Biological Evolution

Cosmic
Evolution
  Life
    Evolution

[Google Search]
☑ only search Palaeos.com

    Paleontology
    Systematics
    Ecology

    Astrobiology (Life in the Cosmos)
    "Tellurobiota" (Life on Earth)

Evolution
  Evolution – the Modern Synthesis
  Glossary
  References

Variability of ladybirds. Theodosius Dobzhansky, one of the founders of the synthetic theory of evolution, began his investigations studying the geographical and intra-population variability of ladybirds. Image copyright Darwin Museum.

In biology, the process of evolution is the change in a population's genetic structure over successive generations. Specifically, it is the change in allele frequency over time. The many sub-processes of evolution account for the diversity of life, such as genetic inheritance, which accounts for the continuity of traits, mutation, which accounts for novel traits, and natural selection, which accounts for the environmental filtering of traits.

There are four common mechanisms of evolution. The first mechanism is natural selection, a process in which there is differential survival and/or reproduction of organisms that differ in one or more inherited traits. A second mechanism is genetic drift, a process in which there are random changes to the proportions of two or more inherited traits within a population. A third mechanism is mutation, which is a permanent change in a DNA sequence. Finally, the fourth mechanism is gene flow, which is the incorporation of genes from one population into another.

Evolution may in the long term lead to speciation, whereby a single ancestral species splits into two or more different species. Speciation is visible in anatomical, genetic and other similarities between groups of organisms, geographical distribution of related species, the fossil record and the recorded genetic changes in living organisms over many generations. Speciation stretches back over 3.5 billion years during which life has existed on earth. It is thought to occur in multiple ways such as slowly, steadily and gradually over time or rapidly from one long static state to another.

The scientific study of evolution began in the mid-nineteenth century, when research into the fossil record and the diversity of living organisms convinced most scientists that species evolve.] The mechanism driving these changes remained unclear until the theory of natural selection was independently proposed by Charles Darwin and Alfred Wallace in 1858. In the early 20th century, Darwinian theories of evolution were combined with genetics, palaeontology and systematics, which culminated into a union of ideas known as the modern evolutionary synthesis. The synthesis became a major principle of biology as it provided a coherent and unifying explanation for the history and diversity of life on Earth.

Evolution is currently applied and studied in various areas within biology such as conservation biology, developmental biology, ecology, physiology, paleontology and medicine. Moreover, it has also made an impact on traditionally non-biological disciplines such as agriculture, anthropology, philosophy and psychology.

A scientific model, or theory, explaining this process is called a theory of evolution (ToE). The current widely-accepted theory of evolution is the modern evolutionary synthesis, also called the Neo-Darwinian theory. Sometimes, the theory of evolution is simply shortened to "evolution" (as in, "Evolution explains the diversity of life"). (Evolution Wiki, Wikipedia)

As with other truly revolutionary scientific hypotheses such as Aristarchus', Copernicus' and Galileo's heliocentric cosmology, Newton's universal theory of gravitation, Einstein's theory of relativity, Darwin's explanation of the origin and diversity of life on Earth through natural selection totally transformed our understanding of the natural world and our place in the universe. Indeed, the evolution and transformation of life on Earth through geological time simply cannot be understood except through Darwinian evolution, any more than the correct movement of the celestial bodies can be understood without reference to Galileo, Newton, etc. The extraordinary amount of data collected by the life sciences in the one and half centuries since Darwin published origin of the species, have allowed us to develop an integrated understanding of the evolution of life through various physical, chemical, and biological processes over millions of years. MAK110719

Page Back: Paleontology	Unit Home (you are here)	Page Top	Page Next: Evolution – the Modern Synthesis

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page last modified MAK111009, edited RFVS111214
Google search box courtesy of Ask Dave Taylor

Page Back | Unit home | Page Next: Glossary
Unit Back: Life | References | Unit Next: Paleontology

Evolution – the Modern Synthesis

Cosmic Evolution
  Life
    Evolution
    Paleontology
    Systematics
    Ecology

    Astrobiology (Life in the Cosmos)
    "Tellurobiota" (Life on Earth)

Evolution
  Evolution – the Modern Synthesis
  Glossary
  References

The Modern Synthesis

A Theory of the Mechanism of Evolution
(version 1.5, January 22, 1993)

Author: Larry A. Moran (from the G.L.K file collection—original url)

Many people do not understand current ideas about evolution. The following is a brief summary of the modern consensus among evolutionary biologists.

The idea that life on Earth has evolved was widely discussed in Europe in the late 1700's and the early part of the last century. In 1859 Charles Darwin supplied a mechanism, namely natural selection, that could explain how evolution occurs. Darwin's theory of natural selection helped to convince most people that life has evolved and this point has not been seriously challenged in the past one hundred and thirty years.

It is important to note that Darwin's book "The Origin of Species by Means of Natural Selection" did two things. It summarized all of the evidence in favor of the idea that all organisms have descended with modification from a common ancestor, and thus built a strong case for evolution. In addition Darwin advocated natural selection as a mechanism of evolution. Biologists no longer question whether evolution has occurred or is occurring. That part of Darwin's book is now considered to be so overwhelmingly demonstrated that is often referred to as the ***fact*** of evolution. However, the ***mechanism*** of evolution is still debated.

We have learned much since Darwin's time and it is no longer appropriate to claim that evolutionary biologists believe that Darwin's theory of Natural Selection is the best theory of the mechanism of evolution. I can understand why this point may not be appreciated by the average non-scientist because natural selection is easy to understand at a superficial level. It has been widely promoted in the popular press and the image of "survival of the fittest" is too powerful and too convenient.

During the first part of this century the incorporation of genetics and population biology into studies of evolution led to a Neo-Darwinian theory of evolution that recognized the importance of mutation and variation within a population. Natural selection then became a process that altered the frequency of genes in a population and this defined evolution. This point of view held sway for many decades but more recently the classic Neo-Darwinian view has been replaced by a new concept which includes several other mechanisms in addition to natural selection. Current ideas on evolution are usually referred to as the Modern Synthesis which is described by Futuyma:

> "The major tenets of the evolutionary synthesis, then, were that populations contain genetic variation that arises by random (i.e.. not adaptively directed) mutation and recombination; that populations evolve by changes in gene frequency brought about by random genetic drift, gene flow, and especially natural selection; that most adaptive genetic variants have individually slight phenotypic effects so that phenotypic changes are gradual (although some alleles with discrete effects may be advantageous, as in certain color polymorphisms); that diversification comes about by speciation, which normally entails the gradual evolution of reproductive isolation among populations; and that these processes, continued for sufficiently long, give rise to changes of such great magnitude as to warrant the designation of higher taxonomic levels (genera, families, and so forth)."

Futuyma, D.J. in *Evolutionary Biology*, Sinauer Associates, 1986; p.12

This description would be incomprehensible to Darwin since he was unaware of genes and genetic drift. The modern theory of the mechanism of evolution differs from Darwinism in three important respects:

1. It recognizes several mechanisms of evolution in addition to natural selection. One of these, random genetic drift, may be as important as natural selection.
2. It recognizes that characteristics are inherited as discrete entities called genes. Variation within a population is due to the presence of multiple alleles of a gene.
3. It postulates that speciation is (usually) due to the gradual accumulation of small genetic changes. This is equivalent to saying that macroevolution is simply a lot of microevolution.

In other words, the Modern Synthesis is a theory about how evolution works at the level of genes, phenotypes, and populations whereas Darwinism was concerned mainly with organisms, speciation and individuals. This is a major paradigm shift and those who fail to appreciate it find themselves out of step with the thinking of evolutionary biologists. Many instances of such confusion can be seen here in the newsgroups, in the popular press, and in the writings of anti-evolutionists.

The major controversy among evolutionists today concerns the validity of point #3 (above). The are many who believe that the fossil record at any one site does not show gradual change but instead long periods of stasis followed by rapid speciation. This model is referred to as Punctuated Equilibrium and it is widely accepted as true, at least in some cases. The debate is over the relative contributions of gradual versus punctuated change, the average size of the punctuations, and the mechanism. To a large extent the debate is over the use of terms and definitions, not over fundamentals. No new mechanisms of evolution are needed to explain the model.

Some scientists continue to refer to modern thought in evolution as Neo-Darwinian. In some cases these scientists do not understand that the field has changed but in other cases they are referring to what I have called the Modern Synthesis, only they have retained the old name.

Page Back | **Page Top** | **Unit home** | **Page Next: Glossary**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page uploaded 9 November 1998, last modified 17 March 2002
checked ATW030421, edited RFVS111214
The Modern Synthesis, by Larry Moran, reproduced from the "G.L.K file collection" (former site)

Page Back: Modern Theory of Evolution	Unit Up: Life	Unit home	Glossary (you are here)	Page Next: References
Unit Back: Paleontology	Page Up: Big Picture Glossary	Page Up: Main Glossary	References	Unit Next: Paleontology

Evolution : Glossary

Cosmic Evolution
  Life
    Evolution
    Paleontology
    Systematics
    Ecology

    Astrobiology (Life in the Cosmos)
    "Tellurobiota" (Life on Earth)

Evolution
  Evolution: the Modern Synthesis
  Glossary
  References

A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z

A

Abiogenesis: The development of life from non-living systems via natural mechanisms. cf. creation. (W. R. Elsberry talk.origins via W.J. Hudson)

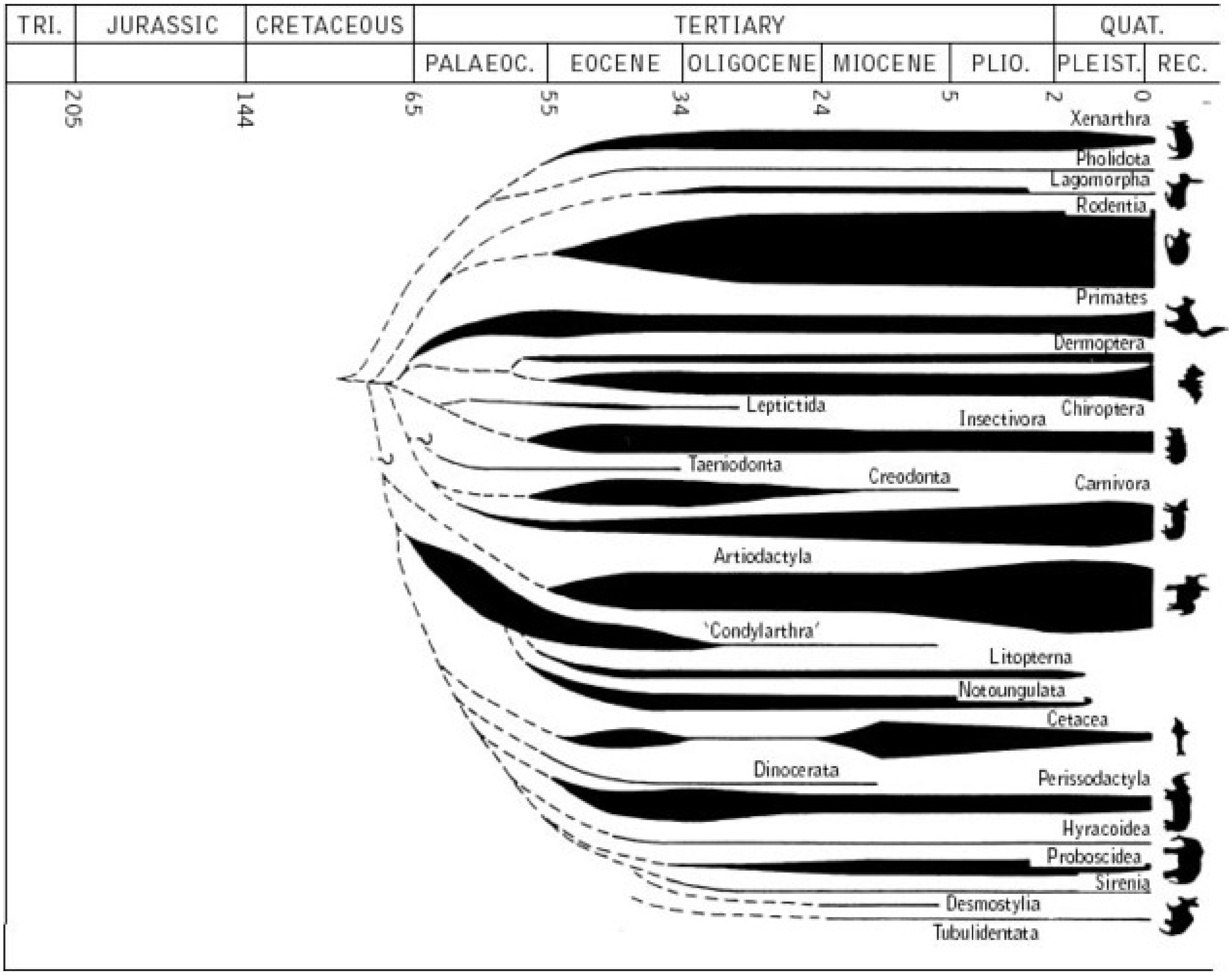
Abiotic factors: The non-biological environmental influences that affect organisms; for example, temperature, rainfall, and humidity. (Wikipedia glossary)

Acquired trait: A phenotypic characteristic, acquired during growth and development, that is not genetically based and therefore cannot be passed on to the next generation (for example, the large muscles of a weightlifter). (PBS evolution Glossary)

Adaptation: the evolutionary process whereby a population becomes better suited to its habitat. Can also refer to a feature which is especially important for an organism's survival. For example, the adaptation of horses' teeth to the grinding of grass, or their ability to run fast and escape predators. Such adaptations are produced in a variable population by the better suited forms reproducing more successfully, that is, by natural selection. (Wikipedia)

Adaptationism or **panselectionism**: a set of methods in the evolutionary sciences for distinguishing the products of adaptation from traits that arise through other processes. It is employed in fields such as ethology and evolutionary psychology that are concerned with identifying adaptations. Critics (most notably Richard Lewontin and Stephen Jay Gould) contend that the adaptationists (John Maynard Smith, W.D. Hamilton and Richard Dawkins being frequent examples) have over-emphasized the power of natural selection to shape individual traits to an evolutionary optimum, and ignored the role of developmental constraints, and other factors to explain extant morphological and behavioural traits. (Wikipedia)

Adaptive radiation: the rapid expansion and diversification of a group of organisms as they fill unoccupied ecological niches, evolving into new species or sub-species; the classic example being Darwin's finches. This occurs as a result of different populations becoming reproductively isolated from each other, usually by adapting to different environments. Radiations specifically to increase in taxonomic diversity or morphological disparity, due to adaptive change or the opening of ecospace, may affect one clade or many, and be rapid or gradual The term can also be applied to larger groups of organisms, as in "the adaptive radiation of mammals" (see diagram below), although in this context it is perhaps better referred to as ***evolutionary radiation***. Evolutionary radiation in this context refers to a larger scale radiation; whereas rapid radiation driven by a single lineage's adaptation to their environment is adaptive radiation proper. Adaptive and evolutionary radiations in this latter context follow mass-extinctions, as when during the early Cenozoic mammals and large flightless birds filled ecological roles previously occupied in the Mesozoic by dinosaurs.



Spindle diagram showing the adaptive radiation of placental mammals in the Cenozoic (Geological timeline at top of diagram). Placentals radiated rapidly after the extinction of the dinosaurs, and the modern diversity of form was established within the first 10 million years of the Tertiary (during the Paleocene). (Based on Gingerich 1984.) from Benton, Mammals – The success of the mammals: chewing and homeostasis, The origin of the mammals, Mammalian evolution.

Advanced: some evolutionary scientists and systematists reject terms like "primitive" or "advanced" when discussing fossil or recent organisms. It is felt that these terms imply ascent or teleology, and that terms like primitive and advanced terms suggest some degree of "improvement" or superiority in the case of organisms considered advanced in relation to those considered primitive. Such associations are of especial concern in cladistics, where an emphasis is on only verifiable empirical methodology. Hence value-neutral words like "derived" are used as an alternative. However, it could be argued that evolution can indeed refer to an increase in complexity and emergence of new characteristics. This being so, there is no reason why these terms cannot be used. (MAK)

Allele: Different versions of the same gene. For example, humans can have A, B or O blood type alleles. (W. R. Elsberry talk.origins via W.J. Hudson)

Allometry: The relation between the size of an organism and the size of any of its parts, first outlined by Otto Snell in 1892 and Julian Huxley in 1932. Allometric growth is the phenomenon where parts of the same organism grow at different rates. For example in various insect species (e.g., the Hercules Beetle), where a small change in overall body size can lead to an enormous and disproportionate increase in the dimensions of appendages such as legs, antennae, or horns. Allometric relations can be studied during the growth of a single organism, between different organisms within a species, or between organisms in different species. Contrast with isometric growth.

Amino acid: The molecular building blocks of proteins. The properties of a protein are determined by its particular amino acid sequence. There are 20 amino acids in the proteins of life on Earth.

Anagenesis: the evolutionary transformation of one species over time into another, or in other words , the emergence of a new character or attribute (which in in this case a new species) from an older one. One of the two main parameters of evolutionary change, the other being branching (either cladogenesis or budding). O'Keefe & Sander 1999 provide a case study of among mid Triassic pachypleurosaurs, and its interpretation using phenetic, cladistic, and stratigraphic methodologies. The diagram at the right by Paul Olsen, Lecture 5 Evolution, showing the relation between anagenesis and cladogenesis. See also fig. 1 at Talk Origins: Macroevolution showing anagenesis and cladogenesis as complementary parameters (see also ancestor, descendant). (MAK)

Analogy/analogous structure: Structures having similar function or superficial appearance, but have a different evolutionary origin. For example the wings of insects and the wings of birds. Contrast with homologous structures.

The Ancestor's Tale: popular science book written by Richard Dawkins. The book charts the evolutionary history of life, which is illustrated as a pilgrimage backward in time heading towards the origin of life. This creates of series of 40 "rendezvous" by following man, as the selected currently existing creature, through the most recent common ancestors (called 'concestor'). The basic structure of the book is modeled after Chaucer's ***Canterbury Tales***. (EvoWiki)

Archaeopteryx: arguably the most famous of all transitional forms, ***Archaeopteryx*** is the earliest and most primitive known bird, most of whose fossil remains were recovered in the 19th century, from the Jurassic Solnhofen limestone in Bavaria. Perfectly intermediate between reptile (or more correctly, theropod dinosaur) and modern bird, its discovery was powerful evidence for Darwinian evolution. (MAK). Wikipedia page (detailed coverage)

Arms race: in evolutionary biology just as is the case between two rival nations, positive feedback between two or more evolutionary lineages coevolving in such a way that each, in turn, develops more and more extreme/efficient defenses and weapons in response to the others' attributes. For example, a predator may evolve larger teeth or claws, resulting in the prey species developing faster speed, larger size or protective armour, requiring the predator lineage itself to develop further to be able to capture its prey. In addition to predator and prey, can also occur with the co-evolution of a parasite and its host. Alternatively, the arms race may be between members of the same species, as in sexual selection or Red Queen effects. See also escalation hypothesis. (MAK, Wikipedia)

Artificial selection: Selectively breeding animals and cultivate crops to select the most desirable traits in a plant or animal population. Most domesticated and agricultural species have been produced by artificial selection. It was Darwin's observations in this area that inspired the idea of natural selection (without human intervention)

Ascent: The premise that evolution directional, moving from primitive and less perfect to more complex and perfect forms, the whole constituting a sort of hierarchical gradation, usually with man at the top. The progression from (what is anthropocentrically considered) a lower to a higher form of life. Zallinger's iconic and often misinterpreted (it was never intended to portray a strictly linear model of evolution) ***March of Progress*** gives the classic representation of the layman's conception of evolution, showing man's progression from an ape-like ancestor through various intervening stages of ape-men, to modern human. . According to popular science writers like Stephen Jay Gould, thes idea of evolution as a straight-line from the slime to man and beyond is a concept that really has very little to do with true Darwinism, despite superficial appearances to the contrary. On the other hand, modern fields such as systems theory and the study of biodiversity through time shows that evolution is indeed directional in that it does progress to more complex forms (while simpler organisms such as bacteria continue alongside, it is a misinterpretation to assume that Darwinian thought and evolutionary theory in general support a naive anthropocentric hierarchy of being.

The Evolution as Progress meme is however immensely influential in human thinking. It appears in Marxism, in Theosophy, in Humanism, in Transhumanism, and elsewhere besides. It is criticized and rebuked by anti-evolutionist religious creationists, who think they are opposing Darwinism, when they are actually opposing something that has nothing to do with Darwinism. Some popular thinkers, such as Teilhard de Chardin, have argued for an anthropocentric cosmology, culminating in a future omega point. (MAK)

Asexual reproduction: (also called Vegetative Reproduction) A form of duplication using only mitosis. Example, a new plant grows out of the root or a shoot from an existing plant. This process produces only genetically identical offspring since all divisions are by mitosis. 1. offspring called clones meaning that each is an exact copy of the original organism 2. this method of reproduction is rapid and effective allowing the spread of an organism 3. Since the offspring are identical, the only mechanism for introducing genetic diversity is mutation. (W.J. Hudson)

B

Base: The information coding part of DNA, the letters of the genetic code. The DNA molecule is a chain of nucleotides; each consisting of a backbone made of a sugar and a phosphate group, with a nitrogenous base attached. There are four bases ("letters" so to speak) in the DNA "language": adenine (A), guanine (G), cytosine (C), or thymine (T). In RNA, uracil (U) is used instead of thymine. A and G belong to the chemical class called purines; C, T, and U are pyrimidines. In a strand of DNA, bases are paired and are lined up across from one another: A pairs with T and G pairs with C. The sequence of bases along the DNA molecule determines what the DNA codes for (such as making a protein, or turning on or off a gene). In protein-coding regions, three base pairs code for a single amino acid. For example, the base pair sequence ATG codes for the amino acid methionine. (adapted from UCMP Understanding Evolution Glossary, and PBS evolution Glossary)

Batesian mimicry: A form of mimicry in which one non-poisonous species (the Batesian mimic) has evolved to imitate the warning signals of a harmful or poisonous species, to deter a predator. It is named after the English naturalist Henry Walter Bates, after his work in the rainforests of Brazil. Contrasted with Müllerian mimicry, a form of mutually beneficial convergence between two or more harmful species. (adapted from Wikipedia)

Biological species concept: An integral part of the modern evolutionary synthesis, defines a species as "a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature." BSC applies well to sexually reproducing animals, but not as well to plant life because there is greater gene flow between plant species. It is also difficult if not impossible to apply to the fossil record. Fossils are divided into species based on taxonomic classification (similarity of physical characteristics—see morphological species concept. See also cladistic species concept, ecological species concept, phenetic species concept, and recognition species concept. (W.J. Hudson. Kutschera & Niklas 2004 p.263).

Bottleneck, **bottleneck effect**: A form of genetic drift that occurs when a population's size is greatly reduced. Gene frequencies in the population are likely to change just by random chance and many genes may be lost from the population, reducing the population's genetic variation. When the population later expands in numbers, the resulting gene frequencies may be distinctly different from those before the bottleneck. (See also Founder effect.) (UCMP Understanding Evolution Glossary, M. W. Strickberger)

Branching: for the sake of convenience I use this term as the counterpole to anagenesis. See also Multiplication of species.

Budding: in a phylogenetic context, the origin of a new taxon (population group, species, or group of species), that does not affect the existence and attributes of the parental taxon (stem population group, or stem group of species). (Horandl & Stuessy 2010, p.1643). Mayr & Bock (2002) coined this term for divergence of a small group of populations, while the rest of the populations remain unchanged. Most obvious are cases of peripatric speciation after geographical isolation of a small group of populations. This is expected to happen mostly after colonizing events by a few individuals, then followed by rapid speciation and adaptation to new environments. Recent evidence from biogeographical studies on both animals and plants suggests that peripatric speciation may be more common than previously thought, since dispersal, even transoceanic dispersal, explains many disjunct distributional patterns. Buddings of this kind are often connected to a high amount of phenotypic change in the derivative species, which undergoes drift and adaptive change in the new ecological situation. In contrast, the source populations are neither in any novel environment, nor under any novel selective pressure." Contrast anagenesis, cladogenesis. (Horandl & Stuessy 2010, p.1644)

C

Cambrian explosion: The sudden appearance of all current animal phyla during the Early and Middle Cambrian.

Cladogenesis (also called **Splitting**): The division of an ancestral parental lineage into two or more daughter lineages or species, rather than the transformation of the ancestral species in toto (anagenesis). In contrast to budding, splitting leads to extinction of the parental lineage. (W. R. Elsberry talk.origins via W.J. Hudson; Horandl & Stuessy 2010, p.1643). As shown by the diagram (right) from Moore, Lalicker, & Fischer 1952 cladogenesis was recognised, along with anagenesis, as one of the two types of gradual evolution. This evolutionary paradigm was replaced in the 1970s and 80s by cladistics. The highly formalised trees that cladistics rely on do not allow for anagenesis, as a result cladogenesis (and then only a division into two daughter species) becomes the standard form of speciation . However, according to Horandl & Stuessy 2010, p.1644 (who argue for recognition of paraphyly): "only a portion of known speciation processes can be categorized as a split of a species in two or more isolated population groups. ***Allopatric speciation***, whereby, e.g., a geographic barrier isolates population groups, does result in a complete disappearance of the original species. Allopatric speciation has been long advocated as the main speciation mechanism, especially in the zoological literature (Coyne & Orr, 2004). This mode of speciation occurs over longer time dimensions, and it divides the ancestral species into more or less equal portions. Allopatric speciation, therefore, fits well the cladistic model of symmetrical divergence, but this is no longer regarded as the predominant mode of speciation, especially in plants (e.g., Rieseberg & Brouillet, 1994). Other evolutionary processes, especially budding and merging, enhance asymmetrical divergence and therefore occurrence of paraphyly." . See also multiplication of species, adaptive radiation. (MAK)

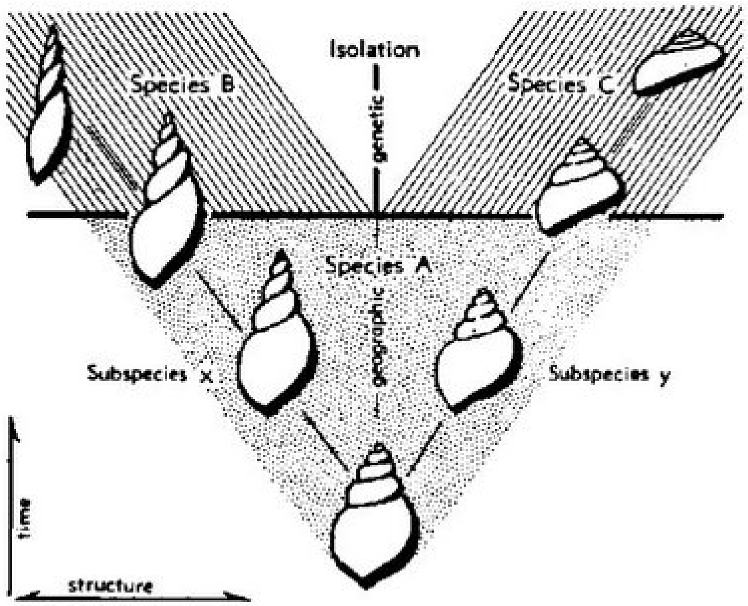


Figure 5–3:
A hypothetical case of geographic speciation viewed from the perspective of phyletic gradualism—slow and gradual transformation in two lineages.
From Moore, Lalicker, and Fischer, 1952; figure 1–15.

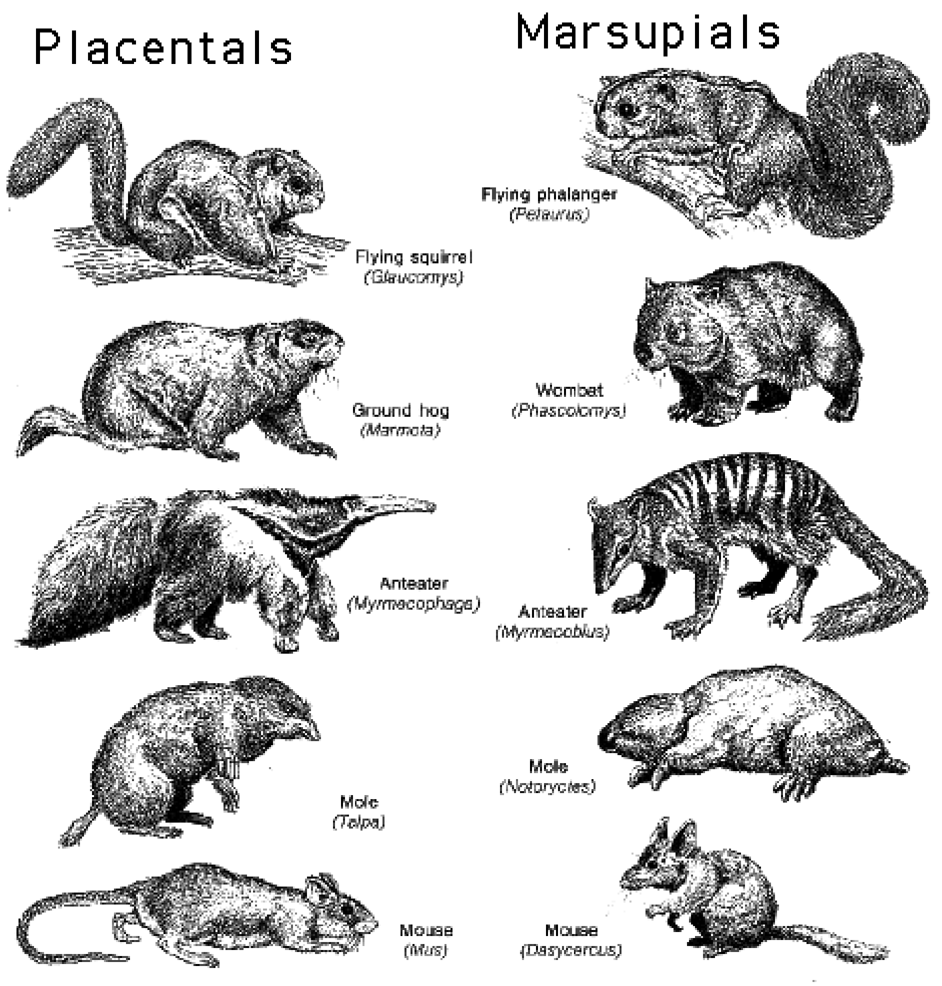
Codon: a three base unit of DNA that specifies an amino acid or the end of a protein.

Co-evolution: Evolution in two or more species, such as predator and its prey or a parasite and its host, in which evolutionary changes in one species influence the evolution of the other species. See also evolutionary arms race. (PBS evolution Glossary)

Co-extinction: the loss of one species due to the extinction of another; for example, the extinction of parasitic insects following the loss of their hosts. Co-extinction can also occur when a flowering plant loses its pollinator, or through the disruption of a food chain. (Wikipedia)

Common ancestor: The ancestral species that gave rise to two or more descendant lineages, and thus represents the ancestor they have in common.

Common descent: the premise that every group of organisms descended from a common ancestor, and that all groups of organisms, including animals, plants, and microorganisms, ultimately go back to a single origin of life on earth. (W.J. Hudson)



Convergence of forms between placentals (left) and marsupials (right). (from Convergent Evolution Examples: Ecological Equivalents.)

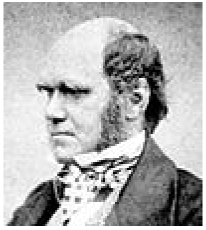
Convergent evolution, **Convergence**: process in which two or more distinct lineages independently evolve similar characteristics of one another. In other words, there is an evolutionary convergence between two unrelated or only distantly related types. This often occurs because both lineages face similar environmental challenges and selective pressures. A form of homoplasy. Compare ***Parallel Evolution***: e.g. the shark, tuna, ichthyosaur, and dolphin all evolved a similar streamlined shape as large aquatic fast-swimming predators. (adapted from UCMP Understanding Evolution Glossary) Two types of convergence that could be distinguished are ***analogy*** (convergent modifications of a non-homologous structure or behaviour, e.g. the wings of insects (presumably derived from tergal paranota) and the wings of birds (derived from the vertebrate fore legs)) and ***homoiology*** (convergent modifications of a homologous structure or behaviour —e.g. The wings of pterosaurs, birds, and bats represent such a homoiology, since they are homologous as tetrapod fore leg, but were convergently modificated to flight devices (wings)). (Glossary of Phylogenetic Systematics by Günter Bechly)

Creation: The bringing forth of matter from nothing, or the development of life from non-living systems. cf. abiogenesis. (W. R. Elsberry ***in*** talk.origins ***via*** W.J. Hudson)

Crossover: The exchange of nucleotides between pairs of homologous chromosomes during mitosis or especially meiosis. (W. R. Elsberry ***in*** talk.origins)

D

Darwin, Charles: 19th-century naturalist considered the father of the science of evolution. His landmark work, ***On the Origin of Species***, published in 1859, presented a wealth of facts supporting the idea of evolution and proposed a viable theory for how evolution occurs, via the mechanism he called "natural selection" (as a natural process analogous to



artificial selection) Also published important works on coral reefs and on the geology of the Andes, and a popular travelogue of his five-year voyage aboard HMS Beagle, and a comprehensive scientific study of barnacles. (adapted from PBS evolution Glossary)

Darwin's theory of evolution through natural selection can be summarised by means of three principles:

1. ***Principle of variation***. Among individuals within any population, there is variation in morphology, physiology, and behavior.
2. ***Principle of heredity***. Offspring resemble their parents more than they resemble unrelated individuals.
3. ***Principle of selection***. Some forms are more successful at surviving and reproducing than other forms in a given environment.

(Griffiths AJF, Miller JH, Suzuki DT, et al. "Introduction", in ***An Introduction to Genetic Analysis***. 7th edition. New York: W. H. Freeman; 2000)

Darwinian: Of or pertaining to natural selection, or Darwin's theory of evolution in general. Sometimes taken to mean natural selection with gradualist assumptions, although it is now considered doubtful that Darwin was a uniformitarian to this degree. (modified from W. R. Elsberry ***in*** talk.origins)

Darwinian classification: see Evolutionary systematics.

Darwinian evolution: See Darwinism.

Darwinism: In 1859 Charles Darwin supplied a mechanism, namely natural selection, that could explain how evolution occurs. Darwin's theory of natural selection helped to convince most people that life has evolved and this point has not been seriously challenged in the past one hundred and forty years. It is important to note that Darwin's book "The Origin of Species by Means of Natural Selection" did two things. It summarized all of the evidence in favor of the idea that all organisms have descended with modification from a common ancestor, and thus built a strong case for evolution. In addition Darwin advocated natural selection as a mechanism of evolution. Biologists no longer question whether evolution has occurred or is occurring. That part of Darwin's book is now considered to be so overwhelmingly demonstrated that is is often referred to as the ***fact*** of evolution. However, the ***mechanism*** of evolution is still debated. cf. Modern Synthesis. (W.J. Hudson). Historically, Darwinism represented the stage in the development of evolutionary thought that began with the 1859 publication of ***On the Origin of Species***. "Specifically, it refers to the Darwin/Wallace principle of natural selection as the major driving force in evolution. Since Darwin (1859, 1872) accepted Lamarck's principle of the inheritance of acquired characteristics as a source of biological variability, it is equally fair to call this the "Lamarck/Darwin/Wallace" period of evolutionary thought. (Kutschera & Niklas 2004, p.259–260)

Descendent: in this context, a population, lineage, or species, that arises through evolution from an ancestor (an earlier species or taxon). Where a number of descendants share the same ancestor (cladogenesis), the ancestor is called a common ancestor. (MAK)

Diploid: Having two alleles for every gene at every locus, one from the mother and one from the father. Most animals, including humans, are diploid. (W.J. Hudson)

Directionality (in evolution): as here defined, the premise that evolution begins with simple or primitive structures or forms of life and moves to greater complexity or perfection; hence some forms of life are more complex, advanced, or evolved relative to others; see Systems Theory's definition of evolution. Results in a tree or hierarchy in which—depending on your perspective—multicellular life, vertebrate animals, or human beings, or self-consciousness, culture, or omega point are at its apex. Whilst the emergence of complexity is a self-evident fact, philosophers and scientists are divided over whether evolution itself is directional. See also complexification, emergence, great story. (MAK)

Diversity: the variation of genomes, populations, species, families, or whatever, within a lineage.

DNA: Deoxyribonucleic acid, the molecule that contains genetic information.

E

Escalation hypothesis: a hypotheses put forward by Geerat J. Vermeij. It states that organisms are in constant conflict with one another and therefore devote a lot of resources to thwarting the adaptations evolution brings to all competing organisms as time advances. This is in contrast to adaptations evolution may bring that are unrelated to competition with other organisms such as adapting to ecological niches based upon other factors such as geology and climate. Vermeij's extensive work with the characteristics of marine gastropod fossils informed his development of thoughts on escalation. One prediction of the Escalation Hypothesis is that individual species having fewer adaptations that enable them to compete with other life forms are more likely to survive a mass extinction event such as one of The Big Five. This is because there is more flexibility to fit into new ecological niches that arduous adaptations such as heavy shells or energy consuming venom production would hinder. (Wikipedia)

Evolution (Biology): A change in the gene pool of a population over time. The process of evolution can be summarized in three sentences: Genes mutate. Individuals are selected. Populations evolve. (W.J. Hudson) A subset of Evolution (Systems Theory). See also Darwinism, Modern Synthesis . Note that in the biological context, evolution does not apply to individuals (in contrast with the premises of Conscious evolution). (MAK)

Evolutionary game theory (EGT): is the application of game theory to interaction dependent strategy evolution in populations. EGT is useful in a biological context by defining a framework of strategies in which adaptive features can be modeled. It originated in 1973 with John Maynard Smith and George R. Price's formalization of evolutionarily stable strategies as an application of the mathematical theory of games to biological contexts, arising from the realization that frequency dependent fitness introduces a strategic aspect to evolution. EGT differs from classical game theory by focusing on the dynamics of strategy change more than the properties of strategy equilibria. Despite its name, evolutionary game theory has become of increasing interest to economists, sociologists, anthropologists, and philosophers.

In Smith's and Price's paper, "The Logic of Animal Conflict", a computer model was used to show why animals had not adapted a “total war” strategy. Adaptations for males focused on maximizing their ability to compete with each other in order to maximize their dominance over a territory and better compete for mates. Using game theory, they were able to test a variety of evolutionary strategies to see which one emerged with the highest average payoff, explaining why animals have only evolved ***limited war*** strategy, in which risk of serious injury is low. (Wikipedia)

Evolutionary psychology: branch of psychology or evolutionary science that examines psychological traits—such as memory, perception, or language—from a modern evolutionary perspective. It seeks to identify which human psychological traits are evolved adaptations , that is, the functional products of natural selection or sexual selection. Evolutionary psychology has its historical roots in Charles Darwin's theory of natural selection.[4] Darwin's theory inspired William James's functionalist approach to psychology. Along with W.D. Hamilton's (1964) seminal papers on inclusive fitness, E. O. Wilson's ***Sociobiology*** (1975) helped to establish evolutionary thinking in psychology and the other social sciences. (Wikipedia)

Evolutionary radiation: see Adaptive radiation.

Evolutionary synthesis: see Modern Synthesis.

Evolutionary Theory: (or **Evolutionary Mechanism Theory**) Any one of several theories in biology dealing explicitly with some aspect of evolution or cumulative evolution. Examples include Sewall Wright's "shifting-balance theory", Eldredge and Gould's "punctuated equilibrium theory", the theory of common descent, Darwin's "descent with modification", Henry Fairfield Osborn's "orthogenesis", and "Gene Flow". While "evolutionary theory" is equivalent, the point that mechanisms are proposed and tested in evolutionary mechanism theories is worthy of stress and repetition. Some mechanisms increase genetic variation (cf. mutation, recombination, gene flow) and some decrease genetic variation (cf. natural selection, genetic drift). (W. R. Elsberry talk.origins via W.J. Hudson)

F

Fitness: the ability of an individual organism to both survive and reproduce; a central element of evolutionary theory. Fitness is equal to the average contribution to the gene pool of the next generation that is made by an average individual of the specified genotype or phenotype. If differences between alleles at a given gene affect fitness, then the frequencies of the alleles will change over generations; the alleles with higher fitness become more common (in other words, natural selection). (Wikipedia)

Fitness landscape: Sewall Wright proposed that populations occupy ***adaptive peaks*** on a fitness landscape. In order to evolve to another, higher peak, a population would first have to pass through a valley of maladaptive intermediate stages. A given population might be "trapped" on a peak that is not optimally adapted. (Wikipedia)

Founder effect: Changes in gene frequencies that usually accompany starting a new population from a small number of individuals. The newly founded population is likely to have quite different gene frequencies than the source population because of sampling error (i.e., genetic drift). The newly founded population is also likely to have a less genetic variation than the source population. For a more detailed explanation, see our resource on adaptation in Evolution 101. (UCMP Understanding Evolution Glossary)

G

Gene: The fundamental physical and functional unit of heredity which carries information from generation to the next. (W. R. Elsberry talk.origins via W.J. Hudson)

Gene family: A set of related genes occupying various loci in the DNA, almost certainly formed by duplication of an ancestral gene and having a recognizably similar sequence. Members of a gene family may be functionally very similar or differ widely. The globin gene family is an example. (PBS evolution Glossary)

Gene flow: An evolutionary mechanism theory. Gene Flow states that new organisms may enter a population by migration from another population. If they mate within the population, they can bring new alleles to the local gene pool. In some closely related species, fertile hybrids can result from interspecific matings. These hybrids can vector genes from species to species. (W.J. Hudson)

Gene frequency: The frequency in the population of a particular gene relative to other genes at its locus. Expressed as a proportion (between 0 and 1) or percentage (between 0 and 100 percent). (PBS evolution Glossary)

Gene pool: The set of all genes in a species or population. (W.J. Hudson)

Gene selection, "selfish gene" theory, or **gene-centered view of evolution**: theory that genes are the unit of selection. The theory states that although individuals are the object of selection, because of crossing over and recombination which shuffles genes around, it is the genes which are selected for over time. The alternatives to gene selection are group selection and individual selection.

Gene selection theory is central to the understanding of contemporary evolutionary theory, and has developed from population genetics and the modern synthesis, and was established as the leading theory of natural selection during the Williams revolution. The revolution was based on the findings of population genetics, and other principal architects of the revolution include W.D. Hamilton, John Maynard Smith, Robert Trivers and Richard Dawkins, who popularised the revolution in ***The Selfish Gene***.

There is still some scientific debate about gene selection, which leading biologists such as Ernst Mayr rejecting the theory. Mayr (2000) states that the gene can not be the object of selection because it is the whole organism that lives, reproduces and dies, not individual genes. This, however, is not a problem for gene selectionism, which has always maintained that part of the environment in which genes are selected includes the other genes in the population, but because of recombination no combination of genes exist more than once, so although individuals may be the object of selection, genes are the units, and evolution consists of a change in independent allele frequencies in populations. (EvoWiki)

Genetic diversity: resulting from sources of genetic variation, it is the variety of alleles and genotypes within a population or species.

Genetic drift: Random changes in the frequency of genes in the population that are not due to selective pressure. This may occur because the different genotypes do not have a noticeable effect on the relative fitness of individuals (such as different mitochondrial haplotypes), or selection may not be strong enough to affect transmission of the genotype (for instance, on a recently-colonised island without predators). Genetic drift is a factor in neutral evolution. The significance of genetic drift in evolution is uncertain. In a large population, most of the factors affected by genetic drift will be minor, and drift is probably not significant over the population as a whole. However, in a small, isolated population drift may have a significant effect on the makeup of the population. CKT061201

Genetic engineering: Removing genes from the DNA of one species and splicing them into the DNA of another species using the techniques of molecular biology. (PBS evolution Glossary)

Genetic recombination: see Recombination.

Genetics: The branch of science which deals with elucidating the attributes and mechanisms of heredity in living systems. On Earth, this involves research into RNA and DNA. (W. R. Elsberry ***in*** talk.origins)

Genome: complete haploid complement of DNA (including all genes) from the chromosomes of the nucleus of an organism. (Developmental Biology 376 Glossary)

Genotype: The heritable information contained in an individual. (W. R. Elsberry ***in*** talk.origins); The set of two genes possessed by an individual at a given locus. More generally, the genetic profile of an individual. (PBS evolution Glossary)

Gradualism or **phyletic gradualism**: evolutionary mechanism theory, based on the premise that evolutionary change takes place through the gradual change of populations and not by the sudden (saltational) production of new individuals that represent a new type. New species evolve through the steady and gradual transformation of the entire population. The standard evolutionary paradigm prior to the early 1970s, as shown by the diagram (right) from Moore, Lalicker, & Fischer 1952. This view is usually attributed to Darwin because of his being influenced by uniformitarian geology by Eldredge and Gould, who instead argued for Punctuated Equilibria. But Richard Dawkins explained that such constant-rate gradualism is not present in the professional literature, thereby the term only serves as a straw-man for punctuated equilibrium advocates. In his book ***The Blind Watchmaker***, Dawkins argues against the idea that Charles Darwin himself was a constant-rate gradualist, as suggested by Niles Eldredge and Stephen Jay Gould. See also comments by John Wilkins and Larry Moran. (MAK; W.J. Hudson, Wikipedia)

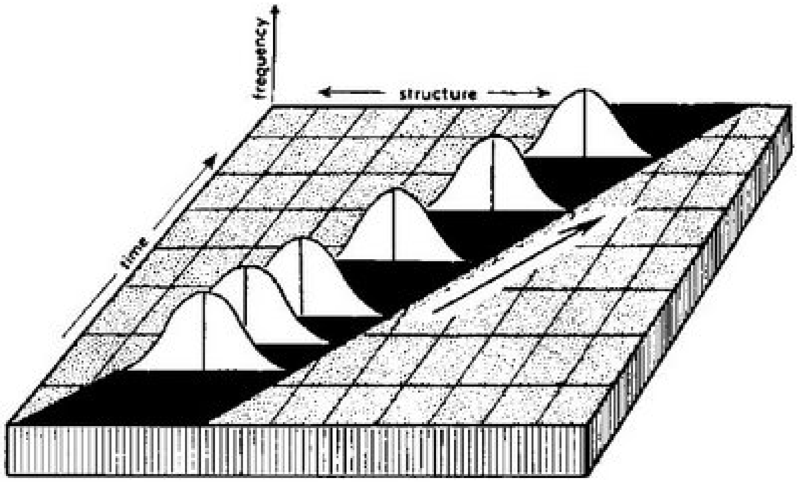


Figure 5–2:
A standard textbook view of evolution *via* phyletic gradualism.
From Moore, Lalicker, and Fischer, 1952; figure 1–14.

Group selection: theory that alleles can become fixed or spread because of the benefits they bestow on groups, regardless of the fitness of individuals within that group. Group selectionist ideas have been around since Darwin mentioned it in the ***Descent of Man*** as a possible mechanism of evolution of human altruism but were further elaborated by V.C. Wynne-Edwards in the 1960s.

More correctly, group selection is defined as the differential survival and reproduction of groups (Wade 1977). A response to group selection occurs when the differences among groups has a heritable basis. For group selection this means not only single locus allelic differences, but also epistatic genetic differences, differences in genetically based interactions among individuals, and even potentially cultural differences. Thus, it is simplistic to speak of group selection simply in terms of the spread of an altruistic allele.

Critiques, particularly by George C. Williams (1966), John Maynard Smith (1964) and C.M. Perrins (1964) cast serious doubt on group selection as a major mechanism in evolutionary history. These responses were part of the lead up to the Williams revolution in which gene selection theory became the prominent paradigm. (EvoWiki)

H

Haploid: having only half the normal complement of chromosomes. (W. J. Hudson)

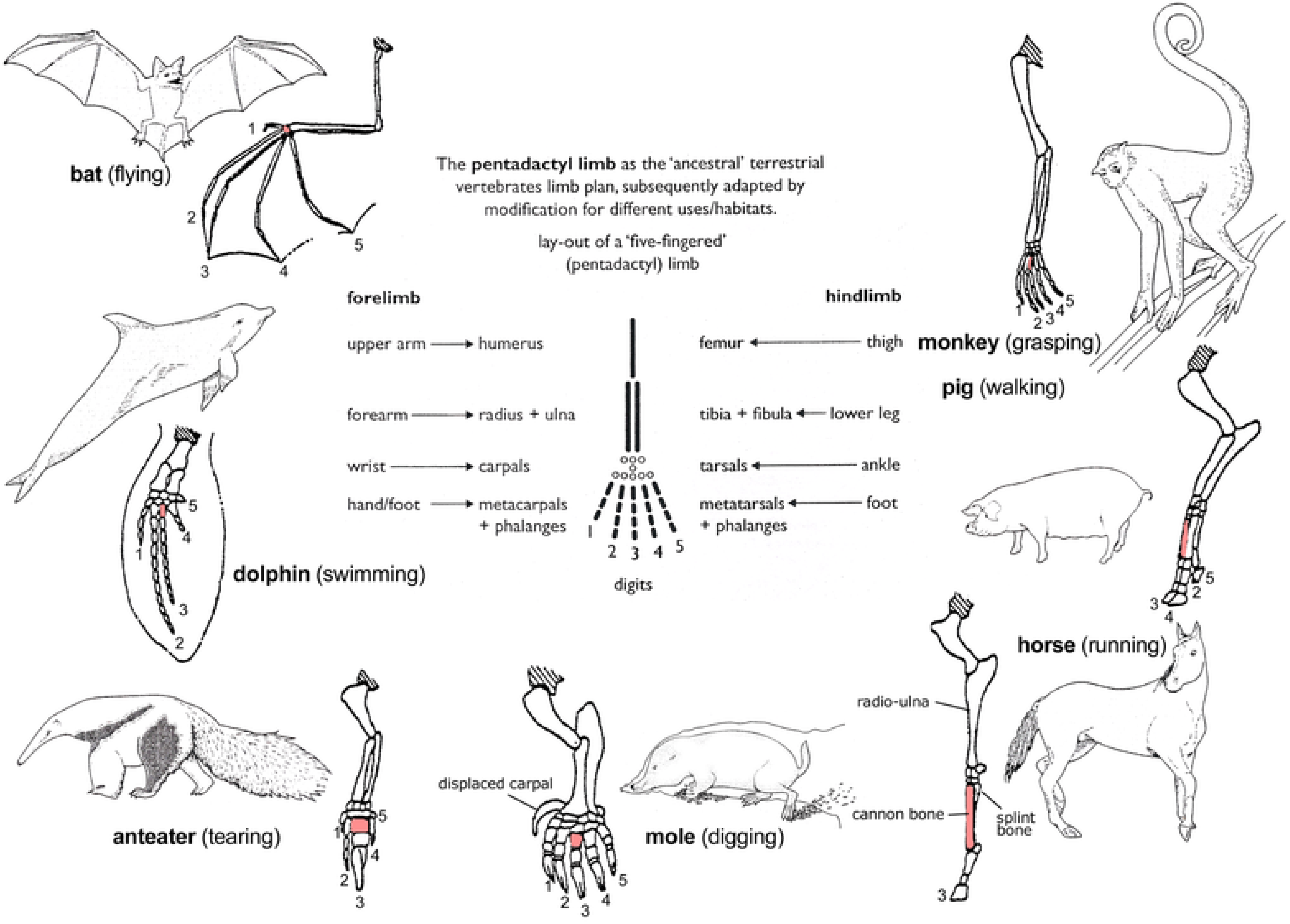
Heterozygous: Having two different alleles at a given locus. (W. J. Hudson)

Heredity: the passing of traits to offspring (from its parent or ancestors). This is the process by which an offspring cell or organism acquires or becomes predisposed to the characteristics of its parent cell or organism. Through heredity, variations exhibited by individuals can accumulate and cause some species to evolve. Evolution in organisms occurs through changes in heritable traits—particular characteristics of an organism. In humans, for example, eye colour is an inherited characteristic and an individual might inherit the "brown-eye trait" from one of their parents. Inherited traits are controlled by genes and the complete set of genes within an organism's genome is called its genotype. The complete set of observable traits that make up the structure and behaviour of an organism is called its phenotype. These traits come from the interaction of its genotype with the environment. As a result, many aspects of an organism's phenotype are not inherited. For example, suntanned skin comes from the interaction between a person's genotype and sunlight; thus, suntans are not passed on to people's children. The study of heredity in biology is called genetics. See also Modern Synthesis, Mendelian inheritance. (Wikipedia)

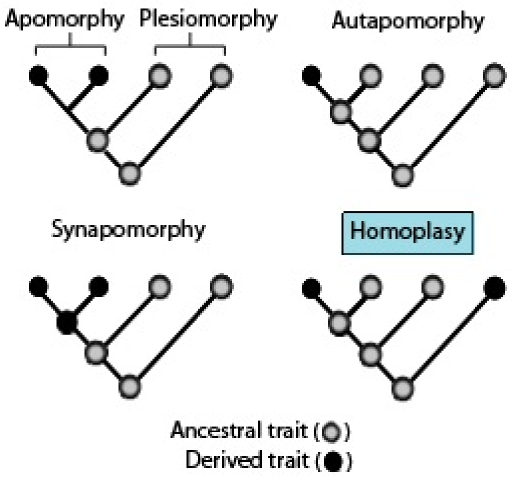
Homoiology: Convergent modifications of a homologous structure (or behaviour). The wings of pterosaurs, birds, and bats represent such a homoiology, since they are homologous as tetrapod fore leg, but were convergently modificated to flight devices (wings). (Glossary of Phylogenetic Systematics by Günter Bechly

Homologous chromosomes: chromosome pairs of the same length, centromere position, and staining pattern, with genes for the same characteristics at corresponding loci. One homologous chromosome is inherited from the organism's mother; the other from the organism's father. (Wikipedia)

Homology/homologous structure: coined by Richard Owen to refer to essential similarity, rather than analogy. With the rise of evolutionary theory, came to mean similarity due to sharing a common evolutionary origin (Rieppel, 1993, pp.2–3). In this definition, which is still the one used, homology refers to a character shared by a set of species and present in and inherited, with or without modification, from their common ancestor. For example, the bones in a bat's wing, a dog's front leg, and a human arm, are the same, although modified to serve different functions (see following diagram). Contrast with homoplasious and analogous.



From Wikipedia. The principle of homology illustrated by the evolutionary radiation of the forelimb of mammals. All conform to the basic pentadactyl pattern but are modified for different usages. The third metacarpal is shaded throughout; the shoulder is crossed-hatched. Diagram by Jerry Crimson Mann.



Homoplasy: having an independent evolutionary origin. Features that are similar but not the result of inheritance from a common ancestor. The two main causes of homoplasious characters are convergent evolution (appearance of the same character in at least two distinct lineages) and character reversion (the return to an ancestral character). Use of homoplasies when building a cladogram is sometimes unavoidable but is to be avoided when possible. (modified from Wikipedia and UCMP Understanding Evolution Glossary)

Homozygous: Having two identical alleles at a given locus. (W.J. Hudson)

Hopeful monster: termed coined by the German-born geneticist Richard Goldschmidt, who thought that small gradual changes could not bridge the divide between microevolution and macroevolution. In ***The Material Basis of Evolution*** (1940), Goldschmidt wrote "the change from species to species is not a change involving more and more additional atomistic changes, but a complete change of the primary pattern or reaction system into a new one, which afterwards may again produce intraspecific variation by micromutation." His thesis however was universally rejected and has been widely ridiculed within the biological community, which favored the neo-Darwinian explanations of R.A. Fisher, J. B. S. Haldane and Sewall Wright. (Wikipedia) **More**

Horizontal gene transfer (HGT) or **Lateral gene transfer (LGT)**: any process in which an organism incorporates or transfers genetic material to or from another organism, without being the offspring of that organism. Often, the transference is between members of different species. By contrast, ***vertical transfer*** occurs when an organism receives genetic material from its ancestor, e.g., its parent or a species from which it has evolved. Most thinking in genetics has focused upon vertical transfer, but there is a growing awareness that horizontal gene transfer is a highly significant phenomenon and amongst single-celled organisms perhaps the dominant form of genetic transfer. Bacteria, for example, frequently pass copies of particular genes to one another and pick up foreign genetic material from their environment, resulting in horizontal transfer. Mechanisms include ***Transformation***, the genetic alteration of a cell resulting from the introduction, uptake and expression of foreign genetic material (DNA or RNA), a process relatively common in bacteria, less so in eukaryotes, and used in laboratories to insert novel genes into bacteria for experiments or for industrial or medical applications (genetic engineering); ***Transduction***, the process in which bacterial DNA is moved from one bacterium to another by a virus; ***Bacterial conjugation***, a process in which a bacterial cell transfers genetic material to another cell by cell-to-cell contact; and ***Gene transfer agents***, virus-like elements encoded by the host that are found in the alphaproteobacteria order Rhodobacterales. (Wikipedia, UCMP Understanding Evolution Glossary) "has had an important role in eukaryotic genome evolution, but its importance is often overshadowed by the greater prevalence and our more advanced understanding of gene transfer in prokaryotes. Recurrent endosymbioses and the generally poor sampling of most nuclear genes from diverse lineages have also complicated the search for transferred genes. Nevertheless, the number of well-supported cases of transfer from both prokaryotes and eukaryotes, many with significant functional implications, is now expanding rapidly." (Keeling & Palmer 2008, abstract)

Hybrid: an offspring resulting from cross-breeding between two different species. Animal hybrids are often infertile. The mule for example is a cross of female horse and a male donkey. The hinny, a cross between a female donkey and a male horse (mule and hinny are reciprocal hybrids). However there are also fertile hybrids, e.g. between coyotes, wolves, dingoes, jackals and domestic dogs. Plant species hybridize more readily than animal species, and the resulting hybrids are more often fertile hybrids and may reproduce, though there still exist sterile hybrids and selective hybrid elimination where the offspring are less able to survive and are thus eliminated before they can reproduce. A number of plant species are the result of hybridization and polyploidy with many plant species easily cross pollinating and producing viable seeds, the distinction between each species is often maintained by geographical isolation or differences in the flowering period. (Wikipedia)

I

Inclusive fitness theory: in evolutionary biology and evolutionary psychology it holds that an organism can improve its overall genetic success by cooperative, social behavior. The theory defines the inclusive fitness of an organism as the sum of its classical fitness (how many of its own offspring it produces and supports) and the number of equivalents of its own offspring it can add to the population by supporting others. (PBS evolution Glossary)

Inheritance of acquired characteristics: theory proposed by Jean Baptiste Lamarck, according to whom evolution occurs through the inheritance of traits or abilities an organism acquires in life. For example, the ancestral giraffe stretched its neck to reach the leaves of trees, and as a result passed on a slightly longer neck and legs to its offspring. Also referred to as the "use–disuse theory." Despited being rejected by Weismannian Neo-Darwinism, Lamarckism remained popular well into the early twentieth century, especially in France, but was supplanted by the synthesis of Darwinian and Mendellian theory.

Intron: "intervening sequence," a stretch of nucleic acid sequence spliced out from the primary RNA transcript before the RNA is transported to the cytoplasm as a mature mRNA; can refer either to the RNA sequence or the DNA sequence that from which the RNA is transcribed. See also exon. (Developmental Biology 376 Glossary)

J

K

L

Lineage: in this context, an evolutionary lineage, a sequence of ancestors and descendants (which may be cells, genes, populations, species) that evolve through time.

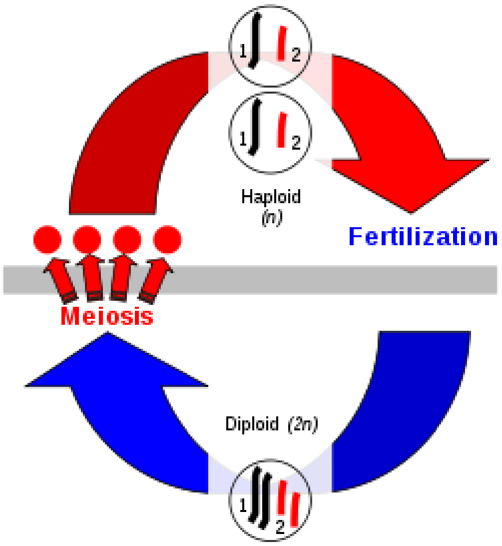
Locus: The location of a gene on a chromosome. At any locus there can be many different alleles in a population, more alleles than any single organism can possess. For example, no single human can simultaneously carry the A, B and an O blood-type allele. (W.J. Hudson)

M

Macroevolution: Evolution at or above the species level. The boundary between macro- and micro- is fuzzy, as some researchers prefer to include speciation in micro- and others reason that the only macro-process that gives distinctive events is speciation. Speciation events are thus, to many scientists, examples of macroevolution. Another definition is evolution too imperceptible to be observed within the lifetime of one researcher . (W. R. Elsberry ***in*** talk.origins ***via*** W. J. Hudson) link: Macroevolution Its Definition, Philosophy and History by John Wilkins

Mass extinction: Event involving higher extinction rates than the usual degree of background extinction. See Big Five for diagram of extinction rates, and synopsis of five major extinctions.

Meiosis: A process which converts a diploid cell to a haploid gamete, and cause a change in the genetic information to increase diversity in the offspring. (W.J. Hudson). In the first stage of sexual reproduction, which is meiosis, the number of chromosomes is reduced from a diploid number (2n) to a haploid number (n). During fertilization, haploid gametes come together to form a diploid zygote and the original number of chromosomes (2n) is restored. (Wikipedia graphic by Stannered)



Meme: controversial concept proposed by Richard Dawkins. A meme is a "a unit of cultural inheritance, hypothesized as analogous to the particulate gene and as naturally selected by virtue of its 'phenotypic' consequences on its own survival and replication in the cultural environment." A meme can be an idea, skill, story, or custom, which is passed from one person to another by imitation or teaching. Some theorists argue that memes are the cultural equivalent of genes, and reproduce, mutate, are selected, and evolve in a similar way. The study of memes is called ***memetics***. (Mavericks of the Mind; PBS evolution Glossary)

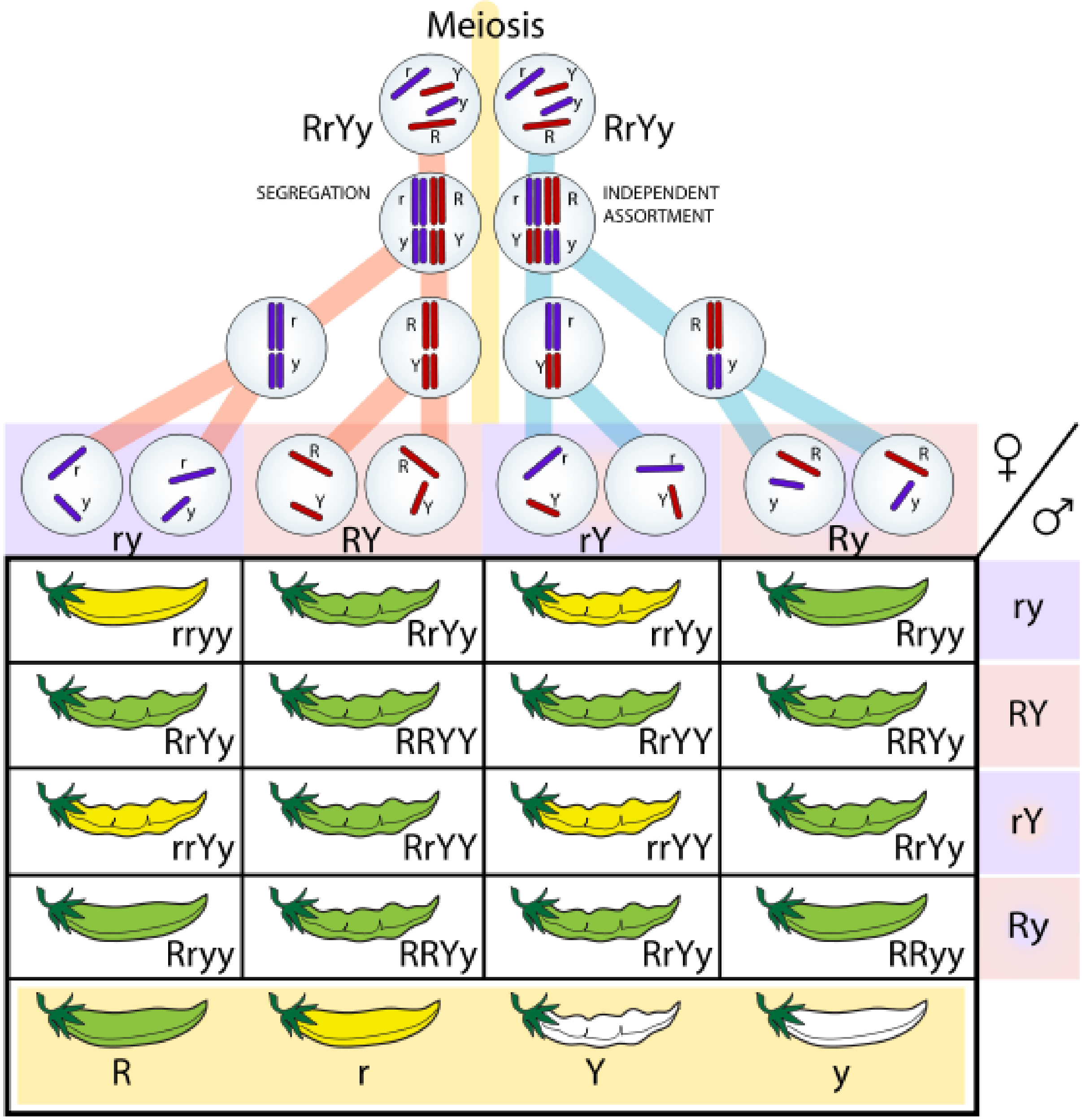


Table showing how genes exchange according to segregation or independent assortment during meiosis and how this translates into the Mendel's Laws. Wikipedia: diagram by Mariana Ruiz Villarreal

Mendelian inheritance: The mode of genetic inheritance of all diploid species, and therefore of nearly all multicellular organisms. Inheritance is controlled by genes, which are passed on to the offspring in the same form as they were inherited from the previous generation. At each locus an individual has two genes—one inherited from its father and the other from its mother. The two genes are represented in equal proportions in its gametes. (PBS evolution Glossary) For quite some time, the rediscovery of Mendel's work was considered to be the conclusive nail in the Darwinian coffin, killing off the idea of natural selection as Darwin proposed it. Since by the publication of the sixth edition of Darwin's "Origin of Species," Darwin had almost inextricably bound natural selection with his hypothesis on the mechanism of heredity, "pangenesis," this view was quite understandable. However, by the early 1940's, the neo-Darwinian synthesis had met and addressed the criticisms of the Mendelists. (Peter J. Bowler. 1984. Evolution: the history of an idea. University of California Press. Review by W. R. Elsberry link)

Microevolution: Evolution within the species level, or a change in allele frequency in a population over time. Note that this connotation is equivalent to evolution. All "Scientific Creationists" so far admit that microevolution is observed. Some Theistic Anti-Evolutionists may not. (W. R. Elsberry ***in*** talk.origins ***via*** W. J. Hudson)

Mimicry: imitative behavior, one species resembling one another, and gaining advantages as a result. For example harmless flies that have the same colouration as bees and wasps. Because predators know that wasps sting they tend to avoid anything that looks like them. See Batesian mimicry and Müllerian mimicry.

(Wikipedia glossary)

Mitochondria (sing. **mitochondrion**): A a small round organelle found in most cells in nearly all eukaryotes. They are surrounded by two membranes, the inner of which is folded into invaginations called cristae, where aerobic respiration takes place. Mitochondria produce enzymes that convert food to energy. They contain DNA that codes for some mitochondrial proteins. Because mitochondria are generally carried in egg cells but not in sperm, mitochondrial DNA is inherited from mothers but not fathers. Hence it is possible to trace ancestry through the mother's line (see also mitochondrial Eve). (PBS evolution Glossary, Wikipedia)

Mitosis: Cell division. All cell division in multicellular organisms occurs by mitosis except for the special division called meiosis that generates the gametes. (PBS evolution Glossary)

Modern Synthesis: Also referred to as "evolutionary synthesis", "synthetic theory", and especially ***modern evolutionary synthesis***. The 1920s saw the emergence of an expanded version of Darwinism, which was founded by Ronald Fisher, J. B. S. Haldane and Sewall Wright. They reconciled the idea of evolution by natural selection with the discontinuous, particulate nature of genes. This was the essence the modern synthesis of Darwin's theory and Mendelian genetics. The new synthesis continued to develop in the 1940s, notably with Julian Huxley's, ***Evolution: The Modern Synthesis*** (1942) and Bernhard Rensch's, ***Evolution Above the Species Level*** (1947). Natural selection was seen as the dominant force shaping evolutionary change. Rensch expressed the view that nothing in biological nature suggests that any evolutionary processes other than natural selection work on the natural genetics of variation within populations. The Great Debate: Darwinism Today. The synthetic paradigm revolution was much broader than the neo-Darwinian concept of Weismann and Wallace, incorporating facts from such fields as genetics, systematics, and paleontology. (Kutschera & Niklas 2004, p.256)

The Modern Synthesis is a theory about how evolution works at the level of genes, phenotypes, and populations whereas Darwinism was concerned mainly with organisms, speciation and individuals. Modern Synthesis differs from Darwinism in three important aspects: 1. It recognizes several mechanisms of evolution in addition to natural selection. One of these, random genetic drift, may be as important as natural selection. 2. It recognizes that characteristics are inherited as discrete entities called genes. Variation within a population is due to the presence of multiple alleles of a gene. 3. It postulates that speciation is (usually) due to the gradual accumulation of small genetic changes. This is equivalent to saying that macroevolution is simply a lot of microevolution. (W. R. Elsberry ***in*** talk.origins ***via*** W. J. Hudson) **More**

Mosaic evolution: Because evolution does not occur uniformly, but rather different characteristics evolve at different rates, transitional organisms tend to have a mosaic of characteristics of both ancestral/primitive and more specialised descendants. So for example early tetrapods had both fish-like and amphibian features, and ***Archaeopteryx*** possessed both dinosaur and bird-like features. (MAK)

Multiplication of species: The theory that species multiply, either by splitting into daughter species or by "budding", that is, by the establishment of geographically isolated founder populations that evolve into new species. (W. R. Elsberry ***in*** talk.origins ***via*** W. J. Hudson)

Mutation: An error in duplication of genetic material which results in a different sequence of and/or a different number of base pairs in the copy than were in the original. Mutation creates new alleles. (W. R. Elsberry ***in*** talk.origins ***via*** W. J. Hudson)

Morphology: The study of the form and structure of organisms, such as animals and plants and their fossil remains. For example, comparing the shape of the femur in different grazing mammals is a morphological study. (UCMP Understanding Evolution Glossary). ***Gross morphology*** refers to the collective structures or an organism as a whole as a general description of the form and structure of an organism, taking into account all of its structures without specifying an individual structure. ***Anatomy*** is the study of the form and structure of internal features of an organism. ***Comparative Morphology*** is analysis of the patterns of the locus of structures within the body plan of an organism, and forms the basis of taxonomical categorization. ***Functional Morphology***: the study of the relationship between the structure and function of morphological features. ***Experimental Morphology*** is study of the effects of external factors upon the morphology of organisms under experimental conditions, such as the effect of genetic mutation. (Wikipedia Morphology pertains to the phenotype rather than the genome ("molecular morphology" has been used for some time for describing the structure of compound molecules, such as polymers and RNA, is a distinct field).

N

Natural selection: The differential reproduction and, thereby, transmission of alleles between generations, of individuals in a population, due to heritable variation in a trait or traits which they possess. This is one mechanism by which evolution can occur. (W. R. Elsberry *in* talk.origins *via* W. J. Hudson). Conceived independently and then jointly published by Darwin and Wallace, and substantially elaborated upon in the early part of the twentieth century with the rediscovery of Mendelian genetics and then advances in population genetics. (Kutschera & Niklas 2004, p.256)

Neo-Darwinism: historically, term coined by Romanes (1895) to refer to the incorporation of Weismann's ideas on heredity into Darwin's theory of natural selection, showing how biological variation is generated and rejecting the Lamarckian inheritance of the earlier Darwinism. (Kutschera & Niklas 2004, p.260). The term is also used as a synonym for Modern Synthesis, or even any modern approach to evolutionary theory

Neutral theory of molecular evolution The neutral theory of molecular evolution was first formally suggested by Motoo Kimura in 1968, and maintains that the majority of mutations occurring within a population are selectively neutral (i.e. have neither a positive or negative effect), and that genetic drift rather than natural selection is a major factor in differences between populations. While debate still occurs about the relative importance of these two processes, the neutral theory has become the null hypothesis for tests of whether natural selection has occurred in a given lineage. One major implication of this theory is that mutations should accumulate at a fairly constant rate, and therefore the divergence times between lineages should be calculable from the degree of divergence—the so-called molecular clock. The usefulness and correct application of molecular clocks remains a highly contentious subject in studies of evolution. References: Kimura, M. 1968. Evolutionary rate at the molecular level. ***Nature*** 217: 624–626. pdf Wikipedia: Neutral theory of molecular evolution. CKT070830

Neo-Lamarckism: Popular alternative to Darwinism during the late 19th and early 20th centuries, based on Lamarck's idea of acquired characteristics. Neo-Lamarckism was supported by natural theology, popular in America at the turn of the century. Spencer supported neo-Lamarckism. "Against selection itself Spencer [1893] used an argument that had considerable force when measured against the pregenetical selection theory (Ridley, 1982a). He pointed out that when a new structure evolved, all the rest of the body would have to accommodate the new development. Thus a series of variations would be required to adjust the overall structure in a manner correlated to the new organ. What would be the chance of all these variations appearing together at the right time, if the species had to depend on random variation? Selection might explain the changes in a single organ, but not an integrated transmutation of the whole body." Lamarckism, as Spencer pointed out, could provide an explanation for the integrated development or elimination of organs. This was seen to be a weakness of natural selection. "The law of "acceleration of growth" was first published in Cope's "On the origin of genera" of 1867 (reprinted in Cope, 1887) and in Hyatt (1868). According to this law, evolution progresses by a series of sudden additions to the growth of the individual. At certain points in time, every individual in a species begins to exhibit a new phase of growth that advances all to the form of a new species. To make room for this addition, the old adult form is compressed back to an earlier phase of growth, hence the "acceleration" of growth to accommodate an extra stage before maturity. Cope denied that evolution on a small scale is a branching process, claiming instead that each genus represents a group of species that have reached the same point in the historical development of their group. Their close relationship is not a sign of common descent but of identical position in the scheme of development." "Cope postulated a growth-force named "bathmism;" concentrated in those parts of the body most in use, it developed them at the expense of other areas. By the last decade of the century, this Lamarckism had been developed to considerable depth (Cope, 1887, 1896; Hyatt, 1880, 1884, 1889)." Referring to the case of the midwife toad: "Was the india ink added by someone wishing to preserve the original marks, or was it deliberate sabotage, perhaps a Nazi plot to discredit evidence hostile to their racial theories? Koestler certainly has suggested that Kammerer's experiments may have been genuinely successful, although others think he was simply dishonest. (Aronson, 1975)." (Peter J. Bowler. 1984. Evolution: the history of an idea. University of California Press. Review by W. R. Elsberrylink)

Nondirectionality (in evolution): as here defined, the premise that evolution does not have a direction, that nature does not tend towards greater complexity, that it is misleading to speak of "lower", "simpler", or "primitive", and that all attempts to impose a narrative are hold-overs of Victorian ideas such as ascent. Non-directionality is favoured by some evolutionists such as Steven Jay Gould. See also cosmicism, reductionism. Contrast with anthropocentrism, ascent, directionality, Evolution (Systems Theory) and teleology. (MAK)

Non-missing link: Although creationists often claim that no transitional forms are known in the fossil record, in fact the reverse is the case. (see Link). As it would be oxymoronic to refer to these intermediate species by their popular moniker as "missing link" (e.g. link link) I have coined the informal term "non-missing link". See also anagenesis, ancestor, common ancestor, basal taxon, stem group. Note that even though, in view of the vagaries of the fossil record, the non-missing link may not necessarily be the actual, literal, common ancestor of all later species in that lineage (although in some cases where stratigraphic preservation is very good it might), but it would certainly be a closely related form. (MAK)

O

Ontogeny: The process of the development and growth of an individual from zygote to adult. (W. R. Elsberry ***in*** talk.origins). See also developmental biology, evo-devo, morphogenesis.

Ontogeny recapitulates phylogeny See Recapitulation.

Orthogenesis: a conjecture related to Lamarckism. "The crucial difference is that the trends of orthogenesis are not adaptive. Far from being a positive response to the environment, they represent a nonutilitarian force that can in some cases drive the species to extinction. In this there is a similarity to Hyatt's concept of racial senility." "A famous case was that of the recently extinct "Irish elk", thought to have died out because its antlers became too large as a result of an internal trend (Gould, 1974b). It seemed as though the trend that produced the antlers, perhaps originally for some useful purpose, had acquired a momentum of its own that had carried it far beyond the point of utility. This "overdevelopment" theory of extinction became widely popular among non-Darwinian paleontologists in the early twentieth century." "Strong support for orthogenesis came from the Russian biologist Leo S. Berg (translation 1926), but perhaps its best known exponent was the American paleontologist Henry Fairfield Osborn." Aristogenesis—Osborn's own term for orthogenesis. Mendelism was originally viewed as an alternative to selection. (Peter J. Bowler. 1984. ***Evolution: the history of an idea***. University of California Press. Review by W. R. Elsberry link)

Organism: individual member of a species, that is, a single biological entity, either unicellular (single-celled) or multicellular (many-celled). A living system such as animal, plant, fungus, or eukaryote or prokaryote micro-organism, capable of response to stimuli, reproduction, growth, and maintenance of homeostasis as a stable whole. Colloquially and informally, the term might also be used in evolutionary narratives to refer to a species or population, rather than just an individual. (from Wikipedia, MAK, Fossil Mall)

P

Parallel evolution: the development of a similar trait or traits in related, but distinct, species descending from the same ancestor, but from different clades or lineages. For example:

- Old and New world porcupines shared a common ancestor, both evolved strikingly similar quill structures; this is also an example of convergent evolution as similar structures evolved in hedgehogs, echidnas and tenrecs.
- Contemporaneous evolution of browsing horses and paleotheres both of which shared the same environmental space.
- Upright posture independently developed among several lines of Triassic Archosaurs.
- Internal fertilization has evolved independently in sharks, some amphibians and amniotes.
- The Patagium is a fleshy membrane that is found in gliding mammals such as: flying lemurs, flying squirrels, sugar gliders and the extinct ***Volaticotherium***. These mammals acquired the patagium independently.
- South American Pyrotherians have evolved a body plan (graviportal limbs, trunk, tusks) similar to early proboscideans.
- Molecular phylogeny indicates that the lophophore, a complex feeding structure, evolved independently among bryozoa and brachiopod, two phyla previously grouped together but now considered only distantly related.

One of the most spectacular examples of parallel evolution is provided by the two main branches of the mammals, the placentals and marsupials, which have followed independent evolutionary pathways following the break-up of land-masses such as Gondwana roughly 100 million years ago. In South America, marsupials and placentals shared the ecosystem (prior to the Great American Interchange); in Australia, marsupials prevailed; and in the Old World the placentals won out. However, in all these localities mammals were small and filled only limited places in the ecosystem until the mass extinction of dinosaurs sixty-five million years later. At this time, mammals on all three landmasses began to take on a much wider variety of forms and roles. While some forms were unique to each environment, surprisingly similar animals have often emerged in two or three of the separated continents. Examples of these include the litopterns and horses, whose legs are difficult to distinguish; the European sabre-toothed cat (Machairodontinae) and the South American marsupial sabre-tooth (Thylacosmilus); the Tasmanian wolf and the European wolf; likewise marsupial and placental moles, flying squirrels, and (arguably) mice. (modified from Wikipedia)

Phenotype: The set of measurable or detectable physical or behavioral features of an individual. The phenotype represents the expression of the genotype of the individual as modified by environmental conditions during the individual's ontogeny. (W. R. Elsberry ***in*** talk.origins)

Phylogeny: term coined by Haeckel (Haeckel 1866): the study of the family history of life, the evolutionary relationships among groups of organisms, often illustrated with a branching evolution tree. More

Piltdown Man: famous 1912 hoax of early fossil man, consisting of a human skull, ape jaw, and filed down teeth. Had a significant detrimental impact on early research on human evolution: discoveries of Australopithecine fossils found in the 1920s in South Africa were ignored and instead the popular (but erroneous) theory argued that the human brain expanded in size before the jaw adapted to new types of food. rather than the reverse. Definitively exposed as a forgery by scientists back in 1953. (MAK, Wikipedia)

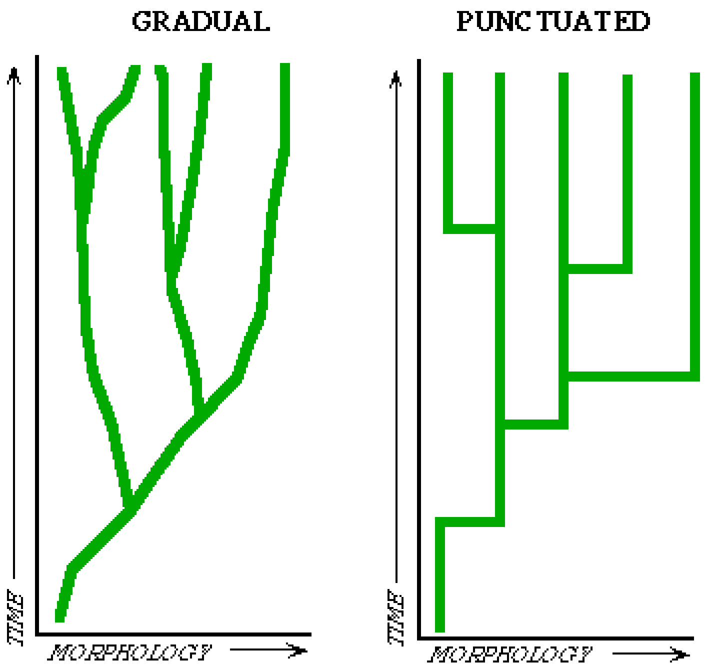
Polyploidy: containing more than two paired (homologous) sets of chromosomes. (Wikipedia)

Population: A group of potentially inter-breeding individuals of the same species found in the same place at the same time (Booth et al. 2003). A group of organisms, typically a single species, and typically isolated from other members of its species in some manner. (W.J. Hudson)

Plasmid: A genetic element that exists (or can exist) independently of the main DNA in the cell. In bacteria, plasmids can exist as small loops of DNA and be passed between cells independently. (PBS evolution Glossary)

Primitive: ancestral, similar or identical to the original forms, basal or stem member of a lineage, tends to be a generalist, lacks the specialised features of its descendants. Cladistics rejects terms like "primitive", instead using the more technical and (to outsiders and non-paleo geeks) obscure plesiomorphy. Nevertheless "primitive" does not have to equate anthropomorphically with advancement, technology, etc, compare "primeval" or "primordial". See also my comments re "advanced". (MAK)

Punctuated equilibria (More popularly known as **punctuated evolution**): an evolutionary theory that argues that new species evolve suddenly and in geographically isolated areas. Most speciation involves cladogenesis rather than anagenesis, and occurs via peripatric speciation. Hence speciation is rarely found in the fossil record, because established, populous and widespread species (the sort that are most likely simply through greater numbers to leave fossil remains) usually change slowly, if at all, during their time of residence. New species tend to develop in a geographically limited region and stratigraphically limited extent, which is small in relation to the overall time and distribution of the species. Sampling of the fossil record will reveal a pattern of most species in stasis, with abrupt appearance of newly derived species being a consequence of ecological succession and dispersion. Adaptive change in lineages occurs mostly during periods of speciation, and trends in adaptation occur mostly through the mechanism of species selection. See punctuated equilibria FAQ on the talk.origins archive site. (W. R. Elsberry ***in*** talk.origins ***via*** W. J. Hudson, modified).



Right: Gradual and Punctuated evolution. Gradual evolution (or phyletic gradualism) occurs where change is small and constant; punctuated evolution where change is very rapid, while most of the time there is virtually no change. (Diagram by Paul Olsen, Lecture 5 Evolution—url; main reference: Eldredge & Gould 1972)

Protein: the building blocks of cells; large molecules made up of a sequence of amino acids. Many of the important large molecules in living organisms—for example, enzymes—are proteins. (Fossil Mall glossary, MAK)

Q

Quasispecies: Darwinian evolution of self-replicating entities within the framework of physical chemistry. Put simply, a quasispecies is a large group or cloud of related genotypes that exist in an environment of high mutation rate, where a large fraction of offspring are expected to contain one or more mutations relative to the parent. This is in contrast to a species, which from an evolutionary perspective is a more-or-less stable single genotype, most of the offspring of which will be genetically accurate copies.

The quasispecies model is useful in providing a qualitative understanding of the evolutionary processes of self-replicating macromolecules such as RNA or DNA or simple asexual organisms such as bacteria or viruses (viral quasispecies), and is helpful in explaining something of the early stages of the origin of life. Quantitative predictions based on this model are difficult because the parameters that serve as its input are hard to obtain from actual biological systems. The quasispecies model was put forward by Manfred Eigen and Peter Schuster based on initial work done by Eigen. (Wikipedia)

R

r-selection, r-selected species: A species that produces a large number of off-spring, each of which receives little care (quantity rather than quality). R-selected species are better suited for variable or unpredictable environments. (Wikipedia glossary)

Racial senility: intriguing but long refuted theory that certain long-lived lineages became old and "senile", by analogy with individual development, as their evolutionary novelty is used up. Developed by Alpheus Hyatt to explain the exotic shapes of some Cretaceous ammonite shells, horns and plates on dinosaurs, and so on. (MAK)

Random: Unpredictable in some way. Mutations are "random" in the sense that the sort of mutation that occurs cannot generally be predicted based upon the needs of the organism. However, this does not imply that all mutations are equally likely to occur or that mutations happen without any physical cause. Indeed, some regions of the genome are more likely to sustain mutations than others, and various physical causes (e.g., radiation) are known to cause particular types of mutations. (UCMP Understanding Evolution Glossary)

Random drift: See genetic drift.

Recapitulation: The **theory of recapitulation**, also called the **biogenetic law** or **Embryological parallelism**, and often expressed as the phrase "ontogeny recapitulates phylogeny". The hypothesis that in developing from embryo to adult, animals go through stages resembling or representing successive stages in the evolution of their remote ancestors. Therefore, each phase of the ontogeny of an individual directly represents the adult phase of some ancestor species in the phylogeny of the species to which the individual belongs. With different formulations, such ideas have been applied to several fields, including biology, anthropology and education theory. In biology, there are several examples of embryonic stages showing features of ancestral organisms, but a "strong" formulation of the concept has been discredited. The concept originated in the 1790s among the German Natural philosophers and, as proposed by Étienne Serres in 1824–26, became known as the "Meckel–Serres Law". In 1866, the German zoologist Ernst Haeckel proposed that the embryonic development of an individual organism (its ontogeny) followed the same path as the evolutionary history of its species (its phylogeny). This principle is recognized to be inaccurate in several respects, and its use is now generally deprecated. The turn of phrase is attributed to Ernst Haeckel, while the "biogenetic law" upon which it was based can be traced back to von Baer. (W. R. Elsberry ***in*** talk.origins, Wikipedia)

Recognition species concept: A definition of a species as a set of organisms that recognize one another as potential mates; they have a shared mate recognition system. Compare with biological species concept, cladistic species concept, ecological species concept, and phenetic species concept. (Fossil Mall glossary) See other species definitions.

Recombination: Recombination creates new combinations of alleles. Recombination primarily occurs through sexual reproduction, where diploid cells form haploid gametes. The organism inherits one gamete each from the mother and the father, and the gametes are 'recombined' to form a new diploid chromosome. Recombination can occur not only between genes, but within genes as well. Recombination within a gene can form a new allele. (cf. mutation) Recombination is a mechanism of evolution because it adds new alleles and combinations of alleles to the gene pool. (W.J. Hudson)

Red Queen's Hypothesis or **Red Queen Effect** is an evolutionary hypothesis. The term is taken from the Red Queen's race in Lewis Carroll's ***Through the Looking-Glass***. The Red Queen said, "It takes all the running you can do, to keep in the same place." The Red Queen Principle can be stated thus: ***In reference to an evolutionary system, continuing adaptation is needed in order for a species to maintain its relative fitness amongst the systems being co-evolved with***. The hypothesis is intended to explain two different phenomena: the advantage of sexual reproduction at the level of individuals, and the constant evolutionary arms race between competing species. In the first (microevolutionary) version, by making every individual an experiment when mixing mother's and father's genes, sexual reproduction may allow a species to evolve quickly just to hold onto the ecological niche that it already occupies in the ecosystem. In the second (macroevolutionary) version, the probability of extinction for groups of organisms is hypothesized to be constant within the group and random among groups. It's counterpart is the ***Court Jester Hypothesis***, which proposes that macroevolution is driven mostly by abiotic events and forces. (Wikipedia)

Reproductive isolation: Isolation of one species or population from another species or population by differences in reproductive traits or habits. The two species or populations may or may not share the same environmental range. An example of two species being reproductively isolated are similar species of animals that breed at different times of the year. (W.J. Hudson)

Ring species: A situation in which two reproductively isolated populations living in the same region are connected by a geographic ring of populations that can interbreed. (PBS evolution Glossary)

Ribonucleic acid (**RNA**): A molecule similar to DNA, but with only a single strand, by which the genetic code of DNA is converted into proteins in cells. It has three forms: ***Messenger RNA***, ***ribosomal RNA***, and ***transfer RNA***. Some viruses carry RNA as their genetic material instead of DNA. There has been speculation that an "RNA world" preceded current life on Earth.

S

Selection: see natural selection.

Selective pressure: any environmental factors such as scarcity of food or extreme temperatures that favour the survival of only those organisms with characteristics that provide resistance or adaptability. (based on PBS evolution Glossary)

Sexual selection: a trait that makes an individual more likely to find a mate than others. A microevolutionary process. (Wikipedia: Glossary of ecology). This process may produce traits that seem to decrease an organism's chance of survival, while increasing its chances of mating.(UCMP Understanding Evolution Glossary)

Shifting Balance Theory: Sewall Wright's 'Shifting Balance' theory argues that populations are often divided into smaller subpopulations. Drift could cause allele frequency differences between subpopulations if gene flow was small enough. If a subpopulation was small enough, the population could even drift through fitness valleys in the adaptive landscape. Then, the subpopulation could climb a larger fitness hill. Gene flow out of this subpopulation could contribute to the population as a whole adapting. (W.J. Hudson)

Social Darwinism: a 19th century political philosophy which attempted to explain differences in social status (particularly class and racial differences) on the basis of evolutionary fitness. Based on the misinterpretation of Darwinian theory, Social Darwinism is generally considered unscientific by modern philosophers of science. (Wikipedia glossary)

Species: Highly controversial term given a variety of definitions by biologists. Currently, the Biological

Species Concept (BSC) is widely popular: Groups of actually or potentially interbreeding populations, which are reproductively isolated from other such groups (Mayr, 1963, Animal Species and Evolution). More (W. R. Elsberry ***in*** talk.origins ***via*** W. J. Hudson) See also cladistic species concept, ecological species concept, phenetic species concept, and recognition species concept. See other species definitions. (Fossil Mall glossary)

Speciation: The the basic process of evolution by which new species appear. Although the theory of evolution is a century and a half old the precise mechanism by which new species make their appearance in the biosphere is still a field of active research, with all the disagreements and debates that go with it. A number of types of speciation have been proposed:

Allopatric speciation is supposed to be caused by the physical separation of specimens of what was one and the same species. The classical example is Darwin's work on the finches of the Galapagos Islands. The presumed scenario is that an ancestral species of finch reached the various islands and evolved in about as many different species as there are islands. The critical factor causing the speciation is usually assumed to be the severing of the gene flow between the population on an island and the mother population on the mainland. Mayr also stressed the small size of the new population and contended that e.g. the emergence of the Isthmus of Panama did not lead to much speciation of biota of the shallow seas at either side because both represented a far too large gene pool to allow allopatric speciation to occur. Jcwf100131

Peripatric speciation is taken to occur in the same geographic area—without severance of the gene flow—due to ecological differences, e.g. the existence of two different ecological niches into which an existing species can specialize. Jcwf100131. Alternatively, a population of an ancestral species in a geographically peripheral part of the ancestral range is modified over time until even when the ancestral and daughter populations come into contact, there is reproductive isolation. See also cladogenesis, anagenesis, punctuated equilibria. (W. J. Hudson)

Splitting: see cladogenesis.

