Evolution lecture #4 -- **Phylogenetic Analysis (Cladistics)** -- Oct. 9th, 2006

• **Overview:**

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). See figure 1, next page.

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, 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.

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 the excludes some of the descendents of the common ancestor. See figure 1 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.
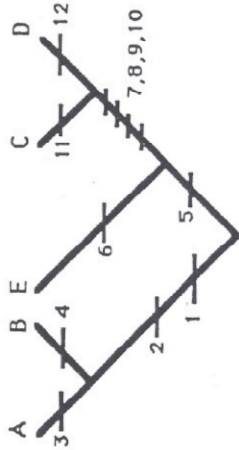
This pattern of character evolution results in the taxonomic distribution of states given in the following character-by-taxon matrix; character states are ancestral (0) or derived (1).

Character

Species	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

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

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

possible higher taxa:

A   B   C

species: 1 2   3 4   5 6
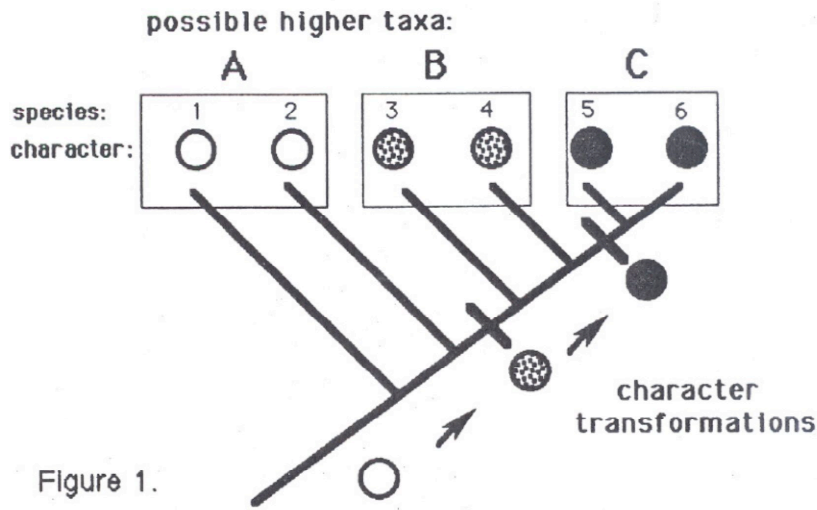
character:

character transformations

Figure 1.

• Cladistics (summary of topics)

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

• 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. 22.14 (6th and 7th)). 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. 25.5 (7th) (Fig. 25.10 6th)). 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.

- **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 examples of convergent evolution is the streamlined bodies of some marine animals, e.g., sharks, icthyosaurs (extinct marine reptile of the Mesozoic), and dolphins (more examples will be considered below).

• 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.

• Weaknesses of Linnaean classification

Linnaeus: developed systematic naming of animals and plants (Figs. 1.14 and 25.8 (7th) (Figs. 1.10 and 25.7 6th))

taxonomy: hierarchical classification system—
kingdom, phylum or division, 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 (see below) for drawing evolutionary relationships while retaining some features of Linnaean nomenclature, and moving towards a new phylogenetic system of classification

• Some terms:

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

• With plants, Linnaeus often used characters that were convergent, i.e., although they looked similar, they were cases of convergent evolution, and did not reflect close genetic relationship. Historically with plants there have been continual arguments as to which is the most important character to base classification on.

• There are no consistent rules to determine when a new genus (or family, order, etc.) is warranted.

• While the Linnaean system is hierarchical it does not describe the evolutionary (genetic) relationships within a group, e.g., all families within an order.

• Further, it can lead to "paraphyletic groupings," e.g., placing humans (*Homo sapiens*) in a separate family (Hominidae) means that the family Pongidae (orangutans, gorillas, and chimpanzees) is a paraphyletic grouping (see below for definition of paraphyletic) (see Fig. 34.38 (7th) (Fig. 34.35 6th)).

Gibbons   Orangutans   Gorillas   Chimpanzees   Humans
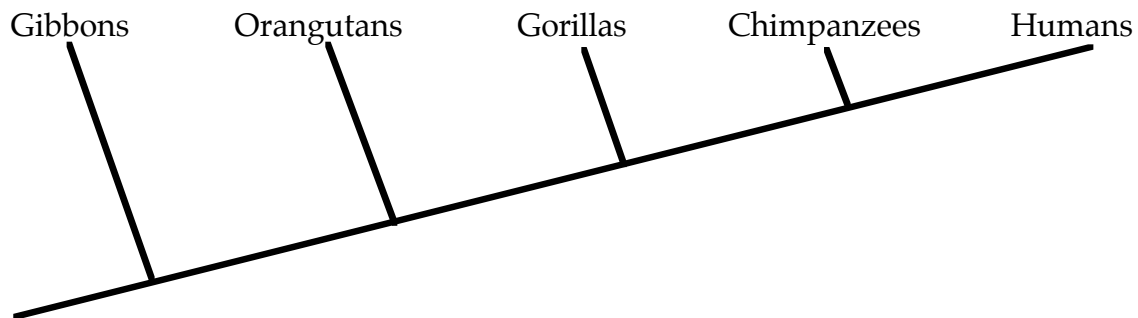
• Similarly, the class "Reptilia" is paraphyletic since birds are not included (see Fig. 34.23 (7th) (Fig. 34.20 6th)). "Dinosaurs" (class "Reptilia") are more closely related to birds, which are in a different class (Aves), than "dinosaurs" are to turtles which are in the same class. Class Reptilia could be divided into separate classes for modern turtles, lizards, snakes, crocodiles, etc.
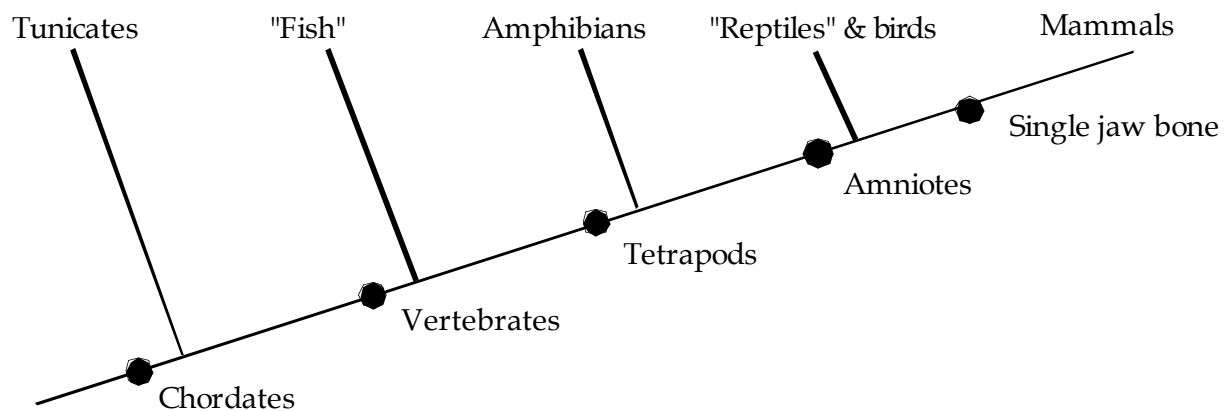
• Why do we want to draw evolutionary relationships?

