

BI694
Bioinformatics & Phylogenetics

Winter Semester 2017

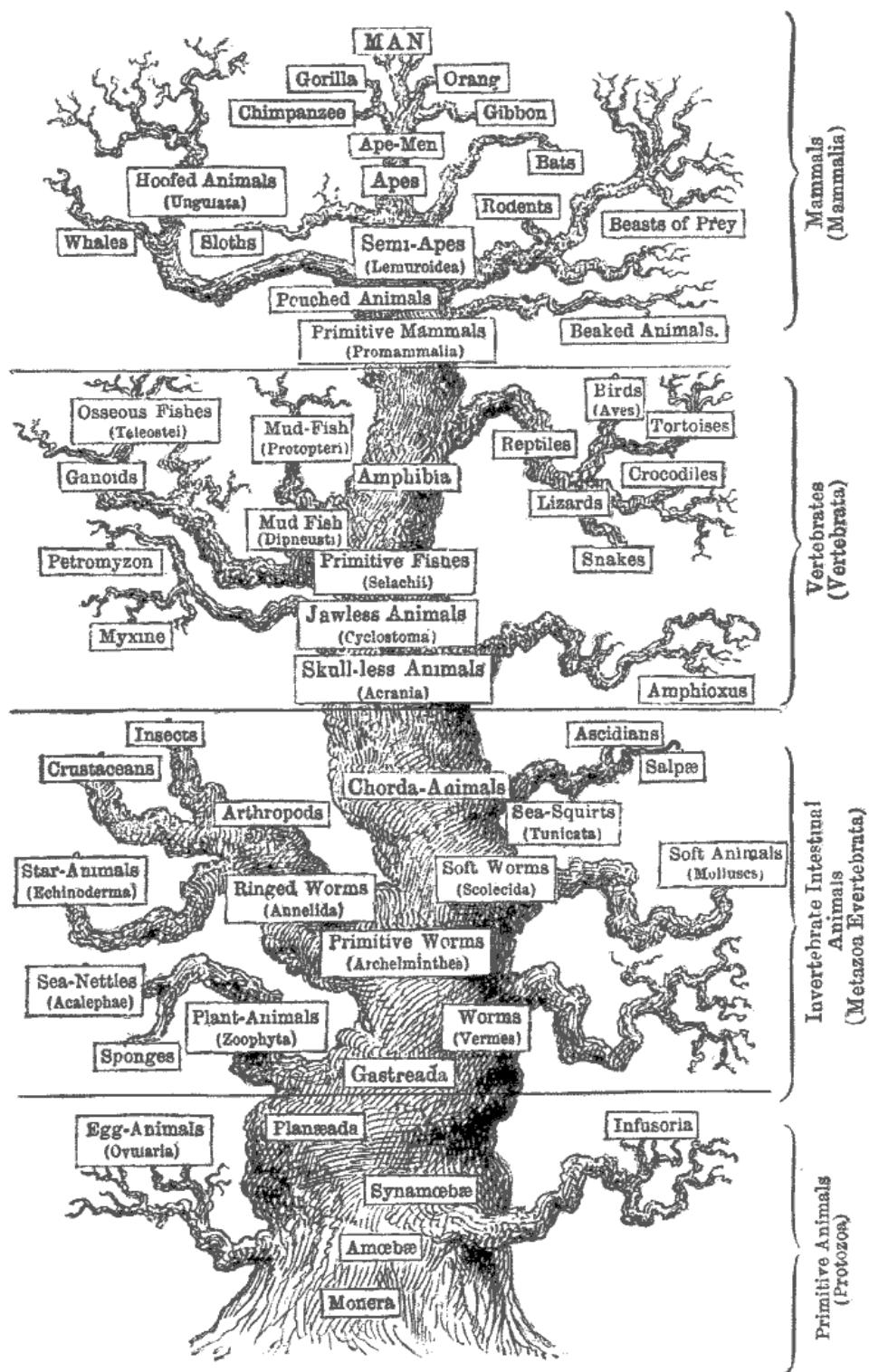
WEEK 10
Intro to Phylogenetics and Parsimony

Phylogenetic Trees

Haeckel's tree of life:

Living (extant) groups (taxa)
are shown on the trunk and
the branch tips.

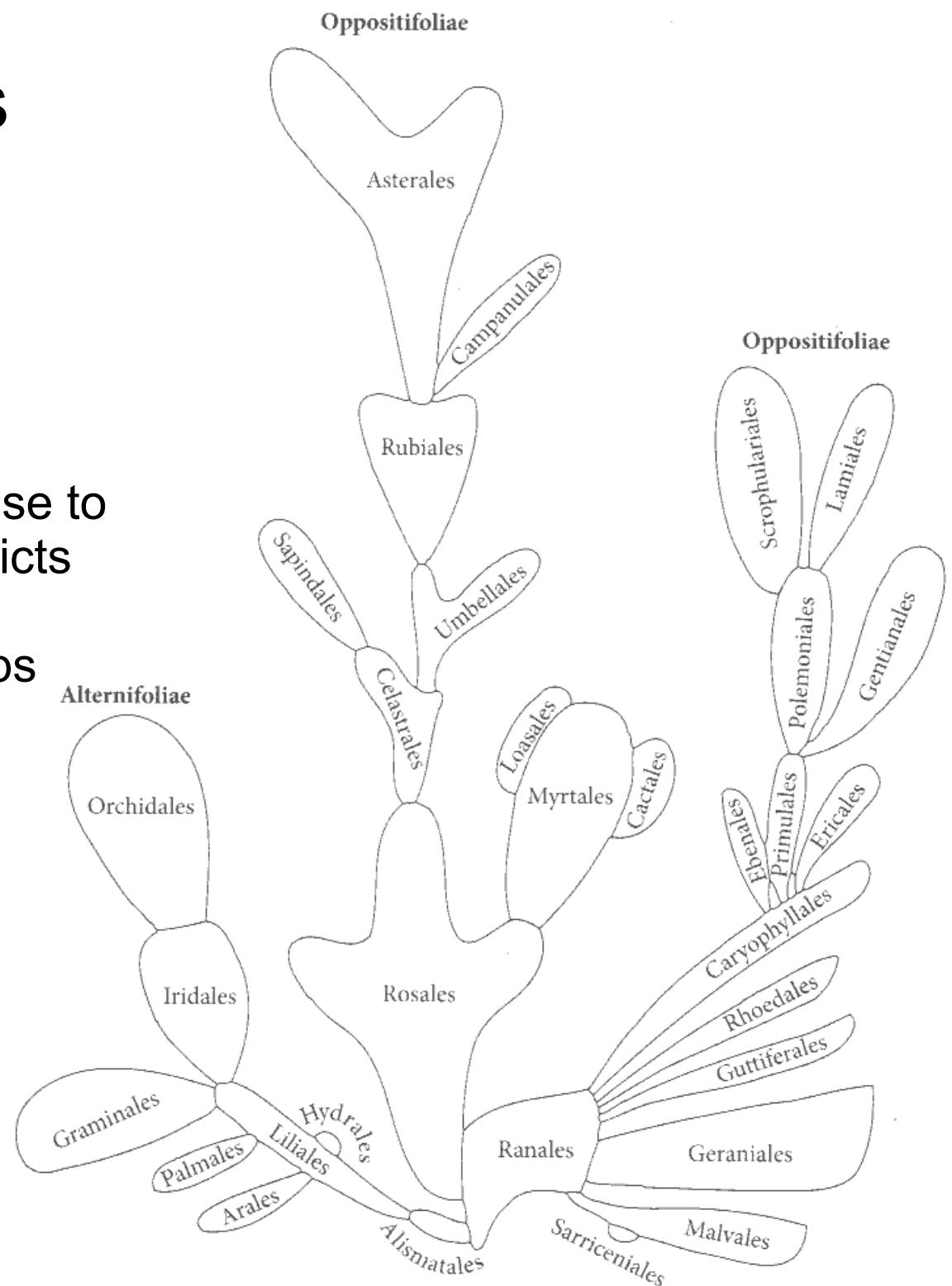
Note how “man” is placed at
the top!



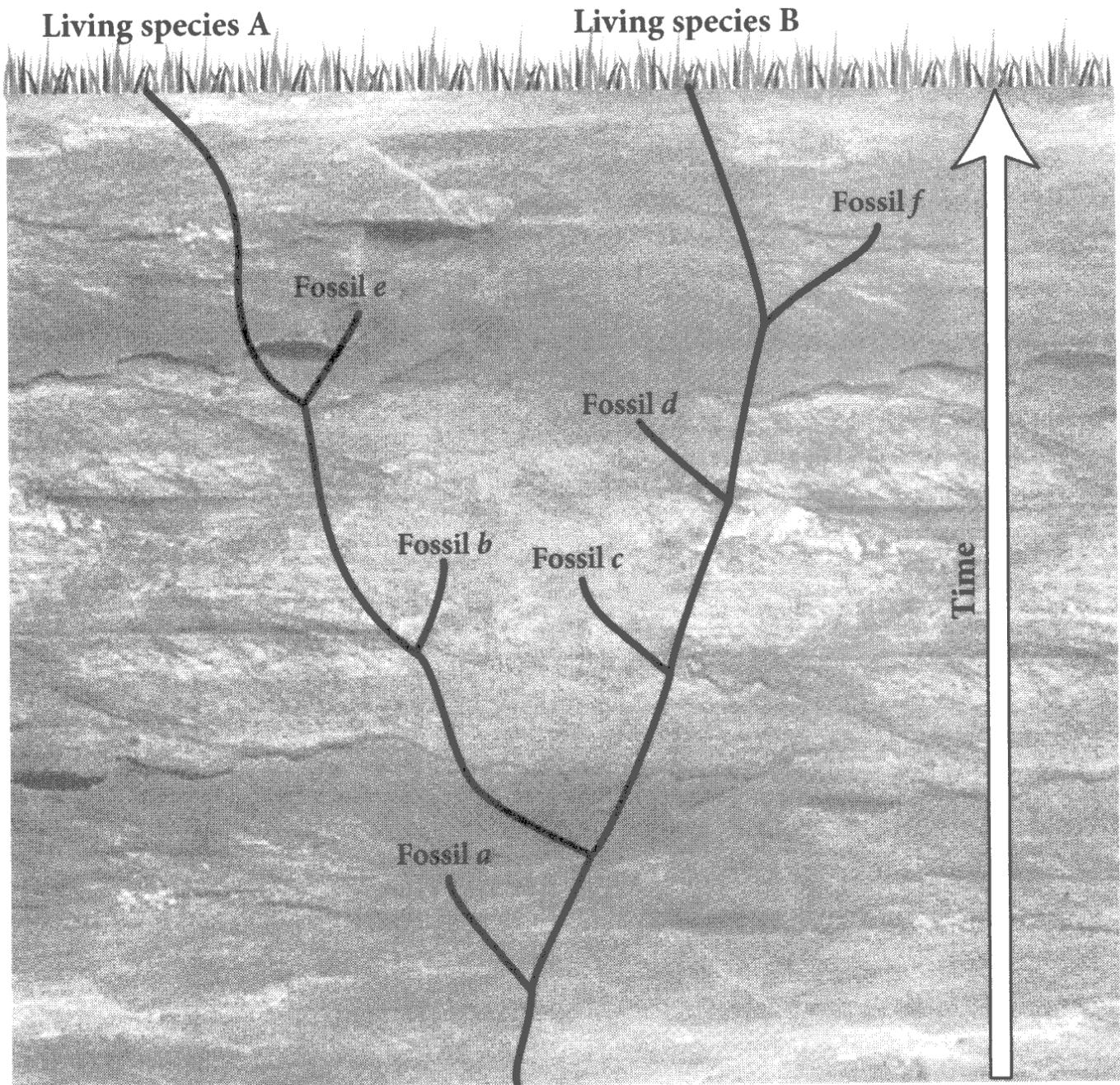
Phylogenetic Trees

Bessey's series of plants:

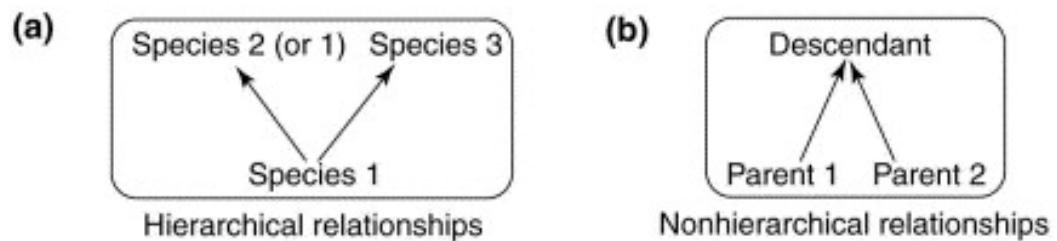
Note how living groups give rise to other living groups. This conflicts with our understanding of evolution in which living groups are related by common ancestors.



