Bonine I

Phylogenetics (Ch 27)

Thursday 29 January 2009 ECOL 182R UofA K. E. Bonine

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Website: For my lecture material:

http://www.eebweb.arizona.edu/courses/182-spring2009-Bonine/182-BONINE-sp2009.htm

There is a link from Dr. Schaffer's 182R website.

Text: The text is Freeman, Scott. 2008. Biological Science (Third Edition). Pearson Benjamin Cummings, San Francisco, CA. Available at UA Bookstore.

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Posted Lecture Notes

Items in orange will not be available on-line (except for today), but they will be presented during lecture.

Note that slides are numbered for easy reference.

I will strive to post the lecture PDF file on your D2L site before lecture.



How do we organize/categorize biodiversity? Why would we want to?







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Linnaean Taxonomy (1700s)

- Taxonomy is the effort to name and classify organisms.
- In Linnaeus' taxonomic system for classifying organisms, each organism is given a unique two-part scientific name consisting of the genus and the species.

(1) A *genus* is made up of a closely related group of species.

(2) A *species* is made up of individuals that regularly breed together and/or have characteristics that are distinct from those of other species.

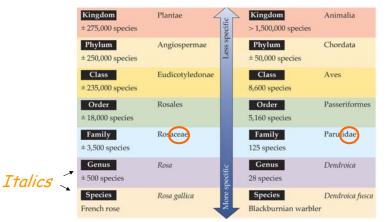
Taxonomic Levels

• Linnaeus' system is hierarchical with nested taxa. The taxonomic levels from least to most specific are as follows:

domain
kingdom
phylum
class
order
family
genus
species

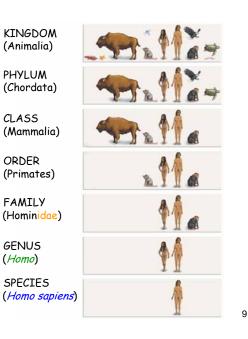
Linnaean hierarchy

- Group of organisms treated as unit is a taxon (plural taxa)
- Hierarchy of taxonomic categories



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Linnaeus' Taxonomic Levels



Theory of common descent

- Any two organisms can trace back to a common ancestor
- We all belong to a big family tree, some more closely related than others
- On the right is a history of individuals: can also draw up the history of species



Phylogeny

- Phylogeny = history of exactly how a group of organisms are descended from their common ancestor
- Phylogenetic tree = representation of that history





1821. From Desmond 1989, p. 43.

http://www.nceas.ucsb.edu/~alroy/lefa/Lamarck.jpg

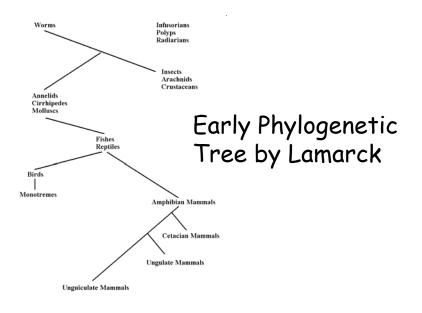


http://www.tulane.edu/~darwin/Herbarium/Herbarium/Koch%20Images/Lamarck2.jpg

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'Cineraria'

Jean Baptiste Pierre Antoine de Monet de Lamarck (1744-1829): Tableau encyclopedique et methodique des trois regnes de la nature... botanique. Paris, 1791-1823



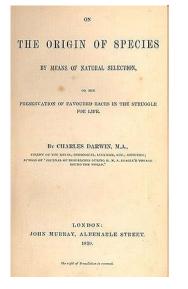
http://bill.srnr.arizona.edu/classes/182/Zool%20Phil%20Tree%20crop-700.gif

