might have evolved once or twice on this tree)
 - ▶ * But this evidence points in the wrong direction
 - ▶ * This is why we combine evidence from different sources

What characters are derived?

- ▶ Derived compared to what?
 - ▶ The common ancestor (characteristics of the common ancestor are called **basal** or **ancestral** characters).
 - ▶ What if our flight example was ostriches, hawks, and sparrows?
 - ▶ * No evidence for similarity between hawks and sparrows
 - ▶ * We believe the common ancestor could fly, so there is no shared, derived characteristic
 - ▶ A **derived** character is a character not shared by the common ancestor of the group that we are currently thinking about
 - ▶ One way to think about cladistic vs. phenetic analysis is that phenetic analysis treats derived and basal characters equally

Inferring the common ancestor

- ▶ We want to know what the common ancestor was like, so we can tell which characters are derived (as opposed to basal)
- ▶ This can be done sometimes by common sense
- ▶ Inferring the common ancestor statistically is difficult, for technical reasons
 - ▶ We can make use of an **outgroup** to study a group. An outgroup is an organism closely related to, but outside, the group being studied.
 - ▶ We assume that the the **root**, or beginning, of the tree is where the outgroup branches from the group

Confusing the phylogeny

- ▶ Two species may have the same trait because the trait evolved twice independently – **convergent evolution**
 - ▶ * Flight, trees, dolphins and ichthyosaurs
- ▶ An organism may lack a character that its ancestors had – **secondary loss**
 - ▶ This can be even more confusing
- ▶ Similarities that are not homologies (ie., not due to common ancestry) are called **homoplasies**

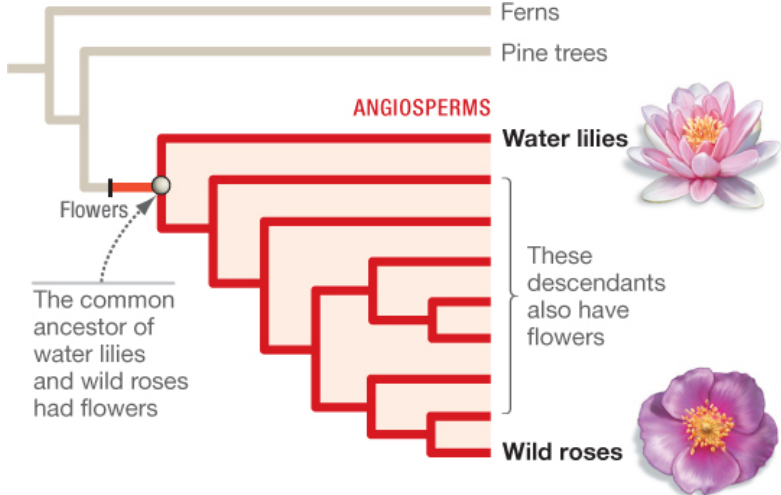


Figure 25.2 Homology: Similarities Are Inherited from a Common Ancestor. Flowers in diverse plants, such as water lilies and roses, are homologous.

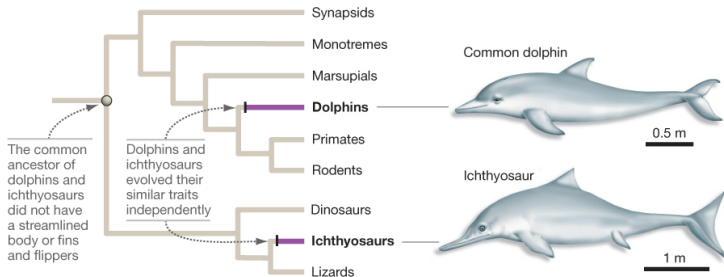


Figure 25.3 Homoplasy: Traits Are Similar but Not Inherited from a Common Ancestor. Dolphins and ichthyosaurs look similar but are not closely related.