Phylogenetic Trees



Phylogenetic Trees

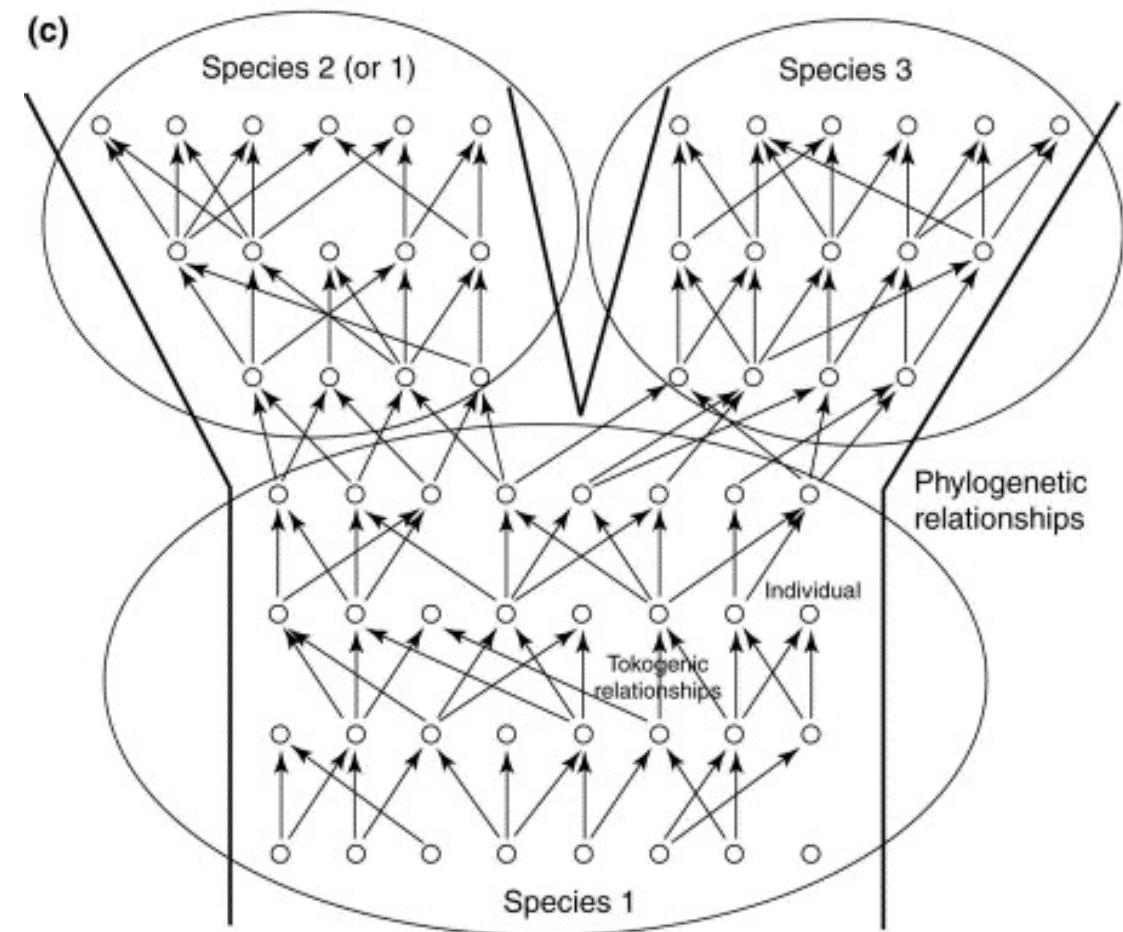


Cladogenesis:

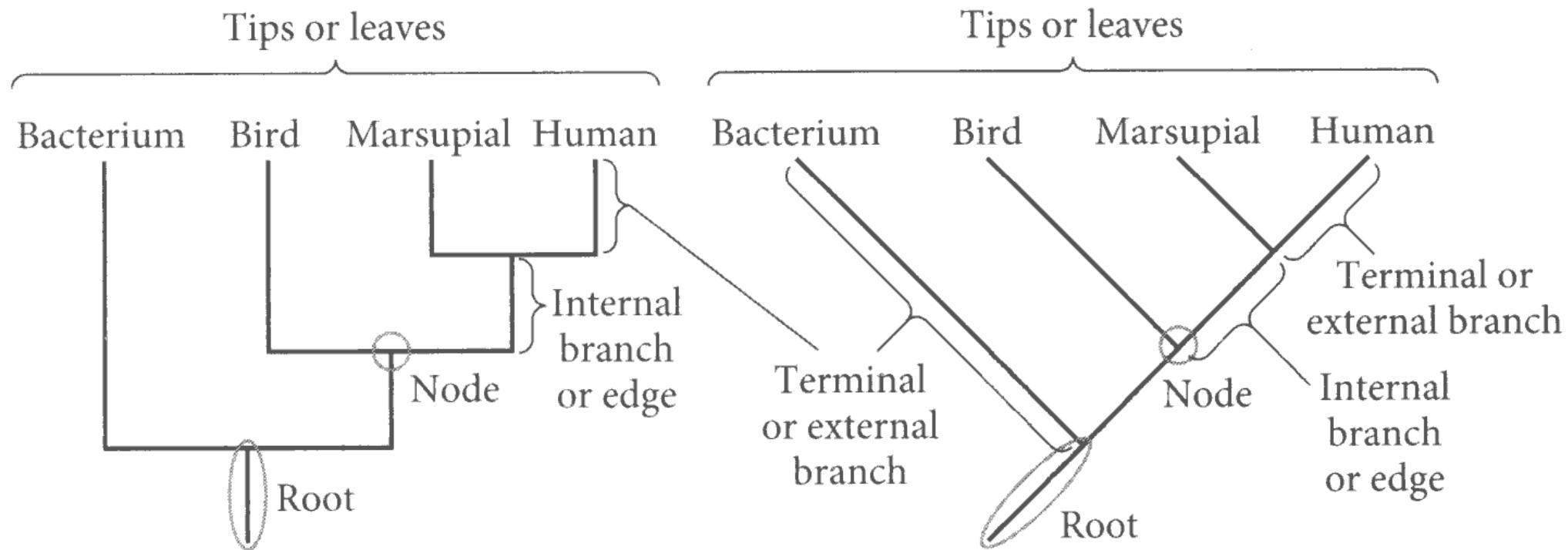
Parent species splits into two

Anagenesis:

Transformation within a species



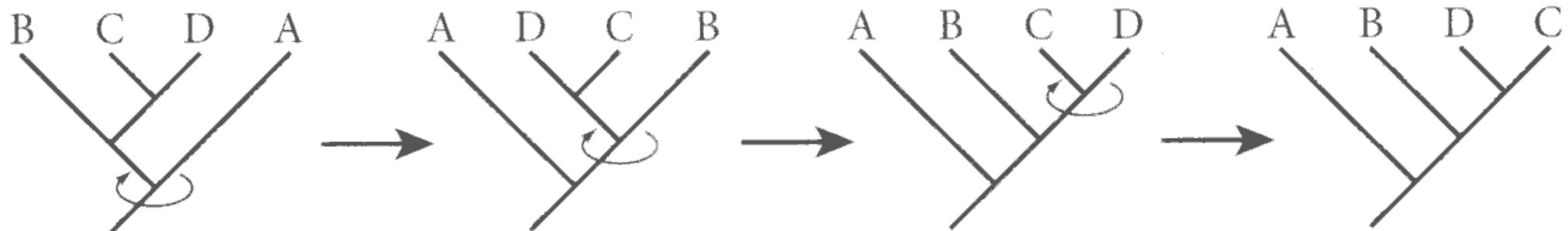
Phylogenetic Trees



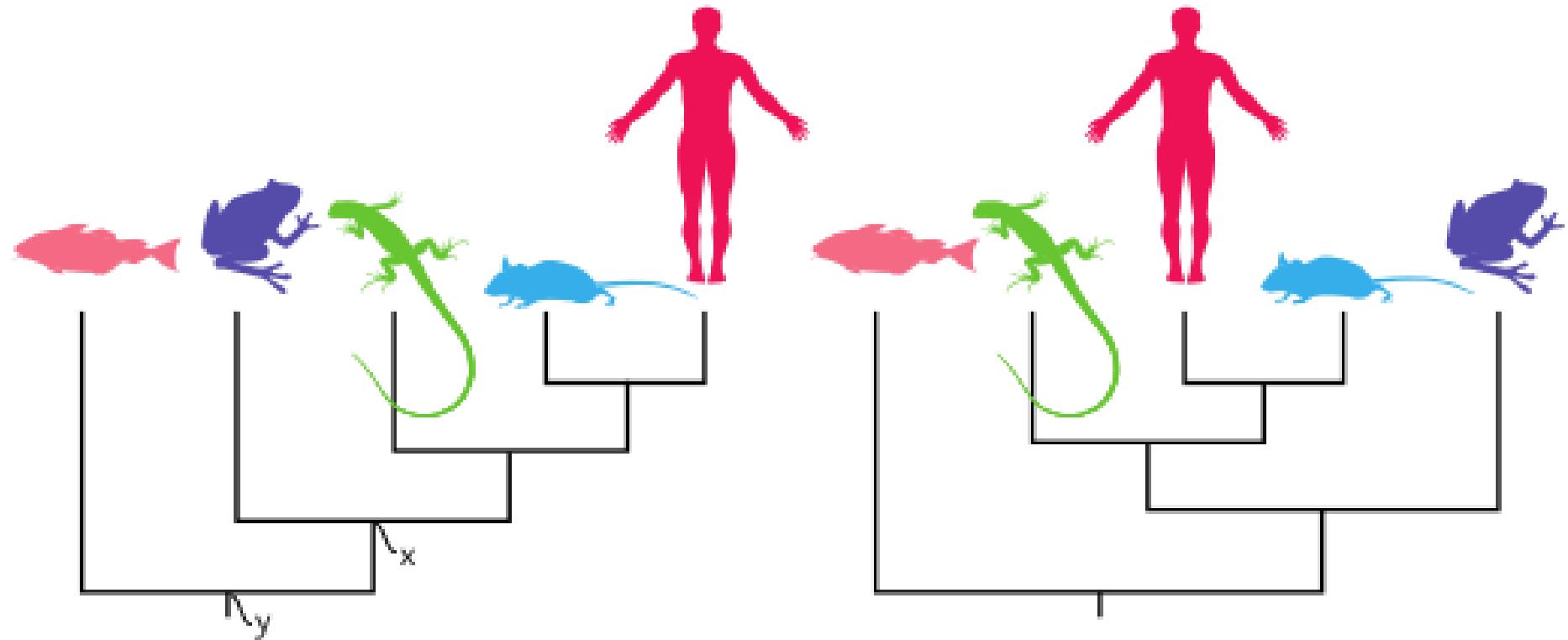
Phylogenetic Trees

Rearranging phylogenetic trees:

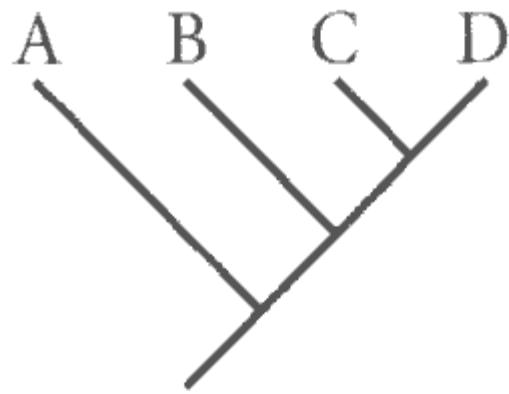
Are the relationships the same or different?



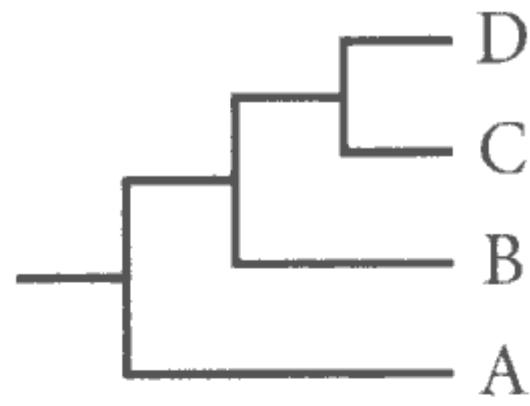
Phylogenetic Trees



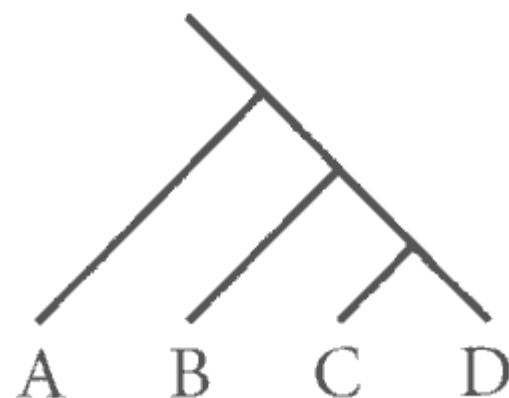
Phylogenetic Trees



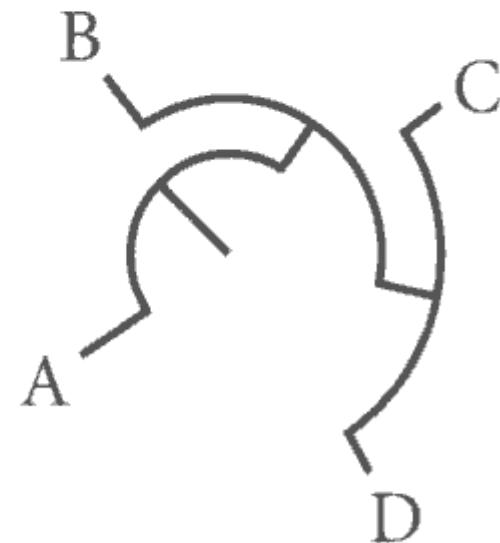
Diagonal-up



Rectangular-right



Diagonal-down

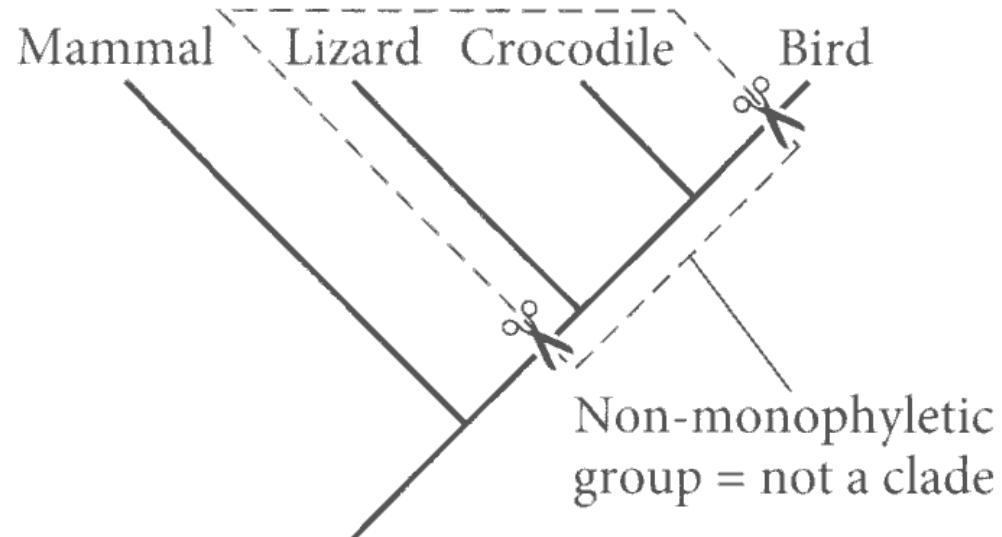
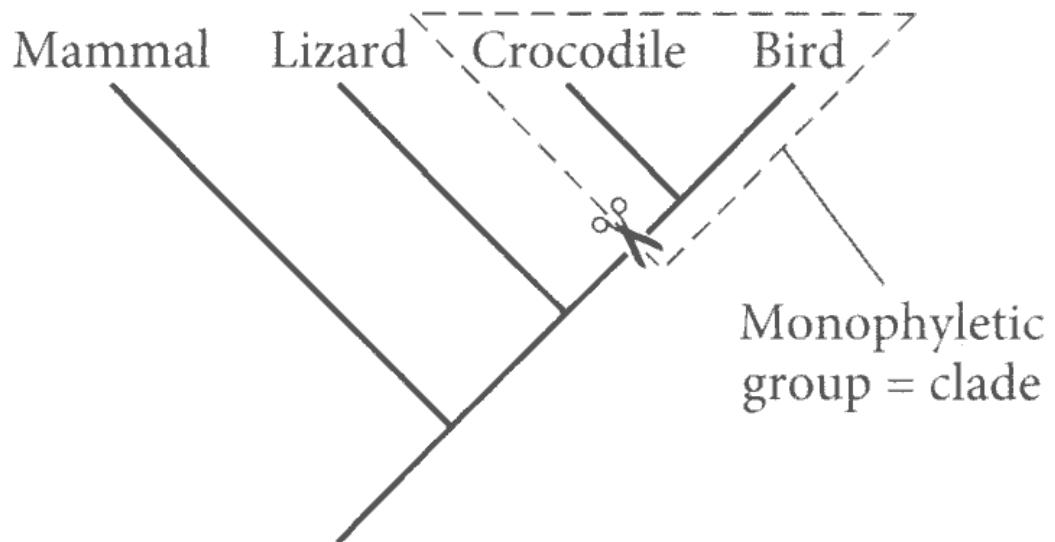