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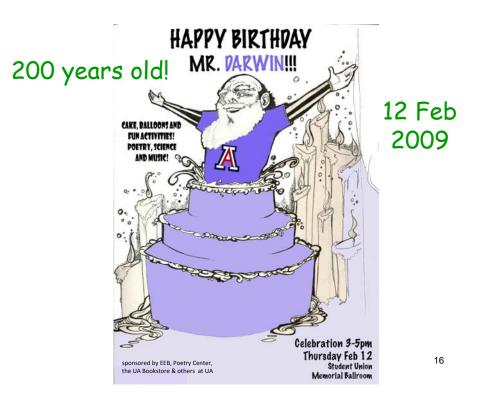
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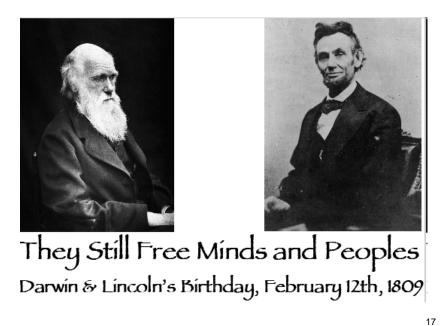
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Tree diagram used to show the divergence of species. It is the only illustration in *The Origin of Species* – Darwin 1859.



Title page of the 1859 edition of *On the Origin of Species*

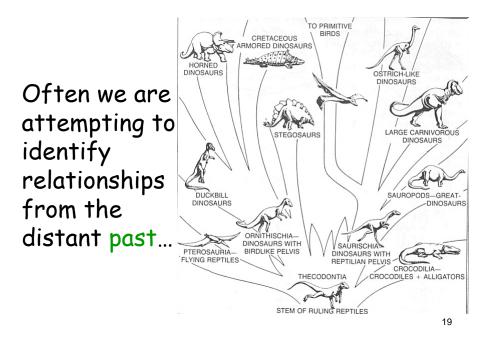




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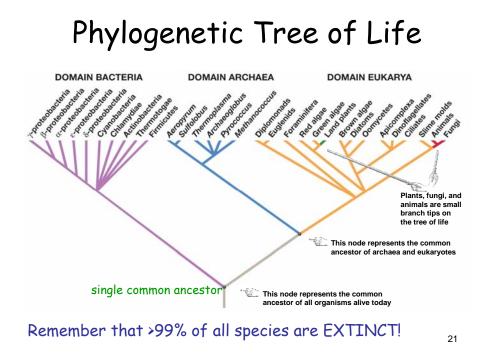
 A phylogenetic tree is a graphical representation of the evolutionary relationships among species.
 Phylogenies can be established by analyzing similarities and differences in traits.





Phylogenetic Trees

- Systematics, the study of organismal diversity with respect to evolutionary (or not) relationships between organisms (patterns of descent).
 - Taxonomy a subdiscipline that relates to classification
- What evolutionary relationships could be useful/helpful to understand?



Old species often become new species...

<u>Darwin's</u> eventual conclusions stemming from his first question about the birds and plants of the **Galapagos** were to feature in one of the most important passages in *Origin of species* (pp. 397-406). The passage ended with one of his key points about evolution by natural selection:

The relations just discussed ... [including] the very close relation of the distinct species which inhabit the islets of the same archipelago, and especially the striking relation of the inhabitants of each whole archipelago or island to those of the nearest mainland, are, I think, utterly inexplicable on the ordinary view of the independent creation of each species, but are explicable on the view of colonisation from the nearest and readiest source, together with the subsequent modification and better adaptation of the colonists to their new homes.

http://darwin-online.org.uk/EditorialIntroductions/Chancellor_Keynes_Galapagos.html

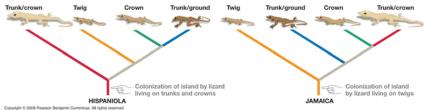


Adaptive Radiation

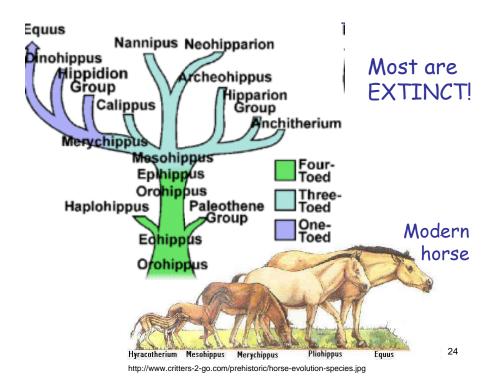
(a) Species of Anolis vary in leg length and tail length. Some species are ground dwelling; others live in distinct regions of shrubs or trees.

