

Evolution lecture #4 -- **Phylogenetic Analysis (Cladistics)** -- Nov. 10th, 2008• **Outline of lecture:**

Overview of task in front of us

An example of putting together characters to make a tree

Summary of cladistic concepts and terms

Going through the steps of phylogenetic analysis at a more detailed level, looking at some of the difficulties

The value of phylogenies in biology

Phylogenetic systematics

• **Overview:**

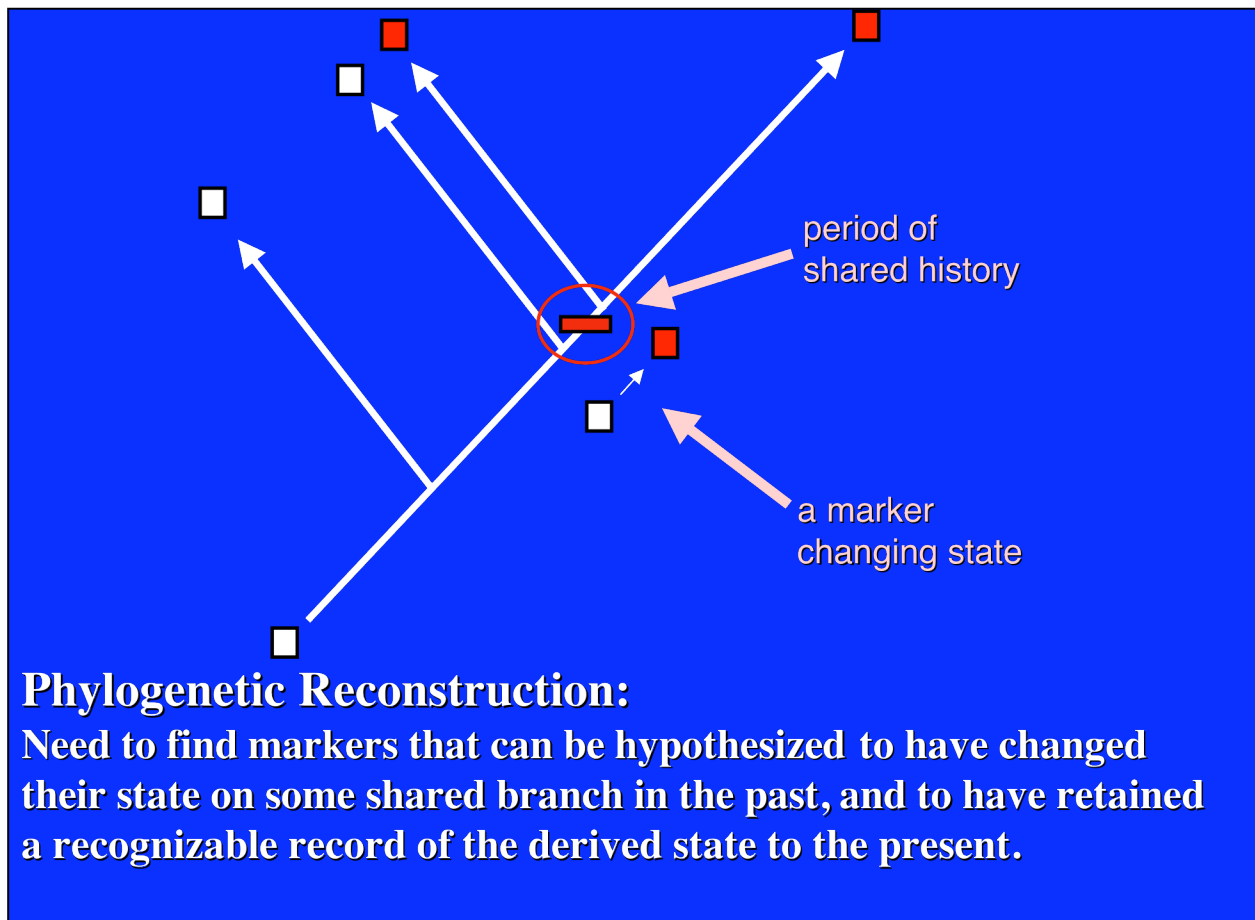
How can we discover phylogenetic history?