Circle

Phylogenetic Trees

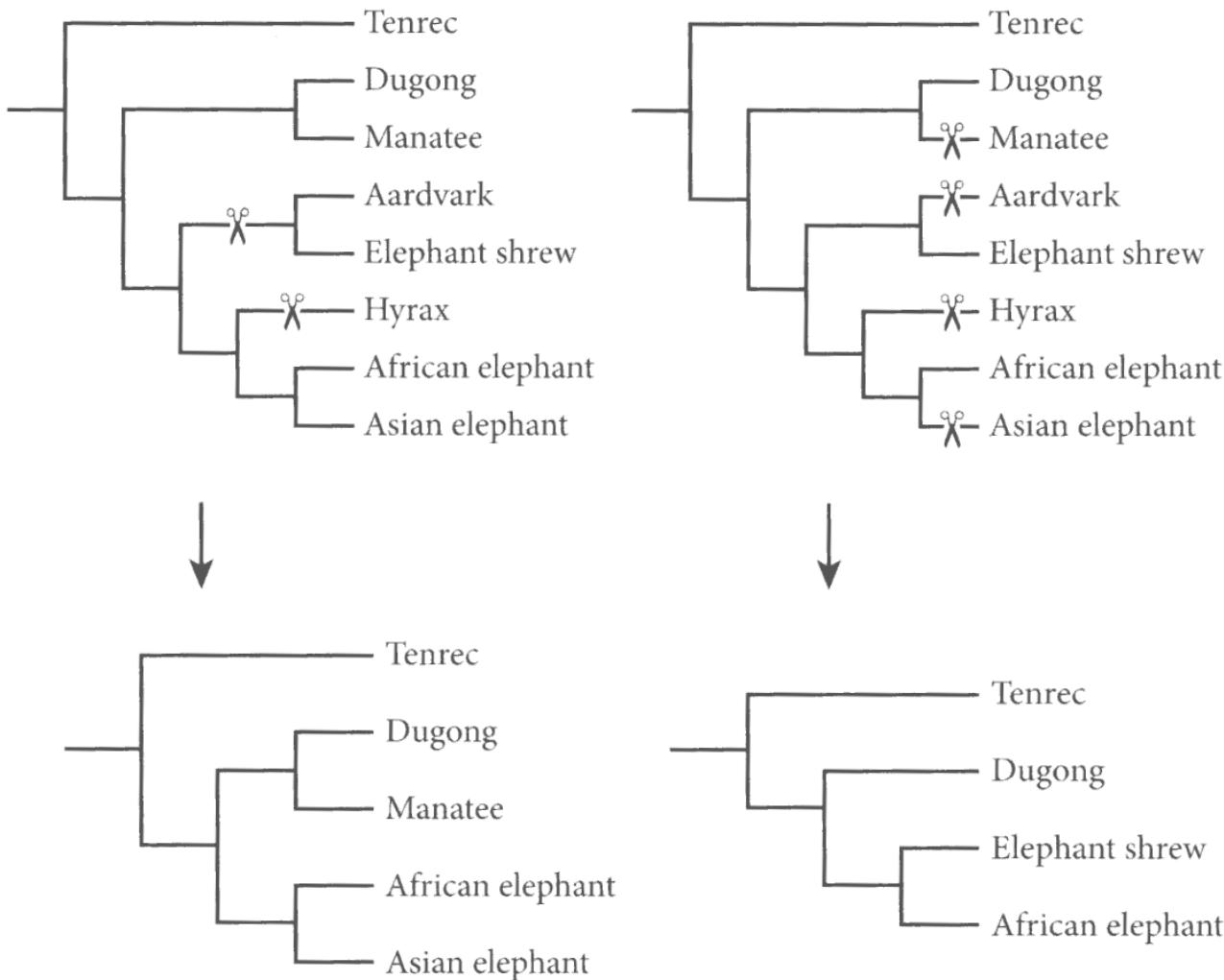
Monophyly, paraphyly, and polyphyly...

Reptiles are not a “natural” group.



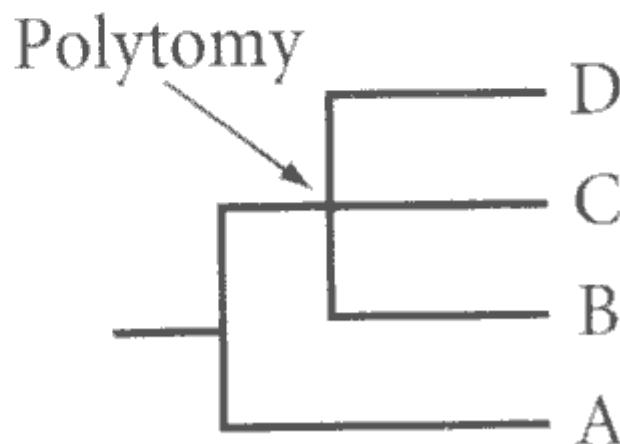
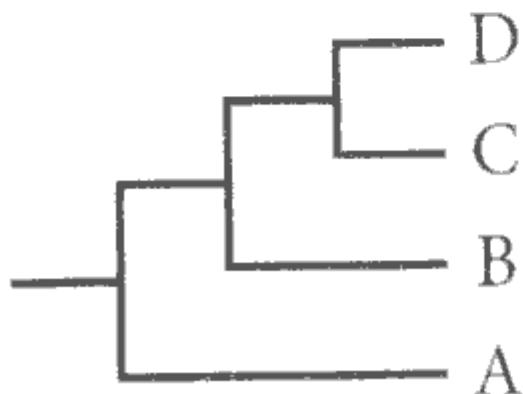
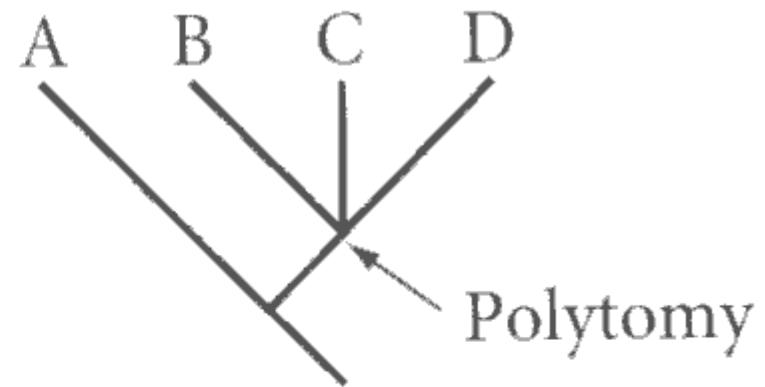
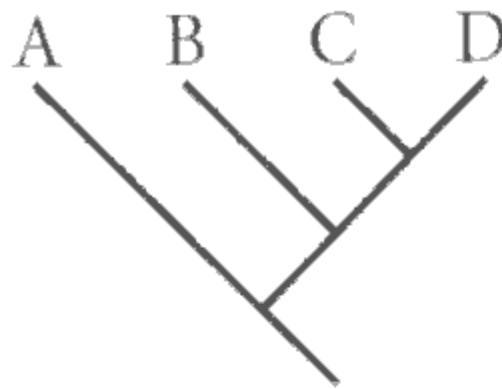
Phylogenetic Trees

Pruning does not change the relationships among taxa



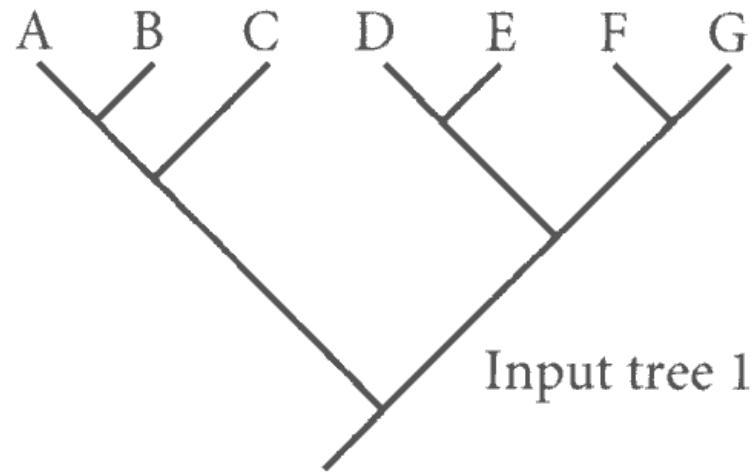
Phylogenetic Trees

Expressing uncertainty of relationships

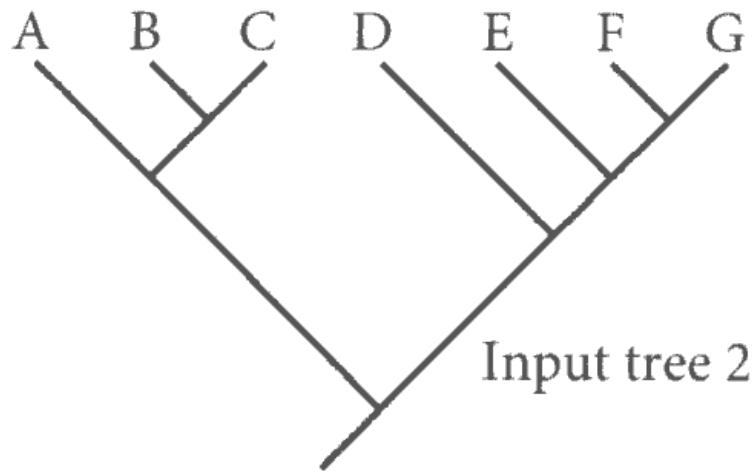


Phylogenetic Trees

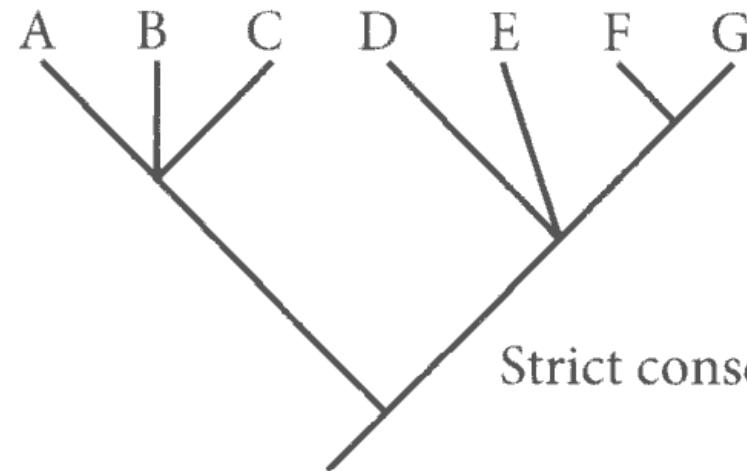
Summarizing competing phylogenetic hypotheses



Input tree 1



Input tree 2

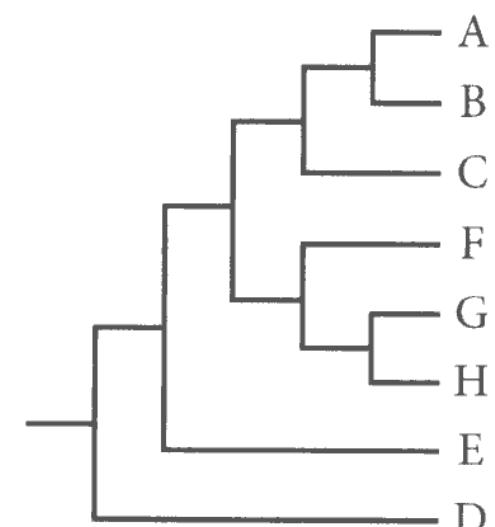
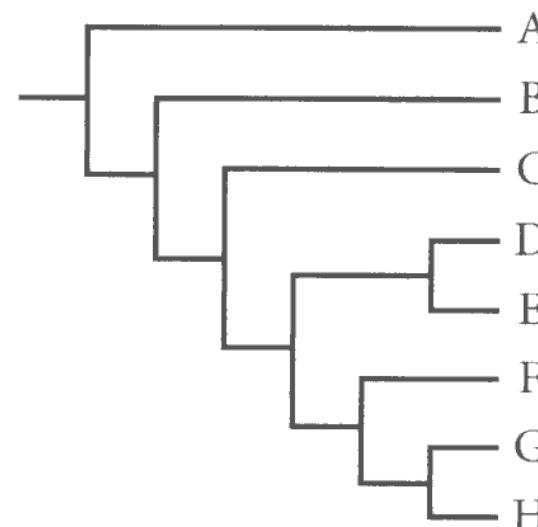
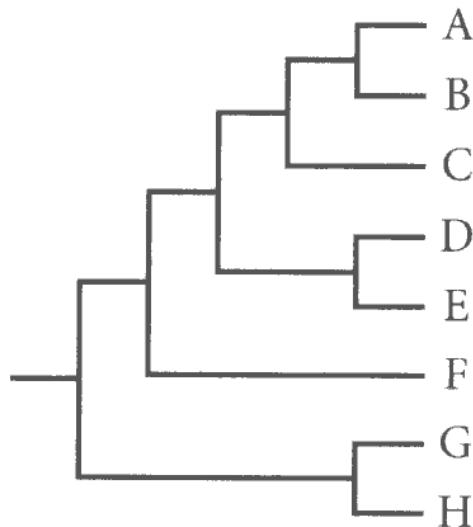


