26th Annual Workshop in Molecular Evolution

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Introduction: David M. Hillis, University of Texas

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(Thanks to Mark Holder, Paul Lewis, and Derrick Zwickl for some of these ideas and slides)

Molecular Evolution

- Using biomolecules to understand evolutionary history and evolutionary processes

- Phylogenetic trees are important to molecular evolution, because many biological phenomena of interest can be modeled as bifurcating processes

Phylogeny

Evolutionary relationships among lineages,
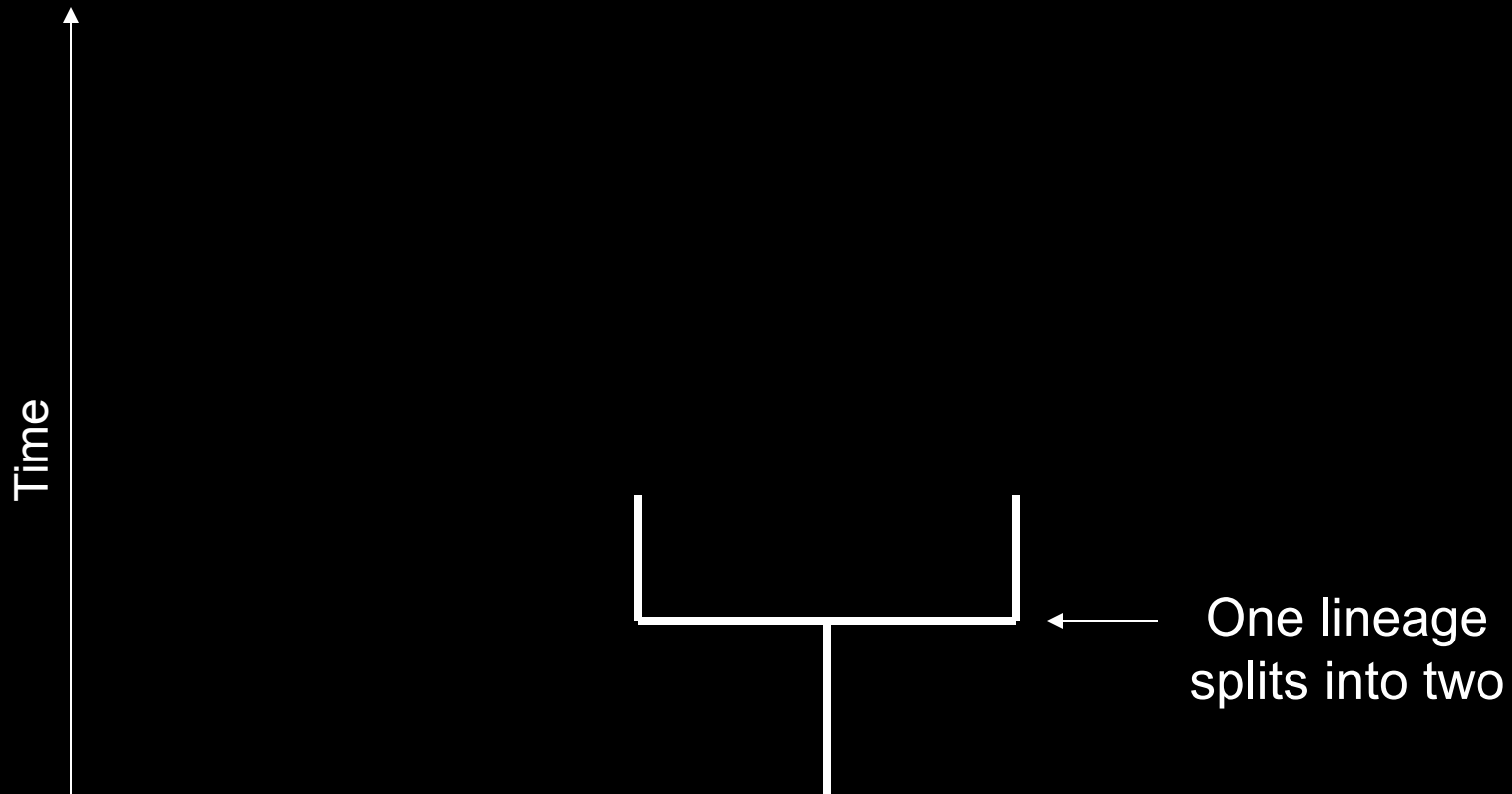such as genes, individuals, populations, species, etc.

Time

Consider an ancestral lineage
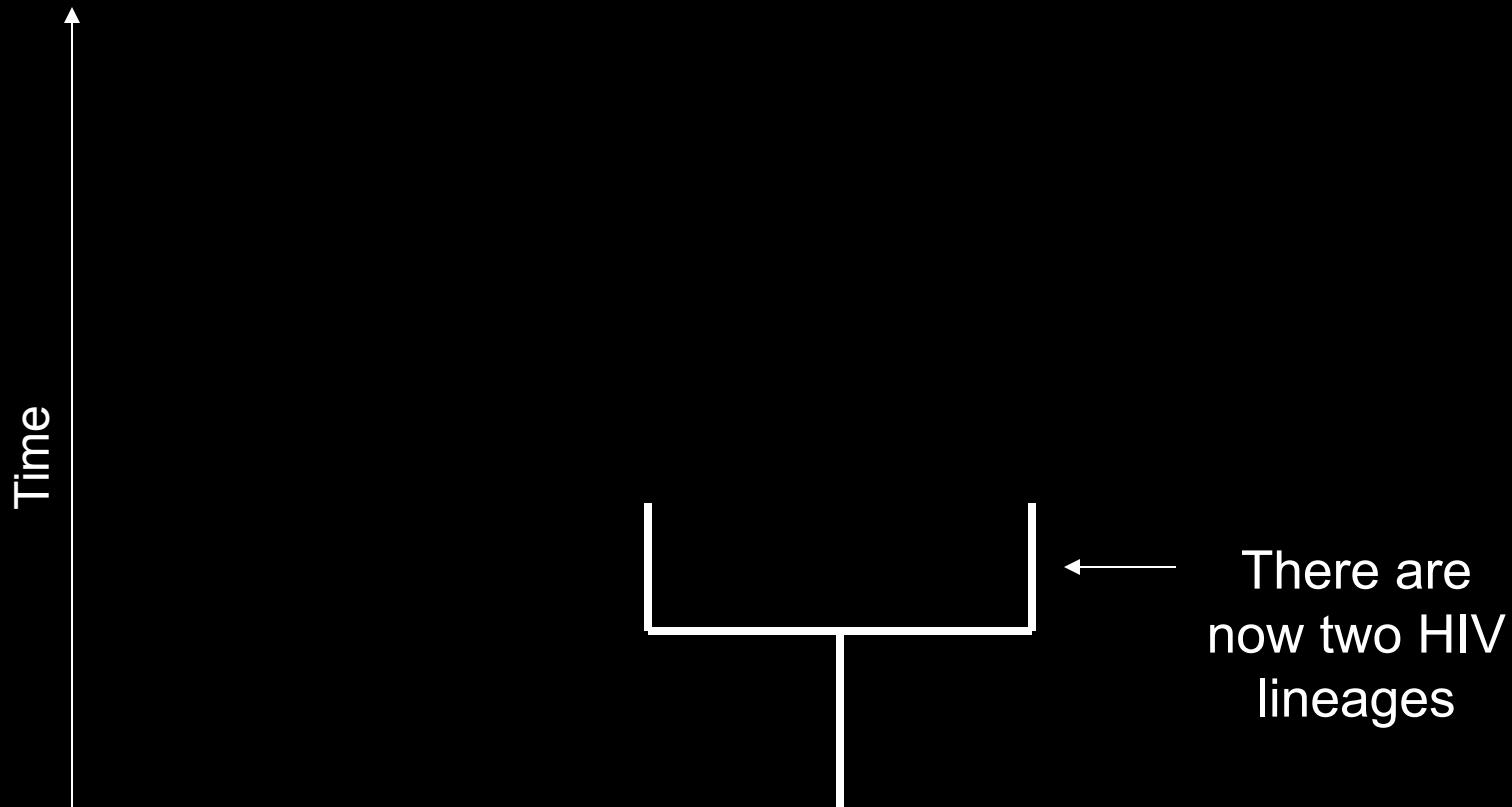(e.g., descendants from one HIV virus)

Phylogeny

Evolutionary relationships among lineages,
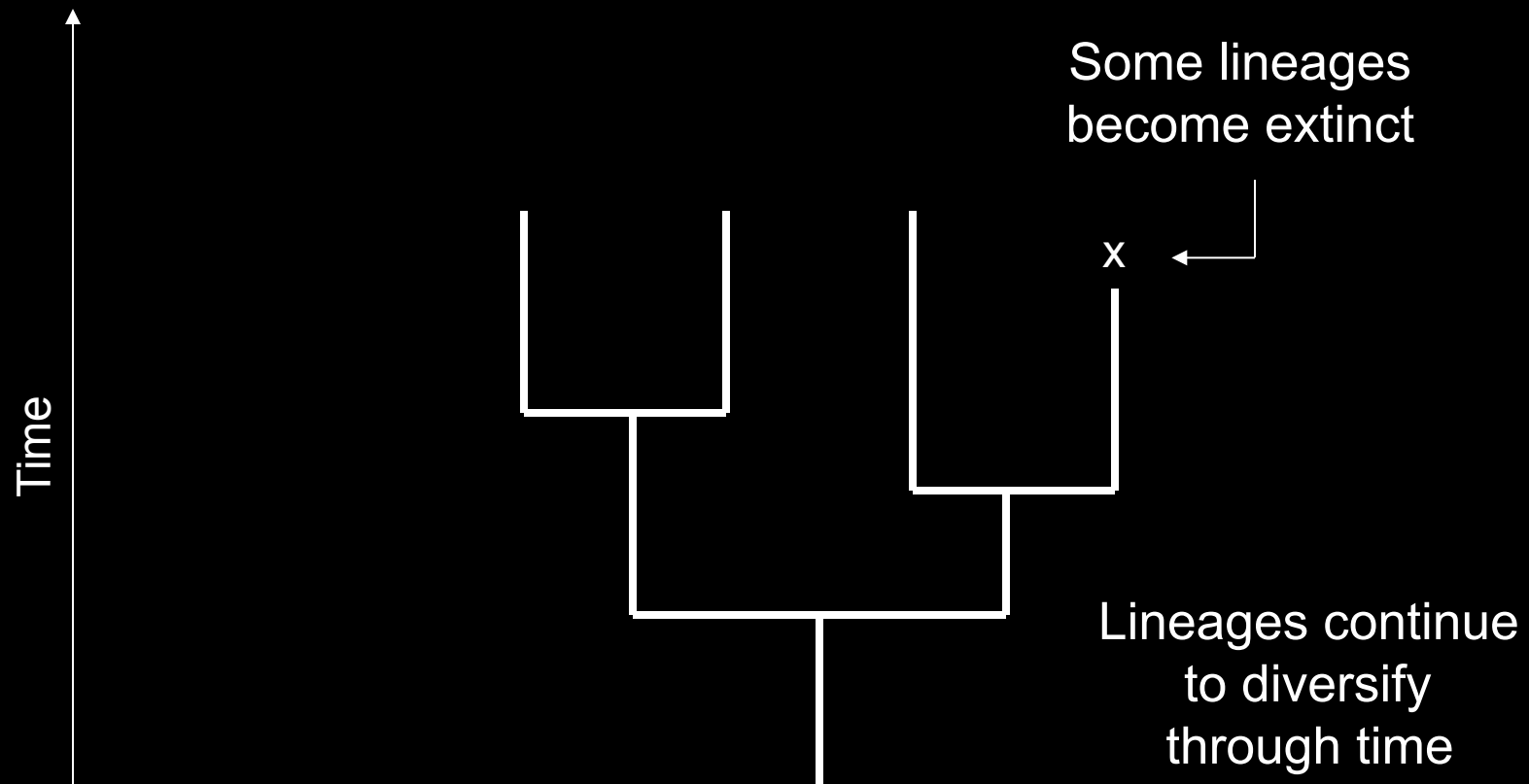such as genes, individuals, populations, species, etc.

Time

One lineage
splits into two

Phylogeny

Evolutionary relationships among lineages, such as genes, individuals, populations, species, etc.