Parsimony

- ▶ Classical cladistic analysis is based on searching for the tree that can explain the observed data most **parsimoniously** – with the fewest number of changes necessary.
- ▶ How do we address the problem of convergent evolution and homoplasy?
 - ▶ * Make use of many different characteristics, when possible
 - ▶ * It may also help to use many different taxa
- ▶ *Modern approaches that use genetic data may use more sophisticated approaches, rather than simple parsimony*

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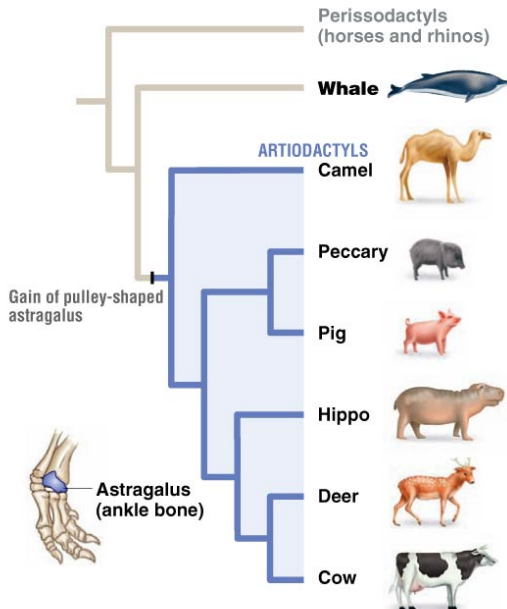
Example: the evolution of whales

- ▶ Whales seem, on the surface, to be pretty different from other mammals, including the closest group, the artiodactyls
- ▶ Early phenetic analyses showed whales in their own group (sisters to artiodactyls)
 - ▶ Whales lack the distinctive artiodactyl ankle structure (surprise!)
- ▶ What about cladistic analysis?

Biology is crazy! (Extra)

- ▶ Which of these doesn't belong?
 - ▶ Whale
 - ▶ Rhinoceros
 - ▶ Hippopotamus
 - ▶ Elephant

(a) Data set 1 (morphological traits):
Whales diverged before the origin of artiodactyls.



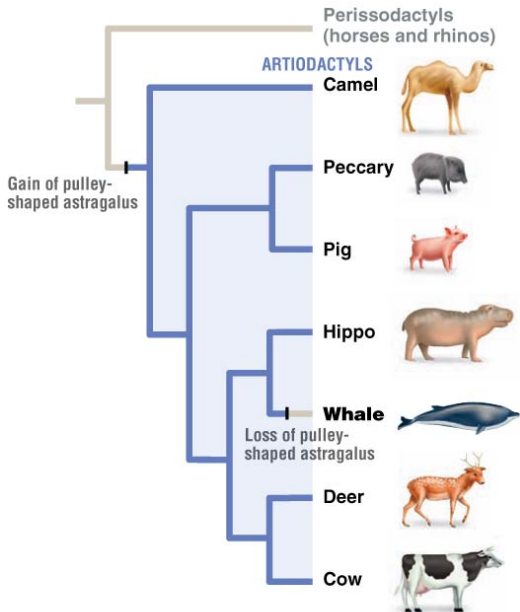
Activity: Tree-construction analysis

- ▶ Hippos have derived characters A, B, C, D, Z
- ▶ Cows have derived character A, Z
- ▶ Whales have derived characters B, C, D, E, F, G, H, I, Z
- ▶ Calculate distances, and make a phenetic tree
- ▶ List synapomorphies, and make a cladistic tree

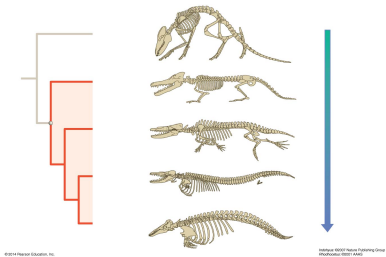
Tree discussion

- ▶ What is the effect of universal characteristics (like Z, above)?
 - ▶ * None
- ▶ What is the effect of unique characteristics (like E, F, G, H, I)
 - ▶ * They affect phenetic trees, but not cladistic trees
 - ▶ * As long as we are sure that they are derived!
- ▶ Why might whales have more derived characters than the other species?
 - ▶ * Because they have had to adapt more since moving to the water

(b) Data set 2 (DNA sequences):
Whales and hippos share a common ancestor.

