Outline

- Finishing up speciation
- Phylogenies–trees of species
    - What are phylogenies good for?
    - How to look at a phylogeny
    - Rooted versus unrooted trees
    - Clocklike versus non-clocklike trees
    - Appropriate data for phylogenies

Homo floresiensis

- One skull and 9 partial skeletons
- Around 3’6” tall and 55 lbs
- Brain of type specimen smaller than that of a chimpanzee
- Last dates initially thought to be 13,000 years ago, but now closer to 50,000

Pro species

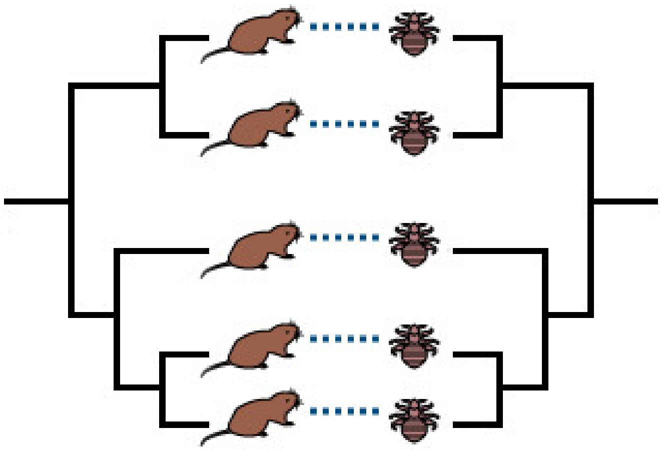
- Other Indonesian island taxa also smaller than average (mammoths, etc)
- *H. floresiensis* also has unusual limb and joint traits
- 700,000 y.o. fossil recently found could be an ancestor/intermediate with *H. erectus*; it's even smaller!

Anti species hypotheses

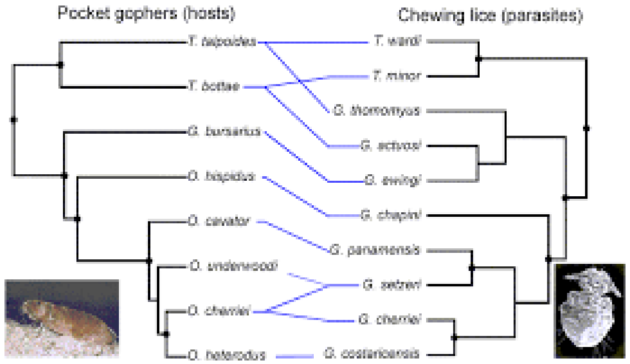
- Laran syndrome:
  - Autosomal recessive dwarfing syndrome
  - *H. floresiensis* smaller body and brain than typical for this, but genetic background could matter
  - (Side note: some modern humans with Laron syndrome have normal IQ)
- Cretinism (lack of functioning thyroid due to environmental factors)
- Question: are these hypotheses mutually exclusive with species status?

Cospeciation

- Host species and parasite species often speciate together
- Species trees of the two groups will look very similar
- Reproductive isolation of hosts may isolate parasites
- Adaptation of hosts may spur adaptation of parasites (or vice versa)



Idealized schematic



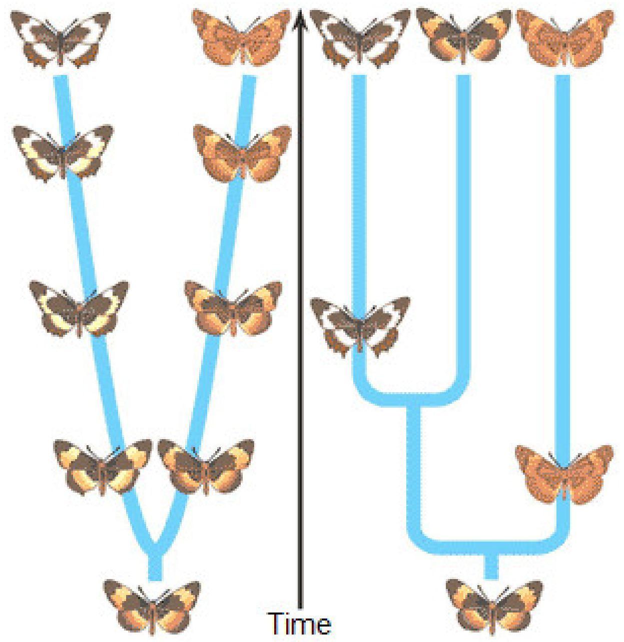
Real data

Gradual versus punctuated

- Classical model: species slowly accumulate differences

- Punctuated equilibrium model (Stephen Gould and colleagues)
  - Burst of change at speciation
  - Relative stasis elsewhere