Time

Some lineages become extinct
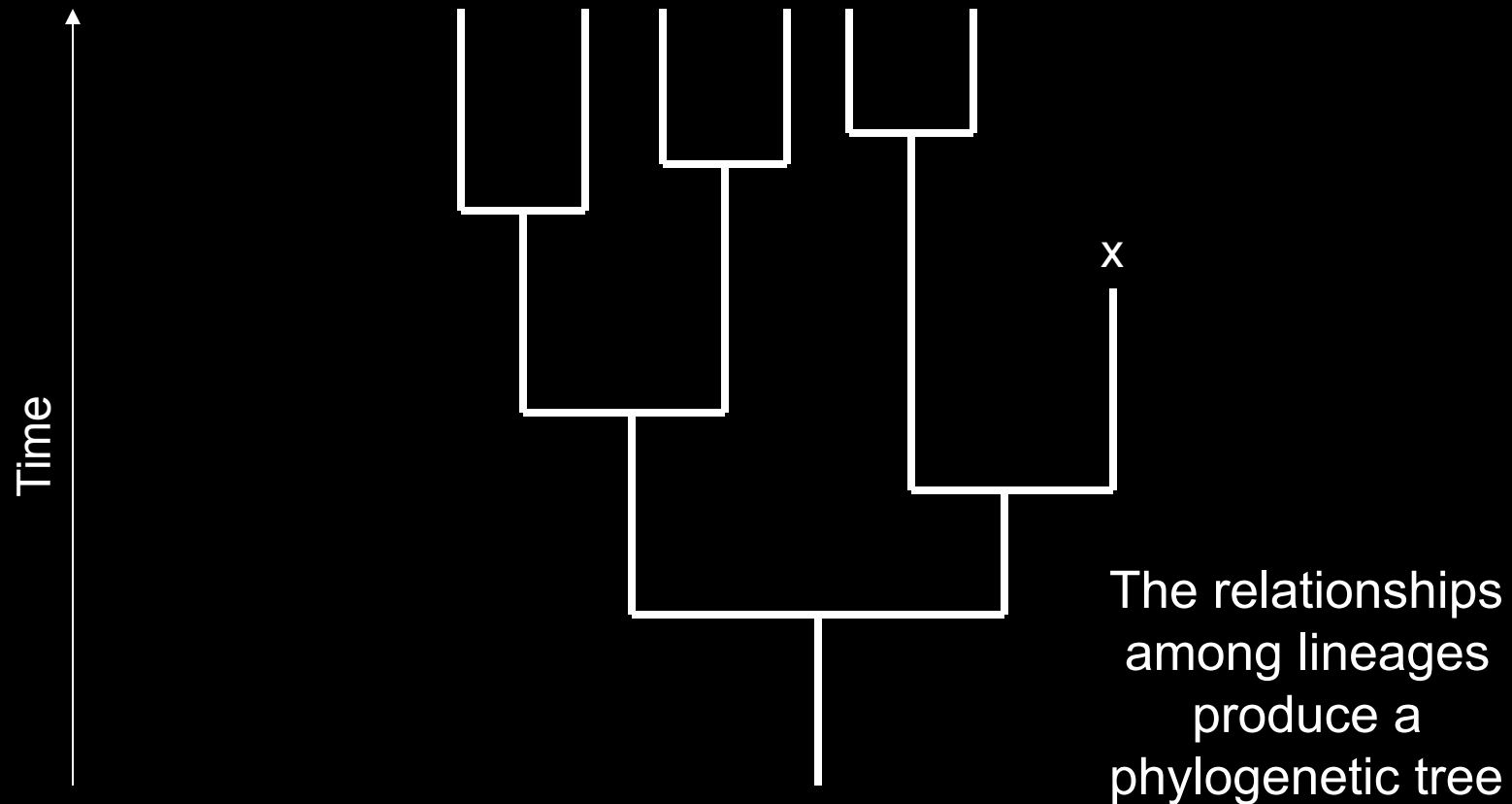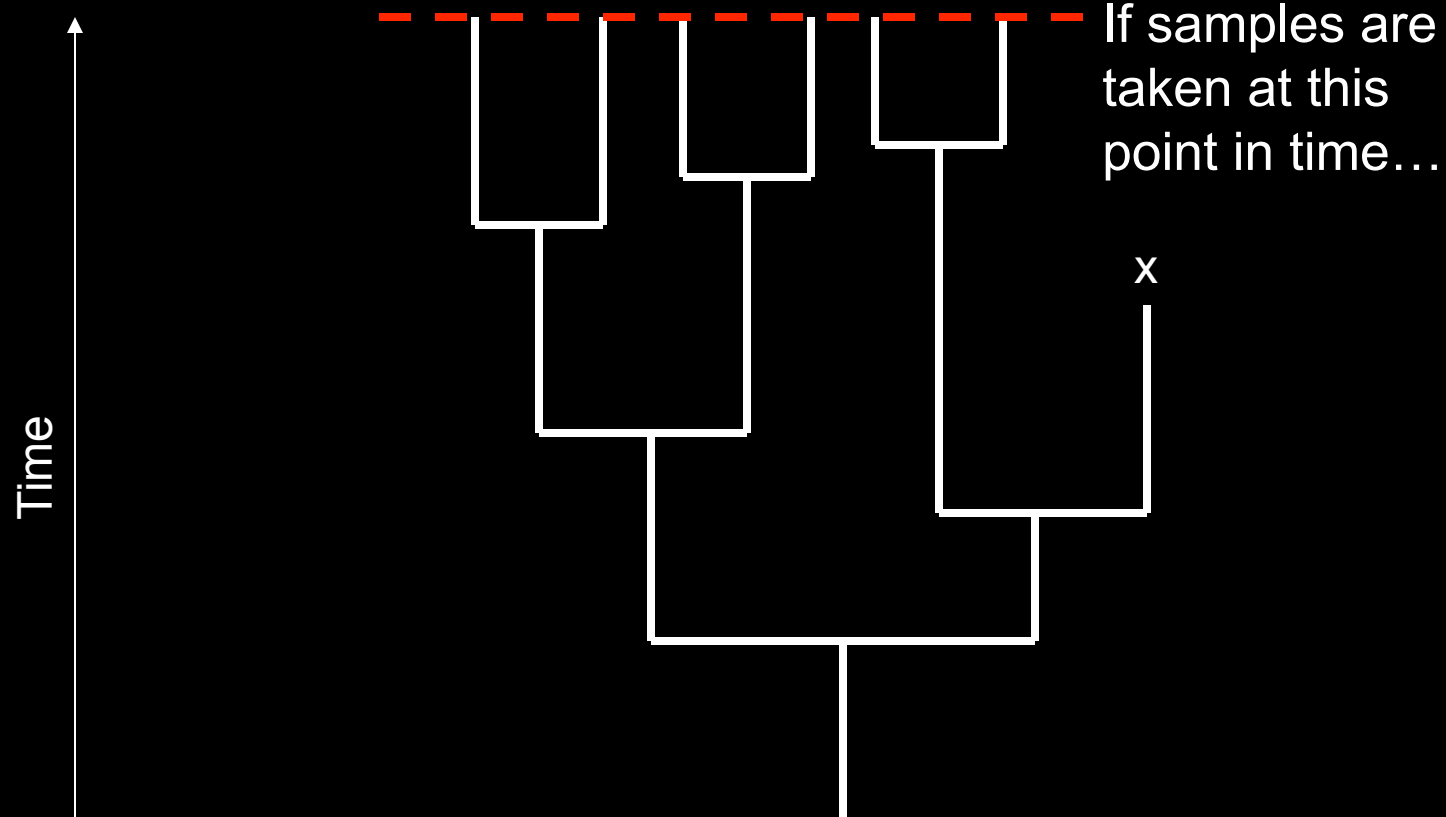
x

Lineages continue to diversify through time

Phylogeny

Evolutionary relationships among lineages,
such as genes, individuals, populations, species, etc.
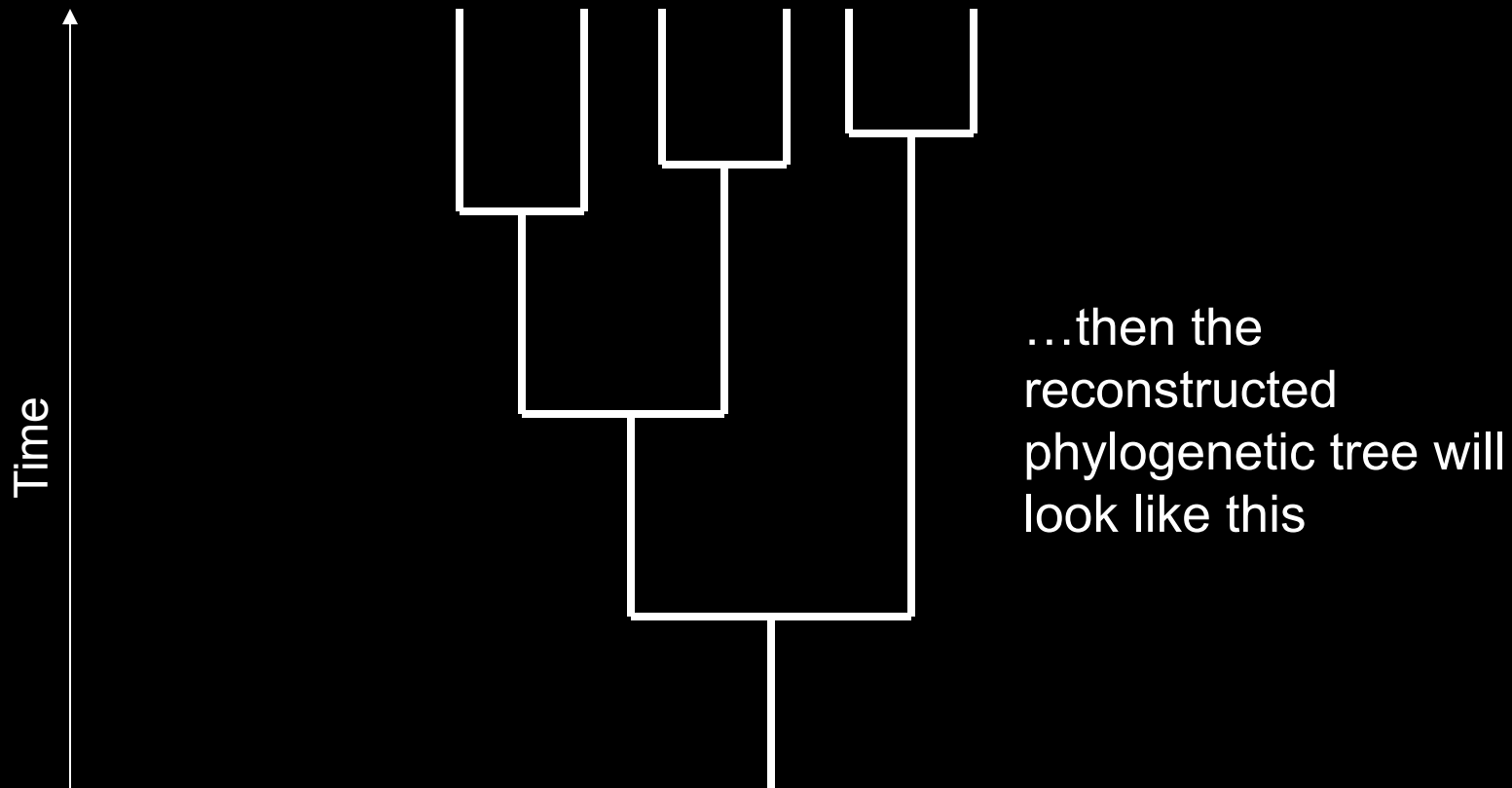

Time

x

The relationships
among lineages
produce a
phylogenetic tree

Phylogeny

Evolutionary relationships among lineages,
such as genes, individuals, populations, species, etc.

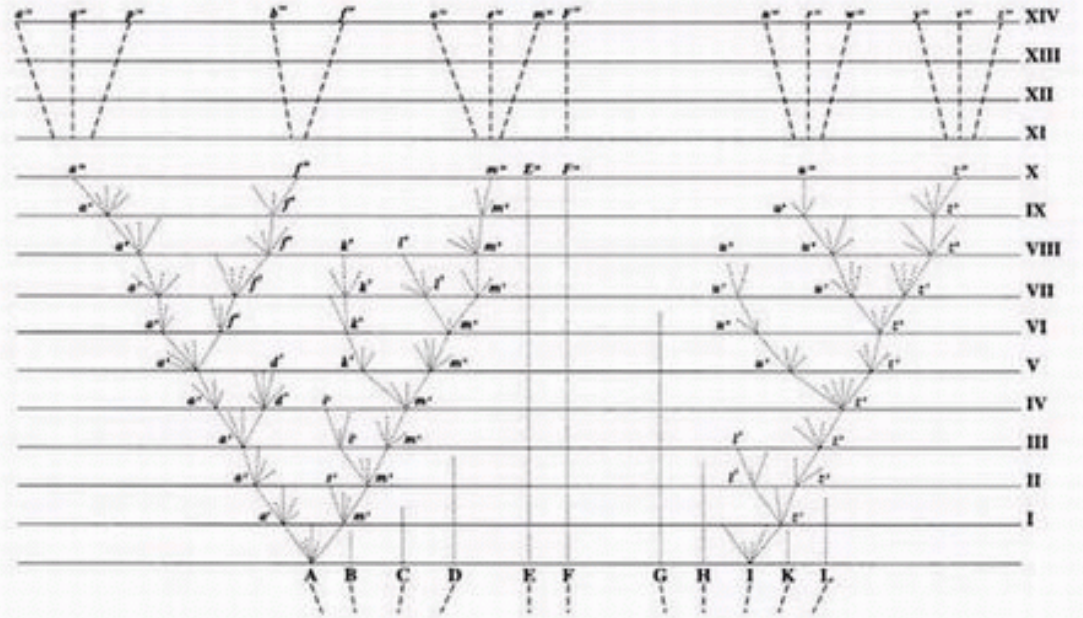Darwin's notebooks contain the sketch (left, from 1837) that was the basis for the only figure in *The Origin of Species* (below, 1859), a conceptual drawing of a phylogenetic tree

"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, 1859: 172
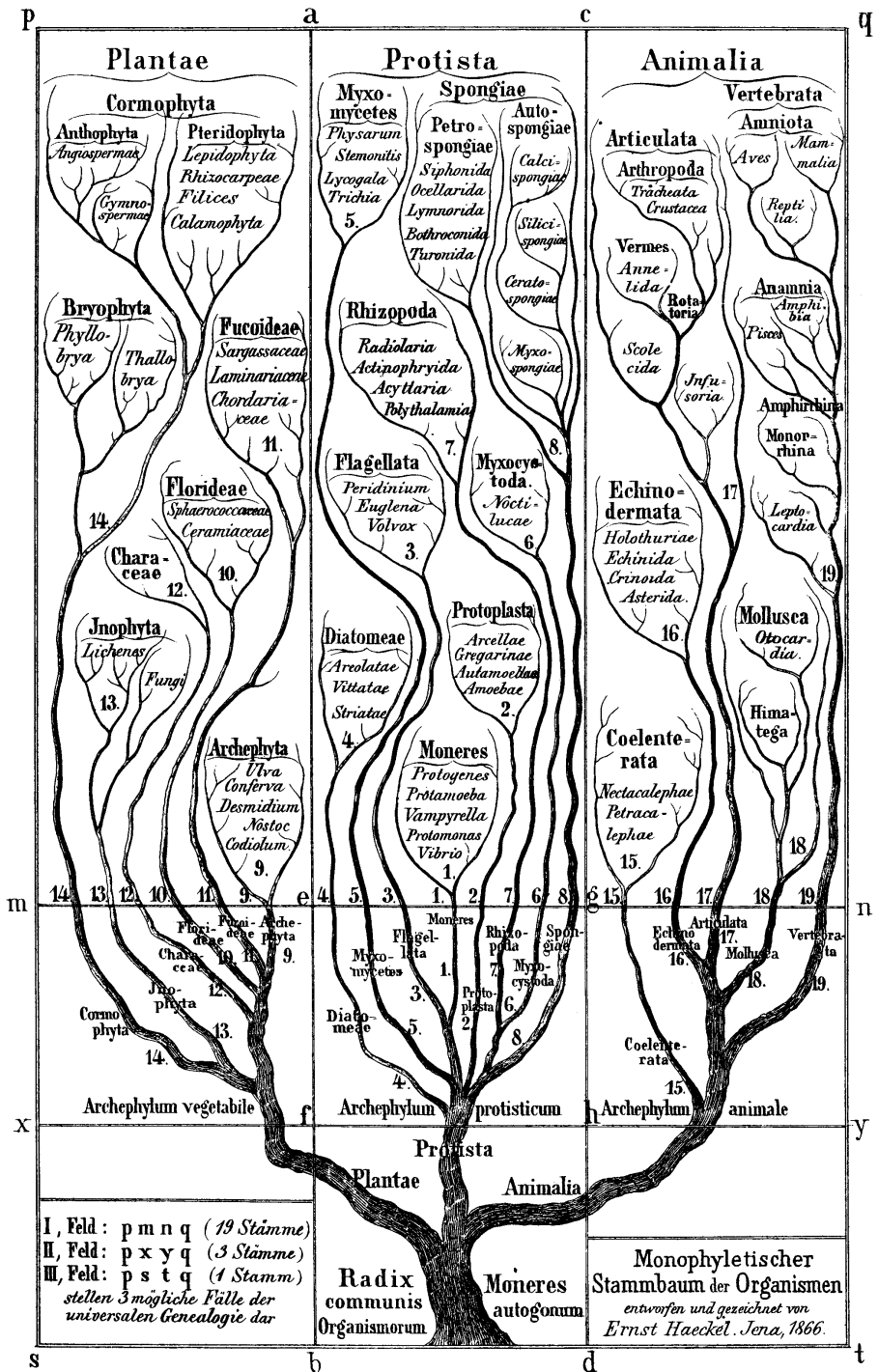
Darwin inspired Haeckel (1866) to construct trees for major lineages of life (and to coin the word "phylogeny")

Dark Ages for phylogeny: 1870s-1950s

E.g., in Julian Huxley's *Evolution: The Modern Synthesis* (1942):

"...the elaborate trees and other diagrams of arrangement (relationship) proposed...are largely contradictory *inter se*, and must be regarded as highly speculative."