T

Tierra: Artificial life simulation of Tom Ray's which demonstrates the utility of natural selection in computer implementations for finding novel approaches to difficult problems. This is prima facie evidence that A. E. Wilder-Smith was premature in declaring "simulations of natural selection 'jam' the best computers". (W. R. Elsberry ***in*** talk.origins)

Transitional form, or **transitional fossil**: A fossil or group of organisms that are intermediate and a link between a more primitive or ancestral group and a more advanced or specialised one, possessing characteristics or traits of both (see Mosaic evolution). Generally any evolutionary lineage constitutes a series of transitional forms; for example in the evolution of birds from dinosaurs, or whales from terrestrial ancestors, there are a number of intermediate forms or non-missing links.An important aspect of evolutionary systematics, see also anagenesis. Note that strict application of cladistics rejects the possibility of identifying transitional forms (it doesn't deny the reality of evolution of course, just that it is possible to know for sure which fossils represent transitional forms) (Systematics and Biogeography: Paraphyly Watch 3: Transitional Fossils, Microbes & Patrocladistics). An alternative approach (given in Wikipedia) would be to make a distinction between "transitional" and "intermediate". ***Transitional*** forms do not have a significant number of unique derived traits, so it is morphologically close to the actual common ancestor it shares with its more derived relative (see also basal taxon and stem group). ***Intermediate*** can be used for those forms with a larger number of uniquely derived traits. According to this definition, ***Archaeopteryx*** is transitional whereas the platypus (an specialised egg laying mammal, descended from very primitive mammals) is intermediate. But rather than multiply terminology, it would be better to retain intermediate in the informal but more grammatically correct sense of meaning the same as "transitional". Some intermediate/transitional forms linking major groups of vertebrates include the fish/amphibian sequence from ***Eusthenopteron*** (fish) to ***Panderichthys*** to ***Tiktaalik*** to ***Acanthostega*** to fully developed amphibians (Devonian period), transitional reptile/mammal forms such as the cynodont ***Thrinaxodon*** and other mammal-like reptiles that show a blend of mammalian and reptilian characteristics (Triassic), ***Velociraptor*** and relatives, and even more so ***Microraptor***, a four-winged gliding dromaeosaurid, and even more advanced forms such as ***Anchiornis*** and ***Scansoriopteryx***, representing an intermediate stage between the flightless theropods and primitive birds such as Archaeopteryx (Jurassic); ***Pezosiren***, an intermediate form of a primitive seacow with both terrestrial (land mammal) and aquatic adaptations (Eocene); ***Pakicetus, Ambulocetus, Rodhocetus*** and similar forms constitute links between amphibious and terrestrial artiodacyl (even-toed) ungulates and aquatic whales (Eocene); and ***Sahelanthropus***, indicating it is close to the common ancestor of chimpanzees and modern humans) the most basal ape-like African hominid. mosaic of primitive (chimpanzee-like) and derived hominid features (Miocene) See Transitional vertebrate fossils FAQ, at the TalkOrigins Archive, and Wikipedia: List of transitional fossils for a much more detailed lists. (MAK; Kutschera & Niklas 2004, p.259).

U

Unicellular organism: a living system consisting of only a single cell. May be simple, as with bacteria, or complex, as with protists. In the case of protists, different parts of the cell takes on the functions that organs and other systems fulfill in multicellular (many-celled) organisms. (MAK)

Uniformitarianism: Assumption that processes acting in the past are the same as those acting in the present. proposed the late 18th century theory of James Hutton that the natural forces now changing the shape of the earth's surface have been operating in the past much in the same way. The most important implication is that the earth is very old (deep time) and that the present is the key to understanding the past. Developed by Charles Lyell in the 19th century, who in turn influenced Darwin. Contrast with catastrophism, punctuated equilibrium.

Universal tree of life: See tree of life.

V

Variation: differences between individual organisms, or populations. An individual organism's phenotype results from both its genotype and the influence from the environment it has lived in. A substantial part of the variation in phenotypes in a population is caused by the differences between their genotypes. The modern evolutionary synthesis defines evolution as the change over time in this genetic variation. The frequency of one particular allele will fluctuate, becoming more or less prevalent relative to other forms of that gene. Evolutionary forces act by driving these changes in allele frequency in one direction or another. Variation disappears when a new allele reaches the point of fixation, when it either disappears from the population or replaces the ancestral allele entirely. Variation comes from mutations in genetic material, migration between populations (gene flow), and the reshuffling of genes through sexual reproduction. Variation also comes from exchanges of genes between different species; for example, through horizontal gene transfer in bacteria, and hybridisation in plants. Despite the constant introduction of variation through these processes, most of the genome of a species is identical in all individuals of that species. However, even relatively small changes in genotype can lead to dramatic changes in phenotype: for example, chimpanzees and humans differ in only about 5% of their genomes. (Wikipedia)

Vestigial, vestigial structure: A non-functional anatomical component retained merely as a matter of contingent history. (W. R. Elsberry *in* talk.origins) Usually, vestigial structures are formed when a lineage experiences a different set of selective pressures than its ancestors, and selection to maintain the elaboration and function of the feature ends or is greatly reduced. UCMP Understanding Evolution Glossary, Many organisms have vestigial organs, which are the remnants of fully functional structures in their ancestors. As a result of changes in lifestyle the organs became redundant, and are either not functional or reduced in functionality. With the loss of function goes the loss of positive selection, and the subsequent accumulation of deleterious mutations. Since any structure represents some kind of cost to the general economy of the body, an advantage may accrue from their elimination once they are not functional. Examples: wisdom teeth in humans; the loss of pigment and functional eyes in cave fauna; the loss of structure in endoparasites. (Wikipedia)

Vicariance: a process in which a species' range is divided even though the species has remained in place. This might happen through tectonic action, geologic activity (like the rise of a mountain range or shift in the course of a river), or other processes. Vicariance is usually contrasted with dispersal as a biogeographic mechanism. (UCMP Understanding Evolution Glossary)

Virus: infectious agent that can replicate only inside the living cells of organisms, and infect all types of organisms, from animals and plants to bacteria. Most viruses are too small to be seen directly with a light microscope. Since the initial discovery of the tobacco mosaic virus by Martinus Beijerinck in 1898, about 5,000 viruses have been described in detail, although there are millions of different types. Viruses are found in almost every ecosystem on Earth and are the most abundant type of biological entity. An enormous variety of genomic structures can be seen among viral species; as a group they contain more structural genomic diversity than plants, animals, archaea, or bacteria. A virus has either DNA or RNA genes and is called a DNA virus or a RNA virus respectively. The vast majority of viruses have RNA genomes. Plant viruses tend to have single-stranded RNA genomes and bacteriophages tend to have double-stranded DNA genomes. Viruses are not typically considered to be organisms because they are incapable of "independent" or autonomous reproduction or metabolism. Their origins are unclear: some may have evolved from plasmids, others from bacteria. Viruses are an important means of horizontal gene transfer, which increases genetic diversity. The study of viruses is known as virology, a sub-speciality of microbiology. (Wikipedia)

W

Web of life: conventionally refers to the food chain or trophic network, describes the feeding relationships between different species in an ecosystem. However, in reference to horizontal gene transfer can also refer to genetic transfer and evolution by non-hereditary means; especially common among bacteria.

Williams revolution: paradigm shift of the 1960s which saw the gene become the focus of evolutionary thinking, which saw evolutionary biology united with genetics. The revolution is named after George C. Williams, whose 1966 book ***Adaptation and Natural Selection*** popularised the theory. Previously most evolutionary thinkers considered selection to favour individuals, groups (group selection) and species, such as individuals acting "for the good of the species". The Williams revolution, however, established gene selection as the principal process of selection, and showed that because genes were the units of selection, selection would favour genes which maximised their own survival, not that of the group or species. (EvoWiki)

X

Y

Z

Zygote: The cell formed by the fertilization of male and female gametes. (PBS evolution Glossary)

Links

Some Links to other glossaries: (some of which have been used here) Evolution: Glossary, very detailed general glossary, Synthetic Theory of Evolution: Glossary of Terms, includes pronunciations; Phylogenetics Glossary, various technical, mostly phylogenetic and cladistic terms. By the Evolution discussion group (fall 1996); Modified from: Hillis, D.M., C. Moritz and B.K. Mable (eds). 1996. Molecular Systematics, Second Edition. Sinnauer Assoc., Massachusetts.; Talk.Origins Jargon, includes not only technical terms but also a list of who's who, slanted to the Creation–Evolution debate, but also of general value.

| Page Back: Modern Theory of Evolution | Unit Home | Page Top | Page Next: References |

content by MAK110419, edited RFVS111214

Evolution : References

Cosmic Evolution
  Life
    Evolution
    Paleontology
    Systematics
    Ecology

    Astrobiology **(Life in the Cosmos)**
    "Tellurobiota" **(Life on Earth)**

Evolution
  Evolution – the Modern Synthesis
  Glossary
  References

Ayala, Francisco J, A Rzhetsky & FJ Ayala (1998), Origins of the Metazoan Phyla: Molecular Clocks Confirm Paleontological Estimates. ***Proc. Natl. Acad. Sci. (USA)*** 95: 606–611.
Cambrian Explosion

Eldredge, N. and Gould, S.J. (1972) Punctuated Equilibria: an Alternative to Phyletic Gradualism. in ***Models in Paleobiology*** T.J.M. Schopf ed., Freemna, Cooper & Co., San Francisco pp. 82–115. **PDF**
Punctuated Equilibria

Hörandl, E. & Stuessy, T.F., 2010 Paraphyletic groups as natural units of biological classification, ***Taxon*** 59 (6) December 2010: 1641–1653 **on line**
budding, cladogenesis

Jewett, S.L. (11 November 1998). "On the Trail of the Coelacanth, a Living Fossil". The Washington Post. Retrieved 2009-05-18.
living fossil

Ulrich Kutschera & Karl J. Niklas. The modern theory of biological evolution: an expanded synthesis. ***Naturwissenschaften*** (2004) 91:255–276 **pdf**
Darwinism, Natural selection

Raymond C. Moore, Cecil G. Lalicker, and Alfred G. Fischer ***Invertebrate Fossils***, 1952, . New York–London: McGraw-Hill
cladogenesis, phyletic gradualism

Romanes GJ (1895) ***Darwin and after Darwin***, vol 2. Open Court, Chicago (cited in Kutschera & Niklas 2004)
Neo-Darwinism

Runnegar, Bruce (1992), Evolution of the earliest animals in JW Schopf [ed], ***Major Events in the History of Life***. Jones & Bartlett.
Cambrian Explosion

Signor III, P. W. and Lipps, J. H. (1982) "Sampling bias, gradual extinction patterns, and catastrophes in the fossil record", in Geological implications of impacts of large asteroids and comets on the Earth (ed. L. T. Silver and P. H. Schultz), ***Geological Society of America Special Publication***, vol. 190, pp. 291–296.
Signor–Lipps effect

Page Back: Glossary | **Page Top** | **Unit home** | **Page Next: Paleontology**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page last modified MAK111012, edited RFVS111214

Page Back: Paleontology	Page Up: Life	Unit Home (You are here)	Page Next: Systematics
Unit Back: Paleontology	Unit Up: Life	Unit Up: Palaeos	Unit Next: Ecology

Systematics, Taxonomy, and Phylogeny

Life
  Evolution
  Paleontology
  Systematics
  Ecology

  Astrobiology
  Life on Earth

Phylogeny and Systematics
  History of Systematics
    "The Great Chain of Being"
    Linnaean taxonomy
    The Phylogenetic Tree
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Stratigraphy and phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

The field of science concerned with studying and understanding of the diversification of life on the planet Earth, both past and present, and the classification of and evolutionary relationships among living things is called ***Systematic Biology***, or Systematics for short. Systematics is concerned both with ***Taxonomy***, the naming and classification of life, and ***Phylogeny***, the science and study of understanding the family tree of all life on Earth. Since classification should be based, ideally, on evolutionary relationships, and since the tree of life can only be understood if we know the names of the various branches and twigs that comprise it, it follows that these two are essentially two aspects of the same field. Systematics, then is the classification of life according to its phylogenetic (evolutionary) relationships.

Phylogeny is only possible with an understanding of evolution. Before the Darwinian revolution, species were considered static, either created by God or as eternal archetypes. Examples of these earlier, static classification schemes are the Scala Naturae (Natural Ladder), the Great Chain of Being, and the original (pre-Darwinian) Linnaean system, the foundation for all nomenclature or naming of species. Today, the Linnaean system remains popular, although some systematists and vertebrate paleontologists are pushing for its abandonment in favour of a new phylogenetic classification.

Currently there are three alternative, rival but also complementary, methodologies for classifying things and mapping out the tree of life. The first is Linnaean classification as modified by the early 20th century evolutionary synthesis (this evolutionary linnaeanism was at one time called Evolutionary systematics, a term that has since fallen into disuse), paleontology, and deep time. The second is Cladistics, itself divided into several types, such as the older single tree parsimony-based approach and the newer computational statistical-based methodologies, and Molecular phylogeny. The modern science of Phylogenetics uses either or both molecular sequencing and computational cladistic methodology to construct and test synapomorphy-based hypotheses. A fourth, phenetics, is little used nowadays but contributed to the statistical and philosophical (such as the distinction between hypothesis and phylogeny) approach of modern phylogenetics. Doubtless more methodologies could be added (e.g. Systems Theory, Evo-Devo, etc). Each methodology and sub-branch thereof claims to be the true one, either accepting the others as subordinates (e.g. many phylogenetic workers consider morphology-based cladistics secondary to molecular phylogeny) or rejecting them as outmoded (e.g. cladistics rejects evolutionary systematics). In fact, each has a different methodology and deals with different aspects of phylogeny and systematics, so it is not a matter of contradiction but complementarity. MAK111009 130323

Page Back: Paleontology	Unit Home (You are here)	Page Top	Page Next: Systematics

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page last modified MAK111014, 130323, edited RFVS111202

Page Back: Home | Unit Home | Page Next: Great Chain of Being
Unit Back: Paleontology | Unit Up: Life | Unit Next: Ecology

Phylogeny and Systematics

Life
  Evolution
  Paleontology
  Systematics
  Ecology

  Astrobiology
  Life on Earth

Phylogeny and Systematics
  History of Systematics
      Symbolic Correspondences
      Aristotle's Scala Naturae
      The Linnaean system
      The Darwinian revolution
      The Cladistic revolution
      The Molecular revolution
    "The Great Chain of Being"
    Linnaean taxonomy
    The Phylogenetic Tree
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Stratigraphy and phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

Systematics

In order to make sense of the natural world, science creates categories and classification systems. In the case of living organisms, which include millions of species that evolved through several billions of years of Earth history, and whose characteristics (especially in the

case of fossil species) and evolutionary relationships are often imperfectly understood, classification often becomes arbitrary. Add to this the fact that specialists working in different fields may have different approaches or preferences, and it is easy to see how the subject can become confusing, and ideas and methodologies have changed radically over time. MAK120229

Systematics - a definition

Systematic Biology - Systematics for short - is the branch of biology that deals with classifying living beings: the diversity and interrelationships of living beings, both current organisms ("neontology") and ancient ones ("palaeontology"). It can be divided into three parts.

- **Taxonomy** - the describing and naming new taxa (a taxon is any specifically defined group of organisms). Taxonomic groups are used to categorize similar taxa for identification-like field guides. These do not necessarily represent evolutionary trends (phylogeny), although the tendency in evolutionary biology (beginning with the school of evolutionary systematics) is that they should. Smaller taxonomic groups used to relate organisms at greater levels of similarities.
- **Classification** - the organization of information about diversity arranging them into a convenient, formal classification into a hierarchical system, and providing means of identifying them, for example diagnostic keys. Generally, classification is the application of taxonomy, e.g. the Linnaean system in a pragmatic way.
- **Phylogeny** - the determination of the ancestral relationships of organisms, and the group's evolutionary history through time. ***Phylogenetics*** is the field of biology concerned with identifying and understanding the evolutionary relationships between the many different kinds of life on earth. Currently phylogenetics is based on a synthesis of cladistics and molecular phylogeny, and has yet to fully incorporate stratigraphy or evolutionary systematics.

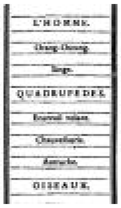
Systematics - history

The protoscience and science of systematic biology has gone through at least six major shifts of worldview, from myth to modern science. The currently preferred system of phyogenetics will no doubt give way to further insights as knowledsge progresses.

Symbolic Correspondences

In pre-modern and pre-scientific cultures, the world (including living organisms and inanimate objects) was classified according to the archetypal mandala - the four cardinal points, each associated with an element, a season, a deity, an animal, and so on, which constituted the underlying structure of the world (much as the elementary particles and forces in quantum physics is considered nowadays). This system of symbolic correspondences by association, which is metaphysical rather than scientific, reached great sophistication in the Chinese system of Five States of Change, the traditional Indian (Samkhyan and Tantric) doctrine of tattwas, and more recently (late 19th century) in Hermetic Kabbalah, as well as in "New Age" thought in general. Especially in China, the doctrine of universal correspondences, in association with the idea of a fundamental cosmic polaritry of yin and ying, developed into something very close to, but noit quite, experimental science (see Jacob Needham, ***Science and Civilisation in China***).

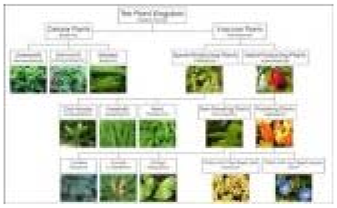
The Scala Naturae (Ladder of Nature)



A different slant on things was given by Aristotle, who introduced the idea of the ***scala naturae*** - the natural ladder. Like the yin-yang school of ancient and medieval China, this represented the beginning of a true science of the natural world. In later centuries, Aristotle's protoscience was subsumed under an elaborate system of metaphysics, according to which the natural world is interpreted in terms of the principle of plenitude, the overflowing abundance of the first principle or Godhead which creates successive beings. The further the beings are from the source the more ontologically impoverished they are. So you have formless matter right at the bottom, then rocks, plants, lower animals, higher animals, man, and finally spiritual and divine beings. This hierarchical view of the world - the Great Chain of Being [see Arthur Lovejoy's classic coverage of this topic], persisted through the middle ages and up until the scientific revolution of the seventeenth and eighteenth centuries, when it was replaced by a sort of monotheistic dualism - there is the material world or creation, and there is God in his heaven. With growing knowledge of the natural world it became impractical to organise everything in existence in a single linear series, and the orientating theme of a ladder of nature gave way to one of a tree of life

The Great Chain of Being

The Linnaean System



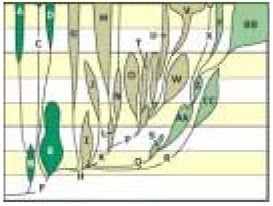
In the 18th century the Swedish botanist Carl von Linné, better known under the Latinized form of his name, Linnaeus, developed what's known as the binomial system of classification, in order to simplify the chaotic state of affairs around at his time. (Some plants were given names ten words long for example). He used Latin because that was the academic language of the time. Linnaeus adopted Great Chain of Being thinking in organising the natural world into three kingdoms, animal, vegetable, and mineral, although his division of each kingdom into class, . The modern system of classification in current widespread use is the binomial hierarchical system introduced by Linnaeus.

The Linnaean system is not a phylogeny, but a system of classifying the living world, developed at a time when species were considered immutablethe same today as when first created by an external God. We now know that species evolve but Linnaean taxonomy is such a useful and adaptable methodology that it has been taken up and become central to botany and zoology as a whole ever since.

Linnaean taxonomy

The Darwinian Revolution

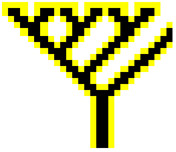
While Linnaeus founded taxonomy and classification, it was left to Charles Darwin in the 19th century to introduce the theory of evolution and hence make possible phylogenetic reconstruction; that is, the evolutionary relationships and history of the



various groups of organisms through geological time (millions of years). That's where things really get interesting, because life as a dynamic process is much more fascinating than life as a static series of unchanging types.

Evolutionary theory replaced the linear Ladder of Nature / Chain of being with a branching **evolutionary tree of life**. Even so, it took a while for the static linnaean classification to be fully incorporated within evolutionary theory. **Evolutionary Systematics** is the integration of the Linnaean system of taxonomy with mid-20th century Evolutionary Synthesis to form a dynamic system of classification. This establishmed the new science of ***Systematic Biology***.

Cladistics (Phylogenetic Systematics)



Cladistics - also called ***Phylogenetic Systematics*** or ***Phylogenetic Taxonomy*** - is a method of classifying organisms by common ancestry, developed by Willi Hennig, an entomologist, in 1950, but was not really accepted until the 1980s. LikeEvolutionary Systematics (which it has currently supplanted) Cladistics is a method of classification based on the evolutionary history of organisms, dividing organisms into meaningful groups and subgroups. Based strictly on determining branching points in the ancestry of organisms, it establishes groups based on their shared, ***derived*** features (synapomorphies), while ignoring primitive features (plesiomorphies) inherited from ancestors. Organisms that share common ancestors (and therefore have similar features) are grouped into taxonomic groups called ***clades***. Clades can be represented in terms of a cladogram. A cladogram is a branching tree-like diagram that depicts species divergence from hypothetical common ancestors. It shows the distribution and origins of shared characteristics.

Originally based only on morphological analysis of obvious synapomorphies, represented by a single branching tree (cladogram), cladistics quickly became a very popular tool in vertebrate paleontology, especially regarding the evolution of reptiles, a group with a rich fossil history, and of dinosaurs into birds. One of the important discoveries cladistics made was proof of the dinosaurian ancestry of birds (previously, birds were cderived from more generalised reptiles called thecodonts).

But organisms can also have share characteristics but have a different evolutionary (phylogentic) history. This is called homoplasy. One of the continuing challenges of Cladistics, and of rival and complementary systems like molecular phylogeny, is how to distinguish the "fake" synapomorphies (homoplasies) from the "genuine" ones (homologies).

Cladistics soon incorporated statistical analysis, resulting in a shift of emphasis and very different cladograms. Computational cladistics has not remained independent for long, as it was brought together with molecular phylogeny to form the science of ***Phylogenetics***.

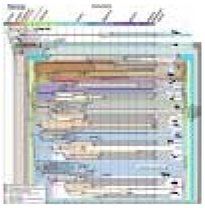
Cladistics

Molecular phylogeny

Molecular phylogeny traces phylogeny uses DNA, RNA, and protein molecular sequences. As with cladistics, molecular phylogenetic analysis results in a branching tree-like diagram, called a phylogram. Both molecular phylogenetics and computational cladistics use statistical analysis to build evolutionary trees, and the tendency now is to combine the two in a single integrated methodology, called computational phylogenetics. But this is not an equal partnership. Molecular analysis is universally privelaged over that of cladistic morphololological analysis whenever there is a contradiction between the two. This means the end of phemonic parsimony, and, very often (for example with mammal phylogeny) an absence of synapomorphies. Only when considering fossil forms alone is morphology-based cladistics still considered authoritative.

Molecular phylogeny

Phylogenetics



Phylogenetics is the name give to the integration of cladistics - especially computational cladistics - and molecular phylogeny. A phylogenetic study may be based just on cladistics on its own, on molecular phylogeny alone, or, increasingly now, the combination of the two, with cladograms that include both morphological (phenomic) and molecular data. It is hoped in this way to resolve the numerous phylogenetic incongruences between morphology and molecular-based studies.

Why a succession of paradigms?

It is hoped the reader will excuse the following rant on the unnecessary self-restrictions of normal (kuhnian) science as applied to systematic biology

The present author (MAK) has noted the tendency, in the history of evolutionary thinking, for each paradigm to replace the preceding one not because the earlier paradigm was refuted, but because the newer one has become more fashionable. Thus Cladistics replaced Evolutionary Systematics in the 1980s and 90s, even though the two use different methodologies and even different data. Evolutionary Systematics deals with problems of geographic isolation, speciation, ancestral taxa, stratigraphy, and large scale (supra-species) lineages. Cladistics uses a highly formalistic approach in order to test different evolutionary trees and arrive at the most likely phylogenetic hypothesis. Why then did evolutionary systematics fall from grace? The reason generally given, and the advantage cladistics has, is that it provides a more quantitative methodology (the same can be said for cladistics early and short-lived rival phenetics).

Although the two methodologies are equally robust, several reasons have been given why molecular phylogeny should be considered more reliable than phenomic morphology, such as larger and easily quantifiable strings of data, and the fact that many DNA sequences are invisible to natural selection and hence would give a more reliable phylogenetic signal. For example, some DNA codes have synonymous effects, e.g. they may code the same amino acid, or if diplicated or "junk" DNA sequences they may never be read at all (Dawkins, 2004, p.132). Yet conversely, the fact that there are only four types of RNA/DNA necleotide bases in every genome makes the problem of homoplasy far worse, and this can only be countered by even more statistical analysis. The premise that molecular phylogeny is more reliable than morphology-based cladistics has almost never been challenged (one of the very few criticisms, by former Palaeos author ATW, here). And while there are certainly advantages in quantification in that it makes computational phylogeny easier, that doesn't mean that Nature herself must work that way. One is reminded of the Mulla Nasrudin story (by popular Sufi author Idries Shah) about the man who lost his keys in his house, but searched for them under the lamp-post, because there was more light there.

All in all, newer taxonomic and phylogenetic methodologies are not necessarily the most inclusive. The newer and older may simply present equally valid but totally opposite methodologies, as regards for example taxonomic rating determined either by diversity or branching sequence, or the contrast between qualitative and quantitative/statistical approaches. The earlier system may be more inconclusive than the later, as for example when evolutionary systematics recognises all three types of speciation, which means it is able to deal with well-sampled groups such as some foraminiferan or ammonite sequences, Neogene molluscs, or Cenozoic and especially plio-pleistocene mammals, whereas cladistics does better with poorly known groyups, and it is usually assumed (see above paragraph) in phylogenetics that molecular phylogeny is better with neontological groups. From this perspective one realises how absurd it is to claim that only one system is the true one for every situation. MAK130331

Links

Taxonomy: Classifying Life - John Kimball - excellent overview (part of Kimball's Biology Pages).

Taxonomy, Transitional Forms, and the Fossil Record - Keith B. Miller - online essay, makes some interesting observations.

Page Back | **Unit Home** | **Page Top** | **Page Next: Great Chain of Being**

---

checked ATW051008, edited RFVS111202
page uploaded 28 April 2002, last modified MAK050104, 120212 130414

Page Back: Taxonomy	Page Up: Glossary	Unit home	Glossary (you are here)	Page Next: References
Unit Back: Paleontology	Unit Up: Life	Unit Down "The Great Chain of Being"	References	Unit Next: Ecology

Systematics, Taxonomy, and Phylogeny: Glossary

Life
  Evolution
  Paleontology
  Systematics
  Ecology

  Astrobiology
  Life on Earth

Phylogeny and Systematics
  Systematics - History of ideas
    "The Great Chain of Being"
    Linnaean taxonomy
    The Phylogenetic Tree
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Stratigraphy and phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z

16S ribosomal RNA *or* 16S rRNA) is a component of the 30S subunit of prokaryotic ribosomes. It is 1,542 nucleotides in length. Multiple sequences of 16S rRNA can exist within a single bacterium. The 16SrRNA gene is used for phylogenetic studies as it is highly conserved between different species of bacteria and archaea. Carl Woese pioneered this use of 16S rRNA. In addition to these, mitochondrial and chloroplastic rRNA are also amplified. (Wikipedia)

A.

Adams consensus: in cladistic analysis, a type of consensus method that uses the idea that a tree should be thought of as a "set of leaf subset nestings" rather than as a "set of clusters." A group nests within a larger group if the most recent common ancestor of the smaller group is a descendant of the most recent common ancestor of the larger group (from the PAUPDISPLAY Manual). This preserves all nested clades common to a set of source trees (Bininda-Emonds, 2004 - glossary) Adams consensus trees are designed to find the maximum number of components for a given set of cladograms by placing conflicting taxa at the most resolved node common to all the trees. (Forey et al 1992 pp.79-80). Only can be used for rooted trees. Usually preserves more structure than the strict methods, but may show clades in the consensus tree that do not occur in any of the trees in the set, which makes interpretation rather difficult. (from the PAUPDISPLAY Manual)

Advanced: see derived.

Algorithm: In mathematics and computer science, an effective method (a procedure that reduces the solution of some class of problems to a series of rote steps that give a specific and correct answer) expressed as a finite list of well-defined instructions for calculating a function. Algorithms are used for calculation, data processing, and automated reasoning. (Wikipedia). Modern cladistics and molecular sequencing use algorithms to create cladograms and phylograms

Allotype: A specimen designated from the type series that is the opposite sex of the holotype. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Alpha taxonomy: the science of finding, describing and naming species of living or fossil organisms. The term "alpha" refers to alpha taxonomy being the first and most basic step in taxonomy. This science is supported by institutions holding collections of these organisms, with relevant data, carefully curated: such institutes include natural history museums, herbaria and botanical gardens. (Wikipedia)

Ancestor: in this context, an organism, or more correctly a population, lineage, or species, that through evolution gives rise to one or more descendants that generally belong to a distinct taxon or species to itself. The identification of ancestors and descendants is a central aspect of evolutionary systematics. In contrast, cladistics denies it is ever possible to know an ancestor (unless one can actually observe evolution in a laboratory). "No matter how well we understand our group, its taxonomy, paleontology and anatomy, we can never know if one taxon is ancestral to another" (Paraphyly Watch blog - Transitional Fossils, Microbes & Patrocladistics). See also Ancestral group, common ancestor. (MAK)

Ancestral group: informal phrase used here to refer to any supra-specific taxon or evolutionary grade which gives rise to another group. Examples include pelycosaurs, thecodonts, and condylarths. Ancestral groups are central to evolutionary systematics and often included in spindle diagrams. cladistics denies the validity of ancestral groups (see paraphyly). (MAK)

Apomorphy: In cladistics, an ***apomorphy*** is a unique derived or specialized character trait found in a particular taxon, which is also possessed by a common ancestor. character.

> "A trait which characterizes an ancestral species and its descendants. This is an evolutionary novelty for the group. These are evidence for the existence of a group. Put another way, attributes shared in common are taken to indicate a shared evolutionary history.
>
> A novel evolutionary trait that is unique to a particular species and all its descendants and which can be used as a defining character for a species or group in phylogenetic terms. Hence, the possession of feathers is unique to birds and defines all members of the class Aves. An apomorphy that is restricted to a single species is termed an autapomorphy. It alone cannot provide any information about the phylogenetic relations of that species, although it can indicate the degree of divergence of a species from its nearest relatives. An example is speech, which is found solely in humans (Homo sapiens) and not in other primates. An apomorphy that is shared by two or more species or groups is termed a synapomorphy. Such traits define the strictly monophyletic groups, or clades, which are the basis of cladistic classification systems (see cladistics). Compare plesiomorphy."

A Dictionary of Biology, Oxford University Press, © Market House Books Ltd 2000

In phylogenetic nomenclature, an ***apomorphy-based clade*** is a clade the members of which are defined through their possession of that particular trait. Contrast with ***autapomorphy***, an apomorphy found only in a single taxon and of no phylogenetic (cladistic) value.

Apomorphy-based taxon (or clade): a group comprising all species descended from a common ancestor characterised by specific apomorphies. Apomorphy-based taxa are rarely used in cladistics because of the difficulty of determining when a particular trait appeared and whether its presence can be reliably determined. In contrast, all Linnaean and Evolutionary systematic taxa are apomorphy-based (either paraphyletic or monophyletic). Contrast with node-based and stem-based MAK120318

Art: in this context we don't mean the Renaissance masters, or the French impressionists, but the role of subjective assessment and intuition in science, a heresy for the advocates of neo-pragmatism and extreme empiricism, but unavoidable if we are to understand something as subtle and complex as the history and nature of life on Earth. I very much like Mike Taylor's comments here on the "How to choose between specific and generic separation" in a Sauropod Vertebra Picture of the Week posting.

> "At this point, I am reminded of when I used to be on a mailing list for wannabe writers...the best advice I saw on that list was from Jane MacDonald: My personal advice is don't overdo, or underdo, anything in your writing. Do it exactly right. That's my attitude to drawing genus boundaries. It is, frankly, an art; and there are no substitutes for taste, experience, judgement, familiarity with the group in question and all those other touchy-feely qualities that uber-cladists would love to find a way to abolish if they could. But they can't. There is no algorithm for this. I also think of an observation by computer scientist Bjarne Stroustrup, the inventor of the C++ programming language: "Design and programming are human activities; forget that and all is lost." The same is true of palaeontology. (And of, well, everything.)"

Artefact: not an ancient extraterrestrial or interdimensional device of great power, but, in the more mundane cladistic and phylogenomic context, a false signal resulting in a distorted phylogenetic view of the group being studied. Examples include Long Branch Attraction and Heterotachy. See also Garbage in, garbage out.

ASCII Phylogenetic Tree: As here defined, an ***ASCII phylogeny***, or more correctly an ***ASCII Phylogenetic Tree***, is a dendrogramor tree diagram which uses ASCII-text format to draw supertrees. ASCII Phylogenetic Trees might also informally be referred to as ***ASCII Cladograms***, but that is inaccurate because cladograms are, pragmatically speaking, not actually phylogenies but branching diagrams depicting patterns of shared similarities (O'Keefe & Sander 1999) from which evolutionary hypotheses can be constructed. The ASCII Phylogenetic Tree format was created by T. Mike Keesey, who used them to show dinosaur phylogenetic relationships in the old ***Dinosauricon***. Mikko Haaramo adopted this format, but refined it with the introduction of the grave (`) for the corners, for his own phylogenetic archive. This useful format was then adopted on the Dinosaur Mailing List and by paleo enthusiast webmasters like Jack Conrad (***The Vertebrate Phylogeny Pages***), Justin S. Tweet (***Thescelosaurus!***), Øyvind M. Padron (***The Dinosauria***), and Toby White and myself (Kheper palaeo and Vertebrate Notes, and finally Palaeos.com, here). The format has now become pretty standard in any paleo geek text-based phylogenetic diagram. (MAK)

Autapomorphy: a character traitunique to a particular unique to a particular taxon; Because autapomorphies do not provide information about the organism's phylogenetic relationships to other taxa, they are of no use in cladistics. However they still provide useful non-phylogenetic information about the species in question. Compare with apomorphy, plesiomorphy, homology, homoplasy.

Available name: A name that is correctly proposed according to the International Code of Zoological Nomenclature. An available name is not necessarily the valid name. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

B.

Basal: Preferred cladistic substitute for "primitive", as it is felt the latter may carry false connotations of inferiority or a lack of complexity. In cladograms, basal taxa are those terminal taxa that first diverged from the root. The term basal is only be correctly applied to clades (species or higher groups) of organisms, not to individual traits possessed by the organisms. There is however a tendency for terms like basal and stem to appear as rather vague alternatives to "primitive" or "ancestral" in cladistic paleontological literature and especially popularised accounts and comments thereof (MAK120318, Wikipedia)

Basal node: the node or base of the cladogram, representing the hypothetical common ancestor of the entire clade (however if the common ancestor or something like it is known, then it is shown as a terminal taxon, see basal taxon. See graphic. (MAK)

Basal taxon: general term in phylogenetic systematics for any terminal taxa that lie at the base of a cladogram, i.e. they are connected by, or else close to, the basal node, and their sister group is the sub-clade that constitutes the rest of the cladogram. Equivalent to primitive or ancestral (these terms not being used in cladistics). Included under or partially equivalent to stem group. (MAK)

Bayesian inference: a method of statistical inference, used for example in phylogenetics, in which some kinds of evidence or observations are used to calculate the probability that a hypothesis may be true, or else to update its previously calculated probability. A form of likelihood analysis that differs from maximum likelihood in that it considers all possible trees (phylograms or cladograms), not just the most likely one, but gives proportionally more credence to the more likely ones. Confidence is measured in terms of probabilities (Dawkins, 2004, p.138-98)

Binomial nomenclature: Linnaean universal standard of biological scientific notation, according to which every species is given a distinct two-part name. The first part, think of it as like the surname, is the genus, which is capitalised, the second part the species, written completely in lower case, is like the given name. Both names are by convention written in ***italics*** (or if that is not possible, underlined, or if even that is not possible say with ASCII text, then there is an underscore character before and after the name, `_like this_`). So in the case of ***Tyrannosaurus rex***, ***Tyrannosaurus*** is the genus (capital "T"), and ***rex*** (small "r") the species. Finally, the name of the discoverer of the species is added (if the species has since been given a new genus the discoverer's name is placed in brackets) along with the year of publication of the scientific paper describing that particular species. This usage is not mandatory in popular and semi-technical books, but is when describing or listing species in a technical journal or a Museum. The species name can also be abbreviated by only using the first letter of the genus and a period, after which comes the species name. The species name on its own can be written as ***T. rex*** (but ***never*** "T-rex", it is not a car!). Any student of natural history will be familiar with this approach. I have noticed however a tendency among paleontologists to give every new discovery a new genus as well as a new species, leading to an over-excess of monotypic genera (each genus only having one species). This was and is exacerbated by the cladistic revolution, where even species previously placed in a genus are moved to their own genus, especially if precise phylogenetic relationship is uncertain (which it almost always is in these cases) only adding to the multiplication of names (Paleo artist and author Greg Paul at one time (***Predatory Dinosaurs of the World***, 1988) went in the opposite direction, lumping species from even fairly distant genera together; e.g. most dromaeosaurids became ***Velociraptor***, although his more recent work ***The Princeton Field Guide to Dinosaurs*** (2010) tends to swing back to less species per genus). There is also a move among several proponents of phylogenetic nomenclature and the Phylocode to abandon the binomial altogether, and emphasise only the phylogenetic relationships (which wouldn't necessarily be evident from the name alone). This would actually only be a small step when considering vertebrate paleontology alone in view of the above mentioned tendency (but not for example Pleistocene mammals which have a very good fossil record!), but would be a nightmare if cataloging or referencing all of the other millions of named and described species. However it is probably unlikely that the Phylocode will become a majority position any time soon. (MAK)

Biological Species Concept: (BSC), this evolutionary systematic pattern-orientated definition is the currently most popular definition of species, according to which species are defined as groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups (Mayr 1963). Other species concepts include cohesion, ecological, evolutionary, phenetic, phylogenetic, and recognition species concept species concepts. (Ptacet & Hankison (2009))

Bootstrap - a sampling method used in phylogenetics. Boostrapping measures how consistently the data support a given tree topology. It does not determine how accurate a cladogram is; it only gives information about its stability, and helps assess whether the sequence data is adequate to validate the topology (branching order) (Holmes 2003)

Bremer support: The Bremer support for a clade is the number of extra steps you need to construct a tree (consistent with the characters) where that clade is no longer present. There are reasons to prefer this index to the bootstrap value. (Øyvind Hammer - PAST - Paleontological Statistics Software) (see also decay index)

Bubble diagram: Informal neologism used by yours truly for a spindle diagram with rounded rather than angular contours. Also called a romerogram. (MAK)

C.

Category: Any rank within the classification hierarchy, e.g., family, subfamily, subspecies. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Change of rank: When a name is moved from one level of the classification system to another, e.g., when De Lotto (1955) moved ***Ceroplastes destructor brevicauda*** from the subspecies to the species rank ***C. brevicauda*** this was a change of rank. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Character any recognizable trait, attribute, quality, feature, or property of an organism, of an organism used for recognizing, differentiating or classifying a taxon. used to reconstruct phylogenies. Characters may be morphological, behavioral, physiological, or molecular. In cladistics, the character is thought to be derived and vary from a corresponding feature in a common ancestor of the organisms being studied. (modified from PBS evolution Glossary, UCMP Understanding Evolution Glossary, Glossary of taxonomy (Doc), and Sereno, 2007)

Character State: the mutually exclusive conditions of a character. (one of the possible alternative conditions of the character). For example, "present" and "absent" are two states of the character "hair" in mammals. Together, characters and character states compose what are termed ***character statements***. (modified from PBS evolution Glossary and UCMP Understanding Evolution Glossary, also definitions from Sereno, 2007)

Character state change: change of the form or state of a character in the course of evolution.

Character optimization, character mapping: interpreting characters on a phylogenetic tree in order to reconstruct ancestral character states.

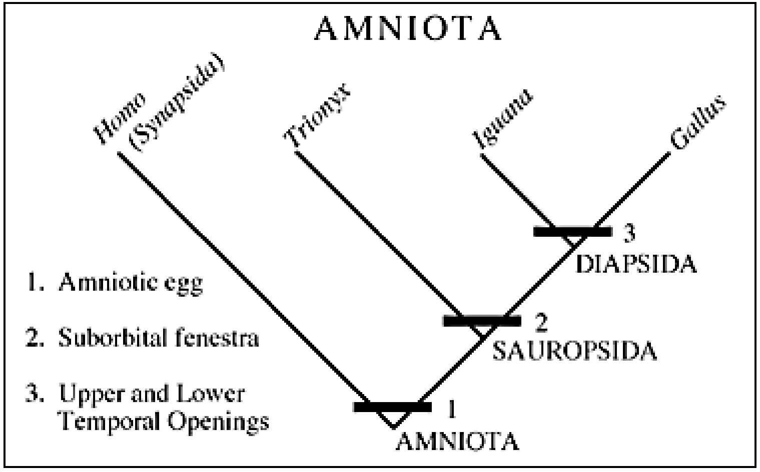
Chronogram: phylogenetic tree that explicitly represents evolutionary time through its branch lengths. In evolutionary systematics and earlier, chronograms took the form of spindle diagrams, emphasising diversity and abundance of clades and grades through time; with the rise of phylogenetics and cladistics they appear as cladogram-like diagrams, emphasising when each new branch (clade) appears in time (MAK).

Chronospecies: One or more species which continually changes from an ancestral form along an evolutionary scale. This sequence of alterations eventually produces a population which is physically, morphologically, and/or genetically distinct from the original ancestors. Throughout this change, there is only one species in the lineage at any point in time, as opposed to cases where divergent evolution produces contemporary species with a common ancestor. Relies on an extensive fossil record, since morphological changes accumulate over time and two very different organisms could be connected by a series of intermediaries. The related term ***paleospecies*** indicates an extinct species only identified with fossil material. To avoid unnecessary multiplication of terminology (and paleontology-neontological distinctions) these terms are here synonymised. For example, changes in the Permian lepospondyl amphibian ***Diplocaulus*** over time may imply a chronospecies (= paleospecies). (MAK, Wikipedia)

Clade: term coined by Julian Huxley, in terms of evolutionary branching and ancestry, to refer to the set of all organisms descended from a particular ancestor. In cladistics, a clade is a monophyletic group of organisms that includes all the descendants of a common ancestor as well as that ancestor itself. For example, birds, dinosaurs, pterosaurs (flying reptiles), crocodiles and their extinct relatives all form the clade Archosauria. In phenotype-based Linnaean and evolutionary systematics, clades are not always suitable as units of classification, as the crown portion of a clade may be very different from its base (compare a pelycosaur reptile to a eutherian mamal for example). The Phylocode attempts to formalise phylogenetic systematic taxonomy based on the use of clades. Contrast grade. (MAK)

Cladistic literalism: informal term coined here by the [present author (MAK) to refer to the belief that cladistic hypotheses describe actual phylogeny, which means that all speciation involves an ancestral lineage dividing into two daughter species, that the fossil record is too incomplete to provide any useful phylogeny, and that no ancestor can ever be known. Cladistic literalism may or may not incorporate molecular phylogeny MAK130318

Cladistics: Rigorous methodology first developed by Wili Hennig, to evaluate and reconstruct phylogenetic hypotheses. The results of cladistic analyses are often represented in the form of a branching diagram, called a cladogram. It is important to keep in mind that cladistics is not the same as phylogeny, and cladograms are ***not*** phylogenetic diagrams of ancestor-descendant relationships! As with Linnaean classification, cladistics provides a nested hierarchy where an organism is assigned a series of names that more and more specifically locate and define it within the hierarchy. However, unlike Linnaean classification, phylogenetic classification only allows monophyletic clades, excludes both paraphyletic and polyphyletic groups. It also does not assign ranks (e.g. class, phylum) to the hierarchical levels.



Cladogram by Paul Olsen (original url), showing four species (human, turtle, lizard and bird) and three clades, each defined buy its own synapomorphies (shared unique characteristics). Most cladogram matrixes involve many hundreds of such characteristics

The late 1970s and early 1980s saw conflict between the two schools of Pattern Cladism and Hennigian systematics, although this has since been resolved, and cladistics today is generally based equally on both. In the 1980s and 90s cladistics became the dominant paradigm in biological systematics, supplanting the previous Linnaean-based evolutionary taxonomy in all fields except botany. Together with molecular phylogeny it forms the current Phylogenetic paradigm.

With the advent of powerful computation, cladistics has come to use statistical procedures such as Bayesian analysis and Maximum Likelihood. Such computer-based cladistics are now used especially in paleontology to determine the relationships between various fossil organisms. Often relying on supermatrixes and incorporating large numbers of species and hundreds of character states, they tend to gives very different results to that of earlier hand-coded diagrams, which emphasied instead a smaller number of well-recognised synapomorphies.

Despite being often referred to as "phylogeny", cladistics today does not seek to describe the actual course of phylogeny in deep time a la evolutionary systematics, but only to select the most viable hypothesis of phylogenetic relationships, given the available data (empirical method).

It is held by cladists that taxa (if recognized) must always correspond to clades, united by apomorphies (derived traits) which are discovered by a cladistic analysis. To this end, cladistics collects character data only from the taxa being studied, and do not consider the inferred characters of ancestors. (MAK) **ATW - Introduction to Cladistics** ; **Links:** What is cladistics? How reliable is it? - Mike Taylor; Cladistics - Wikipedia; 29+ Evidences for Macroevolution: Phylogenetics - Douglas Theobald @ Talk Origins. **More**

Cladogenesis: The division of an ancestral parental lineage into two or more daughter lineages or species. At one time, cladogenesis was recognised, along with anagenesis, as one of the two types of gradual evolution. Because the highly formalised trees that cladistics use on do not show anagenesis, a misplaced literalism led to cladogenesis, in the sense of the division of a common ancestor into two daughter species, being accepted as the standard form of speciation. However, other evolutionary processes, especially budding and merging, involve asymmetrical divergence and therefore paraphyly. (MAK)

Cladogram: A dichotomous phylogenetic tree that branches repeatedly, suggesting a classification of organisms based on the sequence in which evolutionary branches arise; a nested diagram of synapomorphies indicating possible relations between groups; each point of branching represents divergence from a hypothetical common ancestor. Cladograms ***only*** give information about branching order, not about the amount of change or difference (unlike phylograms), the diversity of each taxon (unlike spindle diagrams) or stratigraphic range (unlike chronogram, although a cladogram can also be drawn as a chronogram).

In the 1980s, cladograms used Hennigian methodology and were based on immediately apparent synapomorphies. From the 1990s onwards, computational phylogenetics began to be used in the generation of cladograms, and these have now long since become standard. Characters pertaining to each taxon are run through computer algorithms to determine phlogenetic relationships. Although traditionally cladograms were generated largely on the basis of morphological characters alone, nowadays DNA and RNA sequencing data have been used as well. All have different intrinsic sources of error. For example, ***character convergence*** (homoplasy) is much more common in morphological data than in molecular sequence data, but ***character reversions*** that are unrecognizable as such are more common in the latter (see long branch attraction). Morphological homoplasies can usually be recognized as such if character states are defined with enough attention to detail. The researcher must decide which character states were present before the last common ancestor of the species group (***plesiomorphies***) and which were present in the last common ancestor (***synapomorphies***) and does so by comparison to one or more ***outgroups***. The choice of an outgroup is a crucial step in cladistic analysis because different outgroups can produce trees with profoundly different topologies. Note that only synapomorphies are of use in characterizing clades (Wikipedia, MAK).

Class: In the Linnaean classification the taxonomic rank between phylum and order. It defines a major group of organisms within a particular phylum; e.g. Insects within Arthropods or Reptiles within Chordates. Classes are used in the taxonomic series of evolutionary systematics but are not used in cladistic analysis. Classes are often paraphyletic. This is shown by the spindle diagram showing the evolution of the vertebrates, where only five out of nine classes are holophyletic clades. However this is due to the fact that cladistics uses the species as its basic reference point, whereas evolutionary systematics tends to use families, orders, classes, and phyla. (MAK) **More**

Classification. In biology, a classification is a system of uniting taxa into a system of interconnected units in order to reflect features uniting them. Classifications may be either artificial (built on arbitrarily-chosen features to facilitate the worker's convenience) or natural (supposedly derived from the evolutionary relationships of the taxa). Most authors would currently favour the latter, though artificial classifications may still be in use for groups of organisms (such as anamorphic fungi) in which evolutionary relationships are difficult to establish. Many groups of organisms may have different classificatory systems in use at the same time due to differing opinions between different authors, and classifications may also change as authors refine their investigations. Classification should be distinguished from nomenclature, which is the investigation of correct names for taxa. Classification and nomenclature together form taxonomy. CKT070412

Coalescent Theory: A method for comparison of gene sequences in populations to find the most likely common ancestor sequence. (W. R. Elsberry - talk.origins)

Cohesion Species Concept: defines species as the most inclusive group of organisms having the potential for genetic and/or demographic exchangability (Ptacet & Hankison (2009))

Common ancestor: The ancestral species that gave rise to two or more descendant lineages, and thus represents the ancestor they have in common, and from which later species and groups evolved. The idea of a common ancestor is central to evolutionary thinking from Darwin onwards. In the Modern Synthesis' Evolutionary Systematics the common ancestor is usually shown as the most suitable fossil form at the base of a lineage, where it may or (more likely given the small number of species known from those which actually lived in past ages) or may not be an actual ancestor, more often it is a sort of grand-uncle rather than grandfather). Evolutionary Systematics is based on identifying and determining the actual traits of an ancestral species or, more usually, supra-specific taxa.

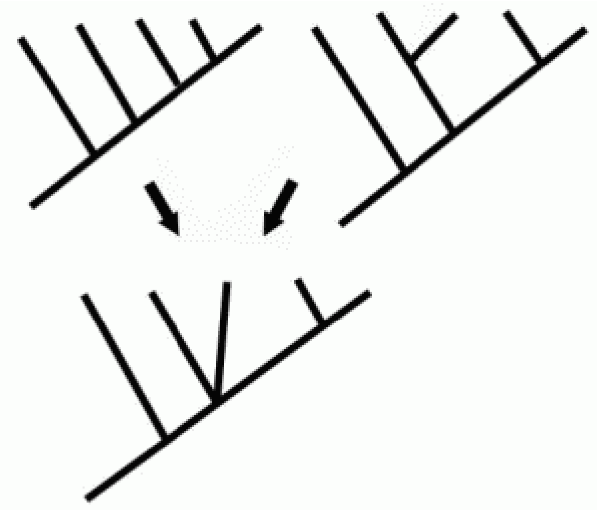
In an attempt to establish greater rigour and precision, Cladistic phylogeny defines the ***most recent common ancestor*** as the originator of a clade; in other words the first species or organism to possess the unique attributes of that clade. Contrary to popular opinion, cladograms do not actually show the actual common ancestor; such an organism or group would be by definition paraphyletic, and hemnce automatically forbidden by cladistic logic. Cladistics therefore rejects the possibity of knowing the actual common ancestor, and instead posits a hypothetical common ancestor. However, a basal taxon may have some features in common witrh the common ancestor. (MAK130318)

Computational cladistics: informal term for modern cladistics following the development of cheap and powerful computers around the turn ofthe 21st century, which provide heavy number crunching to analyse large quantities of data using statistical procedures, the two most common being Bayesian analysis and Maximum Likelihood. The emphasise on small numbers of distinctive and well-recognised apomorphies and synapomorphies - central to both phylogenetic systematics and pattern cladism - is replaced by huge data matrixesincorporating large numbers of species and hundreds of character states. As algorithm-based morphology-based cladistics uses the same statistical methods as molecular sequencing, it becomes possible to combine data from both in supermatrixes to provide a total evidence approach; hence phylogenetics. Whether morphology-based or phylogenetic, algorithm-based cladistics gives very different results to early cladistics. Synapomorphies are often obscure, homoplasy is ubiquitous and rampant, and what were long thought to be well-established monophyletic groups turn out to be paraphyletic, diphyletic, or polyphyletic. MAK130318 **More**

Computational phylogenetics: the application of computational algorithms, methods and programs to phylogenetic analyses. The goal is to assemble a phylogenetic tree representing a hypothesis about the evolutionary ancestry of a set of genes, species, or other taxa. Examples include Computational cladistics, Molecular phylogeny, and Phylogenetics. There is however a tendency, whenever the resolved morphology- and molecular-based trees are found to be incongruent, for the tree topology of molecular phylogeny to be preferred, and the phenomic cladistic trees constrained to follow molecular lines. (MAK130324, Wikipedia)

Congeneric: of species that belong to the same genus

Consensus: in cladistics, a ***consensus tree*** is the agreement between two or more trees (see diagram at right). Obviously there are many different possible solutions, as well as different methodologies. Some consensus methods include strict, majority rule, semi-strict, Nelson, and Adams consensus.



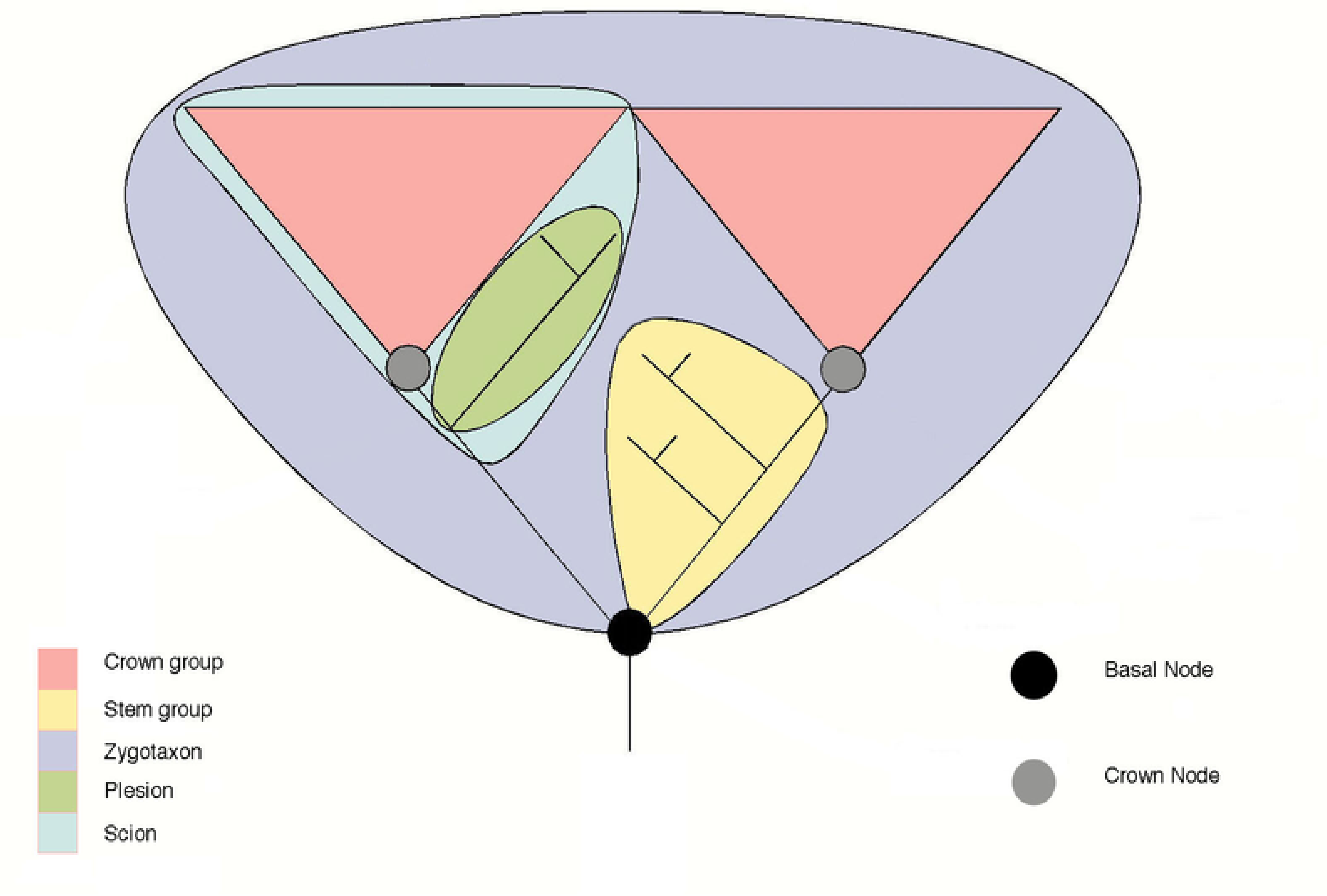
Graphic: A Consensus Cladogram, from How We Look at the Relationships of Taxa

Consistency index (CI): In cladistics, the measure of the parsimony fit of a character to a tree, or of the average fit of all characters to a tree. Varies from 1.0 (perfect fit) to a value asymptotically approaching zero (poorest fit). It is inflated by autapomorphies which can only take the value 1.0; thus a totally uninformative data set (consisting only of autapomorphies) could return a CI equal to 1.0. Compare retention index. (Michael D. Crisp - Introductory glossary of cladistic terms). The per-character consistency index (ci) is defined as m/s, where ***m*** is the minimum possible number of character changes (steps) on any tree, and ***s*** is the actual number of steps on the current tree. This index hence varies from one (no homoplasy) and down towards zero (a lot of homoplasy). The ensemble consistency index CI is a similar index summed over all characters. (Øyvind Hammer - PAST - Paleontological Statistics Software)

Constrain: in the context of phylogenetic analysis, forcing cladograms generated through morphology-based cladistic analysis to follow the branching order of molecular trees, which means rejecting both parsimony and likelihood morphology-based best fit trees as the primary standard. Depends on the premise that molecular phylogeny offers a more reliable phylogenetic signal than morphology-based approaches. The tendency now is towards a total evidence analysis incorporatiing both molecules and morphology. MAK130414

Cotype: (Zoological Code) this term has been used in the past to refer to either a paratype or a syntype. Its use is now discouraged. CKT061027

Crown group: in cladistics, a group consisting of living representatives, their ancestors back to the most recent common ancestor of that group, and all of that ancestor's descendants. The name was given by Willi Hennig as a way of classifying living organisms relative to extinct ones. Though formulated in the 1970s, it was not commonly used until its reintroduction in the 2000s. The usual definition of a crown group is the smallest monophyletic group, or "clade", to contain the last common ancestor of all extant members, and all of that ancestor's descendants. Extinct side branches on the family tree will still be part of a crown group. For example, if we consider the crown-birds (i.e all extant birds and the rest of the family tree down to their last common ancestor), extinct side branches like the dodo or great auk are still descended from the last common ancestor of all living birds, so falls within the bird crown group. (MAK, Modified from Wikipedia)



From Wikipedia. The stem and crown group concept. The two pink groups represent a pair of crown groups, the last common node of which is the basal node. Terminology is from Craske, A. J. and Jefferies, R. P. S. (1989) A new mitrate from the late Ordovician of Norway, and a new approach to subdividing a plesion. *Palaeontology* 32, 69–99 and Budd, G. E. (2001) Tardigrades as "stem-group" arthropods: the evidence from the Cambrian fauna. *Zoologischer Anzeiger* 240, 265-279. Diagram and text by Graham Budd. The diagram shown here is revised from the original to clarify that the stem group does not include the basal node (ancestor) of the crown group. text and revision by Peter Coxhead. For explanation of terminology see Wikipedia - Crown Group page.

D.

Daughter: "Daughter group" is a Cladistic term for the descendant branches of a hypothetical common ancestor that take the form of a node on a cladogram, used in phylogenetic hypotheses. See also Sister group. A "daughter species" however would be an actual phylogenetic descendent, as used in evolutronary systematics MAK130318

Decay index: In cladistic analysis, the number of additional steps required to dissolve a given clade (Michael Allaby, 1999, ***Dictionary of Zoology***). (see also Bremer support)

Dendrogram: There doesn't seem to be an agreed meaning of this term. Michael Crisp's cladistic glossary defines it as any branching diagram or tree, such as a cladogram. Mayr & Bock 2002(for the evolutionary systematics camp) contrast the "Hennigian cladogram" with the "Darwinian dendrogram". The Wikipedia page gives another definition again: "a tree diagram frequently used to illustrate the arrangement of the clusters produced by hierarchical clustering. Dendrograms are often used in computational biology to illustrate the clustering of genes or samples." As used on Palaeos, a dendrogram is any informal phylogenetic cladogram-like diagram, a sort of composite of published trees, or simply the author in question's random opinion. MAK111018 120318

Derived: same as apomorphy; a derived character / trait is inferred to be a modified version of a more primitive condition of that character and therefore inferred to have arisen later in the evolution of the clade.

Descendant: in this context, a population, lineage, or species, that arises through evolution from an ancestor (an earlier species or taxon). Where a number of descendants share the same ancestor (cladogenesis), the ancestor is called a common ancestor. (MAK)

Diagnosis: statement in words that purports to give those characters which differentiate a taxon from other taxa with which it is likely to be confused. (Glossary of taxonomy (Doc))

Diphyly: a taxon that was believed to be monophyletic but instead turns out to be the result of two distinct but convergent evolutionary lineages, for example the mammalian order Insectivora; a form of polyphyly. MAK130318

Distance: phylogenetic or evolutionary divergence. Distances are usually expressed pair-wise among terminal taxa, and can be calculated based on a specified evolutionary model; the model specifies the probabilities of character-state changes through evolutionary time. Distances are popular for building phylogenetic trees from molecular sequence data. Compare with maximum likelihood, parsimony. (Michael D. Crisp - Introductory glossary of cladistic terms)

Doubly paraphyletic group: a group or taxon that is paraphyletic because two of its descendant lineages are not included. e.g. Class Reptilia is a doubly paraphyletic group because reptiles seperately evolved into birds and mammals. cf. singly and triply paraphyletic groups (MAK120318)

E.

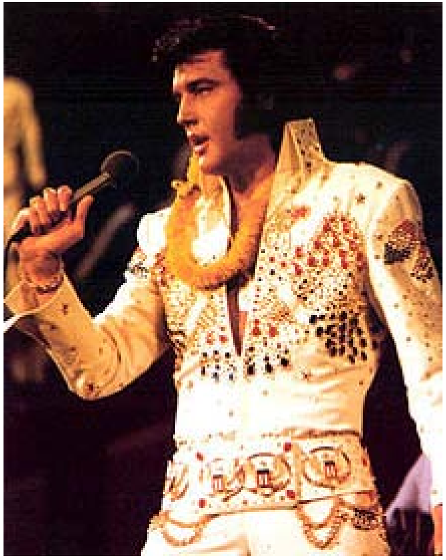
Ecological Species Concept: process orientated species concept in which species are defined as a set of organisms adapted to a single ecological niche and evolving separately from other lineages. (Ptacet & Hankison (2009)). There would seem to be an overlap here with Mayr's biological species concept

Electrophoresis: The method of distinguishing entities according to their motility in an electric field. In evolutionary biology and molecular sequencing, it has been mainly used to distinguish different forms of proteins. The electrophoretic motility of a molecule is influenced by its size and electric charge. (PBS evolution Glossary)

Emendation: In taxonomy, an intentional change to a previously proposed name, e.g., Lindinger proposed the emendation ***Hemiberlesea*** for the armored scale ***Hemiberlesia*** indicating that it was originally improperly formed. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Epitype: (Botanical Code) a specimen designated at a later date to characterise a species, where the original type material is not sufficient to do so. The original type retains name-bearing status, and should the epitype later prove not to be conspecific, the name remains with the holotype (however, it is not uncommon for the International Association of Plant Taxonomy to conserve the common understanding of a name by setting aside the holotype in favour of the epitype). CKT061027

Elvis taxon: a taxon which has been misidentified as having re-emerged in the fossil record after a period of presumed extinction, but is not actually a descendant of the original taxon, instead having developed a similar morphology through convergent evolution. This implies the extinction of the original taxon is real, and the two taxa are polyphyletic. The term was coined by D. H. Erwin and M. L. Droser in a 1993 paper to distinguish descendant from non-descendant taxa: "Rather than continue the biblical tradition favored by Jablonski [for Lazarus taxa], we prefer a more topical approach and suggest that such taxa should be known as Elvis taxa, in recognition of the many Elvis impersonators who have appeared since the death of The King." ***Lobothyris subgregaria***, a brachiopod from the early Jurassic period, is one example of such a taxon. By contrast, a Lazarus taxon is one which actually is a descendant of the original taxon, and highlights missing fossil records, which may be filled



later. A Zombie taxon is a taxon sample that was mobile in the time between its original death and its subsequent discovery in a site of younger classification, like, for example, a trilobite that gets eroded out of its Cambrian-aged limestone matrix, and reworked into Miocene-aged siltstone. (Wikipedia)

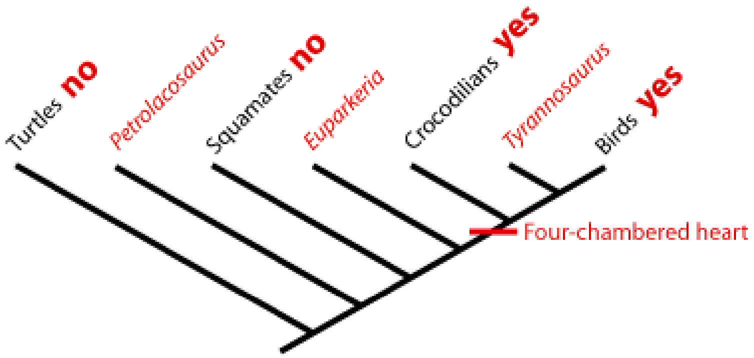
Evolution: For its relevance to systematics, see Phylogeny. For the general biological context see the relevant glossary entry

Evolutionary classification: see Evolutionary systematics

Evolutionary clock: see Molecular clock

Evolutionary Species Concept: evolutionary systematic process orientated species concept in which species are defined as a single and distinct lineage or ancestor-descendant sequence of populations with unique evolutionary tendencies and its own historical fate. This concept, proposed by Simpson but rejected by Mayr, may well be true but is hard to verify empirically. Other species concepts include biological, cohesion, ecological, phenetic, phylogenetic, and recognition species concept species concepts. (Ptacet & Hankison (2009))

Evolutionary systematics, also called Evolutionary classification, i a way to determine natural relationships of organisms by studying a group in detail and comparing degree of similarity. Tends to consider supra-specific taxa rather than single species. The origin of a major new trait or apomorphy (e.g., flowers in angiosperms, endothermy and lactation in mammals) results in the formation of a new "natural group" of the same Linnaean rank as the "natural" group from which it arose (in these examples gymnosperms and reptiles respectively). Often uses spindle diagrams that map taxonomic diversity (usually mapped on the horizontal axis) against geological time (mapped vertically, in keeping with the geologists' tendency to equate time with geological strata and hence verticality). Evolutionary systematics has its roots in the work of Haeckel, but reached its current form in the modern evolutionary synthesis of the early 1940s, especially the work of George Gaylord Simpson and Ernst Mayr. In this school of thought, classification reflects both phylogenetic relatedness as well as morphological disparity (overall similarity). (MAK, Wikipedia, Grant, 2003, IAB blog, quoting Ebach et al 2008, UCMP Virtual Paleobotanical Laboratory) **More**



Extant Phylogenetic Bracket; Phylogenetic bracketing: In 1999, Larry Witmer described how unknown character states for fossil taxa are reconstructed with respect to extant taxa called the ***extant phylogenetic bracket*** (EPB). This is the bracket formed on either side of the taxon with the missing information by extant taxa in which the character state is known. Using it, we can make three types of inference, listed in order of decreasing confidence. Consider the distribution of a soft-tissue character - the four-chambered heart - among three fossil reptiles:

- Type I Inference: ***Tyrannosaurus*** is bracketed by birds and crocodilians, both of which have the derived character. With no contrary positive evidence, the simplest assumption is that Tyrannosaurus had it also.

- Type II Inference: The basal archosauriform ***Euparkeria*** is bracketed by crocodilians and squamates. Crocs have the derived character, squamates don't. Thus, we are much less secure than above in inferring it in Euparkeria , but presence of some sort of hard tissue correlate of that trait might increase our confidence.
- Type III Inference: The basal diapsid ***Petrolacosaurus*** is bracketed by squamates and turtles, neither of which have the derived character. Our confidence in its presence in the extinct form is very low. We would need strong positive fossil evidence to argue for its presence.

Text and diagram by John Merck

F.

Family: In the Linnaean classification the taxonomic rank between order and genus (or order and tribe, tribe being a mostly botanical rank between family and genus), used to define group of related organisms. Used in evolutionary systematics but not cladistics. All members of a family are generally quite similar in appearance. (MAK) **More**

Five Kingdoms: evolutionary classification of life developed by Robert Whittaker and Lynn Margulis, according to which organisms are divided into five kingdoms: Monera, Protist, Plants, Fungi, and Animals. **More**

G.

. **"Gap codings"**. this is not a formal term but refers to the situation in cladistics, when a 'daughter' character is logically dependent upon the state of a 'parent', and cannot be coded when the parent is absent. For example, the position of the frontal appendage in an arthropod can only be coded in taxa that possess a frontal appendage in the first place. In morphological analyses, this assigns double weight a priori to absences in the 'parent' character (because the daughter is always contingent, that is, dependent on the parent character), and can artificially inflate support for particular clades, and hence affect overall tree topology. This situation is hard to avoid when selecting characters across a range of fossils, which include taxa with unusual or differing morphologies. In analyses of nucleotide data the situation is different, because gaps may be the result of shared deletions from an ancestral sequence and hence be informative. (Mounce&Wills2011, Liuetal2011)

"Garbage in, garbage out": self-explanatory phrase borrowed from computer programming. If the characters used in phylogenomics (and cladistic analysis in general) are unreliable, even the most accurate tree reconstruction method can fail. Therefore, methods focusing on the most reliable characters have been developed in order to reduce the impact of inconsistency. (Delsuc et al 2005)

Genealogy: Term derived from Greek γενεά, ***genea***, "generation"; and λόγος, ***logos***, "explanation". The study of families and the tracing of their lineages and history. Genealogists use oral traditions, historical records, genetic analysis, and other records to obtain information about a family and to demonstrate kinship and pedigrees of its members. The results are often displayed in charts or written as narratives. In evolutionary thought, such as cladistics, due to the alternate translation of γενεά as "race" the term can be used as a synonym for phylogeny. (from Wikipedia, Perseus Digital Library, revised RFVS111126)

Genetic Algorithms: Computational systems based upon an implementation of natural selection as an algorithm for classification or optimization. (W. R. Elsberry - talk.origins)

Genus: The taxonomic rank between family or tribe and species, and used to define group of closely related organisms that differ in only very minor ways. In the Linnaean system of binomial nomenclature, the genus is written in italics, with a capital letter, in front of the species name, or on its own. e.g. with ***Tyrannosaurus rex***, the name ***Tyrannosaurus*** is the genus, and ***T. rex*** (no hyphen!) is the species. Used in evolutionary systematics; in cladistic classification every genus is only allowed two species (because of excessive formalism regarding cladogenesis), and Linnaean genera are always oversplit and new names created, resulting in much taxonomic confusion (for example in paleontology the established dinosaur genus ***Iguanodon*** has been split into about a dozen different monospecific genera (link). See also the discussion at Sauropod Vertebra Picture of the Week. It may be that the Phylocode will discard binomial nomenclature altogether (although there is obvious resistance to this). **More** (MAK).

Ghost lineage: in cladistics, a phylogenetic lineage that is inferred to exist, for example by matching a cladogram against geological time, but is not known from the fossil record.

> When we know that two taxa are sister taxa (descendants of the same recent common ancestor), we in essence know that they originated at the same point in geologic time - the time of their last common ancestor and the speciation event that gave rise to them. Say we know one of these taxa from 100 million year old rocks, and the other from 90 million year old rocks. Even without seeing a fossil, we know that the second group must have representatives dating back at least to 100 million years, simply from its sister-taxon relationship with the other. A lineage like this, whose existence can be inferred from the cladogram, but which is not known from actual fossils is called a ***ghost lineage***. The examination of ghost lineages should allow biostratigraphers to refine their models of the stratigraphic ages of organisms.

- John Merck

Ghost lineages are a sign of low stratigraphic congruence. Although ideally the most elegant phylogenetic hypothesis would be the one that has the least ghost lineages, parsimony and morphology-based cladistics, in reducing the number of homoplases, tends to multuiply the number of ghost lineages (this is especially in the case of cladistic literalism and phylopessimism). Stratocladistics is the opposite, it emphasises reducing the number of ghost lineages even if that means increasing the number of homoplasies. (Levinton 2001 pp.76-8). **Links:** UCMP, evowiki, Dave Hone's Archosaur Musings MAK130318

Grade: a paraphyletic evolutionary group showing similarities in morphology, ecology or life history; a horizontal taxon consisting of transitional forms between two other taxa. (MAK). In alpha taxonomy, a grade refers to a taxon united by a level of morphological and/or physiological complexity. The term was coined by British biologist Julian Huxley, to contrast with clade, a strictly phylogenetic unit. (Wikipedia)

Gradism; Gradistics: as used here, the opposite (or complement) of cladistics; understanding phyloigeny in terms of evolutionarey tramnsformation and ancestor-descendent relationships. Includes the evolutionary systematics of .

Great chain of being: metaphysical premise, popular from the classical world until the early 19th century, that all beings constitute a single continuous series of forms in an unbroken gradation from God through countless intermediate spiritual and material stages to formless matter. Also used more profanely to justify feudalism, the Church, etc. With the development of naturalistic theories of evolution, representations of the great chain of being were replaced by phylogenetic trees and secular cosmology. Nevertheless the meme of great chain of being remains popular outside science, including philodsophical and pop cultural refernéces to "ascent". See also The March of Progress. **More** (MAK)

H.

Hapantotype: (Zoological Code) for protists with complex life cycles (such as ***Apicomplexa***), a series of specimens taken from different stages of the life cycle acting as the type. Though composed of multiple specimens, a hapantotype series is treated as a single holotype, and a lectotype may not be designated from within it. Should a hapantotype turn out to contain specimens from more than one species, specimens may be excluded from it until only conspecific ones remain. CKT061027

Heterotachy. Variation in the evolutionary rate of a given position of a gene or protein through time. Can lead to phylogenetic reconstruction artefacts where unrelated taxa have converged in their proportions of invariable sites. Unlike other types of bias, heterotachy does not leave any evident traces in sequences, and therefore are particularly difficult to detect. (Delsuc et al 2005)

Holotype: in taxonomy, a single specimen (or illustration for the Botanical Code) designated by the author in the original publication. Under the Zoological Code since 1999, any species description that does not explicitly designate a type is deemed invalid, and the species name a ***nomen nudum***. CKT061027

Holophyletic, Holophyly: Ashlock 1971 coined the term to resolve the ambiguity between the Haeckelian (evolutionary systematic) and Hennigian (phylogenetic systematic, cladistics) definitions of monophyly, and that usage is followed here. Refers specifically to the definition that a group contains the common ancestor, all organisms descended from the common ancestor, and no other organisms. The term has not gained widespread acceptance in the scientific community, probably because monophyletic is so widely used and has the same meaning. (MAK, Wikipedia)

Homology: shared characteristics inherited from a common ancestor, synapomorphies. A big problem in cladistics is distinguishing genuine homologies from homoplasies (pseudo-homologies). Very often either or both statistical algorithm-based cladistics and molecular sequencing reveal that what were unanimously considered homologies in early cladistic analyses are actually homoplasies. More. MAK130318

Homonym: One of two or more scientific names that are identical but pertain to different organisms, e.g., ***Eriococcus mancus*** Ferris, 1955 and ***Eriococcus mancus*** (Maskell, 1897); ***Onceropyga*** Ferris, 1955 and ***Onceropyga*** Turner, 1904. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Homoplasy: parallel evolution, convergence, the occurance of common sets of characteristics, what appear to be synapomorphies (homologies), in organisms that are similar and appear to be related but are not. The bane of phylogenetics. More. MAK130318

Horizontal classification: as described by Simpson, , a taxon based on overall similarity between its members at a particular time. All members share a common ancestry and are therefore monophyletic at that time slice, however, only the members extant at that particular time are considered. An evolutionary grade. Evolutionary systematics includes the interplay of both horizontal and vertical classification, whereas cladistics only considers vertical. (MAK) **More**

Hypothetical common ancestor: it is necessary to distinguish between cladistics and evolutionary systematics, as the two tend to confused in a sort of mishmash in the popular imagination and on some Wikipedia diagrams. In contrast to the evolution trees (spindle diagrams and so on) that evolutionary taxonomists use, cladograms are not intended to portray ***actual*** phylogeny. i.e. a cladogram does not have a time axis, and it does not portray ancestors, but only branching patterns, that is, sister relationships between terminal taxa and other nodes. This means that the internal nodes that lie at the base of each nested clade do not represent an actual species which can be described in terms of traits and characters, but rather a hypothetical and abstract representation of the common ancestor of that particular clade. (MAK)

I.

International Code of Zoological Nomenclature: widely accepted convention in zoology that rules the formal scientific naming of organisms treated as animals. The rules principally regulate:

1. how names are correctly established in the frame of binomial nomenclature,
2. which name has to be used in case of conflicts among various names,
3. how names are to be cited in the scientific literature.

The rules and recommendations have one fundamental aim: to provide the maximum universality and continuity in the scientific naming of animals. The code is published by the ***International Commission on Zoological Nomenclature*** (ICZN), an organization dedicated to "achieving stability and sense in the scientific naming of animals". The rules in the Code determine what names are valid for any taxon in the family group, genus group, and species group. It has additional (but more limited) provisions on names in higher ranks. Several cladists have argued that the Linnaean based ICZN code needs to be replaced by a new cladistically-based system, the Phylocode. (Wikipedia)

Incertae sedis: A taxon of uncertain identity, classification, or phylogenetic relationship. MAK

Infrasubspecific: category or name of lower rank than subspecies, and, therefore not subject to regulation by nomenclatural Codes; e.g. form, race, variety. (Glossary of taxonomy (Doc))

Intuition: in this context, arriving at a scientific (or any creative) hypothesis through a leap of insight. For example, Einstein discovered Special Relativity by imagining what it would be like to ride on a photon. From another perspective, gut-feelings, hunches, creativity, and more. See also art. In systematics, advocates of Phenetics and Cladistics argue on pragmatic grounds that evolutionary systematics should be rejected because it is too "intuitive", and not sufficiently verifiable. However their use of quantitative empirical data without intuition meant they were not able to distinguish homology from homoplasy. Hence all science will always include some intuition and subjectivity. (MAK)

Isotype: (Botanical Code) a specimen deriving from the same individual as the holotype (for instance, a second cutting from the same tree). CKT061027

J.

Jackknife Value: (***to be added***)

Junior synonym: giving a new name to a species, supra-specific taxon, or clade which already has a scientific name. As a standard, the first applied name is the one that is used in biological and paleontological systematics. Junior synonyms are redundant and hence usually rejected in scientific nomenclature; the exception being when the more recent name is so well known that to change it would cause confusion. For example, the first named fossil which can be attributed to ***Tyrannosaurus rex*** consists of two partial vertebrae found by Edward Drinker Cope in 1892 and named ***Manospondylus gigas***. It was only later realised that they belong to the same animal. In this case, the newer name, ***Tyrannosaurus rex*** (named by Henry Fairfield Osborn in 1905) was retained, and the older one ***Manospondylus gigas***, rejected. If there are only two synonyms, the most recently described one is the junior synonym; if there are more than two synonyms, the junior synonyms are all but the oldest described one which is the senior synonym. (MAK, Wikipedia, ScaleNet - Terms Pertaining to Zoological Nomenclature)

Junior homonym: If there are only two homonyms, the junior homonym is the most recently described homonym; if there are more than two homonyms, the junior homonyms are all but the oldest described homonym which is the senior homonym, e.g., ***Eriococcus mancus*** Ferris, 1955 is the junior homonym and ***Eriococcus mancus*** (Maskell, 1897) is the senior homonym. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Justified emendation: An emendation that is correct according to the International Code of Zoological Nomenclature, e.g., the name ***susani*** is proposed as a patronym for a woman named Susan; according to the Code the name must be changed to ***susanae***and is a justified emendation. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

K.

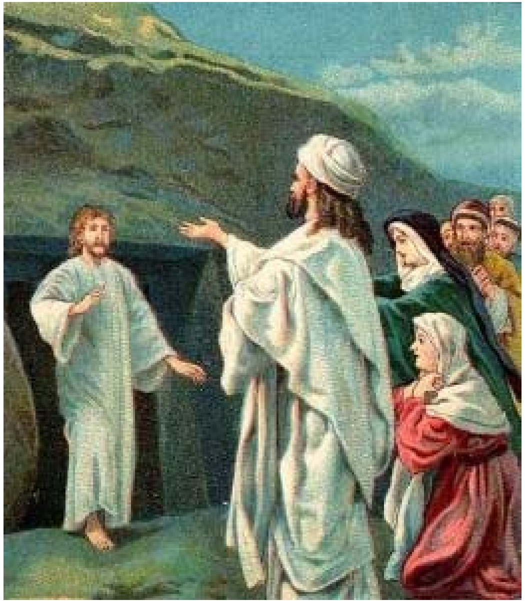
Kingdom: In the Linnaean classification the highest taxonomic rank. Traditionally only included plants and animals; Whittaker-Margulis classification scheme adds three more kingdoms, and other researchers such as Thomas Cavalier-Smith have added additional kingdoms.

L.

Lapsus calumni*:** (abbrev. ***l.c.) slip of the pen, an accidental mispelling; especially common with some of those difficult latin names. e.g. ***Poecilopleuron, Poecilopleurum, Poicilopleuron***, and ***Poikilopleuron*** are all mispellings of the Jurassic theropod ***Poekilopleuron***. MAK120227

Last (or Latest) Common Ancestor (LCA) the most recent common ancestor of any two (or more) species, which is another way of saying it is the earliest member of a particular clade that includes those species but not more distantly related species. So there are still earlier ancestors, and they would also be common ancestors, but they would include other taxa as well as those being studied, and would stand at the base of a more inclusive clade. e.g. the most recent common ancestor of a dog, a cow, a human and a chimpanzee (Boreoeutheria) is also the common ancestor of a human and a chimp (Hominidae), but it isn't the most recent one (it lived much earlier and evolved into far more groups of animals). Therefore, to limit study to the group or clade under consideration, only those members in that clade, and their most recent (not oldest) common ancestor is considered. (MAK120318)

Lazarus taxon: a taxon that disappears from one or more periods of the fossil record, only to appear again later. An example is



Lazarussuchus, an Oligocene member of a clade of freshwater reptiles (Choristodera) thought to have gone extinct at the end of the Mesozoic. As ***Lazarussuchus*** is thought to be outside the clade including other choristoderans, it may indicate a ghost lineage going back to the Late Triassic, a span of over 170 million years. There are also examples of "Burgess Shale type fauna", best known from the Early and Middle Cambrian periods, but which, since 2006, have been found in rocks from the Ordovician, Silurian and Early Devonian periods, in other words up to 100 million years after the Burgess Shale (Kühl et al 2009; Siveter et al 07). The term "Lazarus taxon" refers to the account in the Gospel of John, in which Jesus raised Lazarus from the dead. Lazarus taxa are observational artefacts that appear to occur either because of (local) extinction, later resupplied, or as a sampling artefact. If the extinction is conclusively found to be total (global or worldwide) and the supplanting species is not a look-alike (an Elvis species), the observational artefact is overcome. The fossil record is inherently imperfect (only a very small fraction of organisms become fossilized) and contains gaps not necessarily caused by extinction, particularly when the number of individuals in a taxon becomes very low. If these gaps are filled by new fossil discoveries, a taxon will no longer be classified as a Lazarus taxon. A subtle difference is sometimes made between a "living fossil" and a "Lazarus taxon". A Lazarus taxon is a taxon (either one species or a group of species) that suddenly reappears, either in the fossil record or in nature, while a living fossil is a species that (seemingly) hasn't changed during its very long lifetime. Sometimes however, the two are confused or conflated, as with the coelacanth, which is also called a "living fossil" because it was thought to be extinct for tens of millions of years, but then discovered alive. (modified from Wikipedia)

Lectotype: a specimen selected from a syntype series to become the single name-bearing type of the species in order to confirm the identity of the species. The other previous syntypes become paralectotypes. CKT061027

Length: The length, or number of steps, is the total number of character state changes necessary to explain the relationship of the taxa in a tree. According to the principle of parsimony, the fewer number of character state changes required, the more likely the tree. A tree with a lower length has less homoplasies and so fits the data better than a tree with a higher length. The tree with the lowest length assumes fewer homoplasies and hence is more parsimonious, and so represents the hypothesis of taxa relationship that is selected. Lipscom 1998

Linnaean classification: hierarchical taxonomy developed by the 18th century Swedish botanist Carl von Linné, (Linnaeus). It was the first systematic classification of life on Earth, in which every species is given it's own binomial designation. So for example anatomically modern human beings are ***Homo sapiens***, genus (the "family name") ***Homo*** and species (the specific name) ***sapiens***. In contrast, Neanderthal man is ***Homo neanderthalensis***. Linnaean classification provides a nested hierarchy of levels, each with its own specific characteristics. In this way any organism or species is grouped more and more specifically within the hierarchy. The Linnaean system was originally static, being based on creationism. In the 19th century, applied to the evolution of life and the modern synthesis it became evolutionary systematics, and was used to construct phylogenetic trees. Still foundational to modern biology, Linnaean classification is in the process of being superseded by phylogenetic hypothesis-based cladistic systematics. This latter, with its indefinite series of nested clades, lacks the categorical simplicity and ease of use of the old Linnaean system. Some attempts have been made to integrate the two, but the incompatible methodologies mean that so far these have not been very successful. **More** (MAK)

Long branch attraction (LBA): A phenomenon in molecular phylogenetic analyses, especially those employing maximum parsimony. Unrelated species or lineages sharing rapid evolutionary rates are artefactually grouped together and hence considered closely

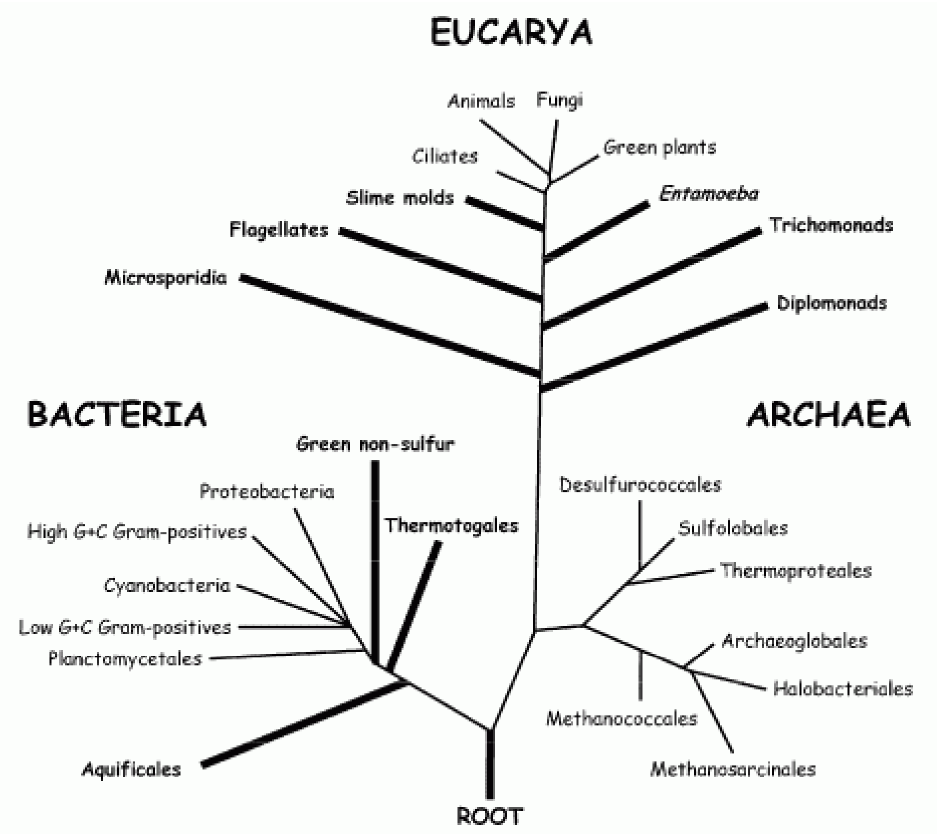


Diagram from Gribaldo & Philippe 2002. "The classical view of the universal tree of life, topology inspired from Stetter 1996, mainly based on rRNA comparison. Branches that could be affected by long branch attraction artefacts (e.g., the placement of the root in the bacterial branch or the early emergence of hyperthermophilic taxa amongst bacteria) are given as thick lines."

related, regardless of their true evolutionary relationships. In other words, unrelated lineages may group on the basis of convergent changes rather than homologies, the long branches being attracted to each other because of chance similarities. For example, in DNA sequence-based analyses, the problem arises when sequences from two (or more) lineages evolve rapidly. For example, rRNA evolutionary rates may vary by a factor of 100 among planktonic foraminifers. As there are only four possible nucleotides, when DNA substitution rates are high, the probability that two lineages will evolve the same nucleotide at the same site increases. When this happens, parsimony erroneously interprets this homoplasy as a synapomorphy (i.e., evolving once in the common ancestor of the two lineages). In phylogenies rooted by a distant outgroup, unrelated fast evolving ingroups will emerge independently as the deepest offshoots, being attracted by the long branch of the outgroup. LBA artefact currently represents a major concern to phylogeneticists, as it is believed to affect the position of virtually every deep-branching lineage. As a result, many organismal relationships in the universal tree, shown as bold lines in the diagram on the right, should be regarded as suspect (note: this particular topology has since been corrected by more recent revisions) This problem can be minimized through improved models of sequence evolution and by using methods that correct for multiple substitutions at the same site, through increased or modified taxonomic sampling and by breaking up long branches adding taxa related to those with the long branches or by using alternative slower evolving traits. Long branche attraction is also a problem with morphology-based cladistics because each branch may have so many unique modifications that tracing shared (ancestral) conditions may be difficult. (Wikipedia, Gribaldo & Philippe 2002, Delsuc et al 2005, Edgecombe 2009))

LUCA (Last Universal Common Ancestor): Also ***Universal Common Ancestor***. The postulated most recent common ancestor of every living thing on Earth; the root of the tree of life. According to Carl Woese, horizontal gene transfer between the three domains early in the history of life makes the idea of a single common ancestor meaningless. **More**

M.