You can't actually see phylogeny, so how do you make inferences about it?

Think of a huge oak tree buried in a sand dune, with only the tips of the twigs showing -- what would you do?

The concept of historical markers -- characters

Need to find something that changed its condition along a lineage, and survived in recognizable form to the present.



Phylogenetics explained:

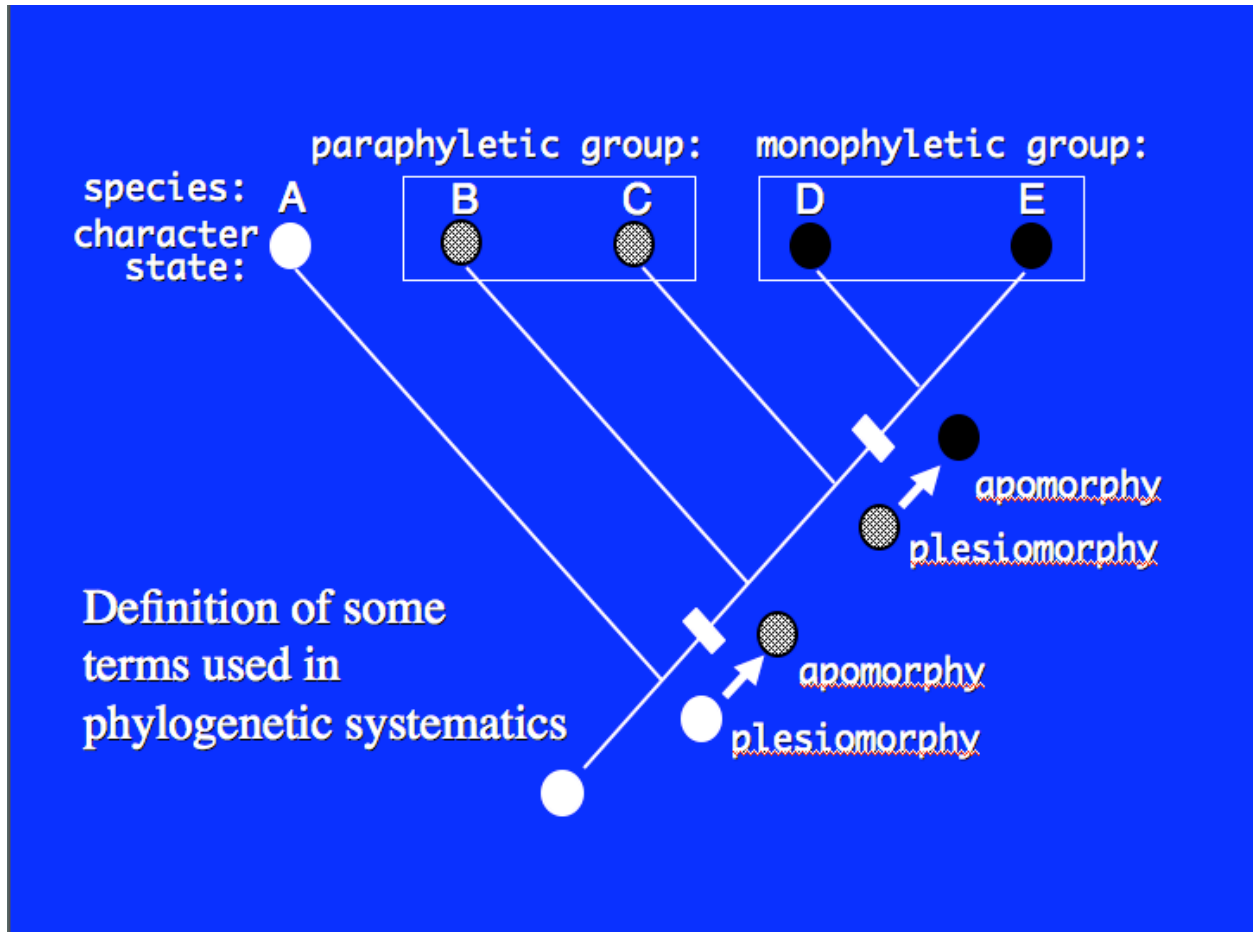
homology -- a feature shared by two lineages because of descent from an ancestor that had the feature.