The primary application of phylogeny was in biological taxonomy during this time

Rebirth of Phylogenetics
1950s-1980s

- Emphasis on explicit analytical methods (development of parsimony, pairwise distance, and likelihood approaches; statistical analysis of results)

- Computer revolution begins to allow efficient implementation of algorithms to large data sets

- Morphology still provided most of the data, but data from proteins and DNA became more important throughout this period

- First non-taxonomic applications (e.g., molecular clocks)

Phylogeny papers, 1978-2008

Rapid increase in applications of phylogeny, beginning in early 1990s

MBL Molecular Evolution Workshop begins

Number of papers published

Year
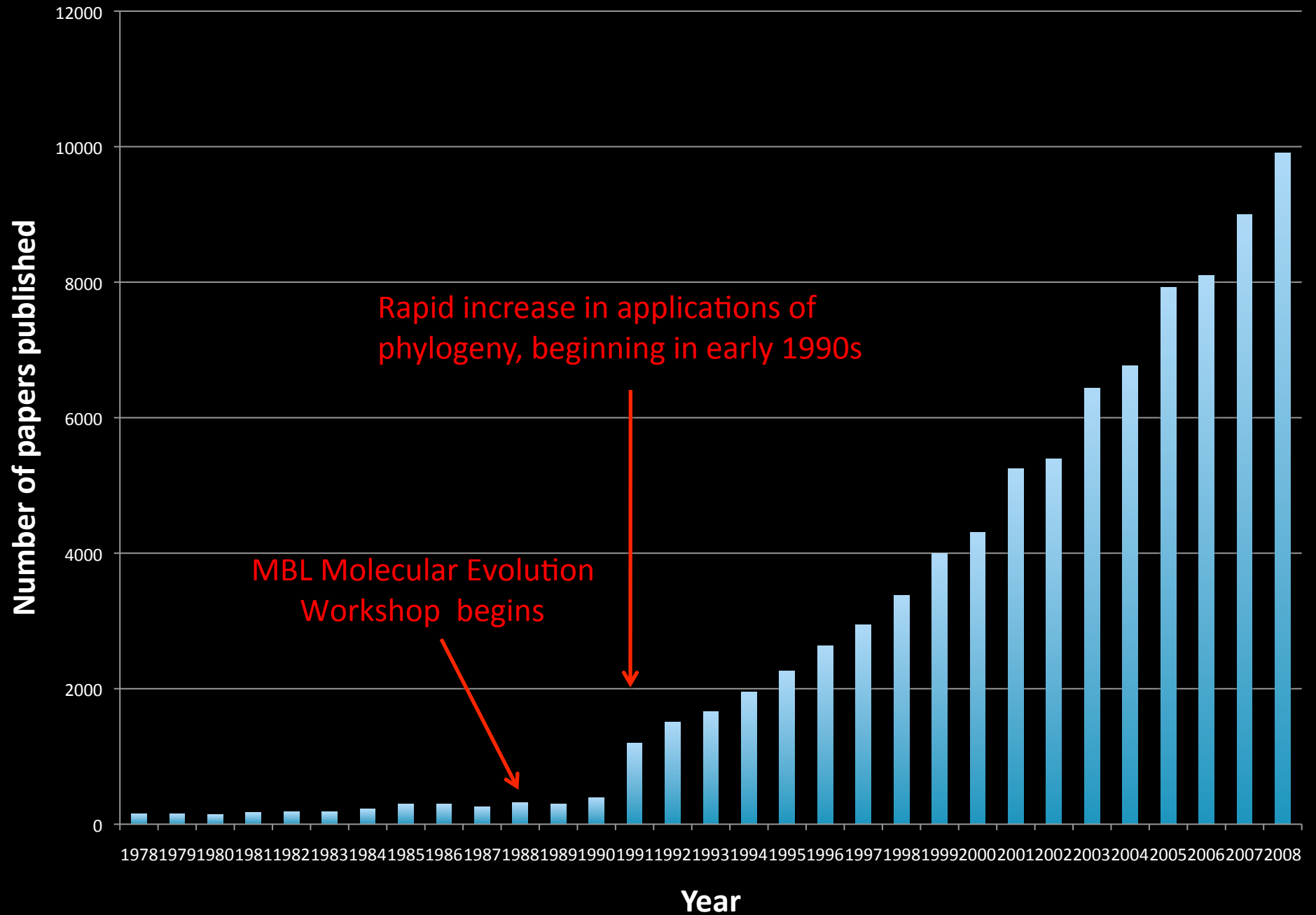
Origins of Emerging Diseases

- Where did HIV come from?
- How did it enter human populations?
- When did it enter human populations?
- How can we prevent similar diseases from entering human populations?

Virus transferred from simian host to humans

HIV-1 (humans)

SIVcpz (chimpanzees)

SIVhoest (L'Hoest monkeys)

SIVsun (sun-tailed monkeys

SIVmnd (mandrills)

SIVagm (African green monkeys)

SIVsm (sooty mangabeys)

HIV-2 (humans)

SIVsyk (Sykes' monkeys)

Common ancestor

Van Heuverswyn et al., *Nature* 444: 164 (2006)

Van Heuverswyn et al., *Nature* 444: 164 (2006)

(A)
1990
1997
1983
1984
1994
1996
1959
1984
1993
1995
1983
1991
1983
1988
1987
1986
1989
1983
1998

Common ancestor of HIV-1 (main group)

Branch length from common ancestor
0   0.03   0.06   0.09   0.12   0.15   0.18

(B)
Average rate of divergence (molecular clock)

Branch length from common ancestor

0.18
0.17
0.16
0.15
0.14
0.13
0.12
0.11
0.10
1980   1985   1990   1995   2000
Year

(C)
0.18
0.15
0.12
0.09
0.06
0.03
0

Confidence limits

1959 sample

Predicted sampling date 1957±10 years

1900 1920 1940 1960 1980 2000
Year

Estimated date for origin of HIV-1 main group

Phylogenetic analysis can be used to trace viral infections through a human population

- Origins of HIV, SARS and other viruses transmitted between animals and humans

- Global virus diversity for vaccine trials

- Epidemiological studies

- Identification of new diseases

- Forensic uses

HIV transmission

Viral transmission events may be traced back
through time among individuals in a population.

To imagine how this is possible, start by considering
the diversity of HIV within one infected individual:

Time 1: Prior to Transmission event

HIV sequence sampled from source
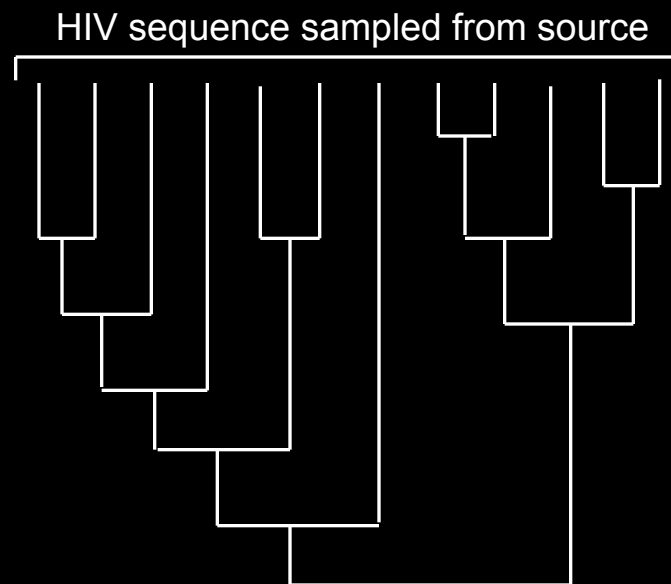
At the transmission event, the HIV in the recipient represents a small subset of the HIV present in the source:

Time 2: The transmission event

To recipient

HIV sequence sampled from source
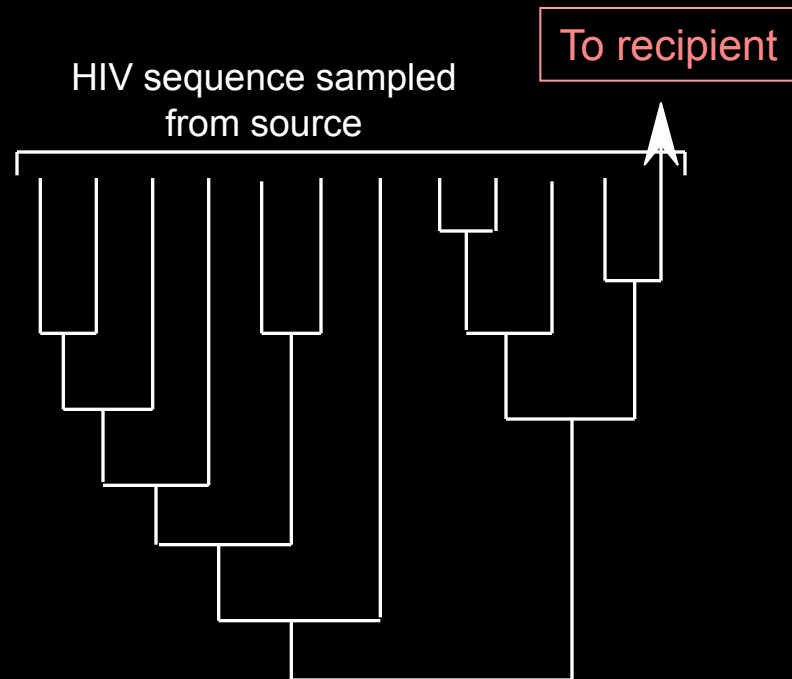
As time passes, HIV lineages in the source and recipient diversify, and other lineages become extinct.

Time 3: Shortly after transmission event
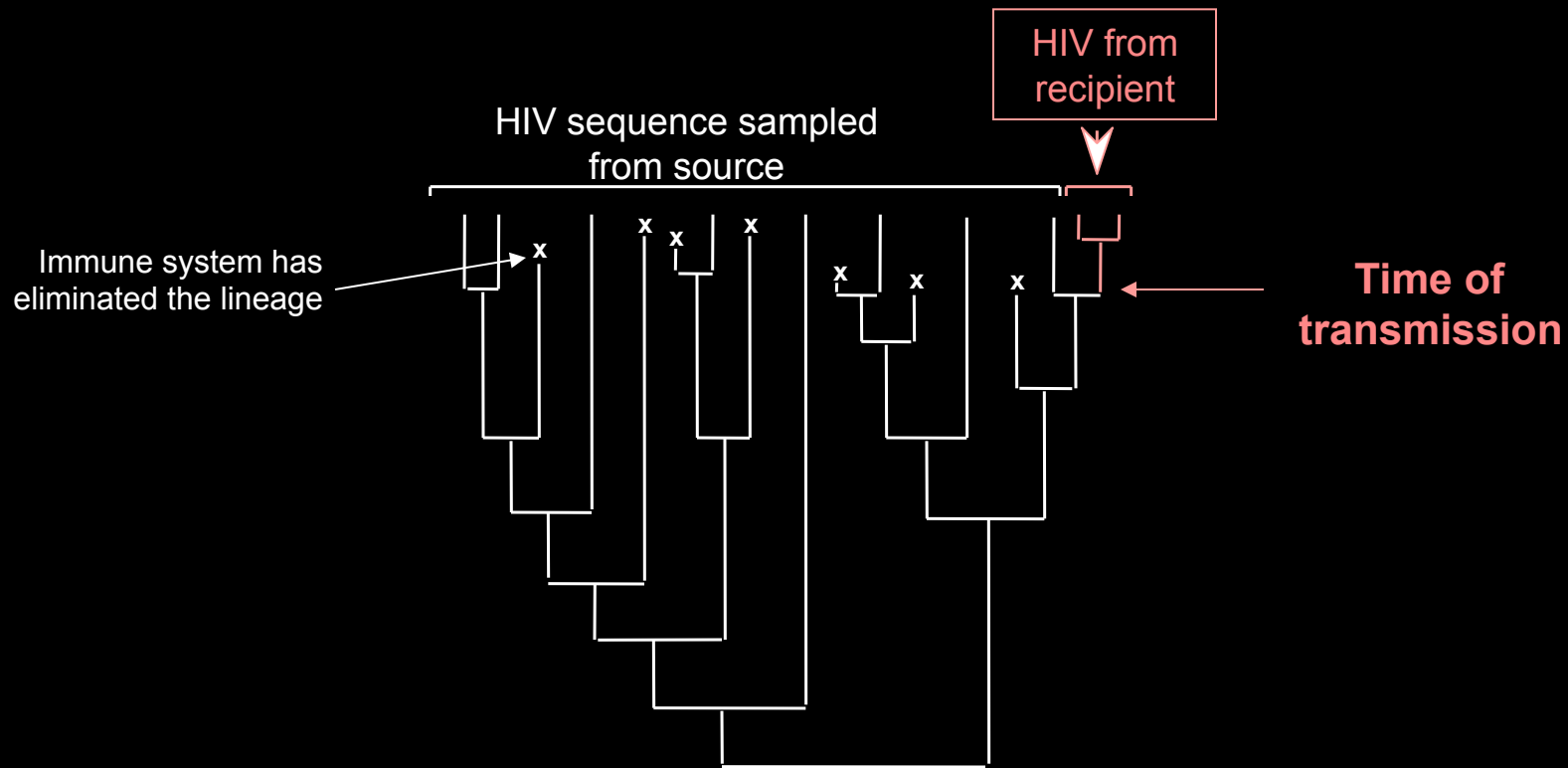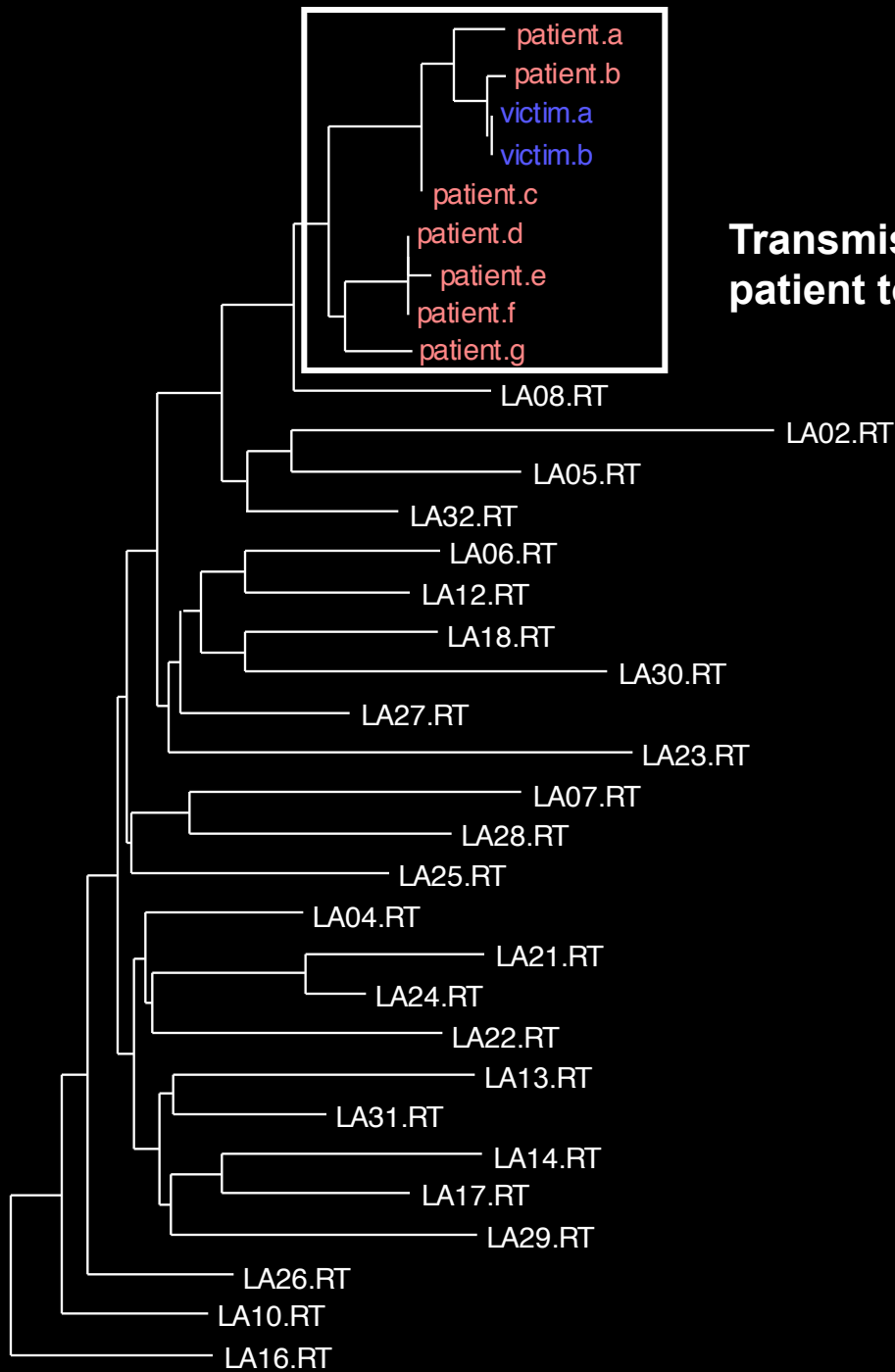
Transmission from patient to victim
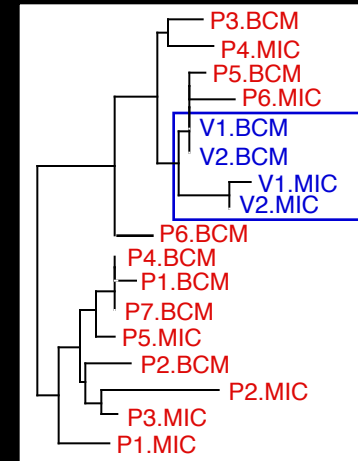
New sequences added