- Favored by paleontologists, who find bursts of change in the fossil record



(a) **Gradualism model.** Species descended from a common ancestor gradually diverge more and more in their morphology as they acquire unique adaptations.

(b) **Punctuated equilibrium model.** A new species changes most as it buds from a parent species and then changes little for the rest of its existence.

Some thoughts on punctuated evolution

- Paleontological species definition encourages this view because “gradual” species can’t be recognized as such
- Not all species evolve the same way
- Major changes in body or lifestyle probably require a burst of changes

Domesticated foxes

- Long-term breeding project started by Belyaev in Siberia, 1959
- Fox kits selected for sociability with humans
- Results not only sociable but oddly dog-like

Wild silver fox: image by Zefram

Russian domesticated foxes

Domesticated foxes

- Complex differences from wild foxes:
  - Very tame even when raised in cages
  - Domestic-like color patterns
  - Wagging tails, whining, barking
  - Can follow pointing finger or gaze
  - A few try to reproduce more than once/year
  - Differences in hormone levels, developmental timing
  - Differences in skull and body plan
- Major change in developmental pathway?

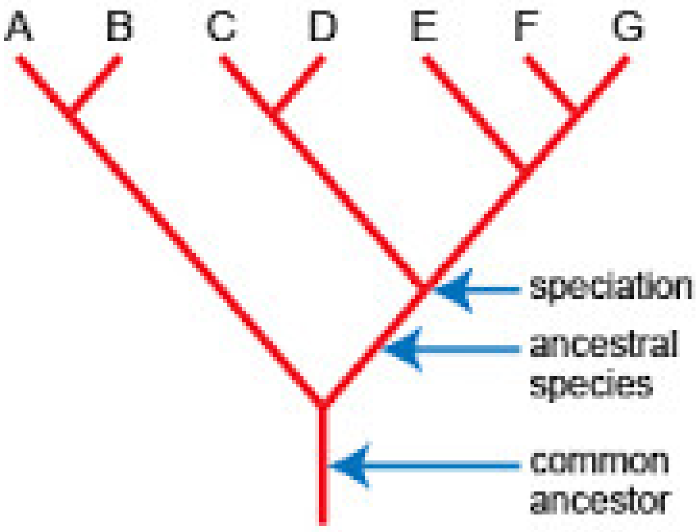
Stasis

- Some organisms appear to change very little over time:
  - ginkgo
  - coelacanth
  - horseshoe crab
- Other organisms change much more rapidly and diversify into multiple species
- Why? Ideas:
  - Change-resistant developmental “program”
  - Broad ecological niche
  - No improvements in easy reach
  - Cryptic species?

What is a phylogeny?

Phylogeny: a branching tree showing inferred relationships among species, populations, or individuals

Synonyms: evolutionary tree, cladogram



Other useful terms

- “Tree” – same as phylogeny
- Taxon, taxa – the units at the tips of the tree (species, populations, individuals)
- Clade – all taxa descending from a common ancestor
- Root – the common ancestor of the whole phylogeny

What are phylogenies good for?

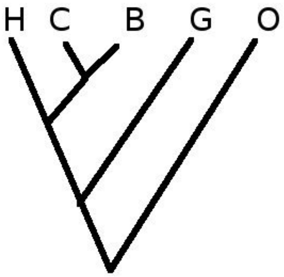
- Relationships between organisms
- Dates of evolutionary events
- Evolutionary patterns–did some features evolve multiple times?
- Removing influence of phylogeny from ecological analyses ("comparative method")
- Relationships among genes
- Patterns of speciation and diversification

How to look at a phylogeny

- Branching pattern shows pattern of relationships
- Right-left ordering is NOT significant; can be rearranged to emphasize or obscure points!
- Branch lengths may or may not be meaningful
- Biologists draw root at the bottom; math and CS types draw root at the top