transformation - a heritable change in a homology along a lineage from a prior state to a posterior state

divergence -- the splitting of one lineage into two lineages

reticulation - the blending of two lineages into one lineage

monophyly -- all and only descendants of a common ancestor



- **An example of putting together characters to make a tree**

Like other areas of biology, this one is loaded with terminology and quantitative methods, yet the basic principle is quite simple. The fundamental idea is known as the Hennig Principle, and is as elegant and fundamental in its way as was Darwin's principle of natural selection. It is indeed simple, yet profound in its implications. It is based on the idea of homology, one of the most important concepts in systematics, but also one of the most controversial. What does it mean to say that two organisms share the same characteristic? The modern concept is based on evidence for historical continuity of information; homology would then be defined as *a feature shared by two organisms because of descent from a common ancestor that had the feature*.

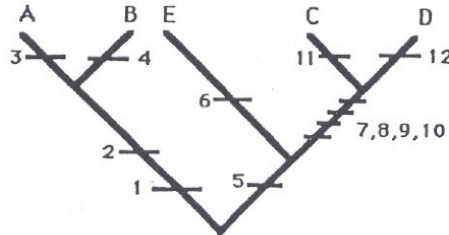
Hennig's seminal contribution was to note that in a system evolving via descent with modification and splitting of lineages, characters that changed state along a particular lineage can serve to indicate the prior existence of that lineage, even after further splitting occurs. The "Hennig Principle" follows from this: homologous similarities among organisms come in two basic kinds, synapomorphies due to immediate shared ancestry (i.e., a common ancestor at a specific phylogenetic level), and symplesiomorphies due to more distant ancestry. Only the former are useful for reconstructing the relative order of branching events in phylogeny -- "special similarities" (synapomorphies) are the key to reconstructing truly natural relationships of organisms, rather than overall similarity (which is an incoherent mixture of synapomorphy, symplesiomorphy, and non-homology).

In the Hennigian system, individual hypotheses of putative homology are built up on a character-by-character basis, then a congruence test (using a parsimony principle) is applied to identify homoplasies (i.e., apparent homologies that are not congruent with the plurality of characters). Examine the data matrix in box 3.4 (above), and be sure you can see why those data support the cladogram shown. Note that the pattern of overall similarity would give a different result, and group E with A and B rather than with C and D (this will be demonstrated on the powerpoint). To see the effect of homoplasy, consider a new character 13, with the distribution 10010 (see next page).

Finally, classifications are applied to the resulting branching diagram (cladogram). A corollary of the Hennig Principle is that classification should reflect reconstructed branching order; only monophyletic groups should be formally named. A strictly monophyletic group is one that *contains all and only descendents of a common ancestor*. A paraphyletic group is one that excludes some of the descendents of the common ancestor. See figure on previous page for the distinction between these two types of groups. *This elegant correspondence between synapomorphy, homology, and monophyly is the basis of the cladistic revolution in systematics.*

Box 3.4 Character State Distribution

The use of ancestral character states (symplesiomorphies) and uniquely derived character states (synapomorphies) to recognize monophyletic groups is illustrated by the phylogeny of species A-E, here diagrammed with 12 numbered character changes from ancestral to derived states.



This pattern of character evolution results in the taxonomic distribution of states given in the following character-by-taxon matrix; character states are ancestral (0) or derived (1).

