# PATHWAYS OF EVOLUTION

## SYSTEMATICS

The diversity of life on earth is overwhelming. So overwhelming that for centuries humans have attempted to organize, or classify, organisms into categories that make sense. The most famous system of classification, developed by Linnaeus in the 1700's and still used today, is the **binomial nomenclature** system. There are two important features of this system. First, *each species has a two-part name*: genus and species. Second, the system classifies species into *hierarchical groupings*, in which groups are nested within larger groups. Similar species are grouped into a genus. Similar genera are grouped into a family, and so on. In short, *organisms are classified together because they are similar*.

Darwin made an extremely important observation about classification: organisms are classified together because they are similar; ***they are similar because they stem from a common ancestor***. This point cannot be emphasized enough. The foundation of taxonomy is evolutionary relatedness; classification reflects the history of species. This idea forms the basis of modern systematics. ***The main goal of modern systematics is to make biological classification reflect evolutionary history***.

### Modern Systematics

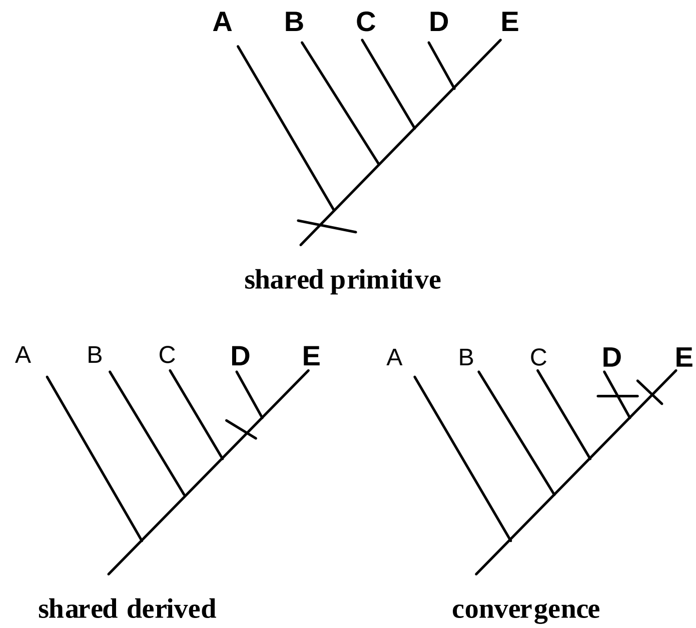
There has only been one history of life on earth. The goal of modern systematics is to discover what this history has been. In other words, how are living and extinct organisms related to one another? What is the genealogy of life? As in all fields of science, systematists develop hypotheses. The hypotheses of systematics are phylogenetic trees, or phylogenies. ***A phylogeny is the hypothesized evolutionary relationship among a group of taxa***.

### Constructing Phylogenies

Constructing phylogenetic hypotheses is in principle a simple thing, but in practice can be quite difficult. Indeed, much of the work in modern systematics is to determine the most appropriate methods for reconstructing evolutionary history.

*Phylogenetic reconstruction begins with* ***choosing characters*** that will be used to compare the taxa of interest. These characters can be morphological, or more commonly, molecular (amino acid or nucleotide sequences). *The various characteristics, or* ***character states*** *(alternate forms of the character) are then defined for each character*. For example, if hair color is the character, then blonde, brown, black, etc. are the character states. If nucleotide sequences are the characters, then for each base pair, A, G, T, or C will be the character states.

Figure 1: Three causes of similarity




Taxa D and E have the same character state (shown in bold). Hash marks indicate where the evolutionary event (from normal text to bold text) took place.

Previously, overall similarity was used to classify organisms: the species that had the greatest number of similar characteristics were grouped together (called phenetics[1]). However, *just using overall similarity to classify does not necessarily reveal evolutionary relationships*, and is rarely used today. The reason for this is that similarity in a character state between two species can have three different origins (also see Figure 1):

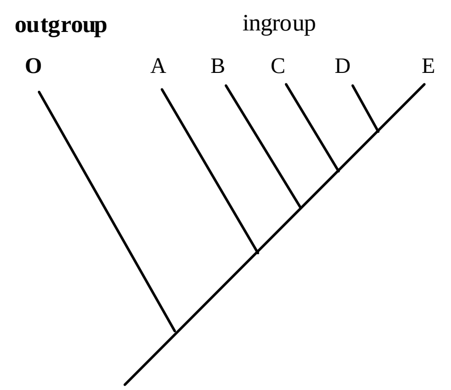
1) **shared primitive state** (character state is older than the most recent common ancestor of the two species)

[1] **Phenetics** is a method of systematic analysis that bases taxonomy on overall similarity, with no attempt to separate homology from analogy (i.e. convergence). **Cladistics** (or **phylogenetics**) attempts to use only homologous, and more specifically, shared derived characters, to define lineages. Today, the vast majority of systematists are cladists.