Strict consensus tree

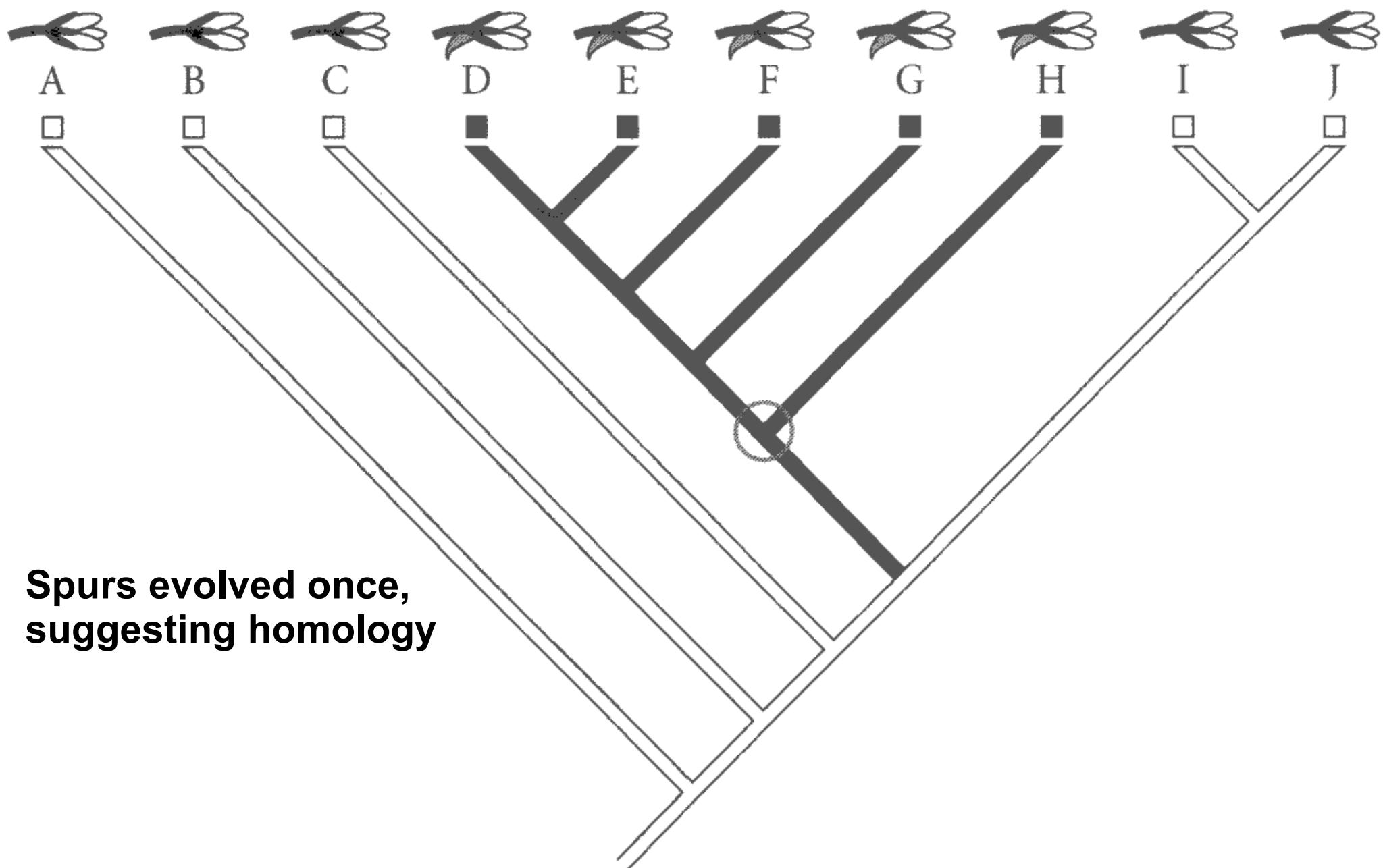
Phylogenetic Trees

Rooting phylogenetic trees
using an outgroup

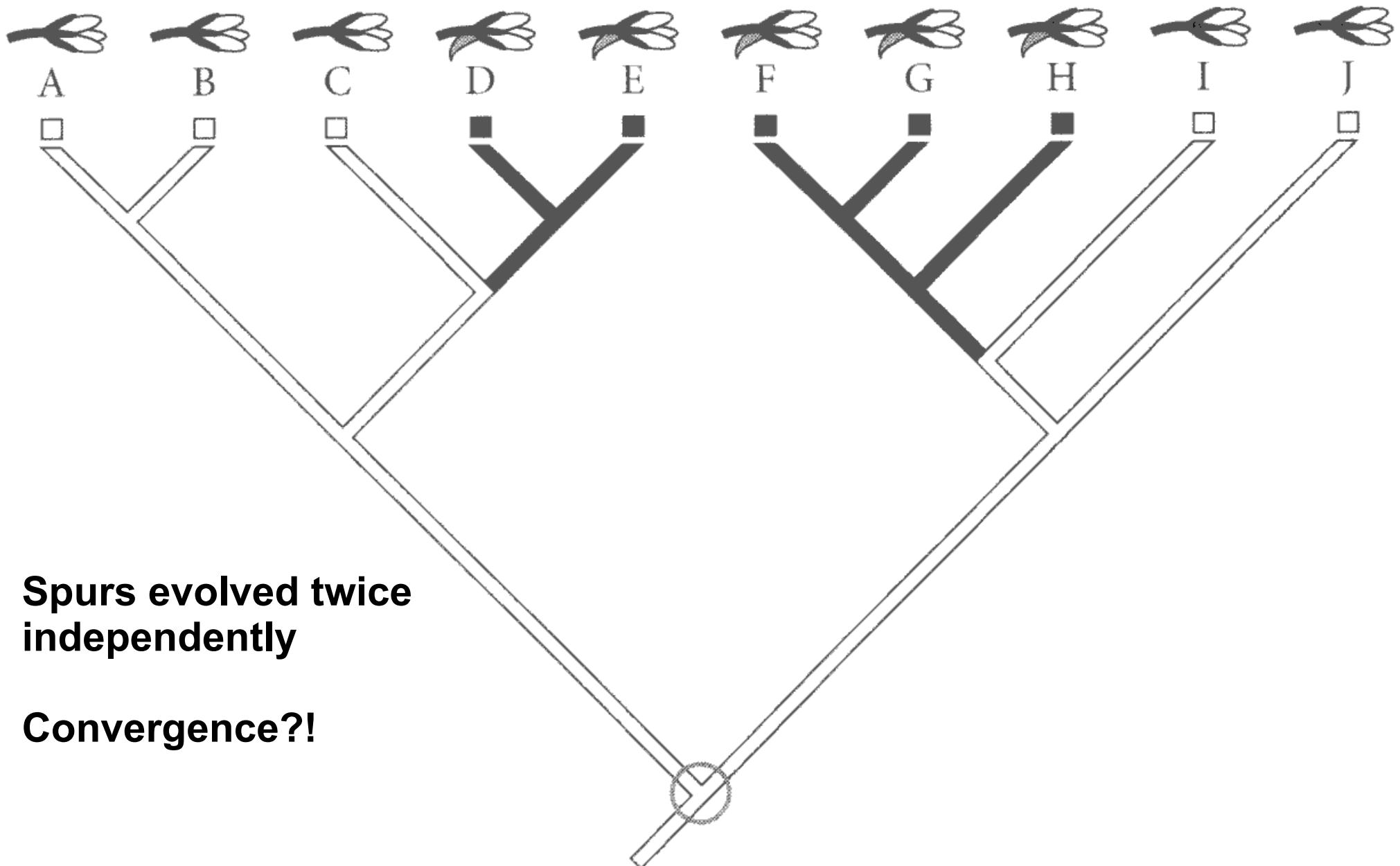
Are the relationships
the same?



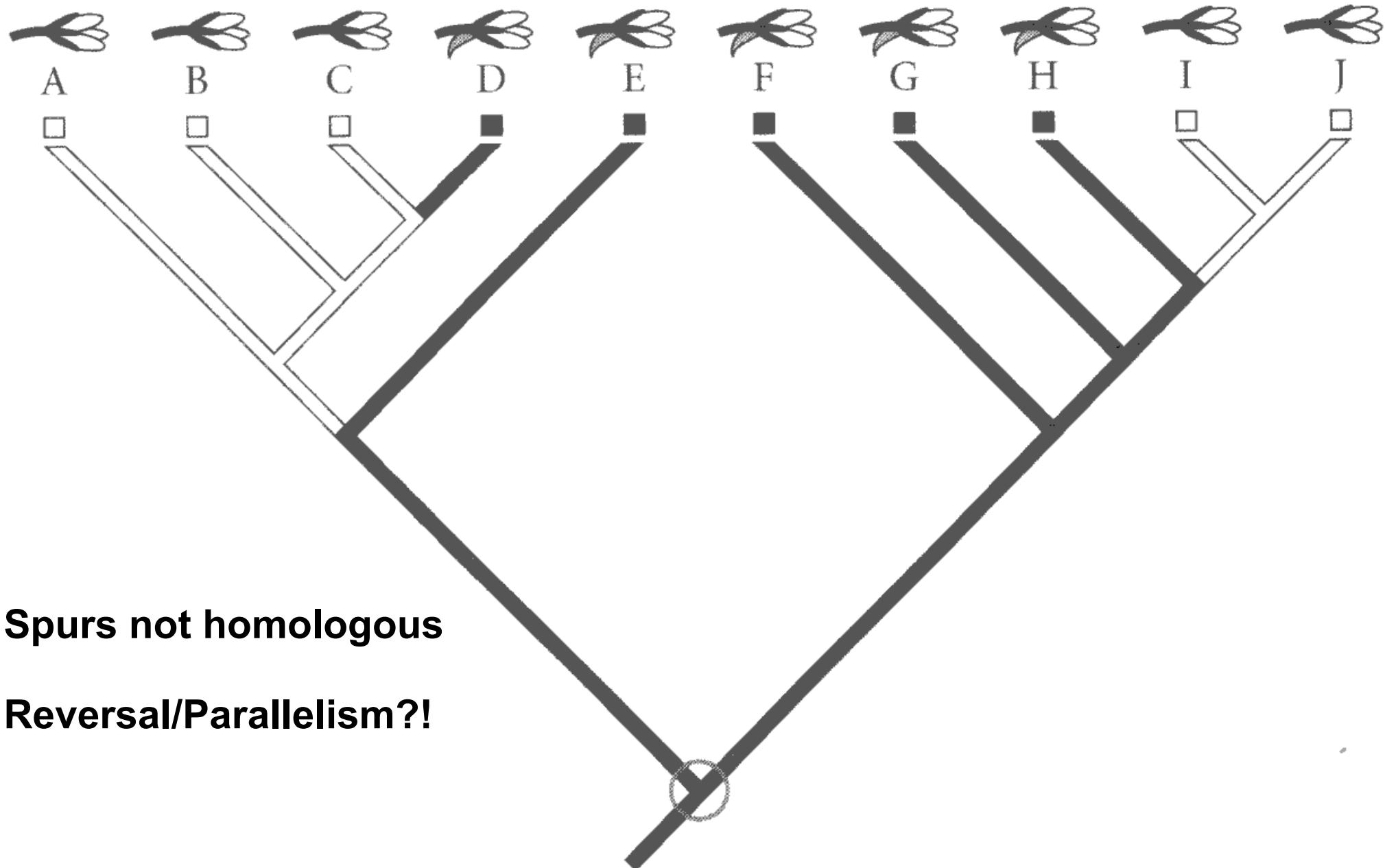
Character evolution: homology



Character evolution: homoplasy



Character evolution: homoplasy



Character evolution

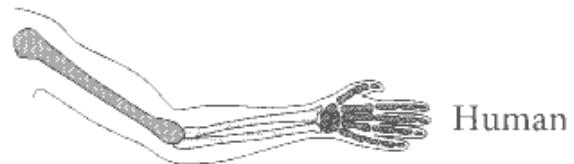
The same structure can be present in different species due to:

Homology (character evolved once in the last common ancestor)

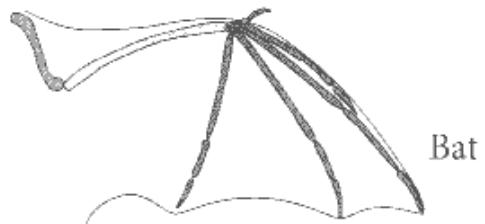
or

Homoplasy (convergence or reversal/parallelism)

Inferring Phylogenetic Trees



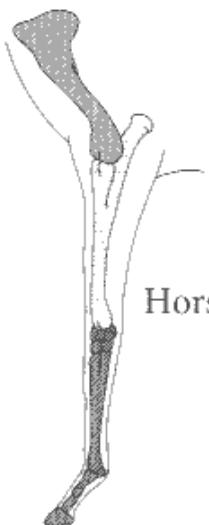
Human



Bat

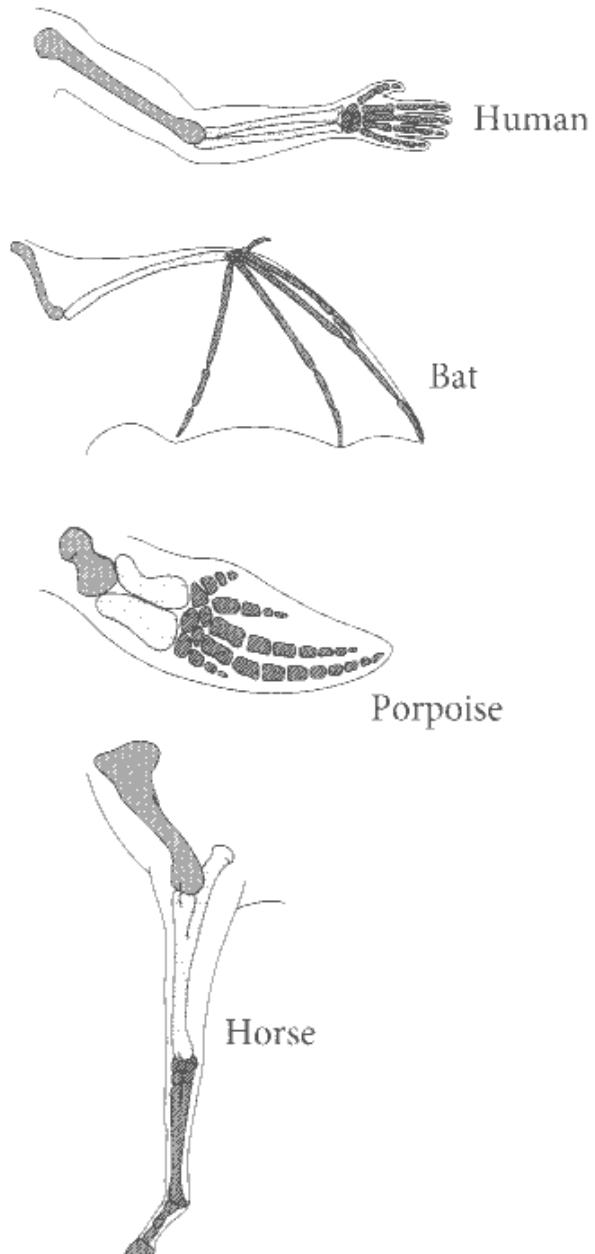


Porpoise



Horse

Inferring Phylogenetic Trees



Homology is assumed prior to phylogenetic tree reconstruction.

Character homology is reassessed in light of the phylogeny. Homology or homoplasy?

Formal way to evaluate character evolution that does not rely on authority opinion...