Species	Character											
	1	2	3	4	5	6	7	8	9	10	11	12
A	1	1	1	0	0	0	0	0	0	0	0	0
B	1	1	0	1	0	0	0	0	0	0	0	0
C	0	0	0	0	1	0	1	1	1	1	1	0
D	0	0	0	0	1	0	1	1	1	1	0	1
E	0	0	0	0	1	1	0	0	0	0	0	0

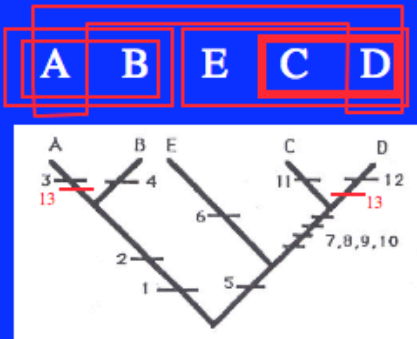
Together, the derived (1) states (synapomorphies) are hierarchically nested and characterize the nested monophyletic groups on the phylogenetic tree.

Characters	Groups sharing "1" state
1,2	A+B
3	A
4	B
5	C+D+E
6	E
7,8,9,10	C+D
11	C
12	D

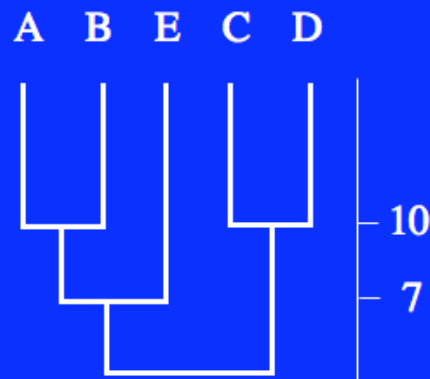
Species	Character												
	1	2	3	4	5	6	7	8	9	10	11	12	
A	1	1	1	0	0	0	0	0	0	0	0	0	1
B	1	1	0	1	0	0	0	0	0	0	0	0	0
C	0	0	0	0	1	0	1	1	1	1	1	0	0
D	0	0	0	0	1	0	1	1	1	1	0	1	1
E	0	0	0	0	1	1	0	0	0	0	0	0	0

New character #13, a homoplasy

Cladogram:



Phenogram:



• **More detail on some topics in Cladistics (summary of the following)**

- The basic methodology of **cladistics**

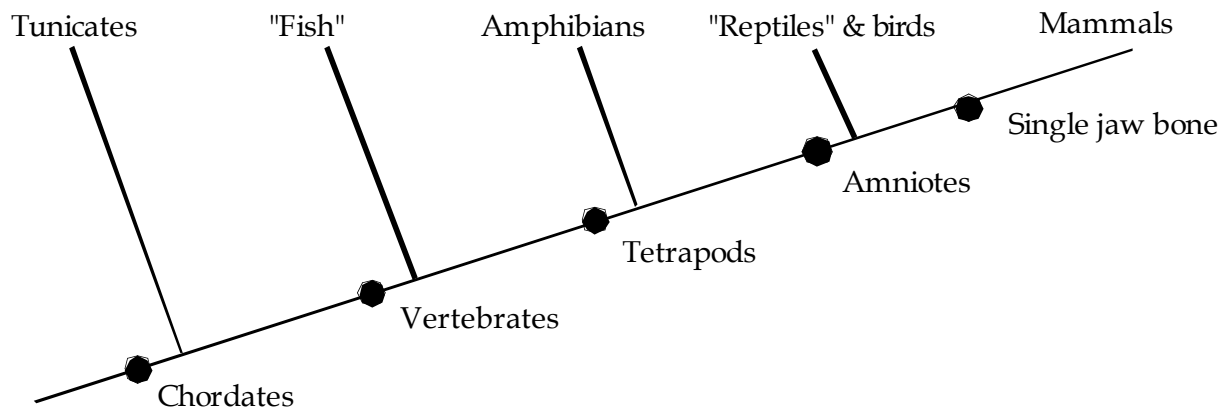
Groupings of organisms are based on their **sharing of a recent common ancestor** with a **new trait** shared by no other groups