Phylogenetic evidence: *pol* sequences

Metzker et al., 2002
(PNAS 99:14292-14297)

- Schmidt was convicted of attempted murder; currently serving term of 50 years of hard labor

- First use of phylogenetic analysis in U.S. criminal case

- Phylogenetics can be used to trace infections of human pathogens among individuals

Outgroups

CC01
CC08
CC01
CC06
CC05
CC07
CC01
CC02
CC01
CC01
CC04
CC01
CC03

0.005
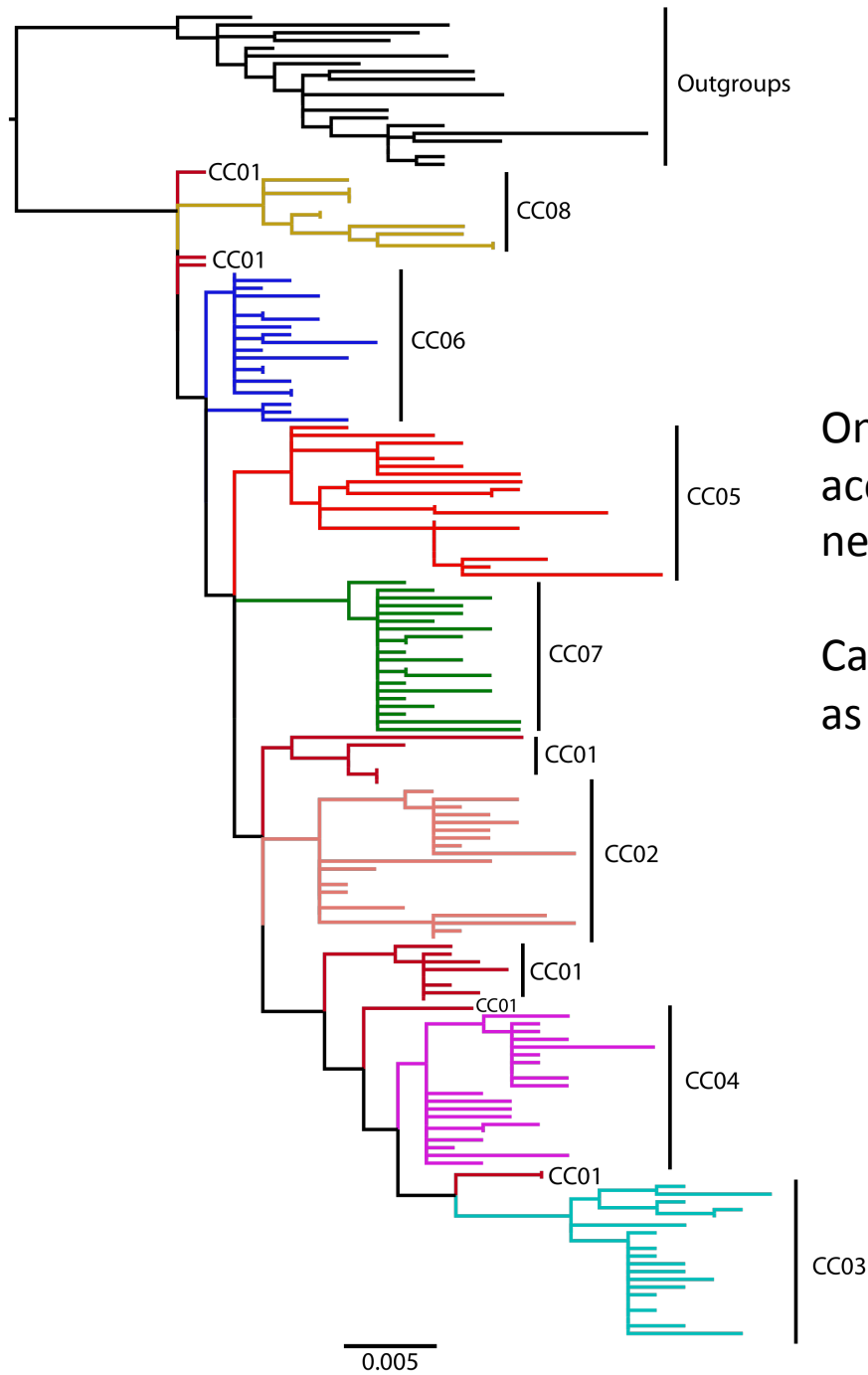
One of these individuals is accused of knowingly and negligently infecting the others.

Can one person be identified as the source of the infections?
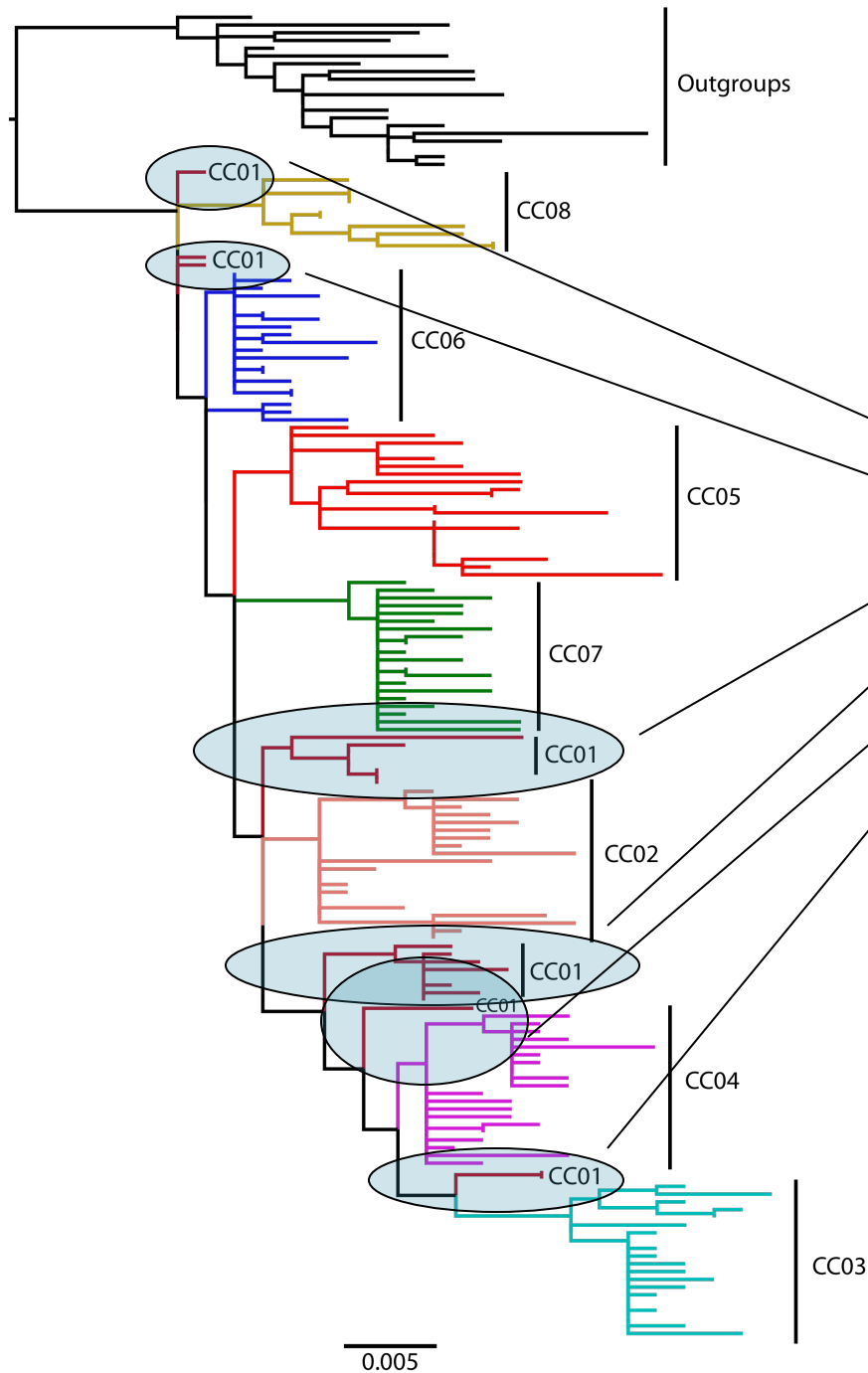
One individual (CC01) is paraphyletic to all the rest. At the trial, CC01 was revealed to be the defendant, who was accused of six counts of motivated assault. He was found guilty by the jury in May 2009.

Outgroups

CC01
CC08
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CC05
CC07
CC01
CC02
CC01
CC01
CC04
CC01
CC03

0.005

Terminology for Trees
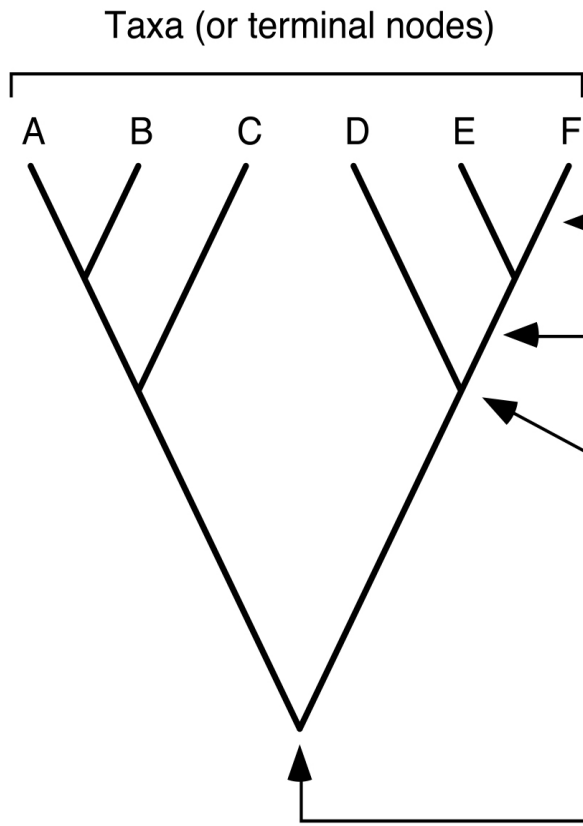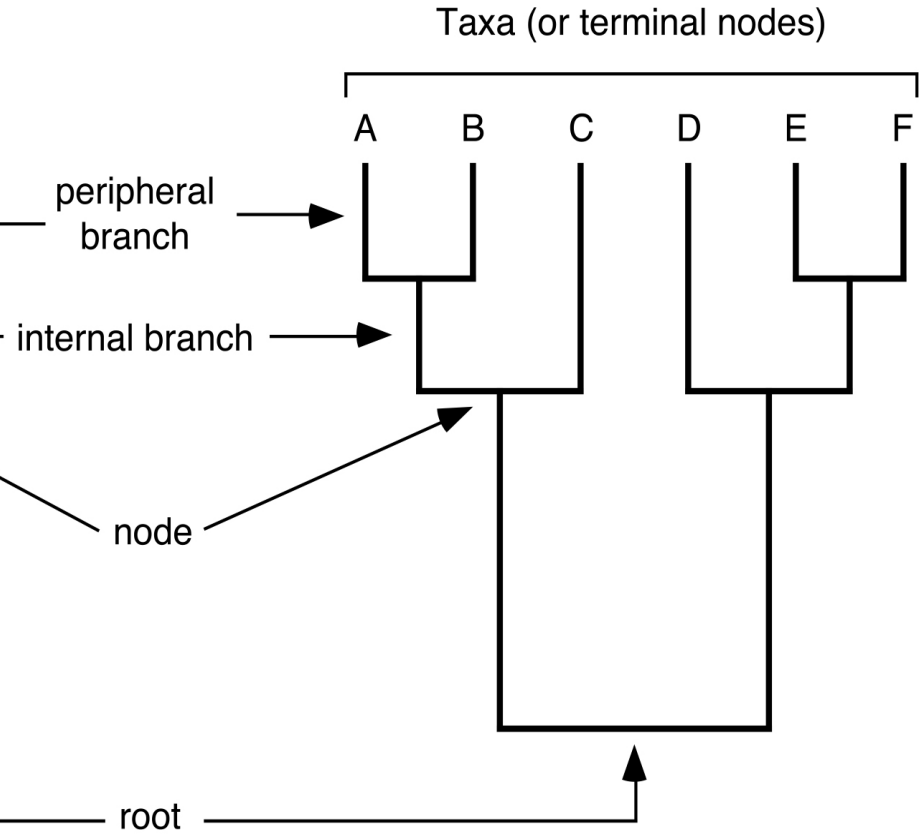
Rooting Trees

- When trees are used to indicate direction of time, they are *rooted*

- One node is identified as the *root*; this can be an existing node or a new node.

- An *unrooted* tree is uninformative with respect to direction of time.

Rooting Trees
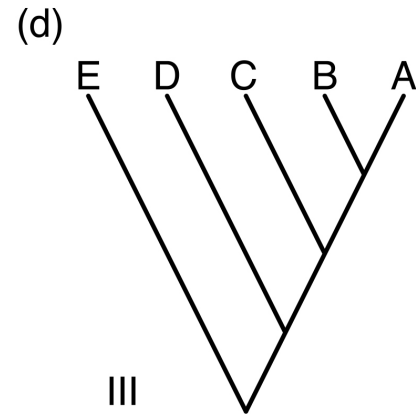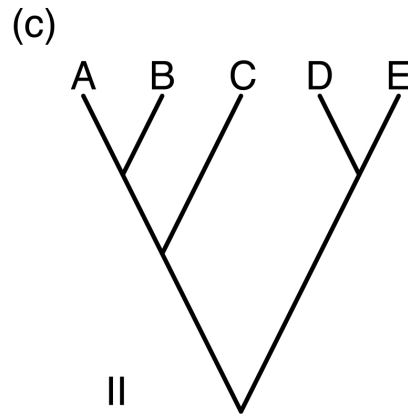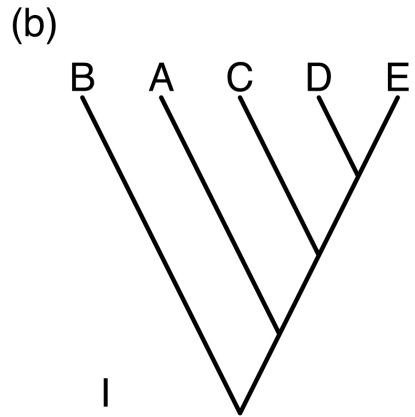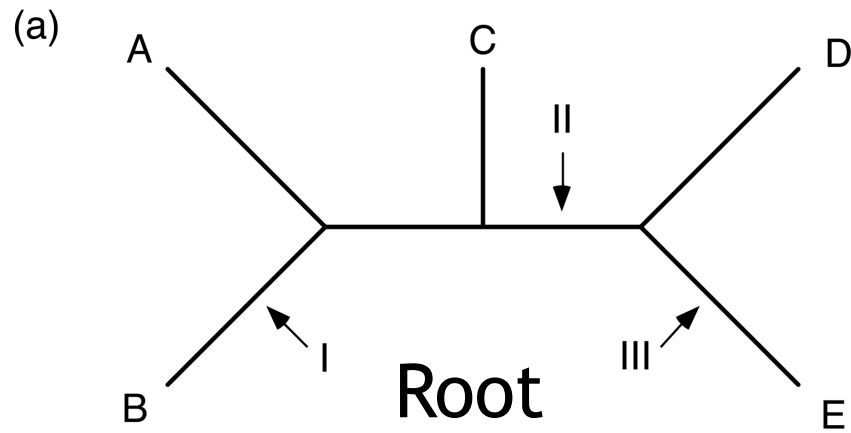
Which are Different?

