Invertebrate Biology is not a stagnant science!

"molecular studies suggest that acanthocephalans evolved from rotifers, the priapulids share common ancestry with all other molting animals (Ecdysozoa), and that flatworms, gnathostomulids and rotifers form a sister group to the remaining, non-molting protostomes (Lophotrochozoa), together forming Spiralia. The lophophorate phyla (phoronids, brachiopods and bryozoans) appear as protostomes, allied with annelids and molluscs rather than with deuterostomes" (Garey and Schmidt-Rhaesa 1998)

Principles of Systematics

"Our classifications will come to be, as far as they can be so made, genealogies" Darwin 1887

It is our nature to identify, name and classify organisms (Berlin 1973)

Systematics, taxonomy, and phylogeny.

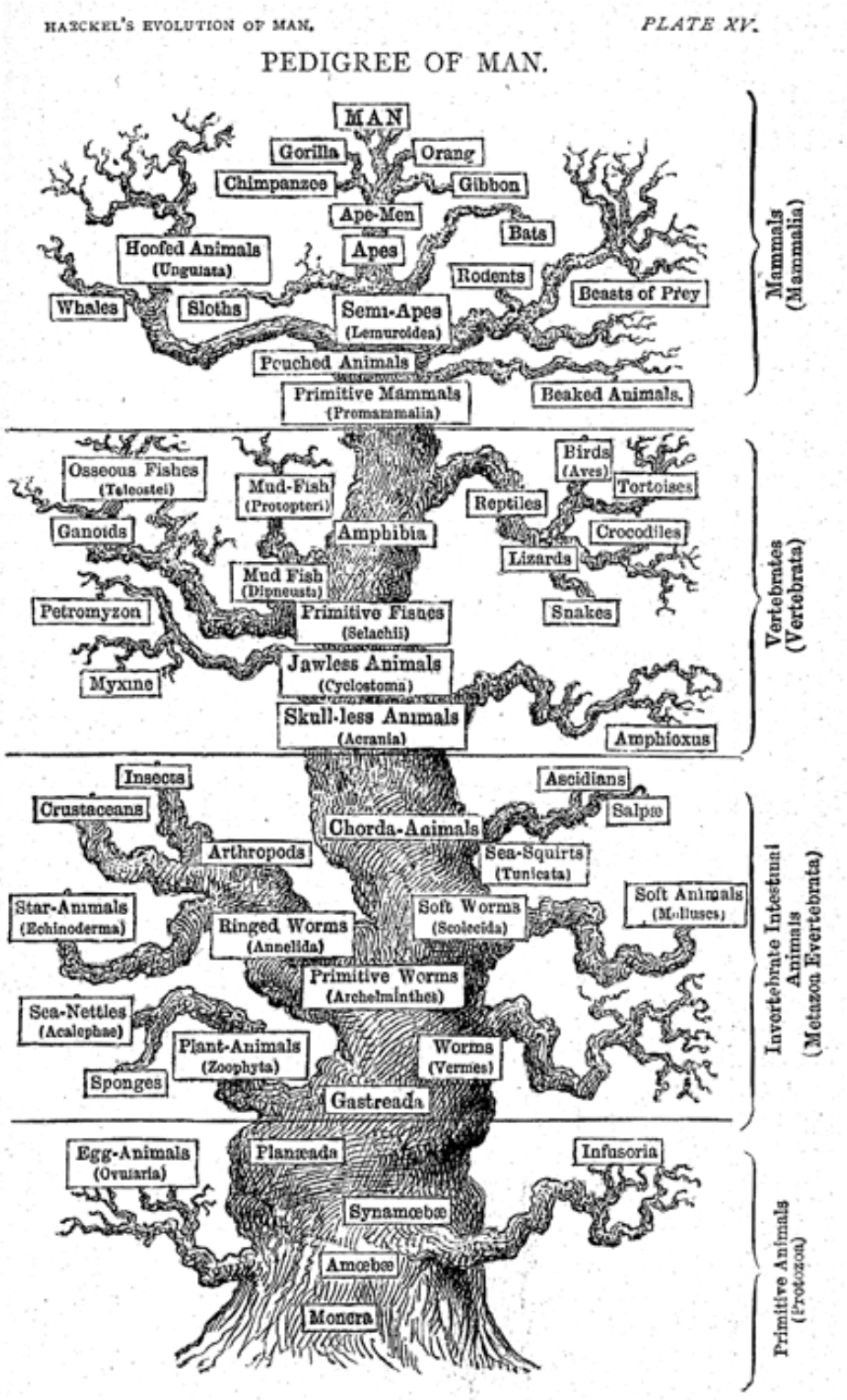
Systematics: The discipline of biology that deals with the diversity and interrelationships of living beings. Systematics consists of 2 sub-disciplines.