- **Choice of traits, relative time, fossils on cladograms**
- Contrast **ancestral** and **derived** (new) traits
- Contrast **homologous** (shared ancestry) and **analogous** (convergent) traits
- Why do we want to draw **evolutionary relationships**?
- **Weaknesses** of the hierarchical **Linnaean** classification system
- **Appendix. Cladistics terms and concepts** (synapomorphies, monophyletic and paraphyletic groups, sister taxa, outgroup, stem and crown groups, etc.)

• The basic methodology of cladistics

- Our aim is to use cladistics to describe the evolutionary relationships of all living and fossil species. We use anatomical, developmental, behavioral, and genetic data on living and fossil species, to draw evolutionary relationships in a systematic and unbiased way (see Fig. 26.11).

- In cladistics, we use new (**derived**) traits shared by all descendants of a common ancestor (**synapomorphies**) to determine **monophyletic** groupings which include the common ancestor and all descendants (terms are defined below). Groupings of organisms are based on their **sharing of a recent common ancestor** with a **new trait** shared by no other groups.



See Fig. 34.2, text

• Choice of traits, relative time, fossils on cladograms

Choice of traits in a cladistic analysis: a cladogram is only as good as the traits used to construct the branching points. However, it does provide us with a potentially unbiased way to determine evolutionary relationships. If we use enough traits, and consistently see the same relationships, we can be pretty certain of the accuracy of the cladogram.

- One must be careful to avoid as much as possible including in the analysis traits which are convergent, or at least to use enough traits and parsimony so that we can detect convergences.

- Also one has to be careful that adaptations have not obscured homologies

- Remember too that in the outgroup there is also evolution via cladogenesis and anagenesis and synapomorphies defining monophyletic groupings. Usually however these traits will differ from those defining the taxa under study.

- The choice of the outgroup is important, one wants to use the closest sister taxa when possible. Still, the assumption that the outgroup retains the ancestral trait may not always be correct. Often more than one outgroup taxon is used.
- A cladogram shows relative time, but not absolute time.
- We have cladogenesis (branching) and anagenesis (evolution along a branch)
- Every species is a mixture of ancestral (plesiomorphic) and new (apomorphic) traits. No species per se is more primitive, it may however retain the ancestral trait with respect to the group being studied.
- We traditionally put the trait before the node defining the most recent common ancestor of the taxa under consideration. We assume there are fossil forms we have not found yet that fall within this monophyletic grouping and these may predate the taxa under consideration.
- We use the parsimony principle (shortest number of steps) to choose the most likely cladogram or evolutionary tree; this may not always be correct. However, if enough traits are examined, and convergent traits are recognized, then the 'correct' tree should emerge.

fossils on cladograms: we can never tell whether or not a fossil form was in a direct lineage leading to current species. We basically treat it as a terminal taxon, just like living organisms.

- **Ancestral, derived, homologous, and analogous traits**

ancestral trait: trait shared by a group of organisms by descent from a common ancestor

derived trait: a new trait found among members of a lineage that was not present in the ancestors of that lineage

homologous: see notes on Darwin (also see Fig. 22.17). A feature that is shared between two organisms by common descent.

Adaptations can obscure homologies: for example, the leaves of plants have diverged during their evolution to form many different structures, some of which bear very little resemblance to each other. For example, the spines of cacti and the bracts of *Heliconia* are both modified leaves (you will see these on the tour for the Botanical gardens lab.)

analogous: similar structure and function but different evolutionary origins (see Fig. 26.7). Analogies can confuse us when drawing evolutionary relationships. Analogies are due to convergent evolution.

convergent evolution (convergence): the independent evolution of similar features by two or more groups. Also, a synonym for analogy. A more general term for characters that appear homologous but are not is homoplasy.