(A,(B,(C,(D,E)))))

(A,(B,(C,(D,E)))) is called Newick or New Hampshire notation for the tree.

You can read it by following the rules:

- start at a node;
- if the next symbol is '(' then add a child to the current node and move to this child;
- if the next symbol is a label, then label the current node;
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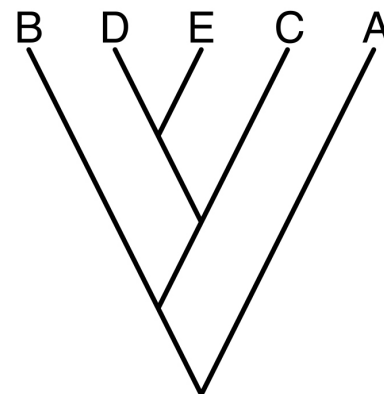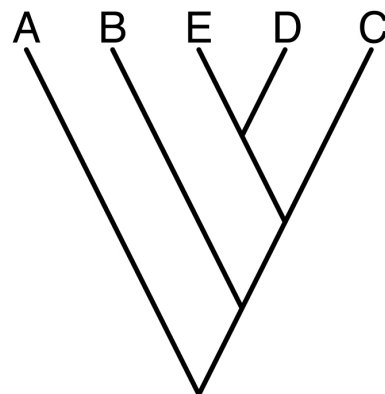
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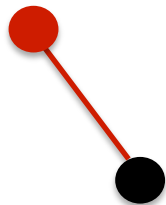
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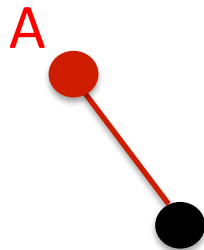
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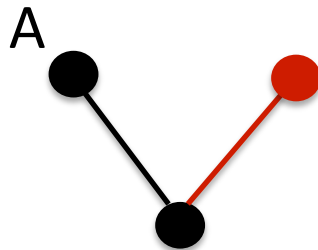
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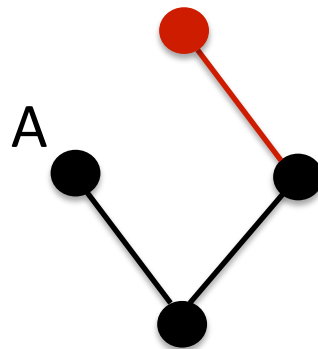
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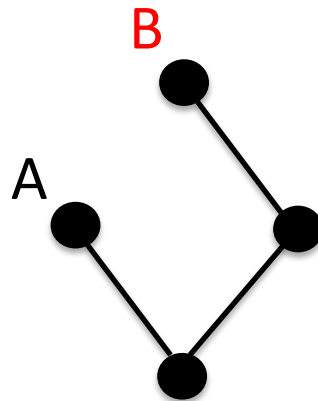
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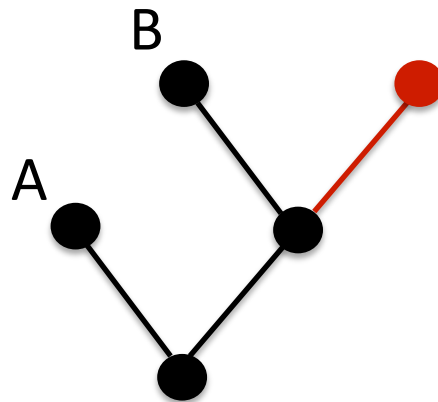
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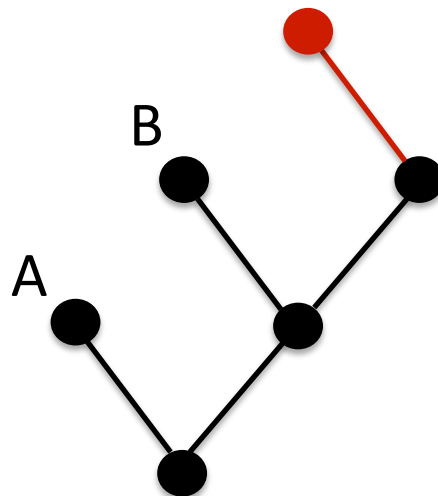
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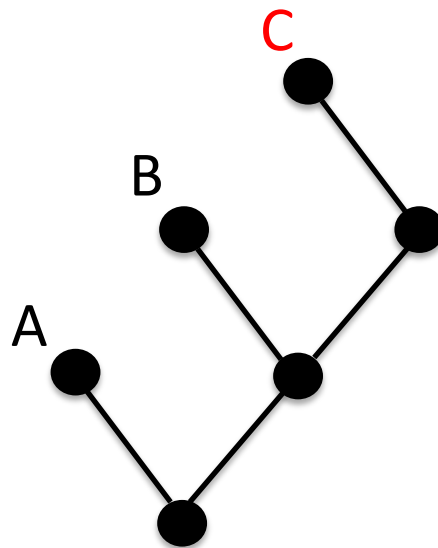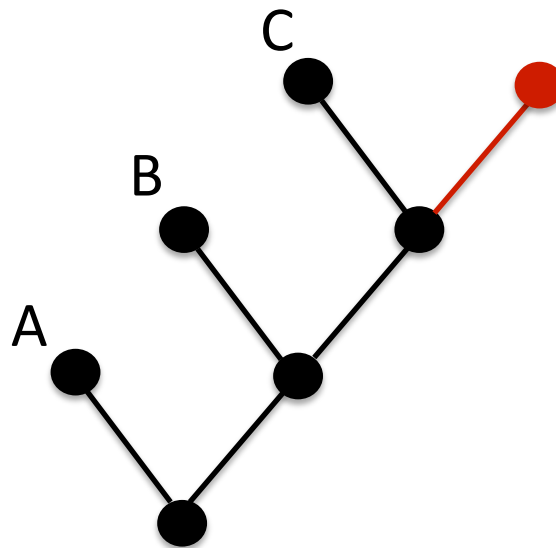•if the next symbol is a ')', then move back to the current node's parent.

(A,(B,(C,(D,E))))

(a) A B C D E

← dichotomy

polytomy →

(b–d) A B C D E   B A C D E   A B C D E

How Big Do Trees Get?

An unrooted, bifurcating tree with T terminal nodes has T – 2 internal nodes. It also has T – 3 internal branches and T peripheral branches, for a total of 2T – 3 branches. Adding a root to the tree also adds a branch, since the root divides one branch into two.

The number of labeled, unrooted binary trees is

$$N_U = \prod_{i=3}^{T}(2i-5)$$

which expands to (2 · 3 – 5)(2 · 4 – 5)(2 · 5 – 5)...(2 · T – 5).

The number of labeled, rooted binary trees is

$$N_R = \prod_{i=2}^{T}(2i-3)$$

which expands to (2 · 2 – 3)(2 · 3 – 3)(2 · 4 – 3)...(2 · T – 3).

Number of Trees

Taxa	Unrooted binary trees	Rooted binary trees
3	1	3
4	3	15
5	15	105
6	105	945
7	945	10,395
8	10,395	135,135
9	135,135	2,027,025
10	2,027,025	3×10^{7}
15	7×10^{12}	2×10^{14}
20	2×10^{20}	8×10^{21}
50	3×10^{74}	
100	2×10^{182}	
1,000	2×10^{2860}	
10,000	8×10^{38658}	
1,000,000	1×10^{5866723}	

What do branch lengths represent?

- They may be drawn of arbitrary length, if not specified

- Or: The estimated, expected, or (rarely) observed amount of character change, measured in some units (e.g., number of substitutions per site)

- Or: They may also indicate time, as estimated from a molecular clock analysis

Phylogenetic methods

- An optimality criterion defines how we measure the fit of data to a given solution

- Tree-searching is a separate step; this is how we search through possible solutions (which we then evaluate with the chosen optimality criterion)

Phylogenetic methods

Three main classes of optimality criteria:

- Nonparametric methods: parsimony and related approaches

- Semi-parametric methods: pairwise distance approaches

- Parametric methods: Likelihood and Bayesian approaches

Advantages of each

Parsimony methods

- Widely applicable to many discrete data types (often used to combine analyses of different data types)
- Requires no explicit model of evolutionary change
- Computationally relatively fast
- Relatively easy interpretation of character change
- Perform well with many data sets

Pairwise distance methods

- Can be used with pairwise distance data (e.g., non-discrete characters)
- Can incorporate an explicit model of evolution in estimation of pairwise distances
- Computationally relatively fast (especially for single-point estimates)

Likelihood-based methods

- Fully based on explicit model of evolution
- Most efficient method under widest set of conditions
- Consistent (converges on correct answer with increasing data, as long as assumptions are met)
- Most straightforward statistical assessment of results; probabilistic assessment of ancestral character states

Disadvantages of each

Parsimony methods

- No explicit model of evolution; often less efficient
- Nonparametic statistical approaches for assessing results often have poorly understood properties
- Can provide misleading results under some fairly common conditions
- Do not provide probablistic assessment of alternative solutions

Pairwise distance methods

- Model of evolution applied locally (to pairs of taxa), rather than globally
- Statistical interpretation not straightforward
- Can provide misleading results under some fairly common conditions (but not as sensitive as parsimony)
- Do not provide probablistic assessment of alternative solutions

Likelihood-based methods

- Require an explicit model of evolution, which may not be realistic or available for some data types
- Computationally most intense

Parsimony Criterion

- Under the parsimony criterion, the optimal tree (the shortest or minimum-length tree) is the one that minimizes the sum of the lengths of all characters in terms of evolutionary steps (a step is a change from one character-state to another).

- For a given tree, find the length of each character, and sum these lengths; this is the tree length.

- The tree with the minimum length is the most-parsimonious tree.

- The most parsimonious tree provides the **best fit** of the data set under the parsimony criterion.

Optimal versus True Tree

There is no guarantee that any criterion
will necessarily identify the "true" tree.
These are simply criteria for choosing
which tree best fits a dataset

Optimization

- In parsimony, this involves minimizing the number of changes of a character across a tree (the *length* of the character)

- The optimization involves estimating the state at all internal nodes.

- It is possible for a character to have more than one best optimization.

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- It is possible for a character to have more than one best optimization.

Observed states at tips

0

1

0

0

0

1

Inferred states at internal nodes

0

0

1

1

1

0

1

A C C G C G A A

{C}

{A}

{GA} | 1 |

{CGA} | 1 |

{G}

{CG} | 1 |

{ACG} | 1 |
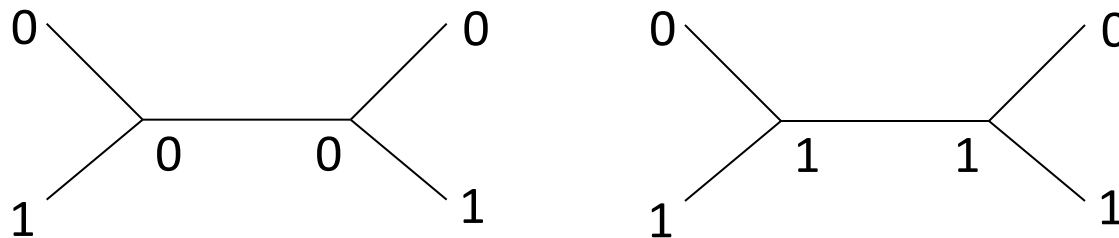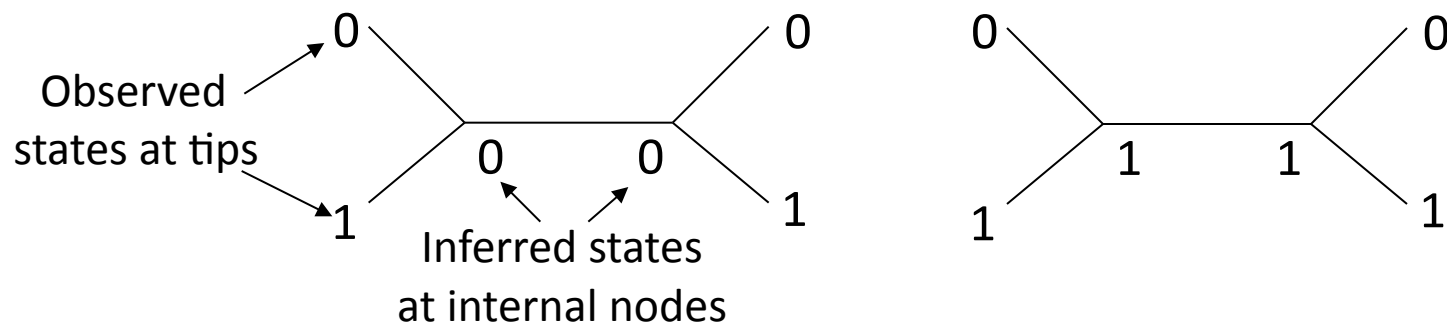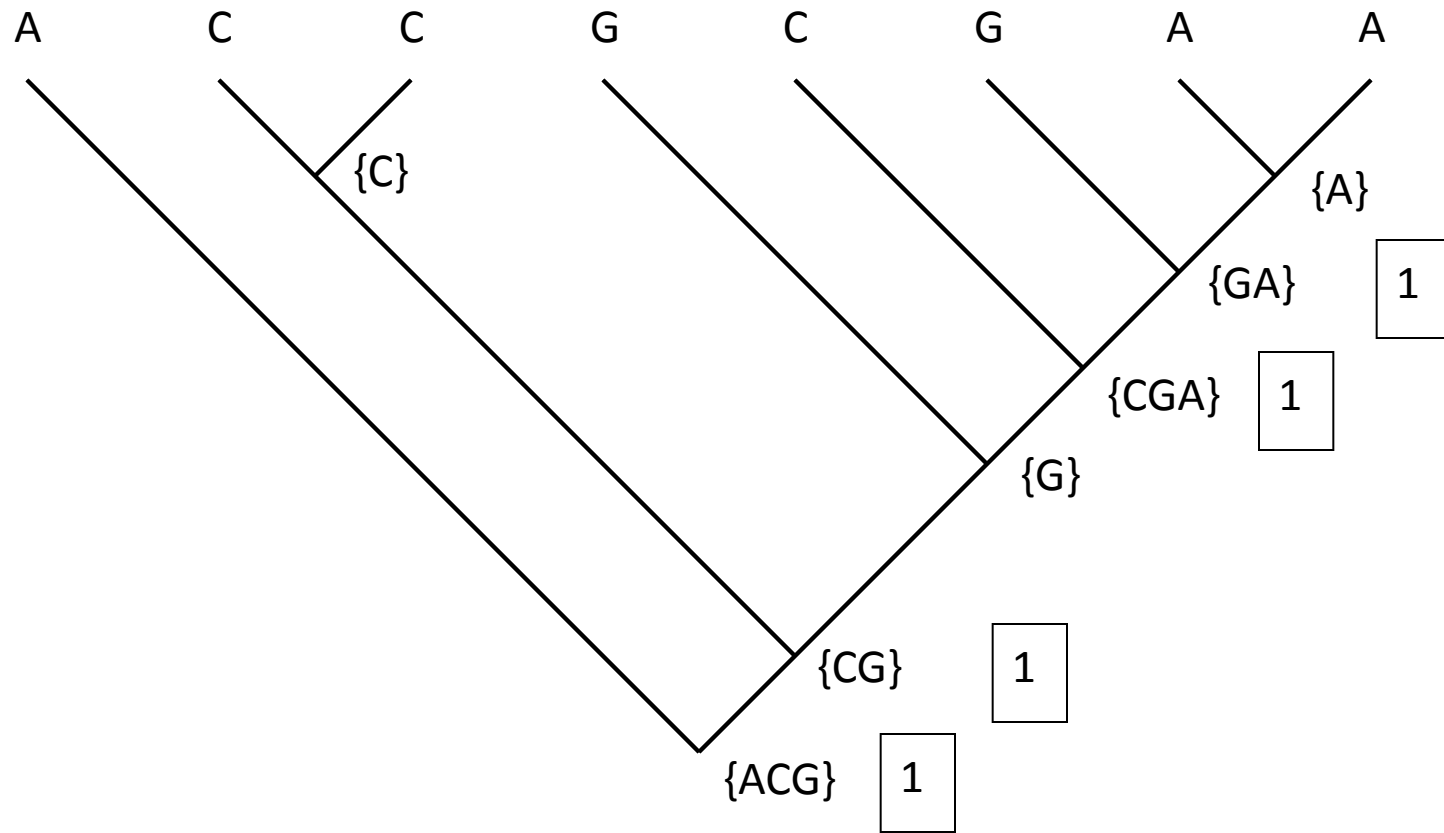
Downpass (postorder traversal)   Length = 4