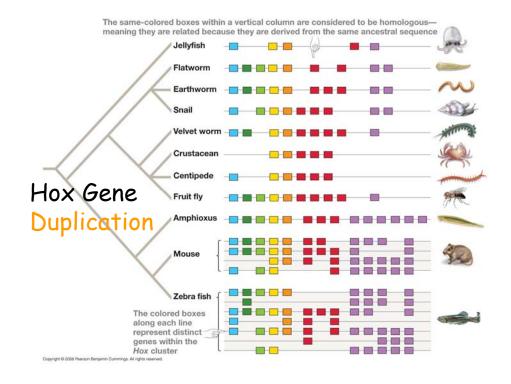


b) The same adaptive radiation of Anolis has occurred on different islands, starting from different types of colonists.



Expand and <u>diversify</u> into areas without competition (Area either 1) new or 2) former residents extinet.)





Living fossils: Gingko

(b)





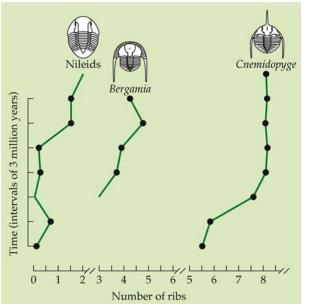
Living fossils: Horseshoe crabs



(b) Limulus polyphemus

~identical for 300 mya

sandy coastlines are harsh environments that changed little, so they didn't need to evolve anything different 27



Gradual change: trilobite rib number

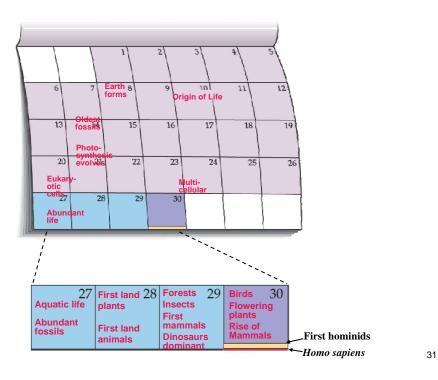
fossils show number of ribs

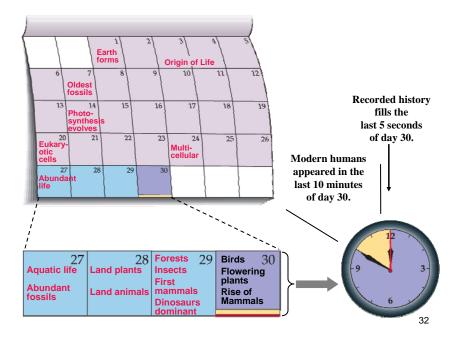
	22.1 Earth's Geological History (Part 2)					
IE	ERA	PERIOD	ONSET	MAJOR EVENTS IN THE HISTORY OF LIFE		
1		Quaternary	1.8 mya ^a	Humans evolve; many large mammals become extinct		
$\left \right $	Cenozoic	Tertiary	65 mya	Diversification of birds, mammals, flowering plants, and insects		
		Cretaceous	144 mya	Dinosaurs continue to diversify; flowering plants and mammals diversify. Mass Extinction at end of period («76% of species disappear)		
11	Mesozoic	Jurassic	206 mya	Diverse dinosaurs; radiation of ray-finned fishes		
		Triassic	248 mya	Early dinosaurs; first mammals; marine invertebrates diversify; first flowering plants; Mass Extinction at end of period (=65% of species disappear)		
	Paleozoic	Permian	290 mya	Reptiles diversify; amphibians decline; Mass Extinction at end of period (=96% of species disappear)		
		Carboniferous	354 mya	Extensive "fern" forests; first reptiles; insects diversify		
		Devonian	417 mya	Fishes diversify; first insects and amphibians. Mass Extinction at end of period (=75% of species disappear)		
		Silurian	443 mya	Jawless fishes diversify; first ray-finned fishes; plants and animals colonize land		
		Ordovician	490 mya	Mass Extinction at end of period (≈75% of species disappear)		
		Cambrian	543 mya	Most animal phyla present; diverse algae		
			600 mya	Ediacaran fauna		
	Precambrian		1.5 bya#	Eukaryotes evolve; several animal phyla appear		
			3.8 bya 4.5 bya	Origin of life; prokaryotes flourish		

