

Bio 1M: Phylogeny and the history of life (complete)

1 Phylogeny

- *Bioskills are in the back of your book*
- 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?
 - * **Answer:** 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?
 - **Answer:** *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

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?
 - **Answer:** By looking for their common ancestor

1.1 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?
 - **Answer:** When genetic information is not available
 - * **Answer:** Most fossil organisms
 - **Comment:** 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?
 - **Answer:** Cladistic analysis
- When should we use the other one?
 - **Answer:** When our data are only distances, with no characters available – e.g., certain molecular techniques
 - **Answer:** 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?
 - **Answer:** These are things that evolved in the relevant context
 - **Answer:** So they are the things our model (the phylogenies) must explain

Flight as evidence

- Oaks and fish don't fly, but birds do
 - **Answer:** We're pretty sure that the common ancestor didn't fly
 - **Answer:** No evidence (any model will have flight evolve once)
 - **Answer:** Flight evolved once in either case
- Mosquitoes and birds fly, but fish don't
 - **Answer:** Evidence (flight might have evolved once or twice on this tree)
 - **Answer:** But this evidence points in the wrong direction
 - * **Answer:** 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?
 - * **Answer:** No evidence for similarity between hawks and sparrows
 - * **Answer:** 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**
 - **Answer:** 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**

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?
 - **Answer:** Make use of many different characteristics, when possible
 - **Answer:** It may also help to use many different taxa
- *Comment:* Modern approaches that use genetic data may use more sophisticated approaches, rather than simple parsimony

1.2 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?

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

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
 - Comment: 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
- Answer: 2. *Stop!* You're done.
 - Answer: I will only give you three species
 - Answer: Seriously.
- Comment: 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
 - * Answer: We would conclude that cows are closely related to hippos

Genetic vs. morphological

- Why was the genetic analysis more effective than the morphological?
 - Answer: It can be hard to tell which traits are derived
 - * Answer: This can also be a problem with the genetic analysis
 - Answer: 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

2 The history of life

2.1 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
 - * **Answer:** Polyploids arising from different (allo-) species
- Wolf-coyote example

Five kingdoms

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

2.2 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
- *Comment:* Does any of this seem likely?

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

2.3 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

3 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)

3.1 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

Competition

- Mammals did very well after the dinosaurs went extinct
- We have seen major tree extinctions due to introduced diseases in the last century
 - **Answer:** 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
 - * **Answer:** 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

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?
 - **Answer:** Because one copy can continue to do the old function, while the other evolves a new function

3.2 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