Inferring Phylogenetic Trees



Inferring Phylogenetic Trees

No.	Character	States
1	Complexity of the mucus-coated surfaces in the nose (maxilloturbinals)	Minimally branched (olfactory surfaces in nasal passage) (0); highly branching (olfactory surfaces excluded from the nasal passage) (1)
2	Bony spur by the auditory bulla (paroccipital process)	Straight and projecting (0); cupped around auditory bulla (1)
3	Number of lower incisors	2 (0); 3 (1)
4	Upper molar 1	Present (0); absent (1)
5	Baculum (bone within the penis)	Present (0); absent (1)
6	Tail	Elongated (0); short (1)
7	Hallux (5th digit, or dewclaw, on hind leg)	Prominent (0); reduced or absent (1)
8	Claws	Nonretractable (0); retractable (1)
9	Prostate gland	Small and simple (0); large and bilobed (1)
10	Kidney structure	Simple (0); conglomerate (1)
11	External ear (pinna)	Present (0); absent (1)
12	Testis position	Scrotal (0); abdominal (1)

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Taxon	Character state scoring											
	1	2	3	4	5	6	7	8	9	10	11	12
Creodont	0	0	0	0	0	0	0	0	?	?	?	?
Cat	0	1	0	1	0	0	1	1	1	0	0	0
Hyena	0	1	0	1	0	0	1	0	1	0	0	0
Civet	0	1	0	0	0	0	0	0	1	0	0	0
Dog	1	0	0	0	1	0	0	0	0	0	0	0
Raccoon	1	0	0	0	1	0	0	0	0	0	0	0
Bear	1	0	0	0	1	1	0	0	0	1	0	0
Otter	1	0	0	0	1	0	0	0	0	1	0	0
Seal	1	0	1	0	1	1	0	0	0	1	1	1
Walrus	1	0	1	0	1	1	0	0	0	1	1	1
Sea lion	1	0	1	0	1	1	0	0	0	1	0	0

Inferring Phylogenetic Trees

Outgroup used to polarize characters
In classic Henningian character argumentation

No.	Character	States
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Hyena	0	1	0	1	0	0	1	0	1	0	0	0
Civet	0	1	0	0	0	0	0	0	1	0	0	0
Dog	1	0	0	0	1	0	0	0	0	0	0	0
Raccoon	1	0	0	0	1	0	0	0	0	0	0	0
Bear	1	0	0	0	1	1	0	0	0	1	0	0
Otter	1	0	0	0	1	0	0	0	0	1	0	0
Seal	1	0	1	0	1	1	0	0	0	1	1	1
Walrus	1	0	1	0	1	1	0	0	0	1	1	1
Sea lion	1	0	1	0	1	1	0	0	0	1	0	0



Inferring Phylogenetic Trees

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Hyena	0	1	0	1	0	0	1	0	1	0	0	0
Civet	0	1	0	0	0	0	0	0	1	0	0	0
Dog	1	0	0	0	1	0	0	0	0	0	0	0
Raccoon	1	0	0	0	1	0	0	0	0	0	0	0
Bear	1	0	0	0	1	1	0	0	0	1	0	0
Otter	1	0	0	0	1	0	0	0	0	1	0	0
Seal	1	0	1	0	1	1	0	0	0	1	1	1
Walrus	1	0	1	0	1	1	0	0	0	1	1	1
Sea lion	1	0	1	0	1	1	0	0	0	1	0	0

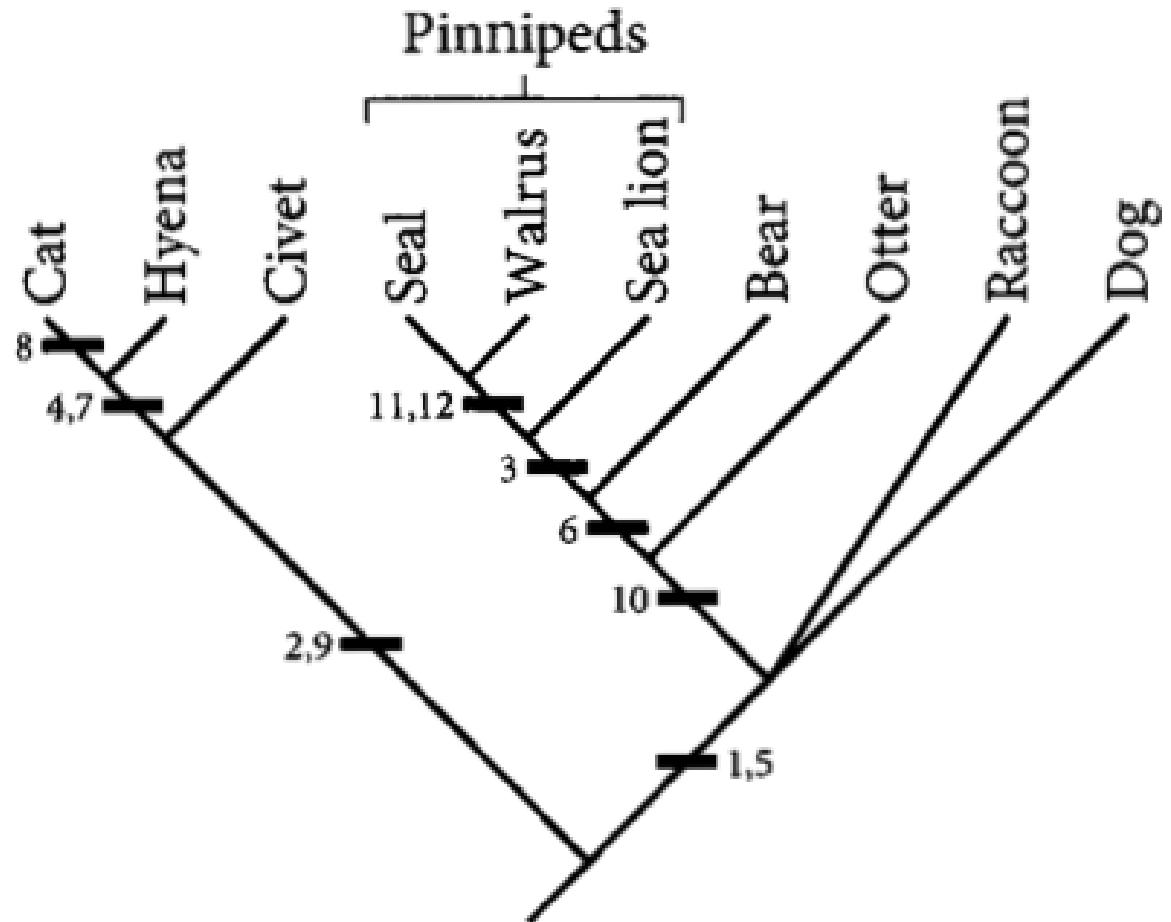
Inferring Phylogenetic Trees

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Civet	0	1	0	0	0	0	0	0	1	0	0	0
Dog	1	0	0	0	1	0	0	0	0	0	0	0
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Bear	1	0	0	0	1	1	0	0	0	1	0	0
Otter	1	0	0	0	1	0	0	0	0	1	0	0
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Inferring Phylogenetic Trees

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Creodont	0	0	0	0	0	0	0	0	?	?	?	?
Cat	0	1	0	1	0	0	1	1	1	0	0	0
Hyena	0	1	0	1	0	0	1	0	1	0	0	0
Civet	0	1	0	0	0	0	0	0	1	0	0	0
Dog	1	0	0	0	1	0	0	0	0	0	0	0
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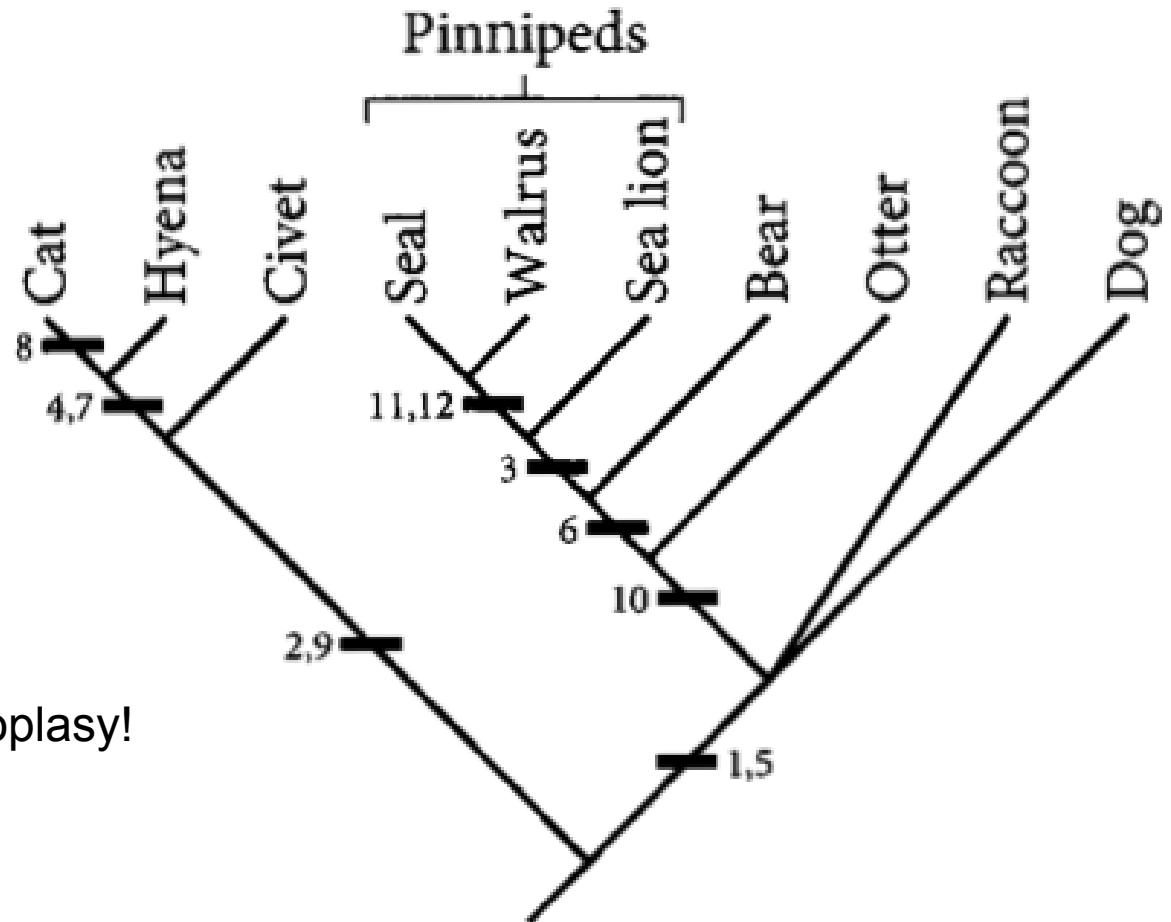
Inferring Phylogenetic Trees

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Civet	0	1	0	0	0	0	0	0	1	0	0	0
Dog	1	0	0	0	1	0	0	0	0	0	0	0
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Otter	1	0	0	0	1	0	0	0	0	1	0	0
Seal	1	0	1	0	1	1	0	0	0	1	1	1
Walrus	1	0	1	0	1	1	0	0	0	1	1	1
Sea lion	1	0	1	0	1	1	0	0	0	1	0	0

If characters display homoplasy it becomes difficult to reconcile tree with character matrix.

We need an optimality criterion:

Find the tree that minimizes homoplasy!
(Maximum Parsimony)

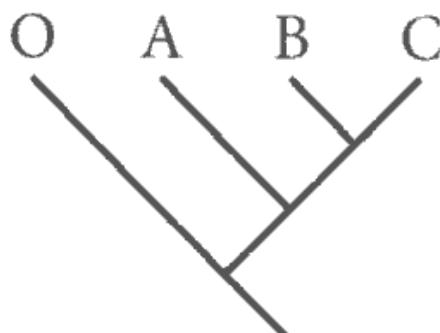


Parsimony: basic principle

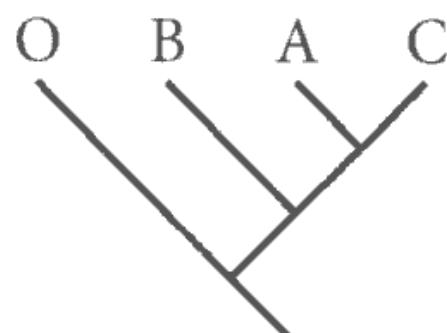
	1	2	3	4	5	6	7	8
O	0	0	0	0	0	0	0	0
A	0	1	0	0	0	1	1	0
B	1	1	0	1	1	1	1	1
C	0	0	1	1	0	0	0	0

Parsimony aims at reducing the amount of homoplasy or number of steps needed to explain the evolution of characters (ie, find the “shortest” tree)

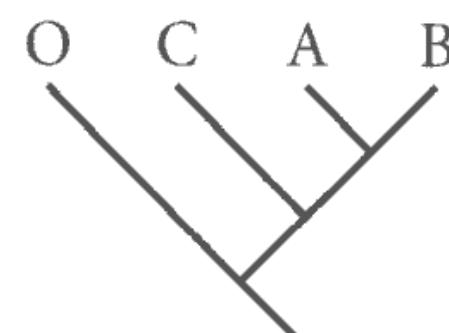
3 possible rooted trees for 3 ingroup taxa



Tree 1



Tree 2

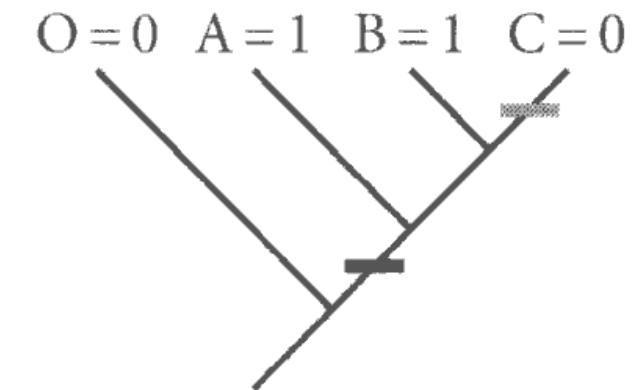
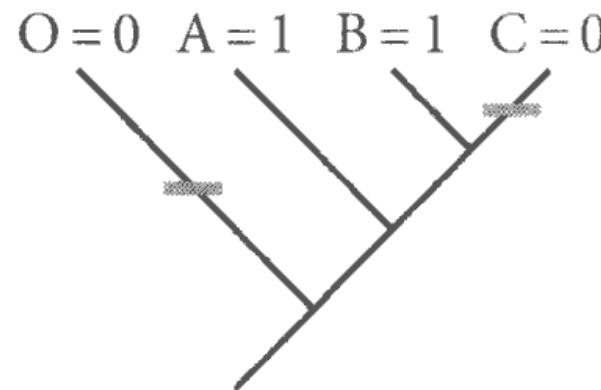
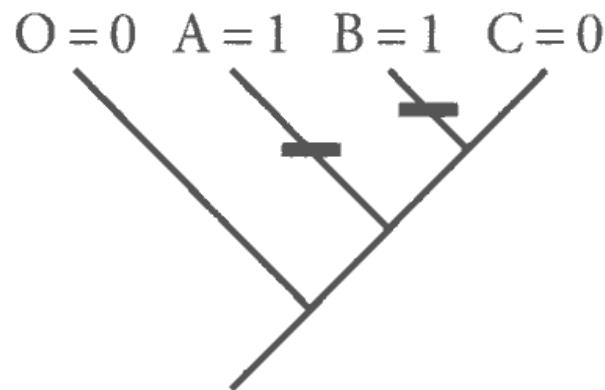