> **Taxonomy:** The naming and classification of organisms
> **Phylogeny:** The study of relationships and patterns among organisms and the group's evolutionary history through time

Phylogenetic Systematics (Cladistics)

The origin of phylogenetic systematics can be traced in **Willi Hennig**'s 1950 book (Hennig 1966). Phylogenetic systematics is based on **recency of common descent (genealogy)** and its goal is to produce hypotheses of genealogical relationships among monophyletic groups of organisms.

Figure 1. Ernst Haeckel's Tree of Life



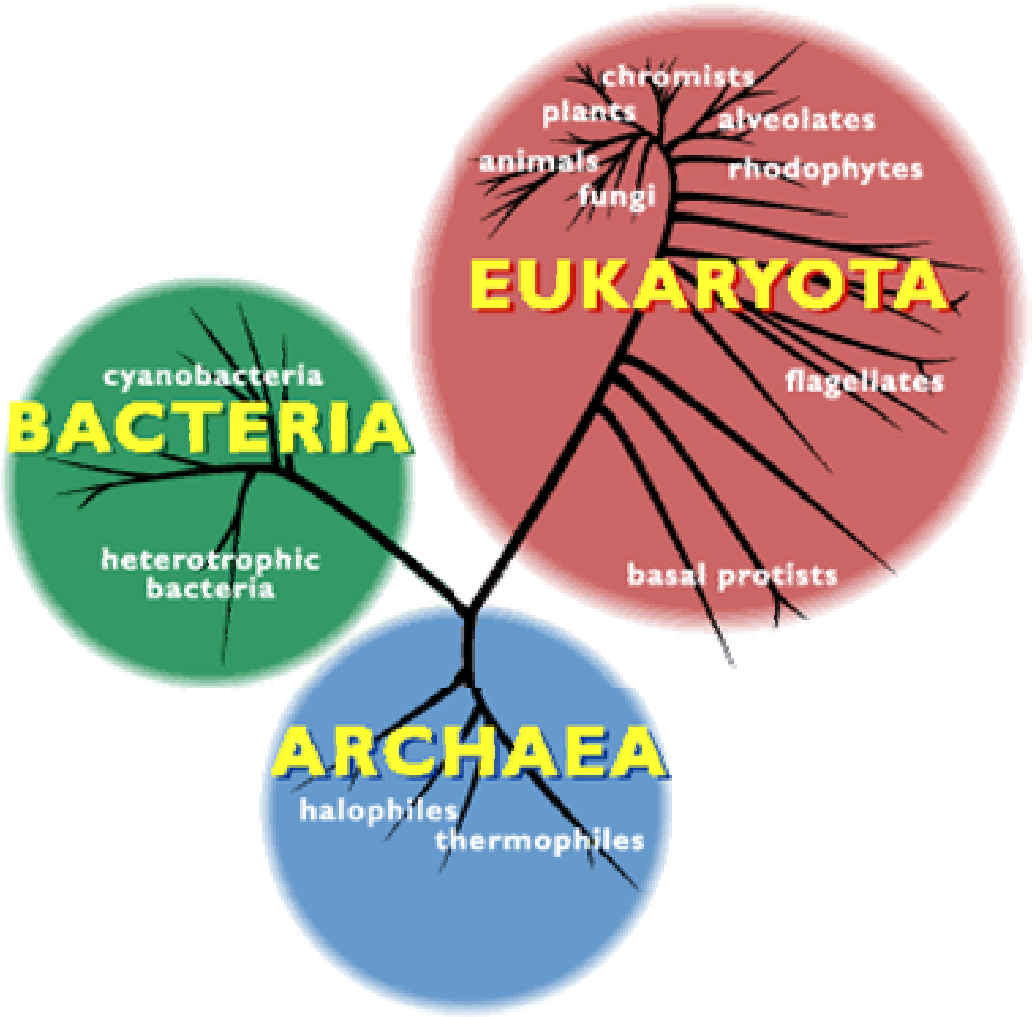
Current view on the phylogenetic organization of life