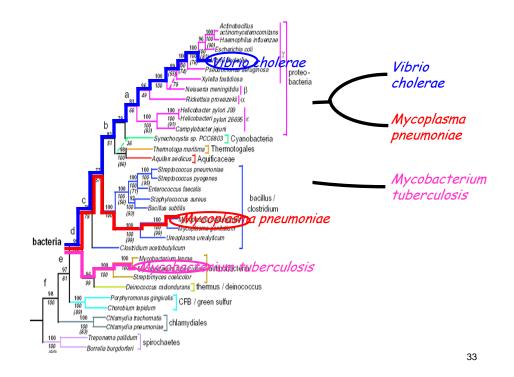
^amya, million years ago; bya, billion years ago.

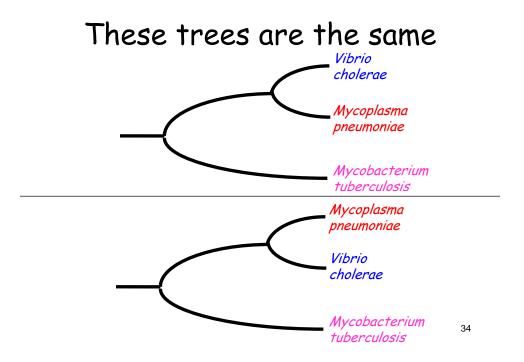
Biological history

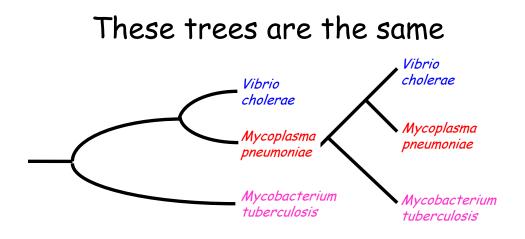
1 day = million y	/ears E	1 arth orms	2	3 Origin of Li	4 life	5
6	7 Oldest fossils	8	9	10	11	12
13	14 Photo- synthesis evolves	15	16	17	18	19
20 Eukaryotic cells evolve		22	23	24 Multi- cellular organisms	25	26
27 Abundant life		29	30			