Majority rule consensus: in cladistic analysis, a consensus method that preserves all relationships appearing in 50% of the source trees. This method allows a group to appear in the consensus even if some of the trees in the set contradict it, as long as a majority of the trees (generally half or more) support the grouping. In fully resolved majority rule consensus, these can appear in the consensus solution so long as they do not contradict relationships that occur more frequently. When comparing only two trees, this method is equivalent to the strict consensus method. (Bininda-Emonds, 2004 - glossary, from the PAUPDISPLAY Manual)

Matrix: tabulated data of the characters of all of the taxa used in a cladistic analysis, arranged in rows (taxon) and columns (character). "0" indicates that a character is absent, "1" that it is present. If there are more than one possible character states, these are inicated by further numbers, such as 2 or 3(very rarely more). if the character state is not known (common in the case of fossils, epsceially fragmentary ones), a question mark is used instead. The tabulated data is used to form phylogenetic hypotheses, which can be diagrammatically represented as cladograms. MAK120227

Maximum likelihood: In phylogenetics, one of several criteria that may be optimised in building trees (phylograms or cladograms) from molecular sequence or morphological data. The maximum-likelihood method is a form of likelihood analysis that is a seemingly more powerful (and computationally intensive) parametric statistical technique than maximum parsimony, that uses an explicit model for character evolution and therefore is not subject to the same pitfalls of homoplasy and long branch attraction. Maximum likelihood will pick the most tree that seems the most likely (hence the name) to explains the observed data. The optimal tree is the one that maximises the statistical likelihood that the specified evolutionary model produced the observed character-state data; the models specify the probabilities of character-state changes through evolutionary time. Compare with distance, parsimony. (Michael D. Crisp - Introductory glossary of cladistic terms; Nobu Tamura - Paleoexhibit)

Maximum parsimony: see parsimony

Molecular clock: the premise that the rate at which mutational changes accumulate is constant over time. The difference between the form of a molecules in two species is then assumed to be proportional to the time since the species diverged from a common ancestor, and molecules can be used to date the tree of life. In the late 1960s, the neutral theory of molecular evolution provided a theoretical basis for the molecular clock, though both the clock and the neutral theory were controversial, since most evolutionary biologists held strongly to panselectionism (Adaptationism), with natural selection as the only important cause of evolutionary change. (Wikipedia, etc). Although subject to certain caveats and continuing debate, the notion of the molecular clock has proven to be an important and useful tool in many contexts Searls, 2003 glossary The tendency now is to calibrate the molecular clock by the fossil record (Donoghue & Benton 2007). Earlier problems associated with this method for example, the evolution of animal phyla during the Precambrian (early in the Proterozoic (ref), for which there is absolutely no fossil evidence) have since been largely rectified. Even so, it is difficult to believe that the molecular clock rate does not vary greatly at particular times, for example accelerating during periods of rapid evolutionary radiation (the Cambrian explosion in this example). In other instances evolution may be more constant, and molecular clocks more reliable. The choice of molecule used may also be significant (reference to be included). (MAK)

Molecular phylogeny, Molecular systematics: Use of data from informational macromolocules (DNA, RNA, and/or proteins) as characters for phylogenetic analyses in order to map out the evolutionary tree of life. That is, the use of the structure of molecules to gain information on an organism's evolutionary relationships. Includes methods based on overall similarity (Phenetics), like electrophoresis, immuno-distance and DNA-DNA-hybridisation, as well as methods that are based on parsimony, like restriction-site-analysis and sequencing sequencing). Generally speaking, the more closely related two organisms are, the more similar their gene sequences will be. By statistically comparing the similarities and differences in the sequence between the same gene from various organisms, we can deduce the pattern of how those organisms are related, and shown in a phylogram. Despite the similarities (both involve dichotomous branched trees), these are not cladograms. Over the last decade or so, molecular phylogeny has supplanted morphology-based cladistic as the primary way of understanding the evolution of life on Earth, giving rise to phylogenetics, the synthesis of molecular phylogeny and cladistics, based on a total evidence approach and supermatrix trees. (MAK) **More**.

Molecules: short for molecular sequencing or molecular phylogeny, and hence any resulting phylogenetic trees that may be derived from this methodology. Frequently contrasted with traditional cladistic morphology-based approaches. Although molecular phylogeny has become the default paradigm in phylogenetics, there is the tendency now towards incorporating morphological data as well in cladistic phylogenetic analyses MAK130414

Monophyletic, Monophyletic group, Monophyly: Originally coined by Haeckel to refer to a group of organisms that is descended from its most recent known or inferred common ancestor (Haeckel, 1866). A monophyletic group in this traditional sense of the word may include all or only a part of the descendants of the common ancestor, and the ancestor may be a taxon of various ranks (Mayr & Ashlock, 1991, Grant, 2003). Hennig (1966) restricts "Monophyly" to the only those groups in which no descendant is a part of any other group. Here monophyletic refers to a group containing all the inferred descendants of a common ancestor. Ashlock 1971 1974 proposed replacing Hennig's redefinition of monophyletic with the neologism holophyletic, but this suggestion has not widely caught on, and Hennig's terminology remains the most popularly accepted and indeed currently standard usage in the the scientific community. (MAK) **More**

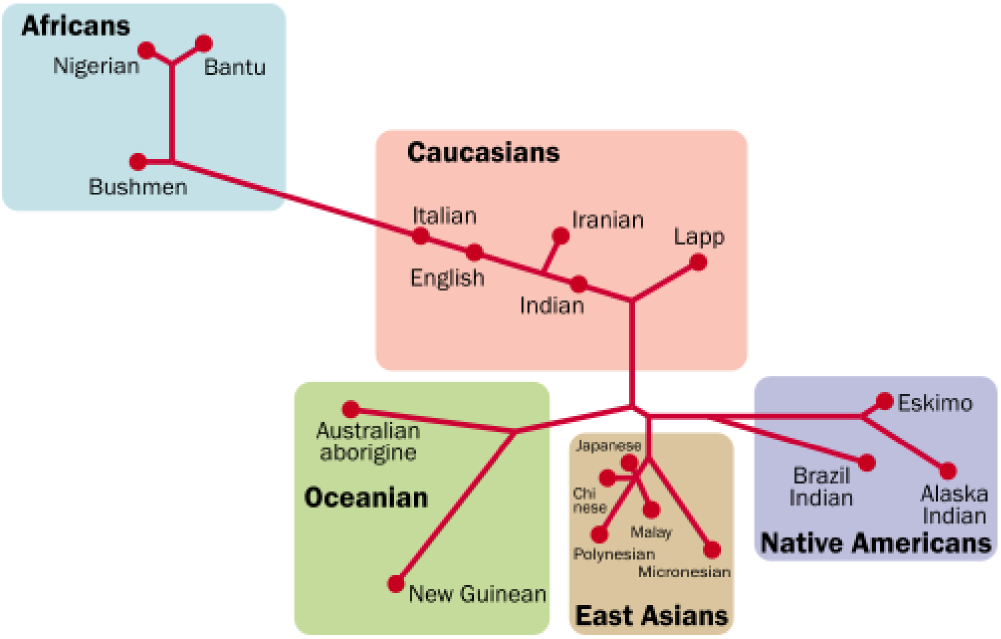
Monotypic: in Linnaean classification, a higher ranked taxon that contains only a single species. e.g. ***Ginkgo*** is a monotypic genus that contains a single extant species, ***biloba***; the family Ginkgoaceae is similarly a monotypic family. In cladistics (and especially vertebrate paleontology), allowing only the type species in that genus; all other species are given their own genera. This is in keeping with a phylocode approach (which rejects supra-specific taxa such as genera, families, phyla etc), and understandable especially when dealing with fossil taxa where there is only very limited information (sometimes all that is known of a species are a few scraps of bone) and phylogenetic placement is uncertain.

Morphology: [1] The gross form and structure of an organism, or of a part of an organism. In paleontology and phylogenetic analysis may refer to the form or structure of a particular bone or shell, and its comparison with that of similar species; phenomic traits. **[b]** Short for ***Morphology-based phylogeny*** (see next entry), and also referring to any resulting phylogenetic trees that may be derived from this methodology. One of the two rival phylogenetic methods currently in use , the other being molecular phylogeny. Although the latter has become the default paradigm (e.g. phylogenetics), here at ***Palaeos*** we have also given equal weight to morphology-based approaches. Morphology-based phylogeny is more or less synonymous with traditional cladistics, newer total evidence cladistic approaches also incorporate molecular sequencing data although the results may sometimes be a little strange (such as pleurodire turtles as highly derived crown group cryptodires) MAK120326

Morphology-based phylogeny: Infrequently used term (and mostly by molecular phylogenists) to refer to, yes, you guessed it, phylogeny based on morphology rather than molecules. Synonymous with traditional Hennigian (synapomorphy-based) and Computational (statistical) cladistics. The tendency now is for cladistic morphological analyses to incorporate molecular data, and morphology-based cladograms to be constrained by the branching order of molecular trees. It is generally now only with analyses using fossil taxa is morphology-based phylogeny retained in phylogenetics MAK130414

N.

Neighbor-joining: a bottom-up clustering method for the creation of phenetic trees (phenograms), created by Naruya Saitou and Masatoshi Nei. Usually used for trees based on DNA or protein sequence data, the algorithm requires knowledge of the distance between each pair of taxa (e.g., species or sequences) in the tree. (Wikipedia. It works something like this. Locate the pair of sequences that are the most similar, and treat this as a single avergaed pair. Match it with the next most similar and so on, to build up a tree of successive nested groups. Not as computation-heavy as other methods. However, because neighbour joining trees do not convey phylogenetic information they have been replaced by parsimony and likelihood statistical methods (Dawkins, 2004, p.134).



This genetic distance map made in 2002 is an estimate of 18 world human groups by a neighbour-joining method based on 23 kinds of genetic information. Public domain diagram by Jason Spatola, via From Wikipedia

Neotype: a new type specimen designated subsequent to the original description. A neotype can only be designated if a type was not originally designated (for species published before 1999), or if the original type(s) is lost or destroyed. In a very few cases in zoological nomenclaure (such as for ***Coelophysis bauri***) a neotype has been designated to replace an unidentifiable holotype - such an action, however, requires a Decision by the ICZN. CKT061027

New combination: When a species is transferred to a different genus for the first time. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Non- As phylogenetics does not allow the use of paraphyletic or ancestral taxa, it becomes difficult to refer to groups at the base of any evolutionary lineage. One way is to use prefixes like ***basal*** and ***stem***, but these can tend to fuzzy vagueness, e.g. "basal archosauria" is not a correct term for all "thecodonts" but only strictly speaking refers to the most basal node or taxon of clade Archosauria. In this context, stem would be more accurate, but seems to be less often used. Another method is to use ***non-***. For example, because the monophyletic clade Dinosauria includes not just dinosaurs but birds (because, cladistically speaking, birds are dinosaurs) dinosaurs as traditionally defined are not called dinosaurs but ***non-avian dinosaurs***. The ancestors of dinosaurs, such as lagosuchids and silesaurids, then become ***non-dinosaurian dinosauromorphs***. This problem does not arise in evolutionary systematics, which recognises and identifies ancestral groups. MAK120326

Numerical cladism: see Phylogenetic systematics.

Numerical taxonomy: same as phenetics; a method of generating phylogenies that is based on large numbers of quantifiable (measurable) characters which groups organisms with respect to overall similarity. (UCMP)

Node: any point in a cladogram where branches diverge or end. In cladistics, nodes of phylogenetic trees represent taxonomic units. Internal nodes (or branches) refer to hypothetical ancestors whereas terminal nodes (or leaves).***External nodes***, which are at the end of a each branch represent terminal taxa, generally extant species but where paleontological data is considered they can also include fossil species. ***Internal nodes*** are where a single ancestral lineage breaks into two or more descendant lineages. In rooted trees, internal nodes represent hypothetical common ancestors. (Modified from Douglas Theobald's Phylogenetics Primer and UCMP Understanding Evolution Glossary)

Node-based taxon (or clade): in phylogenetics and phylogenetic nomenclature, all descendants of the most recent common ancestor of two or more specified taxa. A phylogenetically based taxon that does not require determining the presence or absense of apomorphies. Generally defined as "The least inclusive clade that includes taxon A + taxon B". Compare with stem-based taxon. MAK120318

Nomen conservandum (abbreviation ***nom. cons.***, plural ***nomina conservanda*** � latin for "a name to be preserved") A nomen conservandum is a name that, under strict application of the appropriate code of nomenclature, should be invalid, but which the relevant commision has decided should be upheld in the interests of stability and communication. This may, for instance, involve the preservation of a well-known name for a taxon rather than its otherwise mandatory replacement with an unfamiliar or poorly-defined senior synonym. To what extent a name is conserved depends on the case - a name can be universally conserved, so that it takes priority over any non-conserved synonym, whether already known or recognised later, or it may only be conserved relative to the specific name(s) recognised in competition at the time.

For instance, the name ***Meganthropus africanus*** was established for a fossil hominid by Weinert in 1950. Later, this was synonymised with ***Australopithecus afarensis*** Johanson et al., 1978 within the genus ***Australopithecus***. As there is already an ***Australopithecus africanus*** Dart, 1925, A. afarensis was the correct name. However, some authors have suggested that ***Australopithecus afarensis*** should be removed from ***Australopithecus*** and placed in the genus ***Praeanthropus***. As the homonymy with ***Australopithecus africanus*** would then be removed, the technically correct name for the species would then be ***Praeanthropus africanus*** (Weinert, 1950). However, a request was made to the International Commission on Zoological Nomenclature for the preservation of the species name***afarensis*** (nomen conservandum) due to its high public profile, and to prevent confusion with the equally well-known ***Australopithecus africanus***. The ICZN upheld this request in 1999, meaning that even when placed in a different genus, ***Australopithecus afarensis*** remains ***afarensis***. CKT061016

Nomen dubium (abbreviation ***n. d.***, plural ***nomina dubia***) A nomen dubium (Latin, "doubtful name") is a taxon that has not been characterised in enough detail and whose type material is not sufficient for it to be identified. For instance, a number of dinosaur taxa named in the 1800s such as Trachodon were based on isolated teeth. Unfortunately, teeth in reptiles do not generally differ between species, meaning that fossilised teeth usually cannot be reliably identified to a particular species.

The significance of a taxon being declared a nomen dubium is often misunderstood. Contrary to popular belief, a nomen dubium is not invalid, in the way a nomen nudum is. A nomen dubium is still available for consideration in terms of synonymy and/or homonymy, and if a name previously regarded as a nomen dubium is able to identified with a better distinguished taxon that was named later, the nomen dubium is still the senior synonym, and hence the correct name for the taxon. One well-known example of this involves ***Allosaurus fragilis*** Marsh, 1877, which was suggested in the past as synonymous with ***Antrodemus valens*** Leidy, 1870, and ***Allosaurus*** appeared as ***Antrodemus*** in a number of older sources. However, ***Antrodemus*** is based on a single isolated tail bone, which is not sufficient to characterise the species. Allosaurus is currently regarded as a valid taxon, but this is because ***Antrodemus*** cannot be conclusively identified with it, not because ***Antrodemus*** is a nomen dubium. See New papers in Geobios (and nomenclatoral gripe) and follow-up messages on the Dinosaur Mailing List for an example of an argument on the appropriate application of a nomen dubium. CKT061027

Nomen nudum (abbreviation: ***n. n.***, plural ***nomina nuda***) A nomen nudum (Latin, bare name) is a name that fails to meet the requirements for being validly published under the appropriate code of nomenclature (for instance, no published description). A nomen nudum has no official nomenclatorial standing, and does not compete for synonymy, homonymy, etc. Should a name that was previously a nomen nudum ever be validly published, its priority dates from valid publication, not from original appearance.

In these days of the internet and widespread media, nomina nuda are sometimes a significant issue (especially in vertebrate palaeontology). It is not uncommon for significant and/or interesting discoveries to be popularised in newspapers, newsgroups, etc. before their appearance in the professional literature. Any names that appear in such formats are generally nomina nuda. CKT061016

Nomen oblitum (abbreviation ***n. o.***, plural ***nomina oblita***) A nomen oblitum (Latin, forgotten name) is one that is technically a senior synonym of another, more recent name, but which has been used little or not at all since its original publication, and which would cause confusion if resurrected. Under the International Code of Zoological Nomenclature, to qualify as a nomen oblitum a name must not have been used as valid since 1899, and the competing junior name must have appeared in at least 25 works by at least 10 authors in the immediately preceeding 50 years and over a period not exceeding 10 years. The term "nomen oblitum" has also been used in the past for names suppressed by the International Commission on Zoological Nomenclature. A name that remains in place due to its senior synonym being a nomen oblitum is called a nomen protectum. (see ICZN online for more details)

For example, the name ***Tyrannosaurus rex*** Osborn, 1905 is a junior synonym of ***Manospondylus gigas*** Cope, 1892. However, because of the obscurity of the name ***Manospondylus*** compared to the name ***Tyrannosaurus***, the former has been declared a nomen oblitum, and ***Tyrannosaurus rex*** remains the correct name.

Unlike the ICZN, the International Code of Botanical Nomenclature does not have any provisions for automatic rejection of an old name, requiring an action by the Commission for any name suppression. It is therefore not uncommon in botanical nomenclature for old names to be resurrected. CKT061016

O.

Order: In the Linnaean classification the taxonomic rank between class and family. Describes a major subgroup of organisms within a particular class; e.g. beetles (Order Coleoptera) within Class Insecta (or hexapoda) or lizards and snakes (order Squamata) within Reptilia. Orders are used in evolutionary systematics but not cladistics. (MAK) **More**

Overall similarity: method by which organisms that share the most similarities are grouped together; characters are not distinguished as to whether they are primitive or derived or whether they are evolutionary meaningful; also see numerical taxonomy (phenetics); contrast with phylogenetic systematics. (UCMP)

Outgroup: in phylogenetics, a taxon that is not part of the clade under consideration, but is including in the analysis in order to provide a baseline. In cladograms, outgroups are shown branching off at the base of the tree. (MAK)

P.

Paleontology: the study of ancient life, on thebasis of fossil or other remains. **More**

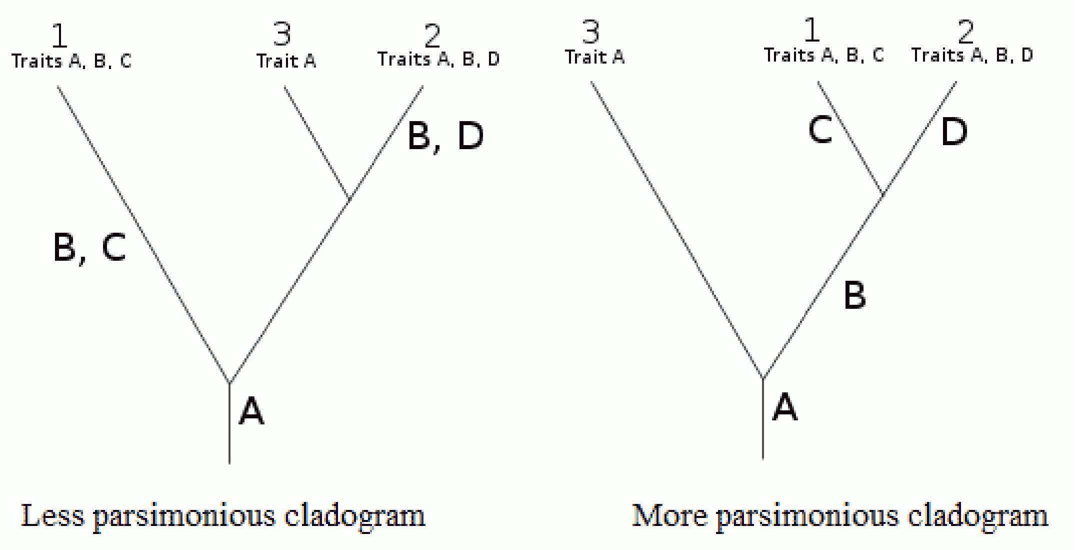
Pan-group, Total group: A crown group and its stem group considered together. The Pan-Aves thus contain the living birds and all (fossil) organisms more closely related to birds than to crocodiles (their closest living relatives). Pan-Mammalia are all mammals and their fossil ancestors down to the phylogenetic split from the remaining amniotes (the Sauropsida). Pan-Mammalia is thus an alternative name for the clade Synapsida. With the exception of a few taxa, such as turtles, the pan-group approach has not caught on because it results in unnecessary junior synonyms. (Wikipedia)

Paraphyly, Paraphyletic group: neologism coined by Hennig (Hennig 1966) to refer to groups that have a common ancestry but that do not include all descendants (Horandl & Stuessy 2010, p.1642). They constitute one of the two types of monophyletic groups ***sensu*** Haeckel ; e.g. protist, reptile (see that entry for diagram), thecodont, condylarth; i.e. an ancestral taxon or evolutionary grade. Constitute "a group of organisms that has descended from a common ancestor but that does not include all descendants from this ancestor. A paraphyletic group of species was holophyletic before a younger derivative species (or derivatives) arose from that group" (Horandl & Stuessy 2010, p.1643). Cladists consider paraphyletic groups invalid (see e.g. Paraphyly watch blog), whereas evolutionary systematics regard them as perfectly acceptable. (MAK) **More**

Paralectotype: In taxonomy, all of the specimens in the syntype series of a species or subspecies other than the l lectotype. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Paratype: In taxonomy, any specimens in the type series other than the holotype (or lectotype in the case of paralectotypes). Paratypes have no official status in determining species identity, but may have historical or practical significance (for instance, if the holotype does not show all the features useful in characterising the species). The term ***allotype*** is sometimes used for a paratype that represents the opposite sex from the holotype. CKT061027

Parsimony: Also known as Occam's Razor (after the medieval theologian William of Ockham (c. 1285-1349), who rejected the idea of universals) is the principle that recommends when choosing between two competing hypotheses, that the simplest explanation of the evidence or observation is to be preferred, when the hypotheses are equal in other respects. A central premise in cladistics, where computer algorithms routinely generate huge numbers of cladistic trees. When reconstructing the phylogenetic relationships of a group of species or taxa, the principle of parsimony implies that we should prefer the branching pattern or phylogeny that requires the fewest number of evolutionary changes (see diagram at right), whether morphological, molecular, or both. Under ***maximum parsimony*** algorithms, the preferred phylogenetic tree is the one that requires the least number of evolutionary changes to explain the observed sets of characters (or traits).



Use of parsimony in cladistics. It is considered more likely that trait B evolved only once (right hand cladogram) rather than twice (left-hand cladogram). Diagram adapted from Wikipedia.

The emphasis on parsimony dates back to the original hand-coded (pre-statistical algorithms) morphology-based cladistics of Hennig, and Hennigian paleontological cladists like Gauthier, Gaffney, and other early workers in the field who emphasised a small number of well-known synapomorphies as a way of constructing phylogenetic trees. Especially with molecular phylogeny, parsimony methods are particular vulnerable to long branch attraction. This is also the case with morphology-based phylogeny, when homoplasy, traits evolving at different rates, and phylogenetic incongruence come into the picture. It now seems that such factors are widespread if not endemic in the evolution of life, making dependence on parsiomony increasingly problematic. An example here is ***Archaeopteryx***, which is resolved as a non-avian deinonychosaur using parsimony-based alogorithms, but as a true bird using maximum likelihood computation (see e.g. Nobu Tamura - Paleoexhibit). The frequent incongruency between morphological and molecular phylogenies is another example, consider for example the Afrotheria which make no morphological sense. (MAK130316)

Pattern cladism, Transformed cladism: Dissenting Cladistic school, distinguished from phylogenetic or process cladism. Sometimes known as Cladists with a capital C (Williams and Ebach 2006). ***Transformed cladism*** is usually included here as well, although following Ebach et al 2008 they are given a separate entry. Founded by Gareth Nelson and Nelson Platnick ("New York Cladists") (Glossary of Phylogenetic Systematics - Günter Bechly although the latter is also associated with transformed cladism. (Ebach et al 2008). As with phenetics, character rooting and synapomorphies are not used, although monophyletic groups are acknowledged. Pattern Cladism asserts that a cladogram is merely a summary of shared characters, that could at best simply ***test*** a historical reconstruction (as a phylogenetic hypothesis), but reject the possibility that a real evolutionary history can ever be arrived at. Pattern cladistics no longer exists as an independent school, although its pragmatic empirical insights, such as cladistics as hypothesis testing, have been incorporated by mainstream cladistics

Phenetic species concept: A definition of a species as a set of organisms that are phenotypically similar to one another. Compare with biological species concept, phylogenetic species concept, ecological species concept, and recognition species concept. See other species definitions. (Fossil Mall glossary)

Phenetics, Phenetic systematics: School of numerical taxonomy that classifies organisms on the basis of overall morphological or genetic similarity. It was abandoned in favour of cladistics for a number of reasons, including numerous difficulties encountered owing to convergence (homoplasy, as individual characters assumed to be homologous were not carefully analysed), mosaic evolution, and a shortage of diagnostic characters. With the rise of molecular systematics, distance methods, which are basically phenetic methods, have become popular, although these are vulnerable to the same problems, especially that of homoplasy. **More**

Phenetic pattern analysis: very similar to Phenetics and generally synonymised, it uses numerical methods for taxonomic classification.

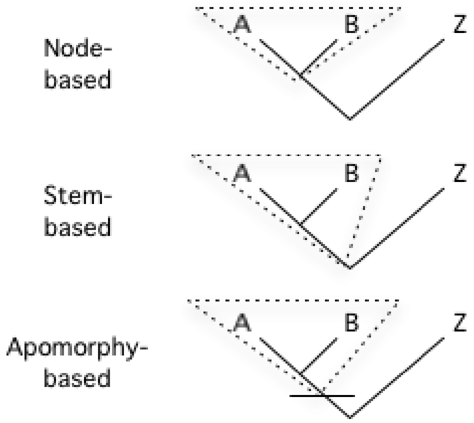
Phenetic Species Concept: phenetics-based definition that defines species as a set of organisms that look similar to each other andare distinct from other such sets (Ptacet & Hankison (2009)). Like phenetics, this is no longer used as it does not reference phylogeny

Phenogram: A branching diagram (tree) showing the phenetic similarity among terminal taxa. Compare cladogram, dendrogram, phylogram. (Michael D. Crisp - Introductory glossary of cladistic terms)

Phenomic: morphology -based character traits, as opposed to molecular traits. The tendency in the total evidence approach is to give equal weight to both. MAK130324

Phenotype: The set of measurable or detectable physical or behavioral features of an individual. The phenotype represents the expression of the genotype of the individual as modified by environmental conditions during the individual's ontogeny. (W. R. Elsberry - talk.origins)

Phylocode: abbreviation for the ***International Code of Phylogenetic Nomenclature***, a developing draft for a formal set of rules governing phylogenetic nomenclature. Its current version is specifically designed to regulate the naming of clades, leaving the governance of species names up to the rank-based codes. Unlike Linnaean-based nomenclatural codes the Phylocode does not require the use of ranks, although it does optionally allow their use. Rather than define taxa using a rank (such as genus, family, etc.) and a type specimen or type subtaxon, the content of taxa are delimited using a definition that is based on phylogenetic relationship and uses specifiers (e.g., species, specimens, apomorphies) to indicate actual organisms. The formula of the definition indicates an ancestor. The defined taxon, then, is that ancestor and all of its descendants. Thus, the content of a phylogenetically-defined taxon relies on a phylogenetic hypothesis. In the Phylocode, clades may be node-based, stem-based, or apomorphy-based (see diagram at right).



The theoretical foundation of the Phylocode was developed in a series of papers by de Queiroz and Gauthier, which was foreshadowed by earlier suggestions that a taxon name could be defined by reference to a part of a phylogenetic tree. The number of supporters for official adoption of the Phylocode is still small, and it is uncertain, as of 2011, whether the code will be implemented and if so, how widely it will be followed. (Wikipedia)

Phylogenetic analysis: See Phylogenetics

Phylogenetic bracketing: see Extant Phylogenetic Bracket.

Phylogenetic hypothesis: an empirical hypothesis regarding evolutionary relationships suggested through cladistic or other phylogenetic methods. Confusingly and despite the name, a phylogenetic hypothesis is not the same as phylogeny, does not purport to describe the actual course of evolution itself, complete with ancestor descendent relationships. Rather it is a stylised or abstract representation of this (usually in the form of a cladogram or similar), based on available data, with the proviso that this can and indeed is likely to change or even be radically revised with new data, discoveries, and analyses. (MAK120318)

Phylogenetic incongruence: when two equally persuasive, verified, robust, and empirically supported methodologies give contrary phylogenetic results. For example, using morphology, the soft shelled turtles (Trionychia) are the most derived group of cryptodires, whereas using molecules, they are the most basal group. The problem here is in deciding which, if any, of the two methodologies provides the more reliable phylogenetic signal MAK120326

Phylogenetic nomenclature (or classification, or taxonomy): classification and taxonomy based on cladistic (Phylogenetic systematic) principles ("vertical" ancestry, not "horizontal" similarity), proposed as a rank-free alternative to the Linnaean system of classification, redefining taxa previously named under evolutionary systematics (e.g. Synapsida), and accepting only monophyletic clades. The goal is to make classification synonymous with phylogeny; i.e. to get rid of similarity altogether. Phylogenetic nomenclature has led to a number of controversial proposals, such as the abandonment of Linnaean binomial nomenclature, the rejection Linnaean ranks, and the migration of established names to crown clades (Benton 2007, p.651); e.g. Tetrapoda (this last reflecting an emphasis on neontology over paleontology that is still found in cladistics). Despite the logical and theoretical appeal of this approach, there are still problems in applying it in practice (Carlson, 2001, p.1113). See also Phylocode. (MAK)

Phylogenetic signal: the amount of information, or "signal" that can be retrieved from the background "noise" of any phylogenetic analysis. It is only to be expected that the advocates of any particular methodological paradigm consider that their own methodology provides the clearest phylogenetic signal. Therefore, in the case of any phylogenetic incongruency between themselves and a rival methodology, their own paradigm is automatically to be preferred. Take the example of molecular phylogeny verses cladistic morphology. Morphology strongly supports a monophyletic Insectivora, based on a large number of unique shared characteristics, whereas molecular sequencing indicates homoplasy and divides the insectivores into two unrelated clades, placing them in groups for which there is no morphological support. Because molecular phylogeny has replaced cladistics as the default option for any analysis that includes extant (recent) taxa, unqualified support of phylogenies resulting from this methodology, despite still being problematic are the standard approach. The unspoken implication here is that molecular phylogney has a much higher and more reliable phylogenetic signal, and that morphology involves so many convergences and reversals as to make extracting any possible phylogfenetic signal almost impossible, without first being grounded in the molecular tree. Here at Palaeos we have tried to adopt a non-partisan approach incorporating all methodolgies, popular and unpopular, the only proviso being that be scientific, verifable, and found in earlier or recent scientific literature. MAK120326

Phylogenetic species concept: also Cladistic species concept: based on cladistics, this is a definition of a species as a lineage of populations between two phylogenetic branch points (or speciation events). The species is the smallest diagnosable cluster of individuals whithin which there iis a pattern of ancetsry and descent. But because most speciation is through budding rather than cladogenesis, this definition can be problematic. Compare with biological, cohesion, ecological, evolutionary, phenetic, and recognition species concept. (MAK)

Phylogenetic systematics: Also known as ***Hennigian systematics***, ***Numerical cladism***, ***Phylogenetic cladism***, and ***Process cladism***. Cladistic methodology that derives from Hennig's work and that of others such as James S. Farris, Walter Fitchand, and Herb Wagner. States that only shared derived characters can provide information about phylogeny. Those taxa that share a greater number of shared features are considered more closely related than those that don't. However, the shared characteristics have to be advanced (derived) rather than on primitive. The relationship between them is shown in a branching hierarchical tree called a cladogram. The cladogram is based on the principle that the fewest number of changes to map all the changes of character states is the most likely one; called the principle of parsimony. Only monophyletic groups are recognised. Unlike pattern cladism , which only aims at the calculation of most parsimonious cladograms from large data-sets, phylogenetic systematics also seeks to reconstruct phylogenetic schemes, in which all branching points are convincingly supported by characters, and using optimization (transformation series) (sensu Farris 1983) to select from a number of possible trees. (W. R. Elsberry talk.origins via W.J. Hudson; IAB blog, quoting Ebach et al 2008, Lipscom 1998, Günter Bechly, UCMP Understanding Evolution Glossary, and Wikipedia) **More**

Phylogenetic tree: See Tree.

Phylogenetics: A term derived from the Greek φῦλον, ***phulon***, "tribe", γενέτης ***genetēs*** "ancestor" and -ικός, ***-ikos***, an adjective-forming suffix. (Perseus Digital Library, Wiktionary) The synthesis of cladistics and molecular phylogeny, phylogenetics is the study of evolutionary relatedness among groups of organisms (e.g. species, populations). It analyses molecular sequencing and morphological data matrices, using statistical methods such as maximum parsimony, bayesian inference and maximum likelihood. This phylogenetic analysis is used to determine the most likely phylogeny that would correspond to an actual tree (phylogram or cladogram) of a particular shape. The tree represents the evolutionary history of a group. Phylogenetics has also begun to incorporate other fields such as evo-devo) which implies this is all leading to a new evolutionary synthesis (replacing the 20th modern synthesis). (Wikipedia, Dawkins, 2004, p.137-8, Telford & Budd 2003, MAK130414). See also Daniel F. Simola - Molecular Evolution and Phylogeny (pdf) for synoptic overview. **More**

Phylogenomics: catch-all label for the intersection between the fields of evolution and genomics. The use of cladistic principles to interpret genome data, and better understanding of gene function. One branch of phylogenomics involves the use of these data to reconstruct the evolutionary history of organisms. It considers molecular data from many genes, or even whole-genome approaches, rather than just a few specific genes, and using broad taxon sampling. Such studies have provided insights into the relationships of protostome phyla that were previously obscure, and allowed resolution of long-standing questions such as the relationships of Arthropoda and Onychophora and various trochozoan phyla. Another application, "Pharmacophylogenomics" is the use of phylogenomics in aid of drug discovery, through improved target selection and validation. (Giribet et al 2009, p.62, Delsuc et al 2005,, Searls, 2003, Wikipedia)

Phylogeny: A distrinction can be made between trhe scioence of phylogeny and phylogeny itself. The term was coined by Haeckel (Haeckel 1866) to refer to the science of the study of the family history of life, the evolutionary relationships among groups of organisms, often illustrated with a branching diagram called a tree. Phylogeny in itself therefore refers to the evolutionary history of a group through deep time; in other words, the evolutrionary tree of life. There are several different forms:

- Haeckelian/evolutionary systematics maps the inferred lines of descent of a group of organisms, in order to reconstruct the common ancestors of that group, map the amount of divergence among the descendants of the common ancestor, and explore the evolutionary history of a group of organisms (Mayr & Bock 2002 p.192). Evolutionary Systematics, which is highly phylo-optimistic, seeks to reconstruct the actual evolutionary history of a group, including the actual common ancestor (either an ancestral species or, more usually, supra-specific taxa), and, with the help of the fossil record, tracing the evolution from ancestor to descendants and from there to further descendants.
- Hennigian cladistics or phylogenetic systematics (Hennig (1950, 1966)) is the analysis of and relationship between monophyly taxa (clades), using shared unique characteristics (synapomorphies). Despite the name, phylogenetic systematics does not describe the actual evolutionary history of life, but rather the construction of phylogenetic hypotheses, represented graphically in the form of cladograms. It rejects the idea of an actual common ancestor a la Evolutionary Systematics, and instead posits a hypothetical common ancestor
- Molecular phylogeny is the use of molecular data (derived for example from DNA, RNA, and/or protein sequencing) for phylogenetic analyses. Generally speaking, the more closely related two organisms are, the more similar their gene sequences will be. By comparing the similarities and differences we can deduce the pattern of how those organisms are related. Because of the emphasis on empiric data it is less convcerned with testing rival hypotheses than cladistics is. However it shares with modern statsitical-based cladistics the emphasis on computer algoritrhms and a bifurcating tree of life.

Other approaches are possible too, for example developmental. In this way, phylogeny is used to understand the evolutionary history of life on Earth. (MAK130318)

More colloqually or informally, phylogeny is also shorthand for any phylogenetic hypothesis or phylogenetic tree (e.g. cladogram). (MAK)

Phylogeography: research field that investigates the principles and processes that govern the geographic distributions of genealogical lineages, especially those within and among closely related species. (Phylogeography)

Phylogram: A phylogenetic, molecular-based dichotomous branching tree that resembles a cladogram, although it differs in that the branch lengths are proportional to the amount of inferred (quantitatively measured) evolutionary change. Phylograms therefore convey more information than cladograms. Whereas cladograms only give information about the branching order and nothing else, phylograms also include information on the amount of change. Unlike chronograms they do not include stratigraphic range (unless one could draw them in three dimensions, like a hologram, perhaps), in a rooted phylogram evolutionary divergence takes the place of the time axis in a cladistic chronogram.

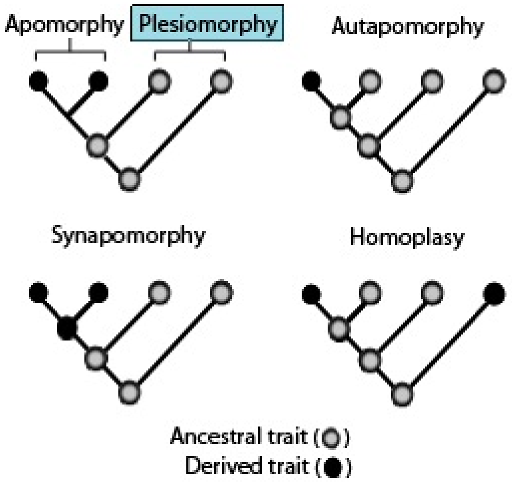
Phylo-optimism: the generally unspoken belief or premise held by some gradists that the fossil record, while admittedly incomplete, is still detailed enough to construct a reliable phylogeny or understanding of the path evolution actually took, as well as the characteristics of ancestral taxa and their descendants. Contrast with phylopessimism (MAK120318)

Phylopessimism: the generally unspoken belief or premise held by some cladists that the fossil record is so incomplete that we can never reconstruct a reliable or objective phylogeny; the best we can do is determine the most viable phylogenetic hypothesis using the incomplete data available to us; in this regard it approaches (or incorporates) pattern cladism. Phylopessimists do not consider stratigraphic congruence important, and emphasise ghost lineages as a way of filling in the gaps and pereserving parsimony. Contrast with phylo-optimism (MAK120318 130318)

Phylum: In the Linnaean classification the taxonomic rank between kingdom and class, and hence one of the highest levels of taxonomic classification, used to define major groups of organisms; e.g. molluscs, arthropods, echinoderms, chordates. Phyla can be thought of as groupings of animals based on a shared general body plan. What this means is that despite the seemingly different external appearances of organisms, they can be classified into phyla based on their internal and developmental organizations. Despite their obvious differences, spiders and barnacles both belong to the phylum Arthropoda; but earthworms and tapeworms, although similar in shape, belong to different phyla. Although Linnaean rankings are not used in cladistic analysis, the majority of phyla are still accepted as they constitute monophyletic clades. (There are a few exceptions; e.g. growing consensus on the basis of molecular phylogeny is that Porifera (sponges) constitute an evolutionary grade. The rank of Phylum was not in Linneaus' original classification system, but was coined later by Haeckel. (MAK, Wikipedia)

Plesiomorphy, Plesiomorphic trait: in cladistic analysis, an ancestral or primitive character state present before the last common ancestor of the species group evolved, and hence not unique to the clade in question. Also called a primitive trait.

> "Features shared more widely than in a group of interest. These are primitive for the group in question and cannot provide evidence for the group. An evolutionary trait that is homologous within a particular group of organisms but is not unique to members of that group (compare apomorphy) and therefore cannot be used as a diagnostic or defining character for the group. For example, vertebrae are found in zebras, cheetahs, and orangutans, but the common ancestor in which this trait first evolved is so distant that the trait is shared by many other animals. Therefore, possession of vertebrae sheds no light on the phylogenetic relations of these three species."



A Dictionary of Biology, Oxford University Press, © Market House Books Ltd 2000

Polarity: in phylogenetic cladistics this refers to the ordering of a particular character state, determined either independently of tree construction (direct method) or more usually from a rooted tree (indirect method) (Michael D. Crisp - Introductory glossary of cladistic terms) To quote Telford & Budd 2003 p.487: "In order for an analysis to be useful in an evolutionary sense, it needs to be rooted, in other words we need to know the polarity of change of the characters that interest us. If we consider two taxa in isolation (say a lizard and a mouse) that differ in a certain character (e.g. hairless or hairy) how do we know which of the two has the primitive character state and which the derived? ...(T)o determine the direction in which the evolution of this character has proceeded...knowledge of the state of the character in a species that is an outgroup (is needed)...in this case, a frog would be appropriate. As the frog is hairless, parsimony suggests that hairlessness is the primitive character and we can infer from this that hair has evolved in the lineage leading to mice after this lineage had diverged from reptiles." Polarity is one of the ways in which phylogenetic systematics is distinguished from non-phylogenetic ordering systems such as phenetics and pattern cladistics.

Polyphyly, Polyphyletic group: A group that does not share a common ancestor, but is defined on the basis of independently acquired or convergent (non-homologous) character states. Examples for polyphyletic groups would be the old taxon Pachydermata which includes the thick-skinned hippos, rhinos and elephants, or the taxon Haemothermia (endorsed at one time by Lovtrup and Gardiner) for a grouping of haemothermic birds and mammals. Polyphyletic groups are considered invalid by both evolutionary and phylogenetic systematics. (MAK, Glossary of Phylogenetic Systematics - Günter Bechly)

Polytomy: in a cladistic phylogeny, a node where more than two lineages descend from a single ancestral lineage. This indicates either that we don't know how the descendant lineages are related or the descendant lineages speciated simultaneously. Where a branching pattern cannot be resolved, the branches in question can be collapsed to show the absence of a hypothesis for the relationships among the lineages that they represent. (UCMP Understanding Evolution Glossary; Keeling & Palmer 2008 p.607).

Primitive trait: same as plesiomorphy; a character that is present in the common ancestor of a clade; a primitive trait is inferred to be the original character state of that character within the clade under consideration; compare to derived trait. (UCMP)

Process cladism: see Phylogenetic Systematics.

Pseudomonophyletic: neologism coined by MAK for an artefact of cladistic methodology (whether morphological or molecular or both) in which a taxon that appears to be a robust monophyletic clade in initial analyses, but is later shown to be a paraphyletic or polyphyletic taxon; e.g. Ceratosauria, Nyctiphruretia, Cyclostomata. Pseudomonophyletic taxa would seme to be the result of widespread reversals among ancestral (basal, stem, plesiomorphic, non-, select your preferred prefix) taxa. The loss of shared character traits among these primitive forms, and hence the absense of what should be plesiomorphic (shared primitive) traits in more derived taxa gives the appearance that the ancestral grade is a monophyletic clade. MAK120326

Q.

R.

Rank: the hierarchical level of a supra-specific taxon, according to the Linnaean approach to classification. The eight ranks are kingdom, phylum (added by Haeckel), class, order, family, tribe (used mostly in botany, much more rarely in zoology and paleontology), genus, and species, plus optional intermediate grades represented by the suffixes ***super***-, ***sub***- and ***infra***-. (In the three domain theory of Carl Woese and co-workers, a further rank, domain, is sometimes added above kingdom, although it seems to me that domain and kingdom are just different ways of approaching the same topic (like evolutionary and phylogenetic systematics)). The highest ranks are the most general, whilst each sub-division or rank adds it own increasingly specific and unique characteristics. In this way any organism or species can be grouped more and more specifically within the hierarchy. A central part of evolutionary systematics, according to which every taxon that evolves from another taxon has the same taxonomic rank. So class Reptilia would give rise to class Mammalia, not subclass Mammalia (although, Reptilia includes a number of subclasses, these are still part of the class Reptilia). Determining the appropriate rank is an art, not a mechanical process, and inevitably ranks don't always equate. e.g. the orders of modern birds are probably equivalent to families or superfamilies of fish or invertebrates. Ranks are strenuously rejected by mostcladists, although some paleontologists such as Michael Benton argues that cladistics and Linnaean ranks are not be incompatible. Moreover, ranks are useful in everything from field guides (compare the muddled organisation of taxa in Greg Paul's otherwise superlative ***Princeton Field Guide to Dinosaurs*** with the clear arrangement of ***Predatory Dinosaurs of the World*** from more than two decades earlier) to measuring the degree of biodiversity through time. (MAK)

Recognition species concept: - species defined as a set of populations that share a common fertrilisation or specific mate recognition system (Ptacet & Hankison (2009)). Basically a rewording of the biological species concept.

Relationship: the way two or more species or other taxa are evolutionarily and phylogenetically related on an evolutionary tree. In phylogenetics, two taxa may have a sister relationship, or one may be more basal or more derived than the other. In evolutionary systematics, one may be the ancestor of another, or they may share an actual common ancestor. (MAK120318)

Replacement name:A name that is assigned to replace a name that is a junior homonym, e.g., ***Onceropyga*** Turner, 1904 is the valid name and ***Onceropyga*** Ferris, 1955 is the junior homonym and must be replaced; Hoy (1963) proposed the replacement name ***Oregmopyga***. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Retention index (RI): Similar to the consistency index, but defined so that the highest possible value for any character is 1.0 and the lowest is 0.0; removes bias due to autapomorphies. (Michael D. Crisp - Introductory glossary of cladistic terms). The per-character retention index (ri) is defined as (g-s)/(g-m), where where ***m*** is the minimum possible number of character changes (steps) on any tree, ***s*** the actual number of steps on the current tree, and ***g*** is the maximal number of steps for the character on any cladogram (Farris 1989). The retention index measures the amount of synapomorphy on the tree, and varies from 0 to 1. (Øyvind Hammer - PAST - Paleontological Statistics Software)

Reversal: in cladistics, the loss of a character trait, or more technically, the evolutionary reversion from an apomorphic to a plesiomorphic character state. Compare with homoplasy.

Robust: a phylogenetic hypothesis or tree topology that is supported by a large number of character states and/or molecular sequencing results, and not destabilised through the addition of one or two phylogenetic steps hence can be considered reliable. MAK120326

Romerogram: A bubble diagram or spindle diagram that plots diversity (horizontal axis, width of bubble or spindle) against time (vertical axis), and showing the phylogenetic divergence of new groups from ancestral lineages. The changing width of the bubbles represents the increase or decrease in diversity or abundance of individuals and species of a particular taxon through time. Named after the great vertebrate paleontologist Alfred Sherwood Romer, who popularised the use of such diagrams. Disliked by cladists because of their use of paraphyletic taxa, although Michael Benton (Benton 2004) uses a modified version that emphasises monophyletic clades. (MAK111018)

Root: in phylogenetics, the common ancestor of all taxa represented in a cladogram or or phylogram. The root is often determined using an outgroup taxon to determine the evolution in the taxa of interest (Delsuc et al 2005). See also base node.

Rooted tree: A cladogram or phylogram with a hypothetical ancestor, which equates to the root. When outgroups are used, this is the node that connects the outgroups to the ingroup, and which thus specifies the direction of evolutionary change among the character-states. Contrast with unrooted tree. (Michael D. Crisp - Introductory glossary of cladistic terms)

S.

Scala Naturae: a Latin expression meaning "natural ladder", is a sort of proto-taxonomy first developed by Aristotle, according to which the natural world can be arranged in a single linear series from inanimate matter through plants, invertebrates, higher vertebrates, and finally man. Along with Plato's Principle of Plenitude it led to the idea of the Great chain of being. Scala Naturae and Great Chain of Being remained central ideas in natural philosophy until the mid 19th century. **More**

Semistrict consensus: also called "combinable component" consensus. If a particular grouping in one tree is not contradicted by the other trees, it will be retained in the consensus. When there is a conflict in grouping, semistrict consensus behaves like strict consensus. (from the PAUPDISPLAY Manual)

Senior homonym: In taxonomy, the oldest described homonym, e.g., ***Onceropyga*** Turner, 1904 is the senior homonym and ***Onceropyga*** Ferris, 1955 is the junior homonym. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Senior synonym: In taxonomy, the oldest synonym, e.g., ***Apiomorpha pharetrata*** Scharder, 1863 is the senior synonym and ***A. nux*** Fuller, 1896 is the junior synonym. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Sequencing: any of several methods and technologies that are used for determining the order of proteins in a cell, or nucleotide bases (adenine, guanine, cytosine, and thymine) in a molecule of RNA or DNA. An essential element in modern biological systematics (molecular phylogeny). The rapid speed of sequencing attained with modern DNA sequencing technology has been instrumental in the sequencing of the human genome (the Human Genome Project). Related projects, often by scientific collaboration across continents, have generated the complete sequences of many animal, plant, and microbial genomes. (Wikipedia)

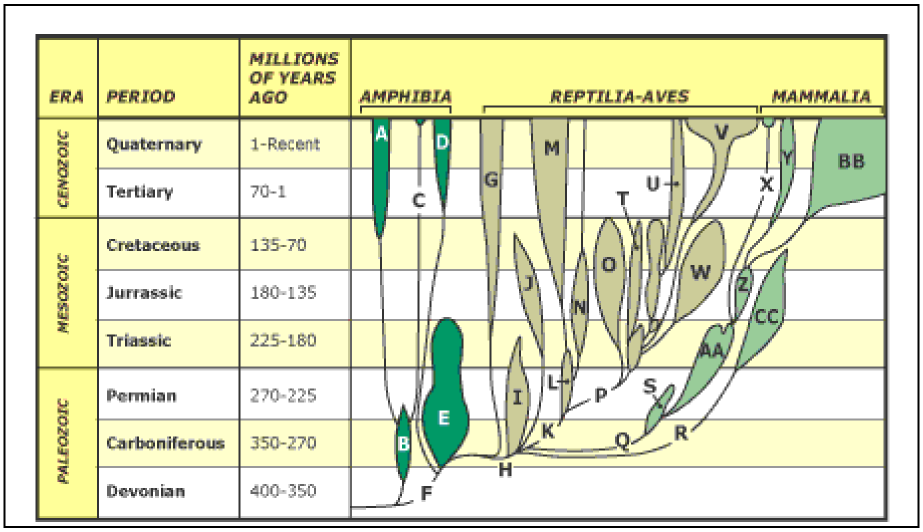
Similarity: the degree to which two or more species resemble or don't resemble each other is one of the two factors that could be considered in any biological classification and taxonomy, the other being phylogeny. Similarity could be the result of common descent and divergence (homology) or convergence (homoplasy). Pre-Darwinian natural philosophy considered only similarity (being unaware of phylogeny), evolutionary systematics gave equal weight to both, phenetics and pattern cladistics rejected phylogeny as impractical and thus revert to similarity only, whilst Hennigian cladistics and phylogenetic nomenclature goes to the other extreme and rejects similarity altogether, emphasising only phylogeny. (MAK)

Singly paraphyletic group: a group or taxon that is paraphyletic because one of its descendant lineages are not included. e.g. Class Amphibia is a singly paraphyletic group because amphibians evolved into reptiles. There are also doubly, triply and so on paraphyletic groups (MAK120318)

Sister group: Cladistic term for any of the descendant branches from a node on a cladogram. In a phylogenetic hypotheses, the descendants of an ancestor are called daughters, while the siblings after a speciation event are called sisters (so a descendant is a daughter relative to its ancestor and is a sister relative to its other sibling). Note that if either of the daughters undergoes further speciation then the sister to a particular terminal taxon may actually be a group of terminal taxa. (Michael D. Crisp - Introductory glossary of cladistic terms)

Species: The most fundamental unit of evolutionary biology, according to which one type of organism is considered a distinct type from another. This highly controversial term is given a variety of definitions by biologists. Currently, the Biological Species Concept (BSC) is widely popular: Groups of actually or potentially interbreeding populations, which are reproductively isolated from other such groups (Mayr 1963) . (W. R. Elsberry talk.origins via W.J. Hudson) Other definitions include the cohesion species concept, ecological species concept, evolutionary species concept, phenetic species concept, phylogenetic species concept, and recognition species concept. **More** MAK120227

Spindle diagram: A evolutionary tree that maps lineage diversity or abundance mapped against geologic time. They are called spindle diagrams because each lineage generally begins at a point, widens in the middle (representing increasing diversity over the course of millions of years), and then declines towards the top (representing the dwindling fortunes of the lineage in question). They are similar to modern chronograms (or clado-chronograms) except that they convey additional information in the form of the diversity and/or



abundance of each lineage at a particular time (as represented by the width of each "spindle". Spindle diagrams are employed in evolutionary taxonomy. They provide a purported map of actual phylogeny rather than a hypothesis, as they emphasise ancestral or paraphyletic groups, transitional forms, and the transformation of one group into another, showing where more recent lineages emerge from earlier ones. Also called a Bubble diagram or Romerogram. Cladistic formalism rejects the use of spindle diagrams. This doesn't mean that spindle diagrams are invalid or untrue, only that cladistics and phylogenetics speak a different language. MAK130409

The spindle diagram shown here is typical of mid 20th century phylogenies. This particular diagram which I found through Google image search is from an online creationist book (original url). The taxa correspond to orders, subclasses, or classes, in the Linnaean ranking. The caption reads: Fig. 20. Family tree of the vertebrates. On the left is a geological time scale. Phylogenetic origins of various groups of vertebrates. A) Urodela, B) Lepospondyli, C) Apoda, D) Anura, E) Labyrinthodontia, F) Apsidospondyli, G) Chelonia, H) Anapsida, I) Cotylosauria, J) Euryapsida, K) Diapsida, L) Eosuchia, M) Squamata, N) Rhynchocephalia, O) Ornithischia, P)Thecodontia, Q) Synapsida, R) Parapsida, S) Pelycosauria, T) Pterosauria, U) Crocodilia, V) Aves, W) Saurischia, X) Prototheria, Y) Metatheria, Z) Pantotheria, AA) Therapsida, BB) Eutheria, CC) Ichthyosauria. The width of the spindle shows taxonomic diversity, numeric abundance (the abundance of fossils of the group in strata of the particular geologic period), or both; the distinction here being often poorly defined. In an effort to introduce precision, spindle width may be drawn according to the number of genera or families known from a particular time period, but even determining what qualifies as a genus or family can be arbitrary (see splitters versus lumpers). Contrast this diagram with cladistic dendrograms and cladograms which show relationships between individual species, without referencing time, transformation, or evolutionary lineage. (MAK)

Splitters versus lumpers: Philosophical conflict among taxonomists, as regards ranking of a taxon. As the name indicates, splitters tend to divide varying individuals from a single species among several different species. Lumpers tend to include specimens or populations normally attributed to different species in a single species. The same principle can be applied at the supra-specific level. (MAK111018)

The earliest use of these terms was apparently by Charles Darwin himself, in a letter to J. D. Hooker in 1857. "(Those who make many species are the 'splitters,' and those who make few are the 'lumpers.')" They were introduced more widely by the biologist George G. Simpson in his 1945 work "The Principles of Classification and a Classification of Mammals." As he put it, "splitters make very small units �"-their critics say that if they can tell two animals apart, they place them in different genera... and if they cannot tell them apart, they place them in different species. Lumpers make large units - their critics say that if a carnivore is neither a dog nor a bear, they call it a cat." - Simpson 1945. (From Wikipedia)

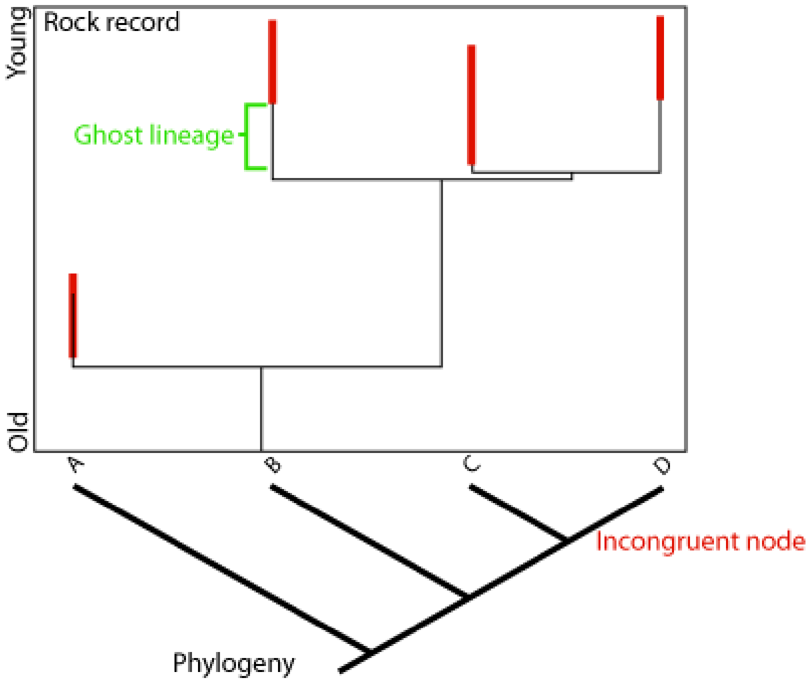
Stem: ancestral forms, species or taxa that constitute the trunk of an evolutionary tree rather than the later ramifications.

Stem-based taxon (or clade, or group): in phylogenetics and phylogenetic nomenclature, all species, living or extinct, that share a more recent common ancestor (or Last Common Ancestor - LCA) with a specified species than with other specied species or taxa. When only two species are refferd to it may be abbreviated to ***Anchor Taxon > Another taxon***. > is the mathematical symbol for "greater than", in this case it means more similar to. A Stem-based group is a phylogenetically based taxon that does not require determining the presence or absense of apomorphies. Compare with node-based taxon. MAK120318

Stem group: Not to be confused with stem-***based*** group (see above entry), the concept of stem group is used in phylogenetics to cover extinct evolutionary "aunts" and "cousins" of living groups. A crown group is a group of closely-related living animals plus their last common ancestor plus all its descendants. A stem group is a set of offshoots from the lineage at a point earlier than the last common ancestor of the crown group; it is a relative concept, for example tardigrades are living animals which form a crown group in their own right, but Budd 1996 and 2001 regarded them also as being a stem group relative to the arthropods. Stem group shown in yellow in this diagram. (Wikipedia). The distinction however between the stem- and crown group is an arbitrary one, because it is determined only by the most basal member of the crown group that is still extant; if ***Branchiostoma*** had gone extinct in the Pleistocene, or even the 15th century, our concept of the euchordate crown-group be radically different, because ***Branchiostoma*** lacks many features of higher chordates (Budd 2001 p.265).

Because cladistics has replaced evolutionary systematics, but does not include all of the concepts provided by the latter, there is a tendency for terms like stem and basal to be used not in their precise phylogenetic nomenclatural definitions but as rather vaguely applied alternatives to "ancestral" in recent paleontological literature and especially popularised accounts and comments thereof. MAK120318 120417

Stratigraphic congruence: also called stratigraphic consistency, the degree to which the terminal taxa that branch off of a cladogram match the order with which they first appear in the fossil record. A simple measure of stratigraphic congruence is the ***Stratigraphic Congruence Index*** (SCI) of Huelsenbeck (1994) is defined as the proportion of stratigraphically consistent nodes on the cladogram, and varies from 0 to 1. A node in the cladogram is consistent with trhw fossil record when the first occurrence of the taxa above it (daughter clades etc) are younger or equal in age to those below it (parent clades etc). Also when it is the same age or than the first occurrence of its sister taxon. (Levinton, 2001, p.76; Øyvind Hammer - PAST - Paleontological Statistics Software)

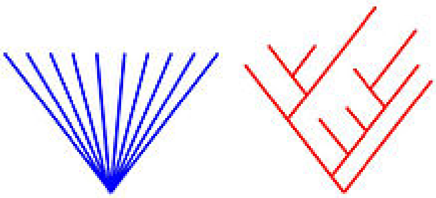


How do we identify ghost lineages and measure their prevalence in a cladogram. All other things being equal, we expect the terminal taxa that branch off of a cladogram first to appear first in the fossil record. When this is true, the cladogram is said to be stratigraphically congruent. Often, cladograms are not stratigraphically congruent. This happens when there are long ghost lineages. - diagram and caption by John Merck.

Stratigraphy: in the phylogenetic context, the chronological and stratigraphic order by which taxa appear in the fossil record, in this context refers to biostratigraphy, rather than stratigraphy as such. Here, the more primitive or ancestral form should always preceed the more advanced type of organism. So, for example, the protodinosaurs ("non-dinosaurian dinosauromorpha" to use the unwieldly cladistic definition) appear in the middle Triassic period, whereas their descendents the true dinosaurs only appear some ten or twenty million years later in the late Triassic. However the vagaries of the fossil record mean that not every evolutionary lineage is recorded, for this reason most cladists, apart from the rarely used stratocladistic approach, ignore stratigraphic sequence and fill in the gaps with ghost lineages. MAK120326

Stratocladistics: a method of making phylogenetic inferences using both geological and morphobiological data. It is similar to cladistics in emphasising parsimony and synapomorphies, but also incorporating stratigraphic information as well; in this way temporal data are used along with conventional character data and Bayesian logic to selecting most parsimonious hypotheses. (Fisher, 2008)

Stratophenetics: phylogenetic method based on (a) the identification of taxa based on phenetic similarities among specimens and (b) stratigraphic interval, so that taxa from different time-intervals are linked in presumed ancestor-descendant sequences according to their similarities. - (from Michal Kowalewski, lecture notes)



Strict consensus: this is the most conservative consensus method used in in cladistic analysis, which only recognises clades that appear in all of the trees. It's advantage is that it only includes data that is totally unambiguous. The disadvantage is that it is thrown off by the slightest difference. For example, two trees may be identical except for the placement of a single sequence, yet their strict consensus tree might be completely unresolved. The resulting is a "star" phylogeny, a broad polytomy with only radiating lines, and very little or no resolution or phylogenetic structure. This is shown by the blue cladogram on theright, which is placed next to a more conventional, branching phylogeny. (from the PAUPDISPLAY Manual, Forey et al 1992 p.78)

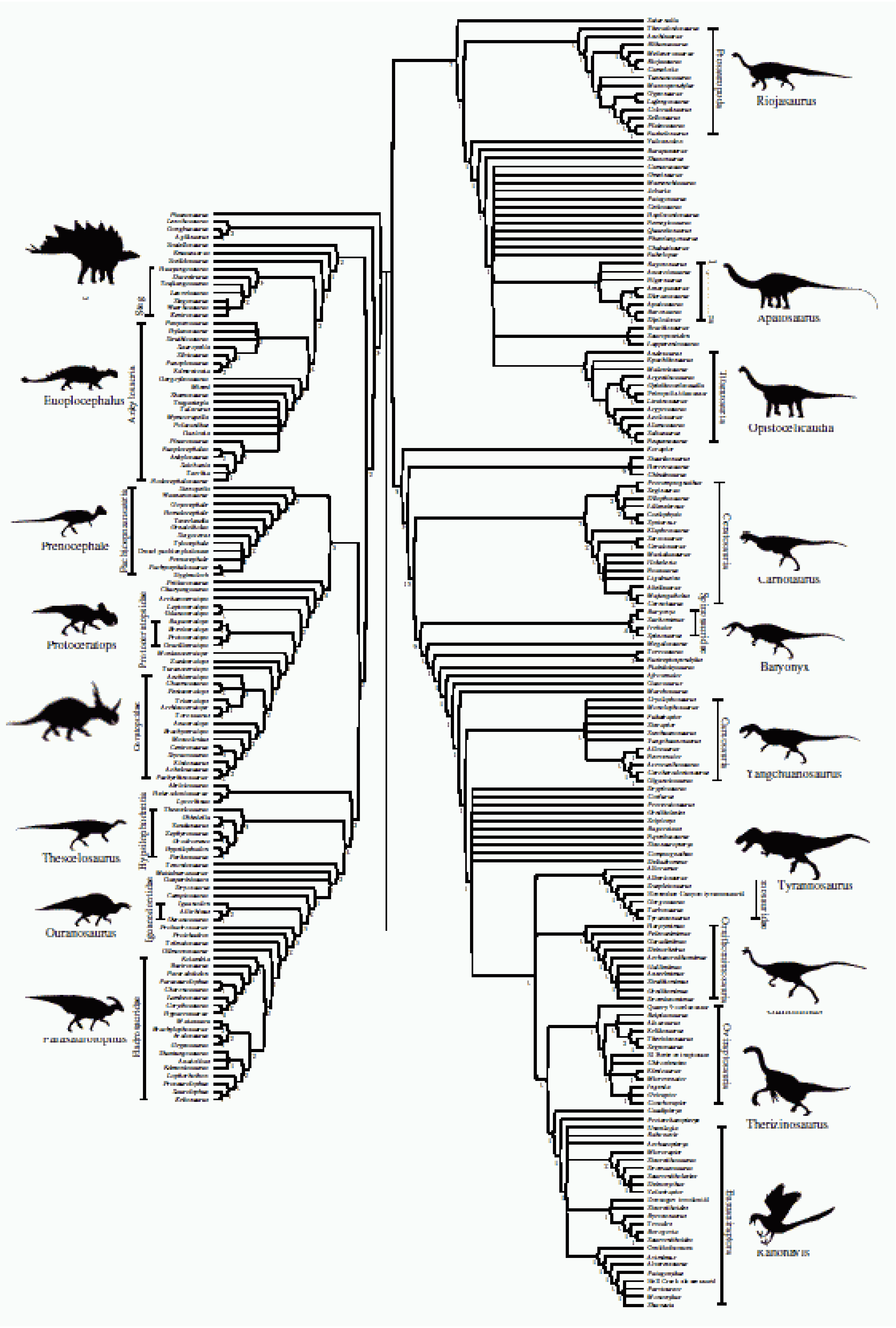
Subgenus: A group of species less inclusive than a genus. The subgenus name is written in italics and brackets, after the genus but before the species. It may be the same as or different to the genus, e.g. ***Cypraea (Cypraea) tigris*** Linnaeus, the tiger cowrie, belongs to the subgenus ***Cypraea*** of the genus ***Cypraea***. However, it is not mandatory, or even customary, when giving the name of a species, to include the subgeneric name. One paleo artist and author of popular books on dinosaurology, Greg Paul, sometimes coins subgenera, although this practice is otherwise very rarely used in vertebrate paleontology

MAK120227,

Subspecies: The smallest taxonmic rank; a group of organisms less inclusive than a species. The term is usually applied to populations or groups within a species that have distinct forms or characteristics and live in a restricted geographic area. In contrast to the species, members of different subspecies can usually interbreed and give rise to fertile offspring. The subspecies name is written in italics after the species, and may or may not be the same as the species name. e.g. The Cape Mountain Zebra is referred to as ***Equus zebra zebra***, as distinguished from Hartmann's Mountain Zebra, ***Equus zebra hartmannae***

Supermatrix: One of the new developments in cladistics that have become possible through cheap and powerful computing, supermatrixes involve simultaneous analysis of all available character data. Rather than separate analyses of data sets and subsequent integration of the resulting trees (supertree), all character data is considered simultaneously to enable incorporation of diverse kinds of data, including characters from fossils, morphology, and molecular phylogeny. (de Queiroz & Gatesy 2007) (MAK)

Supertree: In cladistics, a "supertree" refers to the synthesis of a number of distinct cladograms, combining morphological, molecular, and other data from the different individual phylogenies. Supertrees result from combining many smaller, overlapping phylogenetic trees into a single, more comprehensive tree. They are distinguished from classic consensus techniques in that the source trees need only have overlapping rather than identical taxon sets. Because supertree construction uses other tree topologies rather than the primary data underlying those trees, they can be constructed using all available phylogenetic hypotheses, even those based on incompatible data types, or lacking data entirely. Supertree have produced phylogenies of a number of large taxonomic groups. However supertree strength is also its weakness, and this approach has been harshly criticised by systematists precisely because it only considers the topology of the source trees, effectively discarding primary data. A supertree or quasi-



supertree approach is also standard with ASCII phylogenetic trees. Supertree construction is probably as old as the field of systematics itself, and remains our only way of visualizing the Tree of Life as a whole. References: Pisani et al 2002 who give the example of a dinosaur supertree (see diagram, right), Bininda-Emonds, 2004. (MAK)

Supra-specific taxon: a taxon above the species level: anything from subgenus and genus upwards (family, order, etc). Useful for understanding biotic diversity through time and large scale patterns of evolution. Recognised by evolutionary systematics, but not (or only informerly) by cladistics. See also rank. (MAK)

Symplesiomorphy In cladistics, a shared plesiomorphic character trait, which is shared between two or more taxa, but which is also shared with other taxa which have an earlier last common ancestor with the taxa under consideration. An example is pharyngeal gill breathing in bony and cartilaginous fishes. The former are more closely related to Tetrapoda (terrestrial vertebrates, which evolved out of a clade of bony fishes) that breathe via their skin or lungs, rather than to the sharks, rays, etc. Their kind of gill respiration is shared by the "fishes" because it was present in their common ancestor and lost in the other living vertebrates. Contrast with apomorphy/synapomorphy. (Wikipedia)

Synapomorphy: In cladistics, an apomorphy that is ***shared by*** (syn-) by several taxa, where the trait in question originates in their last common ancestor. Being shared by multiple taxa, synapomorphies can be used to diagnose (describe) a clade (a monophyletic group). Compare with homology. True synapomorphies usually are a given set of terminal groups, shared by two or more terminal taxa, but this is not essential to the concept. Thus, if some descendants of a last common ancestor possess a synapomorphic trait, in the case of reversals it is not strictly necessary that all of its descendants must possess the same trait. Contrast with ***plesiomorphy*** and ***homoplasy***, which are shared primitive and shared convergent characteristics also of no phylogenetic value. (based on Wikipedia, Michael D. Crisp - Introductory glossary of cladistic terms)

Synonym. In taxonomy, the term synonyms is used to refer to two or more names referring to the same taxonomic entity. It is a general principle of taxonomy that any taxon can have only one valid name - usually, this is the oldest name available (the senior synonym, as opposed to a junior synonym) if there is more than one (but see Nomen oblitum for one example of where this rule may be suspended). A list of names used to refer to a taxonomic entity is referred to as a synonymy.

Synonyms may be either objective or subjective. ***Objective synonyms*** have the same type as each other, and as such will always refer to the same taxon. ***Subjective synonyms*** have different types, and authors may differ as to whether they represent the same taxon or not. In synonymies presented on Palaeos.org, we have generally distinguished between the two classes by using "=" for objective synonyms and "incl." for subjective synonyms. CKT070221

Synonymy:A section of a systematic presentation about an organism that lists all of the names that have been used for the organism including synonyms, new combinations, misidentifications, etc. In some cases this section may include only true synonyms. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Syntype: The series of specimens used to describe a species or subspecies when the author did not include a holotype (ScaleNet - Terms Pertaining to Zoological Nomenclature). Where the original description was based on a number of specimens, some or all of them may hold equal status as type specimens. Should a syntype series turn out to contain examples of more than one species, a subsequent reviser may designate a lectotype. CKT061027

Systematics: (short for "Systematic biology") the study of the diversification of life on the planet Earth, both past and present, and the relationships among living things through time. Relationships are visualized as evolutionary trees. Here there are two main paradigms, evolutionary systematics (now rarely used in veretbrate paleontology) and phylogenetic (cladistic) systematics. ***Evolutionary systematics*** interprets Linnaean classification in terms of the modern evolutionary synthesis and provides evolutionary taxonomies above the species level. It maps lineages against a geological time to give a spindle diagram showing diversity or abundance. ***Cladistic phylogenies*** (cladograms) are based at the species level and emphasise greater verifiability. They have two components, branching order (showing group relationships) and (in the case of phylograms) branch length (showing amount of evolution). Almost all systematics nowadays is cladistically-derived. ***Phylogenetic trees*** of species and higher taxa are used to study the evolution of traits (e.g., anatomical or molecular characteristics) and the distribution of organisms (biogeography).

Systematic biology, ***taxonomy***, and ***scientific classification*** are often confused and used interchangeably. However, taxonomy is more specifically the identification, description, and naming (i.e. nomenclature) of organisms, classification focuses on placing organisms within hierarchical groups that show their relationships to other organisms, and systematics alone deals specifically with relationships through time, and can be synonymous with phylogenetics, broadly dealing with the inferred evolutionary hierarchy of organisms. (MAK, Wikipedia)

Systematic paleontology: organising or classifying fossil organisms (paleontology) according to the principles of systematic biology (Systematics). (MAK)

T.

Taxon: (plural: **taxa**) a group of organisms, considered to be a unit, and which generally has been formally named with a scientific (Latin or Greek) proper name and a rank. Defining what belongs or does not belong to such a taxonomic group is done by a taxonomist with the science of taxonomy. It is not uncommon for one taxonomist to disagree with another on what exactly belongs to a taxon, or on what exact criteria should be used for inclusion. Traditionally, a taxon is given a formal or scientific name, which is governed by one of the Nomenclature Codes, which sets out rules to determine which scientific name is correct for that particular grouping. Generally, a good taxon as one that reflects presumptive evolutionary (phylogenetic) relationships, being derived from a common ancestor . Whether or not clades are acceptable as taxons is a matter of dispute; although evolutionary systematists (Mayr & Bock 2002 p.182) deny that they are, whereas cladists have proposed phylogenetic nomenclature and a new Phylocode which requires taxa to be monophyletic and rejects Linnaean supra-specific ranks. (MAK, Wikipedia)

Taxonomic inflation: Pejorative term for what is perceived to be an excessive increase in the number of recognised taxa in a given context, due not to the discovery of new taxa but rather to putatively arbitrary changes to how taxa are delineated. For example, a subspecies may be elevated to species rank, through the arbitrary decision that the differences between the various taxa warrant distinguishing them at species rank. (From Wikipedia). Another form of taxonomic, or rank, inflation is elevating subfamilies to families, families to superfamilies or orders, and so on, which tends to be an on-going process as more taxa are discoevred. For eaxmple in the late 1980s Carcharodontosaur theropods were included under the Allosauridae, now they are given their own family. MAK011227

Taxonomy: The field of science converned with discovering, describing, clasisfying, and naming organisms. It is supported by institutions holding collections of these organisms, with relevant data, carefully curated: such as Natural History Museums, Herbaria and Botanical Gardens. Taxonomy uses taxonomic units, known as taxa (singular taxon). In addition, the word is also used as a count noun: a taxonomy, or taxonomic scheme, is a particular classification ("the taxonomy of ..."), arranged in a hierarchical structure. (Wikipedia) The roots of taxonomy go back to Aristotle at least, although it was only really developed as a modern science by Linnaeus. Modern approaches to taxonomy follow the same principle of organising and understanding the natural world. These taxonomies fall into three major schools: phenetic, phylogenetic (cladistic), and evolutionary. Each of these pertains to a different phylogenetic methodology, a different way of mapping out the history and evolution of life on Earth . . In biological taxonomy there are, according to Ereshefsky (2000, p. 7) "no fewer than four general schools of taxonomy: evolutionary taxonomy, pheneticism, process cladism, and pattern cladism". Each of those schools have their own view on how to get from the characteristics of an individual organism to a species, and also the meaning of the term species varies between schools of taxonomy. (cited from Birger Hjørland) See also Alpha taxonomy , cladistics, Linnaean classification, Systematics. MAK120229

Tetrapod: four-legged, land-living vertebrate, or any secondarily limbless (e.g. snakes) or aquatic (e.g. whales) descendants of such. Cladistic terminology disagrees over whether "tetrapod" should be used to include all four-legged animals (stem-based definition) or only those that include the common ancestor of all living tetrapods and its descendants (crown-based definition). **More**

Terminal, Terminal taxon: Not the end of the evolutionary line, but in cladistic formalism, one of the units whose collective phylogeny is reconstructed; shown diagramatically as the undivided tips of a cladogram. Terminals may be higher taxa, species, populations, individuals, fossils or even genes. There should be some rational basis for accepting the integrity of each terminal (for the purpose of the analysis), e.g. a monophyletic or diagnosable unit. Despite the claims by some authors, terminals do not need to be monophyletic; in fact, many species-level terminals are unavoidably paraphyletic. However, higher taxa used as terminals should be monophyletic. (based on Michael D. Crisp - Introductory glossary of cladistic terms)

Three-domain system: biological classification introduced by Carl Woese that rejects the old prokaryote-eukaryote distinction and divides cellular life forms into Archaea, Bacteria, and Eukarya domains (usually interpreted as a taxonomic grade above kingdom). Woese argued that, on the basis of differences in 16S rRNA genes, the three groups each arose separately from an ancestor with poorly developed genetic machinery, called a ***progenote***. To reflect these primary lines of descent, he treated each as a domain, divided into several different kingdoms. He conjectured an era in which there was a considerable amount of lateral transfer of genes between organisms. Species formed when organisms stopped treating genes from other organisms with equal importance to their own genes. Lateral transfer during this period was responsible for the fast early evolution of complex biological structures. (MAK, corrected from Wikipedia also Wikipedia). Refs Woese et al 1990

Topology: in this context, the particular shape or arrangement of the branches of a cladogram, the evolutionary history of the group in question according to a particular phylogenetic hypothesis. (MAK120318)

Topotype: One or more specimens collected at the same location as the type series regardless of whether they are part of the type series. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Total evidence: the philosophical principle that the best hypothesis is the one derived from all the available data. Incorporates equally phenomic and molecular traits. In phylogenetics, this principle has come to be equated with the supermatrix approach (adapted from Bininda-Emonds, 2004 - glossary). **More**

Total group: see Pan-group.

Transformed cladism: see Pattern cladism.

Tree: also **Phylogenetic tree:** a branching tree-like, diagrammatic representation of the evolutionary relationships and patterns of branching in the history of the organisms being considered. One type of phylogenetic tree, called a cladogram, is central to cladistics, and the equivelent phylogram to moplecular phylogeny). Dendrogram is sometimes used to refer to a more informal diagram. See also chronogram, phylogram, romerogram, and spindle diagram (MAK) **More**

Tribe: In the Linnaean classification a mostly botanical taxonomic rank between family and genus. With the multiplication of ranks in linnaean-cladistic hybrid taxonomies, "tribe" has been used more widely. (MAK) **More**

Triply paraphyletic group: a group or taxon that is paraphyletic because three of its descendant lineages are not included. There would also be quadruply paraphyletic groups and so on. See also singly and doubly paraphyletic groups

Type: The term "type" is tied in biological nomenclature to a very specific concept - that of a designated specifier that provides the definitive concept of a given taxon. For instance, when describing a new species, the author(s) is required to name the specimen or one of the specimens used as the type specimen. The name for the new species then becomes indelibly tied to that specimen, and should any confusion ever arise as to the identity of the species (for instance, if it turns out that two or more species have been mistaken for one, or if the published description turns out to omit some feature[s] required for identification), examination of the type specimen should (hopefully) resolve these issues. Similarly, at higher levels, each genus requires a type species, and each family requires a type genus. See International Code of Zoological Nomenclature Online for more information relevant to animals, and International Code of Botanical Nomenclature for plants. Different nomenclatorial codes may differ in the terminology used. CKT061027

A number of terms are in use to refer to different classes of types, including ***holotype***, (the most important, as it used to define a species), ***allotype***, epitype:, ***hapantotype***, ***isotype***, ***lectotype***, ***neotype***, ***paratype*** , ***syntype***, ***topotype***, ***type series*** and ***type strain*** MAK120227

Type genus:A genus that has been selected as the standard bearer of a tribe, family, or superfamily and provides the stem of the family-group name. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Type locality: The geographic location where the primary type was collected. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Type series: the total group of specimens used in the original description. Ideally, one specimen is the holotype and the remainder paratypes, but if no holotype has been designated, the entire type series become syntypes. CKT061027

Type species:A species that has been selected as the standard bearer of a genus or subgenus. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Type strain: (Bacteriological Code) For prokaryotes, the type is not a preserved specimen, but an isolated culture. The Bacteriological Code of Nomenclature requires that cultures of the type strain be deposited in at least two separate institutes' culture stores. CKT061027

U.

Unavailable name: in taxonomy, a name that is incorrectly proposed according to the International Code of Zoological Nomenclature. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Unjustified emendation: in taxonomy, an emendation that is incorrect according to the International Code of Zoological Nomenclature, e.g., the generic name ***Hemiberlesea*** Lindinger is an incorrect change of ***Hemiberlesia*** Cockerell according to the Code and is an unjustified emendation. - (ScaleNet - Terms Pertaining to Zoological Nomenclature)

Unrooted tree: A cladogram or phylogram for which the ancestor (the root) has not been hypothesized, and which thus does not specify the direction of evolutionary change among the character-states. An unrooted tree can be rooted on any of its branches, and so there are many rooted trees that can be derived from a single unrooted tree. Contrast with rooted tree. (Michael D. Crisp - Introductory glossary of cladistic terms)

V.

Valid name: The correct name of an organism, e.g., if ***Apiomorpha nux*** Fuller, 1896 and ***A. pharetrata*** Scharder, 1863 apply to the same species (and therefore are synonyms), then by the law of priority (the oldest name prevails) ***A. pharetrata*** Scharder, 1863 is the valid name.

Vertical classification: as described by Simpson, a taxon based on ancestor and descendant (phylogenetic) relationship between its members, a clade. Evolutionary systematics considers both horizontal and vertical classification in taxonomy, whereas cladistics and phylogenetics is based on vertical classification only. (MAK) **More**

Vraagteken effect: from the Dutch "question mark", a term introduced by Schram and Hof (1998) to the effect that the absence of critical information has in destabilising cladograms. They found that by introducing fossil taxa, for which, obviously, many character states are unknown, and hence coded as a question mark in the matrix, resulted in a great variation in the topology of the trees recovered by parsimony analysis. Cladistic algorithms respond to the ambiguity caused by the missing data by generating a large number of equally parsimonious phylogenies MAK120417.

W.

Wastebasket taxon: a taxon that includes all species or groups that cannot be easily or conveniently placed elsewhere, e.g., for a while all large theropod dinosaurs that could not be included under the Ceratosauridae, Allosauridae or Tyrannosauridae were named ***Megalosaurus***.

Weighting: in cladistics, the empirically controversial (because non-quantifiable) yet necessary task of determining the phylogenetic significance of a particular character trait. For example, if there are three species of animals, one with brown fur, another with black fur, and one with brown scales, the presence or absence of fur is more important than the external colour, and hence would be given greater weight in phylogenetic analysis. Weighting is unavoidable if one is to address the problem of homoplasy vs homology. (MAK)

X.

Y.

Z.

Zombie taxon, Zombie effect: Before the zombie craze took over geek/nerd culture (perhaps as a counterpole to the excessively feminine/romantic "supernatural romance" vampire story) the technical term for a fossil of this sort was term "reworked". Refers to a fossil such as a dinosaur tooth that was washed out of sediments and re-deposited in rocks and/or sediments millions of years younger. This basic mistake in the interpretation of the age of the fossil leads to its title. The discovered fossil was at some point mobile (or "walking") while the original animal or plant had long been dead. (MAK, Wikipedia)

Page Back: Taxonomy | Unit Home | Page Top | Page Next: References

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

content by MAK110419, edited RFVS111203, last modified MAK120326, merged with taxonomy glossary 130316

Page Back: Glossary | Unit home | Page Next: Ecology
Unit Back: Paleontology | Unit Up: Life | Unit Next: Ecology

Systematics, Taxonomy, and Phylogeny: References

Cosmic Evolution
  Life
  Evolution
  Paleontology
  Systematics
  Ecology

  Astrobiology
  Life on Earth

    Astrobiology (Life in the Cosmos)
    "Tellurobiota" (Life on Earth)

Phylogeny and Systematics
  Systematics - History of ideas
    "The Great Chain of Being"
    Linnaean taxonomy
    The Phylogenetic Tree
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Stratigraphy and phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

J. David Archibald (2009) 'Edward Hitchcock's Pre-Darwinian (1840) 'Tree of Life'.', ***Journal of the History of Biology*** (2009) 42:561-592
Early trees

Ashlock, P.D. (1971). "Monophyly and associated terms". ***Systematic Zoology* 20** (1): 63–69. doi:10.2307/2412223.
monophyletic

Ashlock, P D (1974) The Uses of Cladistics. ***Annual Review of Ecology and Systematics*** Vol. 5: 81-99 (November 1974) DOI: 10.1146/annurev.es.05.110174.000501
monophyletic

Fausto Barbagli (2009) 'In Retrospect: The earliest picture of evolution?', ***Nature*** 19 November 2009
Early trees

Benton, MJ (2000), ***Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead?* Biol. Rev.** 75: 633-648
"Evolutionary phylogeny" - Supraspecific Taxa

Benton, M.J. 2004, ***Vertebrate Paleontology***, 3rd ed. Blackwell Science Ltd;
Romerogram, "Evolutionary phylogeny" - Stratigraphic sequence

Benton, M.J. 2007 The Phylocode: Beating a dead horse? ***Acta Palaeontol. Pol.*** 52 (3): 651–655, 2007
History of Taxonomy, Phylogenetic classification

Bininda-Emonds, O.R.P., 2004, The evolution of supertrees, ***Trends in Ecology and Phylogeny*** Vol.19

No.6 June 2004
Adams consensus, Majority rule consensus, supertree, total evidence

Brian E. Bodenbender and Daniel C. Fisher, 2001, Stratocladistic analysis of blastoid phylogeny, ***Journal of Paleontology*** (March 2001), 75(2):351-369
"Evolutionary phylogeny" - Stratocladistics

Peter J. Bowler (2003) ***Evolution. The History of an Idea***, third edition, p.90-91.
Early trees

Brochu, C.A.; Sumrall, C.D. (2001). "Phylogenetic nomenclature and paleontology". ***Journal of Paleontology*** 75 (4): 754–757. doi:10.1666/0022-3360(2001)075.
Cladistics

Budd, G.E. (1996). "The morphology of ***Opabinia regalis*** and the reconstruction of the arthropod stem-group". ***Lethaia*** 29 (1): 1–14. doi:10.1111/j.1502-3931.1996.tb01831.x.
Stem group

Budd, G. E. (2001). Tardigrades as "stem-group arthropods": the evidence from the Cambrian fauna. ***Zoologischer Anzeiger***, 240, 265�279. **pdf**
Stem group

Joe Cain (2009), "Mayr, Ernst Walter", in Michael Ruse and Joseph Travis ed. ***Evolution: the first four billion years***, Belkna Press of Harvard University Press, Cambridge & London, pp.724-7
Evolutionary Systematics - Methodology

Carlson, Sandra J, 2001. "Ghosts of the past, present, and future in brachiopod systematics". ***Journal of Paleontology***, 75 (6), 2001, pp.1109-1118.
Phylogenetic classification

Coyne, J.A. & Orr, H.A. 2004. ***Speciation***. Sunderland, Massachusetts: Sinauer.
"Evolutionary phylogeny" - cladogenesis

Darwin, Charles (1859), On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life (1st ed.), London: John Murray, ISBN 1-4353-9386-4
Darwin's tree

Darwin, Charles (1872), The Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life (6th ed.), London: John Murray, ISBN 1-4353-9386-4
Darwin's tree

Delsuc, F., Brinkmann, H., & Philippe, H. 2005, Phylogenomics and the reconstruction of the tree of life. ***Nature Reviews Genetics*** 6, 5 (2005) 361-75 **pdf**
"Garbage in, garbage out", heterotachy, Long branch attraction, phylogenomics, root

Donoghue P.C.J. & Benton M.J. (2007) Rocks and clocks: Calibrating the Tree of Life using fossils and molecules. Trends Ecol Evol 22:424-431 **pdf**

molecular clock, "Evolutionary phylogeny" - Rocks and clocks, Stratigraphy and phylogeny

Malte C. Ebach, Juan J. Morrone and David M. Williams 2008 A new cladistics of cladists. ***Biology and Philosophy*** 23 (1). 153-156, DOI: 10.1007/s10539-007-9069-7
Cladistics, Gradists, Numerical cladistics Pattern cladistics

Edgecombe, G.D. 2009, Palaeontological and molecular evidence linking arthropods, onychophorans and other Ecdysozoa. ***Evolution: Education and Outreach*** 2: 178-190. 10.1007/s12052-009-0118-3 **pdf**
Long branch attraction

Ereshefsky, M. (2000). ***The Poverty of the Linnaean Hierarchy: A Philosophical Study of Biological Taxonomy***. Cambridge: Cambridge University Press.
Taxonomy

Felsenstein, J. 2003. ***Inferring Phylogenies***. Sinauer Associates, Sunderland, Massachusetts. review
Gradists

Fisher, D.C. , 1994, Stratocladistics: morphological and temporal patterns and their relation to phylogenetic process. in ***Interpreting the hierarchy of natur***e (Grande, L. & Rieppel, O. eds) 133-171 (Academic Press, San Diego).
"Evolutionary phylogeny" - Stratocladistics

Fisher, D.C. 2008, Stratocladistics: Integrating Temporal Data and Character Data in Phylogenetic Inference ***Annual Review of Ecology, Evolution, and Systematics*** Vol. 39: 365-385 DOI: 10.1146/annurev.ecolsys.38.091206.095752 Daniel C. Fisher
Stratocladistics (glossary), "Evolutionary phylogeny" - Stratocladistics

Peter L. Forey, Christopher J. Humphries, Ian J. Kitching, Robert W. Scotland, D. J. Siebert, D. M. Williams, 1992, ***Cladistics: a practical course in systematics***, Oxford University Press
Adams consensus, Strict consensus

Gauthier, J. 1986. Saurischian monophyly and the origin of birds. In: K. Padian, ed. ***The Origin of Birds and the Evolution of Flight.*** Memoirs California Academy of Sciences 8. pp. 1–55
Cladistics

Marius Dan Georgescu, 2009, Taxonomic revision and evolutionary classification of the biserial Cretaceous planktic foraminiferal genus ***Laeviheterohelix*** Nederbragt, 1991, ***Rev. mex. cienc. geol v.26 n.2 M�xico ago***. Online
Stratigraphy and phylogeny - Diagram

Gonzalo Giribet, Casey W. Dunn, Gregory D. Edgecombe, Andreas Hejnol, Mark Q. Martindale, and Greg W. Rouse 2009, Assembling the spiralian tree of life
phylogenomics

Grant, V. 2003, Incongruence between cladistic and taxonomic systems ***American Journal of Botany*** 90(9): 1263–1270. 2003.
monophyletic, "Evolutionary phylogeny" - ancestors

Gribaldo, S. & Philippe, H. 2002, Ancient Phylogenetic Relationships. ***Theoretical Population Biology*** **61**, 391–408 (2002) doi:10.1006/tpbi.2002.1593 **pdf**
Long branch attraction

Haeckel, E. 1866. ***Generelle Morphologie der Organismen***. Georg Reiner, Berlin, Germany.
monophyletic

Hedges, B and Kumar S. Eds. 2009. ***The Timetree of Life***. Oxford University Press.
"Evolutionary phylogeny" - Stratigraphic sequence

Hennig, W. 1966, ***Phylogenetic Systematics***. (tr. D. Davis and R. Zangerl), Univ. of Illinois Press, Urbana 1966, reprinted 1979,
monophyly, paraphyly

Susan Holmes. 2003. Bootstrapping Phylogenetic Trees: Theory and Methods. ***Statistical Science***, Vol. 18, No. 2, 241�255 **pdf**
Bootstrap

Hörandl, E, 2010. Beyond cladistics: Extending evolutionary classifications into deeper time levels. ***Taxon*** 59 (2) April 2010: 345–350 **pdf**

Hörandl, E. & Stuessy, T.F., 2010 Paraphyletic groups as natural units of biological classification, ***Taxon*** 59 (6) December 2010: 1641-1653 **on line**
"Evolutionary phylogeny" - cladogenesis, budding, paraphyly

Keeling, P.J. & Palmer J.D. 2008, Horizontal gene transfer in eukaryotic evolution
horizontal gene transfer, polytomy

Kr�ger B, Vinther J, Fuchs D. 2011, Cephalopod origin and evolution: A congruent picture emerging from fossils, development and molecules: Extant cephalopods are younger than previously realised and were under major selection to become agile, shell-less predators. ***Bioessays***. 33(8):602-13. doi: 10.1002/bies.201100001.
Total Evidence approach

Kühl, G.; Briggs, D.E.G., and Rust, J. (February 2009). "A Great-Appendage Arthropod with a Radial Mouth from the Lower Devonian Hunsrück Slate, Germany". Science 323 (5915): 771–773. doi:10.1126/science.1166586. PMID 19197061.
Lazarus taxon

Lane, A & MJ Benton (2003), ***Taxonomic level as a determinant of the shape of the Phanerozoic marine biodiversity curve***. **Amer. Naturalist** 162: 265-276 **pdf**
"Evolutionary phylogeny" - Supraspecific Taxa

Levinton, J.S. 2001, ***Genetics, Paleontology, and Macroevolution***, 2nd ed. Cambridge University Press
Ghost lineage, Stratigraphic congruence

Lipscomb, D. 1998. Basics of Cladistic Analysis. George Washington University, Washington D.C. **pdf**
Length, Phylogenetic systematics.