A   C   C   G   C   G   A   A

{C} ⟶ C

{A} ⟶ A

{GA} ⟶ G

{CGA} ⟶ G

{G} ⟶ G

{CG} ⟶ G   (or C)

{ACG} ⟶ A
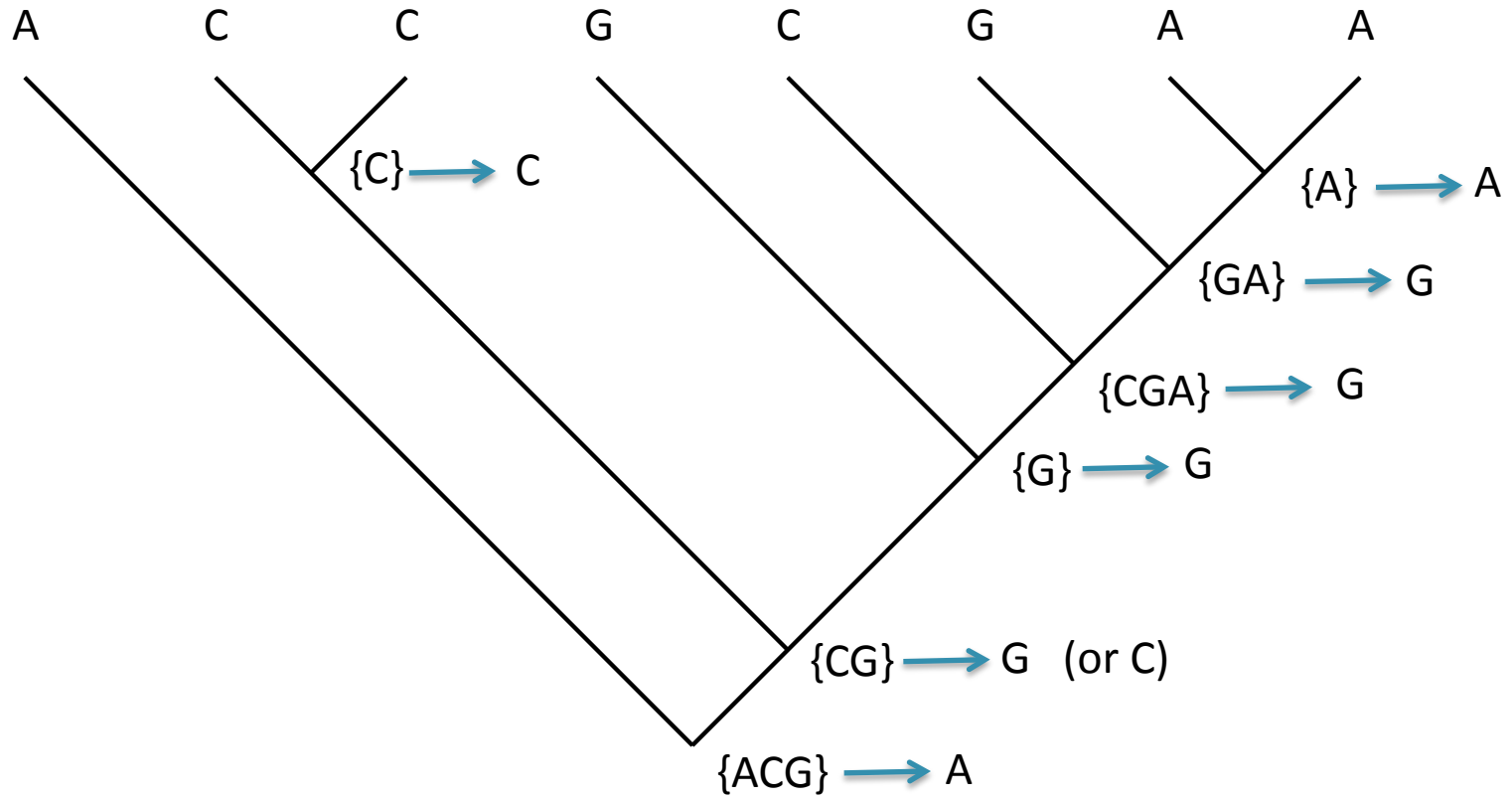
Up-Pass (preorder traversal)

Length = 4
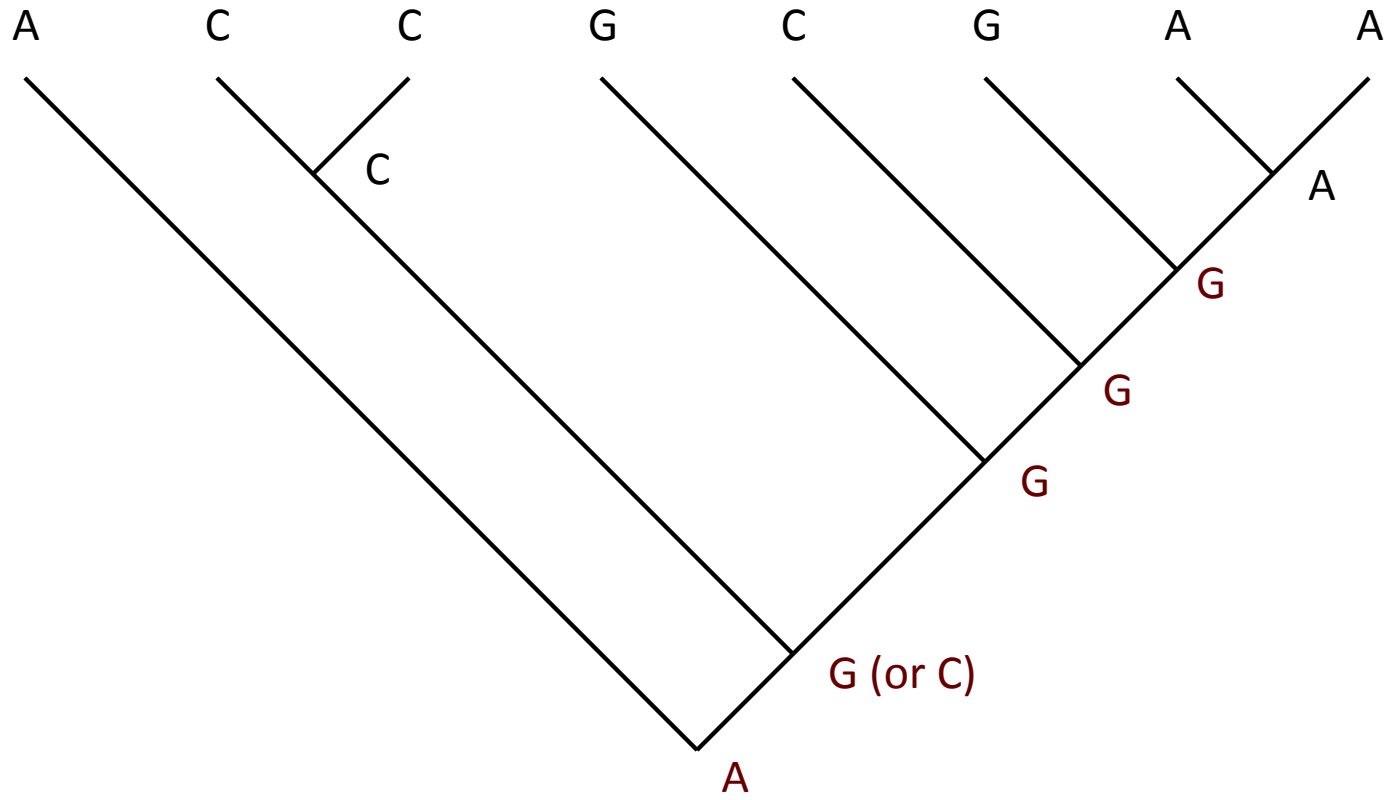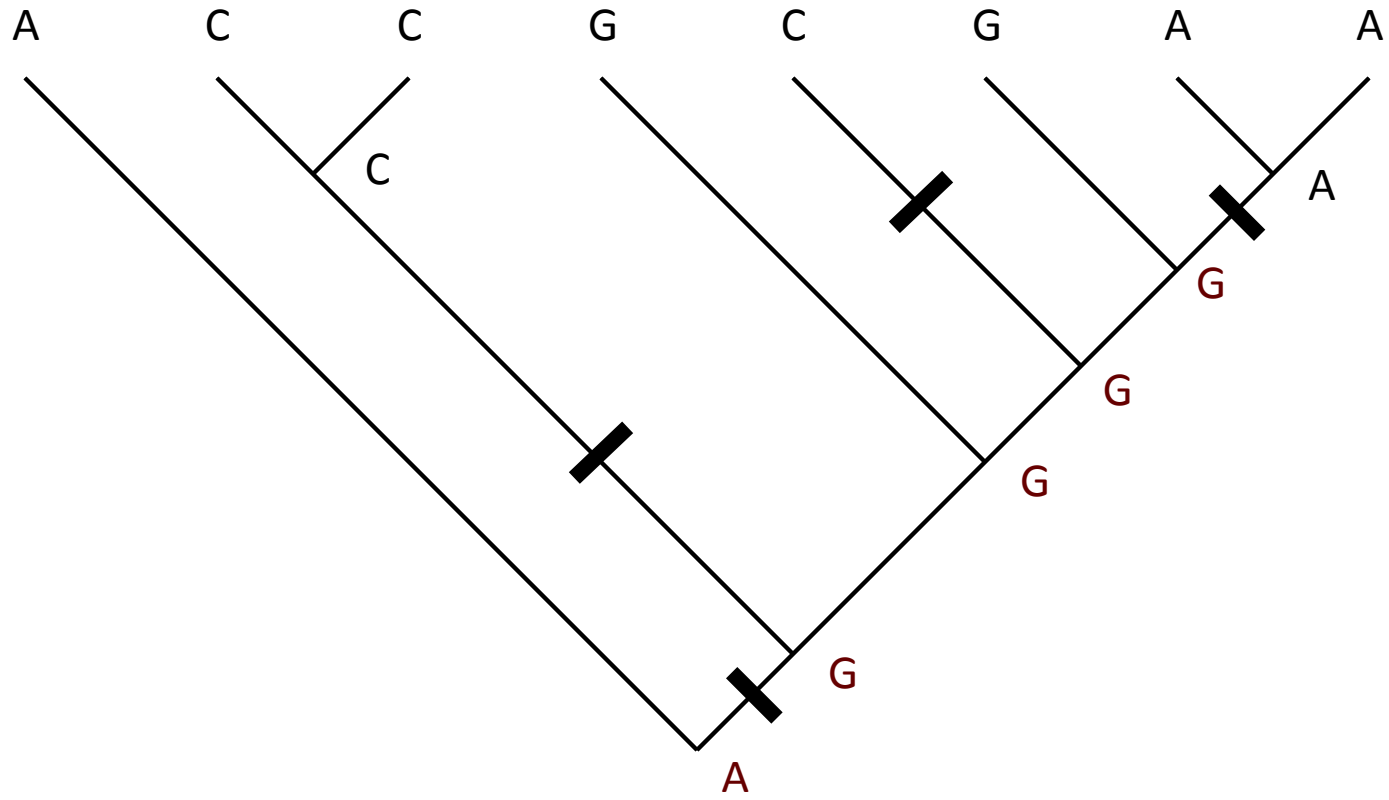
Weighted Parsimony

- Transformations among character-states do not need to be weighted equally

- Can account for different weights between transitions and transversions, for example

- A way to approximately incorporate some aspects of models of evolution

Pairwise distances

- Distances summarize character differences between objects (terminals, taxa).

- Pairwise distances are computationally quick to calculate.

- Character differences cannot be recovered from distances, because different combinations of character states can yield the same distance.

- Characters cannot be compared individually, as in discrete character analyses.

- The distances in a matrix are not independent of each other, and errors are often compounded in fitting distances to a tree.

	Characters				
Taxa	1	2	3	4	5
one	A	G	C	G	A
two	A	G	C	G	T
three	C	T	C	G	T
four	C	T	C	A	A

Start with a data matrix of the usual form

Taxa	Characters				
	1	2	3	4	5
one	A	G	C	G	A
two	A	G	C	G	T
three	C	T	C	G	T
four	C	T	C	A	A
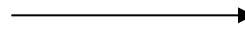
	one	two	three	four
one	-	.2	.6	.6
two		-	.4	.8
three			-	.4
four				-

Compute a distance matrix of observed *proportional* distances

Intuition of sequence divergence vs evolutionary distance

1.0

p-dist

0.0

This can't be right!