- **Similar adaptations** are **independently** acquired through, e.g., living in the same type of environment, adopting the same diet, or defending against similar predators.
- One example of convergent evolution is the streamlined bodies of some marine animals, e.g., sharks, ichthyosaurs (extinct marine reptile of the Mesozoic), and dolphins.
- The wings of birds, bats, pterosaurs, and insects are analogous (they evolved independently), however, the bones in the wings of birds, bats, and pterosaurs share a common ancestry and are homologous.
- **Why do we want to draw evolutionary relationships?**
 - Intrinsic interest in knowing the relationships of all life forms (Fig. 26.21).
 - A summary of all information known about biodiversity
 - Prediction of currently unknown properties of organisms, which is in turn useful for:
 - prospecting for novel chemicals and medicines
 - guiding genomic/biotechnology studies
 - evaluating potential cures for diseases or control measures for pests
 - deciding on conservation priorities
- The Predictive Value of Phylogenetic Classifications
 - The natural evolutionary arrangement of phylogenetic classifications allows us to predict characteristics of an organism based on its position in the phylogenetic tree.
 - Good biological research must consider the evolutionary relationships of the organisms under study.
- How can we use trees? Once we have a phylogeny and traits of interest, what kinds of problems can be solved?

An example given of tree-thinking that saved lives and forests: Taxol and *Taxus brevifolia*: An important drug, e.g., in treatment of cancer, is only available from a plant species that is rare, one can look at closely related plants to see if there is an abundant species from which the drug can be obtained.
- Crop Improvement: Example: Corn. In 1977: the long-lost wild relative of domestic corn was found in a ditch in rural Mexico (Oaxaca). This wild strain of corn is resistant to many viruses that afflict domestic corn

- When we have a good knowledge of the "tree of life" we can study the genetics of new innovations, e.g., the same gene is involved in fin development in "fish" and limb development in tetrapods (Fig. 25.21).
- Knowledge of the tree of life allows us to study convergent traits; how often have they arisen, what are the genetic mechanisms involved, etc.
- If a feature such as antifreeze in some Arctic and Antarctic species of fish can be shown from an evolutionary tree to have evolved independently in these two regions, we can study the molecular basis of these innovations to see if they use a similar molecular solution (they do in this case), or have evolved entirely different solutions. Similarly with other convergent traits such as giving birth to live young, adaptations for living in desert, or other harsh, conditions.
- Knowing the phylogenetic relationships of taxa can be important in study of the biogeography of living and fossil forms found in the same area. The study of closely related species on different continents can provide information on continental drift.
- In the study of behavioral traits, one needs a good evolutionary tree on which to map the trait and determine convergences versus shared ancestry.
- Having solid phylogenetic trees, we can base natural classifications on them, where only monophyletic groups are named.

• **What is phylogenetic systematics?**

- The study of evolutionary relationships among groups of taxa:
 - Phylogenetic systematists make trees that reflect evolutionary relationships based on shared derived traits (whether morphological, chemical, or genetic)
 - Phylogenetic systematists make classifications that describe natural diversity in a meaningful and useful way
 - Phylogenetic classifications name only monophyletic groups
 - These provide a conceptual framework for interpreting biological information of all kinds
 - These allow scientists to make predictions about species and their properties that are of biogeographical, ecological, physiological/behavioral, developmental, or genomic significance.