Practice problem

1



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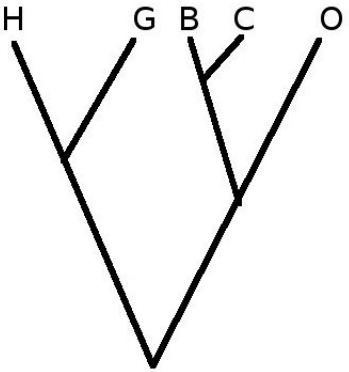

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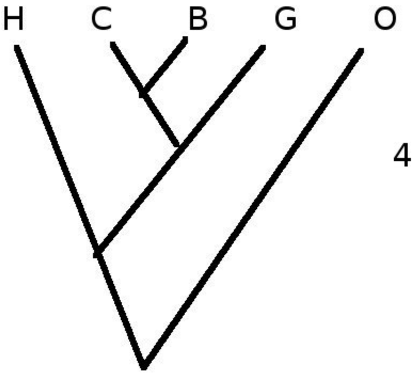

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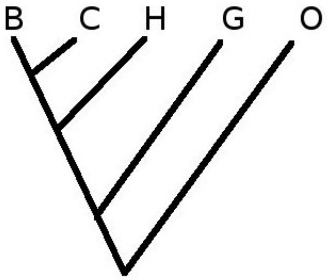


Two of these trees are the same (except for branch lengths). Which two?