Tree 3

Parsimony: basic principle

	1	2	3	4	5	6	7	8
O	0	0	0	0	0	0	0	0
A	0	1	0	0	0	1	1	0
B	1	1	0	1	1	1	1	1
C	0	0	1	1	0	0	0	0

3 possible reconstructions of character 2
on tree 1

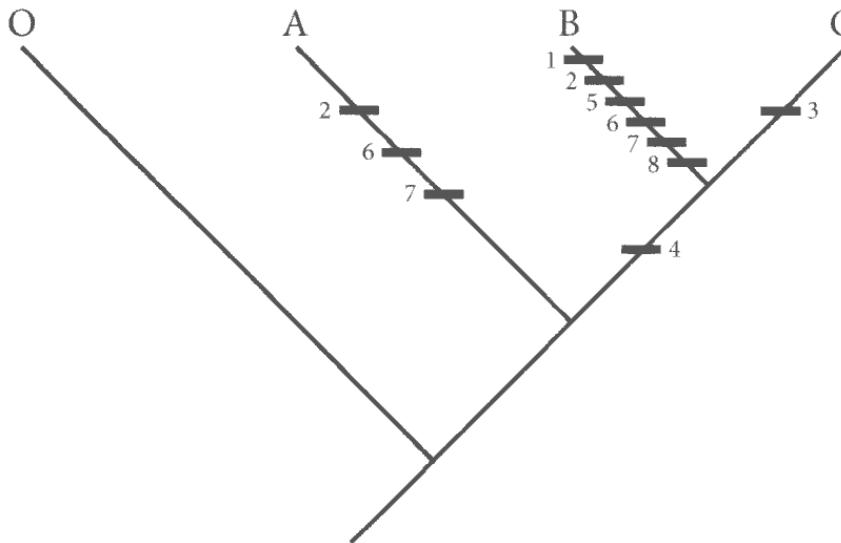


Parsimony: basic principle

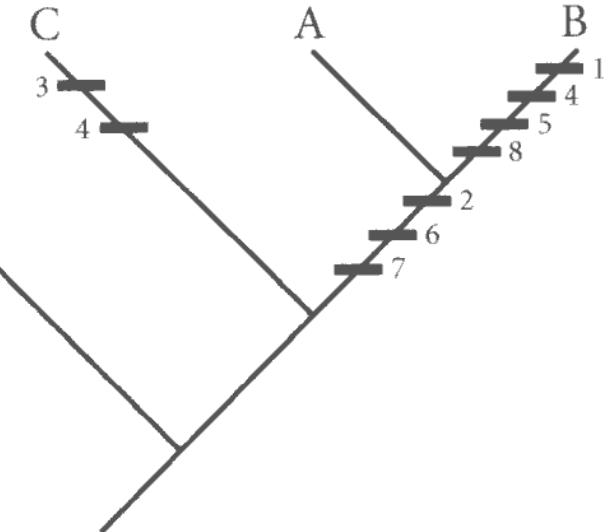
	1	2	3	4	5	6	7	8	
O	0	0	1	0	1	1	0	0	
A	0	1	1	0	1	0	1	0	
B	1	1	1	1	0	0	1	1	
C	0	0	0	1	1	1	0	0	Total length
Length on tree 1	1	2	1	1	1	2	2	1	11
Length on tree 2	1	2	1	2	1	2	2	1	12
Length on tree 3	1	1	1	2	1	1	1	1	9

← Most parsimonious

Tree 1: 11 steps



Tree 3: 9 steps



Parsimony

Taxon	Parsimony-informative							Parsimony-uninformative						
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	1	0	1	0	?	1	0	1	0	0	0	1	0
3	0	1	1	2	1	0	2	0	1	1	0	0	2	0
4	1	1	1	1	?	1	2	0	1	0	1	1	2	1
5	1	1	2	3	1	1	0	0	1	2	?	2	2	2
6	1	0	2	2	1	?	1	0	1	0	?	3	2	?

invariant

Parsimony

Taxon	Parsimony-informative							Parsimony-uninformative						
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	1	0	1	0	?	1	0	1	0	0	0	0	1
3	0	1	1	2	1	0	2	0	1	1	0	0	2	0
4	1	1	1	1	?	1	2	0	1	0	1	1	2	1
5	1	1	2	3	1	1	0	0	1	2	?	2	2	2
6	1	0	2	2	1	?	1	0	1	0	?	3	2	?

Invariant in ingroup

Parsimony

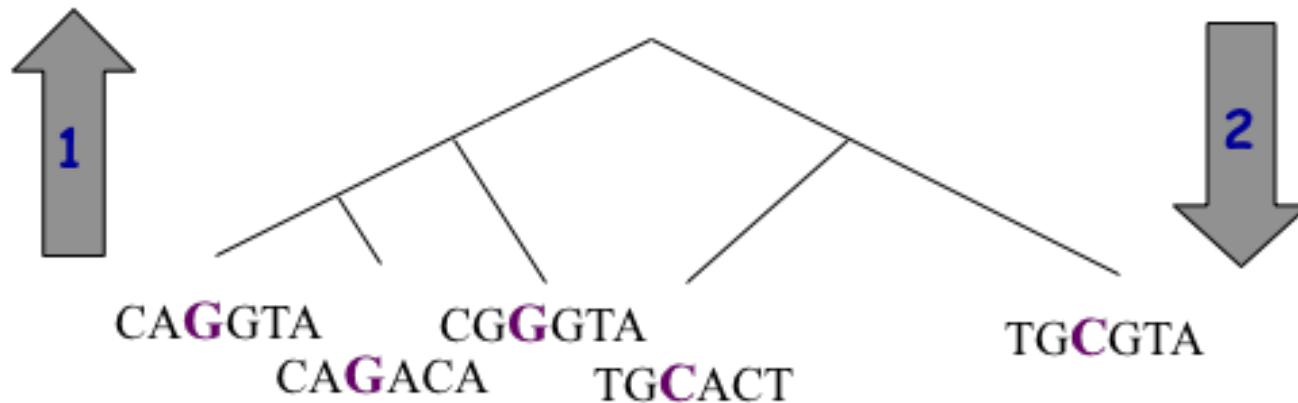
Taxon	Parsimony-informative							Parsimony-uninformative						
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	1	0	1	0	?	1	0	1	0	0	0	1	0
3	0	1	1	2	1	0	2	0	1	1	0	0	2	0
4	1	1	1	1	?	1	2	0	1	0	1	1	2	1
5	1	1	2	3	1	1	0	0	1	2	?	2	2	2
6	1	0	2	2	1	?	1	0	1	0	?	3	2	?

autoapomorphies

Parsimony: Fitch algorithm

Execute independently for each character:

1. Bottom-up phase: Determine set of possible states for each internal node
2. Top-down phase: Pick states for each internal node



Parsimony: Fitch algorithm

- Bottom -Up phase
 - If the children of an as yet unlabeled node have a common possible state, the parent takes that common state
 - Otherwise give the node all possible states of its children – pay 1 point penalty
- Arbitrarily pick a state for the root if there is more than one choice
- Top-Down phase
 - If the set of all possible child nodes from a parent contains the assignment of the parent (*i.e* same character) , assign the state of the parent to the node
 - Otherwise choose one of the possible states arbitrarily and pay 1 point penalty

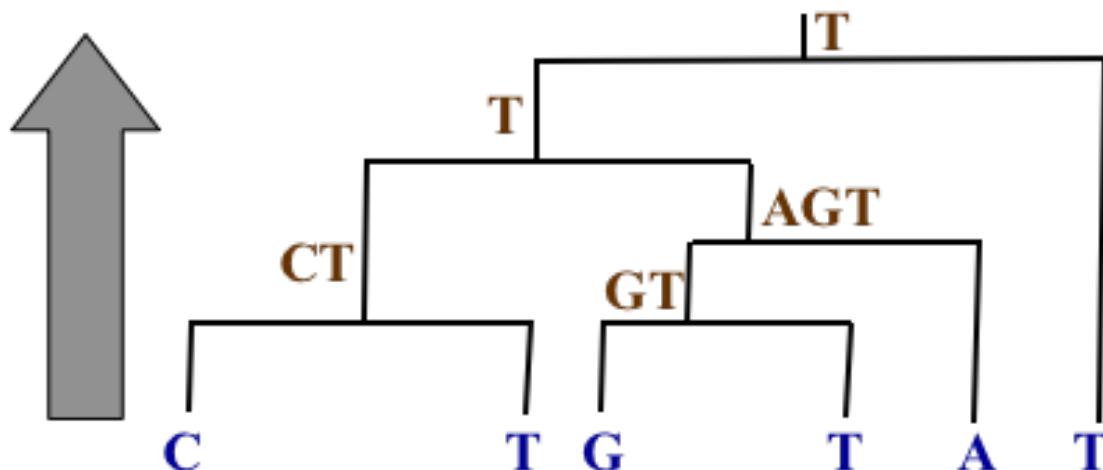
Parsimony: Fitch algorithm

Bottom-Up Phase

Determine set of possible states for each internal node

- Initialization: $R_i = \{s_i\}$
- Do a post-order (from leaves to root) traversal of tree
 - Determine R_i of internal node i with children j, k :

$$R_i = \begin{cases} R_j \cap R_k & \text{if } R_j \cap R_k \neq \emptyset \\ R_j \cup R_k & \text{otherwise} \end{cases}$$



Parsimony-score =
union operations

score = 3

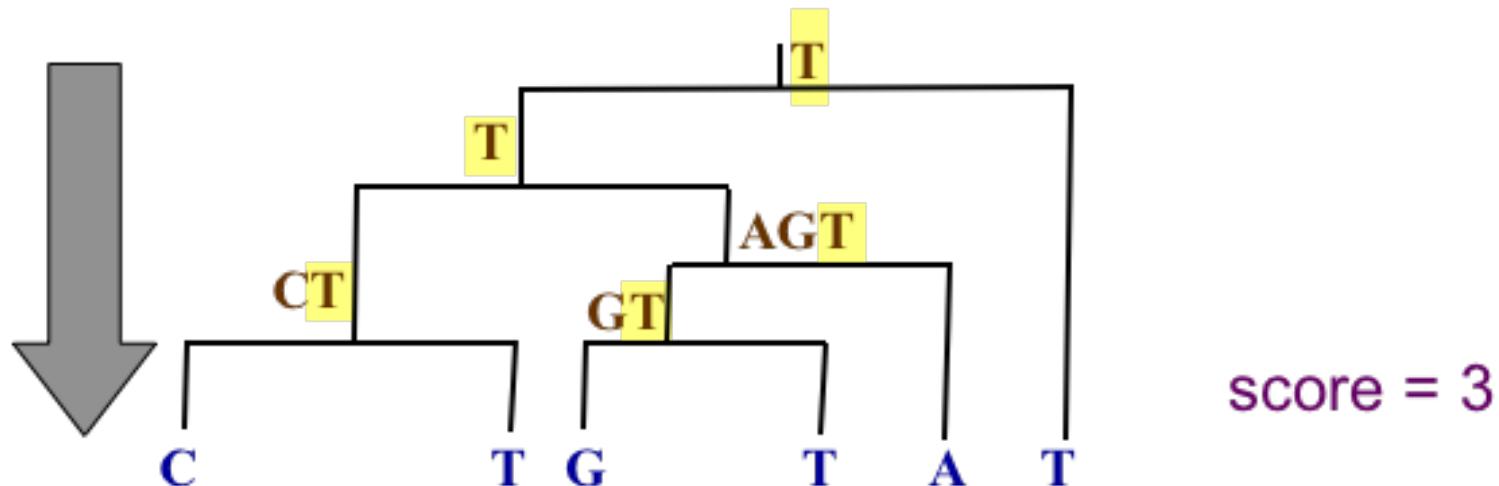
Parsimony: Fitch algorithm

Top-Down Phase

Pick states for each internal node

- Pick arbitrary state in R_{root} for the root
- Do pre-order (from root to leaves) traversal of tree
 - Determine s_j of internal node j with parent i :

$$s_j = \begin{cases} s_i & \text{if } s_i \in R_j \\ \text{arbitrary state} \in R_j & \text{otherwise} \end{cases}$$



Parsimony: Fitch algorithm

Going up, for each character....

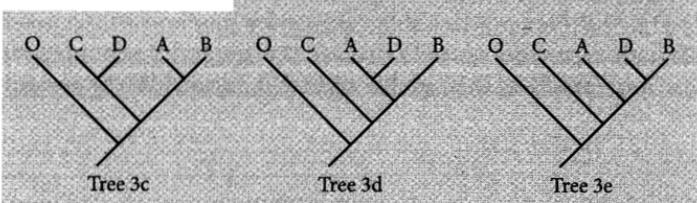
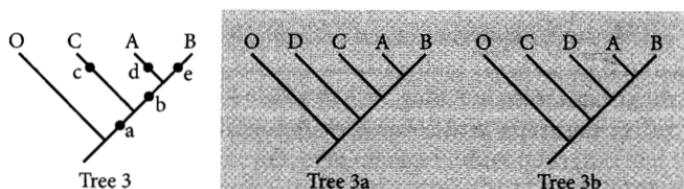
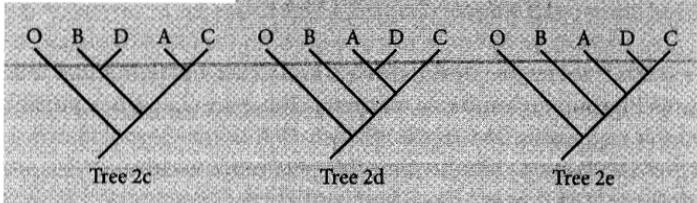
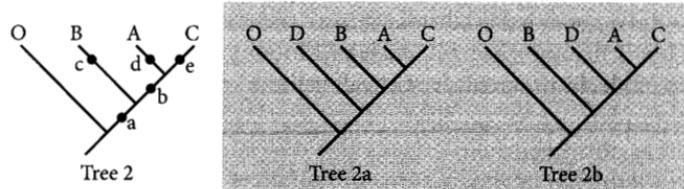
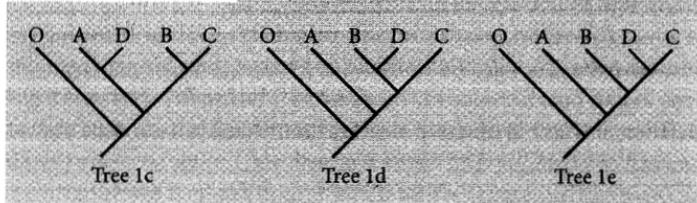
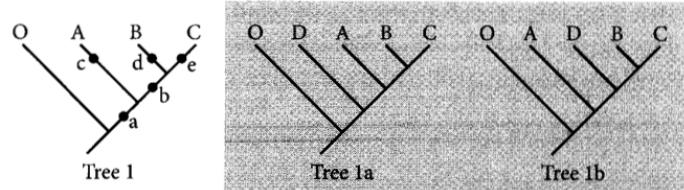
- If there is a common state, keep only it
- Otherwise, keep all the states and pay* a point

Going down, for each character....