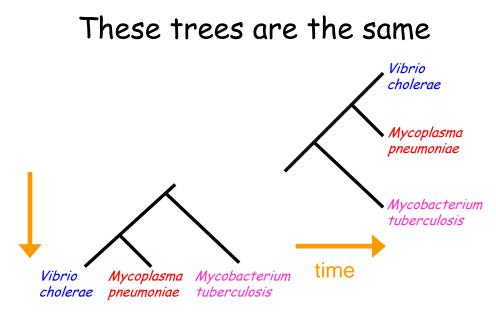


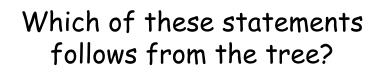


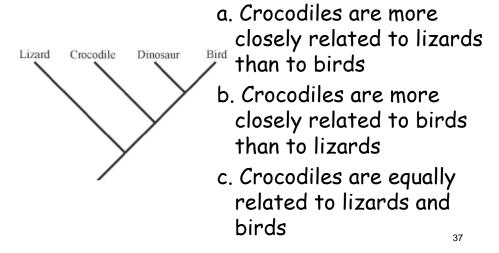


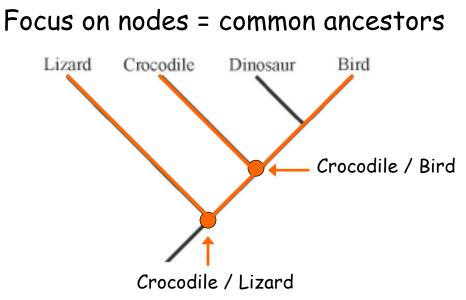




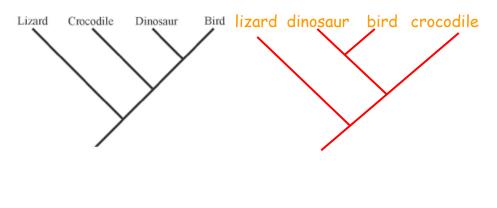


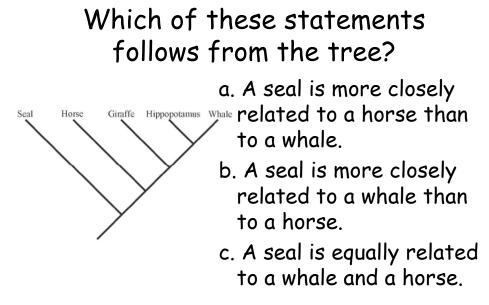






Another method: redraw tree with focus on crocodile





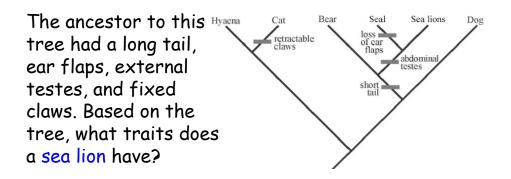
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Ancestral traits

- Traits inherited from ancestor in distant past should be shared by large number of species
- Traits that first appeared in more recent ancestor should be shared by fewer species
- Ancestral trait = shared traits inherited from a common ancestor
- Derived trait = different from ancestral form

Nucleic acids are an ancestral trait

- Nucleic acids (DNA/RNA) as genetic material is ancestral to all life on Earth
- Specific genetic code is ancestral to most



a. long tail, ear flaps, external testes, and fixed claws
b. short tail, no ear flaps, external testes, and fixed claws
c. short tail, no ear flaps, abdominal testes, and fixed claws
d. short tail, ear flaps, abdominal testes, and fixed claws
e. long tail, ear flaps, abdominal testes, and retractable claws

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Ancestral vs derived may depend on scale of taxa

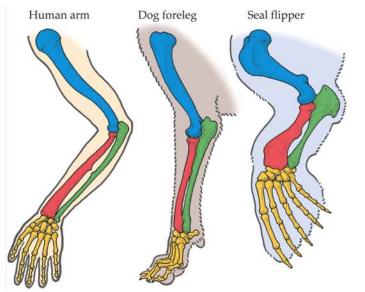
- In rodents: continuously growing incisors are ancestral: all rodents have them
- In mammals they are derived, unique to rodents

Homologous traits

- Features (DNA sequence, behavior, morphology) shared by species descended from common ancestor are called homologous
- e.g., vertebral column is homologous in vertebrates

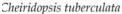
Mammalian limbs are homologous, even with different functions

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Homologous structures derived from leaves





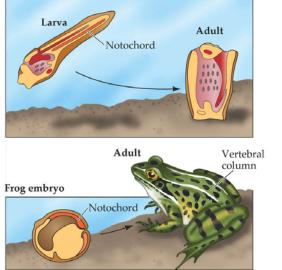
Heliconia sp.



Sarracenia purpurea

Some homologies are hidden by development





Notochord homology seen only in early development, invisible in adult

Both in Phylum Chordata 48

Deducing phylogeny

Look at shared traits

- What is ancestral state?
- How has it been modified?

Two processes make this difficult

- 1. Convergent evolution = similar selective pressures make independently evolved traits look superficially similar
- 2. Evolutionary reversal = character reverts from derived state back to ancestral state

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Bird and bat bones are homologous, but not wings (convergent evolution)



Homoplastic traits

Convergent evolution and evolutionary reversal generate homoplasies: traits that are similar for some reason other than inheritance from a common ancestor

Bird and bat wings are homoplastic

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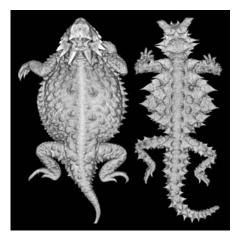


http://digimorph.org/specimens/Phrynosoma_asio/

Moloch horridus, Thorny Devil, AUSTRALIA



Spiny head: Homoplasy or Homology?



Phrynosoma cornutum (left) vs. Moloch horridus (right)



P. cornutum (top) vs. *M. horridus* (bottom); semi-transparent flesh in blue, bone in red

All of the following can result in homoplasy except

- a. similar selection pressures.
- b. reverse evolution.
- c. parallel evolution.
- d. descent from a recent common ancestor.
- e. convergent evolution.