Liu, J. et al.(2011). Jianni Liu, Michael Steiner, Jason A. Dunlop, Helmut Keupp, Degan Shu, Qiang Ou, Jian Han, Zhifei Zhang & Xingliang Zhang. (2011). Liu et al. reply. ***Natur***e 476, 526�530
Gap codings

Mayr, E. 1963, ***Animal Species and Evolution***, Cambridge, MA: Harvard University Press,
species

Mayr, E., & P. D. Ashlock. 1991. ***Principles of systematic zoology***, 2nd ed. McGraw-Hill, New York, New York, USA.
monophyletic, phenetics

Mayr, E., & W. Bock. 2002. Classifications and other ordering systems. ***Zeitschrift fu¨r zoologische Systematik und Phylogenysforschung*** **40**: 169–194. **pdf**
monophyletic, phenetics, "Evolutionary phylogeny" - ancestors, "Evolutionary phylogeny" - budding

Mounce, R. C. P. & Wills, M. (2011). Phylogeny of Diania challenged. ***Nature*** 476, doi:10.1038/nature10266
Gap codings

O'Keefe, F. R. and P. M. Sander (1999) Paleontological paradigms and inferences of phylogenetic pattern: a case study. ***Paleobiology*** 25: 518-533 abstract
"Evolutionary phylogeny" - Anagenesis, ASCII Phylogenetic Tree, Total evidence

O'Leary, M.A., et al. 2013. The placental mammal ancestor and the post-K-Pg radiation of placentals. ***Science*** 339:662-667.
Phylogenetics

Pearson, C.H., 2010. Pattern Cladism, Homology, and Theory-Neutrality. History and Philosophy of the Life Sciences - Vol. 32, no. 4 (2010) abstract

Pattern cladistics

Pisani, D., Yates, A. M., Langer, M., and Benton, M. J. 2002. A genus-level supertree of the Dinosauria. Proceedings of the Royal Society, Series B, 269, 915-921. PDF
Supertree

de Queiroz, A. & Gatesy, J., 2007, The supermatrix approach to systematics, ***Trends in Ecology and Phylogeny*** Vol.22 No.1 pdf
supermatrix

Rieseberg, L. & Brouillet, L. 1994. Are many plant species paraphyletic? ***Taxon*** 43: 21–32.
"Evolutionary phylogeny" - budding

Rieppel, O. 1993 in The Conceptual Relationship of Ontogeny, Phylogeny, and Classification: the Taxic Approach, ***Phylogenyary Biology vol. 27***, edited by Max K. Hecht et al., Plenum Press, New York, pp.1-32,
homology

Scott D. Sampson, Mark A. Loewen, Andrew A. Farke, Eric M. Roberts, Catherine A. Forster, Joshua A.

Smith, and Alan L. Titus (2010). "New Horned Dinosaurs from Utah Provide Evidence for Intracontinental Dinosaur Endemism". ***PLoS ONE*** 5 (9): e12292. DOI:10.1371/journal.pone.0012292. Online
Speciation - Dendrogram

Searls, D.B. 2003. Pharmacophylogenomics: genes, evolution and drug targets. ***Nature Reviews*** Drug Discovery 2, 613-623 (August 2003) | doi:10.1038/nrd1152. **online**
molecular clock, phylogenomics

Sereno, P.C., 2007. Logical basis for morphological characters in phylogenetics. ***Cladistics*** 23 (2007) 565–587 (**pdf**)
Character

Schram, F. R. and C. H. J. Hof (1998), Fossi ls and the interrelationships of major crustacean groups, 233-302. In G. D. Edgecombe (ed.), ***Arthropod Fossils and Phylogeny***. Columbia University Press. New York

Vraagteken effect

Simpson, George G. "The Principles of Classification and a Classification of Mammals." ***Bulletin of the AMNH***, vol. 85, p. 23. 1945. American Museum of Natural History, New York.
Splitters versus lumpers

Siveter, Derek J.; Fortey, R.A., Sutton, M.D., Briggs, D.E.G., and Siveter, David J. (2007). "A Silurian "marrellomorph" arthropod". Proceedings of the Royal Society: B 274 (1623): 2223–2229. doi:10.1098/rspb.2007.0712. PMC 2287322. PMID 17646139.
Lazarus taxon

Michelle Spaulding, Maureen A. O'Leary, John Gatesy, (2009). "Relationships of Cetacea (Artiodactyla) Among Mammals: Increased Taxon Sampling Alters Interpretations of Key Fossils and Character Evolution". In Farke, Andrew Allen. PLoS ONE 4 (9): e7062, doi:10.1371/journal.pone.0007062 **pdf**
Cladogram

Stetter, K. O. 1996. Hyperthermophiles in the history of life, ***Ciba Found. Symp***. 202, 1–10.
Long branch attraction

Stuessy, T.F. Paradigms in biological classification ***Taxon*** 58 (1) February 2009: 68–76 **pdf**
Phenetics

Telford, M.J. & Budd, G.E. 2003. The place of phylogeny and cladistics in Evo-Devo research ***Int. J. Dev. Biol. 47***: 479-490 (2003)
Phylogenetic systematics, Polarity

Dale Tshudy and Ulf Sorhannus, 2003 ***Hoploparia***, the best-known fossil clawed lobster (Family Nephropidae), is a "wastebasket" genus, ***Journal of Crustacean Biology*** 23(3):700-711. 2003 doi: http://dx.doi.org/10.1651/C-2353
matrix

Wagner, P. J. 1995. Stratigraphic tests of cladistic hypotheses. ***Paleobiology*** 21: 153�178.

Wang, Xiaoming, Tedford, Richard H.; Taylor, Beryl E., 1999 Phylogenetic systematics of the Borophaginae (Carnivora, Canidae). Bulletin of the AMNH ; no. 243. online
"Evolutionary phylogeny" - Speciation - Dendrogram

Page Back: Glossary | **Page Top** | **Unit home** | **Page Next: Ecology**

page MAK111009, edited RFVS111127, last revised MAK130324

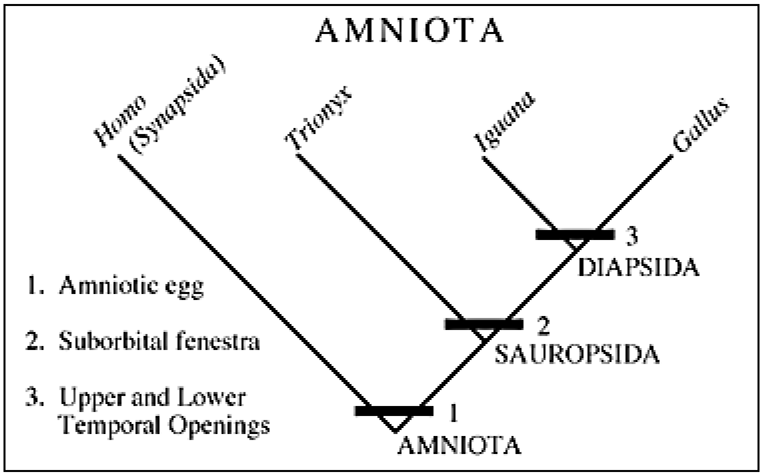
Page Back | Unit Up: Systematics | Page Next
Unit Back: Evolutionary systematics | Glossary | Unit Next: Molecular phylogeny

Cladistics

Cladistics is a rigorous methodology first developed by German entomologist Willi Hennig (who used the term "Phylogenetic Systematics"). It is based on three principles:

1. Groups of organisms are descended from a common ancestor.
2. At each node (divergence of a population), there are two branching lines of descendants.
3. Evolution results in modifications of characteristics over time.

Cladistics acknowledges only Monophyletic groupings as valid. Paraphyletic groups (accepted in Evolutionary Systematics) and Polyphyletic groups are rejected as invalid, as is the whole Linnaean hierarchy above species rank (although sometimes taxa such as family etc are used in a more limited context).



Cladogram by Paul Olsen (original url), showing four species (human, turtle, lizard and bird), according to their synapomorphies (shared unique characteristics). Most computer-generated cladograms involve many hundreds of characteristics

The cladistic revolution of the 1970s and 1980s constituted a major paradigm shift in biology and systematics, with the Evolutionary system falling out of favour and being replaced by the one. Cladistics is based not on ***morphological similarity*** (as in the Linnaean system and more recently phenetics) or on ***ancestor and descent relationship*** (as in Evolutionary systematics) but in sister-group relationships between related taxa. Although originally based on recent organisms (neontology) it also can be used to analyse fossils. Indeed, when computer-based cladistic analysis came into its own in the 1990s, paleontologists were among the first zoologists to almost wholeheartedly adopt the system (Brochu &

Sumrall, 2001).

Although the relation between cladistics and evolutionary systematics could be described as the difference between "Vertical" and "Horizontal" Taxonomy, the two systems are quite distinct and to some degree incompatible. This ***does not mean*** that one is right and the other wrong.

Contrary to popular belief, cladistics does not describe the actual evolutionary path of life. That is, it is not concerned with or describe the evolution of later organisms from common ancestors in the way that, say, Darwin or more recently Richard Dawkins do, and what the Evolutionary systematics of Romer and Simpson also describes. It simply provides a means of determining in which way (i.e. the branching order) living organisms are related to each other. Cladograms, in other words, are not evolutionary trees. What cladistics does do is provide a more precise and verifiable method of creating and testing phylogenetic hypotheses regarding the evolutionary relationships of past and current organisms. In this way, cladistic methodology can even be used to predict properties of yet-to-be discovered organisms.

The current trend in evolutionary thinking is to use statistical-cladistic methods to combine morphological and molecular data in large phylogenetic trees. When there is a conflict between the two methodologies, the tree derived from molecular phylogeny is most often preferred, although there is no empirical reason why molecular sequencing should be preferred over morphological studies, as both are equally robust. The Total Evidence approach provides a more balanced assesment by (ideally) giving equal weight to both methodologies. MAK130324

A few random links: Phylogenetics Primer - Douglas Theobald, (recommended), Introduction to Cladistics - UCMP, also really good, Am I a pattern or transformed cladist? (mail list anecdote on phenetics and cladists); Peter Forey - Cladistics for Palaeontologists (pretty technical). MAK111014

Page Back **Page Top** **Page Next**

page MAK111014, edited RFVS111203, last modified MAK130324

Page Back | Unit Up: Systematics | Page Next
Unit Back: Evolutionary systematics | Glossary | Unit Next: Molecular phylogeny

Cladistics: An Introduction

Cladograms are the heart of paleontology in these opening years of the Third Millennium. The theory and practice of these diagrams is a subject which would fill many pages. In fact it ***does*** fill many pages on this site; and the questions get very technical indeed. Here, we present only a basic introduction.

Cladograms are simply diagrams which show how species, or groups of species, are interrelated. They look like this:

```
Vertebrates
|--sharks
`--Tetrapoda
   |--dinosaurs
   `--+--monkeys
      `--you
```

Notice that we don't have to put in every group. Presumably there are other tetrapods besides dinosaurs, monkeys and you. Nor do we have to name every group. For example, there is some taxon that unites you and monkeys to the exclusion of dinosaurs (***e.g.***, Primates or Mammalia), but it is represented simply by the '+' in the diagram. It's the ***relative*** position that is important.

This cladogram can be written several ways. The most inclusive group always goes at the top, by convention. However, we could describe precisely the same set of relationships like this:

```
Vertebrates
|--Tetrapoda
|  |--+--you
|  |  `--monkeys
|  `--dinosaurs
`--sharks
```

In both diagrams, to go from the first vertebrate to you, we have to split off sharks, go through Tetrapoda, split off dinosaurs and split off monkeys -- ***in exactly that order***. So, we are presenting the same evolutionary sequence, however it is displayed. The path between taxa counts, not where they fall on the page.

For reasons we will not get into here, each group is normally expected to diverge into precisely two others. However, we are often unsure (and unwilling to guess) exactly what the sequence was. Thus, you will frequently encounter:

```
Vertebrates
|--sharks
`--tetrapods
   |--dinosaurs
   `--+--monkeys
      |--Chopin
      |--Mozart
      |--Tansen
      `--you
```

Absent some unexpected miracle of genetics, you do not represent an evolutionary advance over Tansen or Mozart. (As to Chopin -- perhaps the less said the better.) The diagram simply indicates that, for phylogenetic purposes, you, Mozart, Chopin and Tansen are all the same distance from monkeys, dinosaurs, etc. and that all of you are more closely related to each other than to any of the other animals on the list (...with the possible exception of Chopin).

So why do we use cladograms? Cladograms do not necessarily require a "cladistic" view of the world. On the other hand, the cladogram does focus on phylogeny -- how different groups relate to one another. In that sense, cladograms differ a good deal from the usual Linnaean block diagrams. Let's look at a very simple example, a high-level description of the ornithischian dinosaurs in a Linnaean format:

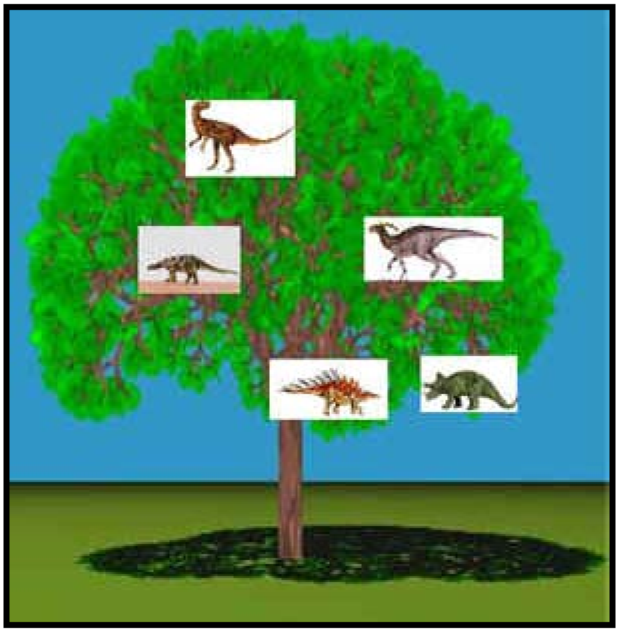
```
Order Ornithischia
    Suborder Fabrosauria
    Suborder Thyreophora
        Superfamily Stegosauria
        Superfamily Ankylosauria
    Suborder Ornithopoda
            Family Hypsiliphodontidae
            Family Heterodontosauridae
        Superfamily Iguanodontia
        Superfamily Hadrosauria
    Suborder Marginocephalia
        Superfamily Pachycephalosauria
        Superfamily Ceratopsia
```

Note that every group has a "rank:" order, family, genus, species, and innumerable gradations in between. Much breath and paper has been wasted arguing the appropriate rank of a group. What does a rank indicate? It cannot be a measure of internal similarity. There is no possible scientific answer to questions such as: "are hypsilophodonts more like each other than ceratopsians are like other ceratopsians?" Even if the question had an answer, it would tell us nothing. All sauropods, for example, are very much alike. Yet no one would argue that they are a mere family. Nor is rank a measure of diversity. Many families have only one member. Others have a hundred or more.

Perhaps a more significant problem is that the scheme doesn't tell us about the evolution or relationships of these groups. The current best guess, for example, is that all ornithischians are descended from "fabrosaurs" (the reason for the quotation marks will be explained later). The hypsilophodonts and heterodontosaurs are independently derived from the ornithopod stem. The iguanodonts may or may not be specialized hypsilophodonts, but the hadrosaurs are definitely of the Iguanodontia. The Linnaean diagram may be good ***systematics***, that is, a reasonable classification scheme. But it tells us nothing about phylogeny. It would be equally valid, and less misleading, to sort them in alphabetical order or by the zodiacal sign of the date of first publication.

Another way of stating this problem is that the Linnaean formalism doesn't tell us whether these taxa are natural groups or just a man-made assortment of similar organisms. Linnaean taxa are defined, if at all, by a list of characteristics. This is sometimes referred to as an "***apomorphy***-based definition" **[1]**. What if another, unrelated, organism were found with the same characteristics, or (as is more usually the case) it turns out that a Linnaean taxon contains organisms that have arrived at the same condition by convergent evolution? Conversely, if, for example, hadrosaurs are descended from iguanodonts, where do we draw the line? ***Ouranosaurus*** has characteristics which are somewhat intermediate between ***Iguanodon*** and "advanced" hadrosaurs. In the Linnaean scheme, we can call it an iguanodont or a hadrosaur, depending on exactly what characteristics we use to define these mutually exclusive terms. But, in doing so, we are arbitrarily putting things in boxes we ourselves have built and labeled. We are not discussing natural groups, but human constructs. Nor are we making testable scientific statements.

The cladistic view of the same group (with some additions) may be represented by the cladogram:



```
Dinosauria
|--Saurischia
|  |--Carnosauria
|  `--birds
`--Ornithischia
   |--"Fabrosaurs"
   `--+--Thyreophora
      |  |--Stegosauria
      |  `--Ankylosauria
      `--+--Ornithopoda
         |  |--Heterodontosauridae
         |  `--+--Hypsilophodontidae
         |     `--Iguanodontia
         |        |--Iguanodon
         |        `--+--Ouranosaurus
         |           `--Hadrosauridae
         `--Marginocephalia
            |--Pachycephalosauria
            `--Ceratopsia
               |--Monoclonius
               `--Triceratops
```

Here, there are no ranks. The phylogenetic relationships are open and obvious. They may not be ***correct***. But we can see what they are posited to be and can challenge the cladogram with evidence. It is testable, unlike a Linnaean scheme. The reason it is testable is that each taxon should (although even scientists are sometimes sloppy about this) have an explicit ***phylogenetic*** definition. The Ornithischia are "all dinosaurs more closely related to ***Triceratops*** than to birds." The phrase "more closely related to" is used in the following special sense: a dinosaur is more "closely related to" ***Triceratops*** than to birds if its last common ancestor with ***Triceratops*** is more recent than its last common ancestor with birds. For example, consider ***Ouranosaurus***. Its last common ancestor with ***Triceratops*** was some primitive cerapod (Cerapoda being the name of the "intersection" just to the left of "Ornithopoda" in the cladogram). The last common ancestor with birds would be much further up on the diagram.

There are four important things to note about this definition:

1) We didn't make up this group. We applied a man-made name, but it is a group which was produced by nature and defined by the actual course of evolution -- even though we may not have full knowledge of what that course was.

2) We don't know ***a priori*** who belongs in each category, or what characteristics the members of each group might have. Instead we use the tools of science to determine the answers to those questions. Taxa may be characterized by having particular physical attributes, but they are never ***defined*** by reference to these attributes. The attributes ("characters") are things we ***discover*** about the taxon.

3) There are no boxes. The Ornithischia are ***all*** dinosaurs closer to ***Triceratops*** then to birds. Not just some dinosaurs who look more like our mental preconception of what an ornithischian "ought" to be like.

4) Ornithischia is an example of a ***stem*** group: "**all organisms closer to x than to y**." A second kind of group used in cladistics is the "***crown group***." Usage has made this term a bit ambiguous. In its most general sense, a crown group is any group defined in the form: "**the last common ancestor of x and y and all the descendants of that ancestor**." For example, Dinosauria is defined as the last common ancestor of ***Triceratops*** and birds and all of its descendants. Cladistics, at its most elegant, describes phylogeny as a series of triads consisting of a crown group and two complementary stem groups:

```
Dinosauria (= birds + Triceratops)
|--Ornithischia (= Triceratops > birds)
`--Saurischia (= birds > Triceratops)
```

As in the diagram above, stem groups are usually described by the shorthand form "x > y". So, Ornithischia = "***Triceratops*** > birds." Crown groups are indicated "x + y." Dinosauria = "***Triceratops*** + birds." Note that the anchor taxa (***Triceratops*** and birds) can be changed without necessarily changing the definition. It doesn't matter what species of bird we might select, for example, if we are correct in believing that all birds have a single common ancestor.

```
Dinosauria
|--Ornithischia
|  |--Thyreophora
|  `--Cerapoda
|     |--Ornithopoda
|     `--Triceratops
`--Saurischia
   |--Carnosauria
   `--+--T. rex
      `--Aves
         |--kiwi
         `--+--flamingo
            `--+--falcon
               `--crow
```

In some cases, of course, those assumptions may be wrong. We should be careful in picking anchor taxa. However, it is much easier to remember Craniata as "hags + hagfish," rather than "***Myxine*** + ***Ausktribosphenos***." Unless something is very wrong with our picture of vertebrate evolution, the two are logically equivalent definitions.

However, it is critical to remember the "all" part of the definitions. Birds ***are*** dinosaurs because Dinosauria includes ***all*** of the descendants of the last common ancestor of birds and ***Triceratops*** -- including all birds. Birds are not "descended from" dinosaurs. Many people, scientists included, are frustrated by this rule. However, it is only by rigorous application of this (and other) cladistic rules that we can be sure that we are doing science and not just making arbitrary boxes. A natural group is called a ***clade***, and only clades are valid taxa for purposes of cladistic analysis. The ultimate reasons for this are well beyond the scope of this essay. For the moment, it will be enough to remember that the use of taxa other than clades invites confusion and ambiguity when we are generally using cladistic principles.

That is the reason that "fabrosaurs" are found only in quotation marks on this page. 'Fabrosauridae" is not a clade. It is simply a collection of primitive ornithischians. The best data available today suggest that their last common ancestor was also the ancestor of some (and perhaps all) other ornithischians. Since "Fabrosauridae" does not contain ***all*** of the descendants of the ancestral "fabrosaur" it is a ***paraphyletic group***, rather than a clade. Conversely, a group which does not contain its own last common ancestor is referred to as ***polyphyletic***.

But how do we go about making these determinations? That is a much longer and more difficult story. In fact, it is the whole subject of the science, theory, practice and art of cladistics. Aspects of this topic are discussed at many different points in **Palaeos**. A more systematic introduction to the subject may be added here in due course.

For the moment, this section contains a master cladogram of the Vertebrata -- a very high level cladogram containing only about 60 of the larger taxa. This is followed by a series of intermediate-level cladograms (incomplete as of this date) which cover the vertebrates in large chunks. For the most detailed level, see the individual units. ATW020430, last modified ATW041013.

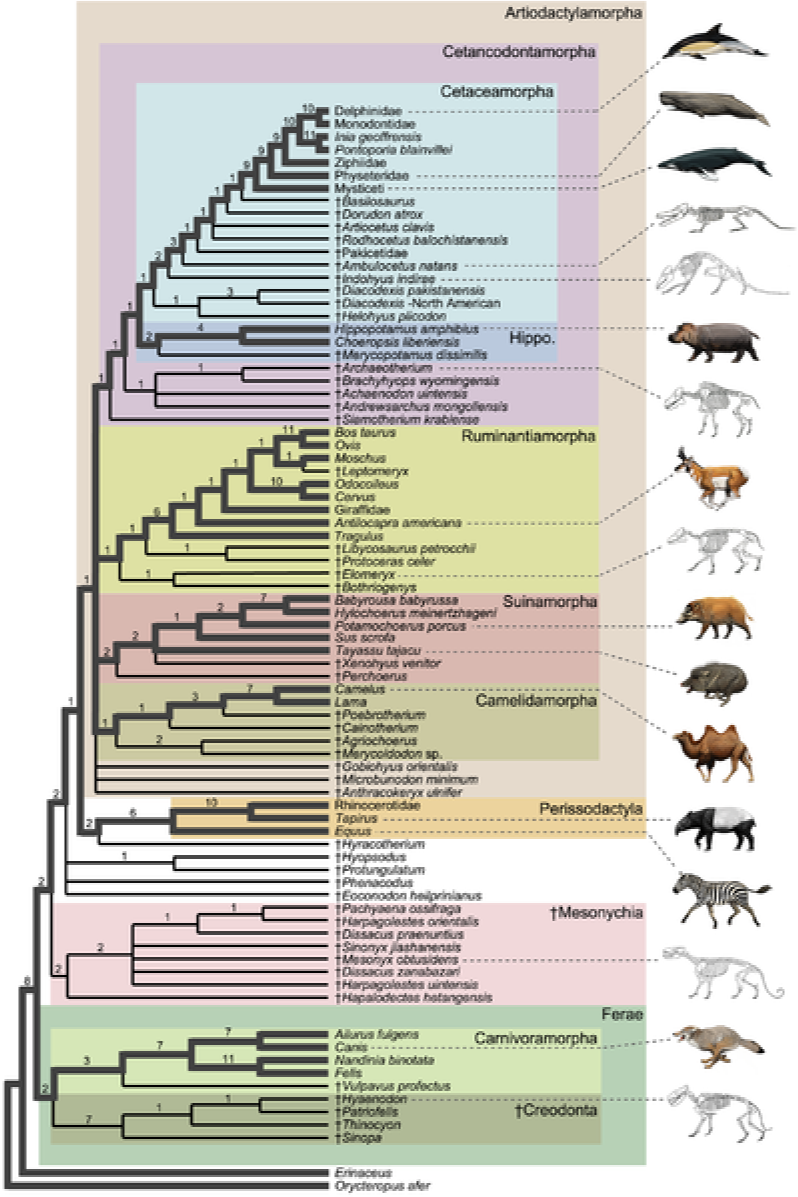
---

[1] That's not quite right. An apomorphy is a characteristic unique to a ***natural*** group -- a group descended from a single ancestor who had this character. The characters listed in a Linnaean definition need not, and often do not, meet this rigorous requirement. By the way, remember that, taken by itself, an apomorphy is inherently useless when it comes to inferring relationships to organisms lacking the apomorphy. The group which shares a derived character has a ***synapomorphy***, and we may infer that they are more closely related to each other than to others. So, for example, Mozart, Tansen, and (presumably) you enjoy good music and form a sort of musical clade. That doesn't mean that Chopin was more closely related to musical monkey than to Mozart. That's ***possible***, of course, and perhaps even likely, but we would need to identify other specific characteristics which Chopin shared with monkeys to the exclusion of Mozart and other tetrapods -- probably a long Liszt. ATW041013, revised ATW070828.

Page Back **Page Top** **Page Next**

Page Back
Unit Up: Systematics
Page Next
Unit Back: Evolutionary systematics
Glossary
Unit Next: Molecular phylogeny

Cladistics: Phylogenetic Systematics



A modern cladogram. Strict consensus of 20 minimum length trees for the equally-weighted parsimony analysis of the combined data set (57,269 steps). The contents of 12 taxonomic groups, including the total clades Cetaceamorpha and Cetancodontamorpha are delimited by different colored boxes (�Hippo� = Hippopotamidamorpha). Lineages that connect extant taxa in the tree are represented by thick gray branches, and wholly extinct lineages are shown as thin black branches. Estimates of branch support scores are above internodes; given the complexity of the data set, these should be interpreted as maximum estimates. Caption and diagram from Spaulding et al 2009, fig.2, Illustrations are by C. Buell and L. Betti-Nash. Creative Commons Attribution 2.5 Generic license, via wikipedia

Cladogram - a definition

A *cladogram* is a phylogenetic tree made up of dichotomous branches, with groups of organisms or individual species represented as terminals (the ends of each branch). Each branching point, or *node* represents divergence from a hypothetical

common ancestor, and is defined in terms of shared characteristics inhereted from that ancestor. A cladogram is not a literal evolutionary tree, but a way of representing phylogenetic hypothesis, regarding the way living organisms are related to each other. Each branch derived from that node is considered a natural grouping, and called a *clade*. Every clade has to be monophyletic, that is, it has to derive from a single ancetsor, and must include every descendent. Nodes do not represent actual ancestral taxa. Were an actual ancestor to be included it would ideally appear (if the cladogram is correct in this regard) as the sister taxon of the sub-clade that includes all its descendants.

Originally, cladograms used Hennigian methodology, and were based on immediately apparent synapomorphies and the simplest branching order (called parsimony). Although easy to draw they were difficult to quantify, as distinguishing a synapomorphy unique to that clade from a shared primitive state or an evolutionary convergence may be problematic.

From the 1990s onwards, cladograms have tended to become bigger and more complex, as powerful computers make it possible to run cladistic analyses using hundreds of traits and taxa, plotted in supermatrixes. Emphasis shifts from a few easily recognised synapomorphies to large arrays of quantifiable data, statistically analysed in terms

of parsimony or likelihood (which may not be the same). A lot depends on how statistically robust the actual branches are. Although some clades are robust, others may not be, for example, including or deleting a few taxa or character states can change the shape (topology) of the entire cladogram. The current trend in cladistics is to incorporate data from molecular sequencing; these total evidence cladograms are important in phylogenetics

Cladograms and other branching diagrams

As a result of the cladistic and phylogenetic revolutions, cladograms have almost entirely replaced Haeckelian and Evolutionary trees in textbooks and popular science books. A distinction should be mnade however between the three superficially similar dichotomous branching diagrams: the chronogram, the cladogram, the dendrogram, the phenogram, and the phylogram

Cladograms give information about branching order, but not about the amount of evolutionary change or stratigraphic range, or even superficial similarity. Cladograms can be drawn in any direction; it doesn't matter, all that matters is the sequence of branching, the topology or shape of the tree (which taxa are related to which). Several types of cladograms are used, depending on the methodology; these are referred to by somewhat unofficial terms:

- ***Hennigian<./em> or Phylogenetic Systematic cladograms identify nodes by synapomorphies (shared characteristics) and often use supra-species taxa as terminals***
- ***Computational cladograms statistically, and should show (using small superscripts and subscriptts) how robust - how strongly or weakly supported - each branch is, depending on the algorithm used; there is the tendency for them to only have individual species in each terminal. Because there rae many possible trees (phylospace), computational cladograms are phylogenetic hypothesis, which are used in phylogenetics***
- ***Supertrees are cladograms of cladograms; they are constructed through using individual cladograms as if they were taxa and avoid the problem of excessive number crunching when using large numbers of taxa. These impressive diagrams have a lot of appeal, especially as regards the goal of large scale tree of life phylogeny, although as with anything they are not without their difficulties; for example they were only as good as the data that generated the component cladograms.***

Phylograms are statistical diagrams used in molecular phylogeny. They not only show the branching sequence, exactly as in cladograms, but also the degree of evolutionary change or difference of each species, as shown by the length of the branch; the longer the branch, the motre change. They can be rooted or unrooted; rooted trees show the ancestors, whereas unrooted ones don't.

***Phenograms** are statistically generated trees used in **phenetics**. They look like cladograms but aren't. They only give information about overall similarity. While they may be useful for identifying species, they are now rarely uised*

***Chronograms** are like cladograms, but use the contrast of thin/unshaded and thick/shaded branches to show the stratigraphic range of the taxon represented by each branch. They are widely used and have replaced **spindle diagrams** in books and scientific papers*

***Dendrograms** as we use the term here, are informal cladograms. They are not intended as hypotheses but as speculative phylogeny, and are informal supertrees and phylogenies. They are popular on paleo discussion mail list, and on some projects like the Tree of Life web project. Here at Palaeos we use dendrograms to organise the taxonomic pages. MAK130417*

Page Back **Page Top** **Page Next**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

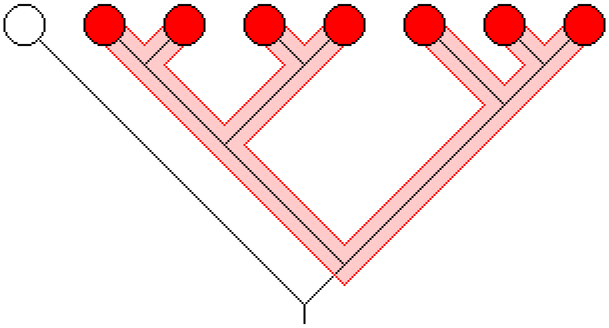
Page Back	Unit Up: Systematics	Page Next
Unit Back: Evolutionary systematics	Glossary	Unit Next: Molecular phylogeny

Definition: Monophyly

Cladistics
  Cladistics - An Introduction
  Phylogenetic Systematics
  Pattern cladistics
  Cladistics and Paleontology
  Computational cladistics

Definition: Cladogram
Definition: Monophyly
Definition: Paraphyly
Definition: Polyphyly

Monophyletic Taxa



graphic © Darren Abbey

The ***Monophyletic taxon***,also called a ***clade***, is the building block of the cladistic system of taxonomy. It refers to any group of organisms that includes the most recent common ancestor of all those organisms and all the descendants of that common ancestor.

Examples: Insects, Vertebrates, Mammalia, Angiosperms, etc, etc.

A definition of monophyly, from Glossary of Phylogenetic Systematics by Günter Bechly:

> "**monophyletic group (= monophylum):** In a hierarchical system of descent, an ancestor (stem-species) and all of his descendants (descendant species) together form a closed community of descent that is called a monophyletic group (***sensu*** HENNIG; =

> holophyletic group ***sensu*** ASHLOCK) or monophylum. Monophyletic groups can be discovered (not defined!) by synapomorphies. The term monophyly is always referring to groups of hierarchically reproducing entities (species) and consequently can not be applied to (or within) a single biospecies or even to a single organism..."

---

images not loading? | error messages? | broken links? | suggestions? | criticism?

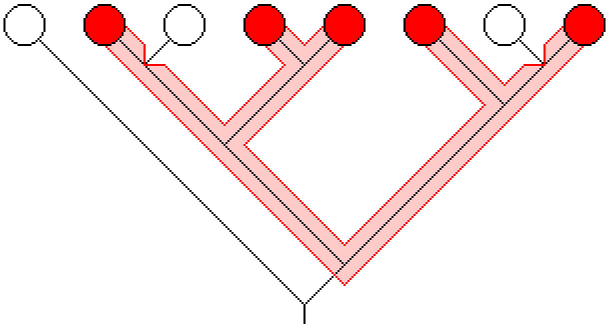
contact us

non-quoted text by M. Alan Kazlev (Creative Commons Attribution 3.0 Unported License), cladogram graphic © Darren Abbey, reproduced with permission
page uploaded 20 May 2002 (originally uploaded on Kheper Site 13 November 1998)
checked ATW040703 last modified MAK090828, edited RFVS111203

Page Back | Unit Up: Systematics | Page Next
Unit Back: Evolutionary systematics | Glossary | Unit Next: Molecular phylogeny

Definition: Paraphyly

Paraphyletic Taxa



graphic © Darren Abbey

The ***Paraphyletic taxon*** is a group of organisms in which the most recent common ancestor of all those organisms and ***some***, but not all, of that ancestor's descendents are included. Paraphyletic taxa are recognized in Linnaean and evolutionary systematics but not in cladistics.

Illustration: the Class Reptilia gave rise to mammals and birds, but neither mammals nor birds are included under Reptilia.

Examples: Invertebrates, Amphibia, Reptilia, Dinosauria if excluding birds, Gymnosperma, etc.

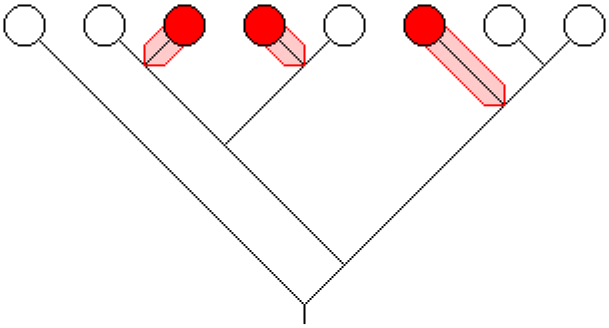
---

contact us

page uploaded 20 May 2002 (originally uploaded on Kheper Site 13 November 1998) last modified MAK090828
checked ATW040703 last modified MAK090828, edited RFVS111203

Definition: Polyphyly

Polyphyletic Taxa



graphic © Darren Abbey

The ***Polyphyletic taxon*** is a group composed of a number of organisms which might bear some similarities, but does not include the most recent common ancestor of all the member organisms (usually because that ancestor lacks some or all of the characteristics of the group). The taxon shares derived characters which originated several times by convergence.

Illustration: it used to be thought (in Victorian times) that all pachydermatous (large stocky hairless thick-skinned herbivores) mammals - e.g. rhinos, hippos, and elephants - were descended from a single large ancestor. It is now known that each of these animals evolved from a separate small ancestor, and the common ancestor of all of them was small and slightly built, with presumably thin skin and fur.

Another Illustration: Some cladists (e.g. Lovtrup and Gardiner) have argued that because warm-blooded birds and mammals share a number of metabolic and anatomical features in common they must have descended from a single warm-blooded Most Recent Common Ancestor and thus constitute the clade

Haemothermia. It is now known that endothermy (warm-bloodedness) evolved independently in each group.

Polyphyletic taxa are considered invalid or unnatural groupings, and are not accepted in either the Linnaean/Evolutionary or the Cladistics taxonomies.

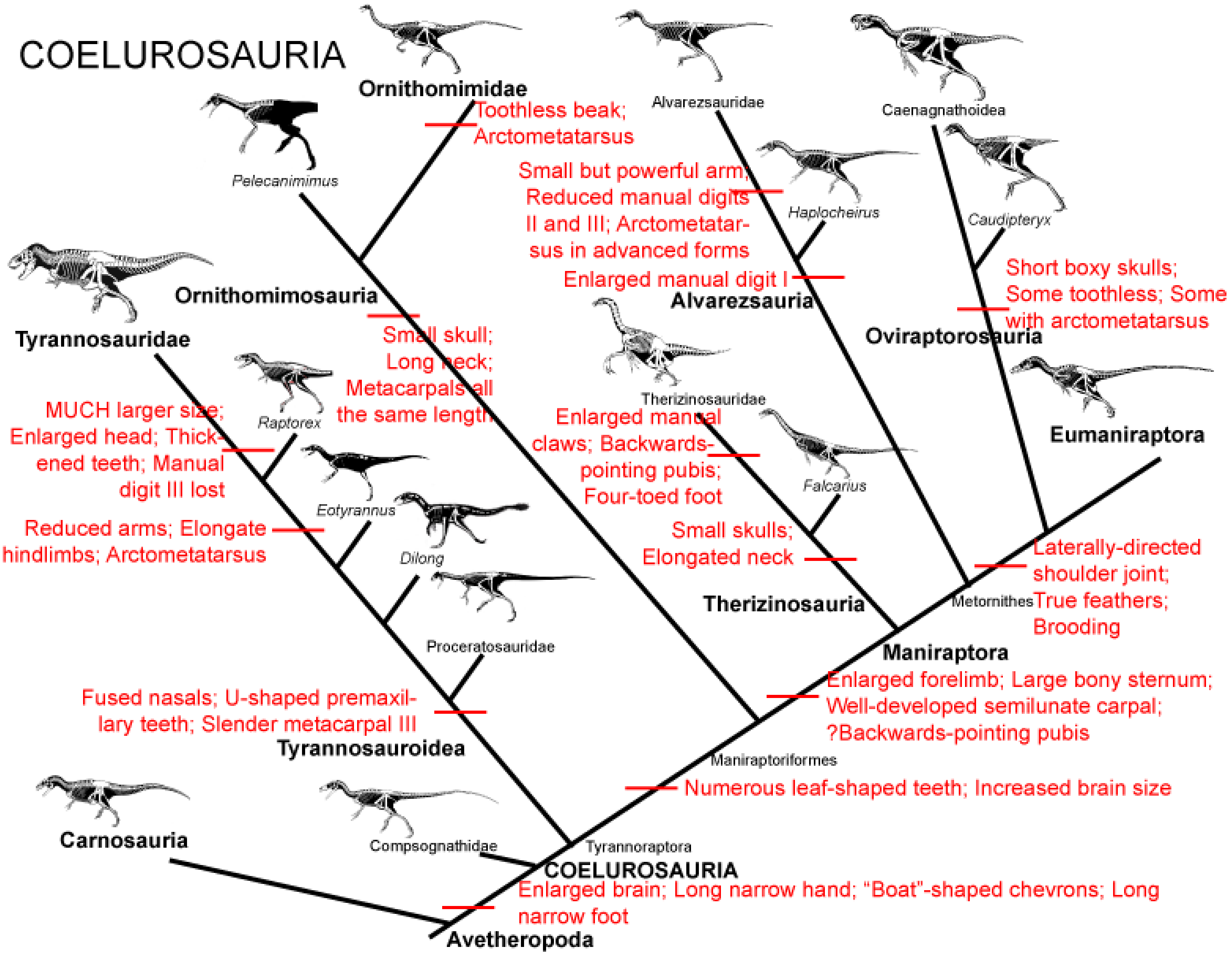
Examples: Pachyderma, Haemothermia, Algae, Vermes (worms).

---

page by M. Alan Kazlev 1998-2002, cladogram graphic © Darren Abbey, reproduced with permission
page uploaded 20 May 2002 (originally uploaded on Kheper Site 13 November 1998)
checked ATW040703 last modified MAK090828, edited RFVS111203

Page Back | Unit Up: Systematics | Page Next
Unit Back: Evolutionary systematics | Glossary | Unit Next: Molecular phylogeny

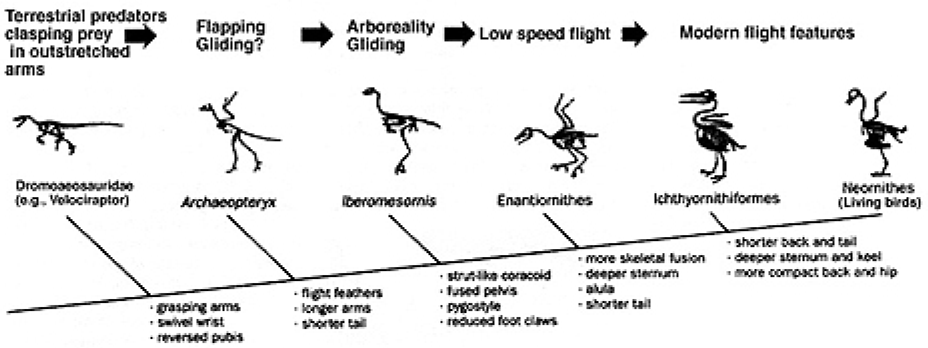
Cladistics: Cladistics and Paleontology



Cladogram of the Coelurosauria, by Tom Holtz, showing synapomorphiesin red. From GEOL 104 Dinosaurs: A Natural History. Tom Holtz, who specialises in theropod evolution, is one of the generation of modern vertebrate paleontologists who have popularised the importance and use of cladistics in the paleo geek consciousness.

Beginning in the mid 1980s, paleontology began to play an essential role in cladistics, thanks to the pioneering efforts of vertebrate paleontologists like Jacques Gauthier (Gauthier 1986), Eugene Gaffney, Susan Evans, Michael Benton, and others. Significantly, all these scientists were concerned with the evolution of reptiles (and in Gauthier's case and those of others such asKevin Padian, of birds from dinosaurs); reptiles having a rich fossil record (of course, being cladists, they weren't allowed to use the "R" word in any formal context). In this way, what began as an obscure alternative to phenetics and evolutionary systematics came to be the defining paradigm for understanding the evolution of life (first vertebrate, than the tree of life in general).

Cladistics never really took off with mammals; as mammals are a group with a large number of extant (recent) taxa, a different methodology, molecular phylogeny, was used to determine their evolution. Only in recent years with the unification of molecular sequencing and statistical cladistics has cladistic methodology been applied to mammals. And as for plants, the influence and prestige of



Cladistic scenario for the origin of birds from dinosaurs and the consequent evolution of flight. Each successive clade (here moving left to right) includes the attributes of previous ones (parent clades). These sorts of diagrams were used to prove the origin of birds from dinosaurs in the 80s and 90s. After Padian, 1996, via original url - note this author does not agree with dino to bird hypothesis

Linnaeaus ensures that cladistic formalism will make little inroads for some time.

By the 1990s, synapomorphy-based cladistics had totally replaced evolutionary systematics in the admittedly specialised field of vertebrate paleontology. Many other fields of biological taxonomy, especially botany, have remained staunchly Linnaean (no doubt due to Linnaeus being a botanist and one of the founders of the field). Despite this paradigm revolution, cladistics and evolutionary systematics are two very different systems. One important difference is that evolutionary systematics deals with ancestor-descent relationships, especially in supra-specific taxa, and cladistic trees with sister relationships of individual species, or even, in the case of fossils, individual specimens. Another is that evolutionary systematics is strongly paleontological, emphasising the stratigraphic sequence in the fossil record in deep time, whereas cladistics place a strong emphasis on neontology, as extant taxa can provide far more information - e.g. soft tissue, molecular, etc. Finally, evolutionary systematics emphasises stratigraphic occurrence, whereas at least early cladistic paleontology considers this phylogenetically unimportant (this is changing with current Phylogenetics).

Synapomorphy-based cladistic paleontology and phylogenetic taxonomy were widely adopted by the online paleo community in the late 1990s (see for example the Dinosaur Mailing list archives), and became the central methodology of earlier iterations of Palaeos (the Vertebrate Notes (1999-2001) and Palaeos mk 1 (2002-6)

By the middle of the first decade of the 21st century, the growing power and easy availability of computers meant that single-tree synapomorphy-based cladistics had completely given way to computational cladistics, and easily recognisable synapomorphies were replaced by obscure combinations of character states thrown up by statistical algorithms. In turn computational cladistics, with its emphasis on fossil reptiles, was assimilated by the more widely applied and popular molecular phylogeny to give the new science of phylogenetics and the rejection of morphological parsimony MAK130321

Page Back | Page Top | Page Next

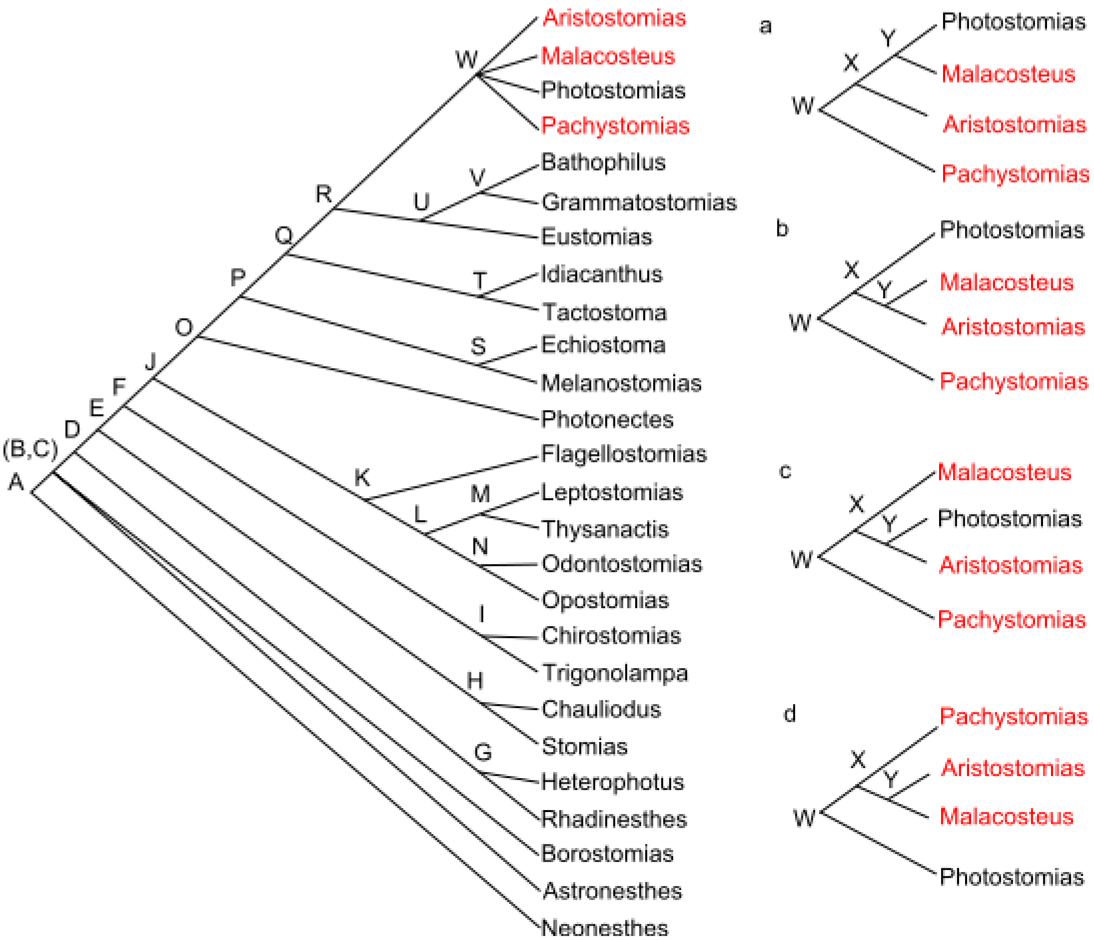
images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

Page Back | Unit Up: Systematics | Page Next

Unit Back: Evolutionary systematics | Glossary | Unit Next: Molecular phylogeny

Cladistics: Computational cladistics



From Wikipedia. An example of an algorithm-derived cladogram. Cladogram of stomiid fishes, according to Fink WL. 1985. Phylogenetic interrelationships of the stomiid fishes (Teleostei: Stomiiformes). *Miscellaneous Publications of the Museum of Zoology*, University of Michigan 171:1-127. Note the absense of easily recognisable synapomorphies. The resolved cladograms of this topology have a length of 496 and consistency index of .494, without the seventy-eight generic apomorphies. With generic apomorphies included, the length is 574, the consistency index is .563. A-D show alternative resolved cladograms for *Malacosteus-Pachystomias-Aristostomias-Photostomias* group. For character conventions, see Fink (1985). Diagram and text by Filip em. The letters A to Y represent nodes, the names at the right of the diagram genera.

After the incorporation of paleontology, the next big revolution in cladistics was statistical computation, methods also used in molecular phylogeny. With the rise of cheap and easily available high powered computing, computational phylogeny and algorithm-based cladistics has replaced the original one-shot cladogram of earlier Phylogenetic Systematics. This meant a change in emphasis from identifying small numbers of easily recognisable and studied synapomorphies (without cheap and powerful computing it was not practical to do otherwise), to statistical analyses of huge data matrixes and supermatrixes, featuring hundreds of character states and millions of possible trees. Cladistics then focuses on evaluating and selecting the most likely or plausible phylogenetic hypotheses. This is because whereas Phylogenetic Systematics would only result in a single, parsimonious cladogram, statistical cladistics calculates millions. The big problem here is the missing data in fossil forms, which are often incomplete and fragmentary, and which therefore act as wildcards. Some taxa can be particularily unstable, jumping around to different positions in different trees. Nevertheless, fossil taxa still provide useful informnation and an additional phylogenetic signal that would not be present if only extant taxa were used.

There are several algorithms available to identify the "best" cladogram. Most algorithms use a metric (a mathematical function which defines a distance between elements of a set) to measure how consistent a candidate cladogram is with the data. Most cladogram algorithms use the mathematical techniques of optimization (choosing the best element from some set of available alternatives) and minimization. In general, cladogram generation algorithms must be implemented as computer programs, although some algorithms can be performed manually when the data sets are trivial (for example, just a few species and a couple of characteristics). Algorithms include least squares (minimising the sum of the squares of the errors made in solving every single equation), neighbor-joining, parsimony, maximum likelihood, and Bayesian inference. (Wikipedia)

Although computational cladistics uses all of the same basic principles of phylogenetic systematics, it results in very different results. Often stratigraphically early monophyletic groups, such as Gauthier's Ceratosauria, which in terms of obvious synapomorphies appear to be simply a large clade of primitive theropod dinosaurs, become paraphyletic step-wise evolutionary grades, thus eliminating excessive ghost lineages and generating cladograms closer to the actual stratigraphic record. Other differences might be previously monophyletic clades now becoming diphyletic, as with protostegid sea turtles that in terms of easily recognised synapomorphies are very close to leatherback sea turtles, but are shown by statistical analysis to be a totally distinct and much more primitive group that are simply convergent with modern sea turtles. These sorts of results tend to be more compatible with both molecular phylogeny and stratigraphy in showing that what were previously considered to be homologies (shared characteristics inhereted from a common ancestor) are actually astonishing instances of homoplasy (convergent evolution). Contrary to the insights of the early cladists, who emphasised parsimonony-based approaches, it seems that homoplasy is rampant throughout nature, making attempts at reconstructing phylogeny difficult at best.

Perhaps because of its far larger data set and its more empirical and quantitative approach, computational or algorithm-based cladistics is considered more reliable than hand-coded Phylogenetic Systematics. In all other respects they are still very similar, in that they both emphasise distinguishing synapomorphies or homologies from plesiomorphies, and from homoplasies (convergences) in order to identify monophyletic clades

In the late 2000s and early 2010s, algorithm-based cladistics has become assimilated intomolecular phylogeny, as the two use exactly the same statsitical algorithms to create the most optimal cladograms. When integrated, statistical cladistics and molecular become the new science of phylogentics. A problem here is that these two methodologies often give strongly incongruent trees. Nevertheless this a victory for the molecules, as in the great majority of published papers wherever there is a clash between molecules and morphology, morphology-based cladistics plays second fiddle to molecular sequencing. The challenge of phylogenetics is to avoid this bias and balance the two methodologies (and others as well). MAK210324

Page Back | Page Top | Page Next

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

Page Back | Unit Up: Systematics | Page Next
Unit Back: Evolutionary systematics | Glossary | Unit Next: Molecular phylogeny

Cladistics: Pattern and Transformed cladistics

Phylogeny and Systematics
  History of systematics
    The Great Chain of Being
    Linnaean taxonomy
    The Tree of Life
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Stratigraphy and phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

Cladistics
  Cladistics - An Introduction
    Definition: Cladogram
    Definition: Monophyly
    Definition: Paraphyly
    Definition: Polyphyly
  Phylogenetic Systematics
  Pattern cladistics
  Cladistics and Paleontology
  Computational cladistics

In the late 70s and early 80s a new school of cladistics, called ***Pattern cladism*** was developed by Gareth Nelson and Nelson Platnick ("New York Cladists") in 1979, and later developed as ***Transformed cladism*** in the works of Colin Patterson (1982). Essentially a reaction to Ernst Mayr's evolutionary systematics, Pattern or Transform Cladism aims at the calculation of most parsimonious cladograms using the pattern of their characters alone, without any recourse to actual phylogeny, through separation of "pattern and process".

Pattern cladistics resembles phenetics in that it does not use character rooting and synapomorphies are not used, although monophyletic groups are acknowledged.

Ebach et al 2008 relate ***Transformed cladism*** to the works of Colin Patterson (1982) and Platnick (1979) and say that in contrast to pattern cladists who are Non-Hennigian, Transformed cladists are Hennigian and root their trees according to either outgroups, ontogeny or concepts such as set theory.... They opt for a definition of monophyly that does not include the most recent ancestor. They do not reject totally transformation, but they do use a concept of character rooting that is inherent within set theory". It seems however that these differences are mostly minor and the two are more usually synonymised.

Like phenetics, pattern and transformed cladists strove to be as objective and empirical as possible. They assert that a cladogram was merely a summary of shared characters, that could at best ***test*** a historical reconstruction (The philosophy of classification Pattern cladism and the myth of theory dependence of observation - John Wilkins) (as phylogenetic hypotheses), but reject the possibility that a real evolutionary history can ever be arrived at. There also tends to be a lack of interest in the fossil record, as fossils were considered to have insufficient characters to be used in a cladogram. Patterson's revision of the British Museum public displays caused something of a stir at the time, being greeted enthusiastically by Creationists who, totally failing to understand the purely pragmatic approach, thought that Darwinists had finally accepted there was no such thing as evolution.

Even so, the idea that science can be theory-neutral is itself philosophically problematic (Pearson 2010). Criticised by Richard Dawkins' ***The Blind Watchmaker***, (quotes and comments here, but see this defense of pattern and transform cladism. (MAK, IAB blog)

Pattern cladism did not last long as a distinct movement, although its pragmatic empirical insights, such as cladistics as hypothesis testing (especially important in computational cladistics, where it is often necessary to choose between hundreds of possible cladograms), have been assimilated into ***Phylogenetic Systematics***, the two together simply being known as Cladistics. MAK130321

Page Back **Page Top** **Page Next**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

Page Back | Unit Up: Systematics | Page Next
Unit Back: Evolutionary systematics | Glossary | Unit Next: Molecular phylogeny

Phenetics

Phylogeny and Systematics
  History of systematics
    The Great Chain of Being
    Linnaean taxonomy
    The Tree of Life
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Stratigraphy and phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

Cladistics
  Cladistics - An Introduction
    Definition: Cladogram
    Definition: Monophyly
    Definition: Paraphyly
    Definition: Polyphyly
  Phenetics
  Phylogenetic Systematics
  Pattern cladistics
  Cladistics and Paleontology
  Computational cladistics

Phenetics, or ***Phenetic systematics***, is not the same as cladistics, but we've placed it here basically because there's nowhere else to put it. It is no longer a distinct school of systematic biology, and has at best limited application. Nevertheless, like cladistics it began as an alternative to evolutionary systematics, and it pioneered the sort of quantitative computational phylogeny and quantative statistical analysis that would later become central to both cladistics and molecular phylogeny. There was even a short-lived school of cladistics, called Pattern cladism, that was very similar to phenetics.

Phenetics started out as a school of numerical taxonomy that was developed in the late 1950s by bacteriologist Peter H. Sneath, entomologist Charles D. Michener, and quantitative geneticist Robert R. Sokal, that classifies organisms on the basis of overall morphological or genetic similarity. It is not the same as cladistics, but it is a prequel to it, sharing many features in common. The school of Pattern Cladism could be considered a synthesis of cladistics and phenetics

Phenetics mainly involves observable similarities and differences irrespective of whether or not the organisms are related. It involves grouping types together in clusters; types with many close relatives would be in a cluster. The development of Phenetics, which was intended to replace evolutionary systematics, was inspired through the quantitative successes and advances in genetics (e.g. discovery of DNA by Watson & Crick (1953)), chemistry and physics, on the other hand as a reaction to positivism and incorporation of a strictly pragmatic approach, which denies that we can know the thing in itself (hence the rejection of phylogeny and evolution). The availability of computers (at this time still big hulking things) also facilitated and encouraged quantitative data comparisons. It uses distance matrix-based methods to construct trees based on overall similarity, which is often assumed to approximate phylogenetic relationships.

Phenetics classifies organisms on overall similarity, usually in morphology or other observable traits, regardless of their evolutionary relationship. It stressed the use of many unweighted characters assessed by overall similarity, purging all intuition and subjectivity and striving to be theory neutral, objective, and quantitative, with observation, description and ordering performed as precisely, objectively and repeatably as possible. Hence all evolutionary and phylogenetic interpretations are rejected as too difficult and subjective. It was considered that phylogenetic reconstruction was nearly impossible to know with any degree of certainty, and therefore, if classification were to be scientific, this futile quest should be abandoned. (Stuessy 2009, UCMP)

In the end Phenetics was unsuccessful and eventually abandoned in favour of cladistics for a number of reasons, including numerous difficulties encountered owing to convergence (homoplasy, as individual characters assumed to be homologous were not carefully analysed), mosaic evolution, and a shortage of diagnostic characters (Mayr & Ashlock 1991, pp. 195-205). Even so, certain phenetic methods, such as neighbor-joining, have found their way into cladistics, as a reasonable approximation of phylogeny when more advanced methods (such as Bayesian inference) are too computationally expensive. (Wikipedia). Also, with the rise of molecular systematics, distance methods, which are basically phenetic methods, have become popular, although these are vulnerable to the same problems, especially that of homoplasy. (Mayr & Bock 2002 p.180). MAK130321

Page Back **Page Top** **Page Next**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

Page Back | Unit Up: Systematics | Page Next
Unit Back: Evolutionary systematics | Glossary | Unit Next: Molecular phylogeny

Cladistics: Phylogenetic Systematics

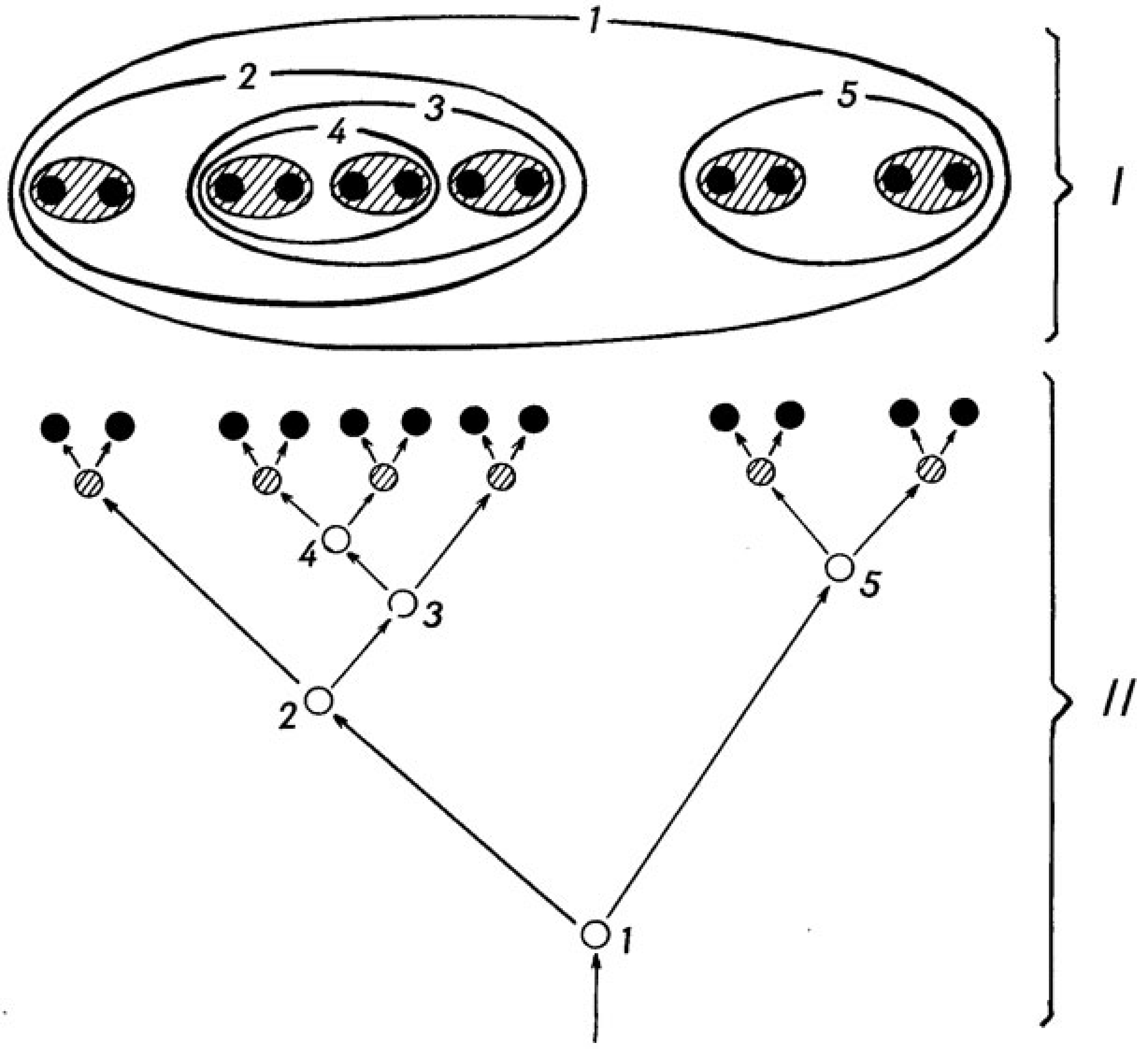


Figure 18. The phylogenetic kinship relations between the species of a monophyletic group, represented in two different ways.

Hennig's two types of cladistic diagrams, from *Phylogenetic Systematics*, figure 18, showing nested clades. The caption reads: "The phylogenetic kinship relationship between the species of a monophyletic group, represented in two different ways." The top drawing (I) shows a set-based, nesting diagram, while the bottom (II) shows a branching tree diagram. This diagram shows the interconnection between branching diagrams and nesting diagrams, but remains equivocal about which is best for displaying the evolutionary relationships phylogenetic methods aim to uncover. - from Rebecca Shapley, *Visualizing the Tree of Life*

History

"Phylogenetic Systematics" is a rigorous methodology first developed by German entomologist Willi Hennig in the 50s and 60s as a means of evaluating and reconstructing phylogenies if fossils are lacking (insects have a notoriously poor fossil record). Hennig's work was translated into English as ***Phylogenetic Systematics*** (University of Illinois Press, 1966), which remains a foundational text for modern phylogenetic studies. Nevertheless his work remained little known until the late 70s, when it was rediscovered and taken up by newer workers in the field such as James S. Farris, Walter Fitchand, and Herb Wagner, and applied in American and British paleontology. Note that Hennig never used the word "cladistics", which was coined by Mayr for an adherent of Hennig's school.

For a short while there was a rival school or schools, known as Pattern or Transformed Cladistics, which rejected Hennig's emphasis on phylogeny in favour of cladograms as tests of a phylogenetic reconstruction, rather than as anything to do with actual evolutionary history, and which had elements in common with phenetics. But such an approach lacked the appeal of Phylogenetic Systematics, and although the idea of hypothesis testing was retained in later forms of cladistics, the rejection of phylogeny was not.

Here we use Phylogenetic Systematics to refer to traditional, Hennigian cladistics and its later and current applications, as opposed to Pattern and Transformed Cladistics, Computational cladistics, and Phylogenetics.

Methodology

Phylogenetic Systematics focuses on identifying unique (derived) shared characteristics, called, synapomorphies. These are distinguished from primitive shared characteristics, which are called plesiomorphies. Only synapomorphies can provide information about the evolutionary history of a group; its phylogeny. The aim is to identify what Hennig called monophyletic groups, that is groups consisting of common ancestor and all its desendents. These are known as clades. This is represented in the form of the now familiar and ubiquitous tree like diagram called a cladogram. In contrast to evolutionary systematics, Phylogenetic Systematics only acknowledges monophyletic groups. The relation between the different clades is shown by a tree-like diagram or cladogram. Because there are any number of possible alternative cladograms (or evolutionary histories), only the simplest one, requiring the least number of changes, is chosen.

In short, Linnaean taxonomy and Evolutionary Systematics are concerned with ***both*** plesiomorphies and synapomorphies, whereas Phylogenetic Systematics is only concerned with synapomorphies only; Evolutionary Systematics is concerned with both monophyletic (also called holophyletic) and paraphyletic groups (made up of a common ancestor and only some of its desendents) , whereas Phylogenetic Systematics only with monophyletic groups. And unlike Evolutionary Systematics it does not use a specific Linnaean hierarchy of ranks (e.g. class, phylum). This is why cladists woin't even recognise Class Reptilia as a natural group; because reptiles evolved into two other taxa, birds and mammals, they are paraphyletic rather than monophyletic. MAK130320

In this context, the following definitions are used

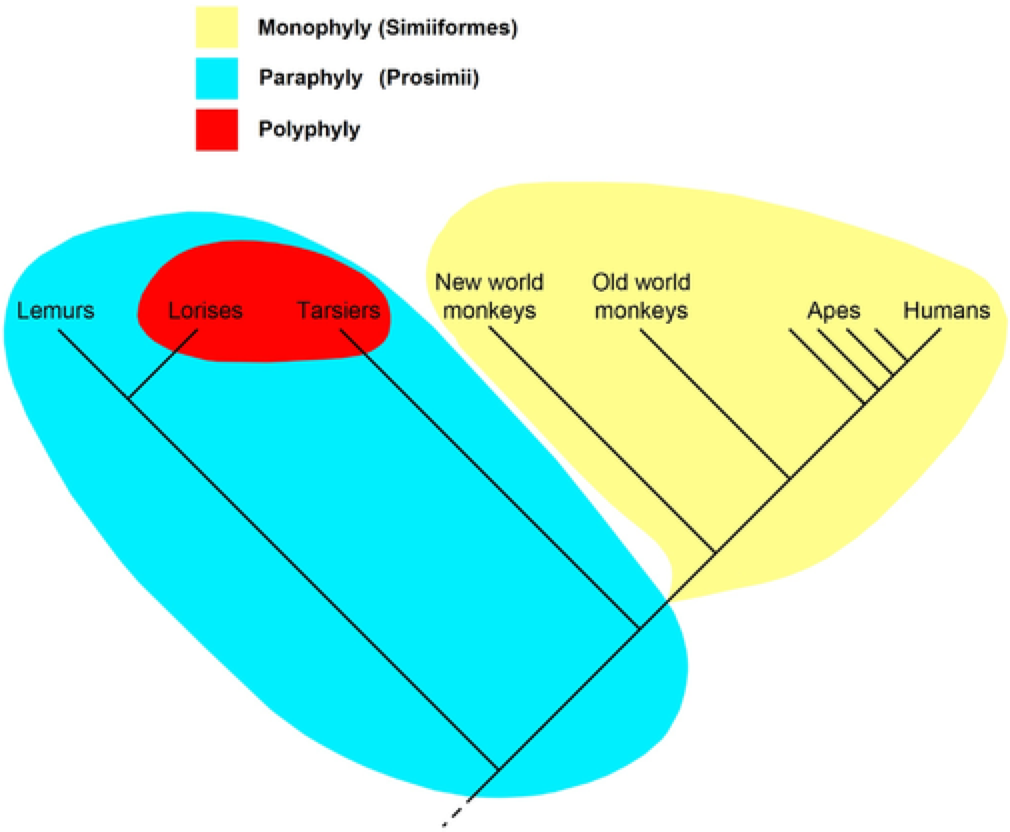
Outgroup We have seen above that a clade is a branch on a tree of descent. Anything occurring outside that branch, further towards the root of the tree, is an outgroup.

The distinction is more than simply contextual: For example, in order to calculate the similarity of genome sequences, it is essential to include within the study one or, preferably, several taxa that lie outside the group in which we are trying to detect relationships. If we are interested in determining the relationships of tigers, we would use close relatives of tigers as our outgroups.

Outgroup comparison is the way we determine how widespread a particular feature may be, whether it is found only within the group (apomorphies) of interest, or beyond that group.

Monophyly (Monophyletic Group) A monophyletic group is one which includes an ancestral species and all its descendants. It is a complete clade.

As we have seen, a monophyletic group can be extremely large and inclusive – for example, most people today would agree the legions of different kinds of insects comprise a monophyletic group – or quite small and exclusive – for example, the enigmatic sea spiders (class Pycnogonida).



A cladogram of the primates with groups showing different phylogenetic units: Monophyly (Simiiformes), paraphyly (Prosimii) and polyphyly (the night active primates, the lorisis and the tarsiers). Diagram by Petter B�ckman, revised by Peter Brown, Creative Commons Attribution, Wikimedia

Paraphyly (Paraphyletic Group) - A paraphyletic group is a clade lacking some of the descendant species.

Today there is a movement away from applying formal names to groups which are known to be paraphyletic, although some of the old taxa are still very useful even though they are now believed to be paraphyletic.

Perhaps the best example is the reptiles. Because both mammals and birds evolved from reptilian ancestors, but are not included in the class Reptilia, the latter is clearly paraphyletic and a cladistic purist might prefer not to use the name. However, the meaning and scope of the reptile class is still a very well understood and useful concept.

What is more, if we were to blindly enforce “Russian doll nomenclature” in this fashion, it seems unlikely the existing hierarchy of taxonomic ranks will cope.

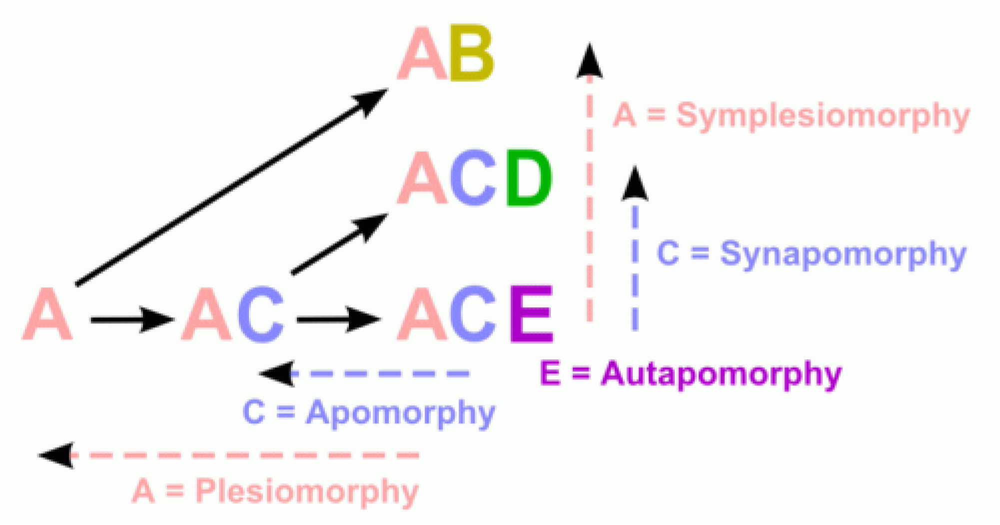
Polyphyly (Polyphyletic Group) - A polyphyletic taxon is an “unnatural” assemblage of two or more clades, united by some characteristic which is not a primitive feature (plesiomorphy).

Groupings which are thought to be polyphyletic truly are avoided by taxonomists, which is one reason there are not too many familiar real examples. An artificial example is “warm blooded animals,” a group which includes both mammals and birds. However, both these groups arose, at different times, from cold-blooded (reptilian) stock: their warmbloodedness is not an apomorphy, but it evolved separately, and is different in detail.

Again, however, all is not plain and simple. Some taxa, even those with a long history of study such as the arthropods, are still subject to on-going controversy. Although most researchers are of the view that the Arthropoda are a “good” monophyletic clade, there remain a few who argue that the arthropod characteristics were arrived at separately by more than one lineage, and thus the group is polyphyletic. They are in a small minority, but some small doubt remains.

Chris Clowes 030219

From Wikipedia



A plesiomorphy ("close form") or ancestral state is a character state that a taxon has retained from its ancestors. When two or more taxa that are not nested within each other share a plesiomorphy, it is a ***symplesiomorphy*** (from syn-, "together") of theirs. Symplesiomorphies do not mean that the taxa that have them are necessarily closely related. For example, Reptilia is traditionally characterized by (among other things) being cold-blooded (i.e. not maintaining a constant high body temperature), whereas birds are warm-blooded. Since cold-bloodedness is a plesiomorphy, inherited from the common ancestor of traditional reptiles and birds, and thus a symplesiomorphy of turtles, snakes and crocodiles (among others), it does not mean that turtles, snakes and crocodiles form a clade that excludes the birds.

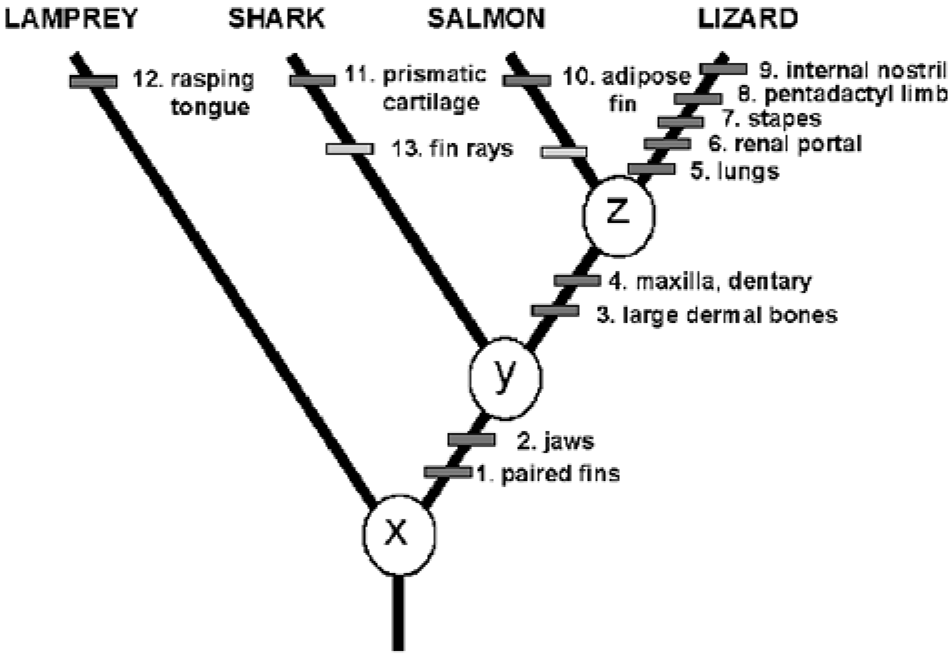
An apomorphy ("separate form") or derived state is an innovation. It can thus be used to diagnose a clade - or even to define a clade name in phylogenetic nomenclature. One clade may have ***autapomorphies*** (from auto-, "self"), two sister-groups may have ***synapomorphies*** (from syn-, "together"). For example, the possession of digits that are homologous with those of ***Homo sapiens*** is an apomorphy within the vertebrates. The tetrapods can be singled out as consisting of the first vertebrate with such digits together with all descendants of this vertebrate (an apomorphy-based phylogenetic definition). Importantly, snakes and other tetrapods that do not have digits are nonetheless tetrapods: they descend from ancestors that possessed them.

A character state is **homoplastic** or "a **homoplasy**" if it is shared by two or more organisms but was not present in their common ancestor. It has evolved by convergence or reversion. Both mammals and birds are able to maintain a high constant body temperature (i.e. they are 'warm-blooded'). However, the ancestors of each group did not share this character, so it must have evolved independently. Warm-bloodedness is separately an apomorphy of mammals and birds, but it is not a synapomorphy of these two clades.

The terms plesiomorphy and apomorphy are relative; their application depends on the position of a group within a tree. An (aut)apomorphy of one clade is a plesiomorphy of each of its members.

- Wikipedia

An actual example of cladistic analysis, showing the way characters can be used to determine the phylogenetic relationship between taxa, is shown below:



An example of a cladogram showing characters by which taxa are recognised. Characters 1 - 4 are synapomorphies, 5 - 12 are autapomorphies and 13 is an attribute seen in the salmon and the shark. Characters numbered 3 and 4 are synapomorphies suggesting that the lizard and the salmon shared a unique common ancestor 'Z'. It suggests that characters 3 and 4 arose in ancestor 'Z' and were inherited by the salmon and the lizard. Shared primitive characters (symplesiomorphies) are characters inherited from a more remote ancestry and are irrelevant to the problem of relationship of the lizard and the salmon. For example, the shared possession of characters 1 and 2 in the salmon and lizard would not imply that they shared a unique common ancestor because these attributes are also found in the shark. Characters 1 and 2 may be useful at a more inclusive hierarchical level to suggest common ancestry at 'Y'. With respect to the three-taxon problem (shark, salmon and lizard) then characters 1 and 2 are symplesiomorphies and they suggest nothing other than that the shark, salmon and lizard are a group. Similarly, characters 5 - 9 and 10 - 12 are autapomorphies and irrelevant to discovering relationships since they are each found in only one of the taxa. Sister-groups are discovered by identifying shared derived apomorphic characters (synapomorphies) inferred to have originated in the latest common ancestor and shared by descendants. These synapomorphies can be thought of as evolutionary homologies: that is, as structures inherited from the immediate common ancestor. Diagram and caption from Cladistics for Palaeontologists © Courtesy The Palaeontological Association.

From Phylogenetic Systematics to Computational cladistics

In the decade or two from the mid-1980s onwards, this methodology was used with great effectiveness to work out the relationship between various taxa of living and fossil vertebrates, such as for example the descent of birds from dinosaurs, or the phylogenetic relationship between early reptiles (amniotes). This type of phylogenetic methopdology became the "gold standard" for determining evolutionary relationships.

But with the development of cheap computing, simple trees constructed from easily recognisable and well studied synapomorphies such as those described in the diagram on the right, have been replaced by a new methodology called computational phylogeny. This relies on statistical analyses of huge data matrixes, featuring hundreds of character states and throwing up literally millions of possible cladograms. It still uses all of the same principles as classical Phylogenetic Systematics, such as distinguishing synapomorphies from plesiomorphies, and homologies from homoplasies (convergences), in order to identify monophyletic clades, and selecting the best phylogenetic hypothesis on this basis, usually (although not always) by means of parsimony. But it often throws up totally different cladograms to those arrived at using the single tree method.

In recent years morphology-based computational cladistics has become assimilated into molecular phylogeny, the two together becoming the statistical science of phylogentics, in which parsimony and morphology play second fiddle to molecular sequencing. MAK130321

Page Back | Page Top | Page Next

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

Page Back	Unit Home (You are here)	Page Next: Evolutionary systematics
Unit Back: Phylogeny	Unit Up: Systematics	Unit Next: Cladistics

Evolutionary systematics

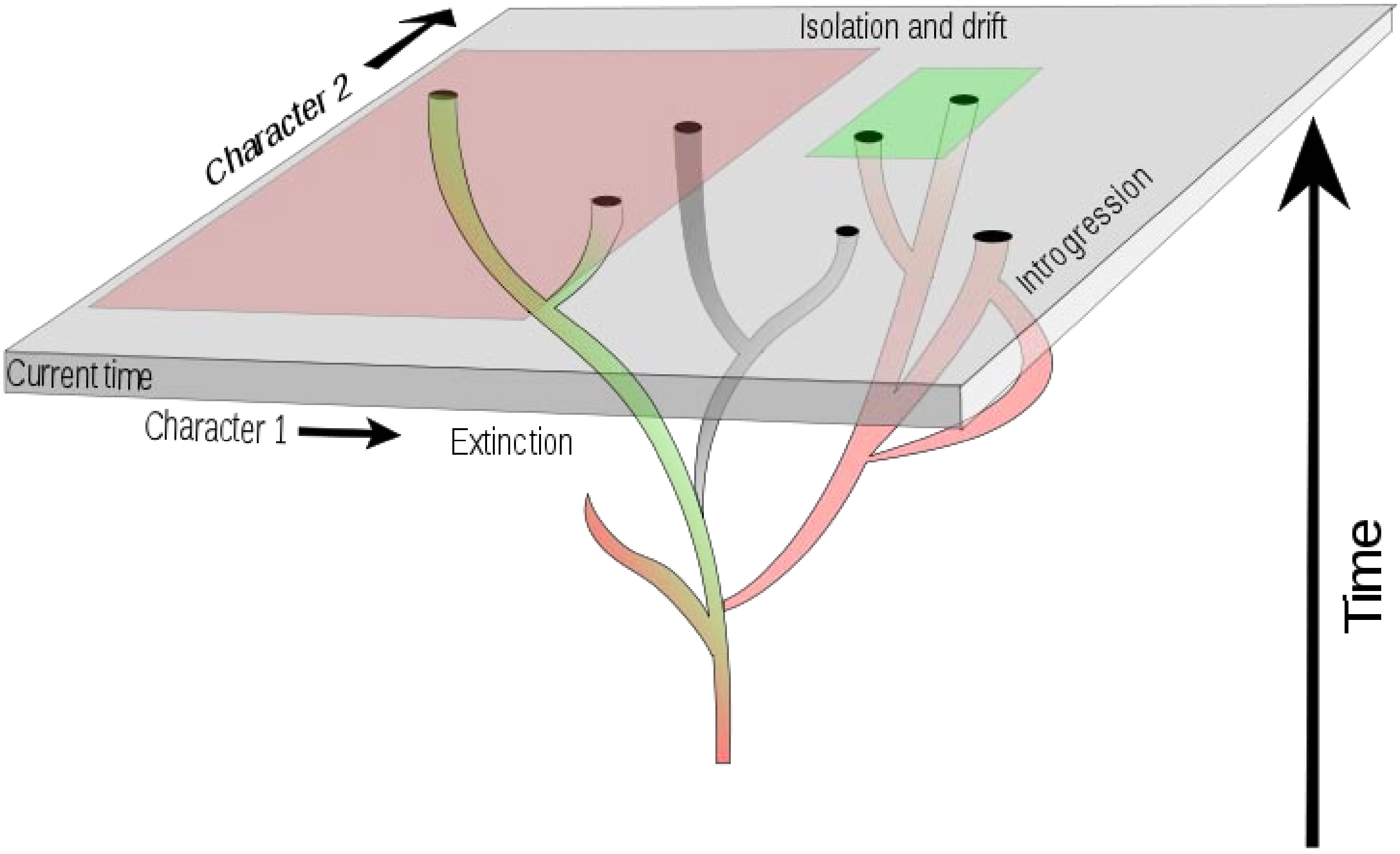
Phylogeny through deep time

Phylogeny and Systematics
  Systematics - History of ideas
  Definitions
  Evolutionary systematics

Phylogeny and Systematics
  Systematics �' History of ideas
    The Great Chain of Being
    The Great Chain of Being
    Linnaean taxonomy
    The Tree of Life
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Stratigraphy and phylogeny
    Phylogenetics

    Taxonomy
  Glossary
  References

  Evolutionary systematics
  Grade and Clade



From Wikipedia: Diagram illustrating phylogenetic (evolutionary history) and phenetic (morphological or phenomic features) concepts. Evolutionary systematics shows how species can diverge through geographic isolation and genetic drift. Graphic by L. Shyamal, public domain.

Evolutionary systematics combines Linnaean classification with ancestor-descendent relationships (phylogeny, evolution) through deep time, emphasising the stratigraphic sequence in the fossil record. Emphasis is placed on supra-specific taxa, such as orders or classes, rather than on species, and paleontology is as important if not more important than neontology. The emphasis is equally on "horizontal" similarity and "vertical" phylogeny. For this reason, generalised ancestral groups are frequently shown in spindle diagrams (""romerograms"), from which later groups radiated. MAK111014

Page Back | **Unit Home** (You are here) | **Page Top** | **Page Next**

Page Back | Unit Home | Page Next
Unit Back: The Phylogenetic Tree | Unit Up: Systematics | Unit Next: Cladistics

Evolutionary systematics

Evolutionary Systematics

History

Linnaeus, like his 18th century contemporaries, had a static, biblical view of the world. All the species that exist and that he described were the same as those originally created by God, and every species that ever lived was still alive today. This simple worldview was undermined in the late 18th and early 19th century by the discovery of fossil species totally different to anything alive. This led to birth of paleontology, under men like Cuvier and Owen. Cuvier, the father of paleontology, who was the first to name and correctly identify many fossil animals (e.g.: ***Pterodactylus, Mosasaurus, Didelphys, Palaeotherium***) was still a creationist, but explained the existence strange armoured fish, ichthyosaurii, tertiary mammals,

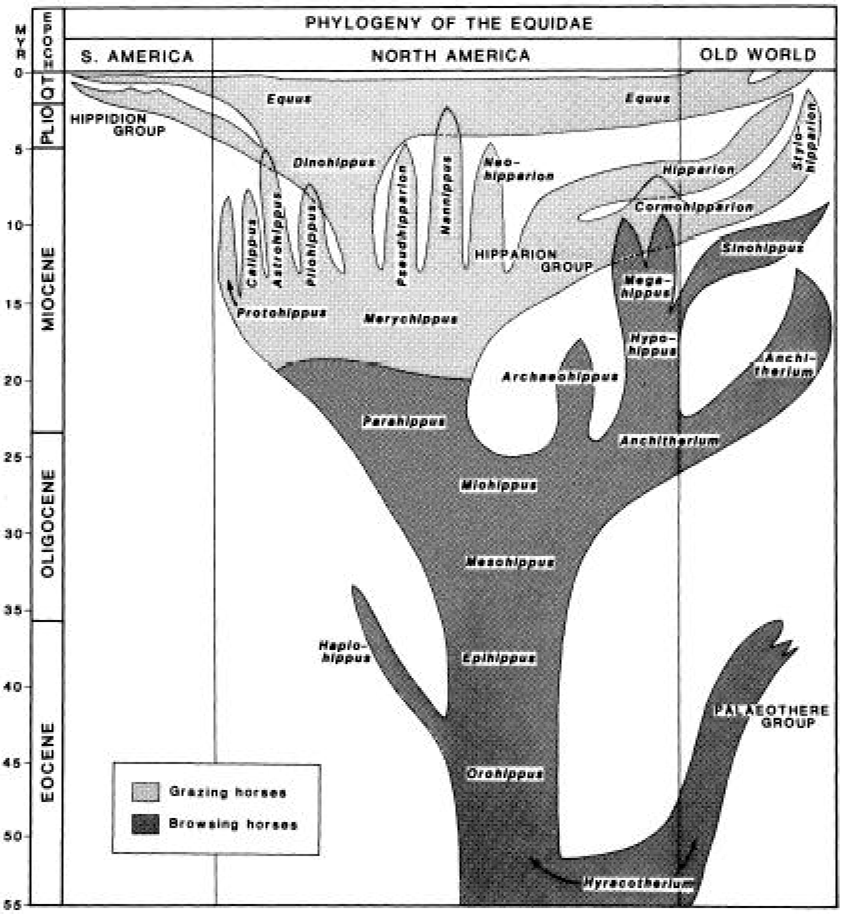


FIGURE 1. Current phylogeny of the Equidae, with particular emphasis on the North American taxa.

Evolution of the Horse, diagram from Bruce MacFadden, 1985. "Patterns of Phylogeny and Rates of Evolution in Fossil Horses: Hipparions from the Miocene and Pliocene of North America" *Paleobiology*, Vol. 11, No. 3. (Summer, 1985), pp. 245-257, retrieved from "Laelaps" blog (Brian Switek), The Branching Bush of Horse Evolution.

mastodons, and the rest in terms of repeated catastrophies, after which God would recreate the world. The biblical flood was considered the most recent of these catastrophes. Owen, who named the order (now superorder) Dinosauria, instead adopted a Goethean concept of evolving archetypes (but not of physical evolution; Owen was strongly opposed to Darwin's theory when it came out). By these sort of mechanisms, Cuvier and Owen could explain the existence of antediluvial (before the flood) monsters. All this changed with Darwin's discovery of the principle of evolution. Darwin, Huxley, and Haeckel established the evolutionary paradigm, and, like Cuvier and Owen, had no problem identifying prehistoric life with Linnaean categories. What evolution did was to make the Linnaean system more dynamic. Thus, Huxley was able to show that ***Archaeopteryx***, the first bird (Class Aves) was also a transitional form between reptiles (Class Reptilia) and modern birds. This synthesis of Darwinian science (specifically the modern evolutionary synthesis) and Linnaean taxonomy was finally fully integrated and systematised in the early 1940s by ornithologist and biological systematist Ernst Mayr, vertebrate paleontologist George Gaylord Simpson, and evolutionary biologist Arthur James Cain. This was the establishment of ***Systematic Biology***, although to distingush it from other schools of biology names like Evolutionary systematics, Evolutionary taxonomy, Evolutionary classification, or Darwinian classification, or Synthetic systematics are used. MAK120229 130331

Methodology

Evolutionary systematics is a way to determine natural relationships of organisms by studying a group in detail and comparing degree of similarity in subspecies, species, and species groups. For example geographical barriers may be sufficient to define subspecies, adaptations to local conditions are features may make a group distinct, and species can be defined as interbreeding local populations. Mayr emphasised geographically determined rings of species, where adjoining races can interbreed, but when the end populations circle back and meet there is geographic isolation. (Cain, 2009 pp.725-6)

As well as considering species, evolutionary systematics also applies to supra-specific taxa, in that groups of species give rise to new groups. Classification reflects both phylogenetic relatedness as well as morphological disparity (overall similarity). The origin of a major new trait or apomorphy (e.g., flowers in angiosperms, endothermy and lactation in mammals) results in the formation of a new "natural group" of the same Linnaean rank as the "natural" group from which it arose (in these examples gymnosperms and reptiles respectively).