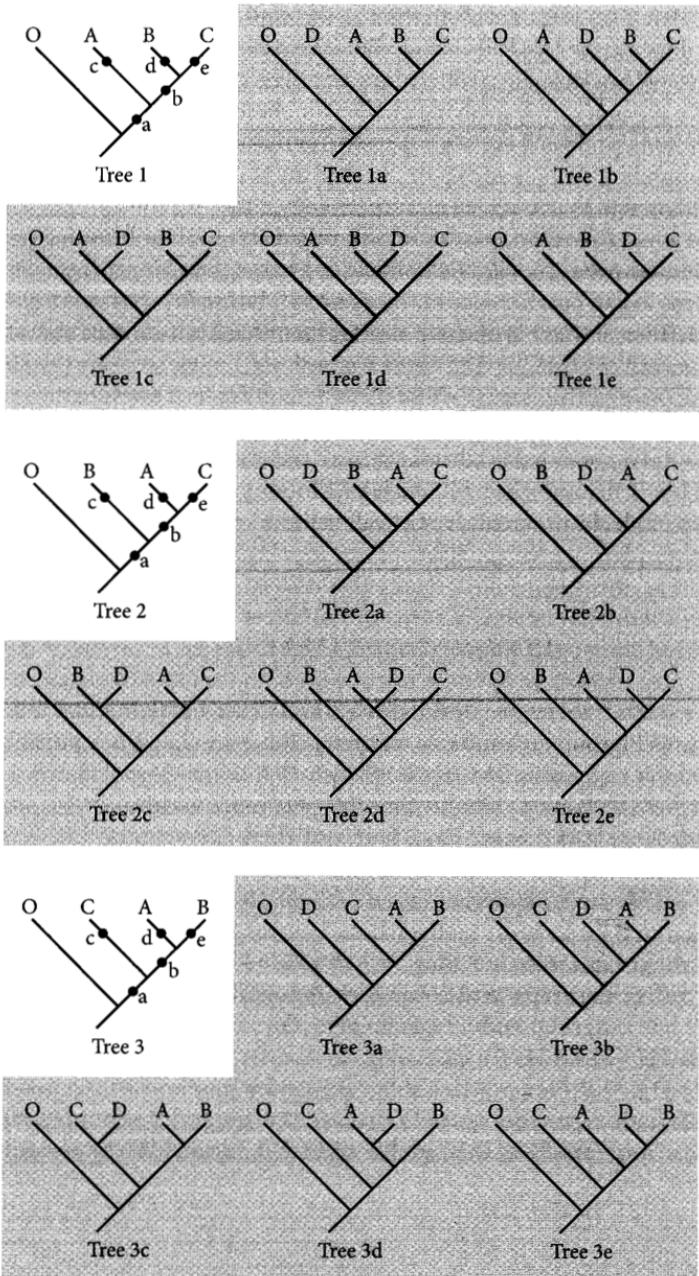
- Keep the common state between parent and child, if there is one
- If not, pick one from the child arbitrarily and pay* a point

*The penalty is paid either going up or going down, but not twice

Parsimony: finding optimal trees



Parsimony: finding optimal trees



Number of rooted tree topologies:

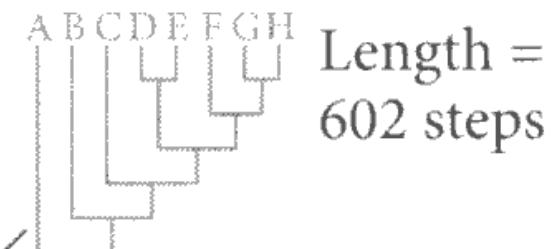
$$(2n-3)! / [2n \times (n-2)!]$$

Heuristic tree searches (hill-climbing algorithm)

Propose a starting tree, rearrange, and evaluate if it is more parsimonious (ie, shorter)

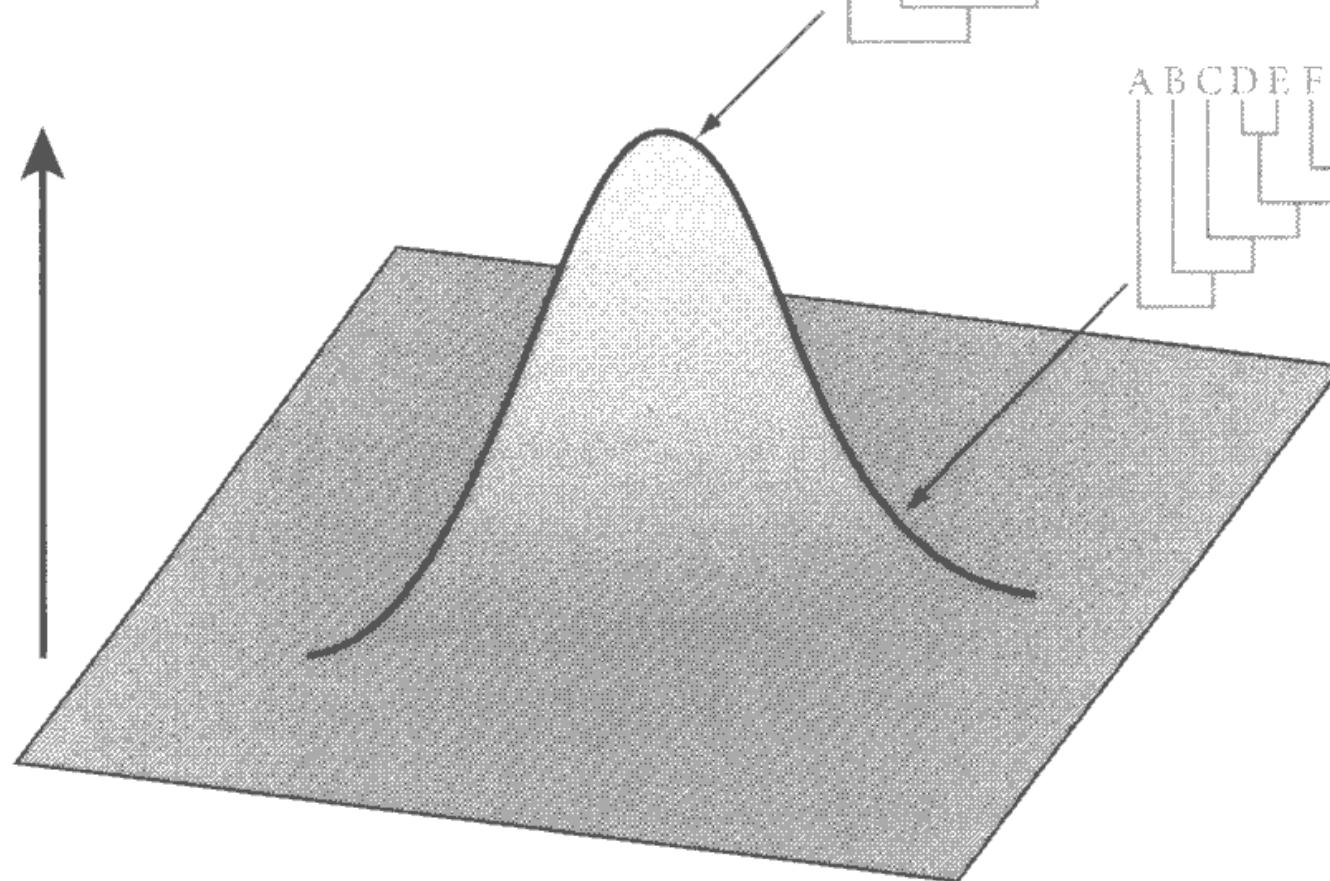


Length =
567 steps



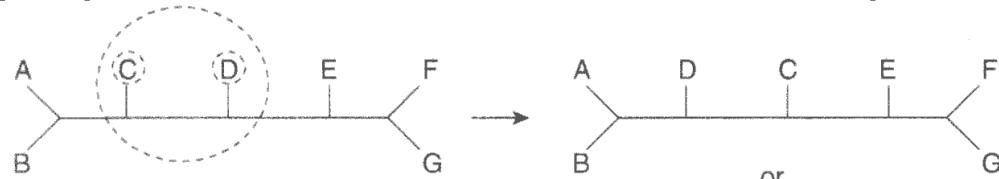
Length =
602 steps

More
parsimonious
(shorter)

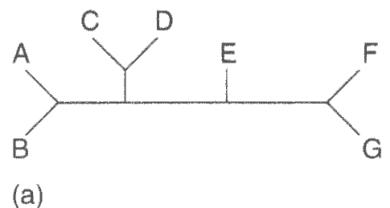


Heuristic tree searches

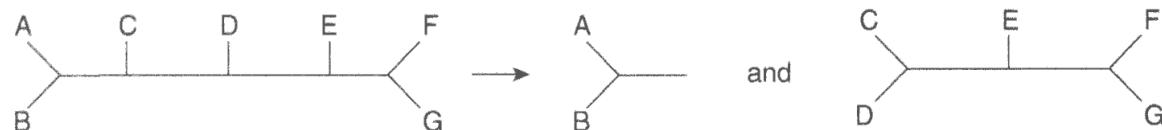
Traversing tree space:
propose new tree; if shorter: accept; else: propose new tree



Nearest-Neighbor Interchange

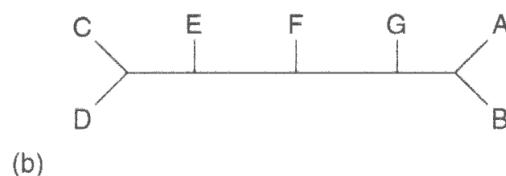


NNI



Subtree Bisection &
Reconnection

SBR

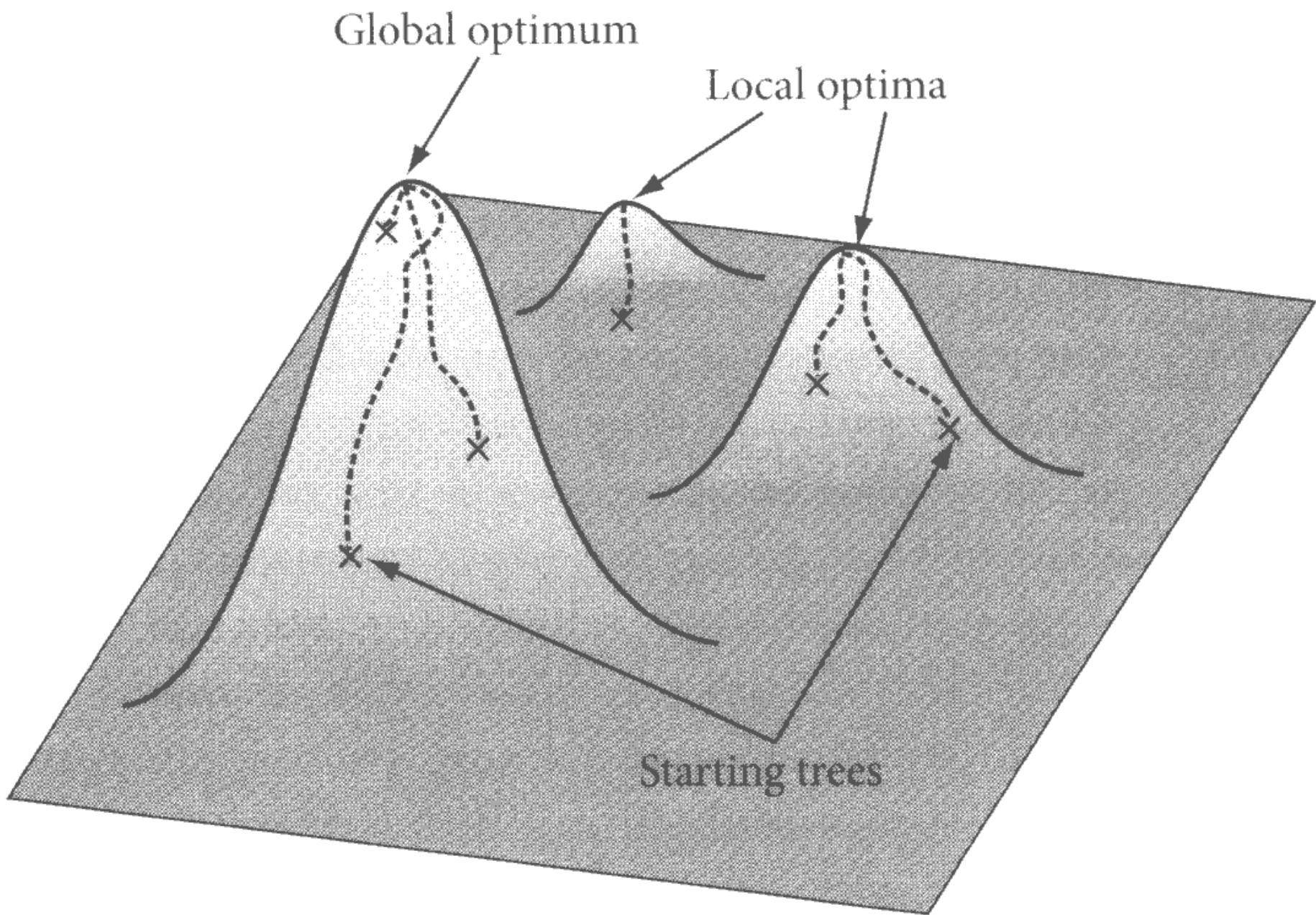


Tree Bisection and
Reconnection

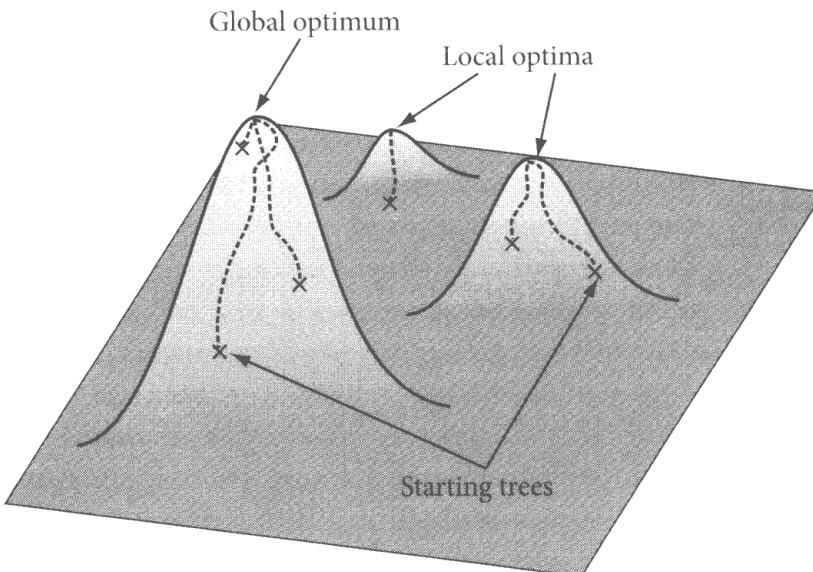
TBR



Heuristic tree searches (hill-climbing algorithm)