Domain Bacteria (e.g. cyanobacteria, never have membrane-enclosed organelles or nuclei or a cytoskeleton. None are methanogens, some use chlorophyll-based photosynthesis, with peptidoglycan in cell wall, with a single RNA polymerase)

Domain Archaea (methane-producing microorganisms, never have membrane-enclosed organelles or nuclei or a cytoskeleton. Methanogens, none use chlorophyll-based photosynthesis, without peptidoglycan in cell wall, with many RNA polymerases)
Note: Bacteria (Eubacteria) and Archaea comprise the now "fading" concept of Prokaryota

Domain Eucarya (Eukaryotes)
(Cells with membrane enclosed organelles, and a membrane enclosed nucleus, cells keep their shape and move by a network of fibrous proteins called the cytoskeleton)
Kingdom Fungi
Kingdom Plantae
Kingdom Protista
Kingdom Animalia

Figure 2. The 3 domains of life

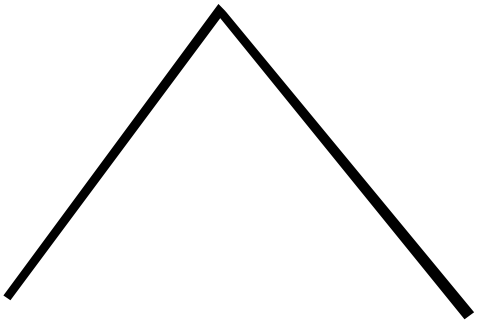


For more info read (Woese, Kandler, and Wheelis 1990; Mayr 1998; Woese 1998)

KINGDOM ANIMALIA

Animalia or Metazoans (34 phyla, about 1.3 million species), monophyletic taxon, heterotrophic, multicellular organisms. Acetylcholine/cholinesterase-based nervous systems, special types of cell-cell junctions, and special connective tissue proteins, the collagens.

10,000 –13,000 new species described every year!! Let alone the revisions! The ironic thing is that at the rate of current extinction 90% of all species will go extinct before they are even described!



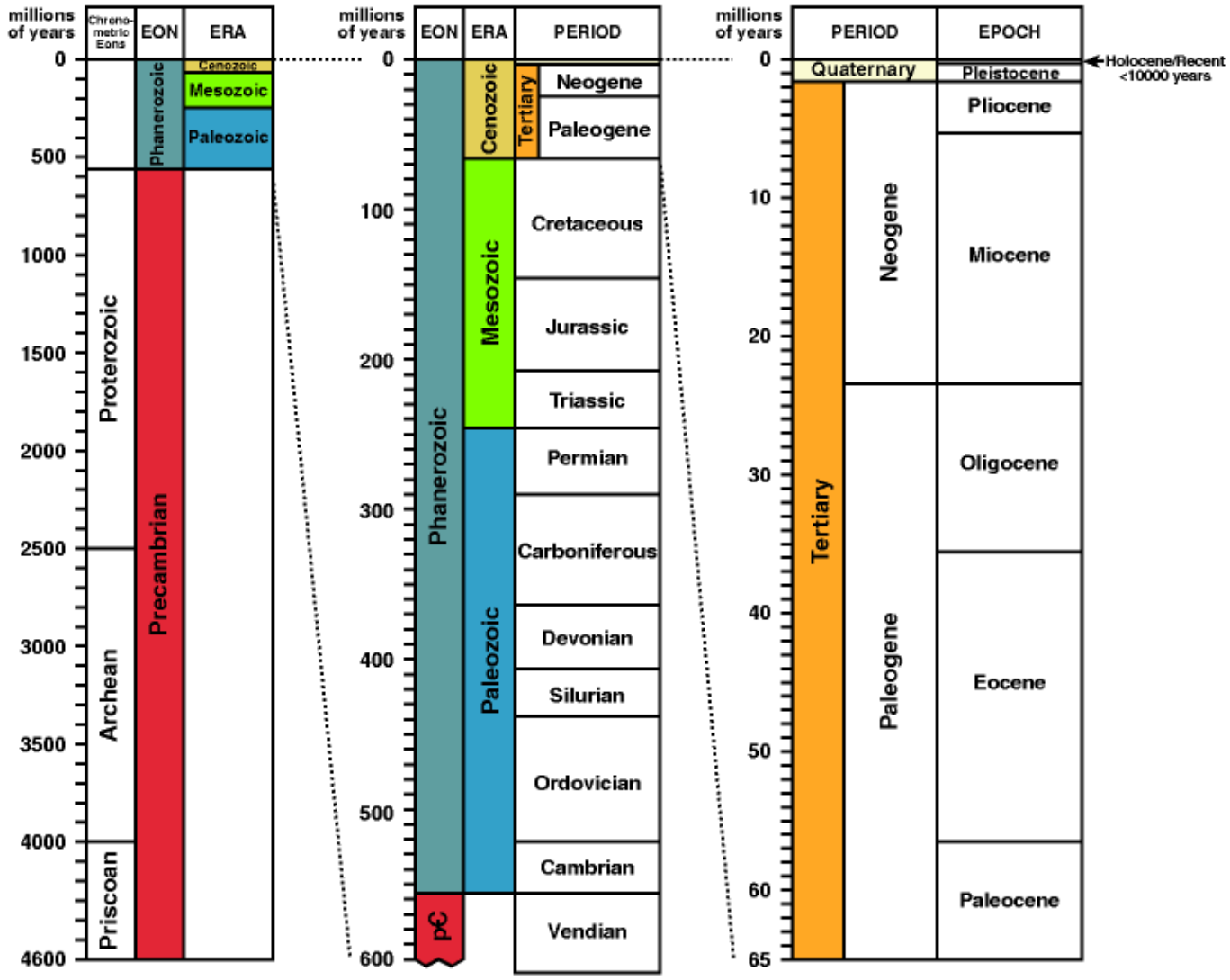
Phylum Chordata
Subphylum Vertebrata
47,000 species