- **Weaknesses of Linnaean classification system**

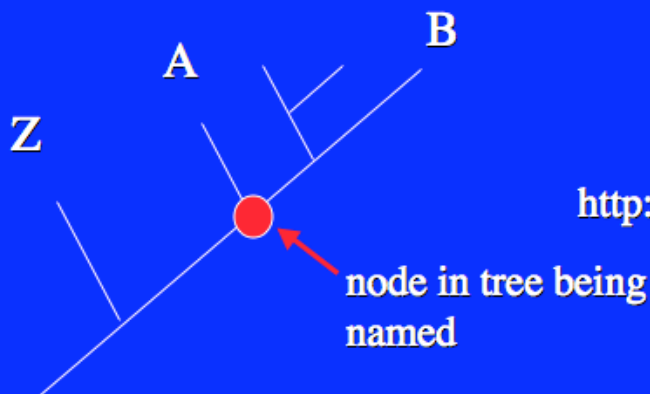
Linnaeus: developed systematic naming of animals and plants (Figs. 1.14 and 26.3)

taxonomy: hierarchical classification system—

kingdom, phylum (animals) or division (plants), class, order, family, genus, species
(King Philip Calls Out For a Good Soup)

- Note that the hierarchical classification system is primarily used for convenience, and there is a great deal of variation between groups with regard to how closely organisms need to be related to be considered in the same family or order, etc. An avian family may have a more recent common ancestor than a family of flowering plants, or vice versa, and similarly with genetic variation.
- Taxonomy is in a state of flux. We currently use a combination of cladistics for drawing evolutionary relationships while retaining Linnaean nomenclature, but are moving towards a new phylogenetic system of classification that would remove the ranks altogether: the PhyloCode.

Advanced topic (not for test): The best approach may be to not designate any ranks at all. There are recent calls for rank-free phylogenetic taxonomy. The main contribution of the PhyloCode is to provide an unambiguous way to name clades:

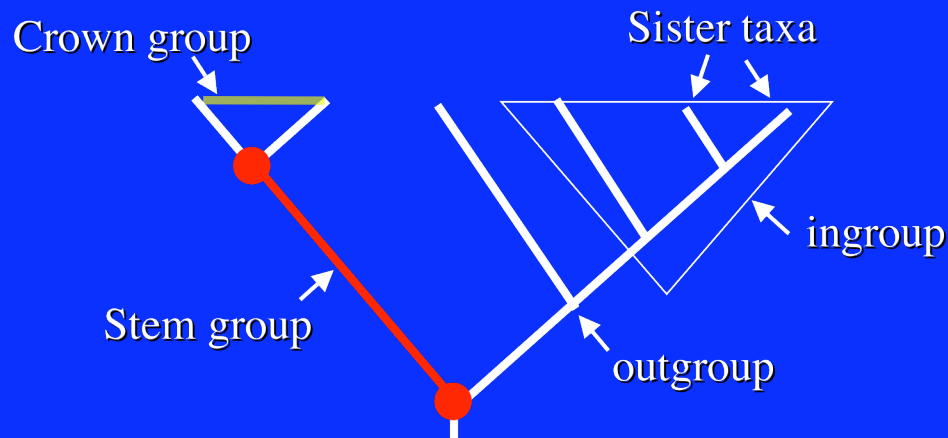


<http://www.ohiou.edu/phylocode/>

A node-based name:

“I name the clade that contains A, B, and all the descendents of their most recent common ancestor”

Some cladistic terms illustrated:



N.B. A cladogram shows relative time, but not absolute time!

Appendix. Cladistics terms and concepts:

taxon (taxa): any named taxonomic group, such as the family Felidae, or the genus *Homo*, or the species *Homo sapiens*

systematics: study of biological diversity and its evolution

phylogeny: "Tree of life": branching relationships among species, showing which species shares its most recent common ancestor with which other species

clade: a group of organisms that have all evolved from a common ancestor, includes the common ancestor and all its descendants e.g., vertebrate amniotes (see below). A synonym for monophyletic group (see below).