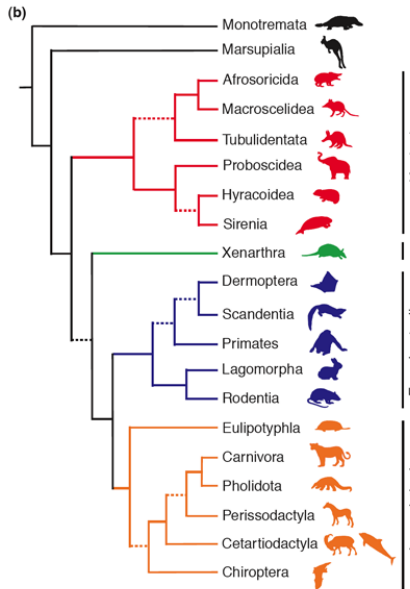
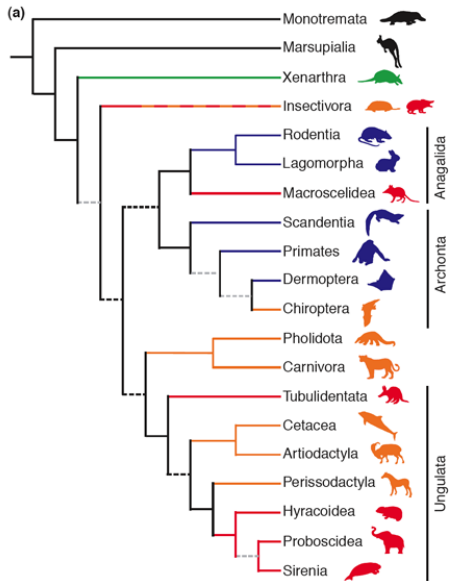


Confirmation



- ▶ Intermediate forms between hippo-like animals and whales
- ▶ Discovered *after* they were predicted from DNA evidence!

Morphological and genetic cladograms (Extra)



How to make a phenetic tree

- ▶ 1. Join the two open nodes that are closest to each other
 - ▶ Shortest distance
- ▶ 2. They are no longer active. Make a new node halfway between them
 - ▶ Average the traits
 - ▶ This step is conceptually simple and practically tricky
 - ▶ *This is why we have computers*
- ▶ 3. Go back to step 1

How to make a phenetic tree in this course

- ▶ 1. Join the two open nodes that are closest to each other
 - ▶ Shortest distance
- ▶ * 2. *Stop!* You're done.
 - ▶ * I will only give you three species
 - ▶ * Seriously.
- ▶ *I'm here to teach you concepts, not to teach you how to be a really bad computer.*

Lessons

- ▶ Phenetic analysis uses less information
- ▶ To do a cladistic analysis, inferences about the common ancestor can be crucial
 - ▶ What if we thought the artiodactyl ancestor was aquatic?
 - ▶ E, F, G, H and I could all be basal characters
 - ▶ * We would conclude that cows are closely related to hippos

Genetic vs. morphological

- ▶ Why was the genetic analysis more effective than the morphological?
 - ▶ * It can be hard to tell which traits are derived
 - ▶ * This can also be a problem with the genetic analysis
 - ▶ * Genetic analyses typically allow us to analyze more traits

Phylogenetic trees are approximations!

- ▶ Phylogenetic trees are tremendously useful and powerful tools for organizing, understanding and analyzing biological data
- ▶ But they have limitations:
 - ▶ The true history of life cannot really be summarized by a tree
 - ▶ Sex, other forms of combination or gene transfer
 - ▶ Trees constructed by humans are not necessarily even the best approximations to the true history of life
 - ▶ Our guesses often change over time