Invertebrates
33 phyla + remaining Chordata
1,253,000 species

Number of extant species in major groups (Brusca and Brusca 2002):

Porifera (5,500)
Cnidaria (10,000)
Ctenophora (100)
Placozoa (1)
Monoblastozoa (1)
Rhombozoa (70)
Orthronectida (20)
Platyhelminthes (20,000)
Nemertea (900)
Gnathostomulida (80)
Rorifera (1,800)
Gastrotricha (450)
Kinorhyncha (150)
Nematoda (25,000)
Nematomorpha (230)
Priapulida (17)
Acanthocephala (700)
Cycliophora (1)
Entoprocta (150)
Loricifera (10)
Annelida (16,500)
Echiura (135)
Sipuncula (320)
Tardigrada (600)
Onychophora (110)
Arthropoda 1,097,631
    Cheliceriformes (70,000)
    Crustacea (68,171)
    Hexapoda (948,000)
    Myriapoda (11,460)
Mollusca (93,195)
Brachiopoda (335)
Ectoprocta (4,500)
Phoronida (20)
Chaetognatha (100)
Echinodermata (7,000)
Hemichordata (85)
Chordata (49,693)
    Urochordata (3,000)
    Cephalochordata (23)
    Vertebrata (46,670)

Geologic Time-Scale



Fossils

Metazoan origins found in the Proterozoic era (600 MYA), but there are trace fossils 1.2 BYA. Representatives of all extant phyla were present in the Paleozoic era (470 MYA). Some phyla have a much better fossil representation than others (e.g. echinoderms, molluscs, arthropods, corals, ectoprocts, and brachiopods).

Naming of Species

The International Commission on Zoological Nomenclature (http://www.iczn.org/code.htm) recognizes the following classification hierarchy:

Kingdom
Phylum (plural: Phyla)
Superclass
Class
Subclass
Cohort
Superorder
Order
Suborder
Superfamily
Family
Subfamily
Tribe
Genus (plural: Genera)
Subgenus
Species (plural: Species)
Subspecies

The symbol of Department of Marine Sciences, the shrimp *Stenopus hispidus* is classified as follows:

Phylum Arthropoda
Class Crustacea
Order Malacostraca
Family Stenopodidae
Genus Stenopus
Species *Stenopus hispidus*

The current naming system was established by **Linnaeus in 1758,** and is known as the **binomial nomenclature**. Linnaeus published the 10th ed. of **Systema Naturae**, where he reported all species known to him, > 4,400 animal species). 5 years before the publication of **Systema Naturae** (1753)**, Linnaeus** published **Species Plantarum** (listing of >8,000 plant species).

Other interesting facts on species nomenclature:

- Publications of scientific names are regulated by sets of rules given by International Commissions of zoological, botanical, and microbiological nomenclature.

- There are about 200 journals publishing manuscripts dealing with taxonomic and systematic issues. Some of them are Systematic Biology, Cladistics, Phylogenetics and Systematic Botany, Journal of Crustacean Biology, Smithsonian Contributions to Zoology, Zoologica Scripta.