In this regard, evolutionary systematics such as palaeontologist Alfred Sherwood Romer, popularised the use bubble or balloon or spindle diagrams that map taxonomic diversity (usually mapped on the horizontal axis) against geological time (mapped vertically, in keeping with the geologists' tendency to equate time with geological strata and hence verticality). The classic example of this, frequently reproduced in old textbooks, is the famous evolution of the horse; see above for a recent version. Thanks to the work of vertebrate paleontologists Romer and Simpson, and later popularisers such as Edwin Colbert, and Romer's student Robert Carroll, evolutionary systematics remained the standard paradigm in paleontology well into the 1990s.

The supremacy of evolutionary systematics in evolutionary theory began to be challenged in the 1960s and 70s by phenetics and especially cladistics, who claimed that it does not have an explicit methodology (much to the surprise of those actually engaged in evolutionary stystematics) or, worse, is "intuitive" (in fact there is no scientific discovery without intuition, as Einstein showed well)

Both Evolutionary systematics and Cladistics use evolution trees, but differ radically in how the tree is drawn. Where each taxon must consist of a single hypothetical ancestor and all its descendants, phylogeny in evolutionary taxonomy allows for groups to be excluded from their parent taxa (e.g. dinosaurs are not considered to include birds, but to have given rise to them). It assumes that ancestor-descendant relationships can be inferred from nodes on phylogenetic trees and considers paraphyletic groups to be natural and discoverable, and at times designated as ancestors (Mayr 1942). Evolutionary systematics also makes possible the organising of organisms into groups (taxa) and hierarchies of such groups (classification systems), in contrast to cladistic, which instead identifies clades and produces cladograms; so both systems can be correct by their own standards. MAK020520 111014 130331

Supraspecific Taxa (Ranks)

It is getting increasingly difficult to find sources which give a balanced comparison of the Linnaean and cladistic methods. Cladistics has simply swept the field. Taxonomy has a good, if somewhat wordy, comparison of the two systems. One of the last, and best, defenses of the Linnaean system -- at least for purposes of nomenclature -- is Benton (2000) which can be accessed here. It would be easy to dismiss these issues as quibbles about nomenclature, but it can make a real difference. The thoughtful student might look briefly at Lane & Benton (2003) . What this paper means, and whether it means anything, depend entirely on on how seriously we take the concept oftaxonomic level and exactly how it is defined. Taxonomic level is a concept almost without meaning in a cladistic scheme; while it is critical to the Linnaean view. Lane & Benton (2003) conclude that the shape of the biodiversity curve over time depends on on what taxonomic level is being considered. That issue has important implications in various areas, including public policy. How can we measure diversity without reference to taxonomic level, particularly for systems in which we cannot account for every species? ATW050802.

The decline of evolutionary systematics

With the rise of phenetics and statistical methods, evolutionary systematics was criticised for being based on imprecise, subjective, and complicated sets of rules that only scientists with experience working with their organisms were able to use. It was argued that the resulting phylogenies became impossible to reproduce other than by the specialists themselves, and there was a call for more repeatable and objective methods. Following the short lived career of phenetics, which due to its purely quantifiable approach was unable to distinguish between homology and homoplasy, evolutionary systematics was replaced by cladistics and molecular phylogeny. Because of a misunderstanding between the respective functions and methodologies of evolutionary systematics (concerned with actual phylogenies in deep time) and cladistics (concerned with statistically evaluating different phylogenetic hypotheses) it came to be wrongly believed that they were saying the same thing, that evolutionary systematics is a quantifiable result, and cladograms have to describe the actual evolutionary path of life. Such misinterpretations do disservice to both methodologies, but is surely one of the reasons for the decline and fall of evolutionary systematics. Nevertheless, a number of scientists, such as Tom Cavalier-Smith and the authors of Res Botanica, support evolutionary taxonomy, although their criticism of cladistics only applies to literalist cladistics that mistakes cladograms for actual phylogenies. MAK111014

Why evolutionary systematics still matters

Even today, many diagrams of hominid (= "hominin" evolution are evolutionary systematic and speciation based rather than cladistic and topology-based. This is not because the various homind species can't be represented cladistically - they obviously can - but because it is no longer necessary to do so. As a great many (although cleary not every) species of hominid is now known, there is much less need to posit "hypothetical common ancestors". Instead we are dealing with "actual common ancestors", and with actual phylogeny, a real evolutrionary tree of life, not just phylogenetics and a choice between any number of statistical hypothesis. The same can be said with any well sampled group, such as Carboniferous and Cenozoic foraminifera, Jurassic Ammonite, Neogene bivalves, or Cenozoic mammals. It is not that one is right and the other wrong but that, for example, evolutionary systematics is better with either well known groups and higher linnaean ranks (e.g. ordinal), whereas cladistics does better with poorly known groups sampled on a species (or even individual fossil) level. This is why attempts to claimthat only one phylogenetic system is right are by their very nature counterproductive to any attempt to understand the complete (and not just partial) evolutionary history of life on Earth. MAK130331

Page Back/Unit Home **Page Top** **Page Next**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page by M. Alan Kazlev (Creative Commons Attribution 3.0 Unported License)
page uploaded 20 May 2002, last revised MAK111018, edited RFVS111202, revised MAK130331
checked ATW031208

Page Back: Evolutionary systematics
See also Linnaean and Cladistics
See also "Evolutionary Phylogeny"
Page Next: Spindle diagrams
Unit Back: The Phylogenetic Tree
Unit Up: Systematics
Glossary
Unit Next: Cladistics

Evolutionary systematics: Grade & Clade

Phylogeny and Systematics
  History of Systematics
    "The Great Chain of Being"
    Linnaean taxonomy
    The Phylogenetic Tree
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

Evolutionary systematics
  Evolutionary systematics
  Grade and Clade
  Spindle diagrams

Grade and Clade

Horizontal and Vertical Classification

The following passage by the great paleontologist George Gaylord Simpson is worth quoting, as it elucidates very well the difficulties inherent in any system of phylogeny and systematics, and the different, indeed opposite, approaches of the Linnaean ("horizontal") and the Cladistic ("vertical") systems. This be it noted was written in 1945, many years before cladistics was founded. Here, "vertical" means phylogenetic - extending through time from ancestor to descendents. "Horizontal" means living at the same time. It is a peculiarity of geologists, and, following them, paleontologists, that time should be measured as an upward march from bottom to top. This is due obviously to the practical fact that the earliest rock strata were deposited first, and hence lie at the bottom of the sequence; the younger strata being deposited above them, leading to the traces of ancient time (as measured in successive rock deposits and the fossils they contain) as measured in terms of vertical succession. This mistaken spatial identification was only reinforced, I feel, by Haeckel and his successors constructing a "tree of life" in which the oldest and most primitive life forms are lower down, in the trunk and main branches, while the younger and later ones are higher up in the smaller branches and twigs (which is not in any way to reject the value of the tree diagram, only excessive literalism). I have however chosen to retain Simpson's jargon, if only because of the certain poetic ring, and assuming these terms are not taken too literally.

> The existence of groups that are ancestral to two or more ultimately quite different phyla and the implication in classification that members of one group are more

nearly related to each other than to members of other groups of the same rank give rise to the most difficult problems of classification of fossils. When the ancestral group is known, how is it to be classified? Can it be more nearly related to one than to the other of its descendent lines? In a sequence, is a group more nearly related to its ancestors, its descendants, or its contemporaries of like origin; in the human family analogy, is a man more nearly related to his father, son, or brother?

In the simplest case of an ancestral unit with two descendent lines, the usual solution in classification is either to extend the name and concept of one descendent group, the one morphologically more conservative if such a distinction is clear, to include the ancestry, or to give the ancestry a separate name and to consider it a group of the same rank as each descendant. Both systems are in common use, and it is impractical to try to use either exclusively and consistently. On lower levels of classification the second solution seems more often useful. For instance, the group immediately ancestral to the genera ***Pliohippus*** and ***Hipparion*** (among others) is also given generic rank and is called ***Merychippus***.

Such simple cases are not particularly confusing, but analogous problems can be very intricate. It has, for instance, frequently happened that a group of, say, about subordinal scope has included numerous phyletic lines, all rather closely related but showing incipient divergence, and that one of these lines has outlived most or all of the others and has itself eventually split up into a group of about equal scope with the first. A concrete example is provided among Mammalia by the Carnivora. The early forms are quite varied, yet they are apparently derived from an immediately antecedent common ancestry. One of these early groups, the Miacoidea, survived and apparently gave rise to all the divergent phyla leading to our modern terrestrial carnivores. In such a case how is the principle of nearness of affinity to be applied?

The Miacoidea are certainly nearly related to the later carnivores, the Fissipeda, for they are ancestral to them. At the same time, they are certainly nearly allied to the more ancient and archaic Creodonta in the way often or customarily expressed by inclusion in one taxonomic unit, for they are derived from the same immediate ancestry. There are two sorts of affinity here, and following either one consistently throughout a classification is a practical impossibility. If the Miacoidea are placed in the Suborder Fissipeda, then consistency might seem to demand placing each of the other early, creodont subfamilies in a separate suborder, since their divergence from each other is equal to that of the Miacoidea, yet logical adherence to this method would make classification absurd by eventually separating virtually every ancient species as distinctive of a suborder or other large group. On the other hand if the Miacoidea are placed in the Creodonta, the implication would seem to be that they are more nearly related to, say, the hyaenodonts than to any fissipeds, which is not the case.

There are only two practical methods of dealing with such a situation, neither one of which is a clear expression of the evolutionary affinities involved. One is to place all the early forms including the Miacoidea in the Creodonta, separating the descendants of the Miacoidea as Fissipeda. The other is to place the Miacoidea in the Fissipeda and nevertheless to lump all other early lines in the Creodonta. These two solutions are equally valid, and both have been proposed and used in this particular example and also in dealing with numerous other analogous cases.

The choice here is between so-called horizontal and vertical classification. Horizontal classification separates ancestral from descendent groups and unites contemporaneous groups, or those in a similar stage of evolution, if they are derived from a common ancestry. Vertical classification unites ancestral and descendent groups and separates contemporaneous groups that are diverging from a common ancestry. It is sometimes stated that these are mutually exclusive principles and that classification must be based on one or the other, but in fact neither can be followed consistently and any classification necessarily combines both methods. The most ardent exponent of vertical classification finds it necessary to separate ancestral and descendent genera, for instance.

> Each point of view has its advantages and its dangers. Horizontal classification is usually easier and more objective. The earlier horses and tapirs, for instance, have more in common than have the earliest and latest horses, and it would be much easier to define and to recognize a horizontal group containing both primitive horses and tapirs than a vertical group containing all the horses and excluding all the tapirs. The horizontal arrangement may also be more stable, because the relative ease of recognition makes it less likely to be disturbed by later discovery, whereas most evolutionary phyla are difficult to distinguish and require considerable material for their proper recognition. Vertical groupings often require extensive rearrangement following new discoveries or new studies that modify ideas of the details of phyletic descent.
>
> The principal advantage of vertical, and disadvantage of horizontal, classification is that the former is more in accord with the whole conception of evolutionary descent. Its principal proponents, such as the late H. F. Osborn, therefore, sometimes speak of it as evolutionary classification, as opposed to the more static and historically pre-evolutionary, more strictly Linnaean, horizontal system. Yet the horizontal affinities are just as real and are just as evolutionary as the vertical. Horizontal classification can, therefore, be as consistent with phylogeny as vertical classification, and since neither can really express phylogeny, there is really no ***a priori***, theoretical reason for preferring one to the other even if one could be employed to the exclusion of the other, which is not possible.

-- G.G. Simpson, "The Principles of Classification and a Classification of Mammals", ***Bulletin of the American Museum of Natural History***, vol.85, (New York, 1945) pp.17-19

Reading this passage, I have the impression that biological systematics is not unlike the wave-particle paradox of quantum physics. Is a photon or an electron a wave or a particle, energy or matter? Is a biological taxon - if indeed such an abstract entity could be considered a "real" (in the sense of objective) thing like a photon at all! (ignoring here the more extreme metaphysical speculation of any Platonizing biology) - best understood "horizontal" or more properly isochronous or evolutionary grade manner - as the Linnaean system does, or in a "vertical" or more correctly phyletic manner, as Cladistics argues it should. If we look at an electron or a photon as a wave of probability or energy we forget it is also (or rather can also appear to our instruments) as a particle of matter - but the electron or photon in itself is beyond wave and particle, energy and matter. Those are only labels we use to make sense of it with our three-dimensional minds.

The Evolutionary Systematics of Mayr, Simpson and others emphasize the horizontal grade, although the vertical dimension of monophyletic clade is accepted as well (but there is no real methodology) Cladists on the other hand have a rigorous methodology that means the rejection of the "horizontal" grade perspective. Terms like say Miacoidea, Thecodontia, Condylartha, Reptilia, or Pteridosperma, because all these groups are paraphyletic; that is they gave rise to descendents that are not included in those groups. But were we living in the Eocene epoch, the Miacoidea would then be monophyletic (and cladistically authentic); were we in the middle Triassic period Thecodontia, Reptilia and Pteridosperma would be too! Ironically the methodology that affirms phylogeny at the same time ignores the passage of time in which that very phylogeny unfolds!

Page Back | **Unit Home** | **Page Top** | **Page Next: Cladistics**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

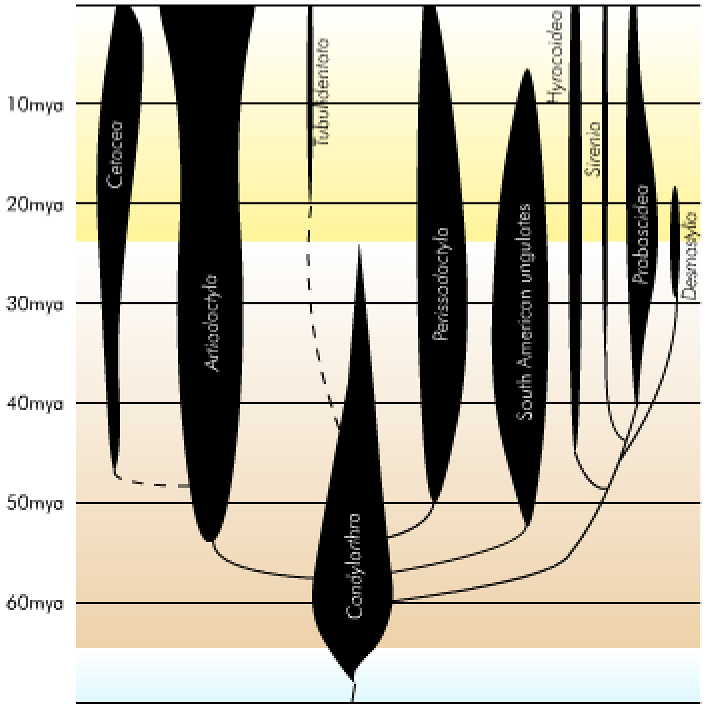
page first uploaded on Kheper site 28 July 2000, on Palaeos site 26 May 2002
checked ATW021107, last modified MAK050104, 111018, edited RFVS111202

Page Back: Grade and Clade | Unit Home | Page Next: Cladistics
Unit Back: The Phylogenetic Tree | Unit Up: Systematics | Unit Next: Cladistics

Evolutionary systematics: Spindle Diagrams

Phylogeny and Systematics
  History of Systematics
    "The Great Chain of Being"
    Linnaean taxonomy
    The Phylogenetic Tree
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

Evolutionary systematics
  Evolutionary systematics
  Grade and Clade Spindle Diagrams



A "romerogram" (spindle diagram), showing the evolution of hoofed mammals plotting diversity (horizontal axis) against time (vertical axis), and showing the phylogentic divergence of new groups as new bubbles or balloons which increase or decrease in diversity of individuals and species through time. Diagram from Trees, Bubbles, and Hooves.

Evolutionary systematics bubble or spindle diagrams were very common in paleontology books from the 1930s to the 70s. This type of diagram being being popularised (but not invented) by Alfred Sherwood Romer (hence the informal term, "romerogram"). It would not be an exaggeration to call Romer the most influential vertebrate paleontologist of the 20th century. Hence the influence of these diagrams on the scientific and educated lay imagination. These diagrams mapped geological time (vertical axis) against taxonomic diversity (horizontal width) and emphasised monophyletic ***sensu*** Haeckel taxa (i.e. both monophyletic and paraphyletic groups). Sometimes width did not reflect diversity but was simply artistic license. For an example of such a tree see the diagram of the evolution of the horse.

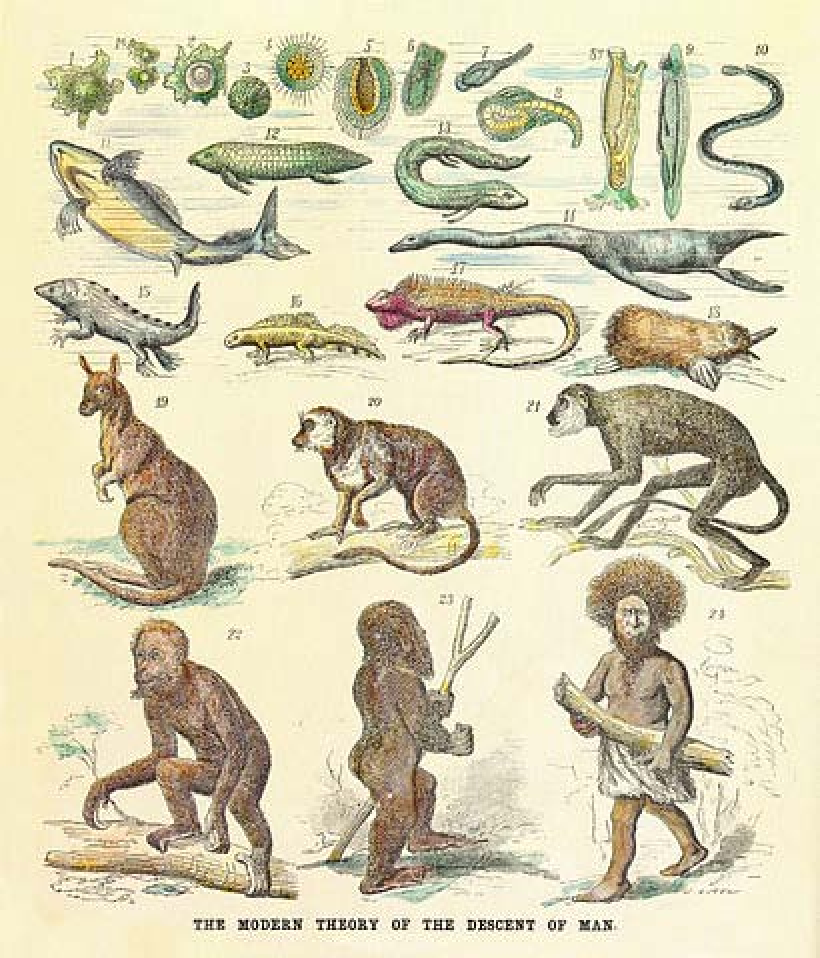
Replacing evolutionary systematics in the 1980s, the cladistic revolution (phylogenetic systematics) also placed great emphasise on tree diagrams, called cladograms, which are based either on gross morphology, molecular phylogeny, or both. Some of these diagrams can be incredibly detailed.

The cladistic revolution meant the end of the romerogram. The rejection of ancestral groups as paraphyletic and the emphasise on precise branching sequence in reconstructing phyloghenies meant that cladograms took over from spindle diagrams. The last serious use of the classic romerogram in a vertebrate paleontology textbook seems to be Carroll, 1988 (not surprisingly, Carroll studied under Romer), although Benton 2004 has revised them in modified cladistic-friendly form (rejecting ancestral groups). One big difference between evolutionary and cladistic trees is that the former include ancestral groups such as Pteridosperms, Ostracoderms, Cotylosauria, Thecodontia, and Condylartha, whereas such taxa, being paraphyletic, are forbidden in cladistic methodology, as they are defined only by shared primitive characteristics. The latter is concerned instead with sister relationships of individual species, or even, in the case of fossils, individual specimens. However, rather than being a replacement for evolutionary systematics, cladistics is a totally different system, with different methodology and taxonomic philosophy, and the present author (MAK) finds no reason why the two cannot be integrated in a larger multi-disciplinary and multi-methodology approach. For example, from an evolutionary systematic point of view, dinosaurs don't have to be called by the unweildly name of "hon-avian dinosaurs", as a paraphyletic assemblage they can still be just dinosaurs (in the classic sense of the word) and yet still be ancestral to birds. MAK130323

Page Back | **Unit Home** | **Page Top** | **Page Next**

page last modified MAK111014, edited RFVS111202

The Great Chain of Being



The human pedigree interpreted chain of being with living and fossil animals. Ernst Haeckel, *Anthropogenie oder Entwicklungsgeschichte des Menschen* (The Evolution of Man), 1874, posted by Petter B�ckman, Wikipedia, Public Domain. The figure show the human pedigree as a Great Chain of Being, illustrated by modern and fossil species. Legend: 1 Amoeba, 1a Asexual reproduction (amoeba dividing), 2 Sexual reproduction (cell with spore), 3 Multi-cellular organism (early embryonic stage), 4 Muliticellular organism with three germ layers (blastula), 5 Organism with primitive mouth (gastrula), 6 Planaria, 7 Worm (leech), 8 Primitive chordate (tunicate larva), 8a Adult tunicate, 9 Lancelet, 10 Jawless fish (lamprey), 11 Cartilaginous fishes (shark), 12 Australian lungfish, 13 South American lungfish, 14 Aquatic reptile (plesiosaur), 15 Early amphibian (labytinthodont), 16 Modern amphibian (newt), 17 Reptile (iguana), 18 Monotreme (platypus), 19 Marsupial (kangaroo), 20 Prosimian (lemur), 21 Monkey (langur), 22 Ape (orangutan), 23 Ape-man (Pithecanthropus), 24 Modern human (a Papuan).

Today we think of life as organised in terms of an evolutionary tree. Little more than one and a half centuries ago this idea was unheard of. Instead there was the Great chain of being. This evocative phrase was coined by historian of ideas Arthur O. Lovejoy in his study, called, what else, *The Great Chain of Being*. The premise was developed by Greek philosophers such as Plato (transcendent ideas), Aristotle (*scala naturae* or Ladder of Nature), and Plotinus. In the Middle Ages this cosmology was the basis for both scholastic theology (ranking all of creation from dirt through to humans to angels) and feudal social stratification; it formed a central element in the Elizabethan understanding of the world still evident in Shakespeare's plays. It continued through 17th, 18th and early 19th century Europe and North America, in an understanding of the universe as the highest good, in which every species of being has its perfect place. The end of the 18th century saw the "temporalization of the great chain of being" with a timeless metaphysical ladder being replaced by a dynamic ascending one. This continues in some contemporary pop cultural approaches such as the "Ascent of Man" (in this context see also the diagram by Haeckel, above). Hard science themes such as complexity theory and emergent evolution, although unrelated, can be considered a modern parallel of this. MAK111018 130319

Page Back: Systematics | **Unit Home** (You are here) | **Page Top** | **Page Next**

Aristotle's *Scala Naturae*

Phylogeny and Systematics
  Systematics �' History of ideas
    The Great Chain of Being
    Linnaean taxonomy
    The Tree of Life
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Stratigraphy and phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

The Great Chain of Being
  Aristotle's *scala naturae*
  The "Great Chain of Being"
  From Ladder to Tree

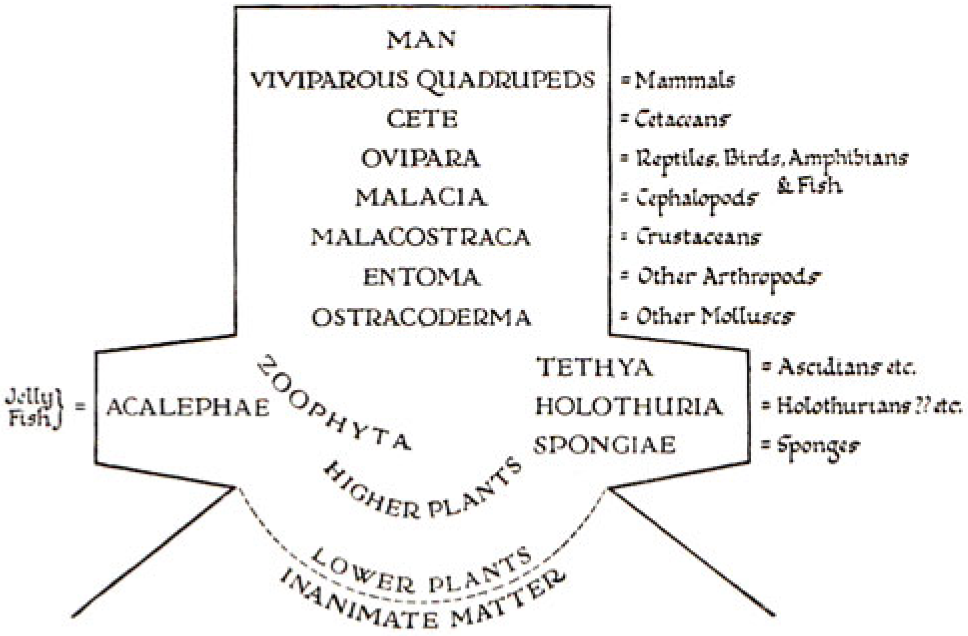


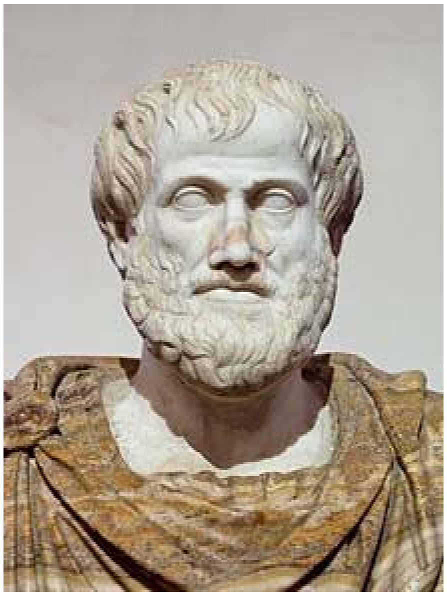
FIG. 18. The *Scala Naturae* or 'Ladder of Life' according to the descriptions of Aristotle.

from Charles Singer, *A Short History of Biology*, via Roger Wotton Blog

Aristotle and the dawn of science

The following is adapted from the UCMP page and Wikipedia

Aristotle (384-322 b.c.e.) was a Greek philosopher and polymath, whose writings range across such diverse subjects as physics, metaphysics, poetry, theater, music, logic, rhetoric, linguistics, politics, government, ethics, biology, and zoology. He was the first to create a comprehensive system of Western philosophy, encompassing morality, aesthetics, logic, science, politics, and metaphysics. Although he observed and wrote about the natural world, he was not a scientist in the Baconian-Galilean mode of empiricism and experimental method; rather he had a qualitative and teleological view of nature.



Marble bust of Aristotle. Roman copy after a Greek bronze original by Lysippus c. 330 BC. Photo by Jastrow, via Wikipedia, Public domain

Aristotle was the first to give the first detailed classification of living things, and hence the first systematists. He did not classify plants or fungi, but his classification of animals was as follows:

- Blooded (vertebrates)
    - Viviparous quadrupeds (land mammals)
    - Birds
    - Oviparous quadrupeds (reptiles and amphibians)
    - Fish
    - Cetaceans (Aristotle did not realize their mammalian nature)
  - Bloodless (invertebrates)
  - Land arthropods (insects, arachnids, myriapods)
  - Aquatic arthropods (mostly crustaceans)
  - Shelled animals (shelled mollusks, echinoderms, etc.)
  - Soft animals (cephalopods, etc.)
  - Plant-animals (cnidarians, etc., which superficially resemble plants)

Aristotle's ideas were essentially based on the idea of the *scala naturae*, the "Natural Ladder" according to which the entire natural world could be arranged in a single continuum. During the medieval period this become incorporated into the idea of the Great Chain of Being.

Though Aristotle's work in zoology was not without errors, it was the greatest biological synthesis of the time, and his work remained the ultimate authority in understanding the secular world until the rise of modern knowledge in the 16th century, and his classification of living organisms contains some elements which still existed in the 19th century. He classified animals by their way of life, their actions, or by their parts. Aristotle described the embryological development of a chick; the chambered stomachs of ruminants and the social organization of bees; and noticed that some sharks give birth to live young, and his observations on the anatomy of octopus, cuttlefish, crustaceans, and many other marine invertebrates were so accurate they could only have been made from first-hand experience with dissection.

Aristotle divided animals into two types: those with blood, and those without blood (or at least without red blood), corresponding to our distinction between vertebrates and invertebrates. The blooded animals, corresponding to the vertebrates, included five genera: viviparous quadrupeds (mammals),birds, whales (which he did not realize were mammals), oviparous quadrupeds (reptiles and amphibians), and fishes. This basic division was to be adopted by Linnaeus, for whom the "genera" became classes. The bloodless animals were classified as cephalopods (such as the octopus); crustaceans (malacostraca); insects (*entoma* - hence "entomology"), which also included arachnids and centipedes; *testacea* or shelled animals such as non-cephalopod molluscs and echinoderms; and *zoophyta*, or "plant-animals," such as corals, which supposedly resembled plants and hence were considered intermediate between the plant and animal kingdoms.

Despite the quite modern nature of his zoological system, Aristotle was not an evolutionist, but an essentialist. For him, species have never changed. There were some eaerlier Greek philosopher naturalists, such as Empedocles, who developed at least in germinal form ideas remarkable similar to those of Darwin's theory of natural selection (ref).

Like Aristarches (spelling?) heliocentriosm, such remarkable insights would have to wait for the rise of modern science becfore beiung rediscovered. MAK130327

Page Back | Unit Home | Page Top | Page Next

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

The Great Chain of Being

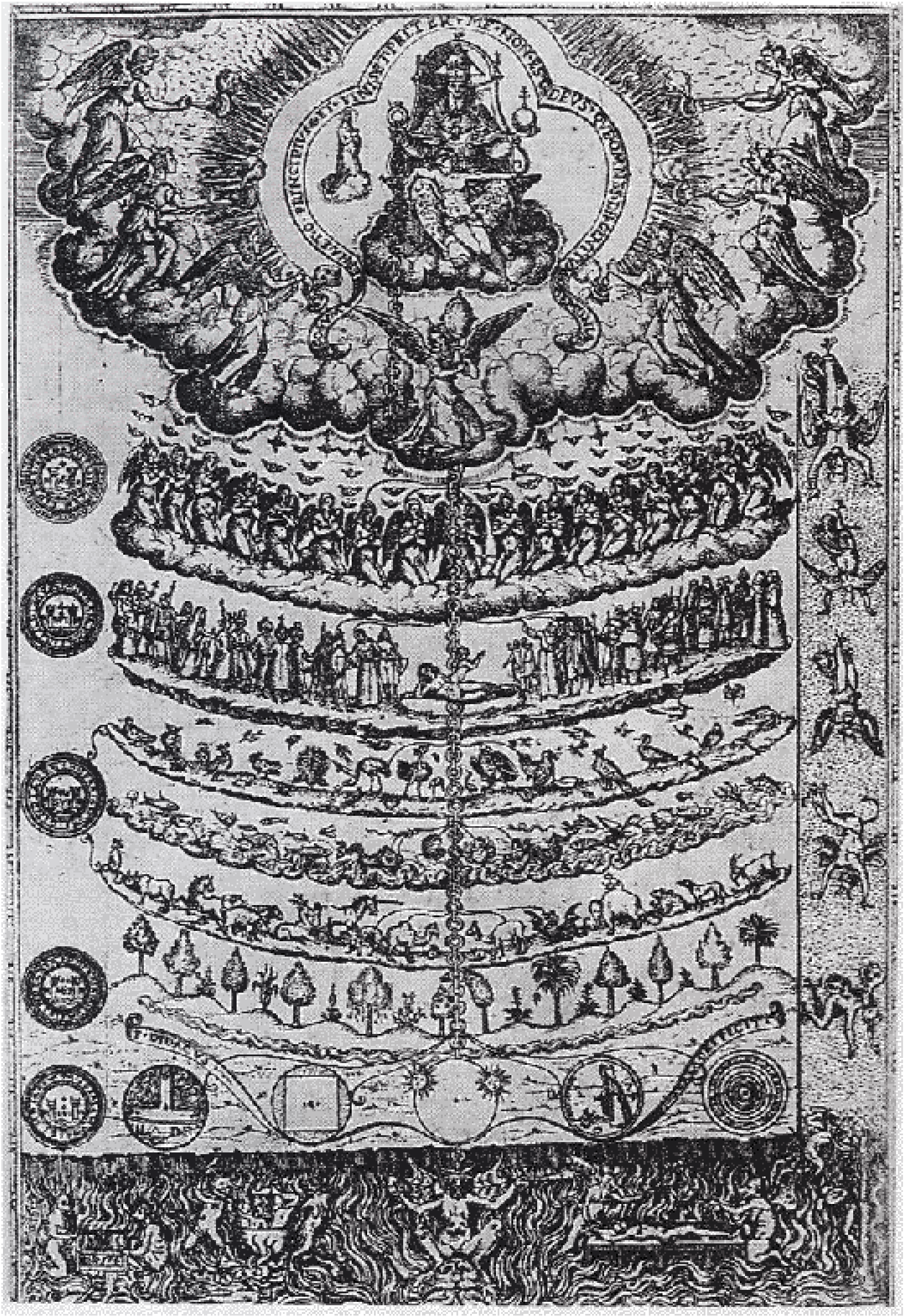
Neoplatonism

The concept of the "Great Chain of Being" begins with a marriage of Plato's Idea of the Good who is bound by its own principle of plenitude to generate every possible Idea and temporal being, and Aristotle's *Scala Naturae* (Ladder of Nature). Later, Plotinus, one of the greatest systematisers and mystics of late Antiquity, integrated Platonic, Aristotlean, and Stoic philosophy, developing a panentheistic metaphysic in which behind the material universe are a series of transcendental realities, called hypostases, as follows:

- The One - the Absolute Reality, source of emanation.
- Nous - the Divine Mind - Platonic archetypes.
- World Soul - the principle behind the cosmos, that moves all things, the universal equivalent of the individual mind or soul.

Following Plato rather than Aristotle, these higher principles were considered distinct metaphysical realities that were the archetypes of the natural world. Each higher higher hypostasis gives rise by a process of emanation to the next, with the lowest one generating the material world. There, "beneath" (although not in any spatial sense) the three hypostases, at the maximum point of emanation, is the world of the senses, the material world of pure quantity (*hyle*), with nature (*physis*) sometimes as an intermediate principle between the world soul and matter. Later neoplatonists such as Iamblichus and Proclus built on Plotinus' scheme, adding ever more hypostases and replacing the mystical immediacy of the One with a series of progressively transcendent strata.

The Medieval Period



The Great Chain of Being. From Didacus Valades, *Rhetorica Christiana* (1579).

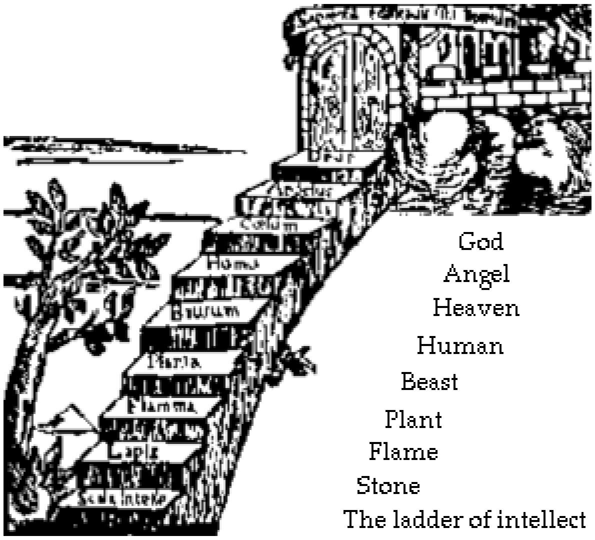
Reproduced here from Anthony Fletcher's *Gender, Sex, & Subordination.* - Original page - Gender and Politics in Literature 1688-1750

With the fall of classic learning the last formulation of pagan metaphysics was lost, and the middle ages reverted to the more classic Platonic and Aristotlean approach, via Augustine and Aquinus. But at the same time, later neoplatonism, especially as propounded by Proclus, the last of the great Neoplatonic synthesisers, was to have a strong influence on both Christian and Islamic medieval metaphysics (via Pseudo-dyonsius and Avicenna respectively). Plotinus himself became one of the major metaphysical sources of Islamic philosophy, via the pseudepigraphical "fourth book" of Aristotle. The elaborate cosmology and theology of mystical Judaism (Kabbalah) was if anything even more strongly influenbced by neoplatonic ideas of emanation.

For the most part though, in the middle ages, the highly metaphysical Neoplatonic concept of emanation and hypostases became God and the hierarchies of angels and archangels bridging the divide between Fisrt Principle and the human world. At the same time, beneath man was the hierarchy of nature as described by Aristotle. Between these two was the feudal system, showing how secular and religious social strata fit into the larger divinely ordained pattern. As a result, during the medieval period The Great Chain of Being represented a visual metaphor for a divinely inspired universal hierarchy ranking all forms of higher and lower life. At the top is God, immediately underneath are His angels, then Kings and Queens (or Pope if one is Catholic), and the whole feudal social stratified sequence of Archbishops, Dukes and Duchesses, Bishops, and so on, down through the ranks of greater and lesser nobles, to commoners and tradesmen, servants, tennant farmers, beggars, pirates, thieves (and actors and gypsies who were likewise placed near or at the bottom) then the various kinds of animals, birds, reptiles, insects, worms, plants, minerals, and rocks. (**Links:** The Great Chain of Being; There were three general roles in society, called the Three Estates.). Drawing from both the Aristotlean and the Biblical (including the modern creationist) understanding of the world (which were synthesised in the theology of Aquinus), the great chain of being presented an essentialist worldview of immutable species, and, in Feudal societry, social strata.

The Elizabethan Age

The idea of the Great Chain of Being was similarily very important during the Renaissance and remained a central element in the Elizabethan understanding of the world as evident in Shakespeare's plays. Shakespeare believed in the Divine Order, the belief that everything in the universe has a specific place and rank due to its importance and spiritual nature. To break the chain of being would upset the established order and bring about universal disorder. Thus when Julius Caesar is assassinated, there is chaos in the heavens as well as on earth. In Macbeth after Duncan is murdered there are frightening omens (Act 2, Scene 4), and only when Malcolm, the rightful king, gains the throne at the culmination of the play is order and harmony to the world restored. ref. Macbeth, Taming of the Shrew, Romeo and Juliet, and Hamlet are just a few of the plays that reflect Shakespeare's belief in the Great Chain of Being and his desire to maintain God's Order. ref



The Great Chain of Being - image from Shakespeare's Life and Times

From Age of Enlightenment to the Present

During the secular enlightenment of the 17th and 18th century Europe and North America, there was an understanding of the universe as the highest good, complete and full, in which every species of being has its perfect place. Lovejoy refers to this belief as "the Principle of Plenitude". It was believed that no species can ever become extinct, as to do so would result in a gap in God's creation. Understanding this harmonious linear order of nature as a product of God's benign creative activity was a meaningful pursuit.

By the late 18th century, the idea of progress that accompanied the enlightenment led to the "temporalization of the great chain of being" . There was still a single linear scale, a ladder of nature, but it was now a progressive, evolutionary one, in which ascent rather than neoplatonic style descent (emanantion) was the rule. In the late 18th to mid 19th century these themes were developed in the form of German Idealism and Naturphilosophie, and in the mid 19th to early 20th century ideas, with the success, popularisation, and misinterpretation of Darwinian and other evolutionary theories, in sociological evolution, social darwinism, spiritialism and theosophy.

A good example in the popular imagination of the temporalization of the great chain of being is Rudolph Zallinger iconic (and universally misinterpreted) 1960s image of the "Ascent of Man". The ubiquity of this iconic graphic shows the power of the meme of progress as the ascending great chain of being

In the late 20th century, a non-evolutionist revival of a neoplatonic style Great Chain of Being, via neo-Sufi Traditionalism, has been presented as an example of the "Perennial Philosophy" (note that this is quite different from the more classically pantheistic or monistic Hindu Vedantic "Perennial Philosophy" taught by Swami Vivekananda, and popularised in a book of teh same name by the novelist Aldous Huxley), by the scholar of comparative religion Professor Huston Smith (formerly of Syracuse University, N.Y.), who (in his books *Forgotten Truth* and *Beyond the Post-Modern Mind*) refers to four levels of physical, intermediate/mental, celestial/soul, and spirit/infinite (the last of these inspired by vedantic monism). These clearly have their roots in Plotinus' hypostases. E.F. Schumacher (author of *Small is Beautiful*) in Chapter 2 of "Guide for the Perplexed" 1977 similarily revived Aristotle's three types of soul (vegetative, a sensitive, and a rational) with together with mineral or inanimate matter made four categories, as another example of the same "Perennial Philosophy". This is also similar to Linnaeus' 18th century great chain of being based three kingdoms but with man as the rational soul anthropocentrically added as a separate kingdom (which is in keeping with the religious idfea of a "special creation" for man).

Finally the creationistr/intelligent design Neo-Sufi, Neo-Platonic, and Aristotlean "Perennial Philosophy", the pantheistic Neo-Hindu (Vivekananda and Aldous Huxley) monism, the evolution of consciousness and temporalised great chain of being "ascent of man" memes, and many other elements (especially Theosophy, popularist Eastern Gurus, and the Human Potential Movement), all converged in the late 20th (1970s onwards) and turn of the 21st century to become the New Age, New Paradigm, Transpersonal Psychology, New Consciousness, and Integral Theory cluster of ideas. As popular metaphysics and religion therefore the confluence of two aspects of the "Great Chain of Being", the descending/emanationist/involutionary and the acending/temporalised/evolutionary remain an influential 21st century meme and an alternative to literalist religion. As non-empirically verifiable it can neither be affirmed nor denied by science, although it can be tied in with themes regarding the evolutionary tramscendence of consciousness (which need not be inconsistent with science or even materialism, consider for example the transhumanist movement). Science itself meanwhile has ever since the 18th and 19th centuries gone its own way, replacing the ladder of nature with the evolutionary tree of life on Earth. MAK130328

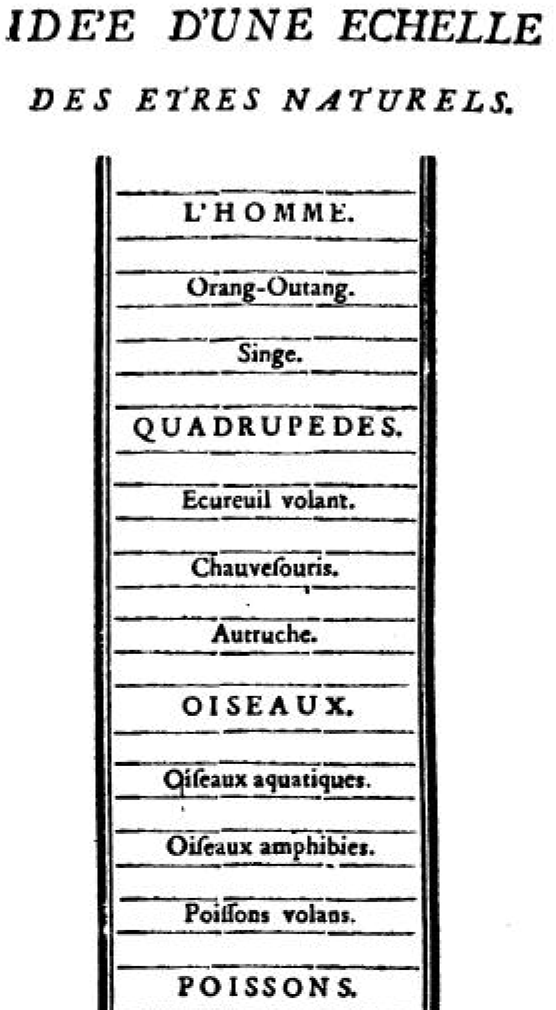
Page Back | Unit Home | Page Top | Page Next

Page Back | Unit Home | Systematics Glossary | Page Next: The Linnaean System
Unit Back: Systematics | Unit Up: Systematics | Systematics References | Unit Next: Linnaean taxonomy

The Great Chain of Being: From Ladder to Tree

Phylogeny and Systematics
  Systematics �' History of ideas
    The Great Chain of Being
    Linnaean taxonomy
    The Tree of Life
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Stratigraphy and phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

The Great Chain of Being
  Aristotle's *scala naturae*
  The "Great Chain of Being"
  From Ladder to Tree


IDE'E D'UNE ECHELLE
DES ETRES NATURELS.

L'HOMME.
Orang-Outang.
Singe.
QUADRUPEDES.
Ecureuil volant.
Chauveſouris.
Autruche.
OISEAUX.
Oiſeaux aquatiques.
Oiſeaux amphibies.
Poiſſons volans.
POISSONS.

There were several factors that brought about the end of the Great Chain of Being or Ladder of Being worldview.

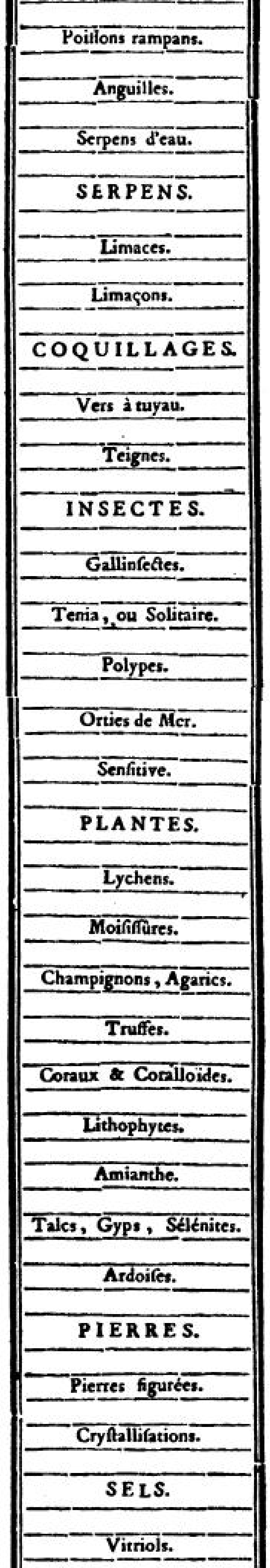
The first was the rise of experimental method, the age of reason, and the secular worldview. Newton for example showed that the same principle of gravitation applied to the celestial bodies - previously believed to be immutable and transcendent - as to the terrestrial, or sublunary realms. Newton's unification of celestial and terrestrial mechanics was as groundshaking a revolution in his day as Darwin's discovery of biological evolution and the demolishment of the fundamentalists' idea of special creation, was in the 19th century. The world was no longer the embodiment of mythological cosmology and theology, but subject to natural laws and amenable to rational explanation throughout.

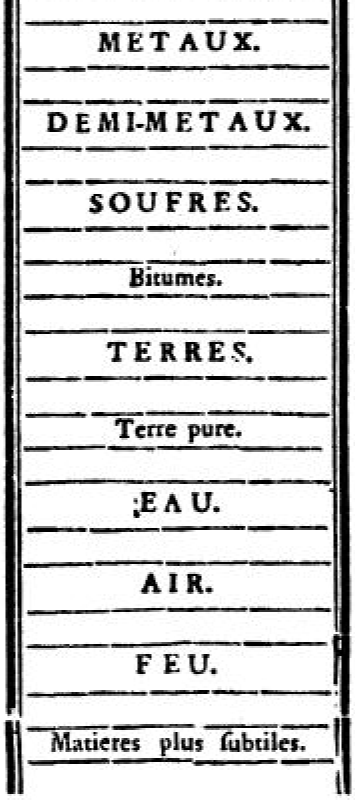
Next, evolution. With the age of enlightenment there was a shift from a religious and metaphysical, emanation and crewation-based worldview to a progressive and proto-evolutionary one. Lamarck's evolutionary theory was actually a "Temporalisation of the Great Chain of Being" [see Frederick Gregory, J.-B. Lamarck and the philosophy of nature in France), although these ideas had to contend with German Idealism and nature philosophy, which retained the idea of archetypes (Goethe) and the transcendental evolutionism of spirit acting in history (Hegel). by the mid 19th to early 20th century ideas of sociological evolution were standard. A temporal evolving sequence of physical, social, and psychological being on the one hand and the transcendental evolution of spirit on the other converged in in the Theosophy of Blavatsky, the cosmic evolutionism of Aurobindo, Teilhard, and others, and more recently the Integral Theory of Ken Wilber, with its strictly linear, ladder-like series of evolutionary stages of consciousness.

Here philosophy moves towards a universal evolutionary worldview. Such a metaphysical cosmology need not conflict with science, Sri Aurobindo and Teilhard de Chardin each replaced the four kingdoms with four evolutionary, stages: matter/geosphere, life/biosphere (which includes all five kingdoms and three domains), mind/noosphere (incorporating the socio-cultural human world), and a future spiritual state of attainmant and collective consumation, which Aurobindo terms the Supramental and Teilhard the Omega Point. Their insights, while not scientific in the empirical hypothesis testing sense, are not incompatible with modern cosmology and tie in with transhumanism and other intriguing and weigh out ideas. MAK130319

A third factor is that the linear or ladder model simply became unable to cope with the weight of knowledge. The extreme development of Great Chain of Being/Ladder of Nature thinking came with Swiss naturalist and spiritual philosopher Charles Bonnet (1720�'1793), who in his 1745 *Traité d'insectologie* traced the scale of nature in such detail that it became an absurdity. *Hydra* became a link between plants and animals, snails and slugs between molluscs and serpents, the ostrich, bat, and flying fox links between birds and mammals. However he also applied the Great Chain of Being to proto-evolutionary theories of ascent �' he believed that catastrophes such as Noah's flood brought about evolutionary change, and that after the next disaster, men would become angels, mammals would gain intelligence, and so on (Wikipedia). It became clear that nature could not be portrayed in a single dimension. The great German naturalist, Peter Simon Pallas (1741�'1811), in his *Elenchus Zoophytorum* (1766) showed that no linear scale can represent the mutual relations of organised beings; the branching tree, he said, is the appropriate metaphor. (see John S. Wilkins, The first use of a taxonomic tree). By the beginning of the 19th century, branching diagrams were used by the French botanist Augustin Augier in 1801, the French evolutionist Jean-Baptiste Lamarck (1744-1829), who produced the first branching tree of animals in his *Philosophie Zoologique* (1809) based on the Great Chain of Being, and the American geologist Edward Hitchcock (1763�'1864), who in 1840 published in his *Elementary Geology*, the first Tree of Life based on paleontology. From here it was only a short step to Charles Darwin, Ernst Haeckel, and the classic evolutionary tree of life. MAK111018.

Diagram, right, the Great Chain of Being, as published in 1745 by Charles Bonnet Charles Bonnet, via John S. Wilkins. For another image of this diagram, along with an early tree-like scheme by Jean Lamarck published 1809 is shown here





METAUX.

DEMI-METAUX.

SOUFRES.

Bitumes.

TERRES.

Terre pure.

EAU.

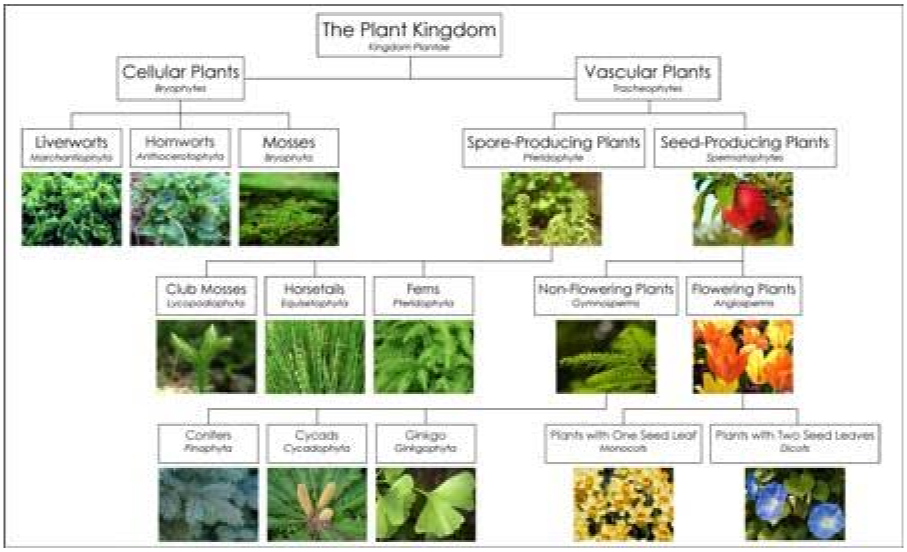
AIR.

FEU.

Matieres plus ſubtiles.

Page Back | Unit Home | Page Top | Page Next: The Linnaean System

The Linnaean System of Nomenclature



The Linnaean System in practice. Image from Montessori for everyone - The Optimization of Classification; © 2005-2011 Montessori for Everyone.

Ever wondered where those fancy names come from? ***Tyrannosaurus rex***, or ***Triceratops***? (actually

Triceratops prorsus and the aptly named ***Triceratops horridus***; every scientific name is binomial, or made up of two parts). Well, there's actually a scientific body (or several) that ensure that every new species is properly named. Once named, the species can be officially referenced in scientific journals, as well as in popular books. This goes not just for prehistoric monsters but for every living thing. Man for example is ***Homo sapiens***. (or more correctly, ***Homo sapiens*** Linnaeus, 1758)

The science of naming the living world is what is known as taxonomy. Taxonomy is the theoretical study of classification and the principles, procedures and rules thereof; the science of finding, describing and naming organisms, thus giving rise to taxa. Essentially, ***taxonomy*** deals with the ways in which we group living things together, in contrast to ***phylogeny*** which refers to evolutionary history.

Basically, taxonomy is like a sort of Dewey Decimal system, by which organisms can be named and categorised, rather like books in a library arranged according to subject. This way species can be identified, for example for environmental research, observing creatures in the wild, growing plants in a herbarium, identifying fossils in order to understand the past ages of life on Earth, or something as banal yet necessary or cataloging specimens in a museum drawer. This system of taxonomy (called Linnaean) was developed even before Darwin's theory of evolution, and even before the modern science of paleontology. MAK120229 120320

Taxonomy is a product of the modern age, specifically, the Age of Enlightenment. Classical and medieval thinkers used logical and philosphical categories, but these were based on the most general principles, and while perhaps useful for abstract philosophy, were not much use in understanding the natural world. In the worldview of the Middle Ages, based as it was on reliance on literalist religion and a fixed social and cosmic order, this didn't matter much, but with the progressive advance of knowledge during the Renaissance, the Age of Reason, and the Enlightenment, there developed an interest in the secular world for its own sake. Botanists especially were fascinated by exoteric new plants discovered during the voyages of exploration. It is not coincidental then that the father of modern biological classification was a botanist, Carl Linne, better known by his Latin name Linnaeus.

Linnaeus's simple yet brilliant idea was to distinguish nomenclature - the science of naming - from description. He therefore rejected the long-winded descriptive names of plants used by his predecessors and contemporaries, and replaced them with a simple two name system, a generic and a specific (think surname and given name, e.g. Smith, John). These where then grouped in hierarchies such as class, order, and so on. With only slight refinements, the Linnaean system is the scientific, biological classification system still used today. Linnaeus's classification of nature involved the three divisions of animal, vegetable, and mineral, although the great Swedish botanist's work on the mineral kingdom is now all but forgotten.

It was scientists and naturalists like Linnaeus in Sweden, and later the anatomist and naturalist Georges Cuvier in France, and Owen in England, and their collegues and co-workers, established in the 18th and early 19th century the science of what we now know as Taxonomy. Taxonomy is concerned with discovering, identifying, describing and naming organisms. For this to work it requires institutions to hold collections of these organisms, with relevant data, carefully curated: such institutes include Natural History Museums, Herbaria and Botanical Gardens. Richard Owen for example established the British Museum of Natural History in London, where his statue still resides. MAK120229

Linnaeus was not an evolutionist. Indeed, there was no such thing as a concept of evolution, in his day. Like Aristotle (and Christian creationists), he thought of species as immutable essences. This is why the Linnaean system is not a phylogeny, but a system of classifying the living world, developed at a time when species were considered the same today as when first created by an external God. Even with the 19th century discovery of evolution and the concept of a tree of life, Linnaean taxonomy remained based on similarity rather than evolutionary (phylogenetic) history. It was left to the great 20th century theorists of evolutionary biology and paleontology such as Mayr and Simpson to adaptable Linnaean methodology and include it in an overall evolutionary synthesis, the result being the methodology known as Evolutionary systematics. This became the standard paleontological worldview until the cladistic revolution of the 1980s. More recently it has been proposed that the venerable Linnaean system should be scrapped in favour of a new, phylogenetically based taxonomy; whether this actually comes to pass is anyone's guess. MAK130327

Page Back: The Great Chain of Being	Unit Home	Page Top	Page Next: Animal, Vegetable, and Mineral

(You are here)

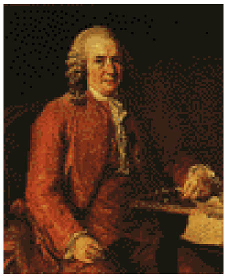
images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page last modified MAK130327

Carl von Linné and the Linnaean System of Nomenclature

Linnaeus



picture from the Linnaean Society of London

I haven't got round to doing his bio yet. In the meantime for info on Linnaeus check out these links.

Carolus Linnaeus - the best coverage.

CARL LINNEAUS - His life and work - short bio at the Linnaean Society of London.

The Linnaean Taxonomic Hierarchy

The Linnaean taxonomy is a formal system for classifying and naming living things based on a simple hierarchical structure, from most general to most similar The basic hierarchy as formulated by Linnaeus, is as follows:

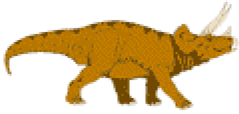
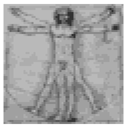
- ***Imperium*** ("Empire") - the phenomenal world
- ***Regnum*** ("Kingdom") - the three great divisions of nature at the time - animal, vegetable, and mineral
- ***Classis*** ("Class") - subdivisions of the above, in the animal kingdom six were recognized (mammals, birds, amphibians, fish, insects, and worms)
- ***Ordo*** ("Order") - further subdivision of the above - the class Mammalia has eight
- ***Genus*** - further subdivisions of the order - in the mammalian order Primates there are four. e.g. ***Homo***
- ***Species*** - subdivisions of genus, e.g. ***Homo sapiens***.
- ***Varietas*** ("Variety") - species variant, e.g. ***Homo sapiens europaeus***.

As can be seen, Linnaeus wrote in Latin, the standard intellectual language of the time. His hierarchical system still reflected the old medieval feudalistic worldview ("Order" for example referred to an order of monks). And concepts like evolution were alien to him. For Linnaeus and his contemporaries, the world and all its creatures was created once and for all, by the Judaeo-Christian God. Nevertheless this basic formula, as set out in the 10th edition of his ***Systema Naturae***, published in 1758, was and still is considered the foundation of all modern taxonomy (at least until the cladists came along! ;-)

As time progressed changes were made. The rank of Empire is obviously superfluous, while Variety came to be used only by gardeners, insect collectors, etc. The use of Latin was replaced by the vernacular, although it is still retained in the actual generic and specific names. And two new ranks were erected - ***Phylum*** (or ***Division*** in the case of Plants) was added between Kingdom and Class, and ***Family*** between Order and Genus, giving seven hierarchical ranks in all. So, in this nested system of rankings, kingdoms are made up of phyla, phyla of classes, classes of orders, and so on; each higher rank including at least one and usually more subordinate members. This seven-layered hierarchy is the version still used today:

Kingdom
  Phylum
    Class
      Order
        Family
          Genus
            Species

This very versatile arrangement can be used to classify every living organism, living or extinct. The following table (below) illustrates this by means of three examples: the tiger cowry shell, the ***Triceratops*** dinosaur, and man

Linnaean rank			
kingdom	**Animalia**	**Animalia**	**Animalia**
phylum	**Mollusca**	**Chordata**	**Chordata**
class	**Gastropoda**	**Reptilia**	**Mammalia**

order	**Mesogastropoda**	**Ornithischia (Predentata)**	**Primates**
family	**Cypraeidae**	**Ceratopsidae**	**Hominidae**
genus	***Cypraea***	***Triceratops***	***Homo***
species	***tigris***	***horridus***	***sapiens***

What's in a name?

The formal international agreement on names, ranks, and so on, is laid out in the International Code of Zoological Nomenclature, The International Code of Botanical Nomenclature, and the International Code of Nomenclature of Bacteria. These set guidelines and publish a reports containing the rules of nomenclature. For example, the ***Law of Priority*** (Article 25) says that if a genus or species has been accidentally given two names, only the earlier one is valid. The later name becomes a "junior synonym". This is the case even when it is better known (or more evocative). To give a famous illustration, the Jurassic dinosaur ***Brontosaurus***, named by the 19th century American paleontologist Othniel C. Marsh in 1879, was later found to be the same animal as ***Apatosaurus***, which was actually named by the same guy two years previously (this was during the great dinosaur rush when Marsh and his rival Edward Drinker Cope were engaged in a bitter feud to see who could discover the most prehistoric animals!). Therefore ***Apatosaurus*** is the correct name, even though "thunder lizard" (***Brontosaurus***) would seem more appropriate than "deceptive lizard" (***Apatosaurus***), and even though the later name honors the same man (maverick paleontologist Dr Bob Bakker has suggested using ***Brontosaurus*** anyway!). A similar thing happened with ***Eohippus*** ("dawn horse") and ***Hyracotherium*** ("hyrax beast"). The better known, more appropriate name was later fond to be describe the same animal as had been previously named. In some cases things are not so clear cut, and a ruling from the Commission in charge of these things is necessary to decide which name to use.

The complete scientific name includes genus and species, the name of the scientist who first described the species in a scientific journal deemed valid for taxonomic purposes, and the year that the paper was published. By convention that the genus and species are written in italics (or, where that is not possible, underlined, or even _underlined ASCII wise_). The generic name is always capitalized, the ***trivial*** or species name is not. So we have (to use the above illustration) ***Apatosaurus ajax*** Marsh, 1877.

When a species is placed in a genus different to the one originally named, then the discoverer's name is placed in brackets, even when it is the same guy who named both. So ***Brontosaurus excelsus*** Marsh, 1879 becomes ***Apatosaurus excelsus*** (Marsh, 1879).

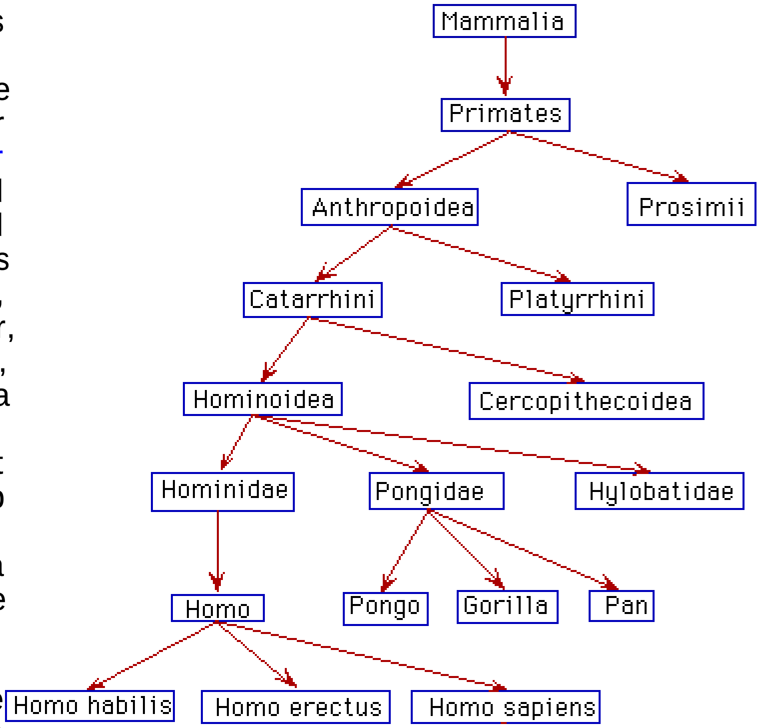
The generic name can be abbreviated to a single capital letter, as in ***A. ajax.*** However just using the generic name alone refers to all species included in that genus, in this case ***Apatosaurus*** includes the species ***A. ajax***, ***A. excelsus*** and ***A. louisae***.

When a new genus is described, it is based on a particular species (i.e. nomenclature-wise the taxonomic hierarchy works from species up, not from kingdom down) which becomes the ***type species*** of that genus. So ***A. ajax*** is the type species of ***Apatosaurus***.

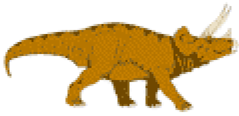
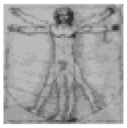
Sometimes a species is deemed too different to belong in the genus it was formally placed in, and so becomes the type species of a new genus. So ***Apatosaurus alenquerensis*** de Lapparent & Zbyszewski, 1957 was recently made the type species for the genus ***Lourinhasaurus***, hence ***Lourinhasaurus alenquerensis*** (de Lapparent & Zbyszewski, 1957). Of course whether a species should be retained in a former genus or placed in a new one is often an arbitrary choice, which brings us to the battle between the splitters and the lumpers.

Infra-orders and superfamilies

Even the seven-fold hierarchical system, with it's multiple ranks, was ultimately not sufficiently detailed. As knowledge of the natural world progressed and the number of groups of organisms identified became larger and larger, it became necessary to create further subcategories. These include Tribe between Family and Genus; and Division and Cohort between Class and Order. Moreover, each category can also have prefixes to create a higher grouping (super-), or lower (sub-, infra-) subdivisions So now there is also superorder, suborder, infraorder, subgenus, and subspecies. Again, each is arranged in nested ranks, e.g. there may be a number of superfamilies in each infra-order, and so on. This is illustrated by the tree-like diagram at the right (showing man's position in the Order Primates - from top to bottom we have class, order, suborder, infraorder, superfamily, family, genus, and species. ***Note***: only a few of the many ramifications of the other branches are shown).



When we look at the preceding three species (see above table) in this light we see straight away that things have become more complex (see table below):

Linnaean rank			
kingdom	**Animalia (Metazoa)**	**Animalia (Metazoa)**	**Animalia (Metazoa)**
phylum	**Mollusca**	**Chordata**	**Chordata**
subphylum	**--**	**Vertebrata**	**Vertebrata**
superclass	**--**	**Tetrapoda**	**Tetrapoda**
class	**Gastropoda**	**Reptilia**	**Mammalia**
subclass	**Prosobranchia**	**Diapsida**	**Theria**
infraclass	**--**	**Archosauria**	**Eutheria**
superorder	**Caenogastropoda** (sometimes considered an order)	**Dinosauria**	**Archonta**
order	**Mesogastropoda (Neotaenioglossa)** (sometimes considered a suborder)	**Ornithischia (Predentata)**	**Primates**
suborder	**Discopoda** (sometimes considered an infra-order)	**Marginocephalia**	**Anthropoidea**
infraorder	**--**	**Ceratopsia**	**Haplorhini**
superfamily	**Cypraeoidea (or Cypraeacea)**	**--**	**Hominoidea**
family	**Cypraeidae**	**Ceratopsidae**	**Hominidae**
subfamily	**Cypraeinae**	**Ceratopsinae**	**Homininae**

genus	***Cypraea***	***Triceratops***	***Homo***
subgenus	***(Cypraea)***	**--**	**--**
species	***tigris***	***horridus***	***sapiens***

Remember that only the seven main categories (i.e. kingdom, phylum, etc, see left-hand column) are actually mandatory under the international codes of nomenclature. But the others, although optional, but often used.

The Splitters and the Lumpers

> "Splitters make very small units - their opponents say that if they can tell two animals apart, they place them in different genera, and if they cannot tell them apart, they place them in different species. Lumpers make large units - their opponents say that if a carnivore is neither a dog or a bear they call it a cat."

G.G. Simpson, "The Principles of Classification and a Classification of Mammals", ***Bulletin of the American Museum of Natural History***, vol.85, (New York, 1945) p.23

One thing the codes of nomenclature are unable to do anything about is personal preference as to how to divide up families, genera etc. Here we have the famous disagreement between the splitters and the lumpers, between those who prefer to lump together a large number of species in each genus, or genera in families, and those who would rather split genera among new families, and put species in new genera. Hence among, say, malacologists (those who study molluscs), there is on the one hand those who would lump all species of cone shells in the old traditional genus ***Conus***, and those who would divide them up among a large number genera - ***Lithoconus, Floraconus, Parviconus***, etc etc. This can be very annoying for amateur naturalists who would like to have the right name for their labels!

The situation becomes even more involved with the large degree of arbitrariness with these finer sub-rankings due to personal preference and bias. One man's superfamily may be another man's suborder! (e.g. the molluscan ranks Caenogastropoda etc in the table above.)

Taxonomic Inflation

When Linnaeus was around there were not really that many types of animals and plants known, so only a few classes, orders, families, and genera would suffice. As the natural world became better known with further voyages of discovery, as well as developments in biology, more and more new generic, family, and higher categories were required to handle it all.

To a large extent this was completely justified, but in the last few decades there has developed a rather unfortunate tendency known as ***Taxonomic Inflation***. This means that a previously considered ranking - e.g. a superfamily, is raised to a higher ranking - e.g. an order, without real justification. Here of course we have again the fact of the arbitrary nature of the Linnaean ranking, as it could be argued either position is valid. And sometimes both versions co-exist (as with the splitters and the lumpers) and are found in different text books (and web pages). For example each of the major taxa of vascular plants may be considered as either Classes (e.g. Lycopsida) or the next higher rank, a Division (e.g. Lycophyta). In keeping with an on-going process of inflation, the latter is more often used now, but one still finds examples of the former approach quite frequently, even in recent books.

In some cases however the degree of taxonomic inflation is completely ridiculous. Take the example of the brachiopod family Cranioidea (a type of marine shelled invertebrate). As these animals are quite distinct from other members of the phylum Brachiopoda they were given their own superfamily Cranioidea. This then became a distinct order - Craniida. Okay, fair enough. But then in a more recent classification they have been raised to the rank of class, the Craniata (containing the Craniida and two other orders, the Craniopsida and Trimerellida) and even a sub-phylum Craniiformea. Many other examples can be given, such as classes of micro-organisms (Protista) raised to kingdom and superkingdom rank! It is clear that this is taking things to excess, but part of the problem here is misguided attempt to combine the Linnaean system with it's rival the Cladistic arrangement; this being impractical if not impossible due to the incompatibility between the two.

Another thing to consider here is that there is also more than a little measure of anthropocentric chauvinism, because those organisms closer to us on the family tree (the old "chain of being") are generally given higher ranking. e.g. the orders of birds or mammals, if they were invertebrates, would never qualify higher than superfamily rank. Moreover the names often change as the classification does. Sometimes either name can be used; sometimes the older name is rendered invalid. In any case it can be seen that this sort of classification, no matter how useful, is not a fixed and absolutely objective system.

Links

Animal, Vegetable or Mineral? by Dan H. Nicolson - a critical analysis, overviewing the arbitrary nature of the Linnaean system and its history up to the time of Darwin (part of the Proceedings of a Mini-Symposium on Biological Nomenclature in the 21st Century).

Nowadays the Linnaean system is increasing losing ground to the non-hierarchical cladistic system of nested branches. But not everyone is pleased about such a change, or even considers it necessarily.

Quite Happy with the Present Code, Thank You by R. K. Brummitt, from the same symposium as the preceding link argues against cladism and in favour of retaining the Linnaean methodology.

Linnaean Society Links

the Linnaean Society of London

Linnaean Society of New South Wales

Page Back: Animal, Vegetable, and Mineral | Page Top | Page Next: Kingdom

---

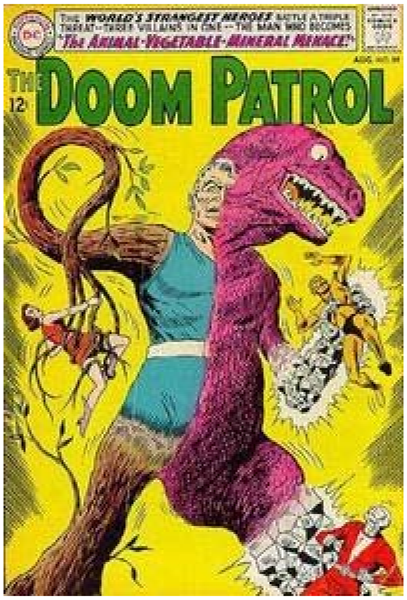
checked ATW031211, edited RFVS111202
(originally uploaded on Kheper site 21 June 1998)

Page Back: Unit home	Unit home	Glossary	Page Next: The Linnaean System
Unit Back: The Great Chain of Being	Unit Up: Systematics	Page Up: Taxonomy	Unit Next: The Tree of Life

Animal, Vegetable, and Mineral

Phylogeny and Systematics
  Systematics �' History of ideas
    The Great Chain of Being
    Linnaean taxonomy
    The Tree of Life
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Synthesis
    Taxonomy
  Glossary
  References

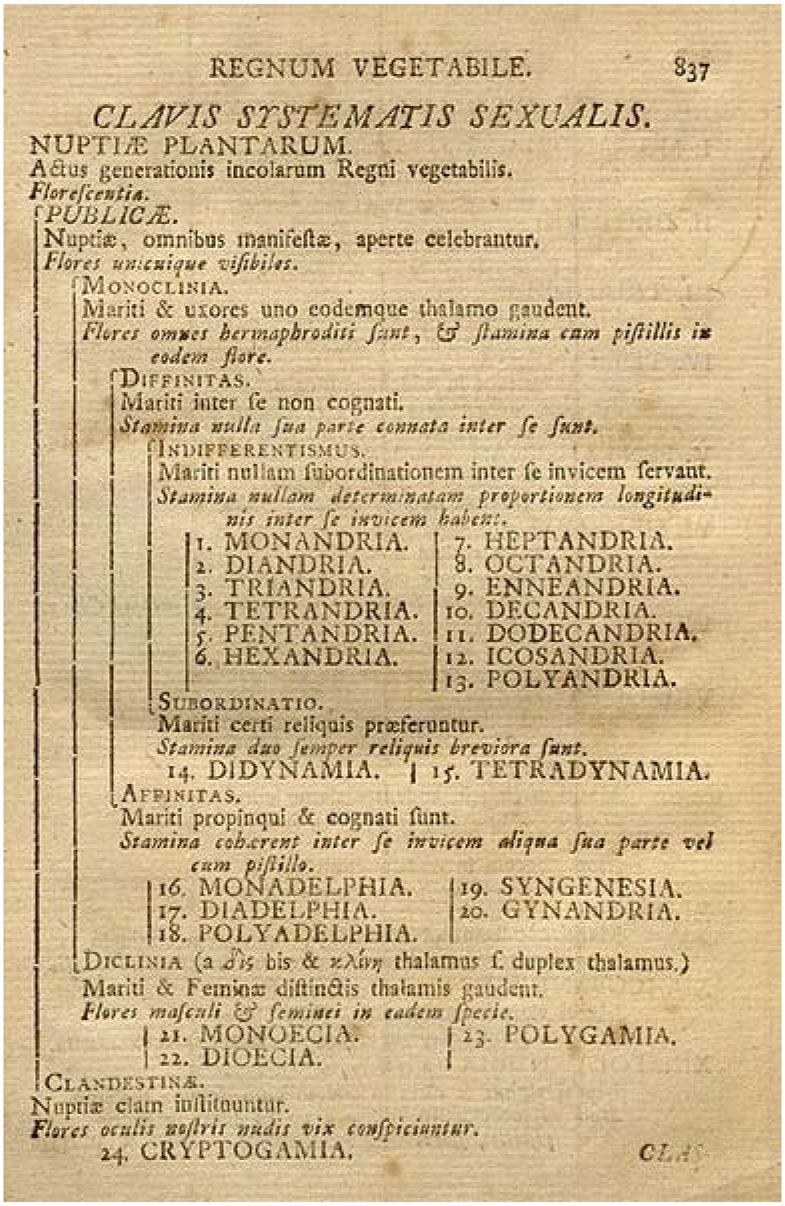
Linnaean taxonomy
  Animal, Vegetable, and Mineral
    The Linnaean system
    The Linnaean Taxonomic Hierarchy
    What's in a name?
    Infra-orders and Super-families
    The Splitters and the Lumpers
    Taxonomic Inflation
    Links
  Kingdom
  Phylum
  Class
  Order
  Family
  Tribe
  Genus
  Species
  Extra ranks



Animal-Vegetable-Mineral Man, from *Doom Patrol* #89, Art by Bob Brown

The division of familiar objects into animal, vegetable and mineral probably dates back to prehistory, and it is commonplace to hear the phrase “animal kingdom” or “plant kingdom.” Most students will be aware, also, of the landmark contribution made by the Swedish naturalist, Carolus Linnaeus (and variations on that spelling) in the mid-1700s. - Chris Clowes 030219

In his *Systema Naturae* (first ed. 1735; 10th ed. 1758) Linnaeus established three kingdoms, namely*Regnum Animale*, *Regnum Vegetabile* and *Regnum Lapideum*, or Animal, Vegetable, and Mineral (a typology that can be derived from ideas regarding the great chain of being), each divided into five ranks: kingdom, class, order, genus, and species. Traces of the Aristotlean system can be seen in the distinction of genus and species, and calling categories classes, while the intermediate level of "order" shows a medieval origin, for example orders of monks. - Wikipedia, MAK130321



REGNUM VEGETABILE. 837

CLAVIS SYSTEMATIS SEXUALIS.

NUPTIÆ PLANTARUM.

Actus generationis incolarum Regni vegetabilis.

Floreſcentia.

PUBLICÆ.

Nuptiæ, omnibus manifeſtæ, aperte celebrantur.

Flores unicuique viſibiles.

MONOCLINIA.

Mariti & uxores uno eodemque thalamo gaudent.

Flores omnes hermaphroditi ſunt, & ſtamina cum piſtillis in eodem flore.

DIFFINITAS.

Mariti inter ſe non cognati.

Stamina nulla ſua parte connata inter ſe ſunt.

INDIFFERENTISMUS.

Mariti nullam ſubordinationem inter ſe invicem ſervant.

Stamina nullam determinatam proportionem longitudinis inter ſe invicem habent.

1. MONANDRIA.
2. DIANDRIA.
3. TRIANDRIA.
4. TETRANDRIA.
5. PENTANDRIA.
6. HEXANDRIA.
7. HEPTANDRIA.
8. OCTANDRIA.
9. ENNEANDRIA.
10. DECANDRIA.
11. DODECANDRIA.
12. ICOSANDRIA.
13. POLYANDRIA.

SUBORDINATIO.

Mariti certi reliquis præferuntur.

Stamina duo ſemper reliquis breviora ſunt.

14. DIDYNAMIA.
15. TETRADYNAMIA.

AFFINITAS.

Mariti propinqui & cognati ſunt.

Stamina cohærent inter ſe invicem aliqua ſua parte vel cum piſtillo.

16. MONADELPHIA.
17. DIADELPHIA.
18. POLYADELPHIA.
19. SYNGENESIA.
20. GYNANDRIA.

DICLINIA (a δὶς bis & κλίνη thalamus ſ. duplex thalamus.)

Mariti & Feminæ diſtinctis thalamis gaudent.

Flores maſculi & feminei in eadem ſpecie.

21. MONOECIA.
22. DIOECIA.
23. POLYGAMIA.

CLANDESTINÆ.

Nuptiæ clam inſtituuntur.

Flores oculis noſtris nudis vix conſpiciuntur.

24. CRYPTOGAMIA.

CLA

Page 837 from the 10th edition (1758) of Linnaeus's *Systema naturae*, classifying plants in terms of an arbitrary "sexual system" .
Botanicus.org, via From Wikipedia, Creative Commons Attribution-Noncommercial 2.5 license.

Of the three kingdoms, only in the Animal Kingdom is the higher taxonomy of Linnaeus still more or less recognizable. He divided the Animal Kingdom into six classes; in the tenth edition (1758), these are:

- Mammalia comprised the mammals. In the first edition, whales and the West Indian Manatee were classified among the fishes.
- Aves comprised the birds. Linnaeus was the first to remove bats from the birds and classify them under mammals.
- Amphibia comprised amphibians, reptiles, and assorted fishes that are not of Osteichthyes.
- Pisces comprised the bony fishes. These included the spiny-finned fishes (Perciformes) as a separate order.
- Insecta comprised all arthropods. Crustaceans, arachnids & myriapods were included as the order "Aptera".

Vermes comprised the remaining invertebrates, roughly divided into "worms", molluscs and hard-shelled organisms like echinoderms.

The orders and classes for the Plant Kingdom, emphasising the sexual organs of plants, was never intended to represent natural groups but only for use in identification (for example species with the same number of stamens were placed in the same class). They were used in that sense well into the nineteenth century. These are

- Classis 1. Monandria
- Classis 2. Diandria
- Classis 3. Triandria
- Classis 4. Tetrandria
- Classis 5. Pentandria
- Classis 6. Hexandria
- Classis 7. Heptandria
- Classis 8. Octandria
- Classis 9. Enneandria
- Classis 10. Decandria
- Classis 11. Dodecandria
- Classis 12. Icosandria
- Classis 13. Polyandra
- Classis 14. Didynamia
- Classis 15. Tetradynamia
- Classis 16. Monadelphia
- Classis 17. Diadelphia
- Classis 18. Polyadelphia
- Classis 19. Syngenesia
- Classis 20. Gynandria
- Classis 21. Monoecia
- Classis 22. Dioecia
- Classis 23. Polygamia
- Classis 24. Cryptogamia

His taxonomy of the Mineral Kingdom has dropped long since from use. In the tenth edition, 1758, of the Systema Natur�, the Linnaean classes were:

- Classis 1. Petr� (rocks)
- Classis 2. Miner� (minerals and ores)
- Classis 3. Fossilia (fossils and aggregates)

The work of Linnaeus had a huge impact on science; it was indispensable as a foundation for biological nomenclature, now regulated by the Nomenclature Codes. Two of his works, the first edition of the *Species Plantarum* (1753) for plants and the tenth edition of the *Systema Natur�* (1758) are accepted among the starting points of nomenclature; most of his names for species and genera were published at very early dates and thus take priority over those of others. Although his taxonomy was not particularly notable in itself (for example the artificial classification of plants), Linnaeus' talent for attracting skillful young students and sending them abroad to collect made his works far more influential than that of his contemporaries. At the close of the 18th century, his system had effectively become the standard system for biological classification - Wikipedia

Animal, Vegetable, and Mineral became a way of classifying and understanding nature even for those who had never heard of Linnaeus (there was even a parlour game and a comic book based on this). In addition to the three kingdoms, a separate human kingdom added (due to the anthropocentric approach of religious thought; this was something Linnaeus did fall for) is still used in a number of religious, spiritual, esoteric and occult systems of thought: the Baha'i faith, Anthroposophy, Rosicrucianism, and contemporary Sufism and the Neo-Sufi Traditionalist or "perennialist" movement. It is assumed here that there is a natural succession from inert mineral to the plant that is alive but not sentient to the animal that has awareness but not reason. Hence the human kingdom as the next rung on the ladder of being. It is easy to see here the influence of Aristotle. This arrangement of the "kingdoms of nature" were modified by the theosophists, who proposed a number of spiritual involutionary kingdoms that represent the downward antecedent of the "evolutionary" kingdoms of plants, animals and man.

> Modern science however has rendered the traditional three kingdom idea obsolete. First the mineral kingdom has been replaced by the hierarchy of particles, atoms, and molecules. This led some "Great Chain of Being" universalists such as Edward Haskell and co-workers (*Unified Science*) and Arthur M. Young (*The Reflexive Universe*) added further kingdoms like subatomic particles, atoms, molecules, etc before the mineral. MAK130319
>
> Today we still use a derived form of the categories first published by Linnaeus, although much of the detail has changed. For example, many single-celled organisms – none of which were known to Linnaeus – are regarded as belonging to a kingdom of their own, the Protista, which stands alongside the Animalia and Plantae. The fungi are no longer considered plants; they too have a kingdom to themselves. -- Chris Clowes 030219

More recently the plant and animal kingdoms were replaced by the five kingdom model of Whittaker (monera, protist, fungi, plant, and animal (including human)), and then the three domains of Carl Woese. Through studies of the genomes of a wide range of organisms, Woese discovered that protists, plants, animals and fungi, collectively known as the Eukarya, are all relatively similar to one another, compared to the far more fundamental differences dividing them from two great lineages of bacteria, the Archaea and the Bacteria. Together these make up the three “domains” – the Archaea, Bacteria and Eukarya –, which are now considered the most fundamental divisions of living things. - Chris Clowes 030219

Page Back: Unit home | **Unit Home** | **Page Top** | **Page Next: The Linnaean System**

page last modified MAK130320. Content by MAK, Wikipedia, Chris Clowes

Kingdom

Linnaean Home
Linnaeus
The Linnaean Taxonomic Hierarchy
What's in a name?
Infra-orders and Super-families
The Splitters and the Lumpers
Taxonomic Inflation
Links

Definition: Kingdom
Phylum
Class
Order
Family
Tribe
Genus
Species

Kingdom

Kingdom

Phylum
Class
Order
Family
Genus
Species

The highest ranking of organisms in the standard Linnaean system. The term is based on earlier medieval and alchemical ideas - e.g. "animal kingdom" "vegetable kingdom," "mineral kingdom". The original Plant - Animal Kingdom divide was replaced by the Five Kingdom model of Whittaker and Margulis. Modern research into micro-organisms however has shown that they are far more diverse than was previously thought, and the kingdom has been relegated to a relatively minor status ***vis a vis*** the Domain, the highest current taxonomic ranking.

---

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page by M. Alan Kazlev (Creative Commons Attribution 3.0 Unported License)
page uploaded 20 May 2002
checked ATW031211, edited RFVS111202
(originally uploaded on Kheper site 13 December 1998)

Phylum

Linnaean Home
Linnaeus
The Linnaean Taxonomic Hierarchy
What's in a name?
Infra-orders and Super-families
The Splitters and the Lumpers
Taxonomic Inflation
Links

Definition: Kingdom
Phylum
Class
Order
Family
Tribe
Genus
Species

Phylum

Kingdom

Phylum
Class
Order
Family
Genus
Species

Referred to as 'Division" in the case of Plants and Bacteria. In the standard Linnaean system (and taxonomic systems based on it), a Phylum is the taxonomic category between Kingdom and Class. A phylum is a major ranking of organisms, defined according to the most basic body-parts shared by that group. e.g. Chordata (animals with a notochord - vertebrates and others), Arthropoda (animals with a jointed exoskeleton) Mollusca (animals with a shell-secreting mantle), Angiosperma (flowering plants), and so on. A number of traditional Phyla - e.g. Protozoa, possibly Arthropoda - are probably invalid (polyphyletic).

---

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page uploaded 20 May 2002
checked ATW021130
(originally uploaded on Kheper site 13 December 1998)

Class

Linnaean Home
Linnaeus
The Linnaean Taxonomic Hierarchy
What's in a name?
Infra-orders and Super-families
The Splitters and the Lumpers
Taxonomic Inflation
Links

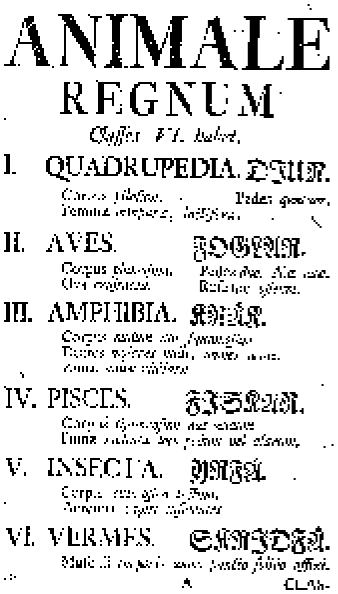
Definition: Kingdom
Phylum
Class
Order
Family
Tribe
Genus
Species

Class

Kingdom

Phylum
Class
Order
Family
Genus
Species

In the Linnaean system (and taxonomic systems based on it), a Class is the taxonomic category between Phylum and Order. A class is a major group of organisms, e.g. Mammalia, Reptilia, Gastropoda, Insecta, etc that contains a large number of different sublineages, but have shared characteristics in common (e.g. warm-blooded, fur, mammary glands in female in the case of mammals, six legs and three body parts in the case of Insects, etc). As with all the groupings whether a group of organisms ranks as a class or not is a subjective decision, although usually based on the traditional status of that group in earlier literature. The cladistic revolution has caused a reappraisal of these rankings, and rejection or modification of many of these rankings.



ANIMALE
REGNUM
Classes VI. habet.

I. QUADRUPEDIA. DJUR.

II. AVES. FOGLAR.

III. AMPHIBIA. KRÄK.

IV. PISCES. FISKAR.

V. INSECTA.

VI. VERMES.

CLAS-

**Originally Linnaeus divided the Animal Kingdom into six classes.
Many more have been proposed since then...**

---

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page by M. Alan Kazlev (Creative Commons Attribution 3.0 Unported License)
page uploaded 20 May 2002 (originally uploaded on Kheper site 13 December 1998)
checked ATW040703, edited RFVS111202

Page Back	Unit Home	Glossary	Page Next
Unit Back	Unit Up: Systematics	Page Up: Taxonomy	Unit Next

Order

Linnaean Home
Linnaeus
The Linnaean Taxonomic Hierarchy
What's in a name?
Infra-orders and Super-families
The Splitters and the Lumpers
Taxonomic Inflation
Links

Definition: Kingdom
Phylum
Class
Order
Family
Tribe
Genus
Species

Order

Kingdom

Phylum
Class
Order
Family
Genus
Species

In the Linnaean system (and taxonomic systems based on it), the Order is a taxonomic category between Class and Family. An order is group of organisms, e.g. Lepidoptera, Squamata, Primates, etc that although differing quite a bit among themselves still have a large degree of characteristics in common (e.g. all Lepidoptera (butterflies and moths) have minute scales on their wings, a soft-bodied herbivorous larval form (caterpillar), mouthparts in the adult specialized for feeding on nectar, etc). As with all the groupings whether a group of organisms ranks as an order or not is a subjective decision, although usually based on the traditional status of that group in earlier literature. There is also a tendency towards taxonomic inflation, especially among tetrapods but also certain groups of invertebrates, with sub- or infra-orders (and even families) being promoted to ordinal status. Also, invertebrate orders tend to differ among themselves much more than vertebrate orders (e.g. an invertebrate order e.g. Coleoptera (beetles) might correspond in diversity to a suborder or cohort or infraclass of Vertebrates). Cladistics tries to solve this arbitrariness by doing away with the Linnaean system altogether.