common ancestor: assuming a single origin of life, then any two taxa have a most recent common ancestor

node: a branch point, it represents a common ancestor at the time of divergence into two or more lineages

cladogram: a graphical depiction of phylogenetic relationships

phenogram: a graphical depiction of overall similarity -- often does not give phylogenetic relationships

sister groups (or taxa): two groups with the same immediate common ancestor

plesiomorphic: an ancestral trait, sometimes (inappropriately) termed primitive

symplesiomorphic: an ancestral character shared by several species (we usually do not use this term, but imply it when we say plesiomorphic)

apomorphic: a derived (new) trait, sometimes (inappropriately) termed advanced

synapomorphies: shared apomorphies (derived) characteristics. To draw a phylogenetic tree, we look for synapomorphies

autapomorphy: a derived character state possessed by only **one** of the taxa under consideration. Autapomorphies demonstrate the uniqueness of taxa but they don't help identify clades.

outgroup: among the states of a character found in the members of a monophyletic group, the **ancestral** character state is the one that is most widely distributed among taxa **outside** this group (unless there is contrary evidence). These latter taxa are called **outgroups** and their features provide valuable information for inferring relationships among the members of the monophyletic group under study.

monophyletic group: a taxon is monophyletic if a single ancestor gave rise to **all** species in that taxon and to no species placed in any other taxon. Monophyletic groups are defined using synapomorphies; they include the common ancestor and all descendants with the new trait. For example, the group tetrapods is monophyletic (amphibians, “reptiles” & birds, mammals, and their common ancestor). Similarly, for living species the class “Reptilia” could be subdivided into monophyletic groups of turtles, snakes, lizards, crocodiles (including respectively their most recent common ancestor) (Fig. 34.24). “Protists” are also paraphyletic (Fig. 28.3).

paraphyletic group: a paraphyletic taxon **excludes** species that share a common ancestor that gave rise to the species included in the taxon. For example, the class “Reptilia”, excluding birds, is a paraphyletic grouping (see Fig. 34.24). “Dinosaurs” (class “Reptilia”) are more closely related to birds, which are in a different class (*Aves*), than “dinosaurs” are to turtles which are in the same class. Class Reptilia could be divided into separate classes for modern turtles, lizards, snakes, crocodiles, etc. For another example, placing humans (*Homo sapiens*) in a separate family (Hominidae) means that the family Pongidae (orangutans, gorillas, and chimpanzees) is a paraphyletic grouping (see Fig. 34.37).

When we talk about the paraphyletic grouping “dinosaurs” (Fig. 34.24) or “fish” (which includes jawless, cartilaginous, and bony fishes) (Fig. 34.2), we use the quote marks to denote that we know we are talking about a paraphyletic grouping.

polyphyletic group: a polyphyletic group includes two or more taxa, but not the common ancestor of those taxa. The members of a polyphyletic group are grouped by **false synapomorphies** - i.e., their similarities are analogous rather than homologous. If we grouped dolphins and sharks based on their physical similarity of a streamlined body adapted for speed in a marine environment, we would be forming a polyphyletic grouping.

stem group and **crown group:** (used especially in discussing taxa with a fossil record), a stem group is an ancestral clade from which a crown group with new derived characteristics has evolved.

terminal taxon: the basic groups whose relationships are being studied in a particular cladistic analysis. Might be genera, species, populations or individual specimens. There is an intrinsic assumption that each terminal taxon is monophyletic with respect to all others.

Questions relating to this lecture on cladistics

1. There are Australian marsupial mammal equivalents of a number of placental mammals, e.g., moles, anteaters, mice, wolves, cats, and squirrels. This convergent evolution proceeded independently due to their _____ due to similar ways of life.
 - A. analogy
 - B. homology
 - C. adaptation
 - D. adaptive radiation
 - E. none of the above is correct
2. Shared **ancestral** characters are:
 - A. nonadaptive
 - B. analogous
 - C. homologous
 - D. convergent
 - E. exaptations
3. Do self quiz questions 1- 6 and 7 on page 555 of the 8th ed. [or 1-5, 6, and 7 on pages 508-509 of the 7th ed.]
4. For Fig. 1.22 (8th) or Fig. 1.23 (7th), define some monophyletic groups, and indicate a grouping which would be paraphyletic.