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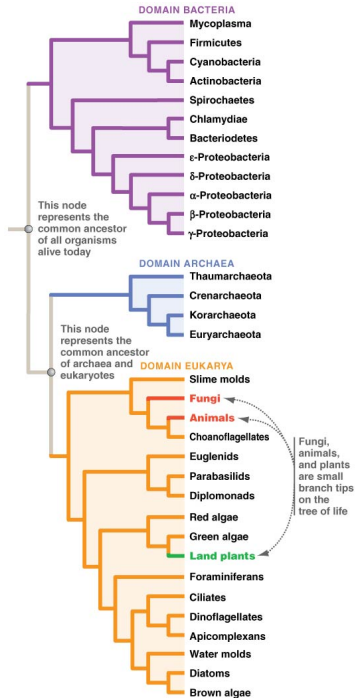
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The shape of the tree

- ▶ Big recent innovations have told us a lot about the history of life
 - ▶ Detailed genetic information
 - ▶ Sophisticated analysis techniques
 - ▶ Electronic computers

Three domains

- ▶ Bacteria
 - ▶ no nuclei; mostly small
 - ▶ most of the micro-organisms you see
- ▶ Archaea
 - ▶ no nuclei; mostly small
 - ▶ rarer, or live in more extreme environments
- ▶ Eukarya
 - ▶ large, nucleated cells

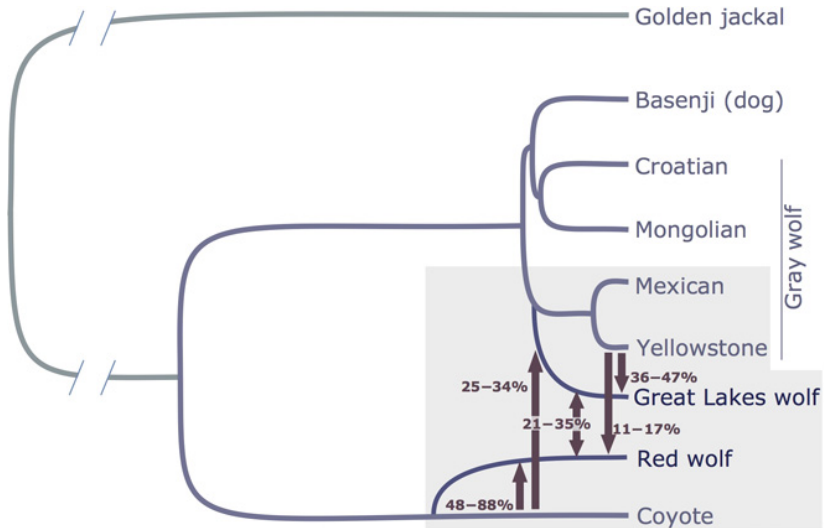


Eukaryotes

- ▶ Seem to be sisters with archaea, according to most of our key genes
- ▶ Characterized by **nuclei** and **mitochondria**
- ▶ Mitochondria came later, and are captured bacteria!
- ▶ Where did the nucleus come from?
 - ▶ Nobody knows

The web of life

- ▶ The tree is only part of the story!
 - ▶ If genes (or even whole bacteria) can be transferred, life is not really a tree
- ▶ Reuniting can create new species
 - ▶ Hybridization
 - ▶ Allopolyploidy
 - ▶ * Polyploids arising from different (allo-) species
- ▶ Wolf-coyote example



Five kingdoms (Extra)

- ▶ Animals
- ▶ Plants
- ▶ Fungi
- ▶ Protists
- ▶ Bacteria

Five kingdoms

- ▶ Not really a good way to describe the evolution of life
- ▶ So why has this idea persisted for so long?
 - ▶ * It matches the way the world *looks* – animals, plants and fungi dominate *visible* life
 - ▶ * Some branches are have organisms that are much smaller, or just have much fewer organisms
 - ▶ * Archaea and bacteria are difficult to tell apart even with a microscope

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The fossil record

- ▶ A **fossil** is a physical trace of an organism from the past
 - ▶ Intact fossils retain their form and substance
 - ▶ Compression fossils are squashed into a thin film
 - ▶ Cast fossils occur when the decomposing piece is replaced by minerals different from the surrounding ones
 - ▶ Permineralized fossils occur if minerals infiltrate cells as they are decomposing
- ▶ *Does any of this seem likely?*