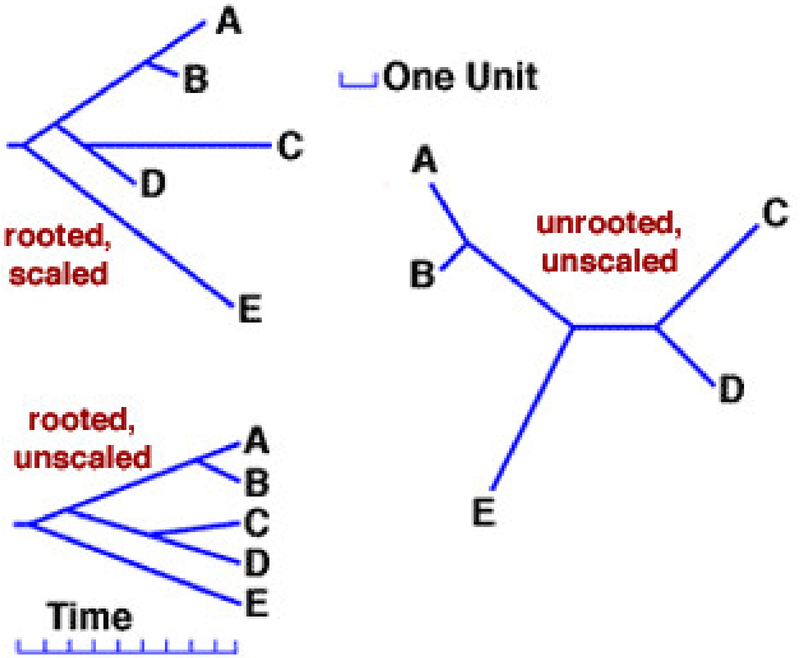
Rooted versus unrooted trees

- A rooted tree (phylogeny) has a specific direction of evolution

- The root is the ancestral form from which the others evolved

- This is the most informative type of tree

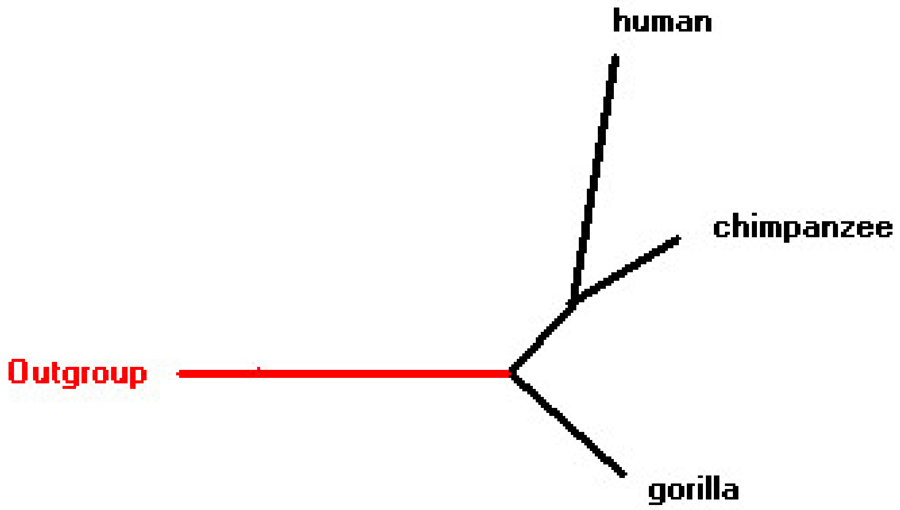
- Unfortunately, most phylogeny inference methods produce unrooted trees

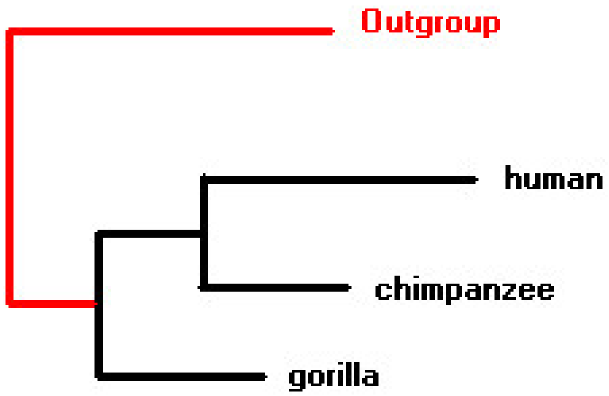


Rooted versus unrooted trees

- An unrooted tree corresponds to a collection of different rooted trees
- We don't know the direction of evolution
- Biological interpretation can be difficult without root
- Ways to root a tree:
  - Outgroup
  - Molecular clock