Creating a phylogeny

- 1. Choose the characters and identify the possible forms (traits) of the characters
- 2. Determine ancestral and derived traits
- 3. Distinguish homologous from homoplastic traits

Traditional character choice

- Most often morphology
 - describes size and shape of body parts
 - can be seen directly in fossil record
- Also physiological, behavioral, molecular and structural traits as available
- The more characters measured, the more the inferred phylogenies should converge on each other and on the real evolutionary pattern

Simple phylogeny example

- Choose 8 vertebrate species and hypothesize their phylogeny
- Traits either present (+) or absent (-)
- Assume that each derived trait evolved only once and that no derived traits were lost

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TAXON	JAWS	LUNGS	CLAWS OR NAILS	GIZZARD
	JANJ	LONGS	ONNALS	GIZZAND
Lamprey	-	-	-	-
Perch	+	-	-	-
Salamander	+	+	-	-
Lizard	+	+	+	-
Crocodile	+	+	+	+
Pigeon	+	+	+	+
Mouse	+	+	+	-
Chimpanzee	+	+	+	-
			MAMMARY	KERATINOUS
TAXON	FEATHERS	FUR	MAMMARY GLANDS	KERATINOUS SCALES
	FEATHERS	FUR _		
TAXON Lamprey Perch	FEATHERS 	FUR 		
Lamprey	FEATHERS 	FUR 		
Lamprey Perch	FEATHERS 	FUR 		
Lamprey Perch Salamander	FEATHERS 	FUR 		
Lamprey Perch Salamander Lizard	FEATHERS +	FUR 		SCALES +
Lamprey Perch Salamander Lizard Crocodile	FEATHERS +	FUR +		SCALES ++ +

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Determine ancestral and derived traits

- Chimp and mouse share mammary glands and fur, other animals lack them
- Ancestral or derived? derived

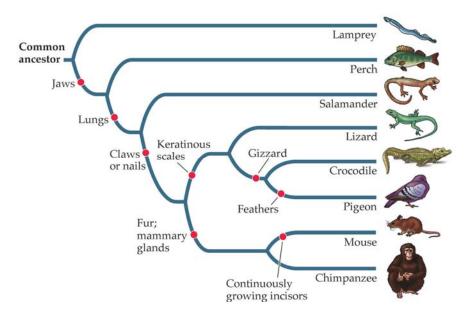
TAXON	FEATHERS	FUR	MAMMARY GLANDS	KERATINOUS SCALES
Lamprey	-		-	-
Perch	-		-	-
Salamander	_	-	-	_
Lizard	-	-	-	+
Crocodile	-	-	-	+
Pigeon	+	-	-	+
Mouse	-	+	+	-
Chimpanzee	-	+	+	-

Determine ancestral and derived traits

- Use similar reasoning on other traits
- Lamprey has no derived traits, so it is an outgroup

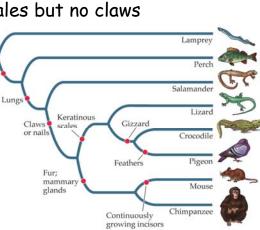
Your Tur	·A	DERIVED TRAIT ^a				
TAXON	JAWS	LUNGS	CLAWS OR NAILS	GIZZARD		
Lamprey	-	-	-	<u> </u>		
Perch	+	-	-	-		
Salamander	+	+	-	-		
Lizard	+	+	+	-		
Crocodile	+	+	+	+		
Pigeon	+	+	+	+		
Mouse	+	+	+	-		
Chimpanzee	+	+	+	-		
TAXON	FEATHERS	FUR	MAMMARY GLANDS	KERATINOUS		
Lamprey	_	-	-	_		
Perch	-	-	-	-		
Salamander	_	-	-	-		
Lizard	-	-	-	+		
Crocodile	-	-	-	+		
Lamprey Perch Salamander Lizard Crocodile Pigeon Mouse Chimmererer	+	-	-	+		
Mouse	-	+	+	-		
Chimpanzee	-	+	+			