(a) Intact fossil (pollen)



(b) Compression fossil (leaf)



(c) Cast fossil (bark)



(d) Permineralized fossil (tree trunk)

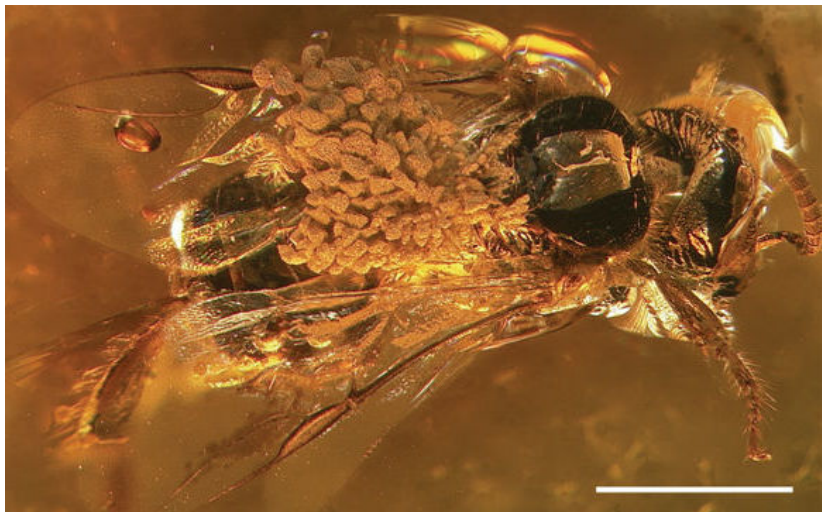


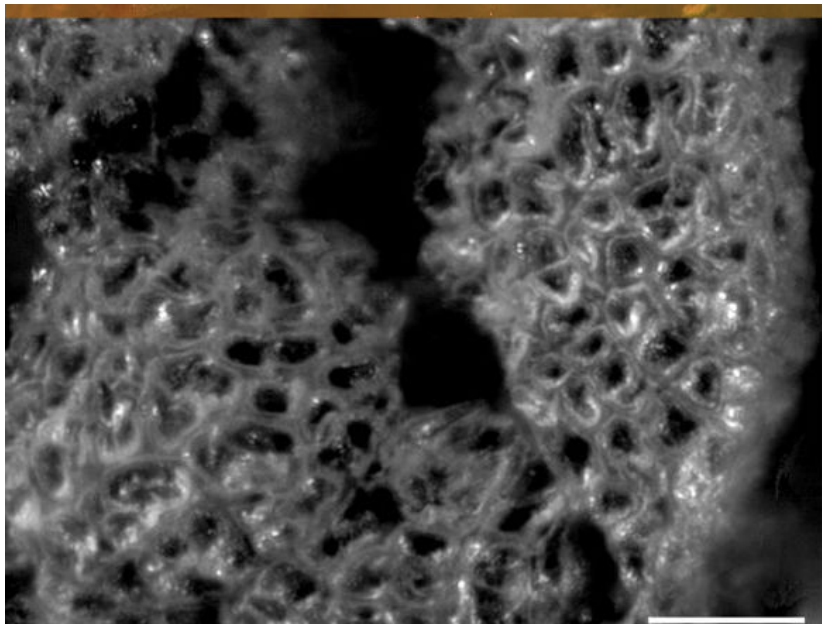
Biases in the fossil record

- ▶ Scientists have learned a lot from studying fossils, but care is needed. Very few things fossilize, and some things are much more likely to fossilize than others, for example:
 - ▶ Things that live in swampy areas, or underground (**Habitat bias**)
 - ▶ Hard things, or hard parts of things (**Taxonomic bias**)
 - ▶ Things that lived more recently have had less time to be destroyed, or to be buried too deep for recovery (**Temporal bias**)
 - ▶ Things that are more abundant have more chances to be preserved (**Abundance bias**)

Accounting for biases

- ▶ Because the fossil record is biased, scientists must be very careful about making inferences from what they see
 - ▶ Just because you don't see it, doesn't mean that it wasn't there
 - ▶ Just because you see a lot, doesn't mean that there were a lot (relatively speaking)
- ▶ Trying to figure out what happened based on what kind of fossils we happen to find is tricky
- ▶ Orchid phylogeny