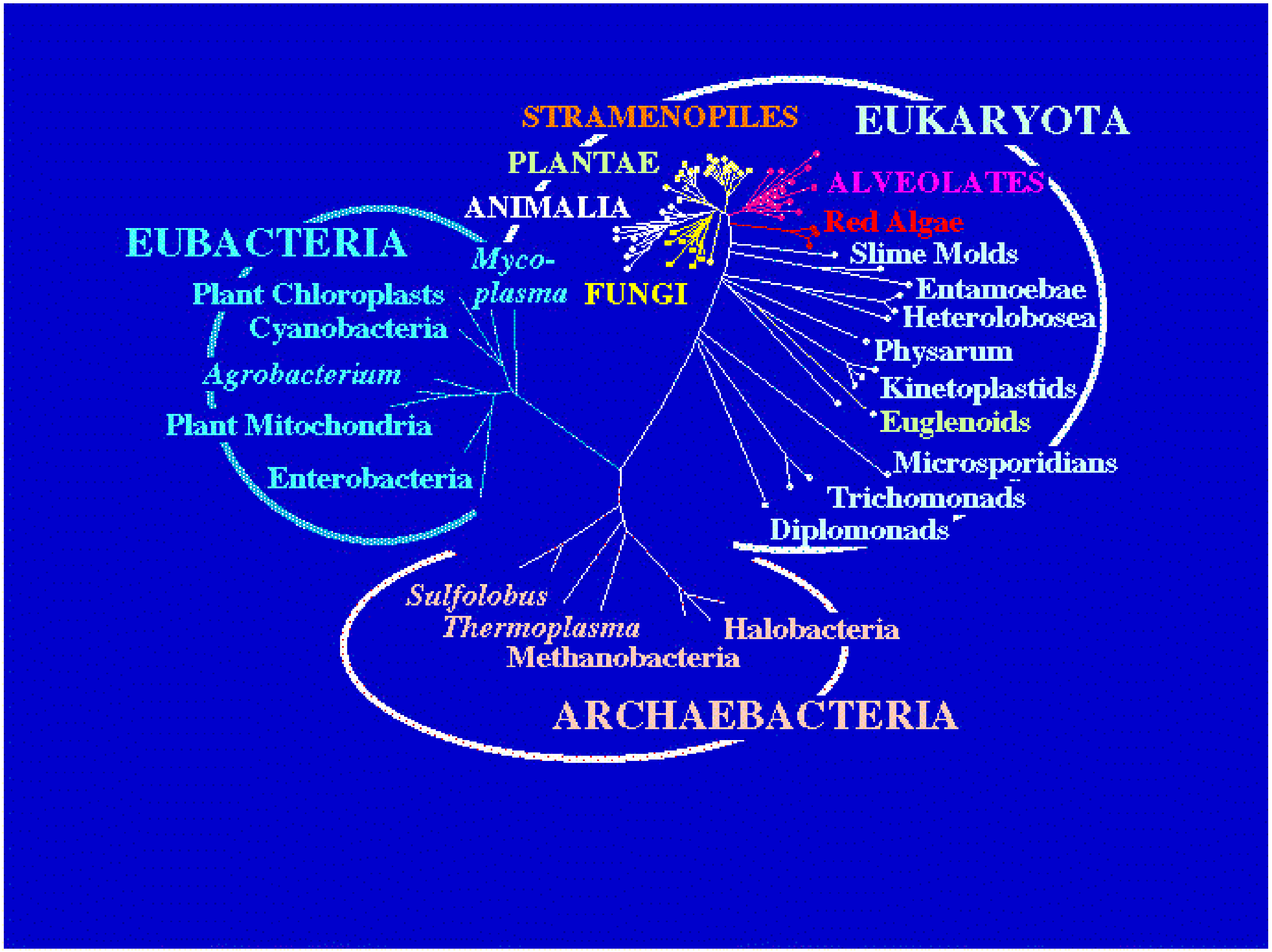
Outgroup rooting





- Outgroup – species known not to belong to clade
  - Wrong outgroup leads to wrong root
  - Too-distant outgroup leads to noise in data

- Some comparisons have no suitable outgroup


STRAMENOPILES
EUKARYOTA
PLANTAE
ALVEOLATES
ANIMALIA
Red Algae
EUBACTERIA
Myco-
plasma
Slime Molds
Plant Chloroplasts
FUNGI
Entamoebae
Cyanobacteria
Heterolobosea
Physarum
Agrobacterium
Kinetoplastids
Euglenoids
Plant Mitochondria
Microsporidians
Enterobacteria
Trichomonads
Diplomonads
Sulfolobus
Thermoplasma
Halobacteria
Methanobacteria
ARCHAEBACTERIA

Molecular clock

- Can we assume rate of evolution the same on all branches?
- If so:
  - Root is point most distant from all tips
  - Branch length is proportional to time
  - If we can date a few points on tree, can date entire tree
- Clock may not hold:
  - Unequal generation time
  - Different selection constraints
  - Different mutation rates
- Clock assumption safest among closely related species

Appropriate data for phylogenies

- Good phylogenetic data has:
  - Enough variation to show relationships
  - Not so much variation that it randomizes signal
  - Ability to establish homology
  - *Relative freedom from convergent evolution*
  - Mode of evolution relatively well understood
  - If possible, a good clock

- No one type of data works for all problems

Some important dates in history

Origin of the universe	–12[a] ±2
Formation of the solar system	–4.6 ±0.4
First self-replicating system	–3.5 ±0.5
Prokaryotic-eukaryotic divergence	–2.5 ±0.3
Plant-animal divergence	-1.0
Invertebrate-vertebrate divergence	-0.5
Mammalian radiation beginning	-0.1

[a] Billions of years ago

Protein family	PAMs[a]/100 res. /10^8 years	Protein Lookback time[b]	
Pseudogenes	400	45[c]	Primates,Rodents
Fibrinopeptides	90	200	Mammalian Radiation
Lactalbumins	27	670	Vertebrates
Ribonucleases	21	850	Animals
Hemoglobins	12	1.5[d]	Plants/Animals
Acid Proteases	8	2.3	Prokayrotic/Eukarotic
Triosphosphate isomerase	3	6	Archaen
Glutamate dehydrogenase	1	18	?

[a] PAMs, point accepted mutations. [b] Useful lookback time, 360 PAMs, 15% identity. [c] Millions of years. [d] Billions of years.