• Intrinsic interest in knowing the relationships of all life forms (Fig. 26.22 (7th) (Fig. 26.1 6th)).

• 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. 34.20 (7th) (Fig. 34.15 6th)).

• If 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.

• 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 genetic 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.

• 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. 25.11 (6th and 7th)).

• 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.

Tunicates   "Fish"   Amphibians   "Reptiles" & birds   Mammals

Single jaw bone

Amniotes

Tetrapods

Vertebrates

Chordates

See Figs. 34.2 and 34.23 (7th) (Fig. 34.7 6th)

• Every species is a mixture of ancestral and new traits.

• We have cladogenesis (branching) and anagenesis (evolution along a branch)

• Cladistics concepts

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

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 (Fig. 25.11 (6th and 7th)).

monophyletic group: a taxon is monophyletic if a single ancestor gave rise to **all** species in that taxon and to <u>no</u> species placed in any other taxon (see Fig. 25.10a (7th) (Fig. 25.9a 6th). 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).

paraphyletic group: a paraphyletic taxon **excludes** species that share a common ancestor that gave rise to the species included in the taxon. The class "Reptilia", excluding birds, is a paraphyletic grouping (see Figs. 25.10b and 34.23 (7th) (Figs. 25.9b and 34.20 6th)).

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 (see Fig. 25.10c (7th) (Fig. 25.9c 6th)).

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.

monophyletic groupings for living taxa: if one just looks at modern taxa of bacteria and archae, then monophyletic groups can be defined.

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. 34.23 (7th) (Fig. 34.20 6th)).

When we talk about the paraphyletic grouping "dinosaurs" (Fig. 34.23 (7th) Fig. 34.20 6th)) or "fish" (which includes jawless, cartilagenous, and bony fishes) (Fig. 34.2 (7th) (Figs. 34.1 and 34.7 6th)), we use the quote marks to denote that we know we are talking about a paraphyletic grouping.

"Protists" are also paraphyletic (Fig. 28.4 (7th) (Figs. 28.2 and 28.8 6th)).

• 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 relation ships, 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.

    • Living sister taxa are always more closely related to each other than to the living outgroup taxon.

    • A cladogram shows relative time, but not absolute time

    • 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.

• Comparative Methods

    • An exciting new area of research, using phylogenies to study evolutionary processes. Areas of emphasis include:
        • Coevolution (which can be broadly defined as congruence between two or more systems undergoing evolution by descent with modification). For example: host/ parasite relationships.

• Vicariance biogeography (organism/ earth coevolution).
• Community evolution (e.g., symbionts, pollinator/plant coevolution, or other long-term ecological associations).
• Cladistic tests of adaptational hypotheses (association between organism phylogenies, putative adaptations, and putative ecological explanations

Questions relating to lecture on cladistics

1. The **correct** hierarchical sequence of animal classification is:
    A. phylum, order, class, family, genus, species
    B. phylum, class, order, family, genus, species
    C. phylum, class, family, order, genus, species
    D. phylum, order, family, class, genus, species
    E. none of the above is correct

2. If two different species belong to the same **class**, then they also belong to the **same** _____, but do **not necessarily** belong to the same _____.
    A. kingdom, phylum
    B. phylum, family
    C. family, order
    D. family, genus
    E. none of the above is correct

3. 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 _____ to similar ways of life.
    A. analogy
    B. homology
    C. adaptation
    D. adaptive radiation
    E. none of the above is correct

4. Shared **ancestral** characters are:
    A. nonadaptive
    B. analogous
    C. homologous
    D. convergent
    E. exaptations

5. Do self quiz questions 1-4, 6, and 7 on pages 508-509 of the textbook (7th) (self quiz questions 2, 3, 5, 6-8, 14, 15, and 17 on pages 506-507 of the 6th edition).

6. For Fig. 1.23 (7th) (Fig. 1.17b 6th), define some monophyletic groups, and indicate a grouping which would be paraphyletic.