Evolutionary distance

0.0 ∞
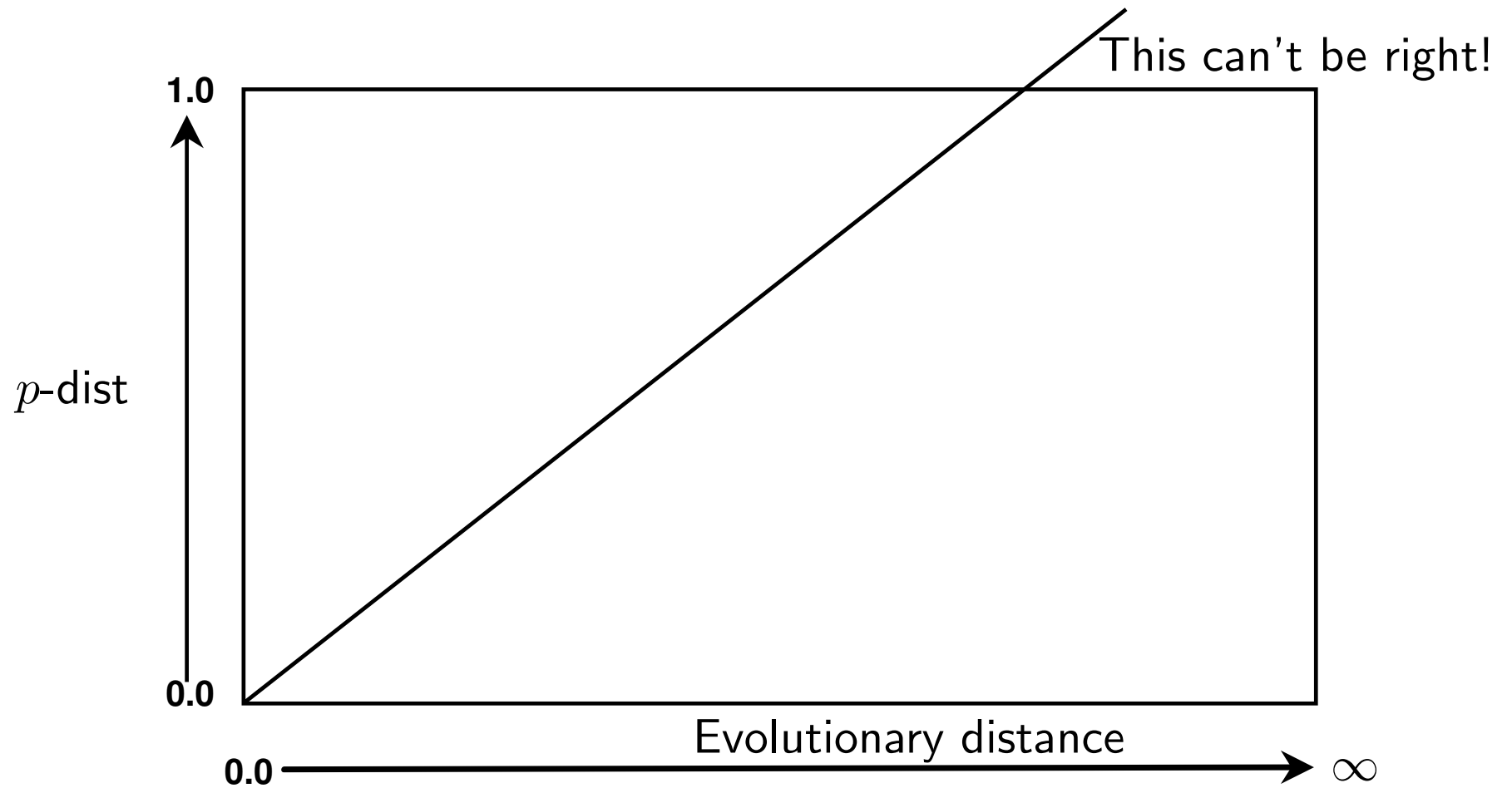
Sequence divergence vs evolutionary distance

	Characters				
Taxa	1	2	3	4	5
one	A	G	C	G	A
two	A	G	C	G	T
three	C	T	C	G	T
four	C	T	C	A	A

	one	two	three	four
one	-	.2	.6	.6
two		-	.4	.8
three			-	.4
four				-

Transform the distance matrix (d_{ij}) into a matrix of evolutionary (corrected) distances, using a model of evolution to account for superimposed changes (reversal, convergences, multiple changes, etc.). This is where the parametric model is applied (to many separate 2-taxon "trees").
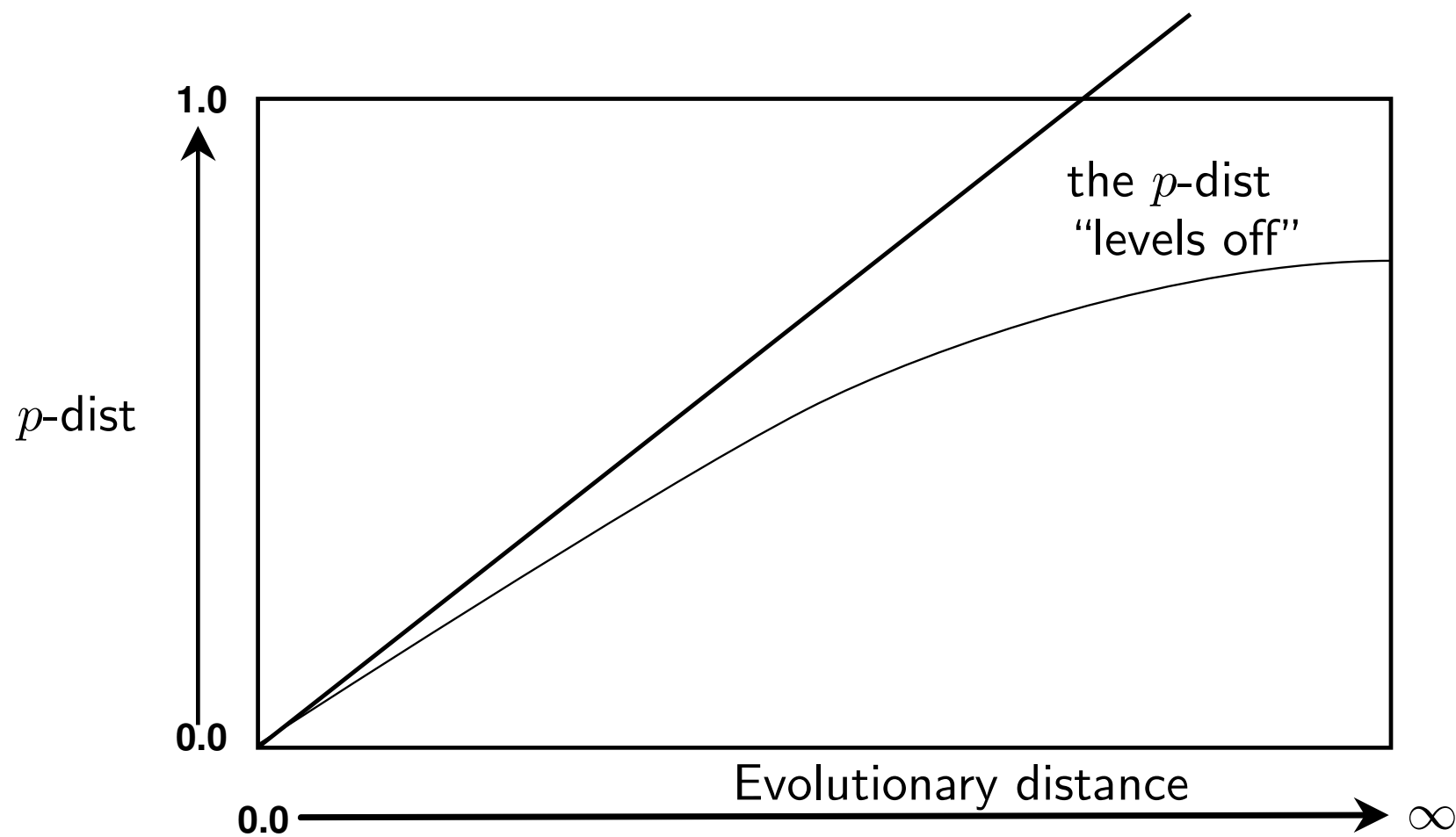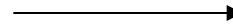
Model of evolution

	one	two	three	four
one	-	.21	.63	.63
two		-	.42	.85
three			-	.42
four				-

Find the tree and branch lengths that result in the best match (using an objective function) between the corrected distance matrix (d_{ij}) and the patristic distance matrix (p_{ij}) (the matrix of path-length distances)

three

0.20

one

0.105

0.21

0.105   two

0.32

four

	one	two	three	four
one	-	.21	.515	.635
two		-	.515	.635
three			-	.52
four				-
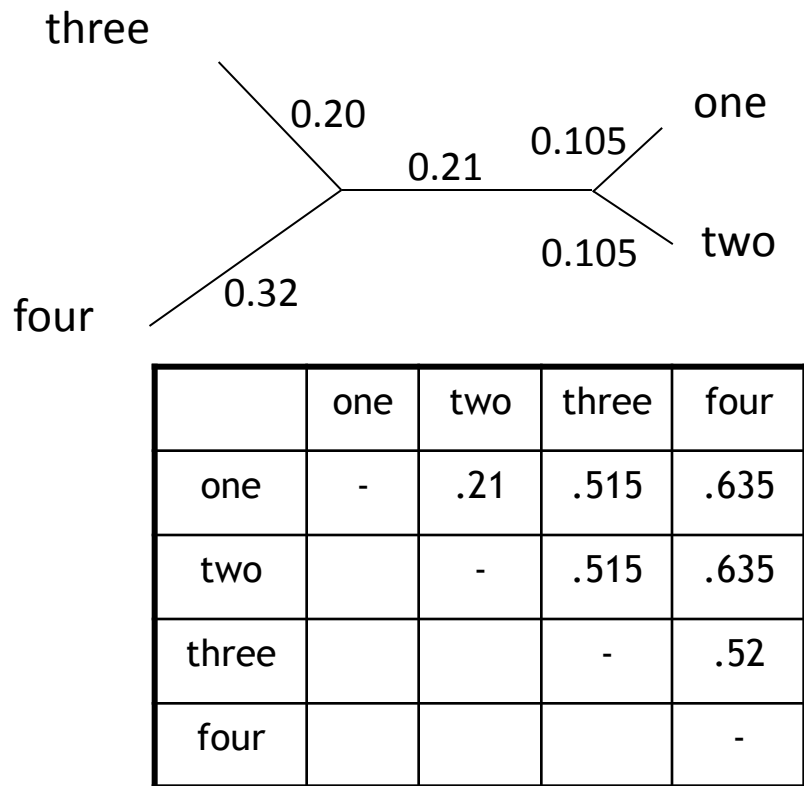
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four				-
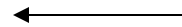
Optimality Criteria using Pairwise Distances

- Two commonly used objective functions:
  - Fitch-Margoliash
  - Minimum Evolution

- The general strategy is to find a set of patristic distances (path-length distances) for the branches so as to minimize the difference between the evolutionary distances and the patristic distances.

Pairwise Distance Methods

- Fitch-Margoliash family

$$Fit = \sum_{1 \le i < j < n} \omega_{ij} \left| d_{ij} - p_{ij} \right|^{\alpha}$$

i = taxon i
j = taxon j, up to n
d = evolutionary distance
p = patristic or tree distance
w = weight
Exponent: 2 = least squares
    1 = absolute difference

Common weights
$w_{ij} = 1$
$w_{ij} = 1/d_{ij}$
$w_{ij} = 1/d^2_{ij}$

Pairwise Distance Methods

- Minimum Evolution

$$Fit = \sum_{1 \le i < j < n} \omega_{ij} \left| d_{ij} - p_{ij} \right|^{\alpha}$$

1. Use w = 1 and alpha = 2 to fit branch lengths l_i
2. Pick the tree that minimizes the sum of the branch lengths, *L*, over all branches (this is parsimony in spirit):

$$L = \sum_{i=1}^{2n-3} l_i$$

Algorithmic Methods for Distance Trees

- UPGMA--unweighted pair-group method using arithmetic means

  (not widely used anymore...requires

   equal rates of change)
- Neighbor-joining--an approximation method for the minimum evolution criterion

Likelihood

- Imagine that we are given a coin, and flip it n times, getting h heads: these are our data (D)
- We can explore various hypotheses (H) about the coin, which may have implicit and explicit components:

  - The coin has a p_h probability of landing on heads
  - The coin has a heads side and a tails side
  - Successive flips of the coin are independent
  - The flipping process is fair
  - etc.

Coin flipping

- The likelihood (*L*) is proportional to the probability of observing our data, given our hypothesis:

$$L(H \mid D) \propto P(D \mid H)$$

- The probability of getting the outcome *h* heads on *n* flips is given by the binomial distribution:

$$P(h,n \mid p_h) = \binom{n}{h} (p_h)^h (1 - p_h)^{n-h}$$

(Likelihood score)

Coin flipping

- The expression $\begin{pmatrix} n \\ h \end{pmatrix}$ gives the binomial coefficients, or the number of different ways to (for example) get 4 heads in 10 flips

- We can ignore that term to look at the probability of a particular sequence of heads and tails (to make it more like the case of a particular observed sequence of nucleotides)

Coin flipping

- Let's try applying this to some data
    - Dataset 1 : A particular sequence of
        H T H T T T H T T H

- Assume a particular hypothesis
    - Try $p_h = 0.5$

- This gives us a likelihood score of

$$L(p_h = 0.5 \,|\, obs) = (0.5)^4 (0.5)^6 = 0.000976563$$

Coin flipping

- What does the likelihood score tell us about the likelihood of our hypothesis? In isolation, nothing, because the score is dependent on the particular data set. The score will get smaller as we collect more data (flip the coin more times).

- Only the *relative* likelihood scores for various hypotheses, evaluated using the same data, are useful to us.

- What are some other models?

$$L(p_h = 0.6 \mid obs) = (0.6)^4 (0.4)^6 = 0.000530842$$

$$L(p_h = 0.4 \mid obs) = (0.4)^4 (0.6)^6 = 0.001194394$$

The likelihood surface
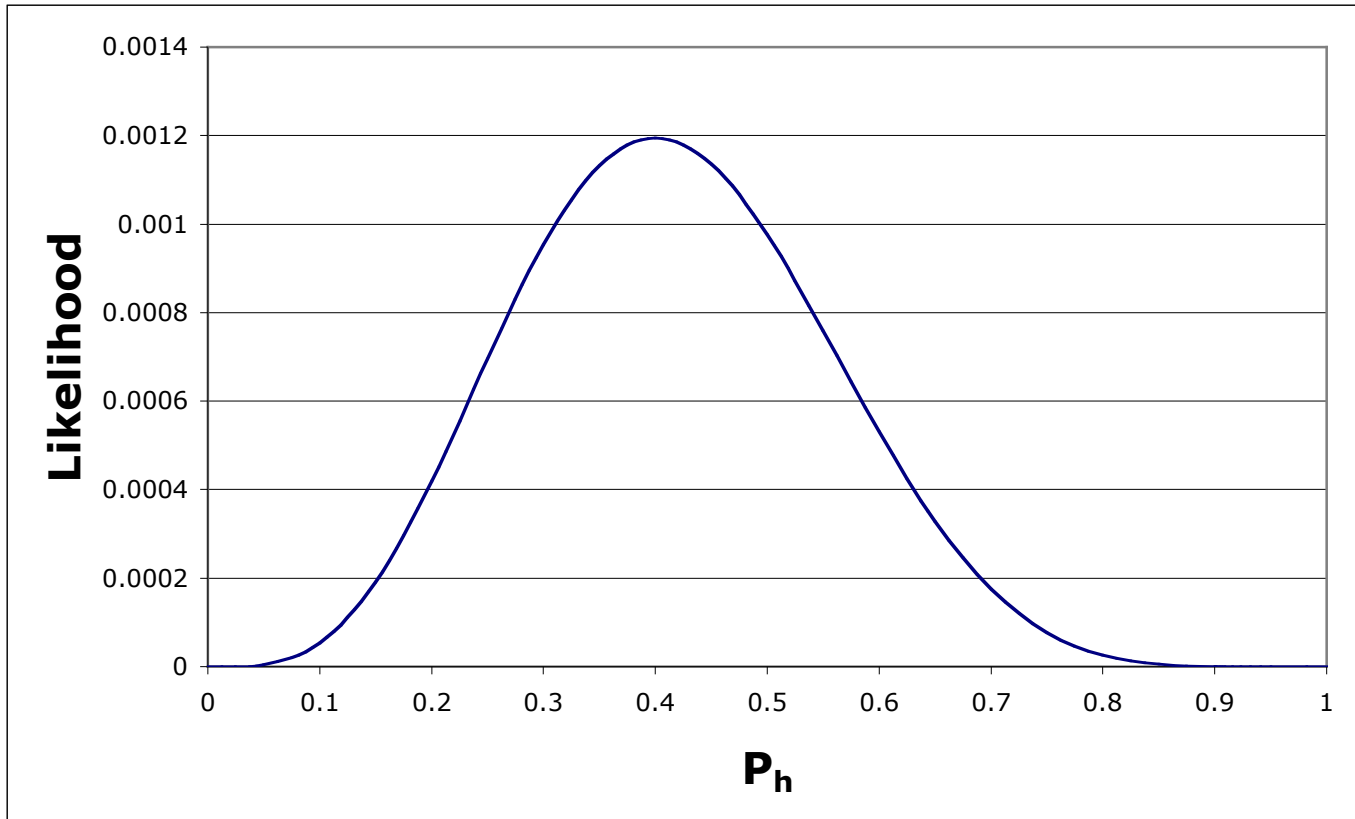
Data: H T H T T T H T T H