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Putting the timeline together

- ▶ Dates of specimens can be inferred using radioactive isotopes (harder than it sounds)
- ▶ Geologic inferences can be made about the relative age of different things (for example, if one was deposited on top of another).
- ▶ Molecular clocks are based on inferences about how fast things are evolving
- ▶ These techniques are complicated, and making the timeline is a difficult and exciting puzzle

Guessing game (*Extra*)

- ▶ For most of Earth's history, there has been:
 - ▶ No life
 - ▶ Life, but no multi-cellular organisms
 - ▶ Multi-cellular organisms, but no plants, animals or fungi
 - ▶ Plants, animals, and fungi, but no flowering plants, birds or mammals
 - ▶ Flowering plants, birds and mammals, but no good espresso

Guessing game (Extra)

- ▶ For most of Earth's history, there has been:
 - ▶ No life
 - ▶ **Life, but no multi-cellular organisms**
 - ▶ Probably
 - ▶ Multi-cellular organisms, but no plants, animals or fungi
 - ▶ Probably not – may depend on definitions
 - ▶ Plants, animals, and fungi, but no flowering plants, birds or mammals
 - ▶ Flowering plants, birds and mammals, but no good espresso

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Processes of diversification

- ▶ Diversity sometimes arises gradually, and sometimes dramatically (**radiation** events)
- ▶ Species (and families, and bigger groups) sometimes disappear gradually, and sometimes dramatically (**mass extinction** events)

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Adaptive radiations

- ▶ An **adaptive radiation** occurs when a single lineage produces many descendant species, in a short period of time, that make their living in a variety of different ways
- ▶ Triggered by opportunity, either in the environment, or because of the evolution of the organisms themselves

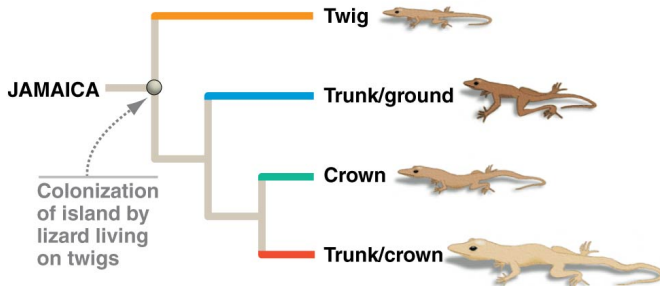
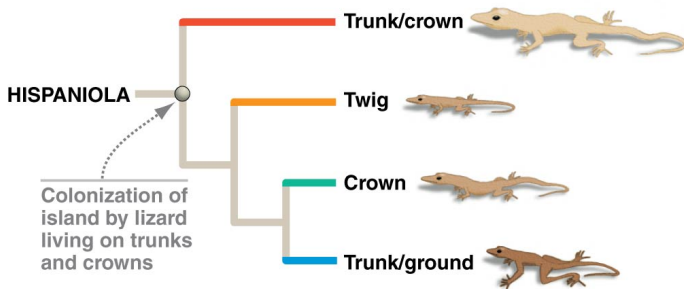
Triggers for adaptive radiation

- ▶ Ecological opportunity
 - ▶ An organism arrives in an area with no similar organisms
 - ▶ A group of competing species is driven extinct (or nearly extinct) by some other cause
- ▶ Morphological innovation: an organism comes up with a good, new idea
 - ▶ Legs in tetrapods
 - ▶ New body plans in the Cambrian explosion
 - ▶ Multi-cellularity
- ▶ Co-evolution: the evolution of one group creates new niches for another group, and vice versa
 - ▶ The insects and the flowering plants

Colonization

- ▶ In many different cases, a new kind of organism has colonized an area, and diversified rapidly
- ▶ This is an opportunity for studying how evolution can go:
 - ▶ What is the same, and what is different, between similar cases?
 - ▶ Finches
 - ▶ Silverswords in Hawaii
 - ▶ Anolis lizards

(c) The same adaptive radiation of *Anolis* has occurred on different islands, starting from different types of colonists.