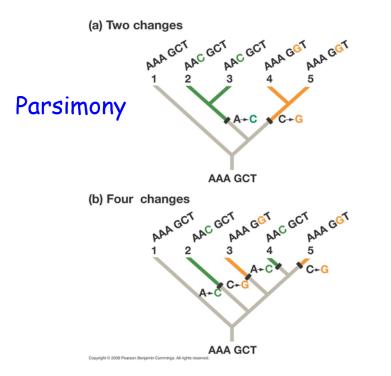
Simple phylogeny example



Not always so simple

- Assumed derived traits appeared once and were never lost
- If we had included snakes, this wouldn't have worked: they have scales but no claws
- Snakes lost limbs and claws during ^{Common} accessor descent from a ^{Jav} common ancestor with lizards
- Parsimony means we assume the smallest possible number of changes





Modern character choice

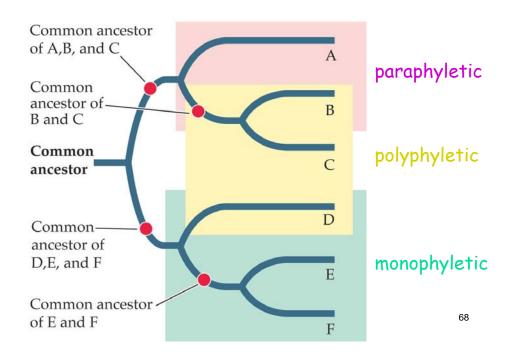
Today, most phylogenies come from gene sequences

- DNA/RNA/protein

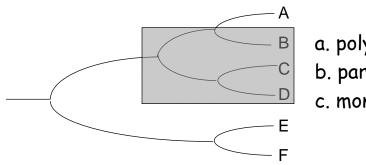
Classification should reflect evolutionary relationships

• A monophyletic group (or clade) best contains all descendents of a particular ancestor and no other organisms

- A polyphyletic taxon contains members with more than one recent common ancestor
- A paraphyletic group contains some, but not all of the descendents of a particular ancestor



A group consisting of the shaded species is best described as



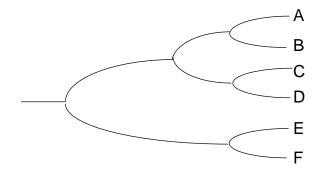
a. polyphyletic.

b. paraphyletic.

c. monophyletic.

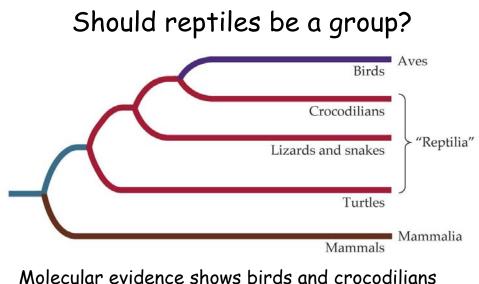
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A particular trait is found only in species A and E. Assuming that the phylogenetic tree is correct, the simplest model describes this trait as



- a. orthologous.
- b. ancestral.
- c. homoplastic.

d. homologous.



closer than crocodilians and other reptiles

Reptiles are paraphyletic, since birds excluded 71

Birds look very different

- Birds have rapidly evolved unique derived traits since they separated from reptiles
- Groups called grades have changed rapidly. May be an appropriate group even if paraphyletic
- General tendency to eliminate paraphyletic groups as we learn more, but some familiar categories, such as reptiles, won't disappear in a hurry

Uses of phylogenetic trees

- 1. How are different species related?
- 2. What traits do you expect a newly discovered species to have?
- 3. How many times has a trait evolved?
- 4. Which molecular change is responsible for adaptation?
- 5. When did lineages split? use DNA sequence and the "molecular clock"

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The Evolution of Macromolecules

- The neutral theory of molecular evolution:
 - postulates that, at the molecular level, the majority of mutations are selectively neutral.
- Thus, macromolecule evolution, and much of the genetic variation within species, does not result from positive selection of advantageous alleles nor stabilizing selection.
- Mutation fixation rate is theoretically constant and equal to the neutral mutation rate - a molecular clock.
 - The concept of the molecular clock states that macromolecules should diverge from one another at a constant rate.