- The most widely accepted species concept (biological species concept) is appropriate for dioecious animals. It may be appropriate for species that hybridize readily (plants) or have asexual reproduction (bacteria)

- Microbiologists use ribosomal DNA (16S) to identify and name species of bacteria.

Some problems with the Linnean system of classification:

1) The ranking is not equivalent across taxa (A fish genus is not necessarily equivalent to a gastropod or primate genus)
2) Very frequently species are moved to other genera and the generic name changes, adding yet another in the literature.

There are efforts to replace the Linnean system of nomenclature, such as BioCode, which is a proposed unified nomenclatural code for all organisms (http://www.biosis.org.uk/zrdocs/codes/biocode.htm)

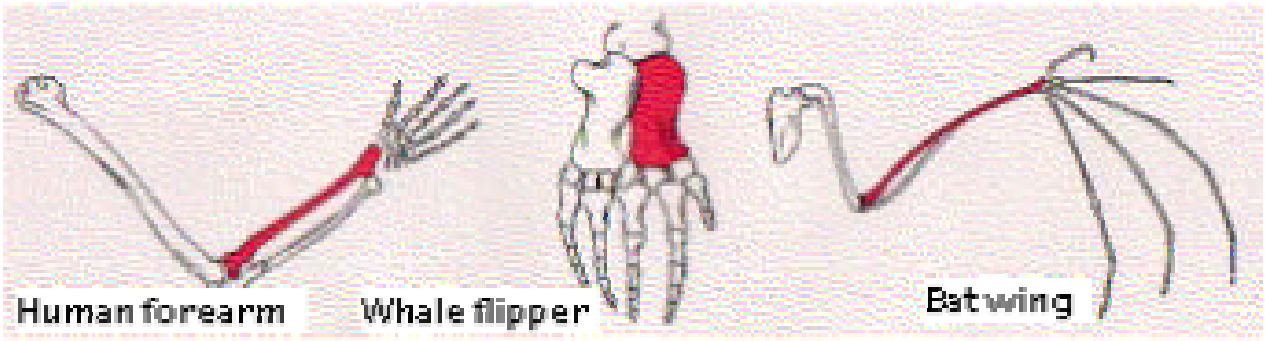
and the

PhyloCode (http://www.ohiou.edu/phylocode/index.html). The PhyloCode is a formal set of rules governing phylogenetic nomenclature. It is designed to name the parts of the tree of life by explicit reference to phylogeny. The development of the PhyloCode grew out of recognition that the current Linnaean system of nomenclature, as embodied in the preexisting botanical, zoological, and bacteriological codes, is not well suited to govern the naming of clades and species. Read (Cantino et al. 1999) for more information.

Homology and Homoplasy
How do we compare different species?

The fundamental basis for **comparative biology is homology.**

Two characters are **homologous** if they have descended from the same ancestor. The principle of homology applies to characters used in comparative biology (e.g. morphological, behavioral, physiological and molecular characters).



Molecular Homology

Molecular homology of cytochrome c															
	1					6				10				14	
Human	Gly	Asp	Val	Glu	Lys	Gly	Lys	Lys	Ile	Phe	Ile	Met	Lys	Cys	Ser
Pig	-	-	-	-	-	-	-	-	-	-	Val	Gln	-	-	Ala
Chicken	-	-	Ile	-	-	-	-	-	-	-	Val	Gln	-	-	-
Dogfish	-	-	-	-	-	-	-	-	Val	-	Val	Gln	-	-	Ala
Drosophila	-	-	-	-	-	-	-	-	Leu		Val	Gln	Arg		Ala
Wheat	-	Asn	Pro	Asp	Ala	-	Ala	-	-	-	Lys	Thr	-	-	Ala
Yeast	-	Ser	Ala	Lys	-	-	Ala	Thr	Leu	-	Lys	Thr	Arg	-	Glu

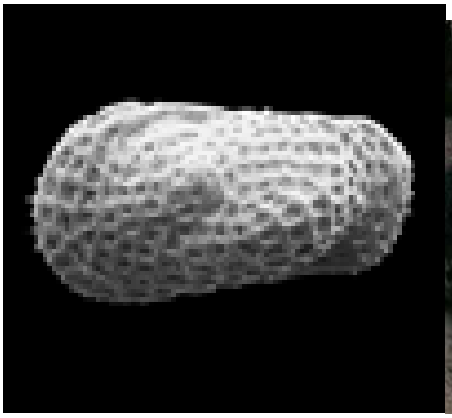
Cytochrome c is part of the respiratory chain down which electrons are passed to oxygen during cellular respiration and is found in the mitochondria of every aerobic eukaryote - animal, plant, and protist. The more identities there are between 2 molecules, the more recently they have evolved from a common ancestral molecule.