Competition

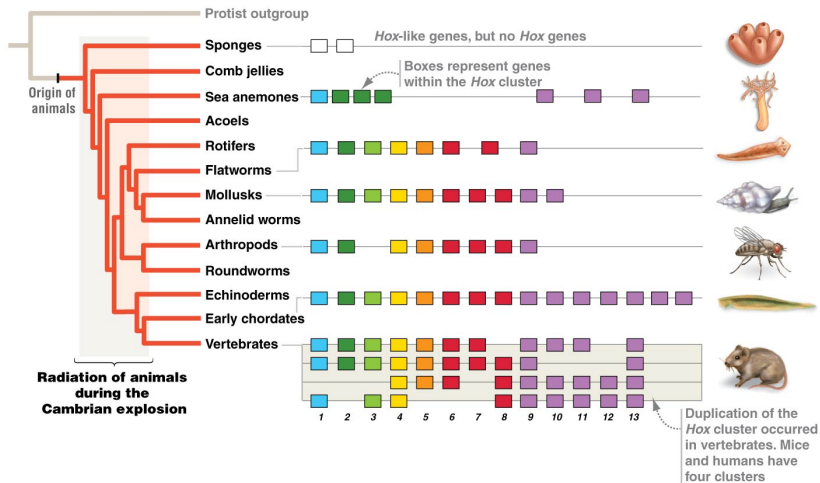
- ▶ Mammals did very well after the dinosaurs went extinct
- ▶ We have seen major tree extinctions due to introduced diseases in the last century
 - ▶ * This opens up ecological niches
 - ▶ * Species may diverge to fill these niches
 - ▶ * Or spread around the world to fill them

Morphological innovation

- ▶ A new adaptive mutation can open up further possibilities for adaptation
 - ▶ **Hox gene** mutations allowed early animals to develop complex body plans
 - ▶ The arthropod body plan
 - ▶ insects, arachnids, crustaceans ...
 - ▶ The tetrapod body plan
 - ▶ reptiles, mammals ...
 - ▶ Flowering plants
 - ▶ This opened many new opportunities for *everyone* (insects, mammals, birds), not just the innovators
 - ▶ * Animals evolved to exploit the flowering plants
 - ▶ * Flowering plants and animals *co-evolved*
 - ▶ * Natural defenses and exploits
 - ▶ * Pollination and dispersal

Hox genes

- ▶ **Hox genes** are involved in determining the identity of different body parts
- ▶ Taxa with simpler body structures tend to have fewer hox genes
 - ▶ Phylogenetic comparisons provide important evidence that hox genes were involved in evolution of complex body plans
- ▶ Evidence that new hox genes were largely created by **gene duplication** events
 - ▶ A rare but important type of mutation
 - ▶ Natural selection must have played a role in the development of this much complexity



Gene duplication

- ▶ One or more genes may be accidentally duplicated so that the genome has two copies of each gene
- ▶ This may make the organism less efficient, and thus be selected against
- ▶ It may also allow for innovation. Why?
 - ▶ * Because one copy can continue to do the old function, while the other evolves a new function

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Mass extinctions

- ▶ Five major mass extinctions so far
- ▶ The last one (and maybe others) was caused by a cosmic impact
 - ▶ It could happen again
- ▶ Are we in the middle of a mass extinction now?
 - ▶ Extinction rate very high over the last 400 years
 - ▶ Time will tell, but we should be worried

Conclusion

- ▶ The best way to reconstruct evolution is with a *model* of how it occurred
 - ▶ Molecular information, and computer modeling has changed our view of the tree of life
 - ▶ life is not really a tree
 - ▶ genetic information can be transferred
 - ▶ sexual mixing occurs at different scales
- ▶ Scientists use many clues to figure out the history of life on earth
 - ▶ Fossils, geology, phylogeny
- ▶ Life has diversified both gradually, and with dramatic episodes
 - ▶ Adaptive radiations, mass extinctions