2) **shared derived state** (character state evolved in the common ancestor of the two species)
3) **convergence** (character state evolved independently in each of the two species)

The first two are homologies (similarity due to shared ancestry), while the third is analogy (similarity due to adaptation to similar environments). Only homologies are useful in phylogenies, as homologies reflect a shared history. Of the two types of homologies, ***only shared derived characters are useful for inferring the true evolutionary relationship among taxa***. Shared derived characters define a group with a shared history: they evolved in an ancestor that was common to all members of the group. They are the distinguishing characteristics of the group.

Figure 2: Outgroup Comparison




Every group of species has a mix of shared primitive states and shared derived states. How is it determined if shared character states are derived or primitive (i.e. how is the **polarity** of the character states determined)? Often, a method called **outgroup comparison** is used. An ***outgroup*** *is a species that is closely related to the group of species of interest (the ingroup),* but clearly not as related as members of the group are to each other (see Figure 2). Character states that are shared by the outgroup species and most/all members of the ingroup are defined as **shared primitive**. Character states of ingroup species that are not found in the outgroup species can be considered to be **shared derived** (i.e. derived more recently than the branch between the ingroup and outgroup). Once shared derived character states have been identified, a phylogenetic hypothesis can be constructed by determining which species have the most shared derived character states.

There are many difficulties involved in phylogeny reconstruction. Choosing independent characters and scoring character states can be tricky. Convergence can be quite common, and this can create complications. Phylogenies are hypotheses. Hypotheses are not just accepted; they are tested and re-tested and modified with new evidence. ***As with any hypothesis, a phylogeny can be strongly supported or weakly supported, depending on the available evidence***.

## Evaluating Phylogenetic Hypotheses

Because of the historical nature of systematics, phylogenetic hypotheses cannot be tested with experiments. However, this does not mean they cannot be tested. Phylogenetic history is reconstructed in a way that is similar to how a criminal investigator reconstructs a crime scene. Investigators are never present when the crime actually happened, but they are very good at determining what most likely occurred. The reason is that clues to past events are always left, and the job of the investigator is to piece together this evidence into a story about what most likely happened. If more clues are found that do not fit the story, then something about the story is wrong, and needs to be modified.

This is what systematists do. After constructing a phylogeny with data, they then test the phylogenetic hypothesis with more data. For example, a tree constructed from morphological data can be tested by comparing it to a tree constructed from molecular data. If the two trees are the same, they are said to **agree**. ***Agreement with independent data is strong support for a phylogenetic hypothesis.***

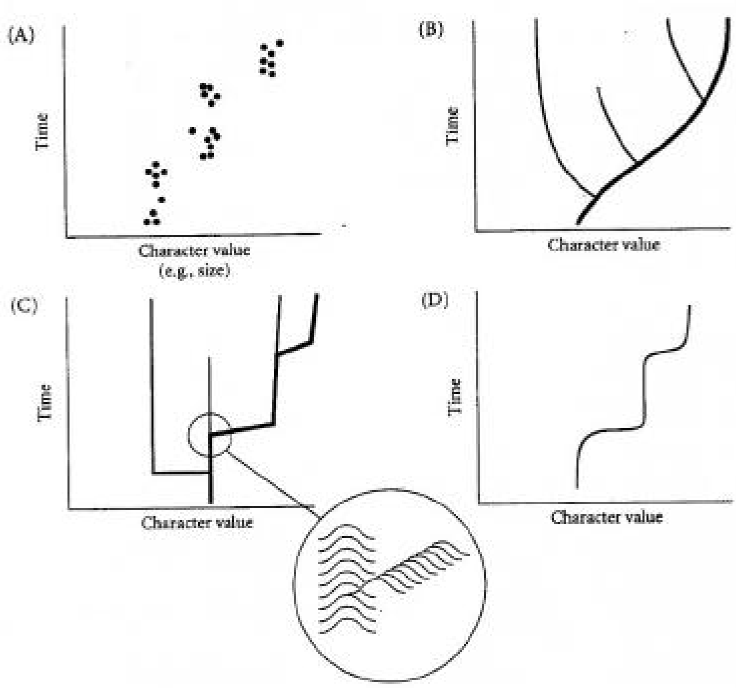
## Uses of Phylogenies

Well-supported phylogenies are extremely useful in many different fields within biology. Their primary uses are to better understand the history of change in a particular character, and to test hypotheses about the evolution of a particular character or characters.