Convergent Evolution

Convergent evolution results in similar-appearing structures (the bivalved shells of ostracods, bivalves and brachiopods). Convergent characters have arisen independently and have separate genetic and phylogenetic origins. Convergence along with parallelism (similar characters arise more than once in different species within a lineage but they share a common evolutionary and developmental basis), and character reversal (a character reverts back to an ancestral condition) constitute **homoplasy. Homoplasy is the recurrence of similarity in evolution.**

Morphological Convergence

Ostracod **Brachiopod** **Bivalve**



Molecular Convergence

Cows and langur monkeys both synthesize a lysozyme that share the same activity, but comparison of their amino acid sequences indicates that each has evolved from a different ancestral molecule.

Characters

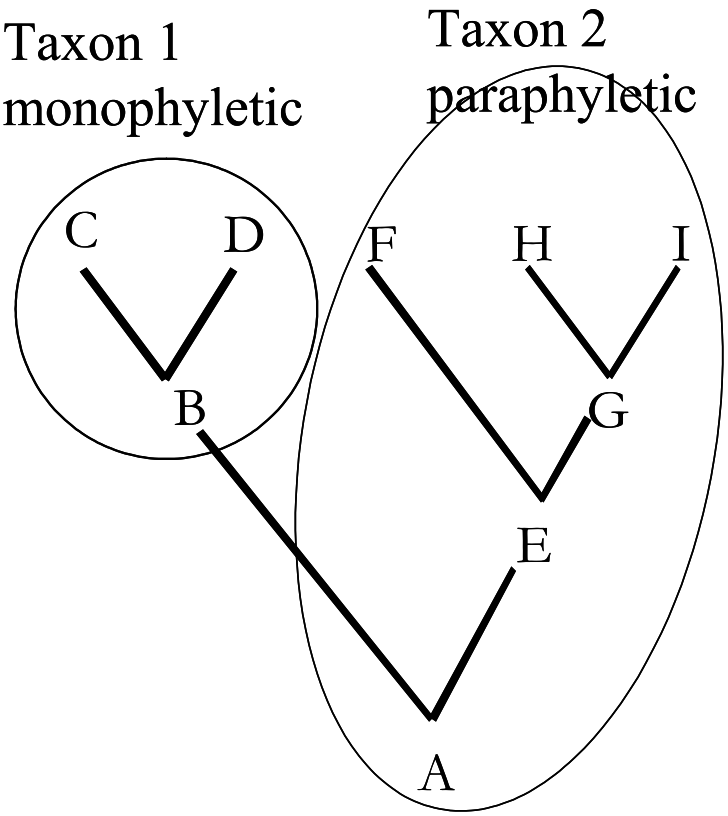
Ancestral (primitive) vs **derived** (advanced) characters.
Ancestral characters are "old" characters retained from some distant ancestor (the possession of a spine in primates is an ancestral character). Derived characters are of recent origin (opposable thumb is a derived character in primates). Note the relative use of these terms.