Superorder
Grandorder
Order

Suborder
Infraorder
Parvorder

---

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page by M. Alan Kazlev (Creative Commons Attribution 3.0 Unported License)
page uploaded 20 May 2002
checked ATW021211
(originally uploaded on Kheper site 27 May 1999)

Page Back | Unit Home | Glossary | Page Next
Unit Back | Unit Up: Systematics | Page Up: Taxonomy | Unit Next

Family

Linnaean Home
Linnaeus
The Linnaean Taxonomic Hierarchy
What's in a name?
Infra-orders and Super-families
The Splitters and the Lumpers
Taxonomic Inflation
Links

Definition: Kingdom
Phylum
Class
Order
Family
Tribe
Genus
Species

Family

Kingdom

Phylum
Class
Order
Family
Genus
Species

In the Linnaean system (and taxonomic systems based on it), the **Family** is a taxonomic category between Order and Tribe. It might seem strange that a family is considered higher than a tribe (i.e. a family can contain many tribes, but not vice versa), but such is the way these names are. When there are no Tribes, the Family is a taxonomic category between Order and Genus. More even then an order, a family is a group of organisms among which the differences are quite minor, e.g. Equidae - horses and their relatives, ***Ceratopsidae*** - horned dinosaurs, or ***Hominidae***, man and ape-men. Some families contain thousands of species, others might only have a single species.

Note: Although again the differences among Hominids are extremely slight, here we see a chauvinistic taxonomic inflation, elevated a probably genus rank to family ranking; more recently cladistics, with its preference for giving each recognised branching point its own linnaean rank (which can be problematic if a cladogram contains dozens of nested nodes) has taken this to the other direction, reducing hominids as traditionally defined to the status as of a subtribe.

rank	suffix
Magnafamily	-idea

Superfamily	**-oidea *or* -acea**
Epifamily	**-oidae**
Family	**-idae**
Subfamily	**-inae**

---

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page by M. Alan Kazlev (Creative Commons Attribution 3.0 Unported License)
page uploaded 20 May 2002
checked ATW031211, edited RFVS111202, last modified MAK130319
(originally uploaded on Kheper site 27 May 1999)

Page Back | Unit Home | Glossary | Page Next
Unit Back | Unit Up: Systematics | Page Up: Taxonomy | Unit Next

Tribe

Linnaean Home
Linnaeus
The Linnaean Taxonomic Hierarchy
What's in a name?
Infra-orders and Super-families
The Splitters and the Lumpers
Taxonomic Inflation
Links

Definition: Kingdom
Phylum
Class
Order
Family
Tribe
Genus
Species

Tribe

Kingdom

Phylum
Class
Order
Family
Genus
Species

In the Linnaean system (and taxonomic systems based on it), the **Tribe** is an optional ranking between the Family and the Genus. It might seem strange that a family is considered higher than a tribe (i.e. a family can contain many tribes, but not vice versa), such is the way these names are. This category has traditionally been more commonly used in botany, but cladistics, with its ever finer subdividing of phylogenetic trees, is encouraging a greater use of this ranking in zoology and paleontology as well. Basically we could say that a tribe is a group of organisms among which the differences are extremely minor but still noticeable. In other words a group of genera which are more closely related to each other than to other genera in that family.

rank	suffix
Tribe	**- ini**
Subtribe	**-ina**

---

contact us

page by M. Alan Kazlev (Creative Commons Attribution 3.0 Unported License)
page uploaded 22 May 2002 (originally uploaded on Kheper site 27 May 1999)
checked ATW030730, edited RFVS111202

Genus

Linnaean Home
Linnaeus
The Linnaean Taxonomic Hierarchy
What's in a name?
Infra-orders and Super-families
The Splitters and the Lumpers
Taxonomic Inflation
Links

Definition: Kingdom
Phylum
Class
Order
Family
Tribe
Genus
Species

Genus

Kingdom

Phylum
Class
Order
Family
Genus
Species

In the Linnaean system (and taxonomic systems based on it), the **Genus** is the first grouping of species, the ranking between Family or Tribe and Species. Only very closely related species are grouped together in a single genus. The genus is sort of like the surname, whereas the species is the first name. So ***Canis lupus***, the wolf, is distinguished from ***Canis familiaris***, the domesticated dog. Although very similar they are still distinct species, but belong to the same genus. Or in man, ***Homo erectus*** and ***Homo sapiens***. Note that the higher ranking (genus) name is written first. This is like the Chinese system of names where the family (sur-)name comes before the individual name. e.g. Kung-fu-tze (Confucius) was literally "Mr Kung" (Kung being the family name). As a formality the genus name, like the species name, has to be written in italics. Where that is not possible it should underlined, e.g. Homo erectus (that one is not a link ;-)).

rank	suffix
Genus	***Genus species***
Subgenus	**Genus *(Subgenus) species***

More on the Genus

Note that the genus name is only one half of the scientific name. That is why it is called the *binomial* system - there is genus and species. Many books on dinosaurs and prehistoric life (and also web sites) only give the genus name as if that was the complete name. But in fact it is actually, to give an example, *Triceratops horridus*, not just *Triceratops*. The only prehistoric animal in which the species name is usually given is of course the famous *Tyrannosaurus rex*. There are actually several species of *Tyrannosaurus* though, the species found in Mongolia is known as *Tyrannosaurus bataar*.

There is a regrettable tendency though to split up vertebrate (especially dinosaurian) genera so that each genus only has a single species - e.g. *T. bataar* is often called *Tarbosaurus*, despite being so similar to *Tyrannosaurus* it is not funny. Such oversplitting also occurs among fossil invertebrates, groups like the Nautiloidea (mollusks) are serious oversplit with much too many genera - especially if you compare them to recent mollusks.

---

page by M. Alan Kazlev (Creative Commons Attribution 3.0 Unported License)
page uploaded 23 May 2002
checked ATW031211, edited RFVS111202
(originally uploaded on Kheper site 27 May 1999)

Species

Linnaean Home
Linnaeus
The Linnaean Taxonomic Hierarchy
What's in a name?
Infra-orders and Super-families
The Splitters and the Lumpers
Taxonomic Inflation
Links

Definition: Kingdom
Phylum
Class
Order
Family
Tribe
Genus
Species

What is a Species
Some different definitions
Species and Archetype
Some books dealing with the definition of "species"

The Problems of Defining a Species

A Voyage from Science to Metaphysics (and vice versa)

What is a Species?

In the Linnaean system and biology in general, a ***species*** is the smallest basic taxonomic unit used to define living organisms. The definition I read when I was growing up was that of Ernst Mayr, the grand old man of modern Evolutionary Biology. He said that two organisms belonged to the same species if they are able to interbreed and produce fertile offspring. This of course ignores simple organisms (bacteria etc) that reproduce by fission (asexually). As John S Wilkins points out (***need current url***) Mayr's reply to that is that these organisms are not species. Well if they're not species what are they? As far as I understand things, every unique biological type (phenotype) is a species. That includes the amoeba, even though amoebas reproduce asexually.

It's obvious that the issue of what constitutes a species in biology is a sticky one. In A Taxonomy of Species Definitions - Or, Porphyry's Metatree (***need current url***), Dr Wilkins gives a detailed analysis of the problem of defining what constitutes a biological species. He points out that the same term is used in a number of different contexts and to mean different things. Fascinating but somewhat heavy going. The following table sets out his list of definitions of "species" (for those who don't wish to plow through the article). First of all, the species can be seen either as a ***theoretical concept*** used in modeling (simulation) and explanation, or as taxonomic units used to differentiate and classify living organisms (allowing for the fact that many definitions combine both approaches). That gives us the ***1st level distinction***. Each of these two categories can be divided into two, and each of those in turn into, giving the following "meta-taxonomic" arrangement:

1st level distinction	**2nd level distinction**	**3rd level distinction**	**definition**	**examples in the literature**	**units**
Species Concepts **SC** species as a ***theoretical concept*** used in modeling and explanation	**Horizontal SCs** - **HSC** Neontological (living organisms)	Reproductive HSCs -**RHSC**	able to interbreed and produce fertile offspring	the traditional biological species concept (Mayr)	genotype
		Ecological HSCs - **EHSC**	use same ecological resources	ecological species concepts (Darnuth, Van Valen)	trophic level
	Vertical SCs - **VSC** Palaeontological (fossil: species over evolutionary time)	Process VSCs - **PVSC**	evolutionary speciation (one species gives rise to others)	Phylogenetic species concepts - **cladistic**, **phenetic** and other phyletic reconstructions (Hennig, Wiley, Cracaft)	monophyletic group, clade, node, character set
		Historical VSCs - **HVSC**	preserved information (phylogenetic and palaeontological)	**evolutionary** species concepts (Simpson)	fossil organism
Taxonomic Units **TU** (species as ***taxa***, used to differentiate and classify)	**Ontological TUs** - **OTU**	Metaphysical OTUs - **MOTU**	species as a metaphysical entity	Plato's transcendent Ideas, the Aristotelian notion of Forms, the Naturphilosophen concept of Bauplans, and the recent proposals of Ghiselin and Hull for the understanding of species as spatiotemporally restricted individuals.	***ideos***, archetype, universal, class, set, subset, member
		Causal OTUs - **COTU**	causal relationship between members	most species concepts - Aristotle's biological implementation of Forms was more causally based on the ability to generate like forms through reproduction.	generally not specified (causal nexus?)
	Epistemic TUs - **ETU**	Morphological ETUs - **METU**	similarity of form	Traditional Linnaean system (also Operational taxonomic units - Sneath & Sokal)	family, genus, species, etc; phenotype
		Dynamic ETUs - **DETU**	similarity of behavior	Game theory (Maynard Smith)	strategy, player/agent

Species and Archetypes

It seems to me that the MOTU group (metaphysical ontological taxonomic unit interpretation) in the above table can in turn be divided. There is the dualistic Platonic theory of "Universals" (Ideal Forms) as transcendent unchanging eternal essences, as opposed to the holistic Aristotelian theory of universals (Forms) as the spirit or soul aspect of an object, the complementary aspect being the body. In the Platonic theory although the body dies the form is eternal. In the Aristotelian approach, when the body dies the spirit or form aspect does likewise. The Creation Science definition of a "species", based on a literal reading of the Hebraic (Mosaic) book of Genesis, is a rather vague and fuzzy version of the Aristotelian position.

The dualistic interpretation of Species/Archetype can in turn be divided into the pure Platonic (the ***eidos*** as a transcendent eternal Truth, and the Theosophical/Anthroposophical/New Age interpretation of the ***species archetype*** as a sort of group consciousness or group soul that all the organisms of that species participate in. The idea of an overshadowing group soul - supraphysical but not eternal and transcendent - goes back to the Neoplatonists, and especially to Iamblichus and Proclus who elaborated this concept in great deal. In a sense modern Theosophy is the true heir to later Neoplatonism, even though Blavatsky was influenced more by Plato, Advaita Vedanta, and Tibetan Buddhism, and Leadbeater more by spiritualism. I have given my thoughts on this matter under the heading Evolutionary Platonism.

Traditional (Greek and Medieval Scholastic) archetype species theories were based on what Aristotle called "privation" - specifying key characters by progressively removing qualities that refer to other entities. The idea of privation - of the diminishing of the plenitude of the Absolute was an important theme in Plotinus's Neoplatonism. With the late Neoplatonists we have "Porphyry's Tree", which is a comb diagram like a modern cladogram.

Hence whereas biological species come about through physical and biological factors, metaphysical species are determined by metaphysical or ontological factors; i.e. their position in terms of planes of existence, and proximity or distance from the Godhead; the emanationist approach.

Some books dealing with the definition of "species"

amazon.com

Species : New Interdisciplinary Essays by Robert A. Wilson

Species Concepts and Phylogenetic Theory ed. by Quentin Wheeler and Rudolf Meier

Phylogeography : The History and Formation of Species by John C. Avise

---

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page by M. Alan Kazlev (Creative Commons Attribution 3.0 Unported License)
page uploaded 20 May 2002 (originally uploaded on Kheper site 18 June 1998)
checked ATW030730

Page Back | Unit Home | Glossary | Page Next
Unit Back | Unit Up: Systematics | Page Up: Taxonomy | Unit Next

Family

Linnaean Home
Linnaeus
The Linnaean Taxonomic Hierarchy
What's in a name?
Infra-orders and Super-families
The Splitters and the Lumpers
Taxonomic Inflation
Links

Definition: Kingdom
Phylum
Class
Order
Family
Tribe
Genus
Species

The Linnaean System - extra hierarchical ranks

The sequence ***Kingdom Phylum Class Order Family Genus Species*** is mandatory in the Linnaean hierarchy. Non-compulsory grades have however been added, such as the ***Tribe*** between genus and family, and more recently the ***Cohort*** between class and order, and ***Domain*** above the level of kingdom. All of which gives the following sequence:

Domain
 Kingdom
  Phylum (= Plant Division)
   Class
    Cohort or (animal Division)
     Order
      Family
       Tribe
        Genus
         Species

And although the subcategories super- sub- and infra- are most widely used, new subdivisions have recently been created, such as subter- parv- magna-, grand-, and mir-, to take into account the extra subdividing due to the influence of cladism. Many of these new sub-divisions are not generally accepted, and are not likely to be, as the cladistic and Linnaean methodologies are completely incompatible in any case. But anyway, here, by way of hypothetical example, is the below sequence using Order as an example:

- ***Super*order**
  - ***Grand*order**
    - ***Mir*order**
      - Order
        - ***Sub*order**
          - ***Infra*order**
            - ***Subter*order or *Parv*order**

The dimmed names are those that are generally unofficial and not often used.

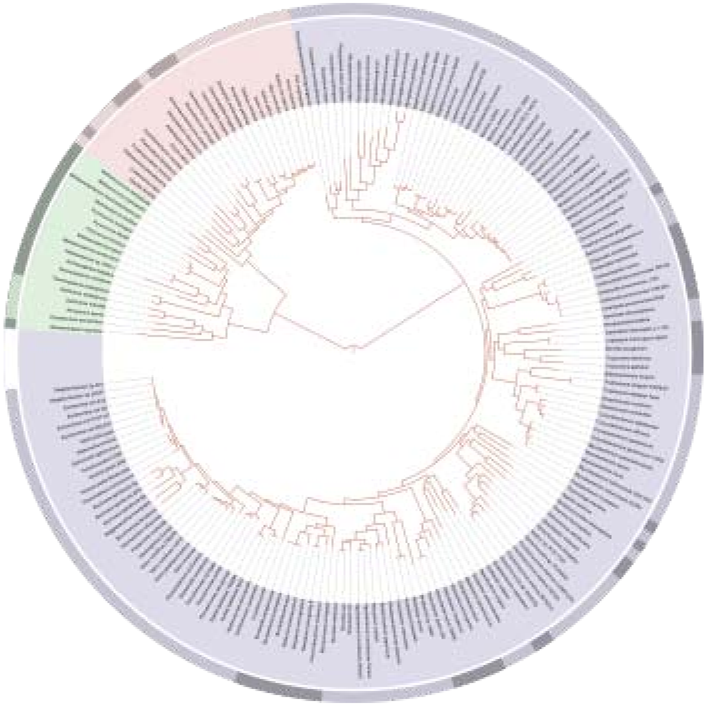
All of this gives a suitably large number of possible hierarchical levels. I do however feel that just as "tribe" was added between family and genus, and "cohort" between order and class, it would be useful to have a further optional grade between family and order.

---

page by M. Alan Kazlev (Creative Commons Attribution 3.0 Unported License)
page uploaded 20 May 2002, (originally uploaded on Kheper site December 1998)
checked ATW031208, edited RFVS111202

Page Back
Unit Home
(You are here)
Page Next
Unit Back: Cladistics
Page Up: Phylogeny
Page Next: Stratigraphy and phylogeny

Molecular phylogeny



Tree of life according to molecular phylogeny (Wikipedia)

Molecular phylogeny, the sequencing and use of informational macromolecules such as DNA, RNA, and proteins for phylogenetic analyses in order to map out the evolutionary tree of life, has been, like cladistics, one of the great late 20th century revolutions in evolutionary understanding.

Like phenetics, molecular phylogeny uses computers to process large amounts of amounts of data for quantitative analysis, generating cladogram-like dichotomous branched trees, called phylograms. These contain more data than cladograms, because whereas cladograms represent branching order only, phylograms include the degree of evolutionary change as well.

Originally, molecular phylogeny used phenetic methods such as overall similarity, generating trees through less computation intense methods such as neigbour joining. With the phylogenetic revolution and the incorporatrion of cladistics, this approach was realised to be unsatisfactory, and molecular phylogeny now uses more sophisticated algorithms such as maximum parsimony, maximum likelihood, and bayesian inference. These methoids have been taken up in computational cladistics.

Because of their strong methodological similarity and cross-fertilisation, molecular phylogeny and computational cladistics have merged into a single discipline, called phylogenetics, and cladistic analyses now regularily use both molecular and morphological data for a combined (or total evidence) approach. But as cladistic morphology based and molecular phylogeny based trees very rarely agree in details of branching order (or topology to use the technical term), and often differ quite radically, the problem arises as to how to resolve this endemic phylogenetic incongruency between two otherwise very reliable phylogenetic systems.

The tendency among both cladists and molecular phylogenists has been to preference molecular-based tree topology, and therefore to force morphology-based cladograms to follow the molecular topology. As a result, paleontological trees tend to use morphology with fossils, but both morphology and molecules with recent taxa. The implication is that rampant and unbiquitous homoplasy means that morphology has a poor phylogenetic signal. Whether this is true or not is still debatable. In any case, molecular sequencing is assumed to give a more reliable signal both because of the larger and more easily quantifiable amount of data it provides, and because many DNA sequences are not affected by natural selection. Conversely, the fact that there are only four types of RNA/DNA necleotide bases makes the problem of homoplasy and long branch attraction artifacts even worse, hence the need for this to be corrected by appropriate statistical analysis, such as bayesian and maximum likelihood. The current emphasis is on incorporating both morphology and molecular data in a total evidence approach. MAK130414

Page Back | Unit Home (You are here) | Page Top | Page Next

page by MAK, edited RFVS111203, last modified MAK130414

Molecular phylogeny

Molecular Phylogeny

Abstract

.

Keywords: .

Introduction

Since the 1960s, when many of the breakthrough ideas of modern molecular biology were first published, the detailed composition ('sequences' – principally amino acid and nucleotide sequences) of biomolecules have become steadily better known. At first only protein sequences were available but later, as technology improved, DNA sequences became available as well. Homologous molecules were discovered in different organisms, and it soon

Related Topics

Further Reading

- Li, W-H (1997), **Molecular Evolution**, Sinauer Associates: 487 pp.
- Liu, F-GR, MM Miyamoto, NP Freire, PQ Ong, MR Tennant, TS Young, & KF Gugel (2001), ***Molecular and Morphological Supertrees for Eutherian (Placental) Mammals*** **Science** 291: 1786-1789.
- Shaffer, HB, P Meylan & ML McKnight (1997), ***Tests of turtle phylogeny: molecular, morphological, and paleontological approaches***. **Syst. Biol.** 46: 235-268.
- Shoshani, J & MC McKenna (1998), ***Higher taxonomic relationships among extant mammals based on morphology, with selected comparisons of results from molecular data***. **Mol. Phylog. & Evol.** 9:

became evident that the basic biomolecular framework of all living things is the same; an observation consistent with the very Darwinian notion that all life is, ultimately, monophyletic.

Molecular sequencing illuminates the evolutionary history of the molecules themselves and, consequently, that of their host organisms. By comparing homologous molecules from different organisms it is possible to establish their degree of similarity, thereby revealing a hierarchy of relationships: a phylogenetic tree. The continuing publication of sequences from diverse taxonomic groups has given rise to what David Penny (2002) describes as a small industry inferring evolutionary relationships.

"The general principle behind phylogenetic methods is to find a tree that minimizes sequence change. For example, if two species have a unique amino acid at a particular site and are joined in the tree, only one change (in their ancestor) is needed to explain this data. Conversely, an additional change would be required if the two species were not joined in the tree, making the other tree less likely to be the true tree. The two tree-building methods that are most often used with molecular sequence data are minimum evolution, such as neighbor joining, and maximum likelihood. These methods, and the Bayesian method [sidebar ®], are flexible enough to include diverse information on the biological nature of molecular sequence change, such as rate variation among sites. A fourth method, maximum parsimony, is also widely used. Although the various methods are quite different from one another, they often result in the same phylogenetic tree. Reliability can be tested in different ways, with the bootstrap method [sidebar ®] being the

572-584.

Related Pages

- One of us (ATW) has been highly critical of molecular studies. See, ***e.g.***, **Insectivora Overview** for a lengthy and obnoxious critique.

Other Web Sites

- .

Bayesian Method: The Bayesian method selects the tree that has the greatest probability that the tree is correct given under a specific model of substitution.

Bootstrap Technique: Randomly sized and positioned pieces of sequence from the same part of the molecule (from each organism) are sampled randomly, with replacement, and a new phylogenetic analysis is performed to produce a tree. This is repeated many times (normally 100). These bootstrap results are compared to the original approximated tree and each branch point is scored (agree or disagree). Scores around 50-60% are considered dubious; those up around 90% provide confidence that the predicted branch is accurate. Controversy arises when a branch is interpreted as meaning something, when in fact the score may say it is insignificant. [Adrian Walden, Vialactia Biosciences, ***pers. comm***.]

most widely used. Phylogeneticists often use and compare several methods in a single study to evaluate the robustness of their results" (Hedges 2002, p. 839).

An assessment of molecular evidence, or of both molecular and morphological evidence, has often proved useful where morphological evidence alone has led to ambiguous results. Many different biomolecules are available for such analyses and this wealth of available characters is perhaps the greatest virtue of the biomolecular technique. Two illustrative examples are:

1. The Pogonophora are not well-known to most people, although one close relative, the giant red tube worms found living near hydrothermal vents along various deep sea trenches, are "almost famous." Pogonophorans long resided in an independent phylum (and some Russian zoologists still maintain this interpretation), but molecular sequencing has confirmed ontological studies placing them in the Annelida, close to the polychaetes (Nielsen 2001, pp. 170-171).

2. Traditionally, zoologists have regarded molluscs and annelids as the

closest relatives of arthropods. However, in 1997 that idea was challenged when Aguinaldo ***et al***. (1997) proposed a clade they named Ecdysozoa, characterized by ecdysis, or moulting, under the influence of ecdysteroid hormones. The ecdysozoans are supposed to include arthropods, priapulids and nematodes. The ecdysozoan hypothesis has not been universally adopted, however. The chitin cuticle of arthropods may not be homologous with the collagen cuticle of nematodes (Adoutte ***et al***. 2000). Additionally, Nielsen (2001, p. 119) mentions some critical 18S rDNA studies which have produced different phylogenies and concludes that the discrepancies will have to be resolved through further study.

Other advances in our understanding of the phylogeny of different groups – notably the protists and the angiosperms – also owe a great deal to molecular analyses.

Neutral Theory

The neutral theory of molecular evolution, proposed by Motoo Kimura in the 1960s, provides the theoretical underpinning for molecular phylogenetic research. The theory posits that the majority of mutations accumulated in any genome were neutral: ‘neither beneficial nor injurious’ in Darwin’s words (Penny 2002). Thus mutations could accumulate continuously, providing the causal mechanism – the ‘ticking’ – of the clock.

"Both DNA and protein sequences are used for estimating phylogenetic relationships and times of divergence among taxa. Typically, DNA sequences are used for relatively recent events – for example, the human and chimpanzee split – when protein sequences are too conserved to be useful. Protein sequences are desirable for more ancient events – for example, human divergence from insects – when DNA sequences are usually too divergent to make accurate estimates on the basis of patterns of nucleotide substitutions. Unequal base or amino acid composition among the genomes of different species is common and makes sequence change more difficult to estimate. In addition, sequence length is a limiting factor, in that the average gene (coding) or protein sequence (~1,000 nucleotides, ~350 amino acids) is usually not long enough to yield a robust phylogeny or time estimate, and therefore many genes and proteins must be used" (Hedges 2002, p. 839).

Caveats

In many cases, phylogenies

based on molecules are found to be robust and they are reinforced by subsequently discovered morphological or behavioral data. Yet, despite these successes, molecules have not proved as unambiguous as had been hoped. "Molecules, like morphologies, vary in their evolutionary rates and are subject to parallel and convergent evolution: and in consequence different molecules often suggest different phylogenies, just as do different morphological characters" (Arthur 1997, p. 53).

"The most useful single molecule has been ribosomal RNA (rRNA), which is homologous for all living organisms and, because it seems to keep evolving in secondary structure, its primary sequence is easier to use to reconstruct ‘good’ trees. Whether the trees are fully correct is another matter. There are at least two reasons why it is very difficult to resolve these deepest divergences. The first is that our models of the processes of mutation, and selection on individual sites of a macromolecule, predict saturation within 500 million years. Thus, we expect lower accuracy further back in time. The second difficulty is the lateral transfer of some genes. The best-established cases are the endosymbiotic origins of mitochondria and chloroplasts where their DNA sequences established an origin from bacteria. Both endosymbiotic and ectosymbiotic living arrangements are common in nature and therefore no unusual biological processes had to be invoked for their origin" (Penny 2002).

The most commonly used rRNA subunit is 18S, comprising about 1800 base pairs, because it evolves slowly. Slow evolution is a prerequisite for probing very ancient phylogenetic events, to minimize the saturation problem. However, this same property makes the molecule unsuited for distinguishing events which occurred close together, perhaps during a rapid radiation. A possible example of this problem is found among annelids and molluscs; analyses which include many representatives of both phyla show a complete mix of the two groups. (Echinoderms, conversely, always appear as a monophyletic group, suggesting the modern forms represent a single lineage which diverged long ago, accumulating many unique mutations.)

"The horizontal transfer of genes is often difficult to confirm by phylogeny alone because the short length of typical proteins (~300 residues) usually precludes the construction of a robust tree, and different methods of detection do not always agree. Therefore, ‘misplaced’ species on a tree might be evidence of horizontal transfer or poor resolution" (Hedges 2002, p. 841).

For further reading, see Nielsen 2001, chapter 57.

Total Evidence Approaches

"Although the cladistic paradigm allows (some might say requires) simultaneous analysis of morphological and molecular data, this combination of evidence is rarely attempted. This is due, in part, to the sampling problems of molecular studies and the use of ground plans and single-character analysis in morphological work. ... Although ‘total’ evidence is something of a misnomer, the concept – that all evidence currently available be used simultaneously – is hard to deny" (Wheeler 1997, p. 87).

The Universal Tree of Life

Although the basic molecular framework is the same for all life on earth, and thus very ancient, organisms are certainly different. More recently acquired physical (morphological) adaptations, adopted to enable their hosts to survive and prosper during the long course of evolution, are the basis for all but a few of the most recent revisions to our taxonomic view of the world. In the latter half of the twentieth century, biochemical studies have also come to compliment traditional comparative morphology. The morphological adaptations and biochemistry, too, are mirrored in the molecules.

The integration of many of these discoveries advanced in a quantum leap in the late 1970s. The standard view of the time, which had held sway for decades, was that the living world is fundamentally divided by the prokaryote-eukaryote dichotomy. This belief was challenged by Carl Woese and George Fox (Woese & Fox 1977) whose sequence analysis of 16S rRNA demonstrated that a division within the prokaryotes was at least as fundamental as that between prokaryotes and eukaryotes (fig. 1). "Analyses involving some unusual methanogenic ‘bacteria’ revealed surprising and unique species clusterings among prokaryotes. So deep was the split in the prokaryotes that Woese and Fox proposed in 1977 to call the methanogens and their relatives ‘archaebacteria’, a name which reflected their distinctness from the true bacteria or ‘eubacteria’ as well as contemporary preconceptions that these organisms might have thrived in the environmental conditions of a younger Earth" (Brown 2002).

cgmrRNA.gif (8205 bytes)

Fig. 1: An early "Universal Tree of Life" deduced from ribosomal RNA (rRNA) data [after Schopf 1999, p.105, fig. 4.2]. The study upon which this figure was based did not resolve the branching of the three kingdoms most familiar to all of us: plants, Fungi and animals. Subsequent analyses, however, have revealed that the biochemistry of fungi (in particular, the synthesis of chitin) is most similar to animals. Thus, counter-intuitively, plants are likely to have diverged first, leaving fungi and animals as sister groups. (However, see Hedges 2002 for discussion of many inconclusive specifics.)

"In 1990, Woese, Kandler and

Wheelis formally proposed the replacement of the bipartite view of life with a new tripartite scheme based on three urkingdoms or domains; the Bacteria (formerly eubacteria), Archaea (formerly archaebacteria) and Eukarya (formerly eukaryotes although this term is still more often used)" (Brown 2002; but refer to Margulis ***et al***. 2000 for an alternate view).

Molecular Clocks

The Coalescence Method of Age Determination

If most mutations are neutral or almost neutral in their selective effects, they will tend to simply accumulate in their respective biomolecules over time. Provided the ***rate*** of this accumulation has not changed over time, then the rate of ‘evolution’ of a particular molecule should be approximately constant over time. The molecular clock hypothesis posits that a given biological molecule exhibits a relatively constant rate of change over time, irrespective of the taxonomic lineage within which it evolves (Zuckerkandl and Pauling 1962). For example, cytochrome ***c*** appears to have evolved at similar rates in vertebrates, in fungi and in plants. Although these organisms are phylogenetically diverse, their genes which code for cytochrome ***c*** exhibit convincingly similar rates of evolution.

If the rate of evolution of a particular molecule is nearly constant over time, we can use the degree of divergence between homologues in different taxa to estimate the time at which their evolutionary lineages separated. Even in those cases where some ***lineages*** have demonstrably different rates of evolution from other lineages (***e.g***. rodents vs. primates), provided we can identify homologous molecules which evolve at a constant rate, they can be used as 'clocks' to calculate the order in which lineages diverged. Furthermore, if we can calibrate the rate of change we observe, it may even be possible to estimate the age at which the lineages diverged from their nearest common ancestor.

Although a given biomolecule with the same function (such as cytochrome ***c***) evolves at approximately the same rate in different taxonomic groups, this characteristic rate differs between different biomolecules. Some, such as the fibrinopeptides, change very rapidly; and others, such as the histones, change very slowly. Thus, for example, the rate for cytochrome ***c*** is considerably slower than the rate for hemoglobin.

Calibration

Before we can draw inferences from a molecular clock, we must calibrate its 'ticking rate.' Most often this is accomplished by pegging it against the known fossil record (keeping in mind that the first occurrence of a representative fossil is always a minimum estimate for the age of the lineage) though, occasionally, major geotectonic events, such as the isolation of a new landmass by rifting, can provide clues also. "Once the homologous gene A has been sequenced in, ***e.g.***, two species and the rate of evolution in this gene is known through prior calibration (let's say 2% per million years) then knowing the percent difference in the DNA sequence of gene A between these two species permits the calculation of the age of their last common ancestor. In this example, if species 1 and 2 differed by 10% in their DNA sequence of gene A, then the common ancestor of these two species would be expected to have lived around 2.5 mya. It would have taken these two lineages this long to both diverge at a rate of 2% per million years to accumulate 10% difference in gene A" (Mayr 2001, p. 198).

"[I]t can be shown that, on average, echinoderms and chordates are about 14% different in terms of their 18S rRNA sequences. [Cnidarian] differences are, on average, much greater – about 22% in each case. It seems, therefore, that as is expected from the comparative anatomy of these organisms, cnidarians left the line leading to chordates some time before the separation between echinoderms and chordates. The echinoderm-chordate split can be no younger than about 520 Ma because fossil echinoderms are found in Early Cambrian rocks [sidebar ®]. So, if it has taken ~500 Ma for a 14% difference to develop between echinoderms and chordates, the split between cnidarians and all other Metazoa – which resulted in a 22% difference – must have occurred some time prior to 520 Ma ago. If the rate of evolution was approximately constant over long periods of time, the split between Cnidaria and the other Metazoa could have been as early as 800 to 900 Ma before the present" (Runnegar 1992, p. 87).

In fact there is a probable echinoderm, ***Arkarua***, described from the Ediacaran.

Molecular dating, while not always in agreement with fossil evidence, offers an opportunity for timing events that are otherwise unobservable. For example, it was by the molecular clock method that the branching point between chimpanzee and man was shown to be as recent as 5-8 million years ago, rather than 14-16 million years, as had been previously generally accepted (Mayr 2001, p. 37; although latest fossil evidence hints that 5-8 Ma might be a slight underestimate [sidebar ®]). For the majority of evolutionary problems, the fossil evidence is either absent or inconclusive. With good calibrations, molecular data can greatly improve the constraints on timing estimates.

The recently described, 6-7 Ma ***Sahelanthropus tchadensis*** discovered at Toros-Menalla in Chad, is the oldest plausible human ancestor known to date. Not much younger, ~6 Ma, is ***Orrorin tugensis***, discovered at Lukeino in Kenya. Together, the two fossil discoveries hint at a diverse and perhaps geographically widespread hominid ancestry, and an older divergence between men and apes than is indicated by most molecular studies. For the present, there is insufficient evidence to be sure.

However, the molecular clock method must be applied with caution because molecular clocks are not nearly as constant as often believed. Not only do different molecules have different rates of change, but a particular molecule may vary its rate over time. These represent cases of ***mosaic evolution***, in which evolutionary change occurs in a taxon at different rates for different structures, organs, or other components of the phenotype (Mayr 2001). This is a failure of the neutral assumption. If the mutations accumulating in a gene begin to express phenotypic effects which are subject to selection, then the rate of change can be effected. As noted above, multiple lines of evidence (‘total’ evidence) are preferable to dependence upon a single datum or technique.

(Also see Smith & Peterson 2002.)

References

Adoutte, A, G Balavoine, N Lartillot, O Lespinet, B Prud'homme & R de Rosa (2000), ***The new animal phylogeny: reliability and implications***. **Proc. Natl. Acad. Sci. (USA)** 97: 4453-4456.

Aguinaldo, AMA, JM Turbeville, LS Lindford, MC Rivera, JR Garey, RA Raff, & JA Lake (1997), ***Evidence for a clade of nematodes, arthropods and other moulting animals***. **Nature** 387: 489-493.

Arthur, W (1997), **The Origin of Animal Body Plans: A Study in Evolutionary Developmental Biology**. Cambridge Univ. Press, 338 pp.

Brown, James R. 2002 (in press): ***Universal Tree of Life***. In ***Encyclopedia of Life Sciences***. Nature Publishing Group, Macmillan.

Hedges, B (2002), ***The origin and evolution of model organisms***. **Nature Rev. Genet.** 3: 838-849.

Penny, David 2002 (in press): ***Molecular Evolution: Introduction***. In ***Encyclopedia of Life Sciences***. Nature Publishing Group, Macmillan.

Margulis, L, MF Dolan & R Guerrero (2000), ***The chimeric eukaryote: origin of the nucleus from the karyomastigont in amitochondriate protists***. **Proc. Nat. Acad. Sci. (USA)** 97: 6954-6959.

Martin, Andrew Peter 2002 (in press): ***Molecular Clocks***. In ***Encyclopedia of Life Sciences***. Nature Publishing Group, Macmillan.

Mayr E (2001), **What Evolution Is**. Basic Books.

Nielsen, C (2001), **Animal Evolution: Interrelationships of the Living Phyla**, [2nd ed.]. Oxford Univ. Press, 578 pp.

Runnegar, B (1992), ***Evolution of the earliest animals*** **in** JW Schopf [ed.], **Major Events in the History of Life**. Jones & Bartlett Publ. pp. 65-93.

Smith, AB & KJ Peterson (2002), ***Dating the time of origin of major clades: molecular clocks and the fossil record***. **An. Rev. Earth & Planet. Sci.** 30: 65-88.

Tamas, Ivica; Klasson, Lisa; Canbäck, Björn; Näslund, A. Kristina; Eriksson, Ann-Sofie; Wernegreen, Jennifer J.; Sandström, Jonas P.; Moran, Nancy A.; Andersson, Siv G. E. 2002: ***50 Million Years of Genomic Stasis in Endosymbiotic Bacteria***. Science 296: 2376-2379.

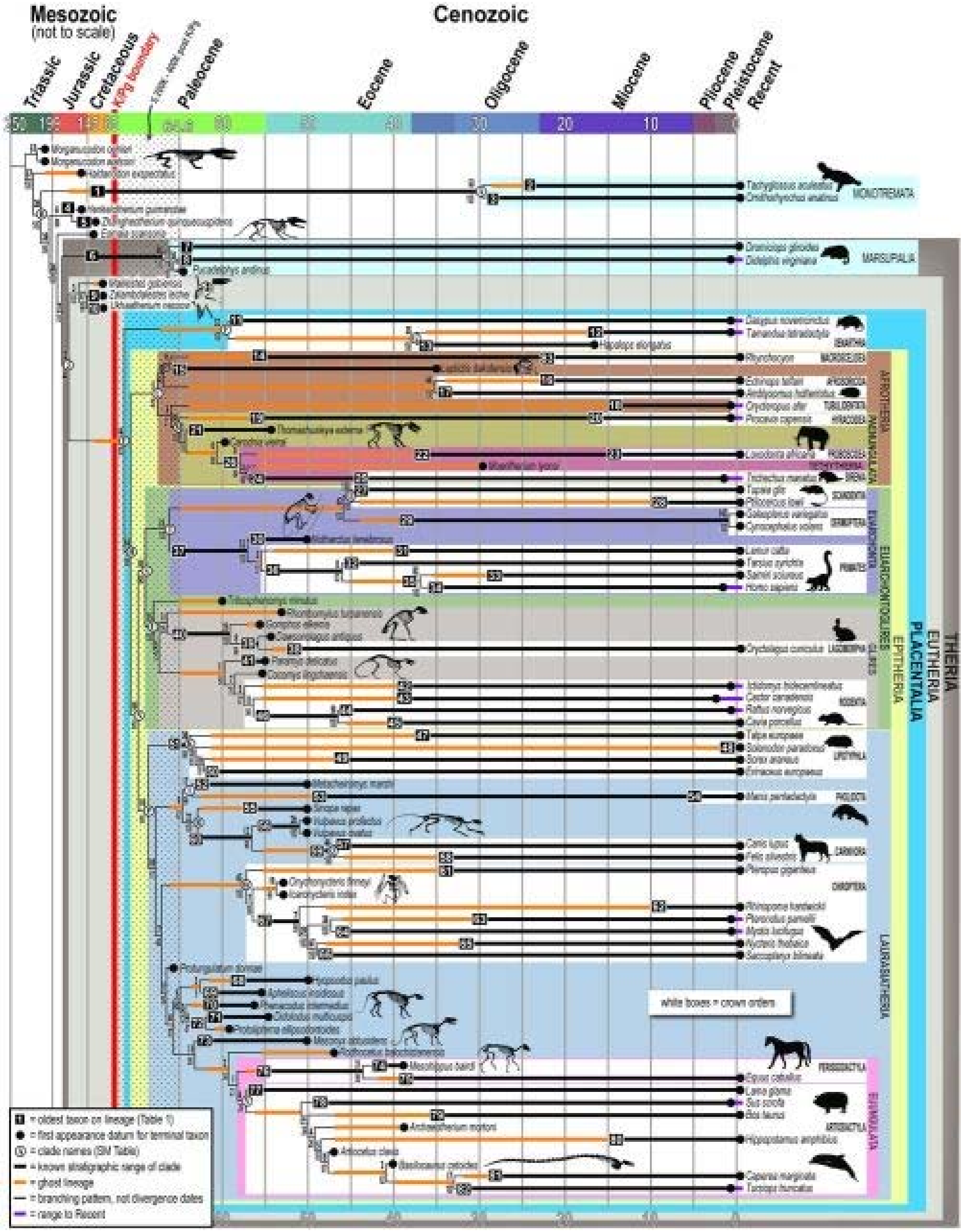
Wheeler, WC (1997), ***Sampling, Groundplans, Total Evidence and the Systematics of Arthropods***, **in** RA Fortey & RH Thomas [eds.], **Arthropod Relationships**. Systematics Assoc. Spec. Vol. 55: 87-96.

Woese, CR & GE Fox (1977), ***Phylogenetic structure of the prokaryotic domain: The primary kingdoms***. **Proc. Natl. Acad. Sci. USA** 74: 5088-5090.

Zuckerkandl, E & L Pauling (1962), ***Molecular disease, evolution, and genic heterogeneity*** **in** M Kasha & B Pullman [eds], **Horizons in Biochemistry**. Academic Press, pp. 189-225.

Page Back	Unit Home (You are here)	Systematics: Glossary	Page Next
Unit Back: Stratigraphy and phylogeny	Unit Up: Systematics	Systematics: References	Unit Next: Taxonomy

Phylogenetics



An example of a statistical-computational total evidence phylogenetic analysis. This tree, chosen from a large number of options, uses parsimony analysis of combined molecular and phenomic (morphological) data mapped onto the stratigraphic record. Crown clade Placentalia is shown to have diversified after the K-Pg boundary with only the stem lineage to Placentalia crossing the boundary. Black boxes indicate fossil taxa hypothesized to be on lineages; black lines indicate stratigraphic ranges; ranges and ghost lineages (orange) provide minimum divergence. Bremer support (BS) is shown above nodes, jackknife values below. - illustrztion and caption from O'Leary et al 2013

Phylogenetics is one of the two main branches of systematic biology today, the other being taxonomy. In the broad definition Phylogenetics is the science of reconstructing of the evolutionary tree of life on Earth (the phylogeny of life), which means it includes everyone from Lamarck, Darwin, and Haeckel upto current workers in the field. Phylogenetics as currently defined and practiced involves the practice of computational cladistics (morphological data matrices) and molecular sequencing, either alone or combined, in order to arrive at the best phylogenetic hypotheses out of the various possible evolutionary trees. There is however a tendency, whenever the resolved trees from each are found to be incongruent, for the tree topology of molecular phylogeny to be preferred, and the cladistic trees constrained to follow molecular lines. MAK130324

Phylogenetic analyses have become essential in researching the evolutionary tree of life. The overall goal of National Science Foundation's Assembling the Tree of Life activity (AToL) is to resolve evolutionary relationships for large groups of organisms throughout the history of life, with the research often involving large teams working across institutions and disciplines. Investigators are typically supported for projects in data acquisition, analysis, algorithm development and dissemination in computational phylogenetics and phyloinformatics. For example, RedToL aims at reconstructing the Red Algal Tree of Life. - Wikipedia

A current trend in phylogenetics is towards a large scale Total Evidence approach, resolving both molecular and morphological data in the same cladistic analysis, testing both parsimony and maximum likelihood trees, and calibrating the nodes by using the first fossil appearances. So for example the placental mammal radiation can be shown to post-date the extinction of the dinosaurs (O'Leary et al 2013) (see phylogenetic tree - a combination of cladogram and chrongram - at top of page), in contrast to both molecular-only calibration and earlier morphological trees, both of which placed the placental radiation deep in the Cretaceous. MAK130324

Page Back | **Unit Home (You are here)** | **Page Top** | **Page Next**

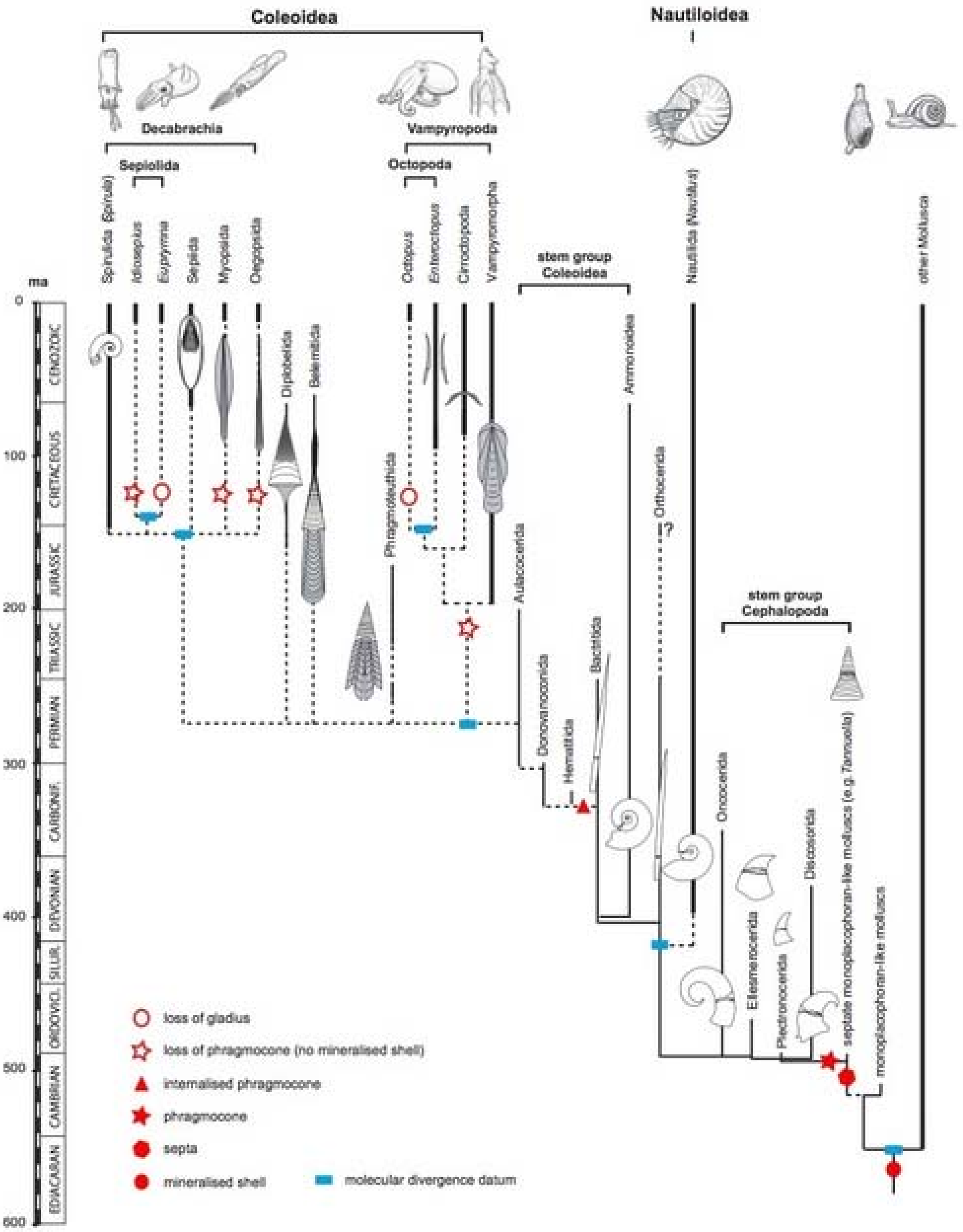
page MAK111014, edited RFVS111203, last modified MAK130324

Page Back
Unit Home
Systematics: Glossary
Page Next
Unit Back: Stratigraphy and phylogeny
Unit Up: Systematics
Systematics: References
Unit Next: Taxonomy

Phylogenetics: Total Evidence approach

Phylogeny and Systematics
  Systematics - History of ideas
    The Great Chain of Being
    Linnaean taxonomy
    The Tree of Life
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Stratigraphy and phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

Phylogenetics
  Total Evidence approach
  "Evolutionary phylogeny"



Cephalopod phylogeny. This interdisciplinary phylogenetic hypothesis resulting from the congruent picture emerging from fossils, development and molecules. First appearance of morphological traits are shown by solid red shapes, parallel loss of external or mineralised shell by open red shapes, molecular clock calibration by blue bars. Diagram from Kr�ger et al 2011

The tendency towards interdisciplinary and multidisciplinary studies, and a conscilience of knowledge, in large scale science in general, shows itself in phylogenetics in theTotal Evidence approach, which brings together data from as many fields as possible to understand and map out the history of life on Earth. For example, both molecular and morphological data can be processed both separately and together using the same computational analysis. Multiple statistical methodologies are now uniformly used and compared, such as testing both parsimony, maximum likelihood, and bayesian trees, with researchers selecting the best fit.

Stratigraphy is used in calibrating the various lineages and nodes by using the first fossil appearances. By these means, and using computational phylogeny, O'Leary et al 2013 were able to show that the placental mammal radiation post-dated the extinction of the dinosaurs, in contrast to both molecular-only calibration and earlier morphological trees, which placed the placental radiation deep in the Cretaceous. Another total evidence paper is Kr�ger et al 2011's synthesis of paleontology, developmental biology and molecular sequencing, as applied to Cephalopod origin and evolution. There tree is shown at the top of this page.

As always, there is scope for further methodologies to be incorporated. Sometimes the reluctance to do so is not practical but ideological. For example the tendency among many cladists to reject both stratocladistics and evolutionary gradism inspired the present author (MAK) to write the following essay arguing for a further synthesis. An example of a total approach of this sort is an intriguing paper on pachypleurosaur anagensis (straight line evolution), that combined stratigraphic, phenetic, and cladistic data and methodologies (O'Keefe & Sander 1999). Such methodologies are well-suited for analysing smaller groups well represented by the fossil record. Although this sort of pluralistic-integrated methodology is not yet widely applied, (prefernce being still given to large-scale phylogenetic reconstructions of the tree of life), there is no doubt that, as science progresses, more data from a more methodologies will be incorporated in increasingly wider total evidence phylogenetic analyses. MAK130414

Page Back | Unit Home | Page Top | Page Next

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

Page Back	Unit Home	Systematics: Glossary	Page Next: Taxonomy
Unit Back: Stratigraphy and phylogeny	Unit Up: Systematics	Systematics: References	Unit Next: Taxonomy

Phylogenetics: "Evolutionary Phylogeny"

Phylogeny and Systematics
  Systematics - History of ideas
    The Great Chain of Being
    Linnaean taxonomy
    The Tree of Life
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Stratigraphy and phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

Phylogenetics
  Total Evidence approach
  "Evolutionary phylogeny"
    The need for a new synthesis
    Mutual misunderstandings
    Ancestors and Ancestral traits
    Stratigraphic sequence
    Speciation and Dendrograms
      Anagenesis
      Cladogenesis
      Budding
      Dendrograms

The need for a new synthesis

I grew up reading books on paleontology and evolution even as a kid in the 1960s. I always felt and still feel at home with the evolutionary systematics of the 50s and 60s. It was so easy, obvious, and intuitively common sense. This was before the cladistic revolution of the late 70s and early 80s. I remember reading about it when I was at University, and being puzzled by the whole thing. It was only much more recently, having gone online in the 1990s that I got a handle on it. More recently in researching for the upgrade of Palaeos I got a better handle on it all. Having thus spanned a major phylogenetic paradigm revolution, I have the advantage of being able to see both perspectives, and the strengths and weaknesses of each. Therefore I have no compulsion to accept one without question, and hence limit myself to a particular viewpoint. Moreover, it seems to me that every advance in science is made by including and adding new insights and methodologies to those that came before, not rejecting them. This is why I reject attempts to force evolutionary systematics into a quantifiable statistical mold, or to use cladistics to map phylogeny through deep time (rather than simply test different hypotheses of how the phylogenetic tree may be ordered). There is no reason why phylogenetic systematics cannot be added to the body of knowledge and insight of evolutionary systematics. It does not also follow that the insights of Hennig and Gauthier disprove or replace the insights of Mayr and Simpson, or vice-versa. A very different matter is incongruencies between Synapomorphy-based and Algorithm-based cladistics, or morphology and molecular based phylogenies. Hence the need for a new approach that includes all perspectives, insights, and methodologies: cladistic, evolutionary, morphological, molecular, developmental, systems approach, and even philosophical and artistic. Nothing less, I honestly believe, would be up to the task of mapping out the history of life on Earth. MAK111014

Mutual misunderstandings

I have noticed that there seems to be no love lost between cladists and evolutionary systematists (the latter being the "old school") . This is due to the misunderstanding of what cladistics is all about, i.e. both camps assume that cladistics is concerned with the same thing that evolutionary systems is, which is describing ***actual*** phylogenies, when it is not. It is simply a statistical method for evaluating different phylogenetic hypotheses. But because both supporters and opponents will often assume that cladograms are actual evolutionary trees with actual evolutionary phylogeny), these are claimed to be more up to date or modern than the bubble diagrams that evolutionary systematics uses. This is an example of cladistic literalism, the confusion of cladistic formalism (essential for hypothesis testing), which confuses cladograms with dendograms.

Because of this misunderstanding, cladistics has been criticised by many big name evolutionists, beginning with Mayr, (who coined the term cladistics for this school because he disliked it; ironically the name was then taken onboard by pattern cladists and became an established term), and continuing through to Richard Dawkins and Thomas Cavalier-Smith, and the authors of Res Botanica, support evolutionary taxonomy, and criticise cladistics among other things for excessive formalism and refusal to consider ancestral ("paraphyletic") groups, or its depreciation of the empirical approach of evolutionary classification as mere "intuition". Similarly, evolutionary systematics has been criticised by cladists for lack of easy repeatability (being based on imprecise, subjective, and complicated sets of rules that only scientists with experience working with their organisms were able to use) and for accepting paraphyletic taxa. That last is not a criticism but just a statement of different methodologies and interpretation. If it could be acknowledged that these two paradigms are not even talking about the same thing, perhaps there could be better relationships on sides. MAK111014

Among the controversial topics that are not given the attention they deserve by the majority of phylogenetics are Ancestral Characteristics, Supraspecific Taxa, Speciation, and Stratigraphic sequence (or Deep Time). MAK111018

Ancestors and Ancestral traits

Highlander

Highlander - There can be only one! (Evolutionary systematics and Cladistics square off for the final showdown). Image from Media Unbound

Evolution is all about the common ancestor. It's not that (as in the standard linear model) humans evolved from (modern) apes, it's that humans and apes share a common ancestor. But one important difference between evolutionary systematics and cladistics is the way they each interpret this common ancestor in their diagrams and methodologies. When people look at a cladogram they assume that, as with an evolutionary systematic romerogram, the ancestors are the nodes. But cladistics is not intended to reconstruct the characteristics of actual deep time ancestors, or transitional forms, or missing or non-missing links. These are all paraphyletic taxa, the attachment to which strict cladistics is highly critical of. It is not that cladistics denies such organisms existed, but rather that, because it works on the species or individual level, it affirms that such taxa are unlikely to be fossilised. ***Archaeopteryx*** may be a close relative of the common ancestor of all birds, but it is not itself the actual common ancestor. Because the remains of the literal ancestor are not available, it is safer to compare the taxa we know of, and postulate hypothetical, ahistorical common ancestors as the nodes at the base of each monophyletic clade.

Most people, including scientists, prefer to think about evolution in terms of actual ancestors, not hypothetical abstractions. Richard Dawkins' criticism of the purely hypothesis-based cladistics and phenetics in his ***The Blind Watchmaker***, might be due to a misunderstanding of cladistics in this regard. In any case, because evolutionary systematics usually deals with supra-specific ranks, it is not necessary to find the exact ancestor, as long as we have the general stem group, the bubble at the base of the bubble diagram. So even if ***Archaeopteryx lithographica*** Meyer, 1861 is unlikely to be the ***exact*** ancestor, another member of the family Archaeopterygidae or the order Archaeopterygiformes certainly would be.[1]

Whether or not actual (as opposed to hypothetic) ancestors are represented has important implications for the overall topology (shape) of an evolutionary tree because of the paraphyly rule. Evolutionary systematics, and authors like Simpson, Mayr, and Dawkins don't accept the paraphyly rule because the ancestral group (whether it be a species or supra-specific taxon) remains, as a taxon in space and deep time, unchanged, regardless of how many newly evolved lineages arise from it in the course of time. The (vertical) side-branch (budding) or daughter taxa (splitting, anagenesis) has no effect on the nature of the (horizontal) ancestors from which it arose. Early Triassic euparkeriids don't stop being small cursorial, armoured terrestrial predators just because some of them in the course of time tended to a more crurotarsal (crocodylian) lineage and others to a more ornithodiran (dinosaur, bird, and pterosaur) lineage. What paraphyly does is make vertical lineages (monophyletic branches) rather than groups of similar organisms the basic units. Application or nonapplication of the paraphyly rule can make a large difference to a taxonomic classification (Mayr & Bock 2002 p.181-2. Grant, 2003 p.1268). Again, this does not make one wrong or the other right. But each still claims "there can be only one". MAK111019

Stratigraphic sequence

Stratigraphic sequence, or the sequence by which fossils occur in geological strata, and hence the deep time chronological sequence of the organisms that they represent, is central to evolutionary systematics (since some of the founding figures there, G.G. Simpson, was a paleontologist). For the most part, this does not figure in cladistics or molecular phylogeny, although both these areas are concerned very much with the branching of clades in deep time (Hedges & Kumar 2009, see also molecular clock). Because the fossil record is known to be complete, the gaps are plugged with ghost lineages. One could say that cladistics puts parsimony ahead of stratigraphy, evolutionary systematics stratigraphy ahead of parsimony. This is why under Romer and Carroll the protothyrids are considered ancestral amniotes (the bubble at the bottom of the romerogram); they are primitive and they include the earliest known reptiles, whereas in cladistics they are considered a more derived or specialised off shoot, already diverged from the ancestral root and on on the road to diapsids. Of course, it may turn out that parsimony isn't everything here, or it is but new discoveries will overturn the current cladograms, and that the eureptilian condition is primitive for amniotes, just as the cryptodire condition (previously considered derived) now seems to be for turtles, but that's just baseless speculation at the moment (another way of looking at it is to understand the protothyrids as paraphyletic (Benton, 2004).

The obvious reason that neontology is emphasised is simply a pragmatic; extant organism prefer far more information than extinct ones. Although special preservation can reveal soft parts of fossil organisms, and although there has been some analysis of fossil genetic material which can be used in phylogenetic analysis, and even a project to sequence the Neanderthal genome, the simple fact remains that this material will never be as complete as that of living organisms. For this reason, cladistics emphasises crown groups (defined by extant, rather than fossil, organisms) as the basis for taxonomic entities.

The problem, from a deep time rather than a pragmatic perspective, with crown groups is that in the grand scheme of things this a purely relative and arbitrary category, as it depends on a particular period in geological or even historical time, and hence is always changing. Because the baseline is uniformly the present, there is almost an anthropocentric bias, because (pragmatic conditions aside), why should the present moment be any superior from an evolutionary, deep time perspective? Regarding the problems of basing crown groups on extant taxa see also Extinct or Extant. An alternative definition does not require all members of a crown group to be extant, only to have resulted from a "major cladogenesis event", but then there is the question of how this is to be defined.

Add to this conflicting definitions of groups like tetrapoda, are tetrapods defined morphologically (first appearance of limbs), phylogenetically (closer to land animals than lungfish or coelacanths), or in terms of crown groups (the common ancestor of all living (not fossil) tetrapods. The ideal of course is to include all perspectives. MAK111019

One field of phylogenetic analysis that ***does*** incorporate both stratigraphic sequence and morphological data is ***stratocladistics***. This follows cladistic principles such as Bayesian logic and parsimony, but adds stratigraphic ordering. In this way, temporal data participate along with conventional character data in determining the most parsimonious hypotheses (Fisher, 1994, Fisher, 2008, Bodenbender & Fisher 2001). Yet after almost two decades stratocladistics is still very much a minority position, although one that deserves greater coverage.

The synthesis of stratigraphic paleontology and molecular phylogeny has been much more successful, with fossils used to determine the minimal age of branching points in the molecular tree of life, and thus calibrate the molecular clock (Donoghue & Benton 2007). The difference here is the premise that that molecules change at a constant rate, and if this can be determined using a few well defined calibration points (e.g. the divergence of synapsids and sauropsids) the whole tree of life can be dated in deep time. For this reason, molecular phylogenists have a greater interest in stratigraphy, where it applies to the branching points of major lineages, than cladists, who are concerned with finer scale divisions on the tree, and often have to deal with an incomplete fossil record and fragmentary material. MAK111020

Speciation and Dendrograms

Speciation is the process by which new species appear through natural evolution. This is a central theme of evolutionary systematics, which grew out of the so-called modern synthesis of Darwinian natural selection and Mendelian heredity. There seem to be at least three modes of speciation.

The Uncanny X Men

This is *not* how speciation works! Wikipedia, graphic copyright © 1941-2011 Marvel Characters, Inc.

Anagenesis is the transformation of one species into another over the course of geological time. Here the original species disappears and is totally replaced by the new species. This is how evolution is thought of in the popular imagination; along with implications of superiority of the new species (which itself ties back to old Great Chain of Being thinking). Hence the classic, and classically misinterpreted, March of Progress meme, and sci-fi and pop sci-fi images and tropes such as mutant superhero (in the X-men comics, ***Homo sapiens superior***, the mutants with superpowers, and the new species emerging alongside ordinary human beings [2], and Transhumanism (posthumanity will succeed humanity). All of which conflates biological evolution with cosmological singularity. A more scientific, less mythopoetic, way of approaching this subject would be to look in the fossil record for instances of change or substitution of one species by another that is very similar to it, but occurs at a higher stratigraphic level. Here there are various taxa - foraminifera, ammonoids, trilobites, cenozoic mammals, with an excellent fossil record, and where many instances could doubtless be found. O'Keefe & Sander 1999 provide a case study of among mid Triassic pachypleurosaurs, and its interpretation using phenetic, cladistic, and stratigraphic methodologies.

Cladogenesis, also less imaginatively referred to as ***Splitting***, involves the division (perhaps through geographic isolation or other factors) of an ancestral species or parental lineage into two or more daughter lineages or species, with the result that, like anagenesis, the ancestral species totally disappears. Only now, rather than one species replacing it, there are two or more. An example of this is ***allopatric speciation***, whereby, e.g., a geographic barrier isolates population groups, results in the disappearance of the original species. Allopatric speciation, which occurs over long time dimensions, and it divides the ancestral species into more or less equal portions has been long advocated as the main speciation mechanism, especially in the zoological literature. (W. R. Elsberry talk.origins via W.J. Hudson; Coyne & Orr, 2004, Horandl & Stuessy 2010, p.1643).

Finally, ***Budding***, which like Splitting is a rather prosaic English term (in this case with nuances of gardening) rather than an interesting and scientific Greek one, is when a new species or population appears, (through the divergence of a small group of populations, without affecting the ancestral of the parental lineage in any way (Mayr & Bock 2002). As a result both the ancestral and the new species or stem group continues alongside each other (although perhaps geographically isolated). Obvious examples include cases of peripatric speciation after geographical isolation of a small group of populations. This is expected to happen mostly after colonizing events by a few individuals, then followed by rapid speciation and adaptation to new environments. Recent evidence from biogeographical studies on both animals and plants suggests that peripatric speciation may be more common than previously thought, since dispersal, even transoceanic dispersal, explains many disjunct distributional patterns. Buddings of this kind are often connected to a high amount of phenotypic change in the derivative species, which undergoes drift and adaptive change in the new ecological situation. In contrast, the source populations are neither in any novel environment, nor under any novel selective pressure." (Horandl & Stuessy 2010, p.1643-4)

Now, when Cladistics is presented simply as an empirical means of testing phylogenetic hypotheses, there is no problem. Mapping speciation is not necessary to cladistics and molecular phylogeny, indeed, it can be highly misleading, because because they are statistical (cladistics) or phenetic (molecular phylogeny) methods of formulating phylogenetic hypotheses, not historical accounts of one species transforming into or giving rise to another. It is only with the misinterpretation of cladograms as literal deep time phylogeny that things get awkward. This is because such a phylogeny could only recognise cladogenesis where the ancestral lineage divides into two (and only two) daughter species. However, something like allopatric speciation fits this model of symmetrical divergence, but this is no longer regarded as the predominant mode of speciation. (Rieseberg & Brouillet, 1994, Horandl & Stuessy 2010, p.1644)

The following is a very interesting dendrogram (which is ***not*** a cladogram!) by Wang et al 1999, in which different modes of speciation are included, as well as deep time (stratigraphy) and chronospecies. This opens the way to a whole new way of doing phylogeny, which can incorporate both cladistics (phylogenetic systematics) and evolutionary systematics. To give it a fancy name I've informally coined it ***evolutionary phylogeny***.

Phylogenetic systematics of the Borophaginae

Diagram by Wang et al 1999, p.339, showing the phylogenetic systematics of the Borophaginae, plotted against time (horizontal axis), and incorporating budding and chronospecies (anagenesis). The caption reads: "Stratigraphic distribution and postulated phyletic relationships for the Borophaginae. Although essentially based on our cladistic analyses, the phyletic relationships represent further speculations about the cladogenetic or anagenetic events, based on our assessment of their morphology and stratigraphy." From American Museum of Natural History Digital Library - Phylogenetic systematics of the Borophaginae, © American Museum of Natural History

A dendrogram such as the above one is however only possible where there is a fairly adequate fossil record. This works for Cenozoic mammals, some marine invertebrates, and even perhaps dinosaurs in a few narrow windows, such as the Morrison Jurassic and Latest (Campanian-Maastrichtian) Cretaceous. Sampson et al. 2010 for example provide a detailed cladogram, plotted against time (so technically a chronogram), of the Ceratopsinae of North America. Looking at their diagram it is not difficult to see where anagenesis might come in, especially where sister taxa occur in the same geographic locality and immediately succeed each other in time. Postulating such paraphyletic taxa does not contradict cladistics, because cladistics, as we often emphasise, is not about actual historical phylogenies. In this way, there is an opportunity for a reconciliation between cladistics and evolutionary systematics, each complimenting the other, so that there is no longer a need for there only to be one. MAK111019

Notes

[1] The reclassification of recent finds of archaeopterygids, like ***Jinfengopteryx*** and ***Anchiornis***, as troodontids and the even more recent find of ***Xiaotingia***, an ally of ***Anchiornis*** and ***Archaeopteryx***, makes the position of the latter within Paraves far less clear cut. One of us (RFVS) thinks troodontids are derived archaeopterygids both because of the phylogenetic confusion and the arm length being the only distinguishing character. One thing we know with the relative certainty of the placement of ***Anchiornis*** within Archaeopterygidae and the uncertainty of the placement of the latter is that ***Anchiornis*** may be the earliest bird (Aves sensu Benton 2005) beating ***Archaeopteryx*** by 5 Ma. RFVS111203

[2] although technically this is budding because mutants and humans co-exist.

Page Back: Total Evidence | **Unit Home** | **Page Top** | **Page Next: Taxonomy**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

content by MAK111019, edited RFVS111203, last modified MAK130316

Page Back	Unit Home (You are here)	Page Next
Unit Back: Molecular phylogeny	Page Up: Systematics	Unit Next: Phylogenetics

Stratigraphy and phylogeny

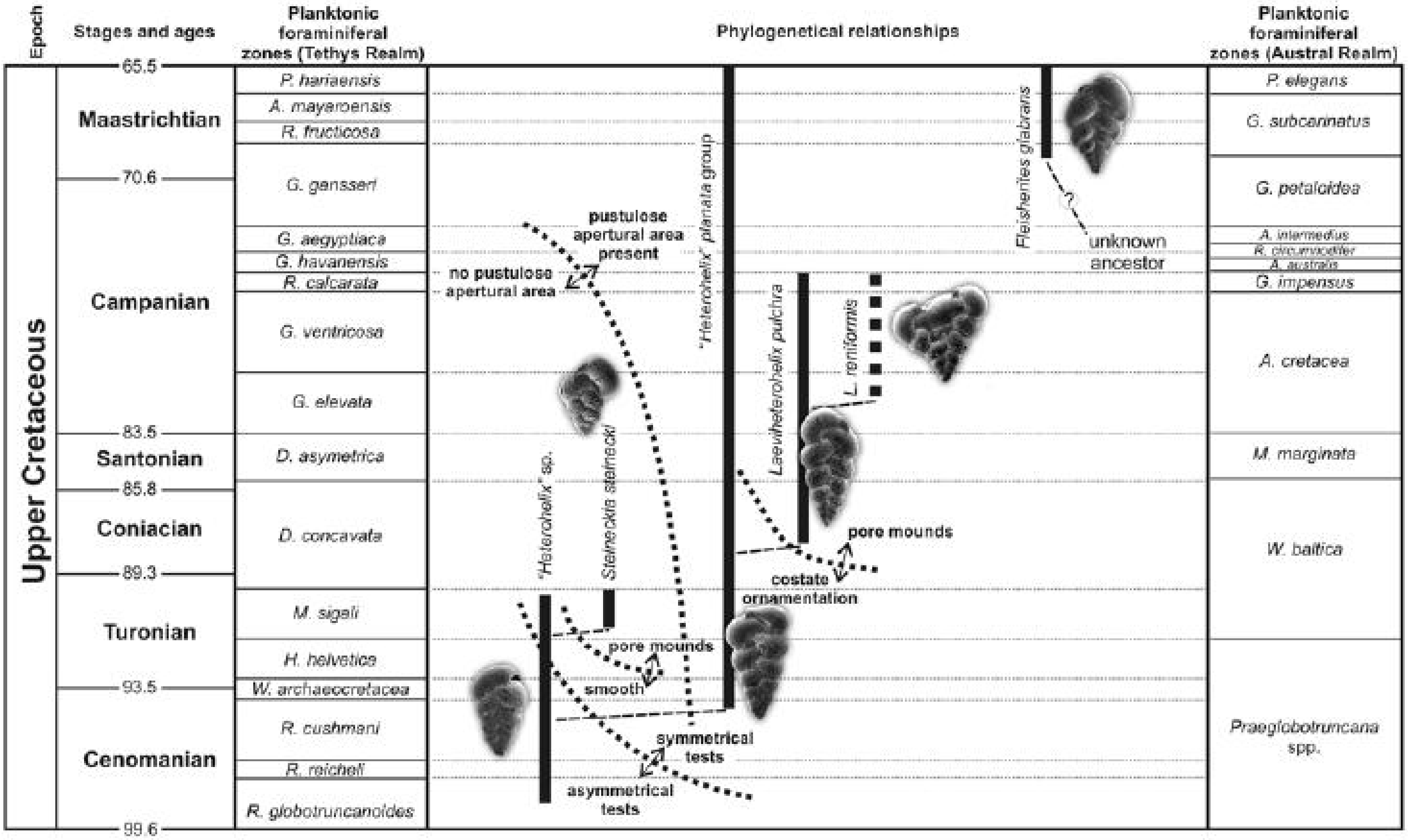


Figure 17. Phylogeny, stratigraphic distribution and major ornamentation differences of the Upper Cretaceous biserial planktic foraminifera with smooth tests or chamber surface ornamented with pore mounds.

A stratophenetic-type diagram showing possible relationship between selected late Cretaceous planktonic foraminifera. From Georgescu, 2009 fig.17

In mapping out the evolutionary tree of life on Earth, we have at least three fields of data at our disposal - gross morphology, the genome, and the fossil record - along with others such as developmental biology, biogeography, and so on. Of the first three named, comparison based on gross morphology, whether obvious shared characteristics (synapomorphies) or statistical parsimony or other computational analyses, is the basis of Cladistics (Phylogenetic systematics). Comparison of the sequence of genes in the DNA and RNA, and proteins and other molcules in the cell, constitutes molecular phylogeny. And understanding life in terms of the fossil record (the sequence of fossils according to younger or older rock strata) is stratigraphic phylogeny.

At one time, the stratigraphic sequence of fossils were essential to understanding the evolutionary relationships of life on Earth. This field of phylogeny is called Evolutionary systematics, and was grounded firmly in paleontology. The cladistic revolution of the 1980s and 90s was an attempt to introduce greater rigor, objectivity, and methodological uniformity and testability into phylogeny. But because cladistics as originally formulated was (and still in large part is) grounded in, on the one hand, neontology, and on the other, the comparison of characters abstracted from temporal and geographic location (i.e. from where the fossils were really found in time and space), temporal or stratigraphic (as well as geographic and paleogeographic) information was considered irrelevant. Inconsistencies between cladograms and stratigraphic sequence in the fossil record (known as stratigraphic incongruencies) were based on the ***ad hoc*** assumption that the fossil record (even for well sampled and easily preserved taxa) is so incomplete as to be absolutely useless for anything other than supplying some extinct taxa for analysis.

By rejecting stratigraphy, mainstream cladistics also limits itself more than it needs to; it has never empirically disproved stratocladistics - the retention index for stratigraphic data is not statistically different to that for morphological data (Levinton, 2001, p.78), so there is no reason why stratigraphy cannot be taken into account when constructing cladograms, other than that it is not included in the traditional set of problem-solving methodologies (Kuhn, 1962) used by the mainstream, cladistic paradigm.

If we assume that the fossil record ***does*** contain useful phylogenetic information, then we are faced with the problem of how to reconcile cladistic analysis with the temporal and stratigraphic information provided by the fossil record, in those instances where they conflict (for example, where the more derived taxa appear earlier than the more basal or stem taxa). There are three possible options here (this list is from Principals of Phylogenetic Systematic)

- ***Strict cladism*** relies solely on character data to determine the pattern of branching. Where there is conflicts between stratigraphic and character data, it is assumed that this is the result from incompleteness in the fossil record. This is the position of the majority of cladists, including workers in the field of vertebrate paleontology, where "ghost lineages" are posited in place of the missing fossils.
- ***Limited use of stratigraphic data***. Stratigraphic data can be used as a tiebreaker to decide between equally parsimonious cladograms, but are never allowed to over-ride parsimony. This option is is primarily associated with Andrew Smith of the BMNH
- ***Full incorporation of stratigraphic data***. Several methods, such as stratocladistics (Fisher, 2008), attempt to estimate phylogeny in light of both stratigraphic and character data. These methods sometimes accept less parsimonious cladograms in order to achieve a better stratigraphic fit.

Here at ***Palaeos*** we have assumed the third option as the default one. As a result, our phylogenies may sometimes differ in details from the official ones. In all these instances, reasons for the new phylogeny or choice of dendrogram is explained.

A few words about molecular phylogeny and stratigraphy. Molecular phylogeny, like the fossil record, frequently conflicts with parsimony-based analyses. In these instances however, phylogenists almost universally reject parsimony, even though the resulting tree topologies are often ridiculous. In the case of mammals, many molecular phylogeny derived clades are unsupported by any synapomorphies at all. In these instances, we have assumed that molecules can at times be unreliable and contain artifacts and convergences just as gross morphology does. Therefore, although molecular phylogeny may provide many useful insights, that is no reason to reject morphology out of hand.

Moreover, the molecular clock is clearly not always reliable, since molecular dating of the emergence of major placental mammal contradicts the fossil record. In these sort of instances, we believe fossils should be preferred over molocules (although in other respects the two systems of data can equally support each other (Donoghue & Benton (2007)).

Summing up. Stratigraphy and stratigraphic based methodologies such as stratocladistics and stratophenetics present an important but neglected source of phylogenetic data and new hypotheses, which can help contrinute to the insights provided by both morphology-based cladistics and molecular phylogeny, and vice-versa. Further fields such as Evo-Devo and systems theory also have great potential. In teasing out the details and even the broad brush strokes of the evolutionary tree of life on Earth, each methodology has something to contribute MAK120212

Page Back | **Unit Home (You are here)** | **Page Top** | **Page Next**

Page Back: Synthesis
Unit Home (You are here)
Page Next: Taxonomy
Unit Back: Phylogenetics
Page Up: Systematics
Unit Next: Ecology

Taxonomy and Nomenclature

Lilium hybrid "Stargazer"
Photgraph by dogmadic, From Wikipedia, Creative Commons Attribution 3.0 by-sa license. GNU Free Documentation License,

Taxonomy is the classification, identification, and naming of organisms. Although the original Linnaean system of taxonomy predates evolutionary (phylogenetic) thinking, taxonomy today is usually richly informed by phylogenetics, but remains methodologically and logically distinct.

The degree to which taxonomy depends on phylogeny differs between schools of taxonomy: phenetics and numerical taxonomy ignored phylogeny altogether, trying to represent the similarity between organisms instead; phylogenetic systematics tries to reproduce phylogeny in its classification without loss of information; and evolutionary taxonomy tries to find a compromise between them in order to represent stages of evolution - (Wikipedia)

One might suppose that classification should reflect phylogeny, and that phylogeny would automatically result in a superior classification system, but this is not necessarily the case. Taxonomiess may involve organisms that appear to be closely related but are not, phylogenies can result in unweildly systems, or phylogenetic definitions can be totally overturned by new discoveries and hypothesis Taxonomies can be overturned as well, but are generally more robust (Benton 2007). The most reasonable approach therefore is to acknowledge the usefulness of both descriptive classification and phylogenetic hypotheses as two equally partial and complementary means of understanding the natural world. MAK120229

Page Back: Synthesis | **Unit Home (You are here)** | **Page Top** | **Page Next: Nomenclature**

page last modified MAK130330

Page Back: Unit Home | Unit Home | Page Next: Nomenclature
Unit Back: Phylogenetics | Page Up: Systematics | Unit Next: Ecology

Taxonomy and Nomenclature

A few definitions:

Taxonomy

The science of organising living things into groups which reflect their natural, phylogenetic relationships, is called taxonomy. The groups are called taxa (sing. taxon, see below).

Taxon (pl. Taxa)

The published groups within each of the divisions in the phylogenetic hierarchy is known as a taxon. Like the relationships themselves, taxa fall into a hierarchy.

The lowest level taxon in most cases is the familiar species, which one can informally think of as a group of organisms which are so closely related that they can inter-breed freely. (This concept obviously fails for organisms which reproduce asexually, and in other circumstances also, but it is sufficient for now.)

Above the species level, grouping together similar species, is the genus (pl. genera). A familiar example of a genus is ***Pinus***, to which several different but related species of pine tree belong. Above that again is the family, and so on.

From highest (most inclusive) to lowest (most specific), the major formal taxonomic units, or “ranks” are:

- Domain (= Superkingdom)
- Kingdom
- Phylum (often called a “Division” in botany)

- Class
- Order
- Family
- Genus
- Species

Intermediate divisions are often used, “subspecies” and “variety” being very commonly employed at the lower end.

Identification

To identify an organism is to determine which taxon it belongs to. An “accurate” identification is not only correct, but will identify an organism with a particular species.

However, it is not at all unusual, in practise, that an identification can only be made to genus or even higher level. There are many possible reasons. Perhaps the organism being identified is incomplete; some part (***e.g***. a flower) which is necessary for a completely accurate identification is not present. This problem is particularly acute when it comes to identifying fossils, which are more commonly fragmentary than not. In some cases, the species may not have been previously recognised, or even if recognised, not formally published.

In such cases, a relationship to a similar species which has been described might be indicated with an ***aff***. indicating “affinity to,” or the less confident ***cf***. meaning “compare with.”

Nomenclature

In order to communicate biological information, it is essential to have universally understood “name tags” for the biological entities we are referring to. This labelling is theoretically possible by means of formulas or letters, though they are not euphonious and would be mnemonically difficult for most people. Instead, latinised names are employed.

“The purpose of formal nomenclature is to provide a precise, simple, and stable system of unique names used by scientists in all countries. The system must allow for reasonable expansion and refinement to accommodate increasing knowledge. In other words, the stability must not become a straitjacket” (Traverse 1996, p. 13). More

Homonyms and Synonyms

Homonyms are identical names for two different taxa.

Synonyms are different names for the same taxon.

Neither can be tolerated in a rational nomenclature. As a general rule, when these situations arise it is the first name to be published which is retained. However, the correct outcome is not always obvious because the distinction between taxa is often quite subjective. In fact, there are colloquial terms in common usage for scientists to tend to create inclusive taxa, with quite broad accommodation for variety (they are called “lumpers”) as opposed to those who subdivide very finely, creating taxa which accommodate very little variation at all (“splitters”). And, in fact, there is no “right” answer: man classifies; nature does not.

Chris Clowes 030219

Linnaean or Cladistic?

Although taxonomy has traditionally been associated with Linnaean nomenclature and classification, which was incorporated into evolutionary systematics, there is a tendency now to prefer to the cladistic system, and hence to create a cladistic taxonomy as an alternative to Linnaean. The problem here is the difference between the Linnaean and Cladistic systems is one of apples and oranges; one is a taxonomic, classification system, the other a means of constructing phylogenetic hypotheses; or in less jargonesque language, deciding which of a number of possible evolutionary trees is likely to be the more correct one (which doesn't mean it ***is*** the right one, as new discoveries can always overturn the current hypotheses). Trying to force Linnaean taxa into a cladistic mould creates endless confusion in the public mind, such as the statement "birds are dinosaurs". For this and other reasons, efforts to develop a formal, cladistic system of taxonomy and nomenclature to replace linnaean taxonomic methodology, while successful within certain specialised fields such paleoherpetology and "dinosaurology", has yet to catch on at a wider level. MAK130330

Links

Proceedings of a Mini-Symposium on Biological Nomenclature in the 21st Century �' suggests replacing the Linnaean system with a cladistic phylogenetic system of nomenclature. However R. K. Brummitt in Quite Happy with the Present Code, Thank You �' argues against the tendency to reduce the Linnaean system to the Cladistic one by eliminating paraphyletic taxa.

Dinosaurs and Evolution part 4 - by Jeff Polling, argues for the cladistic over the Linnaean scheme, with reference to ***Mononykus***, a prehistoric animal that, like Archaeopteryx, was transitional between dinosaurs and birds (note: this page is part of a longer discussion regarding evolution and creationism).

Page Back **Unit Home** **Page Top** **Page Next**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page last modified MAK130330

Taxonomy: Nomenclature

Phylogeny and Systematics
- **Systematics - History of ideas**
  - **The Great Chain of Being**
  - **Linnaean taxonomy**
  - **The Tree of Life**
  - **Evolutionary systematics**
  - **Cladistics**
  - **Molecular phylogeny**
  - **Phylogenetics**
  - **Taxonomy**
- **Glossary**
- **References**

Taxonomy
- **Taxonomy - Definitions**
- **Nomenclature**
- **Taxonomic inertia**
- **Phylogenetic nomenclature**
- **The Incompatibility of the Cladistic and Linnaean Systems**

The butterfly species Morpho rhetenor helena

The species of butterfly called *Morpho rhetenor helena*.
Photograph by Erin Silversmith From Wikipedia, GNU Free Documentation License,.

The criteria by which we group organisms is one thing; the manner in which we give them names, what those names mean and how we define them, is another. The approach to naming groups (nomenclature) most familiar to all of us was invented by Karl von Linne, a.k.a. Carolus Linnaeus. He invented binomial nomenclature by snipping the then-often-used <genus> + <lots of attributes of a species> down to <genus> + <some distinctive attribute of a species>. He also rationalized nomenclature, using the same name for both sexes and for adults and juveniles of a species. Like many of his contemporaries, he used Latin, which has the nice feature of being nationalistically neutral.

His hierarchy of taxa (singular: taxon) was kingdom, class, order, genus, and species, but later taxonomists added phylum, division, family, and various sub- and supertaxa, and even such taxa as domain, cohort, tribe, and section.

Taxonomic names and parts of names come from a variety of sources, though they must all be Latinized. Aside from personal and place names, taxonomic name parts are almost always words drawn from Latin and Classical Greek, with other languages occasionally represented. They are often common names (***Homo, Canis, Bos, Equus, Columba, Salmo, Apis, Lilium, Rosa, Quercus, Pinus***, etc.), and also words for various features and descriptions of them. Compound words are very common, though this sometimes leads to jawbreakers like ***Strongylocentrotus purpuratus*** (the purple sea urchin, found off the North American coast of the Pacific, often used as a model system). Higher-level taxa are often named after genera that they contain.

Several taxonomic ranks have standardized suffixes. Animal families end in -idae, plant families in -aceae, bird orders in -iformes, plant orders in -ales, etc. However, genera and lower-ranking taxa do not; genus names are singular nouns, while species names are either singular nouns, adjectives, or genitives (Latin's of-case). Also, taxon names above the genus are all plurals or collectives, whether or not they have some standardized suffix. Such conventions allow comparison of the ranks of different taxa at a glance.

Many organisms have received different names from different taxonomists; such conflicts are resolved by using the first-bestowed name. Thus, ***Apatosaurus*** pushed out ***Brontosaurus*** and ***Hyracotherium*** pushed out ***Eohippus***. Although the international codes of nomenclature have no rules against it, this rule of priority has meant that some inappropriate names -- names that don't accurately reflect the content or characters of taxa -- have survived. The chimpanzee, ***Pan troglodytes***, got its species name because Linnaeus believed that it lives in caves; it actually lives in forests. Also, ***Basilosaurus*** ("king lizard") turned out to be an early cetacean rather than a marine reptile upon closer examination.

Codes of Nomenclature

Questions of which name is appropriate for any given taxon can become complicated if multiple options exist. For this reason, the various Codes of Nomenclature have developed to guide decisions on name usage. The two most significant codes are the International Code of Zoological Nomenclature (ICZN) for animals and the International Code of Botanical Nomenclature (ICBN) for plants (zoology and botany had become separate disciplines by the time the codes were developed, hence the separate codes). Other organisms -- fungi and protists -- are governed by one or the other code based on whether they were traditionally regarded as plants or animals, so fungi and algae fall under the Botanical Code, while most protozoa fall under the Zoological Code. Bacteria were originally governed by the Botanical Code, but conflicts between the provisions of the Botanical Code and the requirements of bacterial taxonomy led to the establishment of the International Code of Nomenclature of Bacteria (ICNB). Additional separate codes exist for viruses and cultivated plants (horticulturally-developed varieties and hybrids). Different codes may have different opinions on what constitutes a validly-published name, but all codes agree that the oldest name for a taxon is generally valid, and require the identification of some kind of type. Traditionally, names described under different codes do not count as homonyms, so ***Prunella*** is both a genus of birds and a member of the mint family, while ***Bacillus*** is both a bacterium and a stick insect (the Bacteriological Code does forbid the use of names that have previously been used in the other codes, but identical names may exist if the bacterial genus was named first).

A small number of taxa (photosynthetic flagellates and their close relatives, and slime moulds) have been included with both plants and animals at various times in the past, so have been regarded by different authors as falling under both the Zoological and Botanical Codes. This can cause confusion, as the correct name for a taxon may differ between the codes -- a name may be validly published under one code but not under the other, or be a homonym under one code but not the other. Cavalier-Smith (1998) divided eukaryotes into five kingdoms -- the paraphyletic kingdom Protozoa and the monophyletic kingdoms Animalia, Fungi, Chromista and Plantae -- and suggested that Animalia and Protozoa should fall under the Zoological Code, while Plantae, Fungi and Chromista would fall under the Botanical Code. However, Microsporidia in Fungi and various non-photosynthetic taxa in Chromista have been generally treated in the past under the Zoological Code, while dinoflagellates (Protozoa) have probably been more often treated under the Botanical Code than the Zoological Code.

It should be stressed that all codes of nomenclature make a distinction between nomenclaturally valid (or available) names and biologically valid names. The former qualification deals with whether a name is validly published or not, while the latter deals with whether or not it is distinct from other taxa. For instance, the name ***Homo neanderthalensis*** for Neanderthal Man was published by King in 1864, but authors differ as to whether Neanderthal Man (or Woman) represents a separate species from modern humans ***(Homo sapiens*** Linnaeus 1758). Therefore, ***Homo neanderthalensis*** is undoubtably a nomenclaturally valid name, but may not be a biologically valid name.

Occasionally, situations may arise where the correct name for a taxon is uncertain under the Codes, or where strict applications of the Code's regulations would cause confusion for researchers (see entries for nomen conservandum and nomen oblitum). All Codes have an administrative board that adjudicates such cases -- these are the International Commission on Zoological Nomenclature, the International Association for Plant Taxonomy and the International Committee on Systematics of Prokaryotes for the Zoological, Botanical and Bacteriological Codes, respectively. - EvoWiki

Links

- International Commission on Zoological Nomenclature
- International Association for Plant Taxonomy
- International Committe on Systematics of Prokaryotes

Page Back | **Unit Home** | **Page Top** | **Page Next**

Palaeos | Palaeos | **Taxonomy**
Systematics | | **Taxonomic inertia**

Palaeos | Παλαιός | **Taxonomy**
Systematics | | **Taxonomy**

Page Back: Nomenclature | Unit Home | Page Next: Phylogenetic Nomenclature
Unit Back: Phylogenetics | Page Up: Systematics | Unit Next: Ecology

Taxonomy and Nomenclature

Phylogeny and Systematics
  Systematics - History of ideas
    The Great Chain of Being
    Linnaean taxonomy
    The Tree of Life
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

Taxonomy
  Taxonomy - Definitions
  Nomenclature
  Taxonomic inertia
  Phylogenetic nomenclature
  The Incompatibility of the Cladistic and Linnaean Systems

Taxonomy serves two purposes in biology - first, to express the relationships of organisms; second, to facilitate communication between researchers. Unfortunately, these two aims are not always compatible with each other - while communication would usually be perhaps best served by a stable, unchanging structure, taxonomies are often required to change to better reflect increased knowledge about evolutionary relationships.

Taxonomic changes generally take a while to enter the general parlance - this may be referred to as taxonomic inertia. The most common cause of this is simply the time taken for the new taxonomy to become widely known - after all, not everyone who would be affected by the changes will learn about them the very day the paper is published, especially if they don't make a habit of following the taxonomic literature. However, sometimes am old taxonomy will remain in place long after changes have had time to disseminate. Some reasons for this are given below.

First, the organisms involved may have been particularly widely known under the old name, and there may be popular or economic issues with taking up the new taxonomy. The widespread persistence of the name ***Brontosaurus***, despite it being a later synonym of ***Apatosaurus***, is a familiar example of this. Cases such as this are particularly abundant in the horticultural world - plants are much more widely known buy their scientific names than animals, and many gardeners do not take kindly to having to remember to look for something different when they go to the garden centre. The genus ***Azalea*** was sunk into ***Rhododendron*** a number of years ago, but people did not start referring to their azaleas as rhododendrons. Other widely misused genera are ***Cosmos*** (a synonym of ***Bidens***) and ***Datura*** (generally used to refer to the trumpet-flowered trees and shrubs that have been separated off into the genus ***Brugsmansia*** - Datura sensu stricto is a genus of herbaceous plants including the noxious Jimson weed). Interestingly, in 2005 the Commision on Botanical Nomenclature agreed to officially change the type species of the genus ***Acacia***, in order that economically important species might remain as ***Acacia*** when the previously polyphyletic genus was divided.

Second, there may be difficulties in applying the new taxonomy. For instance, a taxonomic revision of members of the small insect order Zoraptera, previously all placed in the single genus Zorotypus, established a number of genera based on characters of the wing venation. However, wings are absent or unknown for many species of Zoraptera (zorapterans usually live as small colonies of wingless individuals in rotting logs, with winged individuals only produced as dispersers when the colony becomes overcrowded or begins to lose its habitat). As the new taxonomy is therefore unusable for most members of the order, the single genus Zorotypus is still used.

Sometimes there are particular barriers to dissemination of new taxonomies. For many years until the end of the Cold War, researchers in Eastern Europe and the Soviet Union were isolated from their peers in western countries. In many cases (for instance, many protozoa), researchers on both sides developed taxonomies in parallel for the organisms they were working on.

Finally, and fairly obviously, researchers may simply not think the new taxonomy is worth adopting. The DNA-DNA hybridisation studies on bird phylogeny by Sibley and Ahlquist lead to the proposal of a new classification for birds differing significantly from the traditional system established by Wetmore in the 1950s. However, right from its proposal there were doubts cast on the studies' methodology and results, and the new classification did not gain wide acceptance. While most researchers were willing to accept that there were problems with retaining the Wetmore classification, they did not accept the Sibley and Ahlquist classification as solving those issues. The Wetmore classification continues to be widely used by default, until a more robust alternative is developed. - CKT061013

Page Back: Phylogenetic nomenclature | Unit Home | Page Next: Systematics Glossary
Unit Back: Phylogenetics | Page Up: Systematics | Unit Next: Ecology

Taxonomy: Cladistic and Linnaean Systems - Incompatible or Complementary?

The difficulty of reconciling the Evolutionary Linnaean and the Phylogenetic Cladistic systems

The Linnaean evolutionary systematic taxonomy, and the Cladistic phylogenetics arrangements are both very useful systems, although they use very different methodologies.