More recently, phylogenetic methods are also being used outside of biology. For example, the various manuscripts of Chaucer's Canterbury Tales have been analyzed phylogenetically (Barbrook, et al. 1998). [[link to resource list]] The various forms of a manuscript that are around today are analogous to living species. Living species (and manuscripts) are related through common ancestry. Changes have occurred through time, so that each species (and manuscript) are now quite different from each other; however, species (and manuscripts) that share a more recent history are more similar. Thus, determining the relationship between the manuscripts using phylogenetic methods is similar to determining the relationship among living species. Various questions about these manuscripts can then be addressed. For example, from these studies, it has been inferred that Chaucer's original manuscript was not a complete version, but rather a draft with his notes, which editors later changed multiple times.

Phylogenies are also now acceptable in U.S. courtrooms as legal evidence, such as in a famous trial in Louisiana in 1998. In this trial a doctor was accused of injecting his ex-mistress with blood from one of his HIV patients, whose blood he had drawn the same day she was injected. To test this story, a phylogeny of her HIV, the patient's HIV, and other HIV from people in the same town was constructed. HIV evolves quickly within a single host, and as it goes from host to host, it changes more and more. Therefore, it can be predicted that if the ex-mistress had indeed been injected with blood from the patient, her HIV should be most closely related to each the patient's HIV, than it was to anyone else's in town. The phylogeny confirmed this prediction, and showed that the ex-mistress' HIV was more similar to the patient's HIV, and very unlike others from around town, suggesting that the doctor did inject her with HIV-tainted blood. He was convicted.

Figure 4: Three Hypotheses about Character Evolution




A) hypothetical series of fossils that need to be explained
B) phyletic gradualism
C) punctuated equilibrium
D) punctuated gradualism

**MACROEVOLUTION**

The study of macroevolution involves the investigation of patterns and processes that are important in evolution above the level of the species. For example, one question is ***what is the <u>pattern</u> of character evolution?*** Does character evolution proceed at a continuous, gradual rate (as

Darwin envisioned), or do characters change relatively little over long periods of time, with this period of stasis "punctuated" with very rapid change? Punctuated equilibrium is a model that describes this second pattern, as well as proposing a hypothesis to help explain it (see below). Detailed fossil records can help address this question for a particular group of organism.

To explain the patterns observed in the fossil record, several hypotheses about evolutionary processes have been suggested. The major difference in these hypotheses is in the driving force of character evolution (Figure 3)[2]. Is the evolutionary diversification of lineages a gradual process that occurs all the time, or is it a special event that results directly from the process of lineage splitting (speciation)? One hypothesis predicts slow, steady changes in fossil species over time, while the other predicts long periods of stasis (equilibrium) "punctuated" by rapid bursts of evolutionary change during speciation events.

1) **phyletic gradualism—**gradual character evolution occurs continuously
2) **punctuated equilibrium—**rapid character evolution occurs only during speciation events, with little change at other times
3) **punctuated gradualism—**rapid character evolution occurs, but not necessarily only during speciation events.

*Another major question about* process *is what is the genetic mechanism responsible for the pattern of large phenotypic differences between taxa?* There are two hypotheses that have been put forward to explain the pattern of phenotypic gaps found between extant taxa. These hypotheses deal with the genetic causes of the phenotypic differences found in higher taxa:

1) **saltation—**these gaps exist because there were never any intermediates: gaps are explained by single events of *macromutations* (single mutations of very large phenotypic effects).
2) **gradualism—**successive fixation of mutations of slight phenotypic effect (i.e. *micromutations*; intermediates did exist, and the gaps are there because the fossil record is incomplete).

Contrary to popular belief, punctuated equilibrium is a gradualistic model (i.e. evolution occurs through the accumulation of mutations of small effects). In this model, intermediates do not appear in the fossil record because the change in morphology occurred so rapidly that the fossil record appears discontinuous. The more rapid the change, the less likely it will have been preserved by fossilization.

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[2] This figure was modified from Futuyma, 1998.

Based on numerous lines of evidence, most biologists agree with a gradualistic model. For example, macromutations do occur, but they usually have diverse pleiotropic phenotypic effects, and end up being selectively disadvantageous. Also, the genetics of species differences reveals a polygenic inheritance of the characters that distinguish species (i.e. many micromutations). Also, gradations (i.e. intermediates) in character states are common among closely related species.