Appropriate data for phylogenies

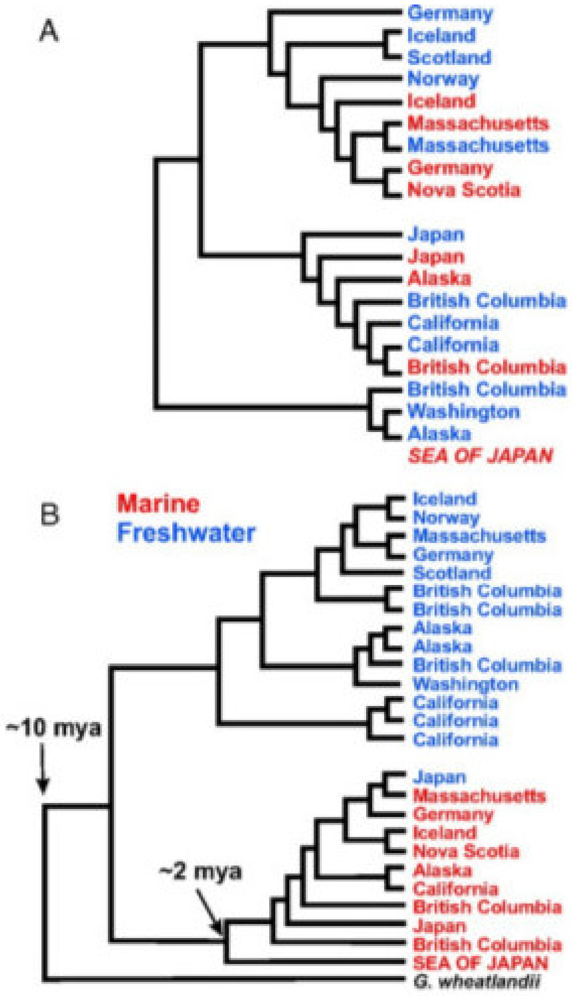
- Within species, between closely related species
  - Non-coding DNA and pseudogenes
  - Microsatellites
  - Very fast-evolving genes
  - mtDNA
- Between moderately similar species
  - Most protein-coding genes, especially housekeeping genes
- Between extremely dissimilar species
  - Ribosomal RNA
  - Very slow-evolving genes

Convergent evolution?

- Why not use loci involved in "exciting" traits of the species?

- Convergent evolution:
  - Two clades are under the same external pressure
  - They independently evolve the same response
  - Not a reliable indicator of relationships

- Upper figure is many random genes; lower is a gene involved in fresh/saltwater adaptation



Why phylogenies are hard

Tips	Topologies
3	3
4	18
5	180
6	2700
7	56700
8	1587600
9	57153600
10	2571912000
15	6958057668962400000
20	564480989588730591336960000000
30	4368466613103069512464680198620763891440640000000000000
40	3027333829948007356546303364551457200042939432053862501707888721920000000000
50	3.28632×10^{112}
100	1.37416×10^{284}

Why phylogenies are hard

- In many cases tree search known to be “NP complete”
- No efficient algorithm is known–none may exist but this is unproven
- Solving any NP-complete problem solves ALL OF THEM
- Three consequences of such an algorithm
  - Reliably find the right phylogeny
  - Crack most/all current codes (business and military)
  - Difficult conversation with the NSA....
- Must use heuristic approximations which will sometimes fail (get the wrong tree)

Phylogeny methods

- Three major approaches to phylogeny inference
    - Parsimony (today)
    - Distance (Friday)
    - Maximum likelihood and Bayesian methods (Friday)