Apomorphy vs. plesiomorphy

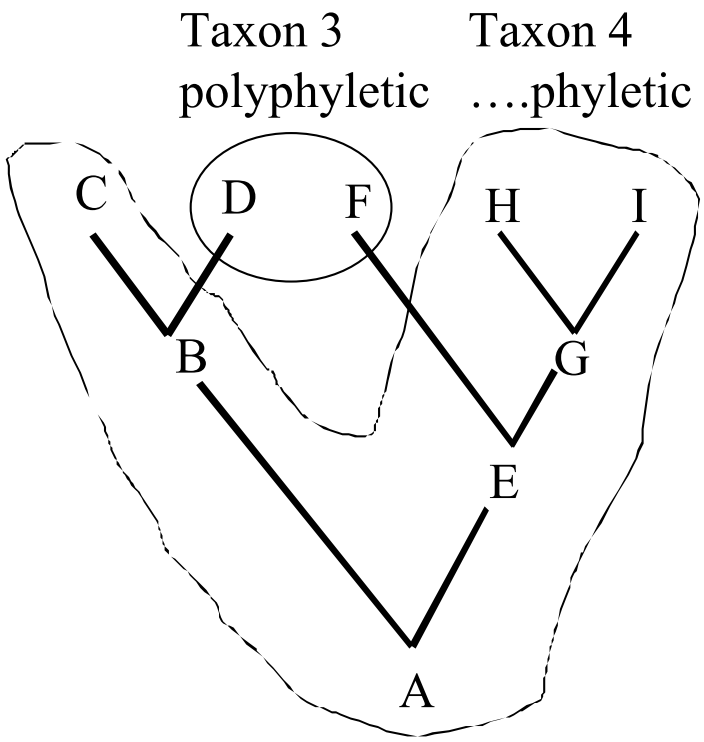
Apomorphy is the derived character state and **plesiomorphy** is the ancestral character state. Example: loss of eyes in cave-dwelling crustaceans and fish is an apomorphy whereas presence of eyes is a plesiomorphy. An apomorphy restricted to one species is called **autapomorphy,** and an apomorphy shared between two or more species is called a **synapomorphy. A synapomorphy** can be considered at only one phylogenetic level; at all lower phylogenetic levels they are referred as **symplesiomorphies**. Example: Broca's center in the brain is an autapomorphy defining humans. Opposing thumbs are a synapomorphy defining primates. Mammary glands are a synapomorphy defining mammals but symplesiomorphy within mammals, e.g. in primates.

Concepts of **Monophyly, Paraphyly, Polyphyly**

A monophyletic group (Taxon 1) is a group of species that includes an ancestral species (species B) and all of its descendants (species C and D). Vertebrates are a monophyletic group. **A paraphyletic group (Taxon 2)** is a group of species than includes an ancestral species (species A), but not all of its descendants (species B,C, and D) are missing. Polychaetes and oligochaetes are probably paraphyletic groups.



A **polyphyletic group** (Taxon 3) is a group of species (species D and F) from different immediate ancestors (B and E). Examples, the former Phylum Protozoa; "slugs that have lost their shells do not constitute a natural monophyletic clade, they are polyphyletic.



Useful Definitions

adaptation -- Change in a organism resulting from natural selection; a structure which is the result of such selection.

anagensis -- Evolutionary change along an unbranching lineage; change without speciation.

ancestor -- Any organism, population, or species from which some other organism, population, or species is descended by reproduction.

basal group -- The earliest diverging group within a clade; for instance, to hypothesize that sponges are basal animals is to suggest that the lineage(s) leading to sponges diverged from the lineage that gave rise to all other animals.

character -- The observable parts, or attributes, of organisms which can be examined for similarity or difference are called characters.

character state -- The alternative forms of a character (e.g. black vs. red hair)

clade -- A monophyletic taxon; a group of organisms which includes the most recent common ancestor of all of its members and all of the descendants of that most recent common ancestor. From the Greek word "klados", meaning branch or twig.

cladogenesis -- The development of a new clade; the splitting of a single lineage into two distinct lineages; speciation.

cladogram -- A diagram, resulting from a cladistic analysis, which depicts a hypothetical branching sequence of lineages leading to the taxa under consideration. The points of branching within a cladogram are called nodes. All taxa occur at the endpoints of the cladogram.

convergence -- Similarities which have arisen independently in two or more organisms that are not closely related. Contrast with homology.

crown group -- All the taxa descended from a major cladogenesis event, recognized by possessing the clade's synapomorphy. See: stem group.

derived -- Describes a character state that is present in one or more subclades, but not all, of a clade under consideration. A derived character state is inferred to be a modified version of the primitive condition of that character, and to have arisen later in the evolution of the clade. For example, "presence of hair" is a primitive character state for all mammals, whereas the "hairlessness" of whales is a derived state for one subclade within the Mammalia.

diversity -- Term used to describe numbers of taxa, or variation in morphology.

endosymbiosis -- When one organism takes up permanent residence within another, such that the two become a single functional organism. Mitochondria and plastids are believed to have resulted from endosymbiosis.

evolution -- Darwin's definition: descent with modification. The term has been variously used and abused since Darwin to include everything from the origin of man to the origin of life.

evolutionary tree -- A diagram which depicts the hypothetical phylogeny of the taxa under consideration. The points at which lineages split represent ancestor taxa to the descendant taxa appearing at the terminal points of the cladogram.

extinction -- When all the members of a clade or taxon die, the group is said to be extinct.

gradualism -- A model of evolution that assumes slow, steady rates of change. Charles Darwin's original concept of evolution by natural selection assumed gradualism. Contrast with punctuated equilibrium.