The log likelihood surface
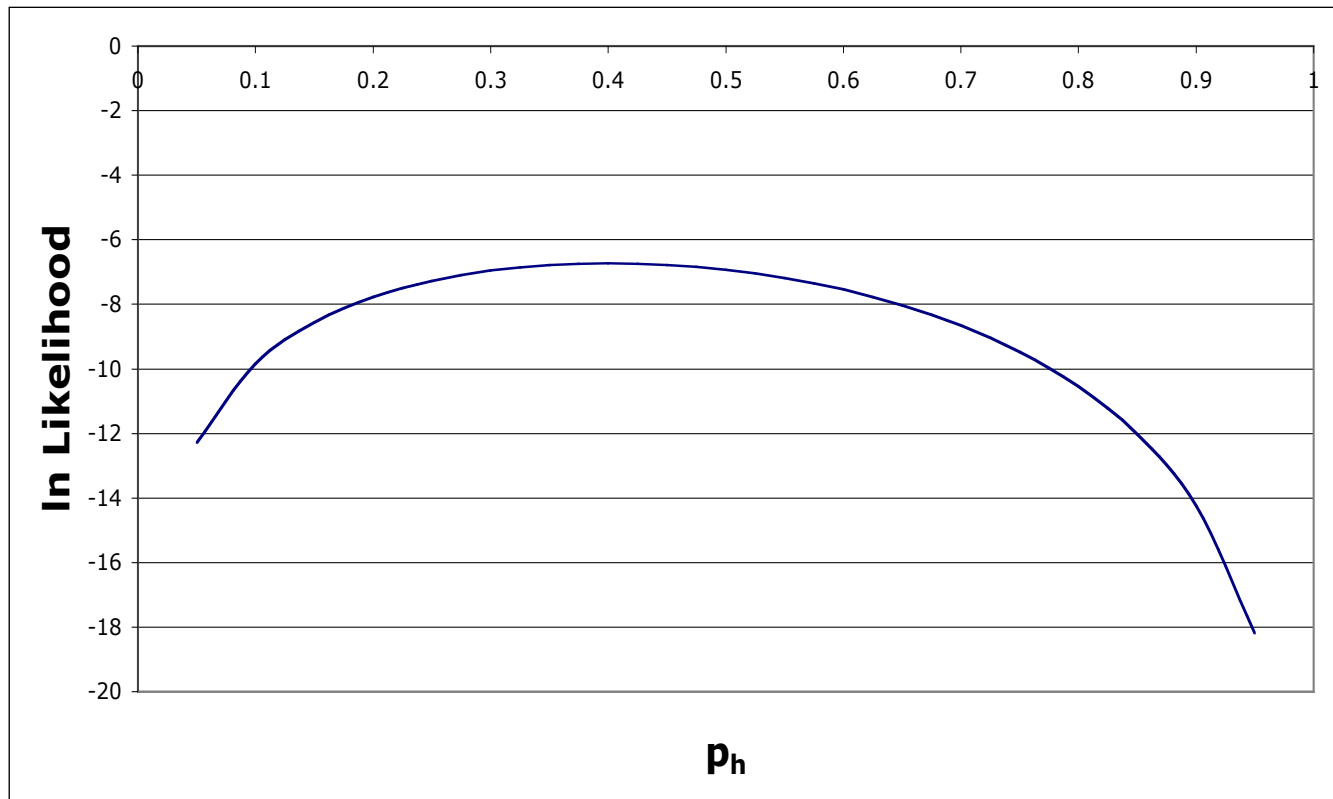
Data: H T H T T T H T T H

Other data
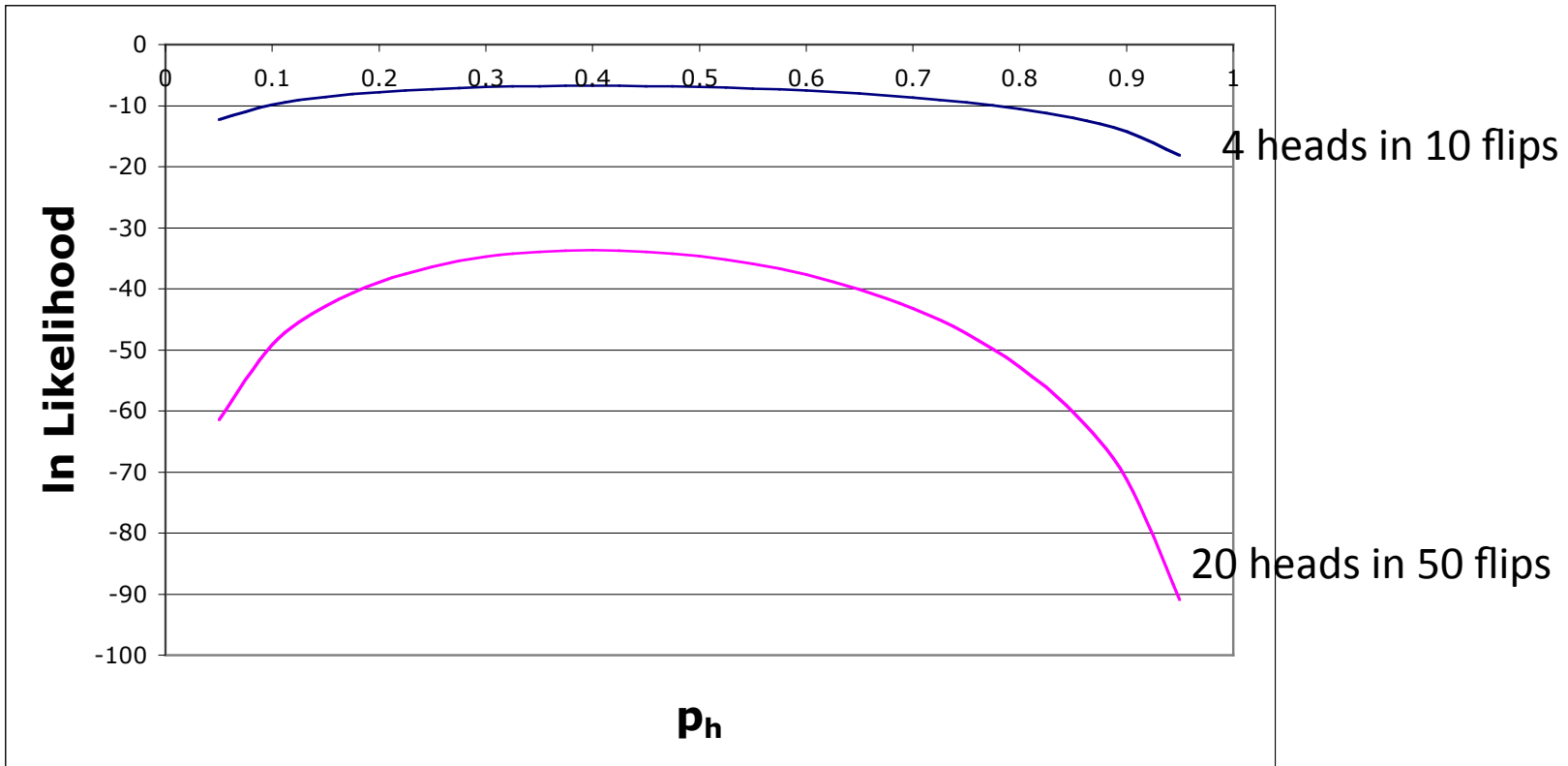
Likelihood

- Likelihood ($H|D$) is proportional to P ($D|H$)
- Components of the hypothesis can be explicit and implicit
- Only relative likelihoods are important in evaluating hypotheses
- The point on the likelihood curve that maximizes the likelihood score (the MLE) is our best estimate given the data at hand
- Likelihood scores can't be compared between datasets
- More data lead to more peaked surfaces (i.e., better ability to discriminate among hypotheses)

Likelihood in Phylogenetics

- In phylogenetics, the data are the observed characters (e.g., DNA sequences) as they are distributed across taxa
- The hypothesis consists of the tree topology, a set of specified branch lengths, and an explicit model of character evolution.
- Calculating the likelihood score for a tree requires a very large number of calculations

Bayesian Approaches

- Take prior information into account

$$P(A|B) = \frac{P(B|A) \; P(A)}{P(B)}$$

(Bayes Theorem)

Reverend Thomas Bayes, 1701-1761

Bayesian Approaches

- Take prior information into account

$$P(A|B) = \frac{P(B|A) \quad P(A)}{P(B)}$$

Posterior probability

Bayesian Approaches

- Take prior information into account

$$P(A|B) = \frac{P(B|A) \quad P(A)}{P(B)}$$

The support that *B* provides for *A*

Bayesian Approaches

- Take prior information into account

$$P(A|B) = \frac{P(B|A) \; P(A)}{P(B)}$$

Prior information about A
(the initial expectation for A)

Bayesian Approaches

- An example:
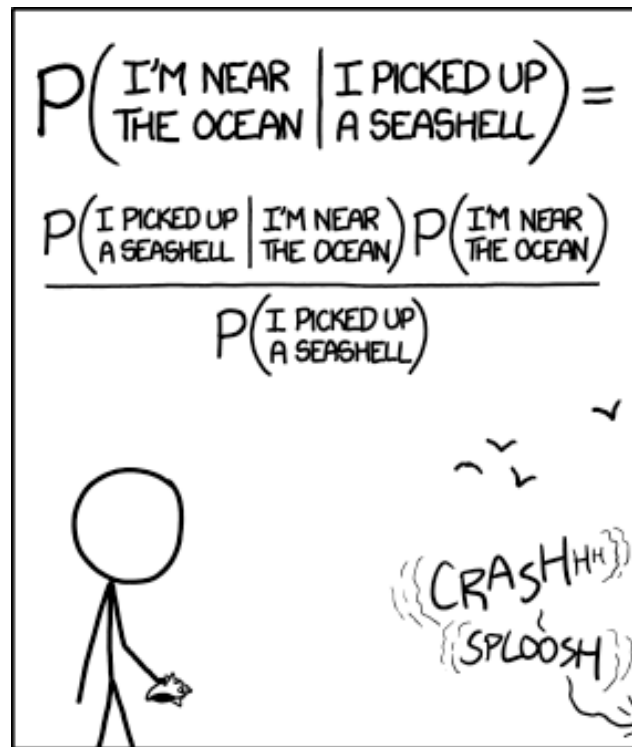
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- Optimality criterion (likelihood-based methods have best performance, as long as assumptions of model are met)

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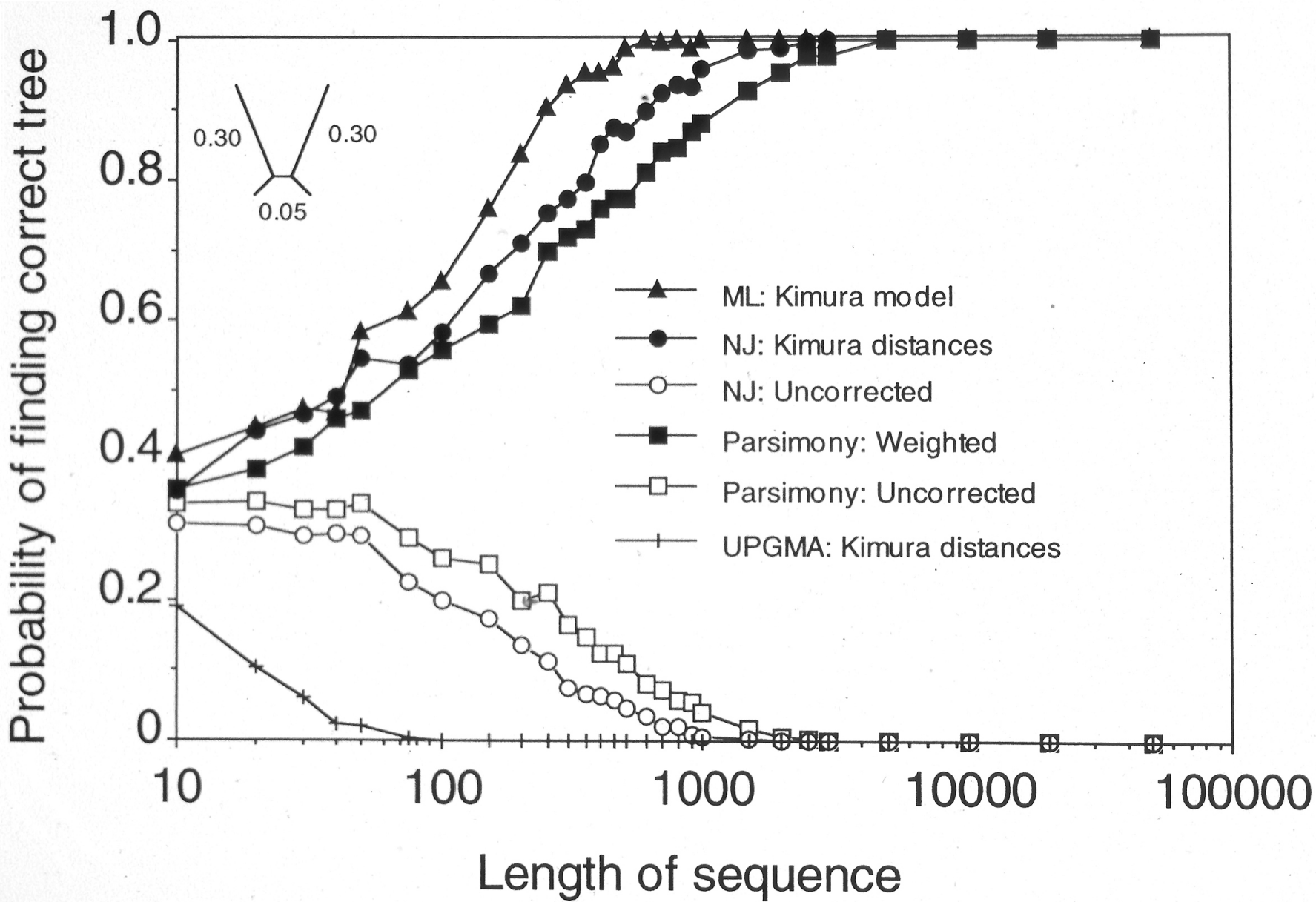
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- Model selection (finding an appropriate model of evolution for the data at hand)
- Sampling density of genes (more genes provide more information, and allow resolution of species trees from gene trees)
- Thoroughness of tree search (finding best solutions)
- Sampling density of taxa (more thorough taxon sampling produces better estimates of parameters and results in better estimates of trees)

A

Lama glama
Sus scrofa
Hippopotamus amphibius
Megaptera novaeangliae
Tursiops truncatus
Tragelaphus eurycerus
Okapia johnstoni
Equus caballus
Ceratotherium simum
Tapirus indicus
Manis pentadactyla
Panthera onca
Felis catus
Leopardus pardalis
Canis familiaris
Ursus arctos
Artibeus jamaicensis
Nycteris thebaica
Pteropus giganteus
Rousettus lanosus
Erinaceus concolor
Sorex araneous
Asioscalops altaica
Condylura cristata
Erethizon dorsatum
Agouti taczanowskii
Cavia tschudii
Hydrochoeris hydrochaeris
Myocastor coypus
Dinomys branickii
Hystrix brachyura
Heterocephalus glaber
Pedetes capensis
Cricetus griseus
Mus musculus
Rattus norvegicus
Castor canadensis
Dipodomys heermanni
Tamias striatus
Muscardinus avellanarius
Sylvilagus floridanus
Ochotona hyperborea
Tupaia minor
Cynocephalus variegatus
Macaca mulatta
Hylobates concolor
Homo sapiens
Ateles fusciceps
Callimico goeldii
Lemur catta
Tarsius sp.
Choloepus hoffmanni
Choloepus didactylus
Tamandua tetradactyla
Myrmechophaga tridactyla
Euphractus sexcinctus
Chaetophractus villosus
Procavia capensis
Trichechus manatus
Loxodonta africana
Echinops telfairi
Orycteropus afer
Macroscelides proboscideus
Elephantulus rufescens
Didelphis virginianus
Macropus eugenii

0.1

B

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