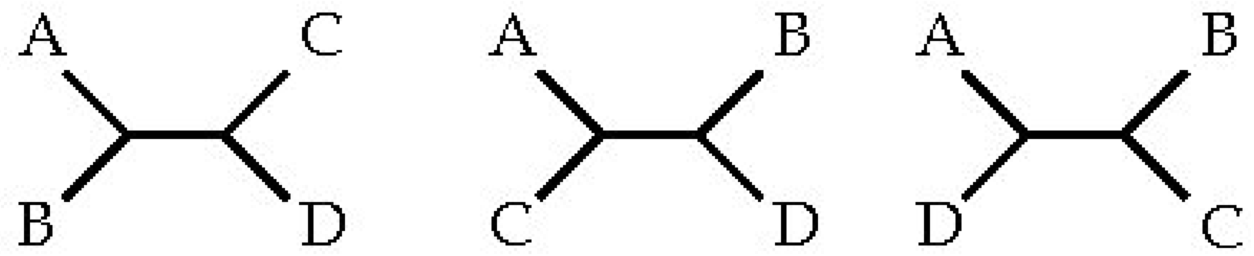
Parsimony methods

- (Philosophical) Principle of Parsimony: Make as few assumptions as possible
- (Phylogenetic) Principle of Parsimony: Prefer the tree that assumes the smallest number of evolutionary changes
- Assumes that changes are fairly rare and evenly distributed

Parsimony methods

- Advantages of parsimony:
  - No explicit mutational model required
  - Applicable to the widest variety of data–including morphological traits (all we have for fossils)
  - Moderately fast
- Disadvantages:
  - No explicit mutational model possible
  - Long branch attraction
  - Limited ability to put error bars on phylogeny estimate

Practice problem–parsimony

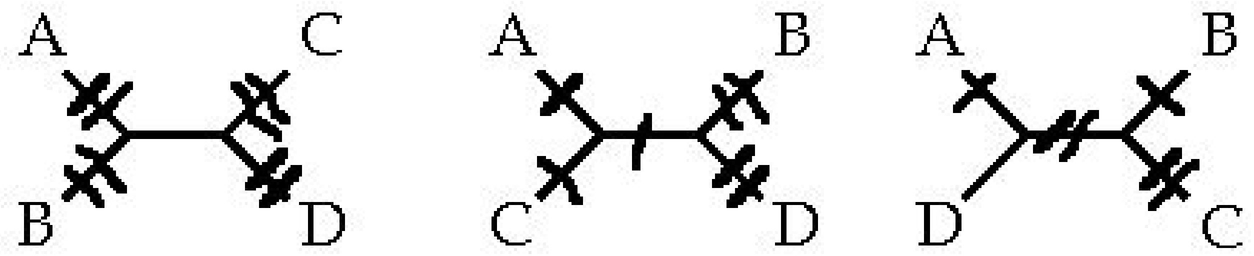


Taxon	1	2	3	4	5
A	A	A	C	G	A
B	T	A	A	T	T
C	T	A	A	G	A
D	A	C	C	G	T

How many changes are needed on each tree topology?

Which topology is preferred by parsimony?

Practice problem–parsimony



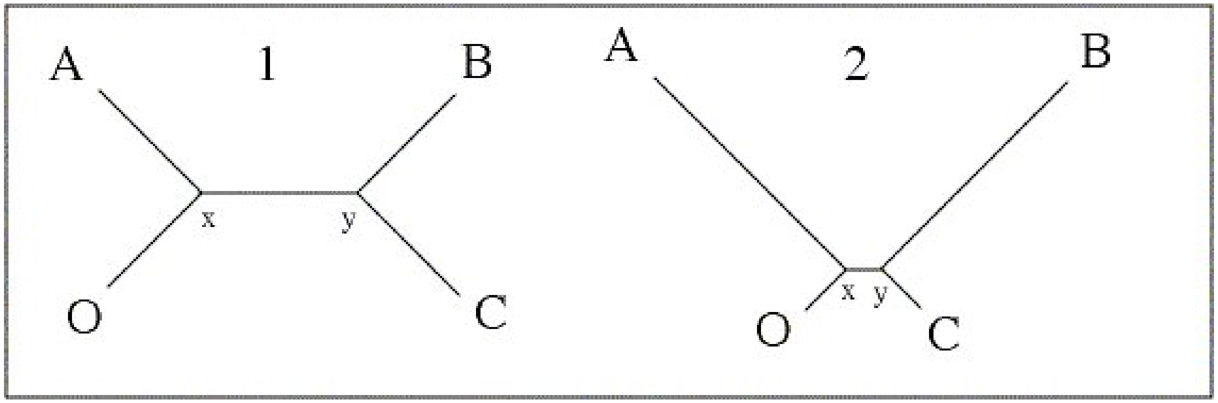
Taxon	1	2	3	4	5
A	A	A	C	G	A
B	T	A	A	T	T
C	T	A	A	G	A
D	A	C	C	G	T