## Resource List


Barbrook, A.C., Howe, C.J., Blake, N. & Robinson, P. 1998. The phylogeny of The Canterbury Tales. Nature 394: 839.

Basolo, A.L. 1990. Female preference pre-dates the evolution of the sword in swordtail fish. Science 250: 808-810.

Basolo, A.L. 1995. Phylogenetic evidence for the role of a pre-existing bias in sexual selection. Proc. R. Soc. Lond. B 259: 307-311.

Campbell, N.A., Reece, J.B. & Mitchell, L.G. 1999. Biology (5$^{th}$ ed). Benjamin/Cummings Publishing Company, Inc. California.

Futuyma, D.J. 1998. Evolutionary Biology (3$^{rd}$ ed). Sinauer Associates, Inc. Massachusetts.

Scott, E.C. 1997. Dealing with anti-evolutionism. Reports of the National Center for Science Education 14: 24-30.

Strahler, A.N. 1999. Science and Earth History—The Evolution/Creation Controversy. Prometheus Books, New York.

# LESSONS ON THE PATHWAYS OF EVOLUTION

## General Lessons on Systematics

The University of California's Museum of Paleontology has a "Phylogeny Wing Exhibit," [[www.ucmp.berkeley.edu/exhibit/phylogeny.html]] which includes a tutorial on phylogenetic systematics. The ENSI website has two general read-and-discuss lessons on systematics: "**Why Cladistics?**" [[www.indiana.edu/~ensiweb/lessons/whyclad.html]], and "**What, If Anything, is a Zebra?**" [[www.indiana.edu/~ensiweb/lessons/zebra.html]].

## Distinguishing Classification from Phylogenetic Systematics

There are several lessons that help introduce the concept of phylogenetic systematics and help students make the jump from the nested hierarchy of classification, to the evolutionary relationships among organisms. They use the concepts of distinguishing characteristics to get across the idea that groups have a common ancestor. In other words, *organisms are classed together because they are similar and they are similar because they share a common ancestry*. The following two lessons are from the ENSI website: "**Primate Classification**" [[www.indiana.edu/~ensiweb/lessons/primclas.html]] and "**Cladistics is a Zip…Baggie.**" [[www.indiana.edu/~ensiweb/lessons/clad.bag.html]] The first uses primates, with the nested hierarchy represented as boxes within boxes, and the second uses vertebrates, with nesting within various sized Ziploc baggies. ENSI also has a whole class activity, "**Classroom Cladogram**," [[www.indiana.edu/~ensiweb/lessons/c.bigcla.html]] in which the class as a whole builds a large tree of vertebrates.

## Constructing and Evaluating Phylogenetic Hypotheses

There are several rather simple exercises on tree building at the Access Excellence web site: “**From Restriction Maps to Cladograms**,” “**Molecular Biology and Primate Phylogenetics**,” and “**Using Amino Acid Sequences to Show Evolutionary Relationships**.” These can all be found at their Activities Exchange’s Evolution Program. [[www.accessexcellence.org/AE/AEPC/WWC/1995/]] You can also find “**Constructing a Phylogenetic Tree Using DNA Sequence Data**” there. In this lesson the students simulate the historical process to produce the sequences, so they know that the tree they make is accurate. They then trade data with another student, and work “backwards” with the data to infer the evolutionary relationship of an “unknown” phylogeny.

The two exercises from ENSI emphasize shared derived characters rather than just overall similarity: “**Making Cladograms**” [[www.indiana.edu/~ensiweb/lessons/mclad.html]] and “**Molecular Biology and Phylogeny.**” [[www.indiana.edu/~ensiweb/lessons/mol.bio.html]] In addition, if you use both of these lessons, you can discuss *evaluating phylogenetic hypotheses*, as they both investigate the relationships among the same animals, but using different data.

The UCMP site also has an activity “**Island Biogeography and Evolution: Solving a Phylogenetic Puzzle Using Molecular Genetics**,” [[www.ucmp.berkeley.edu/fosrec/Filson.html]] which has the students construct several trees using different types of data.

## Macroevolution

ENSI has two lessons on the pattern in the fossil record: “**Macroevolution: Patterns and Trends, and Rates of Change,**” [[www.indiana.edu/~ensiweb/lessons/macroev.html]] and “**A Peek at the Past: Fossil Patterns,**” [[www.indiana.edu/~ensiweb/lessons/peek.html]] which uses caminalcules. They also have a lesson on extinction: “**’Theory’ Choices: What Happened to the Dinosaurs?**” [[www.indiana.edu/~ensiweb/lessons/theor.ch.html]]