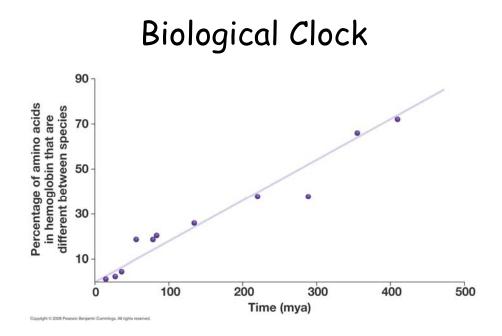
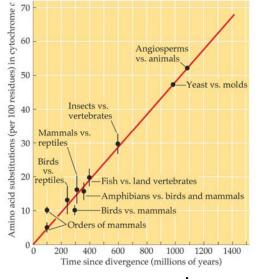


Figure 26.5 Cytochrome c Has Evolved at a Constant Rate



Cytochrome *c* sequences have evolved at a relatively constant rate.

The Evolution of Macromolecules

- Molecular evolution differs from phenotypic evolution in one important way:
 - In addition to natural selection, random genetic drift and mutation exert important influences on the rates and directions of molecular evolution.
 - What does this say about our study of "Evolutionary Theory"?
- Many mutations, called silent or synonymous mutations, do not alter the proteins they encode
- A nonsynonymous mutation does change the amino acid sequence



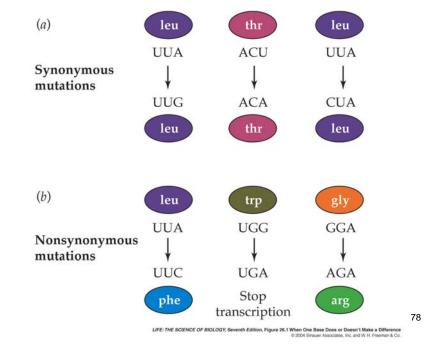


Figure 26.1 When One Base Does or Doesn't Make a Difference

Genetic Code (DNA \rightarrow amino acid)

Second Letter								
		Т	C	A	G			
	т	TTT } Phe TTC } Phe TTA } Leu	TCT TCC TCA TCG	TAT TAC } Tyr TAA Stop TAG Stop	TGT TGC TGA Stop TGG Trp	T C A G		
First Letter	с	CTT CTC CTA CTG	CCT CCC CCA CCG	CAT CAC His CAA CAA Gin	CGT CGC CGA CGG	T C A G		
	A	ATT ATC ATA ATG Met	ACT ACC ACA ACG	AAT AAC AAA AAA AAG Lys	AGT AGC AGA AGA AGG Arg	T C A G	Letter	
	G	GTT GTC GTA GTG	GCT GCC GCA GCG	GAT GAC } Asp GAA GAG } Glu	GGT GGC GGA GGG	T C A G		

http://plato.stanford.edu/entries/information-biological/GeneticCode.png

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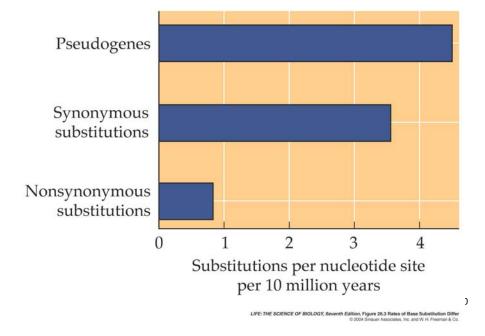


Figure 26.3 Rates of Base Substitution Differ

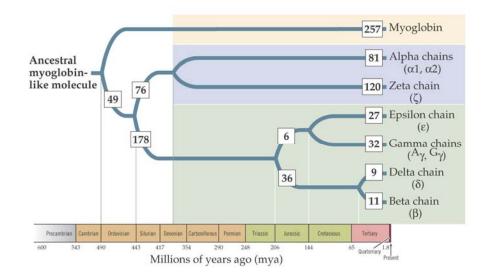
The Evolution of Genome Size

- Several rounds of duplication and mutation may lead to formation of a gene family, a group of homologous genes with related functions.
- There is evidence that the globin gene family arose by gene duplication.

= Neofunctionalization

- To estimate the time of the first globin gene duplication, a **gene tree** can be created.
- Based on the gene tree, the two globin gene clusters are estimated to have split about 450 mya.

Figure 26.9 A Globin Family Gene Tree



LIFE: THE SCIENCE OF BIOLOGY, Seventh Edition, Figure 26.9 A Globin Family Gene Tree © 2004 Strauer Associates, Inc. and W. H. Freeman & Co.

⁸¹