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

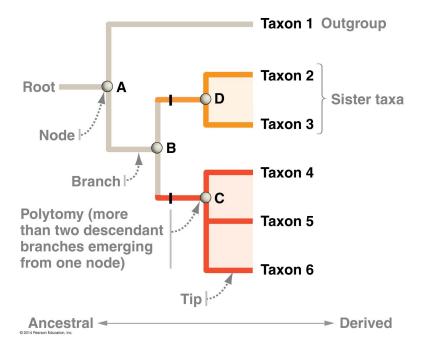
Adaptive radiations
Mass extinctions

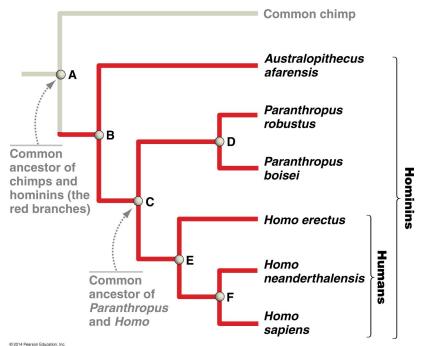
Phylogeny

- ▶ 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

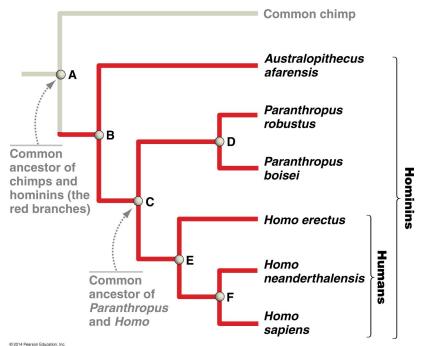
- ► A **phylogenetic tree** is a model of how a group of organisms descended from a common ancestor
- ► The model consists of **nodes**, where groups split, **branches** where evolution occurs, and **tips** representing observed **taxa** which are the endpoints of the process we are trying to model.
- 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

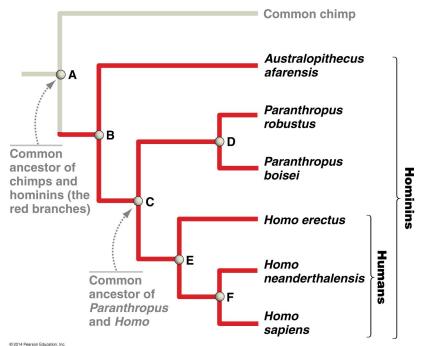


Sister taxa

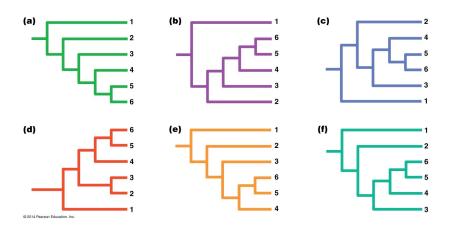
- Sister taxa can be a useful way of thinking about trees
 - two taxa that share a common node
 - You need to take the whole taxon
- ► E.g., sisters of: *Homo sapiens*; *Homo erectus*; humans?
 - * Homo neanderthalensis; Hn and Hs; Paranthropus

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

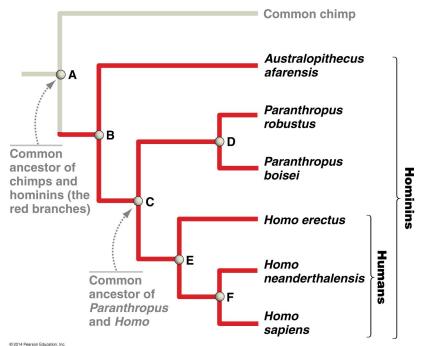


Activity: which of these things is not like the others? (present)



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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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 icthyosaurs
- 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**

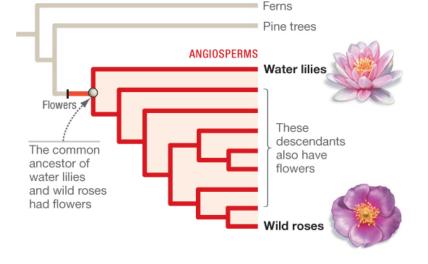


Figure 25.2 Homology: Similarities Are Inherited from a Common Ancestor. Flowers in diverse plants, such as water lilies and roses, are homologous.

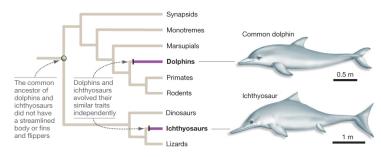


Figure 25.3 Homoplasy: Traits Are Similar but Not Inherited from a Common Ancestor. Dolphins and ichthyosaurs look similar but are not closely related.