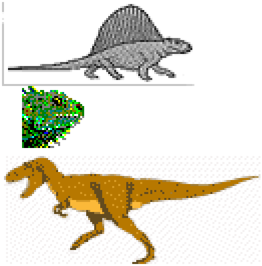
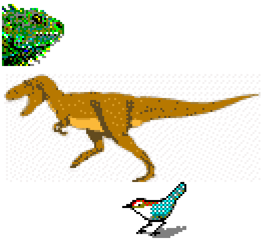
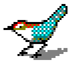
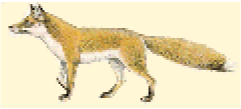
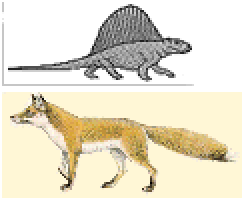
By "Evolutionary Systematics" we mean the linnaean system incorporated with the darwinian modern synthesis and applied to both speciation and higher level phylogeny to understand the evolutionary tree of life on Earth. Often when phylogenetists say "linnaean", what they are really referring to is the incorporation of Linnaean classification by evolutionary science (phylogeny in the original sense of the word) as developed originally by Haeckel, and later in more detail by Simpson, Mayr, Cain and coworkers, and presented in the paleontology textbooks of Romer, Colbert, Carroll, and others.

By cladistics and phylogenetics we mean selecting the most plausible hypotheses of sequence of branching in evolutionary trees (called cladograms and phylograms) based on statistical analysis of morphological and molecular data, as developed by Hennig (phylogenetic systematics using morphology), Fitch (molecular phylogeny), Gauthier (application of paleontology to cladistics) and others

If it assumed that only one is right, then they are incompatible. A better way of looking at things is to say that they are different ways of interpreting the natural world.

To give an example: the Linnaean system distinguishes separate classes for reptiles, birds and mammals. ***Reptiles*** are cold-blooded and scaly and crawl (or slither in the case of snakes) and lay eggs which they then abandon (the only exception being the Crocodylia which guard their nest), and grow new teeth their whole lives. ***Birds*** are warm-blooded, feathered and fly (or with flightless birds descend from flying ancestors), lay eggs and care for their young, and have erect stance and a toothless beak. ***Mammals*** are warm-blooded, furry, have erect stance, give birth to live young and care for them, and replace their teeth only once. So there are clear morphological differences.

But when you trace back the evolutionary tree you find that mammals merge into mammal-like reptiles (cynodont therapsids) and birds into bird-like reptiles (theropod dinosaurs). The cladistic classification has the ancestral amniote (egg-laying) stock giving rise to two lines, sauropsids (reptiles, dinosaurs and birds) and synapsids (mammal-like reptiles and mammals). Both sauropsids and synapsids start as "reptiles," in a colloquial sense, but one is the branch that leads to birds, while the other is the branch that leads to mammals. In fact, in cladistics, ***Amniota*** is often defined as the last common ancestor of birds and mammals and all of its descendants.

Linnaean system - morphology		Cladistic system - sister groups	
Class Reptilia (cold-blooded, scaly, lay eggs)		Division Sauropsida (common ancestor)	
Class Aves (Birds) (warm-blooded, feathered, lay eggs)			
Class Mammalia (warm-blooded, furry, live young)		Division Synapsida (common ancestor)	

The contrast may be clearer if we look at it from a phylogenetic point of view. SeeCladograms. ATW050802

From the cladistic perspective, many conventional Linnaean taxa actually turn out to be paraphyletic (i.e. they include descendants that do not belong within those taxa). As T. Mike Keesey pointed out in an email, such traditional taxa can be shown as nested lists, e.g.:

- Class Reptilia
  - Subclass Synapsida --> Class Mammalia
  - Subclass Anapsida
  - Subclass Diapsida --> Class Aves
- Class Aves <-- Order Diapsida
- Class Mammalia <-- Order Synapsida

The following diagram (cladogram or more correctly dendrogram) shows the ancestor-descendant links for these taxa

```
--o Amniota
   |--Sauropsida
   |   |--Mesosauridae
   |   `--Reptilia
   |       |--Anapsida
   |       `--Diapsida (including Aves)
   `--Synapsida (including Mammalia)
```

(cladograms by T. Mike Keesey)

It is not possible to synthesise these two schemas by doing away with paraphyletic taxa. As R. K. Brummitt points out:

> "Linnaean classification without paraphyletic taxa is a logical impossibility. Every monophyletic genus in a Linnaean classification must be descended from something

> (probably a species) in a different genus, which must be paraphyletic. Similarly every monotypic family must be descended from a species in a genus in a different family. If one denies paraphyletic taxa, where do genera and families come from? Ultimately, one would end up sinking everything into its ancestral taxon, and the whole classification would telescope into its original taxon...
>
> The theory of a Linnaean classification without paraphyletic taxa is nonsensical. Hennig's proposal to eliminate paraphyletic taxa was based on a failure to see the difference between the Linnaean hierarchy in which all taxa are nested in the next higher taxon, and a phylogenetic hierarchy which is not so nested, the lower levels of the hierarchy being not equivalent to the higher levels. Put another way, all the species of a genus together equal the genus but all the offspring of a parent do not equal the parent."

Also, speciation often involves a new species, through geographic isolation, budding off from the parent species, which remains unchanged. This isn't a problem with Linnaean Evolutionary taxonomic ranks, as at bottom these are based on evolutionary systematics and principles of speciation. There can be any number of species derived from and co-existing along with an ancestral species. This is revealed in cases where the fossil record is quite complete, such as Neogene invertebrates, late Cenozoic or Quaternary mammals. At this close in detailed scale, standard cladistic formalism is less useful, and where the actual ancestors are known, the concept of a hypothetical common ancestor (suitable when the fossil record is incomplete) becomes irrelevant. One form of cladistics that can be used in this situation is stratocladistics, as this considers the stratigraphic sequence and hence fossil ancestors.

As far as supra-species taxa go - the Linnaean hierarchy of genus, subtribe, tribe, subfamily, family and so on upto phylum and kingdom (and domain if one wants to include that in the Linnaean ranking) - is that evolutionary taxonomic ranks and evolutionary systematics, as formalised by Mayr, Simpson, and others, uses a combination of Linnaean morphological similarity, specxcies diversity, and evolutionary (phylogenic) branching (ancestor-descendent and sister groups) but, as mentioned, does not reject paraphyly (hence there are valid ancestral gradist taxa such as Thecodontia, Condylartha, etc). Whereas in cladistics, the Linnaean hierarchy is determined solely by phylogenetic (branching) sequence. So the first branch would be into domains, the next into kingdoms, and so on. In order to fit every branching event, Archosauria may have to be a superclass, whereas birds (Linnaean class Aves) may only be an infraorder. Obviously, this is totally impractical, even if additional ranks such as parvorder, microorder, epifamily, and so on, which is why Linnaean suffixes such as -idae and -oidea beyond superfamily notation are very rarely applied in cladistic classifications.

There would be no harm in this, if it weren't that the two systems were often conflated. Take our own Evolutionary Linnaean group, Superfamily Hominoidea. Originally - by which we mean in the classic texts of Romer (1966), Carroll (1988) etc, this included the three families Hylobatidae (gibbons), Pongidae (great apes - gorillas, chimps, orangs, and various fossil forms like ***Dryopithecus***), and Hominidae, the "hominids" of popular science literature, by which is meant humans (genus ***Homo***) and the African plio-pleistocene australopithecines, along with the odd extinct taxon like Pliopithecidae. There are clear morphological differences between these groups; for example Hominids walk upright (with all the physiological novelties that entails), have small canines, and, at least in later forms, have much larger brains and use stone tools and fire. No one denies that hominids evolved from pongids; the latter are, cladistically speaking, a paraphyletic taxon, which is not only permissable but essential for Linnaean-Evolutionary systematics. And what distinguishes the hominid line are morphological and ecological factors: they are an evolutionary offspring of african pongids that came down from the trees and took to savannah foraging, developing bipedality as this had significant locomatory advantages over knuckle walking.

The cladistic, or phylogenetic (for the synthesis of cladistic methodology and molecular phylogeny) version is quite different. Even though there is very little physiological difference between chimps and gorillas, in comparison to the highly derived and mostly hairless naked ape line, molecular phylogeny shows that the common ancestor of chimps and humans branched off from the common ancestor of all extant african apes at the same time as the gorilla ancestor did. In other words, there is approximately the same genetic difference between chimps and gorillas as there is between chimps and humans. And even though the african great apes are very similar to Orang Utans, the ancestor of Orangs (representing a south-east Asian lineage) branched off even earlier. The taxonomic confusion arises when this totally empitrical and plausible branching sequence is appointed ranking according to the ***Linnaean*** ranking system. Remember that Linnaean-Evolutionary systematics requires paraphyletic taxa, whereas cladistics forbids it. The paraphyletic Pongidae is then sunk in its daugher taxon the Hominidae because the latter has priority in the rules of nomenclature. Hominidae then becomes humans and great apes. The next branching in order of sequence is assigned the rank of subfamily, so Hominae (previously genus ***Homo***, exclusive of ***Australopithecus***) is now all the African apes, whereas Ponginae is retained for the Asian branch; orang utans and their fossil relatives. Because gorillas branched from the human and chimp ancestor the latter two share a tribe, the rank below subfamily, although there is far more difference between them than with, say, members of tribes of plants. Finally the old Hominidae as the term was used upto the 1990s now becomes the Subtribe Hominina, a rank barely above genus, even though as mentioned there are important ecological and morphological differences between the Homo-Australopithecine line and even for that matter between ***Homo*** and ***Australopithecus***. Comparing the two gives the following:

Linnaean-Evolutionary taxonomy:

```
Superfamily Hominoidea
     Family Pliopithecidae (early fossil forms)
     Family Hylobatidae (gibbons)
     Family Pongidae (African, Asian, and European apes
              various fossil and recent forms)




     Family Hominidae (hominids)
          Subfamily Australopithecinae
(australopithecines)
          Subfamily Homininae (genus Homo)
```

Phylogenetic (cladistic-molecular) taxonomy:

```
Superfamily Hominoidea

     Family Hylobatidae (gibbons)
     Family Hominidae (great apes)
          Subfamily Ponginae (asian branch)
          Subfamily Homininae (african branch)
               Tribe Gorillini (gorillas)
               Tribe Hominini  (no common name)
                     Subtribe Panina  (chimps and
bonobos)
                     Subtribe Hominina (humans
                            and australopithecines)
```

Linnaean-Evolutionary taxonomy is consistent in that one can apply the same criteria to any species living or fossil, and also extend the hierarchy up to classes, phyla and kingdoms. Phylogenetics describes the branching order of each clade with great precision, but any attempt at use of linnaean nomenclature becomes totally impractical above a certain level. Moreover, new discoveries would require the addition of further branches (and hence further ranks and subranks), so the only way to keep the above schema is to limit it to extant species only.

The simple fact is, the Linnaean and Cladistic systems not only do not speak the same language, they are not only different ways of interpreting the natural world, but they use unrelated methodologies and paradigms to describe toally different things. It's as if an astronomy and a sociologist were arguing, and one said only stars and galaxies are real but human societies are not, and the other said only socio-cultural structures are real and not astronomical bodies. The Linnaean system is a system of taxonomy that classifies living organisms, cladistics a system of phylogeny that presents a methodology for testing rival hypotheses regarding the sequence of branching of living organisms in the tree of life.

This is not to say that it isn't possible to come at workable syntheses. There have been a number of attempts on some sites to reconcile the cladistic and Linnaean/evolutionary-systematic positions. This often results either in a greatly inflated number of classes or in reducing higher grade established taxa to a much lower rank. In either case it doesn't really work out. One attempt that wasn't too bad is found in an excellent book called ***Evolution of the Perissodactyls***, ed. by Donald R. Prothero & Robert M. Schoch (New York & Oxford, 1989) where a number of new hierarchical ranks are introduced. Again, Professor Mike Benton of Bristol University has provided a commendable and very useful new classification of the vertebrates, perhaps the first really useful integration of cladistic and Linnaean methodologies, and this approach is not to be sneered at. At Palaeos however we have however decided to leave these two methodologies side by side, each contributing their own insights, and thus acknowledge the multidimensional and multi-perspectival quality of scientific exploration of the natural world.

Summing up: both Evolutionary/Linnaean and Phylogenetic/Cladistic schemes are complementary rather than exclusive, and both are necessary and useful, each with strong and weak points. Reconciling them however is a nightmare. Monophyletic Linnaean generic and specific taxa can be useful in cladistics, but beyond that the two systems don't work together very well - many higher taxa have very different meanings in each. MAK981204 111014 130408

Page Back | **Page Top** | **Page Next**

Page Back: Taxonomic inertia | Unit Home | Page Next: Incompatibility of Cladistic & Linnaean
Unit Back: Phylogenetics | Page Up: Systematics | Unit Next: Ecology

Taxonomy: Phylogenetic Nomenclature

Phylogenetic nomenclature is a new system of classification, based on based on cladistics and phylogenetic relationships, and intended as a replacement for the venerable Linnaean system. While enthusiastically proposed by some systematists, especially in the field of vertebrate systematics and paleontology (and particularly in mapping out the phylogeny of "amphibians"/tetrapods, "reptiles"/amniotes, dinosaurs and birds), it has yet to catch on in the wider scientific community, and even among vertebrate paleontologists there are those who propose retaining the Linnaean system, arguing that the two approaches can work together. The matter remains controversial and unlikely to be resolved soon (see e.g. papers by Michael Benton of Briston University (Stems, nodes, crown clades, and rank-free lists: is Linnaeus dead? and The Phylocode: Beating a dead horse?), criticism thereof, and a rather badly formatted Phylocode Debate). MAK120126

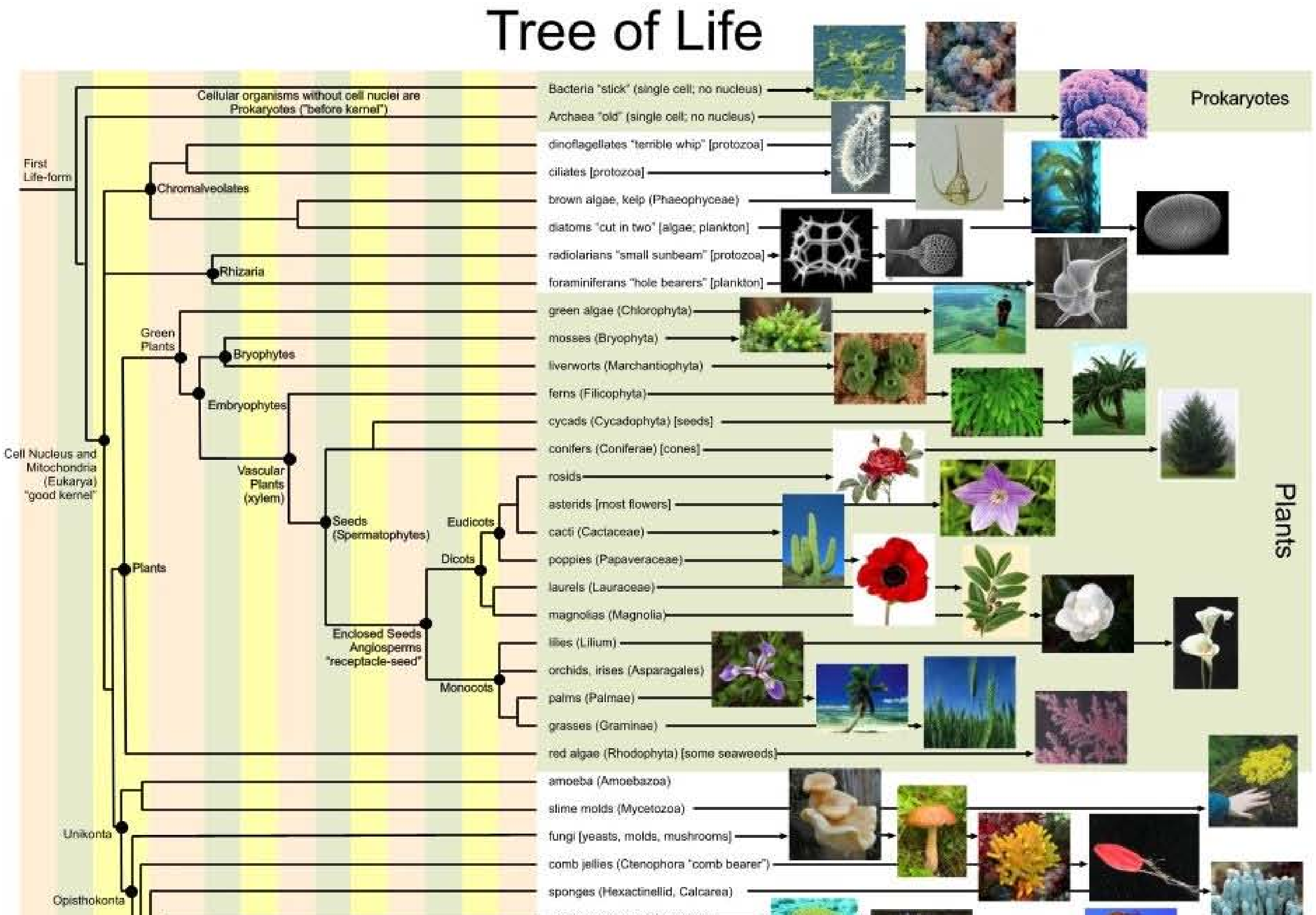
Links

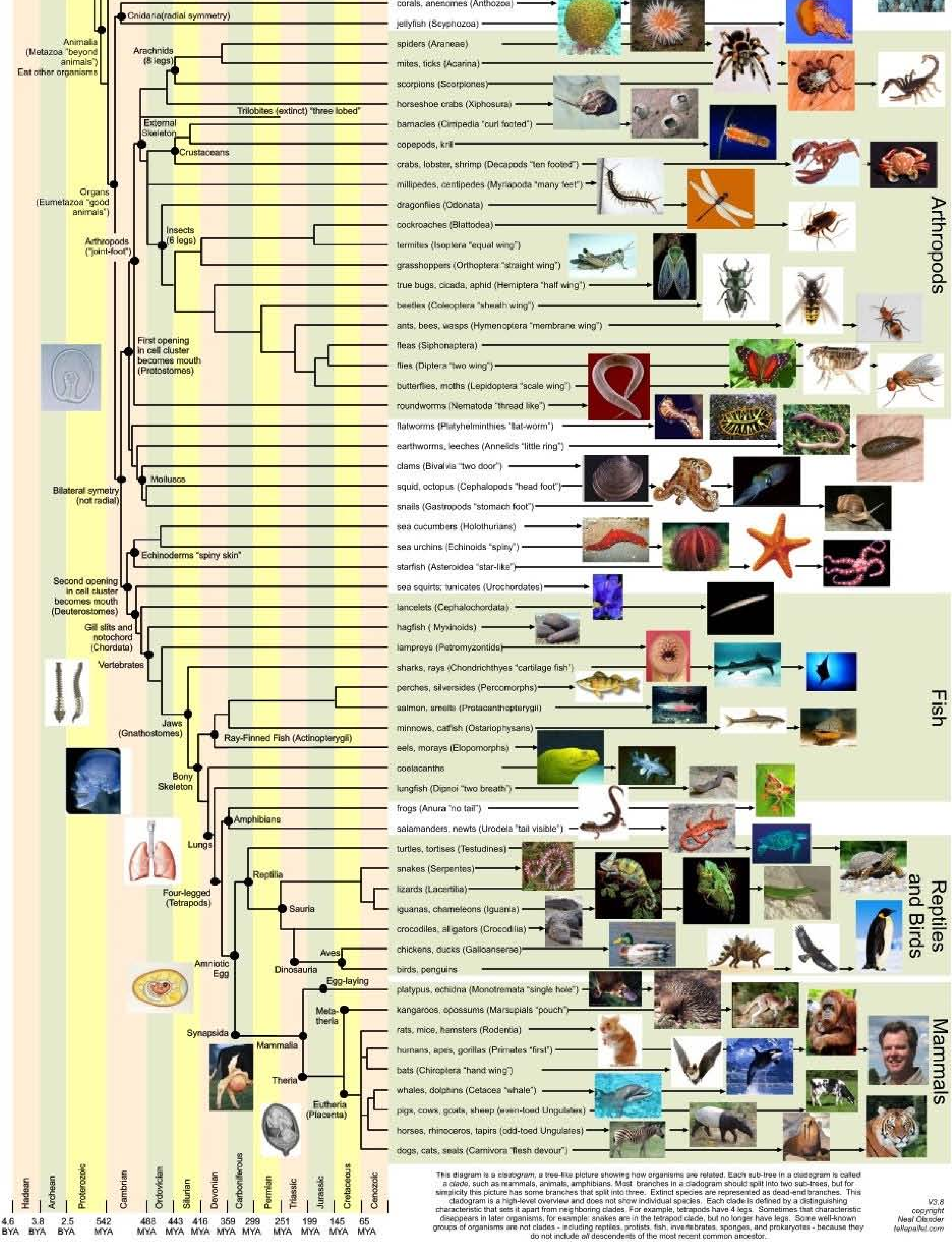
The PhyloCode - website of the The International Code of Phylogenetic Nomenclature; Phylogenetic Nomenclature and the PhyloCode by Kevin de Queiroz, 2001 (pdf); Pushing Phylocode - ***Discover Magazine***; Wikipedia

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

The Phylogenetic Tree





This diagram is a *cladogram*, a tree-like picture showing how organisms are related. Each sub-tree in a cladogram is called a *clade*, such as mammals, animals, amphibians. Most branches in a cladogram should split into two sub-trees, but for simplicity this picture has some branches that split into three. Extinct species are represented as dead-end branches. This cladogram is a high-level overview and does not show individual species. Each clade is defined by a distinguishing characteristic that sets it apart from neighboring clades. For example, tetrapods have 4 legs. Sometimes that characteristic disappears in later organisms, for example: snakes are in the tetrapod clade, but no longer have legs. Some well-known groups of organisms are not clades - including reptiles, protists, fish, invertebrates, sponges, and prokaryotes - because they do not include *all* descendents of the most recent common ancestor.

V3.8

tellapallet.com

Tree of Life diagram by Neal Olander, integrating cladistics (here, vertical axis) with deep time (horizontal axis). Creative Commons Attribution-Noncommercial-Share Alike 3.0 United States License.

The central principle of understanding the evolutionary of life on Earth is the Phylogenetic Tree, sometimes called the "Tree of Life" (not to be confused with the biblical tree of the same name). That is, evolution does not proceed in a simple straight line, but takes the form of a vast tree-like path consisting of various diverging, and sometimes also converging, branches going in many different directions.

This insight, that evolution is tree-like, constituted a huge shift in understanding that still has not totally overthrown the old linear thinking in much of popular culture (consider for example the influence of the iconic and the much misunderstood ***March of Progress*** with its simplistic linear model of human evolution).

Like the geological timescale, the periodic table of elements, of diagrams of the big bang, the evolutionary tree of life is one of those iconic grand vista theory of everything images that are visually associated with science at its most sweeping, in this case with biology and evolution. Hence we felt some space should be devoted to it, even if this section is still a bit scanty. The image featured above presents a modern version of the phylogenetic tree, but it was preceeded my many earlier versions and paradigms, and no dopubt will be succeeded by many future ones

This unit begins with the earliest attempts at evolutionary trees the beginning of the 19th century, and continues through to the grand illustrations of Haeckel, which shaped and still shape our understanding of what an evolutionary tree looks like. After Haeckel came evolutionary systematics and spindle diagrams, and after them cladograms and dendrograms, like the image at the top of the page, which represent the current version of the tree of life. Note that cladograms are not evolutionary trees meant to trace the actual course of evolution, they are phylogenetic hypotheses representing a best guess approach of the branching pattern of that evolutionary tree. Most popular enthusiasts however like to be more concrete, so we pretend (at least until better evidence comes along) that one of these cladograms is an actual phylogeny. Like spindle diagrams and like the image on this page, the dendrograms that feature in Palaeos are modified versions of cladograms which emphasise a purported phylogeny rather than a hypothesis. MAK130328

Links: **The Great Tree of Life diagram**, artistic semi-stylised but still useful representation, by Leonard Eisenberg, evogeneao (evolutionary genealogy) website; **The Tree of Life: Tangled Roots and Sexy Shoots �' Tracing the genetic pathway from the first Eukaryotes to Homo sapiens** by Chris King (Biocosmology and Consciousness Research), huge "big picture" coverage; **Wikipedia Tree of Life** a valuable reference website (albeit still very incomplete, although some taxa, e.g. Agnatha, Ankylosauria, are well represented) with the an interactive presentation of the full "tree of life". Detailed references are supplied on each page about particular organisms. It is not entirely up to date with latest ideas; for example, the tree of Eutheria fails to reflect the recent classification into Laurasiatheria, Afrotheria, Euarchontoglires, and Xenarthra. Link (EvoWiki). MAK111018;

Page Back: Linnaean taxonomy | **Unit Home** | **Page Top** | **Page Next: Early evolutionary trees**

content by MAK130328

Page Back | Unit Home | Page Next
Unit Back: Linnaean taxonomy | Unit Up | Unit Next: Evolutionary systematics

The Phylogenetic Tree: Early (pre-evolutionary and proto-evolutionary) trees

Phylogeny and Systematics
  History of Systematics
    "The Great Chain of Being"
    Linnaean taxonomy
    The Phylogenetic Tree
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References
The Phylogenetic Tree
  Early trees
  Darwin's tree
  Haeckel's trees

The Great Chain of Being

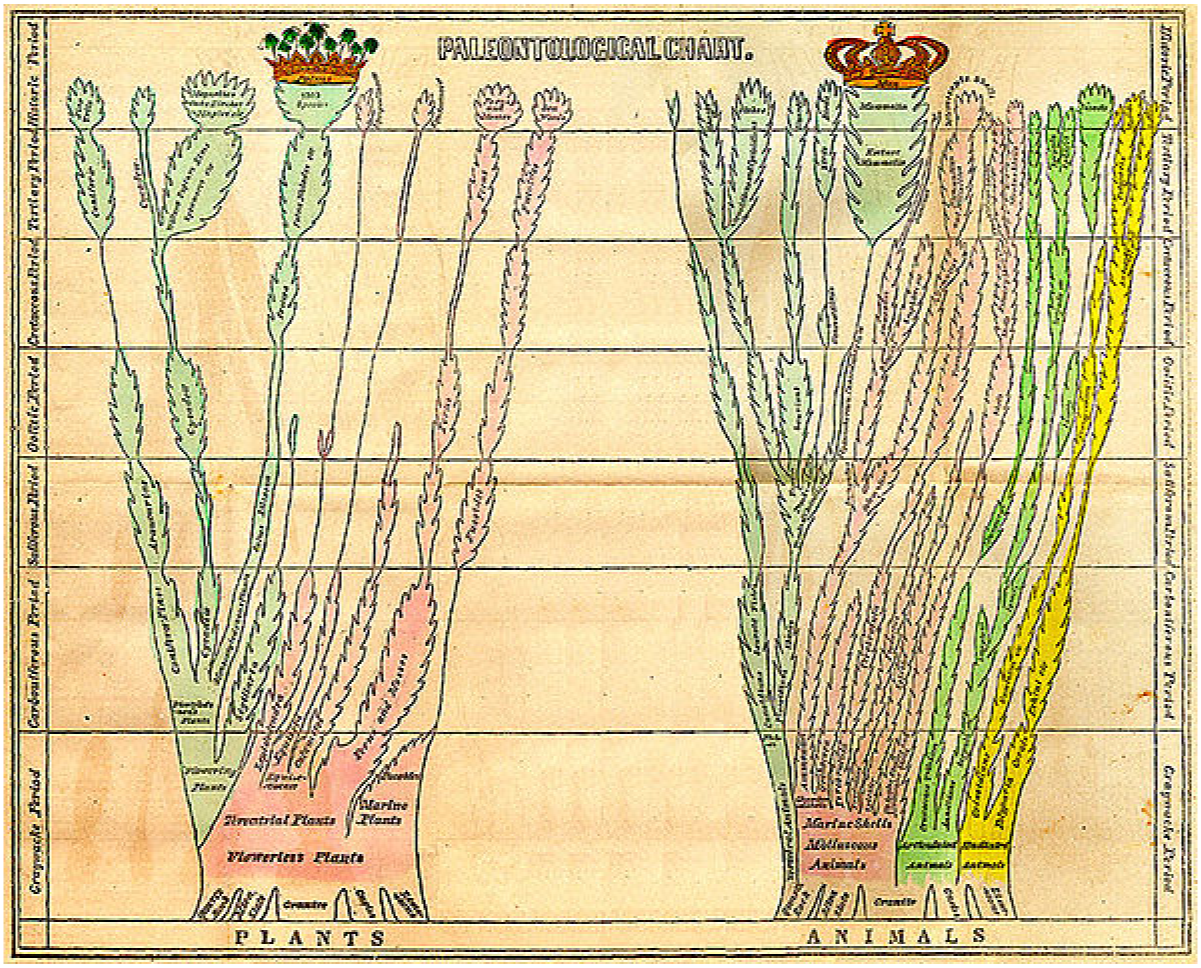
What came before the evolutionary tree was the Great Chain of Being, the idea thatr everything in existence can be arranged in a single linear series. The premise appeared in the Middle Ages through a synthesis of Greek philosophy (chiefly Aristotle), Christian theology and angelology, and justification for social stratification. It continued to form a central understanding of how the world works right up until the 18th century, when it eventually collapsed under its own weight in attempting to organise and incorporate the ever growing amount of knowledge about the natural world.

The Tree of Life

By the late 18th century it had became clear that nature could not be portrayed in a single dimension. The great German naturalist, Peter Simon Pallas, in his ***Elenchus Zoophytorum*** (1766) showed that no linear scale can represent the mutual relations of organised beings; whereas the branching tree is the appropriate metaphor.

Although the mutability of species may have appeared in paintings (Barbagli 2009) and trees have been used as a metaphor for other purposes (Porphyrian tree) earlier than 1800, the combination of the concept of branching evolution and the tree image did not appear before 1800. The earliest tree of life was published by the French botanist Augustin Augier in 1801. It shows the relationships between members of the plant kingdom. (Wikipedia)

the French zoologist and evolutionist Jean-Baptiste Lamarck, produced the first branching tree of animals in his ***Philosophie Zoologique*** (1809). In contrast to the standard format popularised by Haeckel and others, it was an upside-down tree starting with worms and ending with mammals. However, Lamarck did not believe in common descent of all life. Instead, he advocated a temporalised or ascending path along the great chain of being, believing that life consists of separate parallel lines advancing from simple to complex [Bowler 2003]



Paleontological Chart in the publication *Elementary Geology* (1840) by Edward Hitchcock. It shows two trees: one for plants, one for animals. Image scanned by J. David Archibald. Public domain, Wikipedia.

The American geologist and the American geologist Edward Hitchcock, published the first Tree of Life based on paleontology in his ***Elementary Geology*** (1840). (Archibald 2009). On the vertical axis are paleontological periods. Hitchcock made a separate tree for plants (left) and animals (right). The plant and the animal tree are not connected at the bottom of the chart. Furthermore, each tree starts with multiple origins. Although Hitchcock's trees were branching, they were not real evolutionary trees, because Hitchcock believed that a deity was the agent of change. Darwin's abstract tree was the first evolutionary tree of life (Wikipedia)

Page Back **Unit Home** **Page Top** **Page Next**

images not loading? | error messages? | broken links? | suggestions? | criticism?

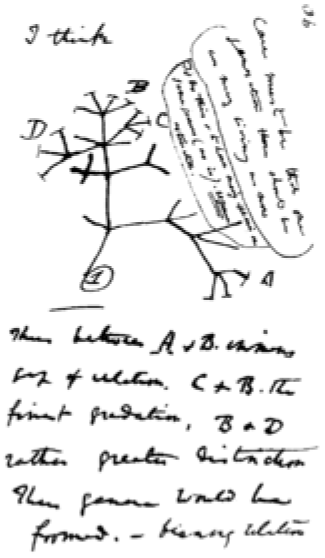
contact us

The Phylogenetic Tree: Darwin's Tree of Life

Phylogeny and Systematics
  History of Systematics
    "The Great Chain of Being"
    Linnaean taxonomy
    The Phylogenetic Tree
    Evolutionary systematics
    Cladistics
    Molecular phylogeny
    Phylogenetics
    Taxonomy
  Glossary
  References

The Phylogenetic Tree
  Early trees
  Darwin's tree
  Haeckel's trees

The following is for now copied verbatum from Wikipedia

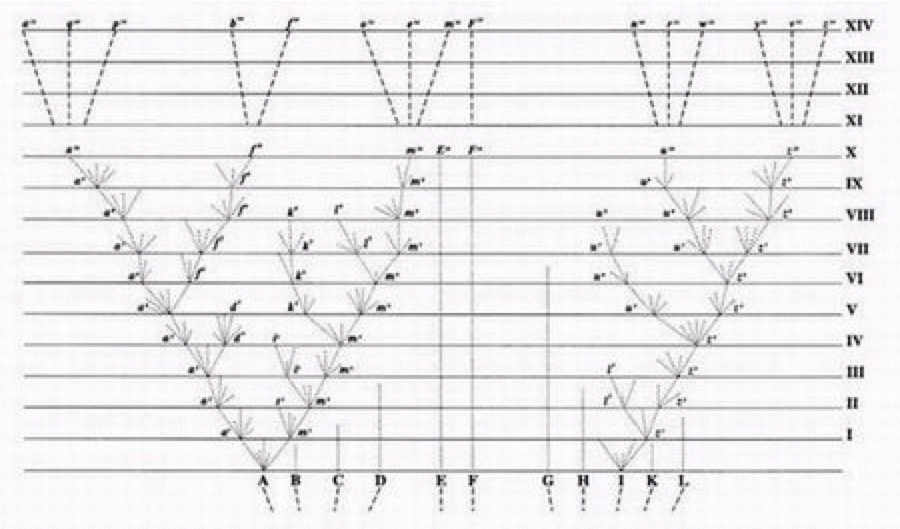


Thus between A & B. immens gap of relation. C & B. the finest gradation, B & D rather greater distinction. Thus genera would be formed. — bearing relation

Page from Darwin's notebooks around July 1837

Charles Darwin (1809-1882) was the first to produce an evolutionary tree of life. He was very cautious about the possibility of reconstructing the history of life. In On the Origin of Species (1859) Chapter IV he presented an abstract diagram of a theoretical Tree of Life for species of an unnamed large genus (see figure). On the horizontal base line hypothetical species within this genus are labelled A - L and are spaced irregularly to indicate how distinct they are from each other, and are above broken lines at various angles suggesting that they have diverged from one or more common ancestors. On the vertical axis divisions labelled I - XIV each represent a thousand generations. From A, diverging lines show branching descent producing new varieties, some of which go extinct, so that after ten thousand generations descendants of A have become distinct new varieties or even sub-species a10, f10, and m10. Similarly, the descendants of I have diversified to become the new varieties w10 and z10. The process is extrapolated for a further four thousand generations so that the descendants of A and I become fourteen new species labelled a14 to z14. While F has continued for fourteen thousand generations relatively unchanged, species B,C,D,E,G,H,K and L have gone extinct. In Darwin's own words: "Thus the small differences distinguishing varieties of the same species, will steadily tend to increase till they come to equal the greater differences between showing his first sketch of an evolutionary tree. (via Wikipedia)

species of the same genus, or even of distinct genera." (Darwin 1859, pp. 116-130).] This is a branching pattern with no names given to species, unlike the more linear tree Ernst Haeckel made years later (figure below) which includes the names of species and shows a more linear development from "lower" to "higher" species. In his summary to the section as revised in the 6th edition of 1872, Darwin explains his views on the Tree of Life:



The Tree of Life image that appeared in Darwin's On the Origin of Species by Natural Selection, 1859. It was the book's only illustration (via Wikipedia)

> The affinities of all the beings of the same class have sometimes been represented by a great tree. I believe this simile largely speaks the truth. The green and budding twigs may represent existing species; and those produced during former years may represent the long succession of extinct species. At each period of growth all the growing twigs have tried to branch out on all sides, and to overtop and kill the surrounding twigs and branches, in the same manner as species and groups of species have at all times overmastered other species in the great battle for life. The limbs divided into great branches, and these into lesser and lesser branches, were themselves once, when the tree was young, budding twigs; and this connection of the former and present buds by ramifying branches may well represent the classification of all extinct and living species in groups subordinate to groups. Of the many twigs which flourished when the tree was a mere bush, only two or three, now grown into great branches, yet survive and bear the other branches; so with the species which lived during long-past geological periods, very few have left living and modified descendants. From the first growth of the tree, many a limb and branch has decayed and dropped off; and these fallen branches of various sizes may represent those whole orders, families, and genera which have now no living representatives, and which are known to us only in a fossil state. As we here and there see a thin straggling branch springing from a fork low down in a tree, and which by some chance has been favoured and is still alive on its summit, so we occasionally see an animal like the Ornithorhynchus or Lepidosiren, which in some small degree connects by its affinities two large branches of life, and which has apparently been saved from fatal competition by having inhabited a protected station. As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth, and covers the surface with its ever-branching and beautiful ramifications. (Darwin 1872, pp. 104-105)

- Wikipedia

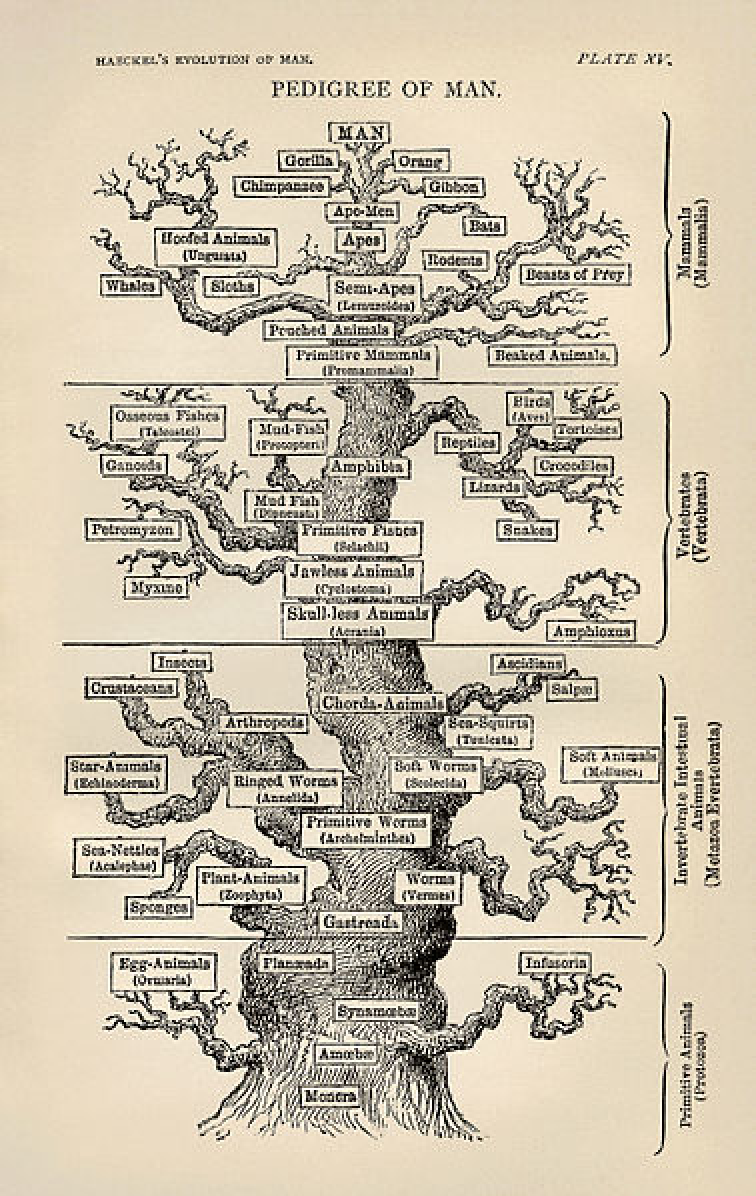
Page Back | Unit Home | Page Top | Page Next

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

Page Back: Darwin's Tree
Unit Home
Page Next: Evolutionary systematics
Unit Back: Linnaean taxonomy
Unit Up
Unit Next: Evolutionary systematics

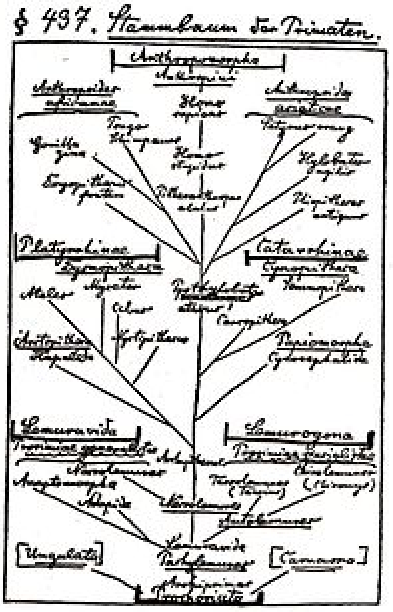
The Phylogenetic Tree: Haeckel's trees



Ernst Haeckel's tree of life. Here Darwin's description of the pattern of universal common descent is presented in beautiful artistic form. With Darwin in England and Lamarck in France, Haeckel in Germany was one of three the great popularisers of evolution. The above is from the English version of *The Evolution of Man*. For Haeckel, as for many early evolutionists, humans were considered the pinnacle of evolution. In fairness to Haeckel he also produced less anthropocentric tree diagrams (see below right). - from Wikipedia

Whilst Charles Darwin was the author of the empirical theory of evolution, it was his German counterpart and follower Ernst Haeckel who established the subfield of phylogeny (one of the many words he coined) as the study and science of the evolutionary relationships of life. Unlike Darwin's abstract trees, Haeckel, who was a brilliant illustrator, enthusiastically constructed several Trees of Life that were intended to convey the actual phylogenetic history of life, in terms of branching taxa. These diagrams, when representing life as a whole, became known (following the biblical phrase) as the "Tree of Life". Several such diagrams are shown on this page.

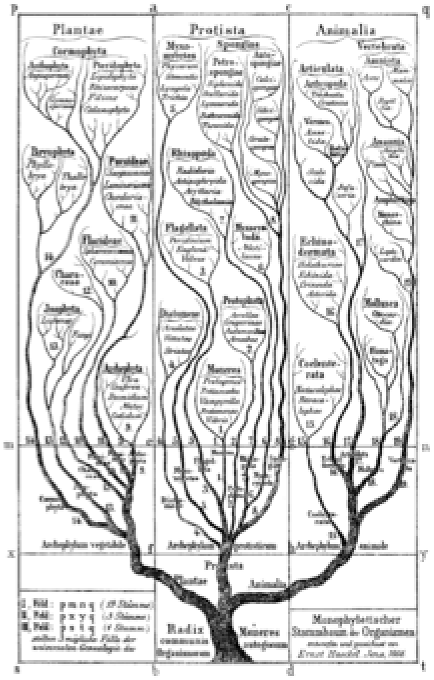
At the left is the first sketch of the famous Haeckel's Tree of Life in the 1870s which shows "Pithecanthropus alalus" as the ancestor of ***Homo sapiens***. Later when Haeckel's student duBois discovered Homo



Haeckel's *Stambaum der Primaten* (1860s). via Wikipedia

erectus in Java he named it ***Pithecanthropus erectus***.

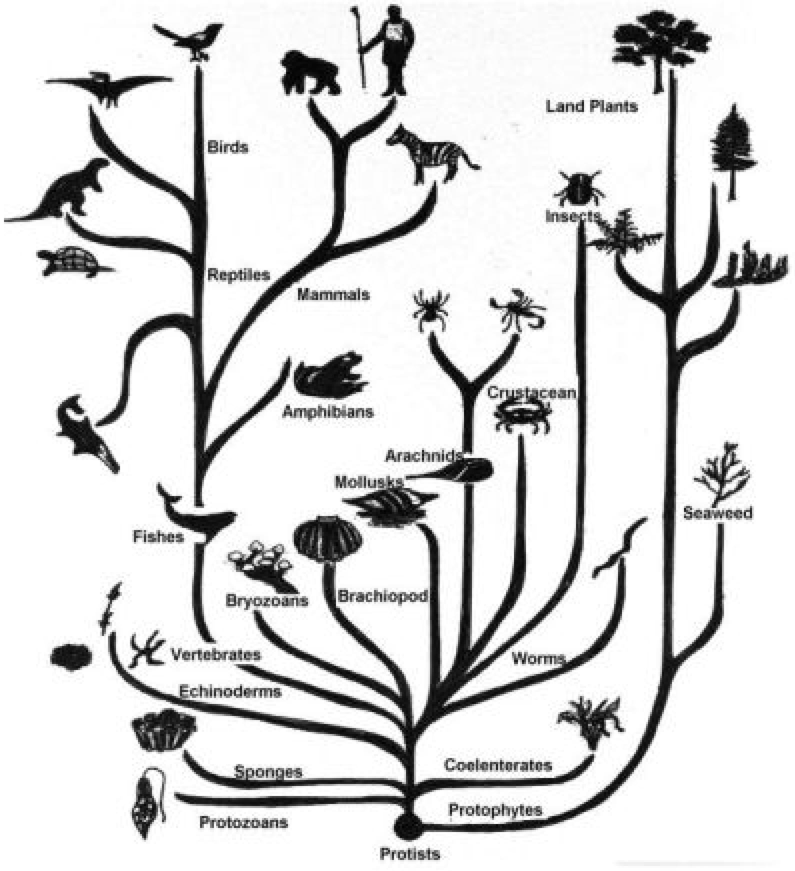
At the top of this page is his famous illustration the "Pedigree of Man" published in ***The Evolution of Man*** (1879), which shows Haeckel's Ladder of Nature/Great Chain of Being perspective with ***Homo sapiens*** at the top, an image as iconic as the much misunderstood ***March of Progress***, and which perhaps was the ultimate inspiration for the latter (although both go back ultimately to great chain of being / ladder of nature thinking). Although this would seem an anthropocentric step backwards in relation to his earlier (1866) but more contemporary-looking three-kingdom model, shown at the right, it should be remembered that for Haeckel, as for many 19th century evolutionists, humans were considered he pinnacle of evolution. Teilhard de Chardin serves as a 20th century example.



Haeckel's Tree of Life in *Generelle Morphologie der Organismen* (1866). This, the first truly modern Tree of Life, shows the three kingdoms of Plantae, Protista and Animalia, via Wikipedia

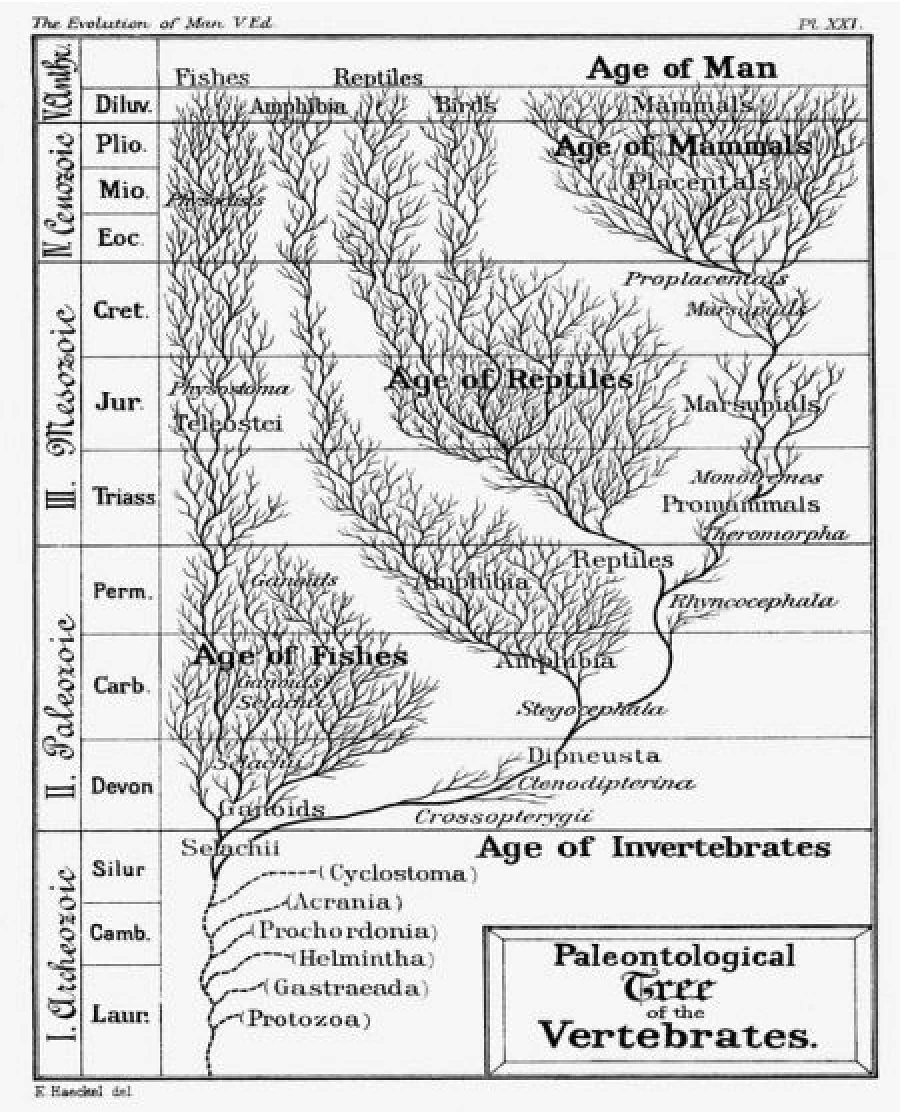
Haeckel's influence was considerable; modern versions of his trees can be seen in any biological textbook or popular science book. Inevitably, these diagrams retain ladder of nature thinking in that they have humans, butterflies, and flowering pants at the summit, with lesser forms of plants, invertebrates, and vertebrates beneath them. A typical diagram is shown here (***left***)

As with this later diagram, Haeckel's original trees showed the branching order only, and often featured purely speculative organisms based on embryology or on Haeckel's theorising regarding the origin of man.



Version of the Tree of Life, from "A Simplified Family Tree of Life" in *The Evidence of Evolution* by Nicholas Hotton III, Smithsonian, c1968 via Think Quest

An interesting diagram widely available online (e.g. Heritage Images, Science Rules!, Wikipedia) shows the transition from mid to late 19th century phylogenetic ladder of nature, shown in the above three diagrams, to a type of representation common in 20th century paleontology textbooks which plots phylogeny and diversity against geological time. This paleontological tree of vertebrates (***right***) is shows the beginning of the spindle diagram. According to the captrion on the Heritage Images page (the only one that gives information about it) it is from the fifth edition of Haeckel's ***The Evolution of Man***, published in 1910. This would put it late in Haeckel's career, reflecting the growing understanding of the diversity of life through time, although this march of life - minus the phylogeny - originates with early 19th century non-evolutionist paleontologists like Cuvier and Owen. Here we see Earth history in terms of successive ages of Invertebrates, Fish, Reptiles, Mammals, and Man, a terminology that was standard in



Tree of Vertebrates, from Ernst Haeckel's *The Evolution of Man*, fifth edition, London, 1910

science books until the cladistic revolution. The individual twigs are no longer labelled, but symbolic only, with diversity represented by the width of each class through time. However even this is quite inaccurate, as for example in real life there are twice as many extant species of birds than mammals, while fish (chiefly teleosts) equal all tetrapods combined. And reptiles themselves were highly diverse during the Permian. Ironically, the geological and paleontological convention of placing the oldest ages at the bottom and the newest at the top fits with Haeckelian (and pop-Darwinian), great chain of being thinking, according to which the "lower" forms of life appear first and hence, mapped against the geological column, would also branch off lower in the geological sequence

By the early 20th century, paleontology and our understanding of the history of life had taken on a mostly modern form. It was left to the evolutionary systematicists of the mid 20th century to eleimante the remnant Great Chain of Being representation integrate Haeckelian style phylogeny with Linnaean taxonomy, Darwin-Mendel evolutionary synthesis, the fossil record and the geological timescale in an empirical synthesis. Evolutionary systematic paleontologists would supplement Haeckelian trees with more sophisticated spindle diagrams that mapped geological time (vertical axis) against taxonomic diversity (horizontal width).

Replacing evolutionary systematics in the 1980s, cladistics used their own tree diagrams, called cladograms, that nevertheless were strikingly similar to Haeckel's in that they emphasise branching sequence (cladogenesis) rather than time or diversity as a way of presenting phylogentic hypotheses. Cladistics however differs from Haeckelian phylogeny in being far more rigorous in approach, and mapping the branching order (the tree shape or topology) with much greater precision. Based on bothgross morphology and molecular sequencing, cladograms became the visual representation of the modern statistical-quantitative science of phylogenetics. These cladograms are strandard in textbooks today. MAK130419.

Page Back | Unit Home | Page Top | Page Next: Evolutionary systematics

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

Paleontology

Life
  Evolution
  Paleontology
  Systematics
  Ecology

  Astrobiology
  Life on Earth

Paleontology
  Paleontology
  Fossils
  Trace Fossils
  Lagerstätten
  Glossary

Asaphiscus wheeleri, a fossil trilobite from the Middle Cambrian Wheeler shale, Millard County, Utah. Photo by DanielCD (Wikipedia)

The study of ancient life, on the basis of fossil remains.

> "To trace that life in its manifold changes through past ages to the present is a... difficult task, but one from which modern science does not shrink. In this wide field, every earnest effort will meet with some degree of success; every year will add new and important facts; and every generation will bring to light some law, in accordance with which ancient life has been changed into life as we see it around us to-day."

O.C. Marsh,
Vice Presidential Address, AAAS, August 30, 1877

Page Back: Evolution | **Unit Home** (You are here) | **Page Top** | **Page Next: Paleontology**

---

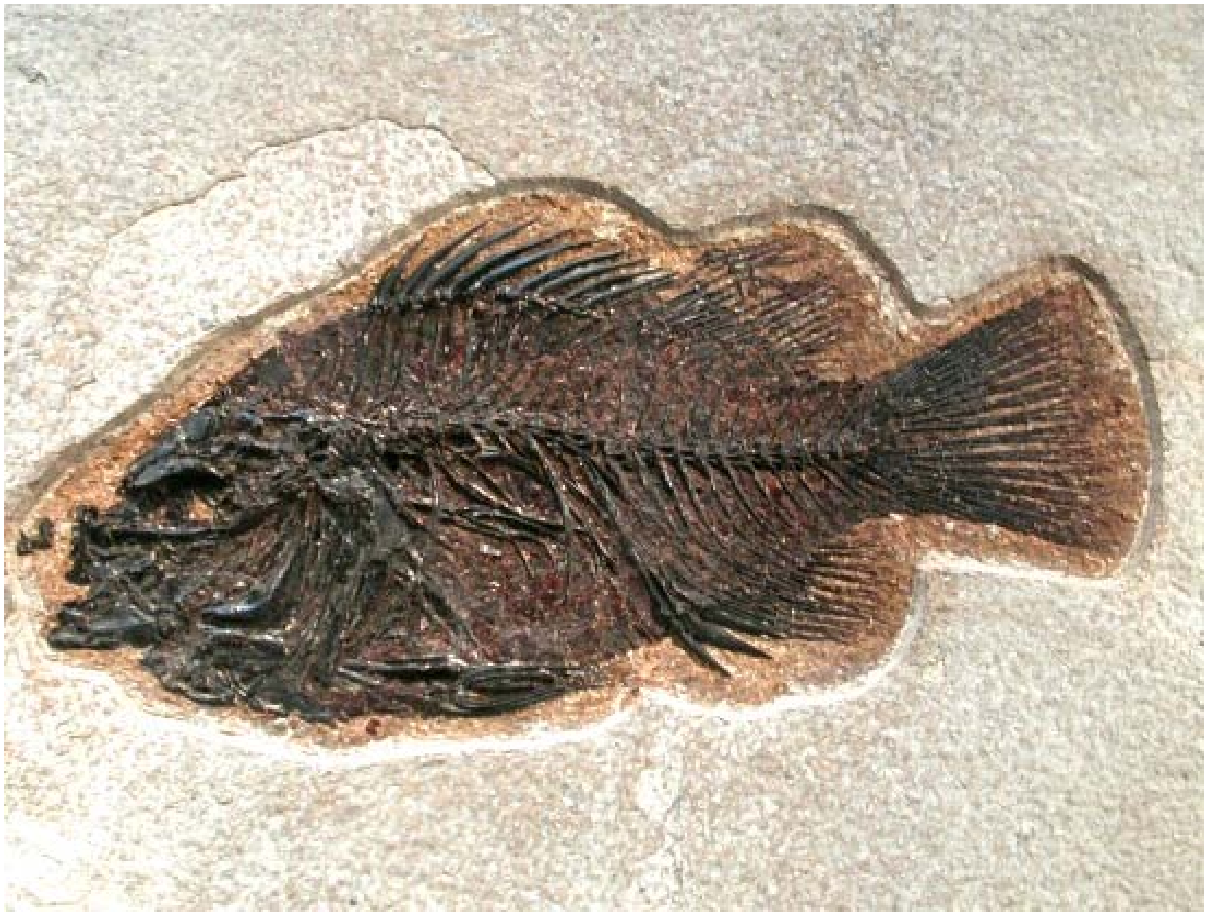
page created 23 April 2001; last modified MAK111005, edited RFVS111204
checked ATW030927

Paleontology

Life
  Evolution
  Paleontology
  Systematics
  Ecology

  Astrobiology
  Life on Earth

Paleontology
  Paleontology
  Fossils
  Trace Fossils
  Lagerstätten
  Glossary



Priscacara liops, a fossilised fish from the Eocene Green River Formation of Wyoming. Photo from Virtual Fossil Museum

Paleontology is the American spelling of Palaeontology, the central subject of the Palaeos website.

The word is roughly equivalent to "old life" -- the study of the life forms that existed before 'modern times'. Evidence of these life forms comes to us mainly through the study of fossils.

Any interested person could spend a happy lifetime studying all the possible implications that arise from these fossils -- and enjoy the lively debates that ensue!

Priestley070528 (Palaeos.org)

Links: (incomplete listing): University of California Museum of Paleontology comprehensive site on Earth History, although with the rise of Wikipedia its systematic coverage of Life on Earth is not as unchallenged as it was in the late 90s and early 2000s. Wikipedia paleontology portal - thanks to the tireless work of paleo geeks Wikipedia has become the single most comprehensive site on paleo matters, even if its coverage is typically unbalanced, giving enormous emphasis on charismatic groups like dinosaurs, while neglecting lesser known vertebrate, invertebrate and fossil plant groups. One of the things the new Palaeos will do (hopefully) is help to address this imbalance. Links for Palaeontologists - absolutely huge list of links and references. Not all links may still be current. International Plant Taphonomy Meeting - hopes to stimulate scientific research and to promote contacts among scientists engaged in the study of plant taphonomy including living and fossil plants of all geological periods. *Palaeontologia Electronica* - online peer reviewed digital journal - it's really cool to see an academic journal take such an innovative approach. Included a movie of *Endoceras* in issue no.1, since surpassed by videos posted to YouTube. Mirror Sites for the *Palaeontologia Electronica*: Texas A&M University, Texas, USA. MAK111005

Page Back: Home | **Unit Home** | **Page Top** | **Page Next: Fossils**

---

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page created 11 June 1998; last modified MAK111005, edited RFVS111204
checked ATW050504

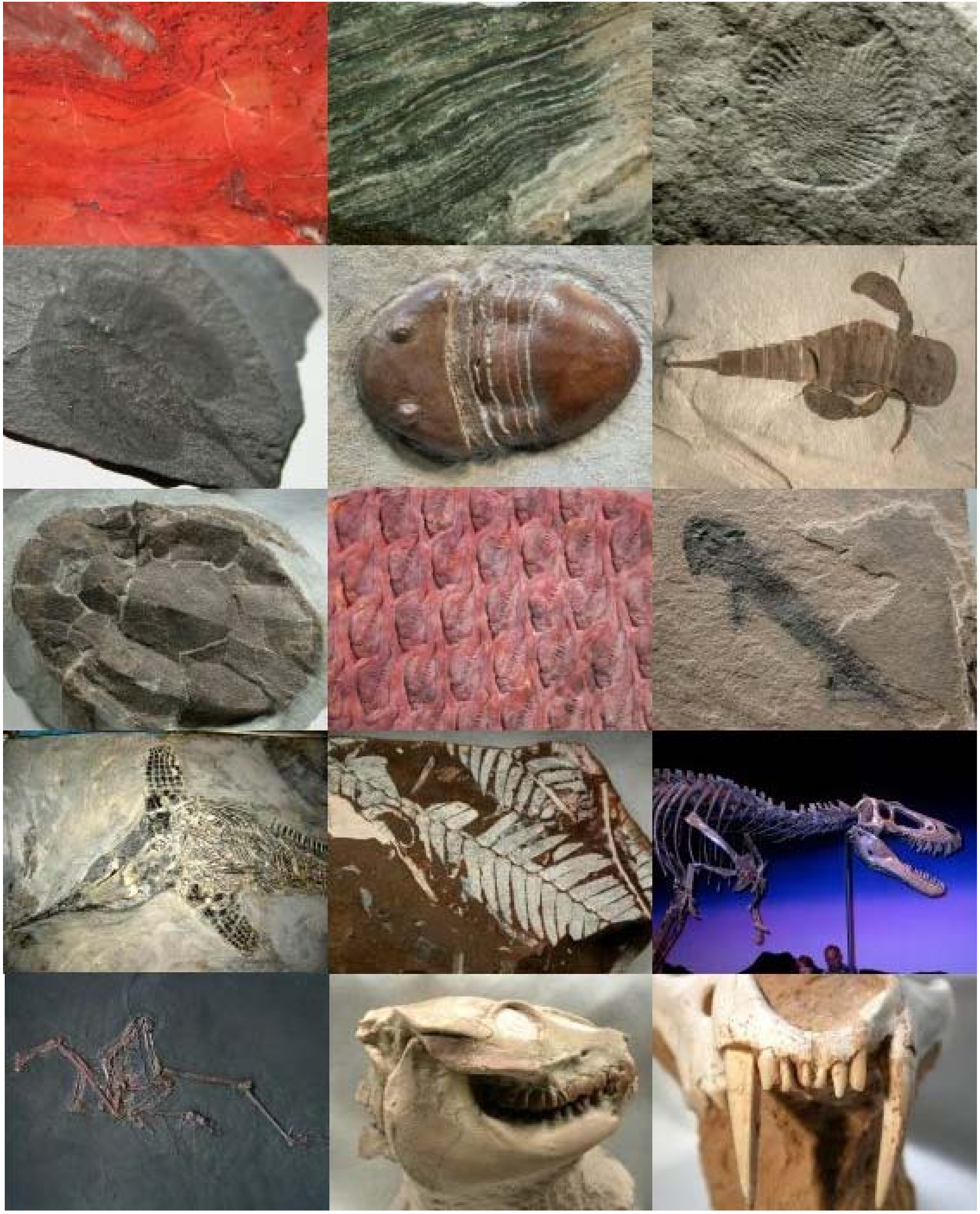
Page Back | Unit Home | Page Next
Unit Back: Evolution | Unit Up: Life | Unit Next: Systematics

Fossils

Life
  Evolution
  Paleontology
  Systematics
  Ecology

  Astrobiology
  Life on Earth

Paleontology
  Paleontology
  Fossils
  Trace Fossils
  Lagerstätten
  Glossary



Some representative fossils from across geological Time. Upper left to bottom right: a) Archean stromatolites from Wyoming, USA; b) Paleoproterozoic stromatolites from Gunflint Formation, Canada; c) Vendian Dickinsonia from White Sea, Russia; d) Early Cambrian Burgessia arthropod from Burgess Shale, B.C., Canada; e) Ordovician Homotelus trilobite from Iowa, USA; f) Silurian Eurypterus from Bertie Group, NY, USA; g) Devonian Bothriolepis Placoderm armoured fish from Quebec, Canada; h) Carboniferous clubmoss tree bark from Poland; i) Apateon Permian Fossil Amphibian from Germany; j) Triassic Ichthyosaur from Guizhou Province, China; k) Jurassic Cycadophyte Plant from Queensland, Australia; l) Cretaceous Tyrannosaurus rex from Hell Creek, Montana, USA; m) Eocene Messelornis Bird from Messel Pit, Germany; n) Oligocene Leptauchenia Oreodont from South Dakota, USA; o) Miocene Saber-toothed cat from Gansu Province, China.

Fossils are the remains of prehistoric animal and plant and micro-organisms, as well as traces, tracks, impressions, etc they may have left. Only a tiny proportion of all the organisms that ever lived became fossils, and even then mostly those with hard shells, bones etc that lived in conditions favourable for preservation. So our understanding of life in past ages is very uneven.

Earlier ideas

The nature of what fossils are was naturally a mystery to a civilization such as the Judaeo-Christian West which considered the entire Earth and all Creation to be no more than 5 or 6 thousand years old. Since the 16th century or so, scholars had engaged in a bitter controversy over the origin of fossils. One group held the modern view that fossils are the remains of ancient plants and animals. The other considered that fossils were either freaks of nature or creations of the devil. During the 18th century, the theory became popular that all fossils were relics of the great flood recorded in the Bible (in the 1960s or so this idea was revived by Young Earth Creationists). It was only around the beginning of the 19th century, when the basic principles of modern geology were established, that a better understand of fossils was possible. And it was not until Darwin published his masterwork on evolution that fossils were truly understood as the traces of ancient life on Earth.

The fossil record

The information revealed to us about the history of life on planet Earth, and the totality of fossils in general, is termed "the fossil record" or sometimes (in older books) the "record of the rocks". The fossil record is one of the most important ways by which we can understand the history and succession of life. However, the fossil record is also extremely capricious, because it creates a bias in terms of organisms with hard parts, while soft-bodied animals are rarely or never preserved. Many organisms probably never produced fossils, and there are a number of phyla of organisms that are not known from fossils. Fossils can only be preserved under certain conditions, and mostly only in sedimentary rocks (although there are rare exceptions, e.g. insects in amber). Also, whereas certain environments - e.g. reefs, ocean bottoms (reduced activity of decomposers and scavengers), swamps (anaerobic conditions mean little decay), and areas with high siltation rates (e.g. river floodplain) - favour fossilization, whereas others, e.g. dry uplands, grasslands, forests, etc are very poor at producing fossils. Thus the fossil record is better for some habitats and essentially non-existent for other habitats. Other factors to consider are that older fossils are less common than recent ones (because of greater time for erosion and degradation of fossil-bearing rocks), and that there are many rocks deep within the Earth's crust that contain fossils.

The rich fossil record

For all its limitations, the fossil record has taught us much about the history of life. There are many beautiful and detailed fossil collections in museums and the homes of private collectors. Images of some of these fossils are available on-line. Eventually the Internet has the potential to become a global database with virtual reality images of representative fossils which anyone can access it (Virtual Museums). In the meantime here are a very few links of what is available at present. MAK990511

Links

Links: . Liste over museets utstilte fossiler - heaps and heaps of images - from : Paleontologisk museum. Fossils, Rocks, and Time - U.S. Geological Survey - talks about the geological study of the earth and time. Includes a number of good specimens from Norway and elsewhere. Collection sorted by Geological age and Biological classification. The Virtual Fossil Museum has an enormous collection of fossil images organized by geological time and taxonomy.

Page Back | Unit Home | Page Top | Page Next

---

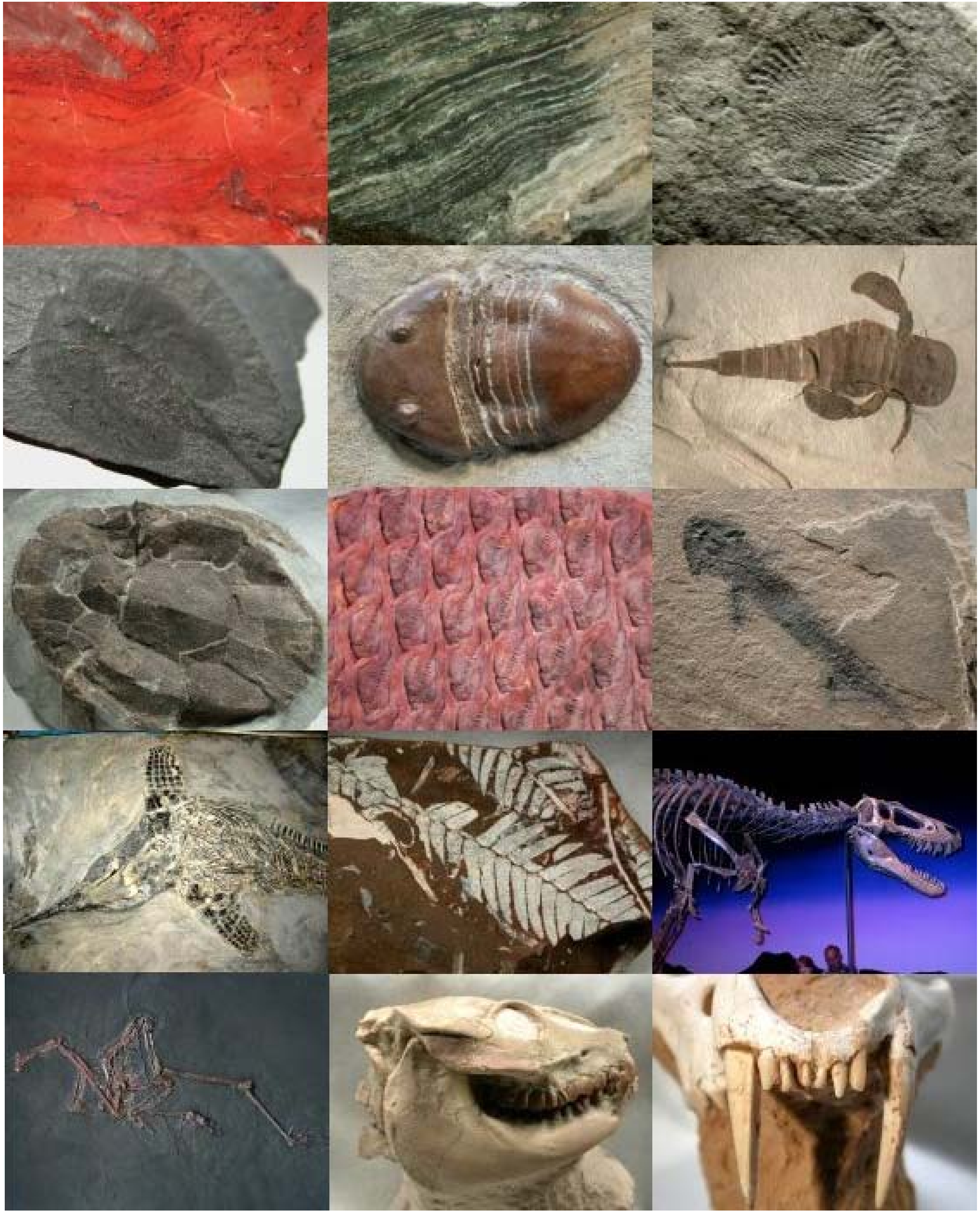
page created 11 May 1999; last modified RGP111101, edited RFVS111204
checked ATW050930

Page Back | Unit Home | Page Next
Unit Back: Life | Unit Up: Life | Unit Next: Classification

Fossils

Life
  Paleontology
  Classification
  Phylogeny
  Astrobiology
  Life on Earth

Paleontology
  Paleontology
  Fossils
  Trace Fossils
  Lagerstätten
  Glossary



Some representative fossils from across geological Time. Upper left to bottom right: a) Archean stromatolites from Wyoming, USA; b) Paleoproterozoic stromatolites from Gunflint Formation, Canada; c) Vendian Dickinsonia from White Sea, Russia; d) Early Cambrian Burgessia arthropod from Burgess Shale, B.C., Canada; e) Ordovician Homotelus trilobite from Iowa, USA; f) Silurian Eurypterus from Bertie Group, NY, USA; g) Devonian Bothriolepis Placoderm armoured fish from Quebec, Canada; h) Carboniferous clubmoss tree bark from Poland; i) Apateon Permian Fossil Amphibian from Germany; j) Triassic Ichthyosaur from Guizhou Province, China; k) Jurassic Cycadophyte Plant from Queensland, Australia; l) Cretaceous Tyrannosaurus rex from Hell Creek, Montana, USA; m) Eocene Messelornis Bird from Messel Pit, Germany; n) Oligocene Leptauchenia Oreodont from South Dakota, USA; o) Miocene Saber-toothed cat from Gansu Province, China.

Fossils are the remains of prehistoric animal and plant and micro-organisms, as well as traces, tracks, impressions, etc they may have left. Only a tiny proportion of all the organisms that ever lived became fossils, and even then mostly those with hard shells, bones etc that lived in conditions favourable for preservation. So our understanding of life in past ages is very uneven.

Earlier ideas

The nature of what fossils are was naturally a mystery to a civilization such as the Judaeo-Christian West which considered the entire Earth and all Creation to be no more than 5 or 6 thousand years old. Since the 16th century or so, scholars had engaged in a bitter controversy over the origin of fossils. One group held the modern view that fossils are the remains of ancient plants and animals. The other considered that fossils were either freaks of nature or creations of the devil. During the 18th century, the theory became popular that all fossils were relics of the great flood recorded in the Bible (in the 1960s or so this idea was revived by Young Earth Creationists). It was only around the beginning of the 19th century, when the basic principles of modern geology were established, that a better understand of fossils was possible. And it was not until Darwin published his masterwork on evolution that fossils were truly understood as the traces of ancient life on Earth.

The fossil record

The information revealed to us about the history of life on planet Earth, and the totality of fossils in general, is termed "the fossil record" or sometimes (in older books) the "record of the rocks". The fossil record is one of the most important ways by which we can understand the history and succession of life. However, the fossil record is also extremely capricious, because it creates a bias in terms of organisms with hard parts, while soft-bodied animals are rarely or never preserved. Many organisms probably never produced fossils, and there are a number of phyla of organisms that are not known from fossils. Fossils can only be preserved under certain conditions, and mostly only in sedimentary rocks (although there are rare exceptions, e.g. insects in amber). Also, whereas certain environments - e.g. reefs, ocean bottoms (reduced activity of decomposers and scavengers), swamps (anaerobic conditions mean little decay), and areas with high siltation rates (e.g. river floodplain) - favour fossilization, whereas others, e.g. dry uplands, grasslands, forests, etc are very poor at producing fossils. Thus the fossil record is better for some habitats and essentially non-existent for other habitats. Other factors to consider are that older fossils are less common than recent ones (because of greater time for erosion and degradation of fossil-bearing rocks), and that there are many rocks deep within the Earth's crust that contain fossils.

The rich fossil record

For all its limitations, the fossil record has taught us much about the history of life. There are many beautiful and detailed fossil collections in museums and the homes of private collectors. Images of some of these fossils are available on-line. Eventually the Internet has the potential to become a global database with virtual reality images of representative fossils which anyone can access it (Virtual Museums). In the meantime here are a very few links of what is available at present. MAK990511

Links

Links: . Liste over museets utstilte fossiler - heaps and heaps of images - from : Paleontologisk museum. Fossils, Rocks, and Time - U.S. Geological Survey - talks about the geological study of the earth and time. Includes a number of good specimens from Norway and elsewhere. Collection sorted by Geological age and Biological classification. The Virtual Fossil Museum has an enormous collection of fossil images organized by geological time and Taxonomy.

Page Back | **Unit Home** | **Page Top** | **Page Next**

---

page created 11 May 1999; last modified MAK111005, edited RFVS111204
checked ATW050930

Page Back: Lagerstätten	Unit Home	Page Next: Glossary
Unit Back: Evolution	Unit Up: Life	Unit Next: Systematics

Trace Fossils

Life
  Evolution
  Paleontology
  Systematics
  Ecology

  Astrobiology
  Life on Earth

Paleontology
  Paleontology
  Fossils
  Trace Fossils
  Lagerstätten
  Glossary

Trace fossils are indirect evidence of life in the rock record. There are several fundamental differences between traces and body fossils, which lead to their unique classification and nomenclature. In general they make poor zone fossils, but they are powerful tools in palaeoenvironmental interpretation. Studies show various general trends in their diversity and range, throughout the Phanerozoic. There are several sites around the world where a wide range and diversity can be observed.

Keywords: bioerosion; bioturbation; ethology; ichnology; trace fossil

Introduction

Trace fossils, or ichnofossils (from the Greek ikhnos meaning "track" or "trace"), are those structures and details preserved in rocks that provide indirect evidence of life in the past, or indeed "traces" of it. The most familiar of these are the tracks, trails, burrows, gastroliths, coprolites, impressions, borings, etc., made by invertebrates of all phyla (Pickerill 1994), but craniates, plants, fungi, and bacteria also contribute significantly to their number.

Ichnofossils are found on and within both hard and soft substrates, especially in sandstones or between two contrasting lithologies (Allaby & Allaby 1999). They constitute an alternative fossil record (Crimes & Droser 1992) from the more familiar physical occurrences of the organisms themselves, i.e. body fossils (bones, shells, carbonised leaves, teeth, etc.) and, although they may be visually less spectacular and inspiring at first glance, they are just as important. On the surface of it there is a considerable overlap between these two fossil realms, both in the information they can yield and in the way they might be studied. However, as one delves in more detail into this area of palaeontology, it becomes clear that traces differ in nature substantially from the traditional fossil type, and should be studied as such, with their own specific schools of thought.

The study of trace fossils, ichnology, can be divided into two distinct fields: palaeoichnology (ancient, fossilised traces) and neoichnology (modern traces created by extant organism groups). This is a subdivision of convenience - it is not to say that a palaeoichnologist would have nothing to do with modern traces or vice versa, it is quite the opposite - the two areas are linked inextricably. In fact, this link is one of the few occasions where the principle of uniformitarianism is turned on its head. Lebensspuren such as traces are much easier to study and much better known in fossil form than they are when freshly created in soft sediments today, therefore in this case "the past is the key to the present". This converse property is one of the major differences identified by Adolf Seilacher (1967) between trace and body fossils. The other differences, as well as many of the major trace fossil properties and points of contention in ichnology today, are discussed below.

Identifying the Trace Maker

The morphology of trace fossils is controlled predominantly by the behavioural (ethological) characteristics of the organisms producing them (eg Osgood, 1970; Häntzschel 1975). The physical dimensions of the organisms also influence most traces to a degree, but usually to a far lesser extent. With this fact in mind, it becomes clear why ichnologists have a hard time identifying the organism that produced a particular trace. Indeed, traces are perhaps the most vulnerable biogenic structures to confusion with pseudofossils (inorganic structures, impressions, or markings that bear resemblances to true fossils) by even the most experienced of palaeontologists, especially in such cases where they are known to occur in the same sequence (Benton & Gray 1981). There have been several such misdiagnoses in the past, prompting Bromley (1990) to note how: “We have inherited a set of names for trace fossils the most venerable of which originated in a series of misconceptions and misidentifications.” Pickerill (1994) provides several examples of dewatering structures assuming such ersatz roles, with various forms morphologically mirroring ichnospecies such as *Dactyloidites ottoi* Geinitz 1849, *Arenicolites variabilis* Fürsich 1974c, and *Skolithos linearis* Haldeman 1840, among others. Therefore great care and attention to detail is often required before one can even verifiably assign trace fossil status to a structure, let alone identify its progenitor.

Once a trace is confirmed, there are several complicating factors that must be considered before and serious effort can be made to verify which organism produced it. Frey & Seilacher (1980) highlighted many of these, including: (1) different behaviours within an individual organism may result in the creation of different traces, so one trace maker may be responsible for two or more trace fossil species; (2) on the other hand, similar behaviours between taxonomically unrelated organisms (possibly members of different phyla) may produce very similar traces, an excellent example being *Chondrites* von Sternberg 1833, which was originally described as plant remains but is now thought to have been created by deposit-feeding animals as they combed the sediment in search of food; (3) the ontogeny of the trace may not necessarily be related to the ontogeny of its maker, ie, as the organism develops, the traces it creates may or may not develop in a similar way (size, relative dimensions, shapes, etc); and (4) a single trace fossil type might represent a number of different behavioural traits.

An additional complexity that is often overlooked is the fact that animals are not machines. Slight variations from one day to the next in the way an organism burrows, for example, might throw up slightly different traces, all reflecting exactly the same behaviour in the same organism. Causes of this might be changes to environmental conditions on a local scale, varying sediment composition and consistency, or there may be no particular factor, just random variations. Furthermore, a trace created by the same organism as a result of the same activity may look quite different if preserved under different depositional and/or diagenetic conditions (Seilacher 1964). These factors may lead to the recognition of separate ichnospecies under the same ichnogenus, when really they should be considered as the same trace. Traces may also occur as the result of a combination of the behaviours of two separate organisms, producing a single structure (Brenchley & Harper 1998).

For these reasons, it is rare for a trace fossil to be assigned to a particular organism or even a higher taxon, with the exception of certain vertebrate and arthropod repichnia (Seilacher 1964, 1967a). Usually, however, it can be determined whether the trace is of metazoan, plant, bacterial, or fungal origin.

An example of a trace that has been assigned to a specific organism is that of a recently discovered eurypterid trackway created by a species of *Hibbertopterus*. This trace is a good example of how ichnofossils can provide valuable information that cannot be gleaned from body fossils. If the interpretation is correct, it shows that giant water scorpions were able to survive out of water for at least short periods 330 Ma ago in the Carboniferous, which could only be speculated until now. It is one of the largest traces of its type known, thought to have been created by the giant invertebrate moving along a soft, sandy beach (Whyte 2005).

Trace Fossil Classification

When considering the immense difficulties in identifying the creator of a biogenic structure, it is hardly feasible to attempt to systematically group their traces into any kind of a phylogeny. Two classification systems have prevailed over the past few decades: (1) the ethological classification scheme proposed by Seilacher (1953, 1964); and (2) the toponymic categorization offered by Martinsson (1970).

The standard suffix used in the technical terminology of trace fossil types is -ichnion (plural -ichnia).

Ethological System

Even if there can be no authoritative taxonomic definition for a trace, there is usually strong evidence for the type of behaviour that produced it (Seilacher 1964). This was the main factor in motivating Seilacher to propose a classification scheme based on behaviour. There are several criteria that can give a trace away as being ethological in origin, many of which are addressed in detail by Ekdale et al. 1984 and Donovan 1994. For example:

- continuity and uniformity of size in an individual structure, which is influenced by the morphology of the trace maker;
- the presence of a body fossil directly associated with the trace which, though rare, affords a chance to identify the specific maker of that trace (though not necessarily the makers of all seemingly identical traces);
- regular occurrences of complex shapes, which would occur in a more random manner if inorganic in origin;
- association with other delicate biogenic features ("spreiten");
- the presence of a lining, e.g. in a burrow wall, that would have had to have been emplaced by an organism;
- the presence of organic residues and/or faeces, indirectly evidencing an organism's association with the trace;
- preservation in full relief

Seilacher based his system upon five major groups: (1) cubichnia, formed on the top of a soft sediment by a resting or hiding animal; (2) domichnia, which reflect the life position of the organism; (3) fodinichnia, burrows found in soft sediments caused by feeding behaviour; (4) pascichnia, grazing traces leaving evidence of an animal scouring a surface for food; and (5) repichnia, which are the impressions of an animal track.

Cubichnia are generally the most morphologically influenced of the ethological trace groups, reflecting the size and shape of the trace maker. Arthropods, cnidarians, and echinoderms are responsible for the majority of them (Brenchley & Harper 1998). Perhaps the most famous examples are *Asteriacites* von Schlotheim 1820, thought to be made by an asterozoan, and *Rusophycus* Hall 1852, created by a trilobite or similar arthropod.

Domichnia are dwelling structures, principally created by infaunal filter feeders, usually in the form cylindrical burrows. They reflect the life position of the organism, which would have remained there until death or some external stimulus caused it to move on. They are most often vertical (e.g. *Skolithos* Haldemann 1840) but some are horizontal or inclined to the bedding strata (Brenchley & Harper 1998), akin to the burrows made by spatangoids. There are many well-known examples, including *Arenicolites* Salter 1857, and *Thalassinoides* Ehrenberg 1944.

Fodinichnia, such as *Teichichnus* Seilacher 1955, represent the three-dimensional feeding patterns of deposit feeders as they scour the sediment, picking up any nutriment contained within (Bromley 1994). Typically the trails created in this way are phobotactic (i.e. they do not overlap or repeat), since the most efficient way for a deposit feeder to acquire maximum nutrition is by not crossing the same area more than once. *Chondrites* von Sternberg 1833 and *Rhizocorallium* Zenker 1836 are other examples.

Pascichnia, like fodinichnia, represent feeding behaviour, but are made by a different trophic group – grazers. They are associated principally with hard, mineral substrates, and are concentrated on surfaces rather than in a 3-dimensional environment, therefore bearing little resemblance to endogenic, soft sediment fodinichnia. A wide variety of patterns result from this grazing activity, from spirals to sinuous furrows, and phobotaxis is again a feature, previously formed branches rarely crossing (Brenchley & Harper, 1998). *Cosmorhaphe* Fuchs 1895 is an example.

Repichnia are locomotory tracks interpreted as evidence of an organism's direct movement from one point to another (Seilacher 1964) on or within soft sediment. This interpretation is usually based on the fact that the track is more or less straight, or with a slight curvature. This group constitutes perhaps the most wide-ranging and best-known traces, from dinosaur footprints (e.g. *Anomoepus* E. Hitchcock 1848) to arthropod trackways (e.g. *Cruziana* d'Orbigny 1842), and even including early human footprints, such as those at Laetoli (fig. 3).

Since Seilacher's pioneering paper, several other ethological trace groups have been recognised, and including Seilacher's original five, eleven are currently accepted by the ichnological community (Bromley 1996), with several others of tentative status. The other currently accepted groups are as follows:

- aedificichnia, erected by Bown & Ratcliffe (1988) as traces created by organisms that built structures above a substrate and cemented them in place, e.g. *Chubutolithes* Ihering 1922 (a wasp nest);
- agrichnia, a group of "gardening traces" proposed by Ekdale et al. 1984, which are the preserved remains of burrow networks created to catch migrating meiofauna or to culture bacteria. The gardening animal passed through this network cyclically, picking up any nutriment acquired in this way. A classic example of this is *Spirodesmos* Andre 1920, a spirally arranged system of burrows and chambers;
- calichnia (Genise & Bown 1994), structures created by organisms that were specifically designed for breeding activity, such as bee cells and the nests of various organisms. An example is the termite trace *Termitichnus* Bown 1982;
- equilibrichnia, put forward for consideration by Bromley (1990) to represent the behaviour of an organism that buried itself deeper or shallower in response to sedimentation rates. These traces can be found in mineral substrates as well as soft sediments, and are typically marked by spreiten showing the various levels the organism had to burrow to. A famous example is the U-shaped burrow *Diplocraterion* Torell 1870;
- fugichnia, or "escape traces", proposed by Simpson 1975 as a trace type formed where an organism has responded to being buried in an event such as a density current. This creates a burrow going upwards instead of the more usual downward trend, typically seen in a chevron pattern produced, and bioturbation can be more severe because of the frantic movements in the animal. An example is *Corophioides* Smith of Kilwinning, 1893;
- praedichnia (Ekdale 1985), predation traces, which are found exclusively on hard substrates such as bones, shells, etc. They reflect predatory behaviour, be it by rasping gastropods boring into shells or the tooth marks found on the bones of large vertebrates. A well-known example is *Oichnus* Bromley 1981, which are drill holes created by carnivorous cephalopods and gastropods.

The other, more tentative, groups (e.g. the polychresichnia, suggested by Hasiotis 2003) are shown in table 1. They tend to be subsets of this core set of eleven ethological classes. An exception to this might be fixichnia which, as defined by Gibert et al. 2004, cannot be fully accommodated in any one of the more established classes.

Metazoan Traces

Group	**Subgroup**	**Definition**	**Status**
aedificichnia		traces formed from structures built above the substrate and cemented in place by an organism.	accepted
calichnia		structures that were used for breeding purposes, e.g. bee cells or any of various nests.	accepted

agrichnia		networks of burrows designed to catch migrating meiofauna or culture bacteria within.	accepted
	chemichnia	agrichnia that are specifically designed to culture bacteria for harvesting.	tentative
fodinichnia		burrows created by deposit feeders (e.g. nematodes) as they scoured the sediment for nutriment.	accepted
pascichnia		patterns on the surface of a substrate (esp. a hard substrate) that reflect the feeding patterns of grazing organisms.	accepted
praedichnia		evidence of predatory behaviour, e.g. bite marks on bones, shell borings, etc.	accepted
	mordichnia	praedichnia that show evidence of the death of an organism after it has been predated.	tentative
cubichnia		impressions left on the surface of a soft substrate that show where an organism was resting or hiding.	accepted
domichnia		traces, e.g. burrows, that reflect the life position of the organisms that created them.	accepted
fixichnia		the superficial etchings left after a sessile organism has used a soft or skeletal body part to anchor itself to a mineral substrate.	tentative
equilibrichnia		traces showing the response of an organism to accommodate varying sedimentation rates, e.g. U-shaped burrows with spreiten.	accepted
fugichnia		sediment disruption caused by an organism attempting to escape a sudden burial from increased sedimentation.	accepted
	taphichnia	fugichnia showing an unsuccessful attempt to escape burial, which resulted in the organism's death.	tentative
repichnia		ichnofossils created by an organism moving from one station to another in a definite direction.	accepted
	cursichnia	track traces that reflect locomotory behaviour in the form of crawling, walking, etc in the organism that created them.	tentative

	natichnia	repichnia that were caused by natatorial behaviour, e.g. a fish disturbing soft sediment by swimming low over it.	tentative
	volichnia	impressions (chiefly of insects) that show the position in which a flying organism landed on a soft sediment.	tentative
polychresichnia		trace fossils caused by multiple behaviours, e.g. calichnia also serving as domichnia, or cubichnia caused by ambush predators.	tentative
Metaphytan traces			
Group	**Subgroup**	**Definition**	**Status**
cecidoichnia		abnormal outgrowths of plant tissues that are produced in response to invasion by insect parasites, viruses, bacteria, and fungi.	tentative
corrosichnia		rhizocretions arising because of the corrosive action of plant roots.	tentative
sphenoichnia		bioturbation that reflects root growth growth and spreading down into a soft sediment.	tentative

Table 1: Ethological ichnofossil groupings and characteristics.

A further proposal, put forward by Mikuláš 1999, is the idea of distinguishing traces created by metazoans from those of metaphytan origin. He identified three separate classes relating to plant traces: corrosichnia and sphenoichnia being those rhizoliths caused by the action of roots corroding and bioturbating lithic sediments respectively; and cecidoichnia, in which animal-plant (rarely plant-plant, fungus-plant or moneran-plant) interactions leave a gall on a xylic substrate (i.e. the plant itself). Little work has been subsequently added to this area of ichnology but it remains an intriguing prospect.

It is possible to further classify ethological groups into the bioerosive and bioturbational realms, according to the nature of the substrate. Bioerosion represents the actions of animals, plants, and microbes that sculpt and penetrate hard substrates (Bromley 1994). Bioturbation occurs in soft sediments, where a range of behaviours can disrupt the grains and leave patterns that are subsequently preserved upon lithification. When one analyzes each trace-producing behavioural trait in this regard, it becomes clear that a wider ethological diversity of traces is produced within soft sediments than hard substrates (Gibert et al. 2004). As fig. 1 shows, most of the accepted ethological groups are exclusively bioturbational, praedichnia being the only exclusively bioerosive class. Furthermore, of those groups overlapping between the two, only pascichnia is found more commonly on hard substrates.