How many changes are needed on each tree topology? *8, 7, 6*

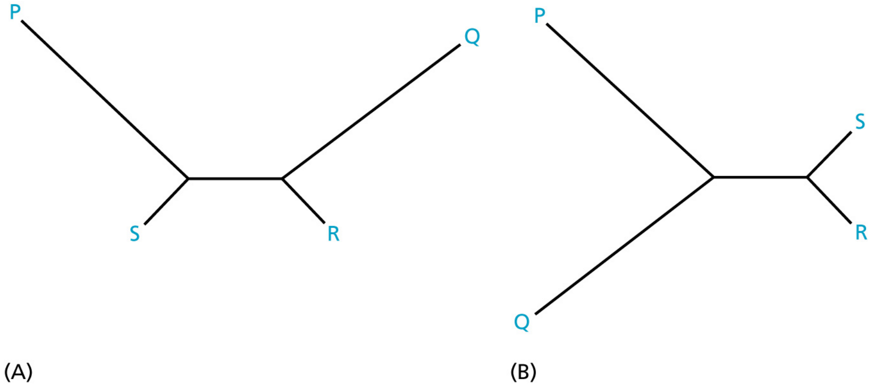
Which topology is preferred by parsimony? *Third topology*

Parsimony methods

- Felsenstein showed a four-tip tree which gives inconsistent results with parsimony
- “Inconsistent” – wrong answer becomes more probable as data increases
- With infinite data you would be 100% sure to get the wrong answer



Long branch attraction

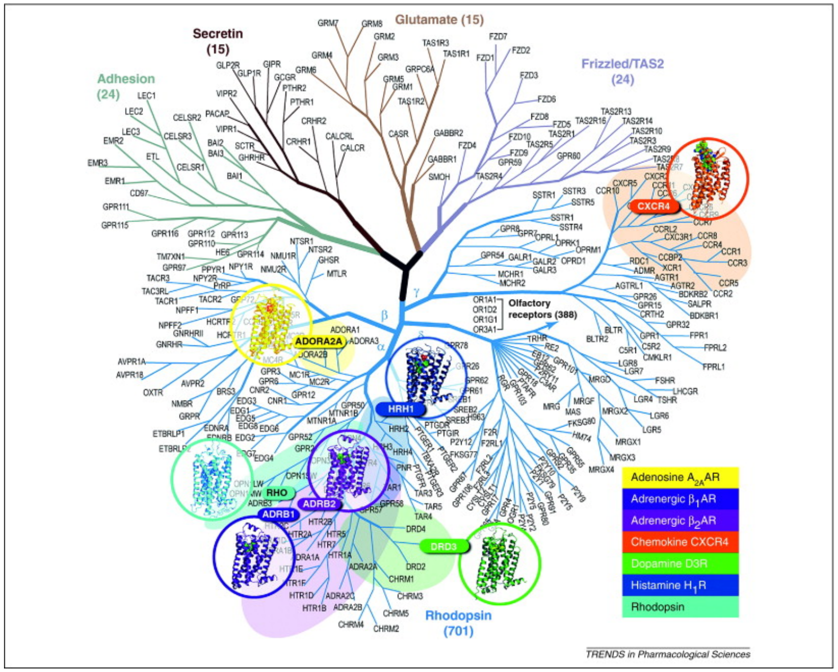


- Data from tree A leads to inference of (wrong) tree B
- Two convergent changes on the long branches are more likely than a single change on the short branches
- This violates the basic principle of parsimony
- Fast-evolving sites and data sets are particularly problematic

Betting on your trees

- Ken Rice makes parsimony trees of G-protein coupled receptors
  - Maximum likelihood too slow
  - Distance methods didn't perform well

- If new gene groups with:
  - Odor receptors – ignore
  - Neurotransmitter receptors – spend $2K to validate



TRENDS in Pharmacological Sciences

G-protein coupled receptor genes

One-minute responses

- Tear off a half-sheet of paper
- Write one line about the lecture:
    - Was anything unclear?
    - Did anything work particularly well?
    - What could be better?
- Leave at the back on your way out