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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
 - Rhinocerous
 - Hippopotamus
 - Elephant
- ► Aadd FUNSLIDE needs an annotation on complete notes

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

Perissodactyls (horses and rhinos) Whale 2 **ARTIODACTYLS** Camel Peccary Gain of pulley-shaped astragalus Pig Hippo Astragalus Deer (ankle bone)

Cow

Activity: Tree-construction analysis

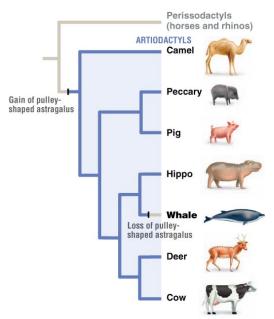
- Hippos have derived characters A, B, C, D, Z
- Cows have derived character A, Z
- Whales have derived characters B, C, D, E, F, G, H, I, Z
- Calculate distances, and make a phenetic tree
- List synapomorphies, and make a cladistic tree

Tree discussion

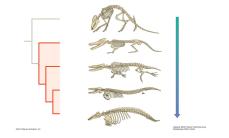
- ▶ What is the effect of universal characteristics (like Z, above)?
 - ► * None
- What is the effect of unique characteristics (like E, F, G, H, I)
 - * They affect phenetic trees, but not cladistic trees
 - ▶ * As long as we are sure that they are derived!
- Why might whales have more derived characters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

(b) Data set 2 (DNA sequences):

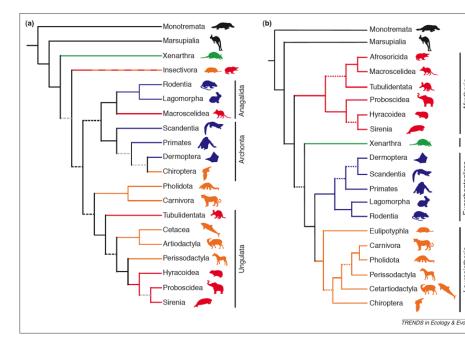
Whales and hippos share a common ancestor.



Confirmation



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



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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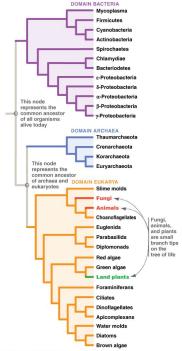
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The shape of the tree

- 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

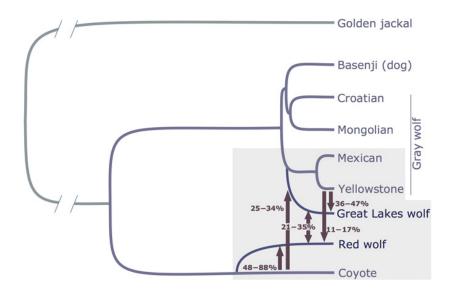


Eukaryotes

- ► 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)

(b) Compression fossil (leaf)





(c) Cast fossil (bark)

(d) Permineralized fossil (tree trunk)



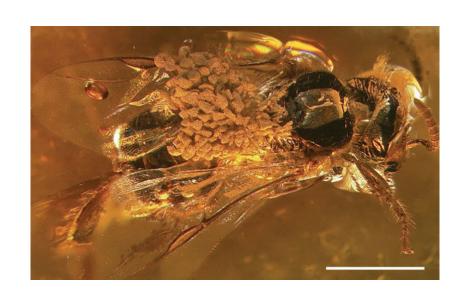


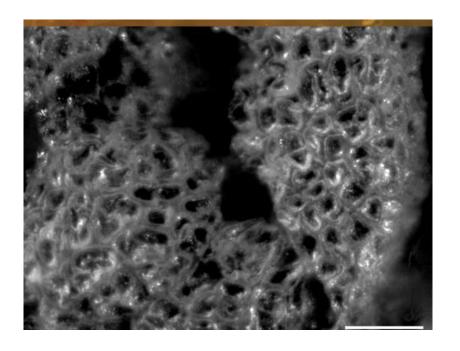
Biases in the fossil record

- 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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- ▶ 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

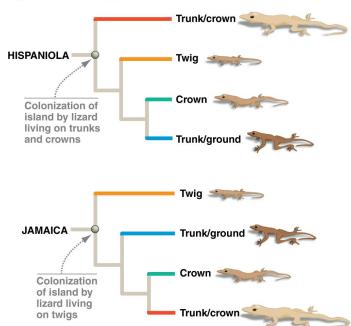
Triggers for adaptive radiation

- 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

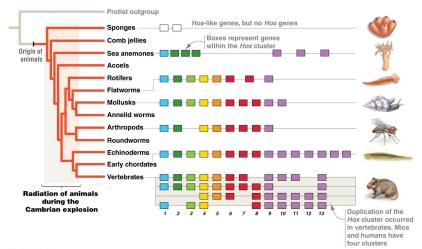
- ▶ Mammals did very well after the dinosaurs went extinct
- We have seen major tree extinctions due to introduced diseases in the last century
 - * It remains to be seen whether new evolution will fill this opportunity

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
 - ► * Co-evolution

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



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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