Hennigian cladistics – the most important feature is that synapomorphic character states must be identified and that they alone provide the basis for clade identification.

homology -- Two structures are considered homologous when they are inherited from a common ancestor which possessed the structure. This may be difficult to determine when the structure has been modified through descent.

hypothesis -- A concept or idea that can be falsified by various scientific methods.

ingroup -- In a cladistic analysis, the set of taxa which are hypothesized to be more closely related to each other than any are to the outgroup.

lineage -- Any continuous line of descent; any series of organisms connected by reproduction by parent of offspring.

monophyletic -- Term applied to a group of organisms which includes the most recent common ancestor of all of its members and all of the descendants of that most recent common ancestor. A monophyletic group is called a clade.

outgroup -- In a cladistic analysis, any taxon used to help resolve the polarity of characters, and which is hypothesized to be less closely related to each of the taxa under consideration than any are to each other.

paraphyletic -- Term applied to a group of organisms which includes the most recent common ancestor of all of its members, but not all of the descendants of that most recent common ancestor.

parsimony -- Refers to a rule used to choose among possible cladograms, which states that the cladogram implying the least number of changes in character states is the best.

phylogenetics -- Field of biology that deals with the relationships between organisms. It includes the discovery of these relationships, and the study of the causes behind this pattern.

phylogeny -- The evolutionary relationships among organisms; the patterns of lineage branching produced by the true evolutionary history of the organisms being considered.

plesiomorphy -- A primitive character state for the taxa under consideration.

polarity of characters -- The states of characters used in a cladistic analysis, either original or derived. Original characters are those acquired by an ancestor deeper in the phylogeny than the most recent common ancestor of the taxa under consideration. Derived characters are those acquired by the most recent common ancestor of the taxa under consideration.

polyphyletic -- Term applied to a group of organisms which does not include the most recent common ancestor of those organisms; the ancestor does not possess the character shared by members of the group.

primitive -- Describes a character state that is present in the common ancestor of a clade. A primitive character state is inferred to be the original condition of that character within the clade under consideration. For example, "presence of hair" is a primitive character state for all mammals, whereas the "hairlessness" of whales is a derived state for one subclade within the Mammalia.

pseudoextinction -- The apparent disappearance of a taxon. In cases of pseudoextinction, this disappearance is not due to the death of all members, but the evolution of novel features in one or more lineages, so that the new clades are not recognized as belonging to the paraphyletic ancestral group, whose members have ceased to exist. The Dinosauria, if defined so as to exclude the birds, is an example of a group that has undergone pseudoextinction.

punctuated equilibrium -- A model of evolution in which change occurs in relatively rapid bursts, followed by longer periods of stasis.

radiation -- Event of rapid cladogenesis, believed to occur under conditions where a new feature permits a lineage to move into a new niche or new habitat, and is then called an adaptive radiation.

rank -- In traditional taxonomy, taxa are ranked according to their level of inclusiveness. Thus a genus contains one or more species, a family includes one or more genera, and so on.

relatedness -- Two clades are more closely related when they share a more recent common ancestor between them than they do with any other clade.

reticulation -- Joining of separate lineages on a phylogenetic tree, generally through hybridization or through lateral gene transfer. Fairly common in certain land plant clades; reticulation is thought to be rare among metazoans.

selection -- Process which favors one feature of organisms in a population over another feature found in the population. This occurs through differential reproduction -- those with the favored feature produce more offspring than those with the other feature, such that they become a greater percentage of the population in the next generation.

sister group -- The two clades resulting from the splitting of a single lineage.

stasis -- A period of little or no discernible change in a lineage.

stem group -- All the taxa in a clade preceding a major cladogenesis event. They are often difficult to recognize because they may not possess synapomorpies found in the crown group.

synapomorphy -- A character which is derived, and because it is shared by the taxa under consideration, is used to infer common ancestry.

systematics -- Field of biology that deals with the diversity of life. Systematics is usually divided into the two areas of phylogenetics and taxonomy.

taxon (plural taxa)-- Any named group of organisms, not necessarily a clade.

taxonomy -- The science of naming and classifying organisms.

vicariance -- Speciation which occurs as a result of the separation and subsequent isolation of portions of an original population.

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