The groupings in Fig. 1 are somewhat superficial and do not constitute viable ichnotaxa or, for the most part, ichnotaxobases. They are loosely-defined “ichnoguilds” based on their sharing of particular resources or behaviour, and provide nothing more than a general idea of which classes are more closely related to others. For example, it can be seen at a glance that cubichnia only share one characteristic with three other groups, in being made by an organism that was not moving around at the time. On the other hand, fodinichnia and agrichnia share facets of organismal behaviour with all classes except cubichnia, in being made by mobile organisms that were feeding, and may also have used this feeding area as a life site.

Toponomic System

The toponomic (or morphotopographic) system provides a completely different way to consider trace fossils, being more or less unrelated to the organisms producing them. The idea is to look at where the traces occur in relation to the casting medium, since an important consideration when classifying traces is how its morphological expression can be influenced by preservation processes (Bromley 1990). The most common environment for trace fossil observation is on the tops and soles of sandstones, a feature that indeed triggered the introduction of several stratinomic terms in this regard, which has prompted several authors to organise them into classification systems (Bromley 1990).

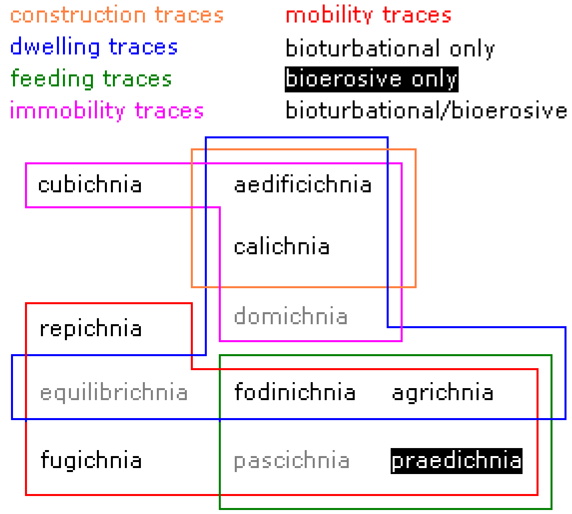


Fig. 1: Diagram illustrating the nature of the eleven established ethological trace fossil classes, and ichnoguilds within which they can be included (modified from Gibert et al. 2004).

The first attempt at classifying traces in this way was by Seilacher (1953), in a system he subjected to subsequent revision and modification (1964a, 1964b). He split traces into two basic types, those in full relief ("Vollformen", in which the full structure is preserved wholly within a sediment) and those in semirelief (or "Halbformen", traces preserved at an interface between two strata). Full reliefs can only be created by infaunal animals, reflecting their behaviour within the sediment, and have two main forms: fills, which contain sediment of the same nature as the surrounding medium or perhaps some other lithology; and cavities, which are open burrows. Several ways in which semireliefs can form were also detailed, with this category further split into boundary reliefs and cleavage reliefs. Boundary reliefs are those traces that occur strictly at the contact between two beds, reflecting reworking of the sediment by the animal at the upper or lower interface immediately before preservation. Boundary reliefs found on the upper surface of the substrate are called epireliefs, with those on the soles of strata termed hyporeliefs. Cleavage reliefs show deformation of subsurface laminae, before some subsequent event such as erosion has brought the trace to a stratal boundary, and as such an individual specimen may resemble a true boundary relief. Most of these trace categories are heterogeneous in nature.

In addition to these descriptive classes Seilacher also identified a genetic basis for categorisation, introducing three terms to this end: endogene, meaning the trace is filled with material of the same origin as the host sediment; exogene, used to describe traces with a composition alien from the casting medium due to coverage by a different sediment; and pseudexogene, describing the scenario whereby a structure is actively filled by the organism with a material other than the surrounding sediment (e.g. a burrow with a mud lining).

Simpson (1957) introduced an alternative scheme, perhaps a little less aesthetic, with poorer organisation and more ambiguity due to its openness to interpretation. He recognised four distinct categories for all trace fossils to fall within regarding the nature of their preservation:

- bed junction preservation, which forms as a result of the organism's activity at a lithological contact. The trace is preserved at the stratal interface;
- burial preservation, which may result in the trace's occurrence within a bed or at a lithological interface. A filled burrow gets exposed upon dissociation of surrounding soft sediments, e.g. by currents, and are thus left on the sediment surface. Subsequent burial, either by the same sediment type or that of varying composition, preserves the trace;
- concealed bed junction preservation, which provides a mechanism for traces to be preserved within a casting medium of a different lithology to its own, with no obvious connection to a stratum with a lithology reflecting the trace's composition. This simply occurs where the trace structure has been infilled by different material, the associated stratum of which is subsequently

removed by some process, e.g. erosion, leaving no evidence in the rock record.
- diagenetic preservation, in which the traces are preserved as nodules prior to compaction upon burial, probably during the eogenetic phase.

The most recent of the major toponomic classifications has been provided by Chamberlain (1971). His system more or less regurgitated previous work, but it is a very simple scheme in which traces can be placed in one of three categories: (1) endogene traces, which are structures filled within the host sediment, and therefore are homogeneous with the casting medium. The sediment infilling may have occurred either actively (by the organism itself) or passively (by some other process, after the organism has created the structure); (2) epigene traces, which are traces produced on the upper surface of a sediment then preserved by being quickly covered by a sediment of a different lithology; (3) intergene traces, which are endogenic structures formed at a lithological interface or the junction between two beds.

Perhaps the most authoritative and widely-used toponomic system, however, is that proposed by Martinsson (1965, 1970). He identified four ichnofossil groups with the morphotopographic basis: (1) endichnia, which are found within the casting medium; (2) epichnia, ridges or grooves found on the upper surface of the bed; (3) exichnia, traces found within a medium other than the sediment of origin; and (4) hypichnia, which are basically the opposite of epichnia, being ridges or grooves on the underside of the bed. This is again very similar to the Seilacherian system, as well as Chamberlain's offering, but is broadly regarded as the most aesthetic and all-encompassing of the schemes, although Seilacher's system would certainly seem the most thorough. The two are compared in Fig. 2, a classic diagram found in many works (e.g. Bromley 1990; Brenchley & Harper 1998) showing the parallels between the two most popular schemes.

Trace Fossil Nomenclature

The ambiguities faced by ichnologists in determining the creator of a trace means that the naming of trace fossils needs to have its foundations on completely different principles from that of more familiar, organismal taxonomy which is more or less based on phylogeny. In 1961, the International Committee for Zoological Nomenclature, having regarded the various complexities assigned to trace fossil nomenclature and its inconsistencies with established codes for animals and plants, ruled that any name proposed after 1930 would be no longer available. Traces described after this time therefore had no legal status, but those that were already established did. This action led many to propose a new, separate nomenclatural code specifically for trace fossils (e.g. Sarjeant & Kennedy 1973). There were problems with this, however (see Pemberton & Frey 1982 for fuller discussion), and in 1985 trace fossil names were again brought under the provisions of the International Code of Zoological Nomenclature.

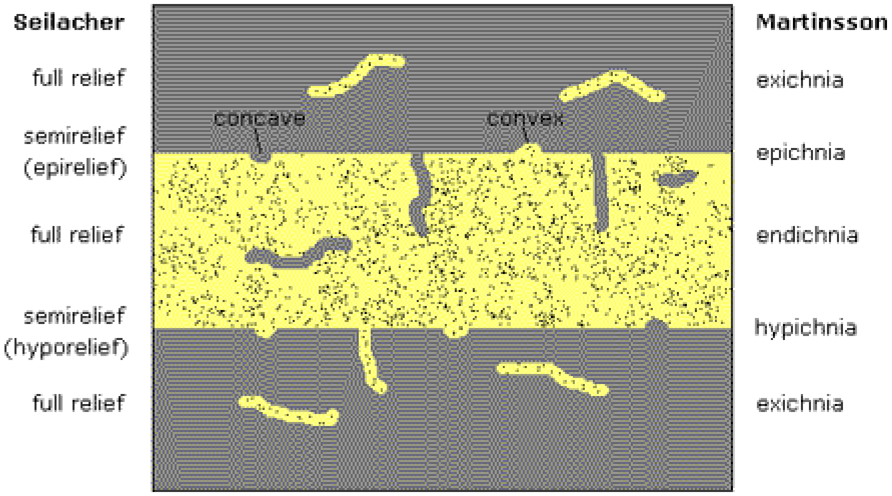


Fig. 2: comparison of the stratinomic trace fossil terminology between the systems proposed by Seilacher and Martinsson.

Whilst this has ameliorated some of the problems faced by ichnologists, the world of trace fossil nomenclature is still somewhat inadequately satisfied in several regards (Pickerill 1994). Some of the difficulties remaining today include: (1) the absence of any real formulated guidelines outlining recommendations with respect to how one should name a newly-discovered trace; (2) the historical "mess" left by early ichnologists who named many ichnotaxa upon the basis of misconception and misidentification (Bromley 1990); and (3) the incredible amount of misspelled ichnotaxa in primary literature and textbooks, among the most common of which is *Zoophycus*, which even appears in lowercase in Allaby & Allaby 1999 (on the whole, an excellent lexicon).

In addition to the general complicating factors touched upon above, there are many other more specific considerations, which vary in significance depending upon the type of trace. For discussion see Frey 1973, Sarjeant & Kennedy 1973, Häntzschel 1975, Basan 1979, Sarjeant 1979, Bromley 1990, Pickerill 1994, and references therein.

Development Through Time

The first trace fossils are very simple trails: The earliest clear indications of animals are trace fossils from about 570 Ma – structures, such as trails, that record animal activity. Before Cambrian time these traces are rare and minute, 1 mm or so wide for the most part, and were probably formed by creeping worms. Younger trace fossils progressively increase in complexity through time.

The beginning of the Cambrian Period at 543 Ma is marked by the first records of larger, vertical traces, and from then until the beginning of the explosive metazoan radiation ~530 Ma, the traces become an order of magnitude wider, more diverse, and more complex, suggesting a gradual diversification of larger animals (Crimes & Droser 1992). Indeed, the lower boundary of the Cambrian is now defined by the occurrence of a distinctive horizontal burrow trace fossil, *Trichophycus pedum* in the reference section at Fortune Head, southeastern Newfoundland (Fig. 3).

The abrupt appearance of many different kinds of trace fossils at the end of the Proterozoic is regarded as a singular biological event. It represents either the evolutionary origin of soft-bodied metazoans (Cloud 1948; Sepkoski 1978) or the first appearance in the fossil record of common animals capable of leaving preservable traces (Towe 1970; Durham 1978; Runnegar 1982a, b).

Traces are mostly found in marine sediments, but some of the most famous are terrestrial. The earliest evidence we have for for terrestrial activity by animals is provided by trace fossils. Among the oldest are Late Cambrian to no younger than Arenig (Early Ordovician) tracks made by multiple ~50 cm-sized, many legged animals, and preserved in an aeolian sandstone in the Nepean Formation (Potsdam Group) near Kingston, Ontario. However, these track-makers were probably amphibious arthropods - possibly euthycarcinoids - which only left the sea for a limited time, rather than fully terrestrial animals (MacNaughton *et al*. 2002).

Among larger and more recent animals, dinosaur trackways are relatively common, intensively studied, and have engendered an entire literature of their own. Perhaps the most famous, however, is the hominid trackway discovered by Mary Leakey's team at Laetoli (Fig. 4).

Fig. 3: The horizontal burrow trace fossil, *Trichophycus* (formerly *Phycodes*) *pedum* defines the lower boundary of the Cambrian in the reference section at Fortune Head, southeastern Newfoundland. [Image courtesy of Dr. Gerd Geyer, Institut für Paläontologie, Bayerische Julius-Maximilians-Universität, Würzburg, Germany.]

Trace Fossils as Paleoenvironmental Indicators

Although individual traces can yield important information about the rocks within which they are found, e.g. U-shaped burrows make excellent geopetal indicators, generally, a single trace fossil alone is a poor indicator of the environment in which the trace maker lived. Trace fossil associations, however, can prove to be extremely useful tools in palaeoenvironmental interpretation. The two most powerful concepts in this regard are ichnocoenoses and ichnofacies, which are quite similar and might easily be confused with each other, so some initial definitions are perhaps in order. An ichnofacies is a rock sequence, the defining characteristics of which include its lithology and sedimentary structures (of which the only lebensspuren considered are specific trace fossils). An ichnocoenosis is an assembly of trace fossils that were all generated by members of the same community (Allaby & Allaby 1999). They are used as components of ichnofacies, comprising less ichnodiversity than the broader range provided by the trace fossil signature of a full rock sequence.

Specific types of ichnocoenosis and ichnofacies are given taxonomic names that distinguish them from other types, e.g. the *Fuersichnus* ichnocoenosis, which falls into the *Cruziana* ichnofacies (Bromley & Asgaard 1991). The names are supplied by the ichnogenus that is most typically found within the ichnocoenosis or ichnofacies, but this ichnogenus does not necessarily have to be present in each individual occurrence. On the other hand, a certain ichnogenus or ichnocoenosis may not always be restricted to one particular ichnofacies, with many having features that overlap between two different groups. For example, *Cruziana* ichnospecies are prevalent in the *Cruziana* ichnofacies, but are also present as part of the *Scoyenia* ichnofacies, as are *Skolithos* ichnospecies (which also occur in the *Glossifungites* ichnofacies).

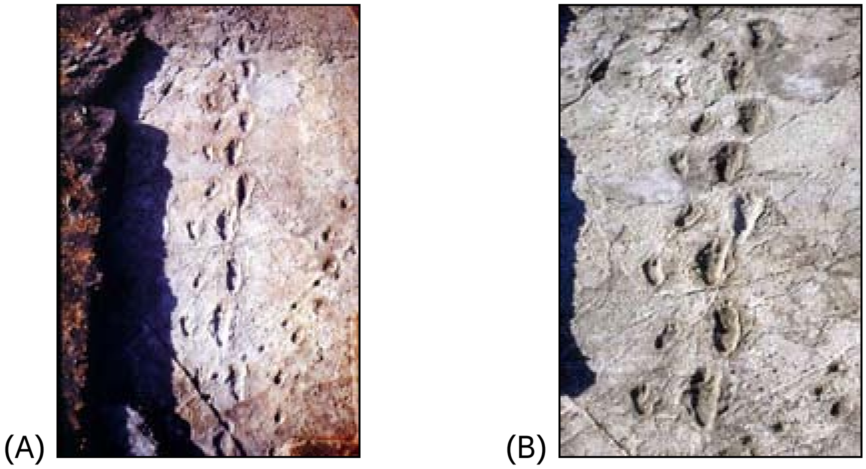


Fig. 4: Fossil hominid trackway site, known as Laetoli Site G, located in northern Tanzania. One of its trackways records unique evidence of bipedalism in hominids 3.6 million years ago. A team led by Mary Leakey originally excavated the site during 1978-1979. [Image (B) courtesy of University of Liverpool.]

There has been some confusion as to the true application of ichnofacies, with many authors (e.g. Lockley et al. 1987) suggesting there is a strong palaeobathymetric link. Indeed, this was the manner in which they were first introduced by Seilacher 1963, following his work on trace fossil associations throughout the fifties (e.g. Seilacher 1955). Where ichnocoenoses and ichnofacies occur, however, most attention should be paid to depositional conditions or environmental gradients, with palaeo-bathymetry being a prominent control only where certain environmental parameters are also related to bathymetry (Frey et al. 1990). There is also a stronger taphonomic control than many authors seem to appreciate, with trace assemblages not necessarily accurately reflecting the work of the original community (Bromley 1990). Bromley & Asgaard (1991) argue the importance of taphonomic control with a strong example in that the *Nereites* and *Zoophycos* ichnofacies may well reflect identical communities. The *Nereites* ichnofacies represents shallower tiers of the community, which are often destroyed by the deeper-tiered *Zoophycos* traces. Therefore "these would appear to be two taphonomic aspects of the same incipient ichnocoenosis, and therefore have the attributes of a taphofacies."

There are several currently recognised ichnofacies, some of which are more poorly defined and established on more tenuous grounds than others. The original four were proposed by Seilacher (1964) as a succession (*Skolithos* ® *Cruziana* ® *Zoophycos* ® *Nereites*) to aid palaeoenvironmental interpretation from shallow- to deep-water rock sequences respectively. All four are marine ichnofacies produced chiefly by bioturbational behaviour. Upon refinement of Seilacher's original scheme more ichnofacies have been identified, not all restricted to the marine realm, also including those of a bioerosive nature, and the palaeobathymetric link has lost much of its credibility (as discussed above). Seilacher (1967) himself began to argue against the reliability of ichnofacial bathymetric profiling, when he proposed two further ichnofacies, *Glossifungites* and *Scoyenia*, both independent of water depth. The *Scoyenia* ichnofacies has since come under scrutiny, with several authors (e.g. Bromley & Asgaard 1991) highlighting certain problems with it, such as low ichnodiversity and its similarity to other assemblages. The *Psilonichnus*, *Teredolites*, and *Trypanites* ichnofacies make up the rest of the nine "major" currently accepted ichnofacies.

The *Cruziana* ichnofacies is characteristic of a low-energy environment, best developed in circalittoral substrates below a normal fair-weather wave base (but not below the storm wave base) in well-sorted sands and silts (Brenchley & Harper 1998, Frey et al. 1990). Such quiet conditions might be expected in estuarine, lagoonal, and shelf environments, as well as certain non-marine scenarios, where lower ichnodiversity occurs. The traces are made up of burrows created by suspension and detritus feeders, and most prominently, repichnia reflecting the activities of mobile carnivores (the facies is named after a crawling trilobite trace).

The *Glossifungites* ichnofacies was erected by Seilacher 1967 to accommodate firm, often exhumed substrates such as dewatered muds (e.g. Brenchley & Harper, 1998). It occurs in conditions of moderate energy or in high-energy settings where semi-consolidated micritic/siliciclastic substrates offer some resistance to erosion (Frey et al. 1990). It has been recognised as a transitional phase of benthic community succession, as a hardground develops from an original softground in the natural evolution of an omission surface (Goldring & Kazmierczak 1974, Fürsich 1978), and therefore has little bathymetric restriction. Borings prevail in this predominantly bioerosive facies, along with burrows, some of which are quite complex (e.g. *Spongeliomorpha* Saporta 1887).

One of the original ichnofacies proposed by Seilacher 1964 as a set of recurring, palimpsest ichnofossil assemblages, the *Nereites* ichnofacies is thought to develop on and in quiet but moderately well-oxygenated seabeds (Brenchley & Harper 1998). The palaeodepth is usually from bathyal to abyssal, and it is common in flysch sequences where the area has been disrupted by down-canyon bottom currents and turbidity flows (Frey et al. 1990). A wide diversity of agrichnia, pascichnia, and repichnia is seen, the bioturbation taking the form of complex structures that are allowed to form in slowly-accreting, distal abyssal conditions (Frey et al. 1990). Seilacher 1964 identifies two distinct suites: (1) pre-turbidite assemblages, developing in mud softgrounds and representing the topmost and shallowest tiers of benthic activity; and (2) post-turbidite assemblages, occurring in and on sand softgrounds in the form of flysch systems. Some authors (e.g. Bromley & Asgaard 1991) hold only the pre-turbidite suite to truly represent the ichnofacies.

The *Psilonichnus* ichnofacies was proposed by Frey & Pemberton (1987) and based on traces associated with well-sorted, variably laminated to cross-stratified sands, to root- and burrow-mottled, poorly-sorted muddy sands. This implies moderate- to low-energy marine and/or aeolian conditions, such as sand dunes in both beach and backshore environments, and the coastal setting may extend to washover fans and supratidal flats (Frey et al. 1990).

Introduced by Seilacher 1967, and perhaps the most debated of the nine major ichnofacies, *Scoyenia* is characteristic of terrestrial redbed sequences (e.g. Brenchley & Harper 1998). These are formed in conditions intermediate between fully aquatic and non-aquatic, non-marine environments, at low-energy sites. The moist to wet sandy sediments may also support semi-aquatic vegetation (Frey et al. 1990).

Perhaps one of the best-known ichnofacies, and indeed ichnogenera, is *Skolithos*. The trace itself is a simple, straight, vertical burrow with a circular cross-section, created by suspension-feeding animals. The ichnofacies is marine, representing moderate- to relatively high-energy conditions, such as a beach foreshore or shoreface, other possible settings including estuarine point bars, tidal deltas, and deep-sea sand fans (Frey et al. 1990). The trace fossil signature of the facies is, as one might expect, on the pattern of *Skolithos*-type burrows, such as *Diplocraterion* and *Monocraterion* Torell 1870. Such burrows are often abundant, but the ichnodiversity is usually low.

The *Teredolites* ichnofacies is unique in developing in xylic skeletal material as wood-boring structures (Bromley et al. 1984). It represents predominantly a marine environment, where the borings are produced chiefly by bivalves, but freshwater ichnocoenoses can occur, in which case the borings consist primarily of those made by isopods (Frey et al. 1990).

The bioerosive *Trypanites* ichnofacies reflects production in hard substrates, such as hardgrounds and rockgrounds (Frey & Seilacher 1980). Typical casting media include omission surfaces on rocky coasts, beach rock, carbonates, and organic substrates such as reefs and shell beds (Frey et al. 1990). Originally described as marine, it can also occur in non-marine conditions, being produced on rigid skeletal material. This property, together with the occurrence of hardgrounds and rockgrounds at all water depths, gives the *Trypanites* ichnofacies perhaps the widest distribution of all ichnofacies (Bromley & Asgaard 1991). Because of the sequentiality of hardground development, the *Trypanites* suites may be seen to cross-cut previously formed ichnofacies such as *Glossifungites*, or even earlier assemblages attributable to the *Cruziana* ichnofacies (Frey et al. 1990).

Seilacher 1964 introduced the *Zoophycos* ichnofacies as one requiring quiet water and (presumably) nutrient-rich conditions on the outer shelf and slope. It can also develop in both shallower and deeper environments where similar conditions prevail (e.g. a lagoonal environment or a deep-sea setting supplied by rich down-welling nutriment). It is dominated by complex fodinichnia and pascichnia created by deposit feeders. There is some debate as to the degree of oxygenation on the seafloor represented here, with many authors (e.g. Frey & Pemberton 1984; Frey et al. 1990) suggesting a deficiency. Others (e.g. Bromley & Ekdale 1984, Bromley & Asgaard 1991) propose that this is not the case, the organisms being able to burrow to reach their required reducing pore-water environments.

Several authors have proposed additions and/or augmentations to the current ennead of major ichnofacies. For example, Bromley & Asgaard 1991 suggests the dissolution of the *Scoyenia* ichnofacies and inclusion of the *Arenicolites* ichnofacies instead, and the same two authors in 1993 divided the *Trypanites* ichnofacies into the *Gnathichnus* and *Entobia* ichnofacies. It has been suggested that the *Nereites* ichnofacies should be split into the *Nereites* and *Palaeodictyon* ichnofacies (Brenchley & Harper 1998), because of the apparent mutual exclusivity of some of the trails and burrows, and there are many more examples. Other less important ichnofacies are generally non-marine in nature and include, among others, the lacustrine *Mermia* (Buatois & Mángano 1995) and palaeosolic *Coprinisphaera* (Genise et al. 2000) ichnofacies. This section has focussed on the palaeoenvironmental implications of the nine ichnofacies that have been most prominent since the proposal of Seilacher's original four in 1964.

The basic fact is that, despite their usefulness, ichnofacies are by no means absolutely consistent; variations will always be observed. If one were to base an ichnofacies in any rigorously specific way then a potentially indefinite number would be discovered, due to local variations in (e.g.) ecology, taphonomy, and diagenetic/depositional controls. It is thought, however, that many more terrestrial ichnofacies are yet to be recognised and defined (Buatois & Mángano 1995). As far as current ichnological understanding allows, ichnofacies provide a reasonable proxy for palaeoenvironments.

Links

Links: Emory University (Atlanta, Georgia) – Introduction to Ichnology; University of Arizona site

References

Allaby, A.; Allaby, M. 1999: *Oxford Dictionary of Earth Sciences*. Oxford University Press, London.

Andre 1920

Basan, P.B. 1979: *Trace fossil nomenclature: the developing picture*. Palaeogeography, Palaeoclimatology, Palaeoecology, 28: 143-6.

Benton, M.J.; Gray, D.I. 1981: *Lower Silurian distal shelf storm-induced deposits in the Welsh Borders: sediments, tool marks and trace fossils*. Journal of the Geological Society of London, 138: 675-94.

Bown 1982

Bown, T.M.; Ratcliffe, B.C. 1988: *The origin of* Chubutolithes *Ihering, ichnofossils from the Eocene and Oligocene of Chubut province, Argentina*. Journal of Paleontology 62: 163-167.

Brenchley, P.J.; Harper, D.A.T. 1998: *Palaeoecology: Ecosystems, environments and evolution*. Chapman & Hall, London, 402 pp.

Bromley, R.G. 1981: *Concepts in ichnotaxonomy illustrated by small round holes in shells*. Acta Geologica Hispanica 16: 55-64.

Bromley, R.G. 1990: *Trace fossils: biology and taphonomy*. Unwin Hyman Ltd, London, 280 pp.

Bromley, R.G. 1994: *The palaeoecology of bioerosion*. In Donovan, S.K. (ed.) 1994: *The paleobiology of trace fossils*. John Wiley & Sons, Chichester: 134-154.

Bromley, R.G. 1996: *Trace Fossils: biology, taphonomy and applications* (2nd edition). Chapman & Hall, London, 361 pp.

Bromley, R.G.; Asgaard, U. 1991: *Ichnofacies: a mixture of taphofacies and biofacies*. Lethaia 24: 153-163.

Bromley, R.G.; Asgaard, U. 1993: *Endolithic community replacement on a Pliocene rocky coast*. Ichnos 2: 93-116.

Bromley, R.G.; Ekdale, A.A. 1984: Chondrites*: a trace fossil indicator of anoxia in sediments*. Science 224: 872-874.

Bromley, R.G.; Pemberton, S.G.; Rahmani, R.A. 1984: *A Cretaceous woodground: the* Teredolites *ichnofacies*. Journal of Paleontology 58: 488-498.

Buatois, L.A.; Mángano, M.G. 1995: *The paleoenvironmental and paleoecological significance of the lacustrine Mermia ichnofacies: an archetypical subaqueous nonmarine trace fossil assemblage*. Ichnos 4: 151-161.

Chamberlain, C.K. 1971: *Morphology and ethology of trace fossils from the Ouachita Mountains, southeast Oklahoma*. Journal of Paleontology, 45: 212-246.

Cloud, P.E. 1948: *Some problems and patterns of evolution exemplified by fossil invertebrates*. Evolution 2(4): 322-350.

Crimes, T.P.; Droser, M.L. 1992: *Trace fossils and bioturbation: The other fossil record*. Annual Reviews of Ecology and Systematics 23: 339-360.

Donovan, S.K. 1994: *The palaeobiology of trace fossils*. John Wiley & Sons Ltd, 308 pp.

d'Orbigny 1842

Durham, J.W. 1978: *A Lower Cambrian eocrinoid*. Journal of Paleontology 52: 195-199.

Ehrenberg 1944

Ekdale, A.A. 1985: *Palaeoecology of the marine endobenthos*. Palaeogeography, Palaeoecology, Palaeoclimatology 50: 63-81.

Ekdale, A.A.; Bromley, R.G.; Pemberton, S.G. 1984: *Ichnology: Trace fossils in sedimentology and stratigraphy*. Society of Economic Paleontologists and Mineralogists Short Course, no. 15, 317 pp.

Frey, R.W. 1973: *Concepts in the study of biogenic sedimentary structures*. Journal of Sedimentary Petrology 43: 6-19.

Frey, R.W.; Pemberton, S.G. 1987: *The* Psilonichnus *ichnocoenose, and its relationship to adjacent marine and nonmarine ichnocoenoses along the Georgia coast*. Bulletin of Canadian Petroleum Geology 35: 333-357.

Frey, R.W.; Pemberton, S.G.; Saunders, T.D.A. 1990: *Ichnofacies and bathymetry: a passive relationship*. Journal of Paleontology 64: 155-158.

Frey, R.W.; Seilacher, A. 1980: *Uniformity in marine invertebrate ichnology*. Lethaia 13: 183-207.

Fuchs 1895

Fürsich 1974

Fürsich, F.T. 1978: *The influence of faunal condensation and mixing on the preservation of fossil benthic communities*. Lethaia 11: 243-250.

Geinitz 1849

Genise, J.; Bown, T.M. 1994

Genise, J.F.; Mángano, M.G.; Buatois, L.A.; Laza, J.H.; Verde, M. 2000: *Insect trace fossil associations in paleosols: the* Coprinisphaera *ichnofacies*. Palaios 15: 49-64.

Gibert, J.M. de; Domènech, R.; Martinell, J. 2004: *An ethological framework for animal bioerosion trace fossils upon mineral substrates with proposal of new class, fixichnia*. Lethaia 37 (4): 429-437.

Goldring, R.; Kazmierczak, J. 1974: *Ecological succession in intraformational hardground formation.*

Palaeontology 17: 949-962.

Haldeman 1840

Hall 1852

Häntzschel, W. 1975: *Trace fossils and problematica*. In Teichert, C. (ed.) 1975: *Treatise of Invertebrate Paleontology (2nd Edition), part W, Miscellanea, Supp 1*. University of Kansas and Geological Society of America, Boulder, Colorado, and Lawrence, Kansas, 269 pp.

Hasiotis, S.T. 2003: *Complex ichnofossils of solitary and social soil organisms: understanding their evolution and roles in terrestrial paleoecosystems*. Palaeogeography, Palaeoclimatology, Palaeoecology 192 (1-4): 259-320.

Hitchcock, E. 1848

Ihering 1922

Lockley, M.G. Rindsberg, A.K.; Zeiler, R.M. 1987: *The paleoenvironmental significance of the nearshore* Curvolithus *ichnofacies*. Palaios 2: 255-262.

Page Back: Lagerstätten | **Unit Home** | **Page Top** | **Page Next: Glossary**

---

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page by Kristian Saether & Christopher Clowes - original url
edited RFVS111204

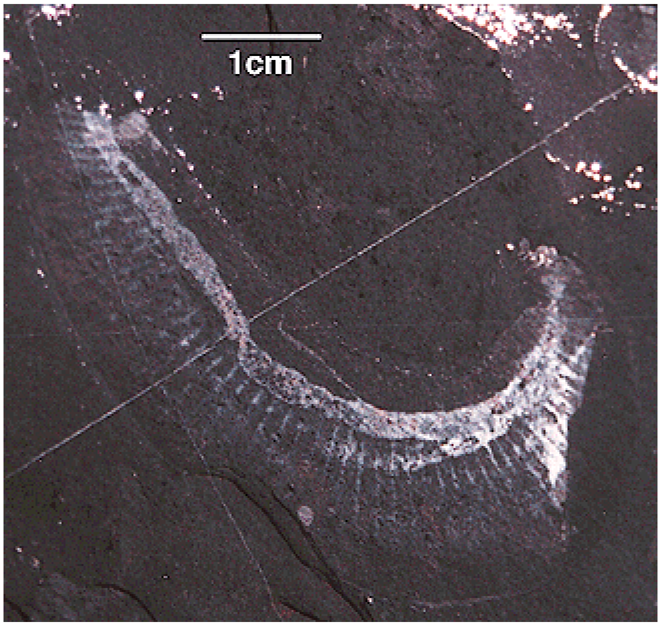
The Lagerstätten

Unique windows into the past

Life
  Evolution
  Paleontology
  Systematics
  Ecology

  Astrobiology
  Life on Earth

Paleontology
  Paleontology
  Fossils
  Trace Fossils
  Lagerstätten
  Glossary



Ottoia prolifica, showing muscle bands and gut.
Ottoia is a priapulid worm found commonly in the Burgess Shale. Image copyright © 1995 by Andrew MacRae

As far as fossil remains go, almost always, only scraps of bone or shell or a few carbonized leaves are all that remain of past organisms. Too often the soft parts decompose, and even the hard parts degrade.

In some exceptional instances however, usually anaerobic environments, or a sudden mudslide or volcanic eruption, organisms are buried before their bodies can be broken down by bacteria, or consumed by scavengers. Eventually their bodies are carbonized or mineralized, and so even soft-bodied creatures become fossilized. Such environments provide a unique, rare and precious window to the past.

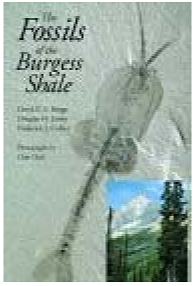
These extraordinary fossil deposits, where organisms are so well preserved that even their soft parts remain as carbon films, are referred to as Lagerst�tten, a German word meaning "deposit places". These are geological fossil deposits that are rich with varied, well-preserved fossils, representing a wide variety of life from a particular era. These spectacular fossil deposits represent a window into the past, a kind of "snapshot" of the type of organisms (hard and sometimes soft-bodied) that lived at that particular time and place.

Some Lagerstätten	Location	Period/Epoch	Age of Deposits
Chengjiang Maotianshan Shales	Yunnan Province, China	Early Cambrian	535 million years old
Burgess Shale	British Columbia, Canada	Middle Cambrian	530 million years old
Kaili Formation	Guizhou Province, China	Middle Cambrian	513 million years old
House Range	Millard County, Utah, USA	Middle Cambrian	507 million years old
Orsten	Sweden	Furongian	500 million years old
Hunsrück Slates	Bundenbach Germany	Early Devonian	370 million years old
Mazon Creek	Northeastern Illinois, USA	Late Carboniferous	300 million years old
Holzmaden	Württemberg, Germany	Early Jurassic	190 million years old
Solnhofen Limestone	Bavaria, Germany	Late Jurassic	150 million years old
Auca Mahuevo	Patagonia, Argentina	Late Cretaceous	80 million years old
Green River Formation	Wyoming and Colorado, USA	Eocene	50 million years old
Messel Oil Shale	Hessen, Germany	Eocene	49 million years old
Ashfall Fossil Beds	Nebraska, United States	Miocene	10 million years old
Rancho La Brea	Southern California, United States	Late Pleistocene	20,000 years old

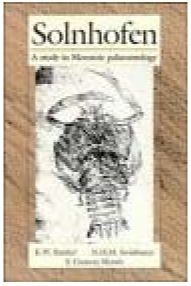
Links:

General: Looking Back Through Lagerst�tten - good intro - with links. Lagerst�tten - very brief intro - has a useful table listing the main Lagerst�tten

Specific (this list is incomplete...) Burgess Shale fossils - by Andrew MacRae - short intro to Burgess Shale and representative fossil organisms - **best on the Web**; Mazon Creek Fossils - the Illinois State Museum Mazon Creek homepage; The Solnhofen Limestone of Germany; Chengjiang Fossils - I don't like commercial fossil sites, but this one has some nice photos; 'Orsten' Research and Dieter Waloszek's View of Arthropod and Crustacean Phylogeny - includes info on arthropods from this important but less well-known Furongian Lagerst�tten



The Fossils of the Burgess Shale
- by Derek E. G. Briggs



Solnhofen - a study of Mesozoic Palaeontology
by K. Werner Barthel, S. Conway-Morris, and N. H. Swinburne

Page Back **Unit Home** **Page Top** **Page Next**

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact me

page created 19 June 2001; last modified MAK111005
checked ATW050504

Page Back | Unit Home | Page Next: Systematics
Unit Back: Evolution | Unit Up: Life | Unit Next: Systematics

Paleontology : Glossary

Life
  Evolution
  Paleontology
  Systematics
  Ecology

  Astrobiology
  Life on Earth

Paleontology
  Paleontology
  Fossils
  Trace Fossils
  Lagerstätten
  Glossary

A | B | C | D | E | F | G | H | I | J | K | L | M | N | O | P | Q | R | S | T | U | V | W | X | Y | Z

A.

Acanthodians: A primitive group of Silurian to Permian jawed bony fishes, bearing bony spines in front of all but their caudal fins. (USGS Paleontology glossary)

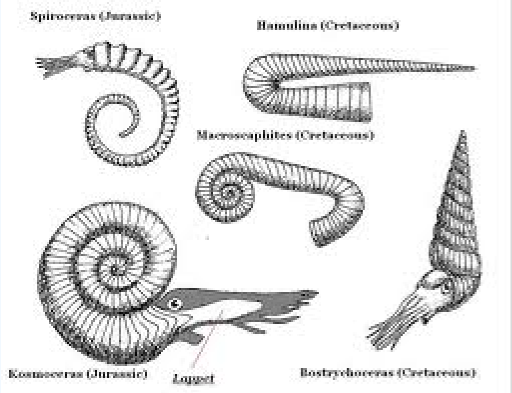
Age of Mammals: term found in popular books on evolutionary systematics for the Cenozoic era, beginning with the Paleocene Epoch when following the K-T (end Cretaceous) mass extinction, mammals underwent a huge evolutionary radiation and thus replaced reptiles as the dominant life on Earth. Paleontologist Björn Kurtén wrote a popular intelligent layperson book with the same title. *The Age of Mammals* is also the name of a mural by Rudolph Zallinger for the Yale Peabody Museum (link), which follows his earlier and better known *The Age of Reptiles*. The Age of Mammals has in turn been replaced by the Anthropocene or Age of Man, (Holocene) when humans dominate every conceivable environment and most other life forms (apart from weedy species) are suffering a mass extinction (Yes I know humans are also mammals, so technically speaking this is still the age of mammals, but I tend to think of age of mammals as a period of flourishing biodiversity). (MAK)

Age of Reptiles: term found in popular books on evolutionary systematics for the Permian through to Cretaceous periods (but obviously originating with Victorian discoveries of "antediluvian monsters"), when reptiles (first mammal-like reptiles, then archosaurs and marine reptiles) were the dominant life on Earth. Paleontologist Edwin Colbert wrote a popular intelligent layperson book with the same title. The Age of Reptiles was followed by the Age of Mammals. (MAK). *The Age of Reptiles* is also the title of a 110-foot (30 meter) mural painted by Rudolph Zallinger depicting the time from the Devonian to the Cretaceous and featuring dinosaurs and other prehistoric animals (His *The Age of Mammals* mural is similar and covers the Cenozoic). The fresco sits in the Yale Peabody Museum in New

Haven, Connecticut, and was completed in 1947 after three years of work. *The Age of Reptiles* was at one time the largest painting in the world, and depicts a span of nearly 350 million years in Earth's history. Painted in the Renaissance fresco secco technique, *The Age of Reptiles* was an important cultural influence during the 1950s-60s, images of which are often found in earlier books on paleontology, and was also the model for dinosaur toys. Despite its somewhat outdated view of dinosaurs (presenting them as slow, sluggish creatures), *The Age of Reptiles* is still notable for its historical and artistic merit and as the largest natural history painting in the world. It has been an inspiration to many visitors including both Robert Bakker and Peter Dodson, who credit it with influencing them to become paleontologists. Dodson was nearly moved to tears upon first seeing it as a college senior. (Wikipedia). *Editors note*: In my own case, a photo of this mural in a book (I no longer remember which one) when I was still a young child (maybe 10 or so) exerted a huge influence on me, like a revelation, and for the first time gave me a visual appreciation of deep time in terms of succession and transformation of various forms of plant and animal life. To this day, this mural, along with a spindle diagram of vertebrate evolution in G.G. Well's *Science of Life*, have been the two central influences that determined the way I think about deep time and the evolution of life on Earth. I think of Palaeos com as in many ways simply an extension, update (in keeping with more recent discoveries) and commentary on this magnificent work. (MAK) Link - Age of Reptiles at the Yale Peabody Museum

Agnatha: name given to what was previously considered a class of jawless fish, including both Paleozoic ostracoderms and extant lampreys and hagfish. With the cladistic revolution, the term has been replaced by more phylogenetically accurate terms such as "basal vertebrate" (MAK)

Ammonite: A coiled, chambered fossil shell of a cephalopod mollusc of the extinct subclass Ammonoidea. Traditionally divided into three types, according to suture: *goniatites* (Devonian to Permian) have simple lobes, *ceratites* (Triassic) have a saw-toothed pattern, and *ammonites* proper (Jurassic and Cretaceous) are the most complex, have fractal sutures with rounded lobes and saddles. Ammonoids appear in the Devonian and become very important as fossils from the Carboniferous through to the Cretaceous. There abundance, wide distribution, and short stratigraphic range make them excellent index fossils. (USGS Paleontology glossary)



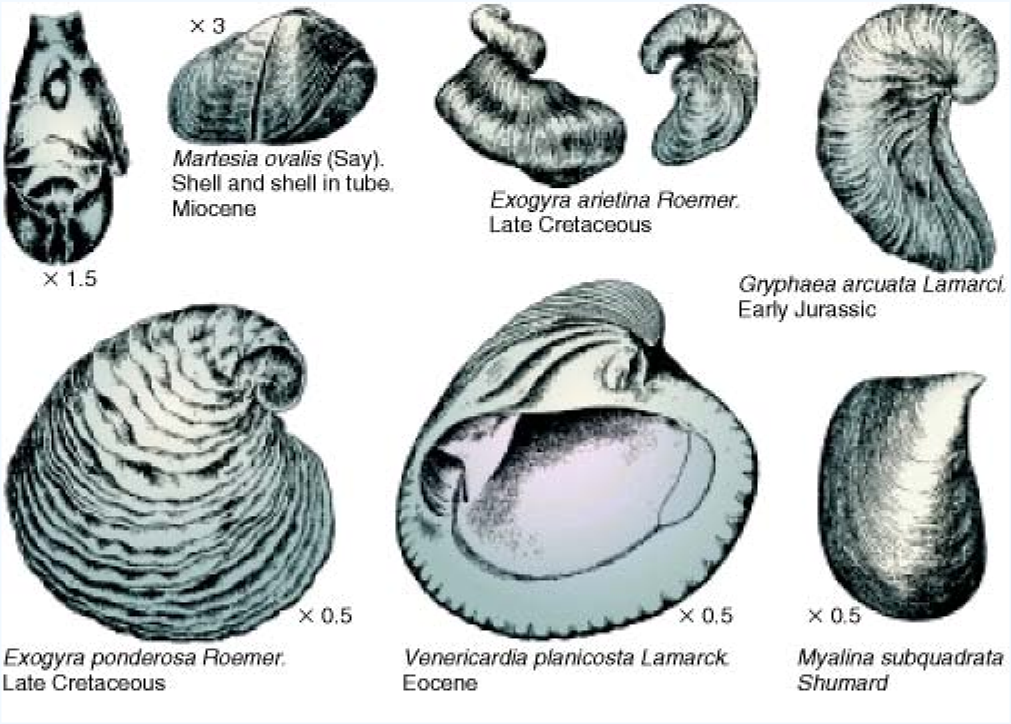
Graphic: selected ammonites, from Phil Eyden, Ammonites: A General Overview

Aperture: A relatively large opening on the last-formed chamber of a foraminiferal shell; the mouth of a mollusc shell. (USGS Paleontology glossary, MAK)

B.

Belemnite: a Mesozoic to early Tertiary cephalopod mollusc with an internal cone-, bullet-, or cigar-shaped shell. In life a squid-like animal, along with their cousins the ammonites they were important members of the Mesozoic marine ecosystem.

Bivalve: names any a mollusc that is a member of Class Bivalvia, a clade characterised by having two shells hinged together, as the oyster, clam, scallop, or mussel. The term is sometimes also used to refer to any animal with two halves to its shell such as an ostracod or brachiopod. Here Bivalve is used to refer specifically to the molluscan class. In contrast to brachiopods, the plane of symmetry is primitively between the valves (the two shells), although many types, for example oysters, developed different sized



valves. The second largest class of mollusc, after gastropods. Common as fossils, especially during the Mesozoic and Cenozoic, and these animals remain an important element in marine ecologies, especially in the littoral region. (MAK)

Graphic (right) A variety of bivalve fossil, After C. L. Fenton and M. A. Fenton, *The Fossil Book*, Doubleday, 1958., original url)

Brachiopod: meaning "arm foot", names any member of a major phylum of marine organisms with bivalved shell, in contrast to molluscan bivalves the plane of symmetry is through the mid-line of the shell, not between the valves. Filter feeding by means of a specialised organ called a lophophore. Abundant during the Paleozoic (most especially from the Ordovician to the Devonian), where, along with corals, they make up the majority of invertebrate fossils. Less common in the Mesozoic, and even less frequent in the Cenozoic. Cambrian-Recent. (MAK)

Bryozoa: meaning "moss animal", is a phylum of exclusively aquatic and mostly marine colonial organisms. At one time thought to be related to brachiopods because of the common possession of a lophophore, this is now considered the result of convergence. Ordovician-Recent. (MAK)

Burgess Shale: *Konservat-Lagerstätten* from the Middle Cambrian of British Columbia, preserves carbonised films which give a unique preservation of soft-bodied organisms and soft parts of hard-shelled organisms, provides an important window on the Cambrian explosion. The inspiration for Stephen Jay Gould's book *Wonderful Life*.

C.

Calcareous: Of, containing, or like calcite (calcium carbonate). (USGS Paleontology glossary)

Calcareous nanofossils: Fossil remains of calcareous nanoplankton. *Calcareous Nanoplankton* are protists that normally produce coccoliths during some phase in their life cycle. (USGS Paleontology glossary)

Calcite: A common rock-forming mineral: $CaCO_3$. Calcite can be white, colorless, or pale shades of gray, yellow, and blue. It readily effervesces (bubbles) in hydrochloric acid and is the principal component of limestone. (USGS Paleontology glossary)

Cambrian: The earliest period of the Paleozoic era, spanning the time between 544 and 505 million years ago. Its name derives from Cambria, the Roman name for Wales, where rocks of this age were first studied. (USGS Paleontology glossary) Major diversification of life in the Cambrian Explosion. Numerous fossils; most modern animal phyla appear. First chordates appear, along with a number of extinct, problematic phyla. Reef-building Archaeocyatha abundant; then vanish. Trilobites, priapulid worms, sponges, inarticulate brachiopods, and many other animals numerous. Anomalocarids are giant predators, while many Ediacaran fauna die out. Prokaryotes, protists (e.g., forams), fungi and algae continue to present day. Gondwana emerges. Petermann Orogeny on the Australian Continent tapers off (550–535 Ma). Ross Orogeny in Antarctica. Adelaide Geosyncline (Delamerian Orogeny), majority of orogenic activity from 514–500 Ma. Lachlan Orogeny on Australian Continent, c. 540–440 Ma. Atmospheric CO2 content roughly 20–35 times present-day (Holocene) levels (6000 ppmv compared to today's 385 ppmv). (Wikipedia) **More**

Carboniferous: A period of time in the Paleozoic era that includes the Mississippian and Pennsylvanian subperiods and extended from 360 to 286 million years ago. The later Carboniferous was the time of great Coal Swamps. (USGS Paleontology glossary) **More**

Cartilaginous fishes: Class Chondrichthyes; fish having a skeleton composed mostly of cartilage, as sharks and rays. Cartilage is gristle or a firm, elastic, flexible type of connective tissue. (USGS Paleontology glossary)

Cenozoic: ("new animal life") the current of the three Phanerozoic eras in the geological timescale. It began 65.5 million years ago. The era when the modern continents formed, mammals and birds filled the ecological niches vacated by dinosaurs, and modern taxa of plants and invertebrates evolved. The later part of the Cenozoic was marked by a pronounced cooling, culminating in the Pleistocene ice age. Includes two periods, the Tertiary and Quaternary, and seven epochs, the Paleocene, Eocene, Oligocene, Miocene, Pliocene, Pleistocene, and Holocene. **More**

Chalk: soft, earthy, fine-grained white to greyish limestone of marine origin. It is composed almost entirely of by shallow-water accumulations of coccoliths and other microscopic organisms and forms in a sea predominantly free from terrestrial sediment. (from Glossary - Bristol University)

Chelicerate: "claw horn bearing". Subphylum Chelicerata , Morphologically distinct arthropod clade characterized by have chelicera (a pair of pre-oral appendages), including arachnids (spiders, mites, etc), horseshoe crabs, scorpions and eurypterids ("sea scorpions"). Cambrian to recent. (University of Arizona Geosciences 308 Paleontology glossary)

Chronospecies: One or more species which continually changes from an ancestral form along an evolutionary scale. This sequence of alterations eventually produces a population which is physically, morphologically, and/or genetically distinct from the original ancestors. Throughout this change, there is only one species in the lineage at any point in time, as opposed to cases where divergent evolution produces contemporary species with a common ancestor. Relies on an extensive fossil record, since morphological changes accumulate over time and two very different organisms could be connected by a series of intermediaries. The related term *paleospecies* indicates an extinct species only identified with fossil material. To avoid unnecessary multiplication of terminology (and paleontology-neontological distinctions) these terms are here synonymised. For example, changes in the Permian lepospondyl amphibian *Diplocaulus* over time may imply a chronospecies (= paleospecies). (MAK, Wikipedia)

Cnidaria: meaning "nettle bearing", is a phylum of solitary or colonial, sessile or free-living, predatory organisms with specialized stinging cells called *nematocytes* (or *cnidoblasts*), and frequently having distinctive morphologies for asexual and sexual reproduction. Cnidarians include jellyfish, corals, hydrozoans and others. In older books the name *Coelenterate* is used instead. (University of Arizona Geosciences 308 Paleontology glossary) **More**

Coal swamp: name given to the vast equatorial tropical forests and swamplands of the late Carboniferous, from which most modern black coal comes from (brown coal in contrast is Tertiary in age). Despite the name, coal swamps did not themselves contain any coal. (MAK) Page with links to dioramas

Coccoliths: Microscopic structures of varying shape and size that are made of calcite, are secreted by calcareous nanoplankton, and are found in marine deposits from the Triassic period to the Recent. Coccoliths range in size from one to thirty-five micrometers in size. (USGS Paleontology glossary), found only in warm, low-latitude waters and hence useful for understanding ancient climates. (Glossary - Bristol University)

Coral: Class Anthozoa, sessile Cnidaria, solitary or colonial polyp-like animals, may be soft-bodied (sea anemone) or secret a stony skeleton (this is the familiar coral). Often reef-building organisms. Include the Paleozoic Rugose and Tabulate corals, both common or very common as fossils in rocks of Ordovician to Permian age, and the Mesozoic to Recent scleractinian corals.

Cretaceous: The final period of the Mesozoic era, spanning the time between 145 and 65 million years ago. The name is derived from the Latin word for chalk ("creta") and was first applied to extensive deposits of this age that form white cliffs along the English Channel between Great Britain and France. (USGS Paleontology glossary) Flowering plants proliferate, along with new types of insects. More modern teleost fish begin to appear. Ammonites, belemnites, rudist bivalves, echinoids and sponges all common. Many new types of dinosaurs (e.g. tyrannosaurs, titanosaurs, duck bills, and horned dinosaurs) evolve on land, as do Eusuchia (modern crocodilians); and mosasaurs and modern sharks appear in the sea. Primitive birds gradually replace pterosaurs. Monotremes, marsupials and placental mammals appear. Break up of Gondwana. Beginning of Laramide and Sevier Orogenies of the Rocky Mountains. Atmospheric CO2 close to present-day levels. (Wikipedia) **More**

Crinoid: sea lily, (Subphylum Crinozoa, Class Crinoidea) a type stalked and filter-feeding echinoderm that was very common during the Paleozoic, especially the early Carboniferous, and continues to flourish today, mostly in deep sea environments.

Crustacean: Subphylum Crustacea. Large group of mostly marine arthropods (although there are also some freshwater types and even a few terrestrial ones). Include shrimps, lobsters, crabs, barnacles, krill, ostracods, and terrestrial slaters and pillbugs. Morphologically distinct from other arthropods (hence given their own subphylum), but according to molecular phylogeny closely related to insects. Cambrian to recent.

Cyanobacteria: common name "blue-green algae", a type of photosynthetic Eubacteria, one of the most primitive forms of life on Earth. Form stromatolites, and the "scum" on rocks and in showers. Archean to recent.

Cynodont: mostly Triassic mammal-like reptiles, from which true mammals evolved. (MAK)

D.

Devonian: A period of the Paleozoic era, spanning the time between 410 and 360 million years ago. It is named after Devonshire, England, where rocks of this age were first studied. (USGS Paleontology glossary) First clubmosses, horsetails and ferns appear, as do the first seed-bearing plants (progymnosperms), first trees (the progymnosperm *Archaeopteris*), and first (wingless) insects. Strophomenid and atrypid brachiopod, rugose and tabulate corals, and crinoids are all abundant in the oceans. Goniatite ammonoids are plentiful, while squid-like coleoids arise. Trilobites and armoured agnaths decline, while jawed fishes (placoderms, lobe-finned and ray-finned fish, and early sharks) rule the seas. First amphibians still aquatic. "Old Red Continent" of Euramerica. Beginning of Acadian Orogeny for Anti-Atlas Mountains of North Africa, and Appalachian Mountains of North America, also the Antler, Variscan, and Tuhua Orogeny in New Zealand. (Wikipedia) **More**

Dinocyst: A resting stage or reproductive stage in the life cycle of a dinoflagellate. (USGS Paleontology glossary)

Dinoflagellate: Small organisms with both plant-like and animal-like characteristics, in earlier taxonomies usually classified as algae (plants). They take their name from their twirling motion and their whip-like flagella. (USGS Paleontology glossary); found as fossil from the mid Triassic to the present. Modern dinoflagellates are often responsible for the phosphorescence of the sea and toxic red tide. Fossil dinoflagellates are used to date and correlate rocks from the Triassic to the Quaternary. (Amateur Geologist Glossary)

E.

Echinoderm: meaning "spiny skinned", names any member of Phylum Echinodermata; a large group of primarily pentamerally radially symmetrical exclusively marine metazoans with internal calcite skeletons and hydrostatic vascular system. Includes crinoids (sea lilies), echinoids (sea urchins, sand dollars, sea biscuits), holothurians (sea cucumbers), asteroids (starfish), ophiuroids (brittle star), and many exclusively Paleozoic groups such as blastoids, edrioasteroids, carpoids, and others. (University of Arizona Geosciences 308 Paleontology glossary) **More**

Echinoid: Subphylum Echinozoa, Class Echinoidea. Sea urchins and their relatives. Echinoderms with spherical or flattened bodies, often protected by long spines, like starfish they move about on tube feet. Very common as fossils, especially in the Cretaceous and Tertiary. Ordovician - Recent (rare prior to the

Jurassic). (MAK)

Ediacaran: most recent period of the Proterozoic era, characterised by the appearance of both enigmatic Vendobionta and trace fossils that seem to pertain to more conventional organisms. The term Ediacaran was replaced for a while by Vendian, but now it seems that Ediacaran is back in fashion. (MAK)

Ediacaran biota: enigmatic life forms from the Ediacaran period; the first large to appear. Their affinities remain highly controversial; they have been interpreted as the first representatives of current animal phyla (Cnidaria, Annelida, Arthropoda, etc), as sister group to all metazoa more derived than sponges, as a totally distinct kingdom (Vendobionta, Vendozoa), and even as marine fungi and giant Rhizarian protists. Each hypothesis has advantages and disadvantages going for it. (MAK)

Eocene: An epoch of the early Tertiary period, spanning the time between 55.5 and 33.7 million years ago. Its name is from the Greek words ἠώς (*eos*, dawn) and καινός (*kainos*, new)). It was a period of global greenhouse climate and lush forests, in which small to large archaic mammals, large reptiles, and giant flightless birds all flourished. (USGS Paleontology glossary, MAK, Perseus Digital Library) Moderate, cooling climate. Archaic mammals (e.g. Creodonts, Condylarths, Uintatheres, etc) flourish and continue to develop during the epoch. Appearance of several "modern" mammal families. Primitive whales diversify. First grasses. Reglaciation of Antarctica and formation of its ice cap; *Azolla* event triggers ice age, and the Icehouse Earth climate that would follow it to this day, from the settlement and decay of seafloor algae drawing in massive amounts of atmospheric carbon dioxide, lowering it from 3800 ppmv down to 650 ppmv. End of Laramide and Sevier Orogenies of the Rocky Mountains in North America. Orogeny of the Alps in Europe begins. Hellenic Orogeny begins in Greece and Aegean Sea. (Wikipedia) **More**

Eurypterid: colloquially known as "sea scorpions", these were medium-sized to gigantic, marine to freshwater to amphibious Paleozoic chelicerates, include the largest arthropods ever to live (up to 2.5 meters long). Ordovician to Permian, most common during the late Silurian and early Devonian, although also flourished in Carboniferous swamps. (MAK)

F.

Foraminifer: Amoeboid protozoans traditionally included under the subclass Sarcodina, order Foraminifera, but more recently reclassified as Rhizaria. They have a test (shell) of one to many chambers composed of secreted calcite or agglutinated particles. They have a comprehensive fossil record, and are very important in stratigraphy. (USGS Paleontology glossary)

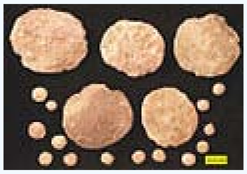


Image (right): Nummulitid foraminiferans from the Eocene near Al Ain, United Arab Emirates. Microspheric and megalospheric specimens shown. Scale in mm. Photo by Mark A. Wilson, Wikipedia

Form taxon: binomial name given to a fossilized plant organ when it is found in isolation, i.e. when the taxonomic affinities of the organ are not known with certainty; for example spore and pollen taxa have their own binomial names, since it is rarely known which fossil genus may have produced them. (UCMP)

Fossil: mineralized or otherwise preserved remains or traces (such as footprints) or impressions of animals, plants, and other organisms. (from Wikipedia glossary); Evidence of past life on earth. Can include the preserved hard and soft parts of plants and animals, tracks and burrows, whole organisms preserved intact in amber or tar, and fossilized dung. *Any* evidence of life constitutes a fossil. (GeoMan)

Fossil record: the history of life on Earth through geological time, as preserved through fossil remains in sedimentary rock (sometimes referred to poetically in older books as the record of the rocks). Also the fossil history of any particular group.

Fossilization: All the processes that involve the burial of a plant or animal in sediment and the eventual preservation of all, part, or a trace of it. (USGS Paleontology glossary)

G.

Gondwana: The southern land mass derived from the supercontinent of Pangea, which continued until its break-up during the Cretaceous and early Tertiary. It comprised of Antarctica, Africa, South America, Australia and India. The term is also used to describe these same continents when connected as a supercontinent in the Paleozoic, prior to Pangea. Gondwana means "Land of the Gonds" (a tribe from the Indian subcontinent). Note, the popular term Gondwana*land* is therefore redundant. **More**

Graptolite: "painted stone", mostly planktonic, Paleozoic, colonial hemichordates with a chitinous skeleton (periderm), commonly preserved as carbon films in black shales, common during the Ordovician, Silurian, and early Devonian, important as index fossils 240 genera are known. (MAK, University of Arizona Geosciences 308 Paleontology glossary)

Gymnosperm: "naked seeds", after the unenclosed condition of their seeds (called ovules in their unfertilized state). Their naked condition stands in contrast to the seeds or ovules of flowering plants (angiosperms) which are enclosed during pollination. Includes conifers, cycads, Ginkgo, Gnetales, and extinct groups such as "seed ferns". (Wikipedia)

H.

Hadean: First of the four eons of the geological timescale, the earliest subdivision of the Precambrian, spanning the time between the formation of the Earth, about 4.5 billion years ago, and the start of the Archean era, 3.8 billion years ago. This interval predates the period of true geologic time since no rocks of this age are known on Earth, with the exception of a few meteorites. Except possibly for the very end of the Hadean, conditions were too harsh to support life (hence the name, after the underworld of Greek mythology). (USGS Paleontology glossary, MAK) **More**

Holocene: An epoch of the Quaternary period, spanning the time from the end of the Pleistocene (10,000 years ago) to the present. The most recent period of geologic history, which extends from 10,000 years ago to the present. It is named after the Greek words ὅλος (*holos,* entire) and καινός (*kainos*, new). See also Anthropocene. (MAK, USGS Paleontology glossary, Perseus Digital Library) The last glacial period ends; rise of human civilization. Quaternary Ice Age recedes, and the current interglacial begins. Younger Dryas cold spell occurs, Sahara forms from savannah, and agriculture begins, allowing humans to build cities. Paleolithic/Neolithic (Stone Age) cultures begin around 10000 BC, giving way to Copper Age (3500 BC) and Bronze Age (2500 BC). Cultures continue to grow in complexity and technical advancement through the Iron Age (1200 BC), giving rise to many pre-historic cultures throughout the world, eventually leading into Classical Antiquity, such as the Roman Empire and even to the Middle Ages and present day. Little Ice Age (stadial) causes brief cooling in Northern Hemisphere from 1400 to 1850. Also refer to the List of archaeological periods for clarification on early cultures and ages. Mount Tambora erupts in 1815, causing the Year Without a Summer (1816) in Europe and North America from a volcanic winter. Following the Industrial Revolution, Atmospheric CO2 levels rise from around 280 parts per million volume (ppmv) to the current level of 390 ppmv, due to anthropogenic emissions, very likely causing global warming and climate change. (Wikipedia) **More**

I.

Ichnology: branch of paleontology that deals with traces of organismal behavior, such as burrows and footprints. Thus, burrows, trackways, trails and borings are all examples of biogenic structures, but not casts or molds of dead shells or other bodily remains. To keep body and trace fossils nomenclatorially separate, *ichnospecies* are erected for trace fossils. Ichnotaxa are classified somewhat differently in zoological nomenclature than taxa based on body fossils. Examples include:

Dinosaur footprints

- Late Cambrian trace fossils from intertidal settings include *Protichnites* and *Climactichnites*, amongst others
- Mesozoic dinosaur footprints including ichnogenera such as *Grallator*, *Atreipus* and *Anomoepus*
- Triassic to Recent termite mounds, which can encompass several square kilometers of sediment

(from Wikipedia)

Image (right) Dinosaur footprints, preserved at Dinosaur Ridge, Morrison Formation (late Jurassic), Colorado

Ichnotaxon: defined by the International Code of Zoological Nomenclature as "a taxon based on the fossilized work of an organism". Ichnotaxa are names used to identify and distinguish morphologically distinctive ichnofossils, more commonly known as trace fossils. They are assigned genus and species ranks by ichnologists, much like organisms in Linnaean taxonomy. These are known as *ichnogenera* and *ichnospecies*, respectively. Ichnotaxa include trace fossils such as burrows, borings and etchings, tracks and trackways, coprolites, gastroliths, regurgitaliths, nests, leaf mines, bite and gnaw structures, secretions modified by organismal activity, such as cocoons, pupal cases, spider webs, embedment structures and plant galls. (from Wikipedia)

Index fossil: A fossil that identifies and dates the strata in which it is typically found. To be most useful, an index fossil must have broad, even worldwide distribution and must be restricted to a narrow stratigraphic range. (S.M. Richardson)

J.

Jurassic: The middle period of the Mesozoic era, spanning the time between 213 and 145 million years ago. It is named after the Jura Mountains between France and Switzerland, where rocks of this age were first studied. (USGS Paleontology glossary). Gymnosperms (especially conifers, Bennettitales and cycads) and ferns common. Many types of dinosaurs, such as sauropods, carnosaurs, and stegosaurs. Mammals common but small. First birds (*Archaeopteryx*) and lizards. Ichthyosaurs and plesiosaurs diverse. Bivalves, ammonites and belemnites abundant. Sea urchins very common, along with crinoids, starfish, sponges, and terebratulid and rhynchonellid brachiopod. Breakup of Pangaea into Gondwana and Laurasia. Nevadan orogeny in North America. Rantigata and Cimmerian Orogenies taper off. Atmospheric CO2 levels 4–5 times the present day levels (1200–1500 ppmv, compared to today's 385 ppmv). (Wikipedia) **More**

K.

Konservat-Lagerstätten: see Lagerstätten.

L.

Lagerstätten (more correctly called **Konservat-Lagerstätten**): a term coined by German paleontologists for exceptionally preserved fossil assemblages. Most contain direct evidence of soft part morphology. Examples include Mazon Creek (concretions, Carboniferous, Illinois), Solnhofen Limestone (extremely fine grained (lithographic) limestone, Jurassic, Germany), La Brea (tar pits, Pleistocene, California), Burgess Shale (carbonization, Cambrian, Canada). (University of Arizona Geosciences 308 Paleontology glossary)

Limestone: the most abundant of the non-clastic sedimentary rocks that is produced from the mineral calcite (calcium carbonate) and sediment. The main source of limestone is the limy ooze formed in the ocean. The calcium carbonate can be precipitated from ocean water or it can be formed from sea creatures that secrete lime such as algae and coral. (Fossil Mall)

Living fossil: informal term for any living species (or genus or clade) of organism which appears to be the same as a species otherwise only known from fossils and which has no close living relatives. These species have all survived major extinction events, and generally retain low taxonomic diversities. For example, the inarticulate brachiopod *Lingula* has not noticeably changed since the Ordovician period. One famous example is the coelacanth, which was thought to have become extinct with the dinosaurs at the end of the late Cretaceous, until a live specimen was caught in 1938 (Jewett1998). A species which successfully radiates (forming many new species after a possible genetic bottleneck) has become too successful to be considered a "living fossil". Lazarus taxon would seem to be a more or less synonymous term. (MAK, Wikipedia)

M.

Macrofossil: A fossil that is large enough to be studied without a microscope. (USGS Paleontology glossary)

Mesozoic: the second of the three Phanerozoic eras of the geological timescale, between the Paleozoic and the Cenozoic, and lasting from 251 to 65.5 million ago. More or less equivalent (especially in the popular imagination) to the "age of reptiles". Dinosaurs, pterosaurs, marine reptiles, ammonites, gymnosperms, and primitive mammals and birds all flourished. The word Mesozoic is from Greek and means "middle life." Includes three periods: the Triassic, Jurassic, and Cretaceous. (MAK, USGS Paleontology glossary) **More**

Microfossil: A fossil so small that it must be studied with a microscope. (USGS Paleontology glossary)

Micron: Micrometer, a unit of measure, used for example when describing protists and microfossils. There are one million micrometers in one meter. (MAK, USGS Paleontology glossary)

Miocene: A epoch of the late Tertiary period, spanning the time between 23.8 and 5.3 million years ago. It is named after the Greek words μεἰων (*meion*, less) and καινός (*kainos*, new). (USGS Paleontology glossary, Perseus Digital Library) Moderate Icehouse climate, punctuated by ice ages; Orogeny in northern hemisphere. Modern mammal and bird families become recognizable. Horses and mastodons diverse. Grasses become ubiquitous. First apes appear (for reference see the article: "Sahelanthropus tchadensis"). Kaikoura Orogeny forms Southern Alps in New Zealand, continues today. Orogeny of the Alps in Europe slows, but continues to this day. Carpathian orogeny forms Carpathian Mountains in Central and Eastern Europe. Hellenic orogeny in Greece and Aegean Sea slows, but continues to this day. Middle Miocene Disruption occurs. Widespread forests slowly draw in massive amounts of CO2, gradually lowering the level of atmospheric CO2 from 650 ppmv down to around 100 ppmv. (Wikipedia) **More**

Mississippian: A subperiod of the Paleozoic era, spanning the time between 360 and 325 million years ago. It is named after the Mississippi River valley, which contains good exposures of rocks of this age. The term is used by American geologists as a period ranking of geological time, but not European ones, who refer instead to the "Lower Carboniferous". The Mississippian has since been standardised as subperiod of the Carboniferous (MAK, USGS Paleontology glossary) Large primitive trees, first land vertebrates, and amphibious sea-scorpions live amid coal-forming coastal swamps. Lobe-finned rhizodonts are dominant big fresh-water predators. In the oceans, early sharks are common and quite diverse; echinoderms (especially crinoids and blastoids) abundant. Corals, bryozoa, goniatites and brachiopod (Productida, Spiriferida, etc.) very common, but trilobites and nautiloids decline. Glaciation in East Gondwana. Tuhua Orogeny in New Zealand tapers off. Variscan orogeny occurs towards middle and late Mississippian Periods. (Wikipedia) **More**

Mold: fossilised impression of organism preserved in rock. *External molds* are impressions of the outside of a structure, while *internal molds* (also known as *steinkerns*) are impressions of the inside of structure. *Composite molds* are formed when the original material dissolves, and the external and internal mold are pressed together. Both external and internal features are preserved on a composite mold. (University of Arizona Geosciences 308 Paleontology glossary)

Mollusca: also *mollusk* (American spelling) major phylum of invertebrate animals distinguished by a shell-secreting mantle and radula teeth. Includes chitons, bivalves, gastropods, cephalopods, and various minor groups. An important component in marine ecosystems, also many freshwater and terrestrial forms. Cambrian to recent. **More**

Morphological species concept, population-based concept, defines a species by its body shape, size, and other structural features. Unlike the Biological Species Concept in that it can be applied to the systematic study of fossil organisms, and hence adopted by paleontologists. Compare with Paleontological species concept.

Mosasaur: giant marine reptiles, probably related to the ancestors of snakes. They dominated the seas during the late Cretaceous. (MAK)

N.

Nautiloid: the pearly nautilus and its ancestors. Include a large assemblage of mostly Paleozoic cephalopods with straight, curved, loosely or tightly coiled shells and simple sutures. Common and most diverse from the Ordovician to the Devonian, after which time they were increasingly supplanted by ammonoids. Nevertheless, nautiloids much like the modern Nautilus continued virtually unscathed even when the various groups (goniatites, ceratites, ammonites) of their advanced ammonoid cousins died out, perhaps because they inhabited deeper water and were not so dependent on the plankton-based food chain. The largest Paleozoic nautiloids had straight shells several meters or more in length, but most species were of more modest proportions. MAK

Neogene: A subperiod of the Tertiary period of the Cenozoic era, Includes the Miocene and Pliocene epochs. A move to have the Paleogene and Neogene replace the Tertiary was not successful, and they now seem to have become subperiods. (MAK) **More**

Neontology: An infrequently used word, and used only then by paleontologists to refer to those aspects of biology that, in contrast to paleontology, deal with now living or extant organisms. From *neos* = new, *ontos* = being, *logos* = study of). In another sense, more or less equivalent to biology. Neontologists have access to data that is difficult or impossible for paleontologists to access for extinct species, such as anatomy and soft-part morphology, physiology, molecular sequences, embryology, histology, and more, and therefore make essential contributions to systematic paleontology and phylogeny. In general, and understandably because of the far greater amount and diversity of data that neontology provides, cladistics tends to be more orientated to neontology (hence taxonomy orientated to crown clades) and evolutionary systematics to paleontology. However the tendency in the total evidence and supermatrix approach now is to integrate and consider both paleontological and neontological data. (MAK)

O.

Oligocene: An epoch of the early Tertiary period, spanning the time between 33.7 and 23.8 million years ago. It is named after the Greek words ὀλίγος (*oligos*, little, few) and καινός (*kainos*, new). (USGS Paleontology glossary, Perseus Digital Library) Warm but cooling climate, moving towards Icehouse; Rapid evolution and diversification of fauna, especially mammals. Major evolution and dispersal of modern types of flowering plants. (Wikipedia) **More**

Ordovician: The second earliest period of the Paleozoic era, spanning the time between 505 and 440 million years ago. It is named after a Celtic tribe called the Ordovices. (USGS Paleontology glossary) Invertebrates diversify into many new types (e.g., long straight-shelled cephalopods). Early corals, articulate brachiopod (Orthida, Strophomenida, etc.), bivalves, nautiloids, trilobites, ostracods, bryozoa, many types of echinoderms (crinoids, cystoids, starfish, etc.), branched graptolites, and other taxa all common. Conodonts (early planktonic vertebrates) appear. First green plants and fungi on land. Ice age at end of period. (Wikipedia) **More**

Osteology: literally, the "science of bones"; the study of the various parts of the vertebrate skull and skeleton. Regardless of how much neontology and soft-part morphology, paleobiological reconstruction (especially popularised by the dinosaur renaissance of Ostrom, Bakker, and Paul), developmental biology, and molecular phylogeny increase in importance in studying the evolution of vertebrates, along with trace fossils and footprints, the study of the most durable and commonly preserved parts of the organism, the teeth (in small delicate animals such as Mesozoic mammals) and bones will always remain an essential element in any analysis of vertebrate phylogeny and paleontology. Classic vertebrate paleontology textbooks and papers such as the works of Zittel, Romer and Carroll are full of dense descriptions on the skeletal and cranial minutiae of various extant and extinct taxa, and even more so this is the case with technical journals. Thus material, essential for listing traits for cladistic analysis, makes up a large part of the "Vertebrates" section of Palaeos.com (originally, "Vertebrate Notes"). (MAK)

Ostracod: Class Ostracoda - small crustaceans with dorsally located bivalved carapace which is commonly heavily calcified, common as microfossils and very useful for biostratigraphy. (University of Arizona Geosciences 308 Paleontology glossary, MAK)

Ostracoderm: name given to a diverse assemblage of highly distinctive armoured jawless fish from the Ordovician, Silurian and Devonian periods. The term is now rarely used in scientific literature, as they are now known to consist of a number of different lineages, and are a paraphyletic or even a polyphyletic grouping. Nevertheless it is a useful label for referring to these bizarre creatures from the early days of vertebrate evolution. (MAK)

P.

Paleoanthropology: the study of fossil hominids, especially human ancestors.

Paleoart: informal term first coined by Mark Hallett for art that depicts subjects related to paleontology. These may be representations of fossil remains or depictions of the living creatures and their ecosystems (Wikipedia). Paleoartists therefore are any of those wonderfully talented people who produce those beautiful reconstructions of prehistoric organisms that help to brighten up the web (and Palaeos too). (MAK)

Paleobiogeography: The branch of paleontology that deals with the geographic distribution of plants and animals in past geologic time, especially with regard to ecology, climate, and evolution.

Paleobiology: The study and understanding of fossil organisms from a biological perspective. Whereas paleontology looks at the fossil bone, shell, or leaf for its own sake, paleobiology seeks to understand the organism that produced those remains.

Paleoceanography: The study of oceans in the geologic past, including its physical, chemical, biologic, and geologic aspects. (USGS Paleontology glossary)

Paleocene: Earliest epoch of the Tertiary period, spanning the time between 65 and 55.5 million years ago. It is named after the Greek words παλαιός (*palaios,* old) and καινός (*kainos*, new). (USGS Paleontology glossary, Perseus Digital Library) Climate tropical. Modern plants appear; mammals diversify into a number of primitive lineages following the extinction of the dinosaurs. First large mammals (up to bear or small hippo size). Alpine orogeny in Europe and Asia begins. Indian Subcontinent collides with Asia 55 Ma, Himalayan Orogeny starts between 52 and 48 Ma. (Wikipedia) **More**

Paleogene: A subperiod of the Tertiary period of the Cenozoic era, Includes the Paleocene, Eocene, and Oligocene epochs. A move to have the Paleogene and Neogene replace the Tertiary was not successful, and they now seem to have become subperiods. (MAK) **More**

Paleomagnetism: Refers to the study of the magnetic properties of rocks and minerals. This demonstrates to us that both the strength and direction of Earths magnetic field is not constant. Each rock and mineral tells its own story at a particular moment in time. (A. Atwal, Wikiversity)

Paleoneurology: branch of neurology concerned with the study of the evolution of the brain by using fossil evidence, such as brain endocasts of extinct vertebrates. This little known field has been pioneered by American biopsychologist Harry J. Jerison. more/link

Paleontological species concept: Species concept which focuses on morphologically discrete species known only from the fossil record, the Morphological species concept would be similar or synonymous.

Paleontology. The scientific study of ancient life (*palaeos* = ancient, *ontos* = being, *logos* = speech, reason, hence study of), through examination of fossil remains and the fossil record. Includes subdivisions such as Vertebrate, Invertebrate, and Micro- paleontology. Contrast with neontology. Paleontologists have access to many extinct forms of life, including many transitional and ancestral forms, and information regarding their stratigraphic or temporal position in the geological timescale, paleobiology, paleoecology, paleoclimatology, etc extend this to environmental, geographic, and other areas to provide a comprehensive history of the Earth. Because of the fragmentary or partial nature of many fossils, reconstructing extinct life and extinct environments is often more like forensic science than biology or ecology. (MAK)

Paleosol: A fossil soil or soil horizon. (MAK)

Paleozoic: the first and longest of the three Phanerozoic eras of the geological timescale, , lasting from 542 to 251 million years ago. Characterised by the emergence and dominance of multicellular life in the Cambrian explosion, and the succession of invertebrates, fish, and early land plants, amphibians and reptiles. Includes six periods: the Cambrian, Ordovician, Silurian, Devonian, Carboniferous, and Permian. The word Paleozoic is from Greek and means "ancient animal life." **More**

Palynology: The study of pollen, living and fossil. (Amateur Geologist Glossary)

Pangea, **Pangaea**: meaning "all the earth", is a supercontinent that existed during the Permian and Triassic, and included most of the Earth's continental crust. During this time, terrestrial faunas were often quite uniform, as there were few geographic barriers, although there were distinct vegetation zones (biomes). Beginning in the Jurassic, Pangea divided into Laurasia in the north and Gondwana in the south. **More**

Pennsylvanian: A subperiod of the Carboniferous period of the Paleozoic era, spanning the time between 325 and 286 million years ago. It is named after the state of Pennsylvania where rocks of this age are widespread. (USGS Paleontology glossary) Winged insects radiate suddenly; some (esp. Protodonata and Palaeodictyoptera) are quite large. Amphibians common and diverse. First reptiles and coal forests (scale trees, ferns, club trees, giant horsetails, *Cordaites*, etc.). Highest-ever atmospheric oxygen levels. Goniatites, brachiopod, bryozoa, bivalves, and corals plentiful in the seas and oceans. Testate forams proliferate. Uralian orogeny in Europe and Asia. (Wikipedia) **More**

Period: a unit or division of geological time, usually lasting several tens of millions of years, and hence intermediate in duration between era and epoch. By convention, each period is divided into two or more epochs. In terms of geological strata, rather than time, the word "system" is traditionally used, although this now seems to be falling out of favour, and only found in older books. (MAK)

Permian: The final period of the Paleozoic era, spanning the time between 286 and 248 million years ago. It is named after the province of Perm, Russia, where rocks of this age were first studied. (USGS Paleontology glossary) Landmasses unite into supercontinent Pangaea, creating the Appalachians. End of Permo-Carboniferous glaciation. Synapsid reptiles (pelycosaurs and therapsids) become plentiful, while parareptiles and temnospondyl amphibians remain common. In the mid-Permian, coal-age flora are replaced by cone-bearing gymnosperms (the first true seed plants) and by the first true mosses. Beetles and flies evolve. Marine life flourishes in warm shallow reefs; productid and spiriferid brachiopod, bivalves, forams, and ammonoids all abundant. Permian-Triassic extinction event occurs 251 Ma: 95% of life on Earth becomes extinct, including all trilobites, graptoloids, and blastoids. Ouachita and Innuitian orogenies in North America. Uralian orogeny in Europe/Asia tapers off. Altaid orogeny in Asia. Hunter-Bowen Orogeny on Australian Continent begins (c. 260–225 Ma), forming the MacDonnell Ranges. (Wikipedia) **More**

Permo-Carboniferous: informal period of time encompassing the Carboniferous and Permian periods, or alternatively the latter parts of the Carboniferous and early part of the Permian period. Important in considering late Paleozoic geology, global climate change (glaciation), and plant, invertebrate, and tetrapod ecology and evolution. (MAK)

Phanerozoic: the most recent, and current, of the four eons of the geological timescale, the time of diverse and complex life, complex ecosystems, and an oxygen-rich atmosphere. Divided into Paleozoic, Mesozoic, and Cenozoic. The Phanerozoic begins with the start of the Cambrian period, and continues to today. **More**

Placoderms: A peculiar group of primitive armored jawed fish, superficially similar to Ostracoderms, and found almost exclusively in rocks from the Devonian Period. (USGS Paleontology glossary, MAK)

Pleistocene: An epoch of the Quaternary period, spanning the time between 1.8 million years ago and the beginning of the Holocene at 8,000 years ago. It is named after the Greek words "pleistos" (most) and "ceno" (new). The period of the last ice age, characterised by many large mammals, as well as modern plants and invertebrates. Modern humans evolved during this time. (USGS Paleontology glossary, MAK) Flourishing and then extinction of many large mammals (Pleistocene megafauna). Evolution of anatomically modern humans. Quaternary Ice Age continues with glaciations and interstadials (and the accompanying fluctuations from 100 to 300 ppmv in atmospheric CO2 levels[20]), further intensification of Icehouse Earth conditions, roughly 1.6 Ma. Last glacial maximum (30000 years ago), last glacial period (18000–15000 years ago). Dawn of human stone-age cultures, with increasing technical complexity relative to previous ice age cultures, such as engravings and clay statues (e.g. Venus of Lespugue), particularly in the Mediterranean and Europe. Lake Toba supervolcano erupts 75000 years before present, causing a volcanic winter that pushes humanity to the brink of extinction. Pleistocene ends with Oldest Dryas, Older Dryas/Allerød and Younger Dryas climate events, with Younger Dryas forming the boundary with the Holocene. (Wikipedia) **More**

Pliocene: Final epoch of the Tertiary period, spanning the time between 5.3 and 1.8 million years ago. It is named after the Greek words πλεῖον (*pleion*, more) and καινός (*kainos*, new). The Miocene and Pliocene represented the time of greatest abundance and diversity of the mammals. Characterised by a cooling climate and ice sheets in Antarctica. (USGS Paleontology glossary, MAK, Perseus Digital Library) Intensification of present Icehouse conditions, present (Quaternary) ice age begins roughly 2.58 Ma; cool and dry climate.

Australopithecines, many of the existing genera of mammals, and recent mollusks appear. *Homo habilis* appears. (Wikipedia) **More**

Precambrian: older term, now rarely used, to refer to the expanse of geological time prior to the Cambrian period. Because the Cambrian was when animal fossils first appear, it, and the following periods to the present, were called the Phanerozoic, and was contrasted with earlier ages and their corresponding rock strata, often highly metamorphosed, and devoid of fossils (or characterised only by stromatolites). The Precambrian was also known as the Cryptozoic (hidden life), and originally referred to as "Primary" strata. Current understanding and research has revealed the Precambrian to be a time of diverse geological, climatological, and microbiological activity and evolution. Current usage replaces "Precambrian eon" with three distinct eons, Hadean, Archean, and Proterozoic, with complex life forms only appearing at the end of the latter, during the Ediacaran period. (MAK) **More**

Proterozoic: the most recent, and current, of the four eons of the geological timescale, during which occurred the oxygen crisis, snowball earth, the rise of Eukarya, and the origin of multicellular life. It followed the Archean, and lasted from around 2.5 to half a billion years. **More**

Pterosaur: "winged lizard" or "winged finger" (pterodactyl); Order of Mesozoic flying archosaurian reptiles characterised by a greatly elongated fourth digit that supported a membranous wing (in contrast to bats in which all five digits are elongated; artwork and movies that give pterosaurs bat-like wings are inaccurate). They include the largest animals ever to fly, although others were of more modest proportions. Pterosaurs were not dinosaurs, but were closely related, both are included under the clade Ornithodira. (MAK, Fossil Mall glossary)

Q.

Quaternary: The second period of the Cenozoic era (following the Tertiary), spanning the time between 1.8 million years ago and the present (in terms of duration, this is the shortest period, equivalent to a standard age). It contains two epochs: the Pleistocene and the Holocene. It is named after the Latin word "quatern" (four at a time), and refers to the earliest (19th century) stratigraphic systems (Primary, Secondary, Tertiary, and Quaternary). Although there was a movement to scrap both Tertiary and Quaternary in favour of more modern terms such as Paleogene and Neogene, this was not successful, and in current geological timescales the Quaternary has been restored or retained. The Quaternary includes both the Ice Age with its distinctive megafauna, and the modern, human-dominated period of Earth history. (USGS Paleontology glossary, MAK)

R.

Rudist: A type of extinct bivalve mollusk from the Jurassic and especially the Cretaceous that had two different sized and shaped shells; they usually were attached to the substrate and were either solitary or in reeflike masses. (USGS Paleontology glossary)

Rugose: "wrinkled". Order Rugosa: Paleozoic group of mostly solitary, but some colonial, stony corals; 800 genera known. Common as fossils. (adapted from University of Arizona Geosciences 308 Paleontology glossary)

Reworked: a fossil that was eroded out of its original strata and then redeposited in more recent strata, giving the impression that the organism lived at a later date than it did. e.g. some isolated dinosaur fossils have been found in Paleocene strata, leading some to argue that they survived the end Cretaceous extinction. (MAK)

S.

Sauropod, sauropodomorph: "lizard footed", a misleading name for these giant creatures with their chubby elephant-like feet. One of the three main clades of dinosaurs, the other two being theropods and Ornithischia. Early sauropodomorphs, called *prosauropods*, were small to medium sized animals, but they quickly grew to become *sauropods* proper, the largest animals to walk the Earth. Sauropods are characterised by very small heads (relative to the overall body), long to very long necks and tails, solid pillar-like legs, and massive dorsal vertebrae. At one time they were believed to be sluggish semi-aquatic wallowers in swamps, unable to walk on land. It is now known that they were active and fully terrestrial animals, much like elephants. Adults were so large they were immune to predation even from the biggest theropods. (MAK) **More**

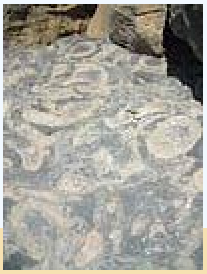
Scanning Electron Microscope (SEM): A microscope in which a finely focused beam of electrons is scanned across a specimen, and the electron intensity variations are used to construct an image of the specimen. This type of microscope is ideal for magnifications from 200 to 35,000. (USGS Paleontology glossary)

Signor-Lipps effect: Principle that states that, since the fossil record of organisms is never complete, neither the first nor the last organism in a given taxon will be recorded as a fossil. (Signor&Lipps82). The Signor-Lipps effect can reduce the apparent severity of a catastrophic extinction by making it appear to be extended in time. It is named after its authors, Philip W. Signor and Jere H. Lipps . (Wikipedia)

Silurian: A period of the Paleozoic, spanning the time between 440 and 410 million years ago. It is named after a Celtic tribe called the Silures. (USGS Paleontology glossary) First Vascular plants (the rhyniophytes and their relatives), first millipedes and arthropleurids on land. First jawed fishes, as well as many armoured jawless fish, populate the seas. Sea-scorpions reach large size. Tabulate and rugose corals, brachiopod (Pentamerida, Rhynchonellida, etc.), and crinoids all abundant. Trilobites and mollusks diverse; graptolites not as varied. Beginning of Caledonian Orogeny for hills in England, Ireland, Wales, Scotland, and the Scandinavian Mountains. Also continued into Devonian period as the Acadian Orogeny, above. Taconic Orogeny tapers off. Lachlan Orogeny on Australian Continent tapers off. (Wikipedia) **More**

Suture: the line of partition between gas-filled chambers in shelled cephalopods. Sutures can only be seen when the outside of the shell has been removed, and suture pattern is used to characterize many ammonoid groups. Nautiloids have simple sutures, ammonites more complex ones. (MAK, University of Arizona Geosciences 308 Paleontology glossary)

Stratigraphy: Branch of geology concerned with the formation, composition, ordering in time, and arrangement in space of sedimentary rocks. (USGS Paleontology glossary) **More**



Stromatolite: algae mats, formed in shallow water by microorganisms, especially cyanobacteria accreting grains in layers. Rare now, but common during the Proterozoic. The oldest stromatolites are known from the Archean, they are among the oldest records of life on Earth. Image (right) Wikipedia; (MAK)

Subperiod: optional unit of geological time intermediate between period and epoch. (MAK)

T.

Tabulate: Order Tabulata. Paleozoic group of exclusively colonial organisms traditionally classified as stony corals, although other interpretations have been suggested (e.g. sponges). Common as fossils, 280 genera known. (adapted from University of Arizona Geosciences 308 Paleontology glossary)

Tethys: during the time of Pangea (Permian and Triassic) this was the sea that separated the northern half (Laurasia) of the supercontinent from the southern (Gondwana). If Pangea can be imagined in the shape of a giant "pac-man", then the Tethys is the "mouth". During the Triassic especially, the borders of the Tethys were populated by unique animals, such as the walrus and turtle like placodonts. (MAK) **More**

Tertiary: The first period of the Cenozoic era (after the Mesozoic era and before the Quaternary period), spanning the time between 65 and 1.8 million years ago. This was the Age of Mammals proper, before the rise of man. It is divided into two subperiods, Paleogene and Neogene, and five epochs, Paleocene, Eocene, Oligocene, Miocene, and Pliocene. (USGS Paleontology glossary)

Trace fossil: fossil not of an organism itself (e.g. shell, bone, mold, carbonised impression) but of the traces and impressions it left behind while alive (footprints, burrows, resting traces, etc. The study of trace fossils is called Ichnology. (MAK)

Treatise on Invertebrate Paleontology: massive multi-authored multi-authored work-in-progress (beginning 1953 and still ongoing), with contributions by more than 300 paleontologists, and covering every phylum, class, order, family, and genus of fossil and extant invertebrates. Published by the Geological Society of America and the University of Kansas Press. Raymond C. Moore, the project's founder and first editor, originally envisioned this Treatise in invertebrate paleontology as comprising just three large volumes, and totaling only three thousand pages. It has already run to some 50 volumes and tens of thousands of pages; some groups have not yet been covered, while others are being revised. The work is so large and on-going that it spans paradigms; the first volumes followed the standard evolutionary taxonomy of the day, more recent revisions, for example brachiopods, involve phylogenetic systematics. The Russian (at the time Soviet) equivalent, *Osnovy paleontoligii* (Fundamentals of paleontology) (editor in chief Yuri Orlov) was a less ambitious but still huge 15 volume work that was began in 1962. (MAK, Wikipedia)

Triassic: The earliest period of the Mesozoic era, spanning the time between 248 and 213 million years ago. The name Triassic refers to the threefold division of rocks of this age in Germany. (USGS Paleontology glossary) Archosaurs dominant on land as dinosaurs, in the oceans as Ichthyosaurs and nothosaurs, and in the air as pterosaurs. Cynodonts become smaller and more mammal-like, while first mammals and crocodilians appear. *dicta* flora common on land. Many large aquatic temnospondyl amphibians. Ceratitic ammonoids extremely common. Modern corals and teleost fish appear, as do many modern insect clades. Andean Orogeny in South America. Cimmerian Orogeny in Asia. Rangitata Orogeny begins in New Zealand. Hunter-Bowen Orogeny in Northern Australia, Queensland and New South Wales ends, (c. 260–225 Ma). (Wikipedia) **More**

Trilobite: important class of Paleozoic marine arthropods, distinguished by a three-fold division of the exoskeleton. Most were small (a few centimeters) although a few giants reached half a meter or so. Abundant during the Cambrian, where they make up the majority of invertebrate fossils. Also very common during the Ordovician to the Devonian, but declined thereafter. Their exquisite forms and great variety of species make them a favourite o\f most fossil collectors. Morphologically distinct; relationships with other arthropods unclear, hence included in a distinct subphylum, the *Trilobitomorpha*. Cambrian-Permian. (MAK)

Photo (right): *Olenoides erratus* from the Mt. Stephen Trilobite Beds (Middle Cambrian) near Field, British Columbia, Canada. photo by Mark A. Wilson, Wikipedia

U.

V.

Victorian age: in Britain and the British colonies, the period of Queen Victoria's reign (from 1837 to 1901). A long and prosperous period, and also a time of great scientific, technological, and social advancement. Evolutionary thinking and the science of paleontology are among the developments that stem from this period (and also from equivalent contemporary developments in France, Germany, and the United States).

Vertebrates: animals with backbones. Because bones easily fossilise, the vertebrate fossil record is excellent in comparison to that of other more delicate organisms, e.g. insects, or soft-bodied invertebrates. **More**

W.

X.

Y.

Z.

Page Back | Unit Home | Page Top | Page Next: Systematics

---

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

page last modified MAK111005, edited RFVS111204