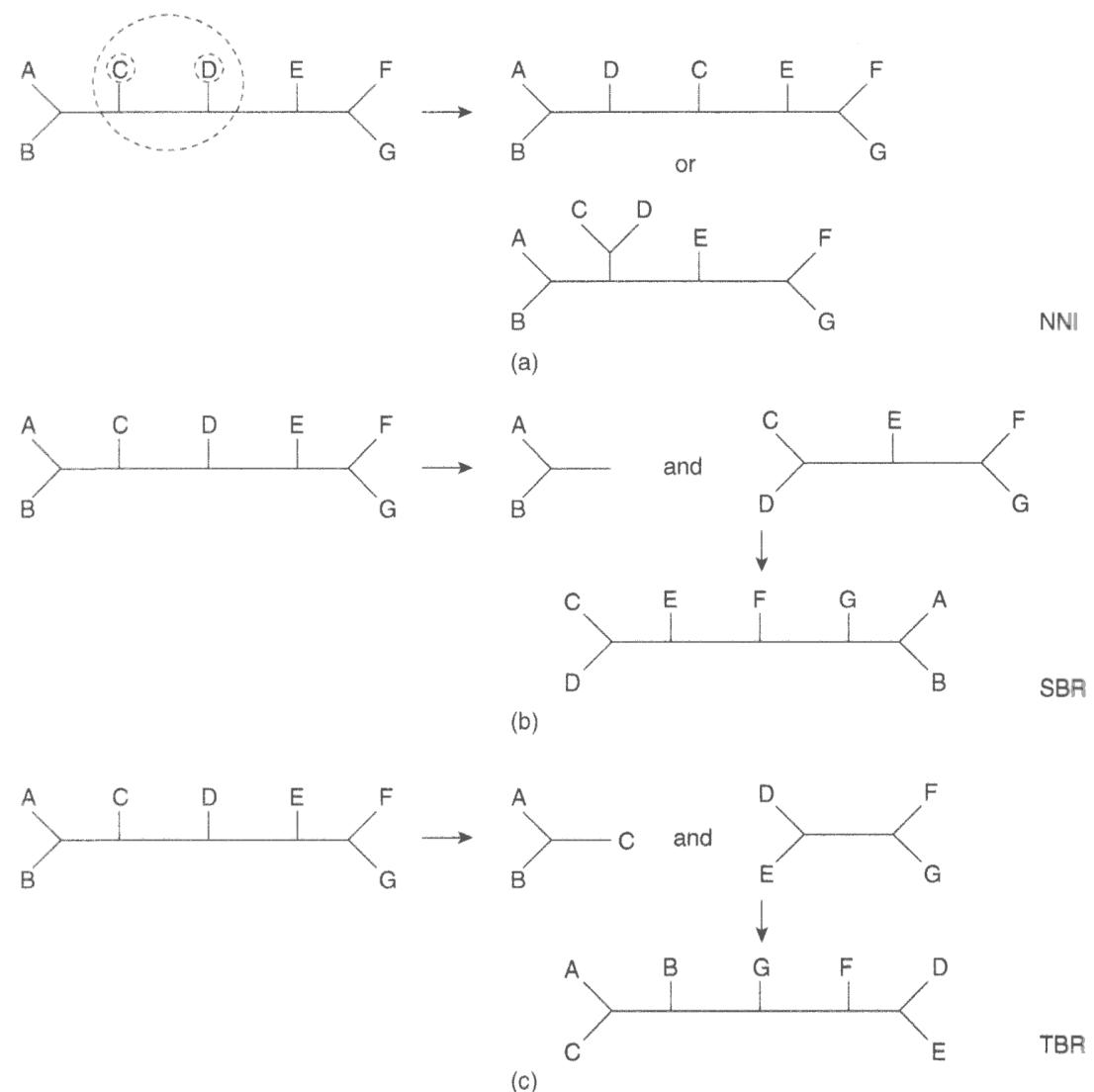
Heuristic tree searches (hill-climbing algorithm)



How can we escape local optima and find the global optimum?

Accept sub-optimal trees
Sometimes...

Choose several random starting points...



Parsimony: heuristic versus exhaustive

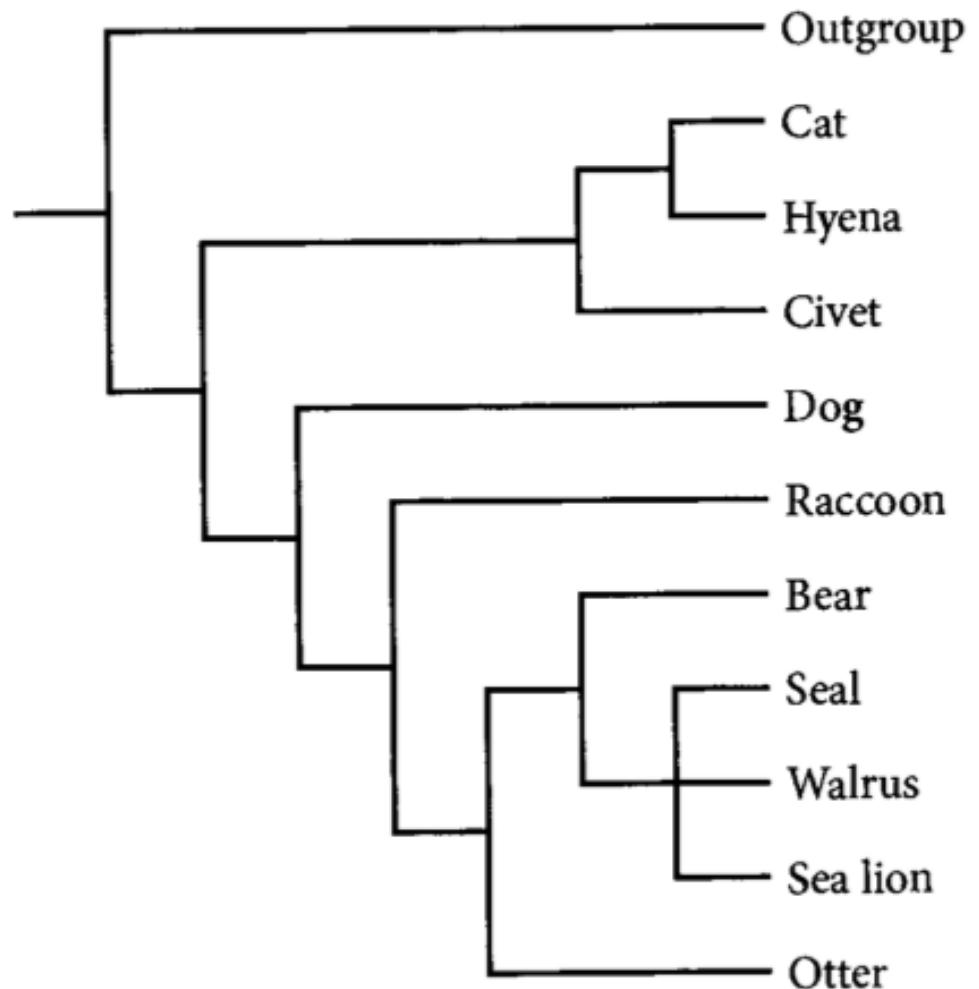
Expanded carnivore matrix. Let's compare run times of heuristic (approximate) and exhaustive (exact) searches

	1 (4)	2 (21)	3 (32)	4 (45)	5 (52)	6 (54)	7 (56)	8 -	9 (59)	10 (60)	11 (61)	12 (62)	13 (40)	14 (50)	15 (51)	16 (1)	17 (2)	18 (3)	19 (24)	20 (26)
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cat	0	1	0	1	0	0	1	1	1	0	0	0	1	1	1	0	0	0	0	0
Hyena	0	1	0	1	0	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0
Civet	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Dog	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Raccoon	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Bear	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1
Otter	1	0	0	0	1	0	0	0	0	1	0	0	1	0	1	1	1	0	0	0
Seal	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	1	?	0	1	1
Walrus	1	0	1	0	1	1	0	0	0	1	1	1	0	0	1	1	0	1	1	1
Sea lion	1	0	1	0	1	1	0	0	0	1	0	0	0	1	1	1	0	1	1	1

Parsimony: heuristic versus exhaustive

Expanded carnivore matrix. Let's compare run times of heuristic (approximate) and exhaustive (exact) searches

	1 (4)	2 (21)	3 (32)	4 (45)	5 (52)	6 (54)	7 (56)	8 -	9 (59)	10 (60)	11 (61)	12 (62)	13 (40)	14 (50)	15 (51)	16 (1)	17 (2)	18 (3)	19 (24)	20 (26)
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cat	0	1	0	1	0	0	1	1	1	0	0	0	0	1	1	1	0	0	0	0
Hyena	0	1	0	1	0	0	1	0	1	0	0	0	0	1	1	1	1	0	0	0
Civet	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0
Dog	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Raccoon	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Bear	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1	0	1
Otter	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	1	1	0	0
Seal	1	0	1	0	1	1	0	0	0	1	1	1	0	1	1	1	?	0	1	1
Walrus	1	0	1	0	1	1	0	0	0	1	1	1	0	0	1	1	0	1	1	1
Sea lion	1	0	1	0	1	1	0	0	0	1	0	0	0	1	1	1	0	1	1	1



Parsimony: Models of Evolution

Character weighing

	1	2	3	4	5	6	7	8	Total length	Total cost
O	0	0	1	0	1	1	0	0		
A	0	1	1	0	1	0	1	0		
B	1	1	1	1	0	0	1	1		
C	0	0	0	1	1	1	0	0		
Weight	1	1	1	5	1	1	1	1		
Cost of tree 1	1	2	1	5	1	2	2	1	11	15
Cost of tree 2	1	2	1	10	1	2	2	1	12	20
Cost of tree 3	1	1	1	10	1	1	1	1	9	17

← Most parsimonious

Parsimony: Models of Evolution

Step Matrix with character state changes receiving same weight

From:	To:				
	A	C	G	T	
A	0	1	1	1	
C	1	0	1	1	
G	1	1	0	1	
T	1	1	1	0	

Step Matrix upweighting transversions compared to transitions

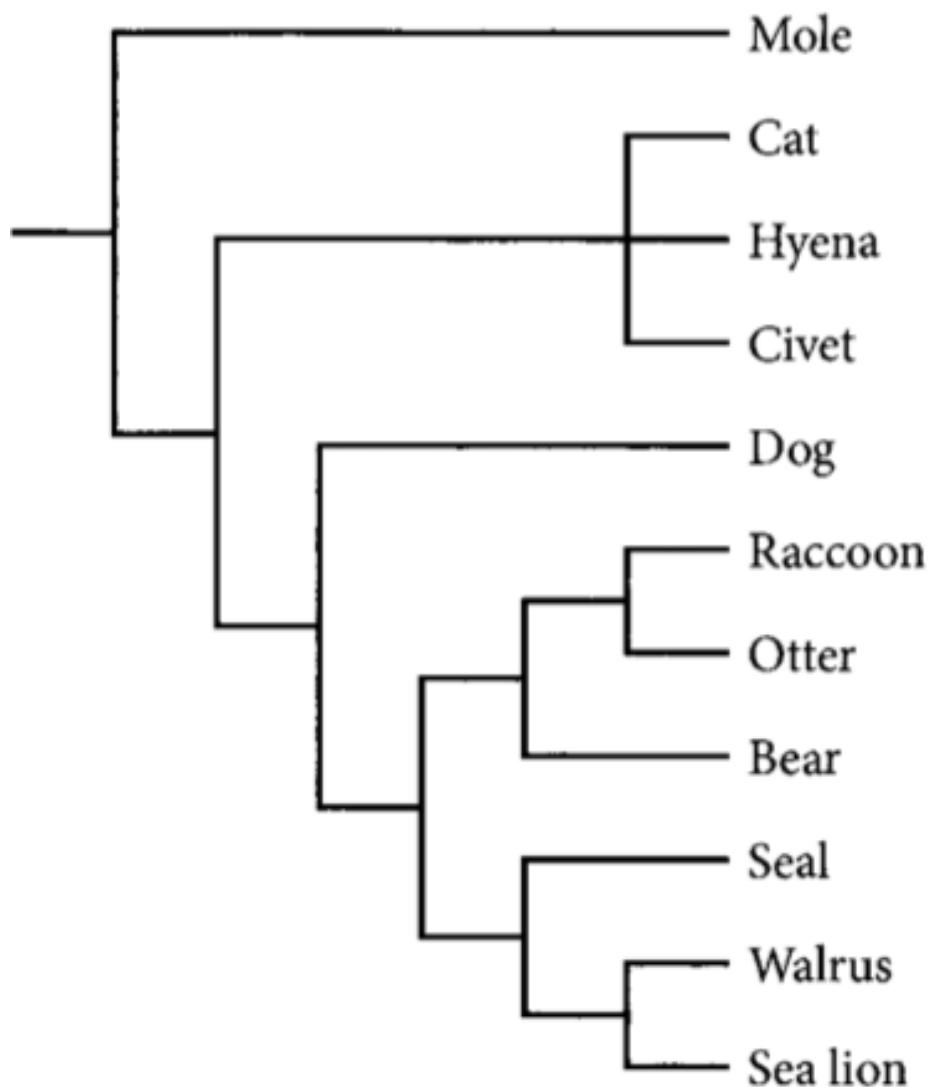
From:	To:				
	A	C	G	T	
A	0	2	1	2	
C	2	0	2	1	
G	1	2	0	2	
T	2	1	2	0	

Parsimony: Molecular Data

Taxon	Positions in DNA sequence														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Mole	G	T	T	A	A	-	C	T	T	C	T	C	A	C	T
Cat	G	T	T	G	A	-	C	C	T	C	T	T	A	C	T
Hyena	G	T	T	G	A	-	C	C	T	C	T	C	A	C	T
Civet	G	T	T	G	A	-	C	C	T	C	T	C	A	C	T
Dog	G	T	T	A	A	G	C	A	T	C	T	G	C	C	T
Raccoon	G	T	T	A	A	G	G	G	T	C	T	G	C	C	T
Bear	C	T	T	A	A	G	T	G	T	C	T	G	C	C	T
Otter	G	T	T	A	A	G	G	G	T	C	T	G	C	C	T
Seal	G	T	A	A	A	G	C	G	T	C	T	G	C	C	T
Walrus	G	T	A	A	A	G	C	G	T	C	T	G	C	C	T
Sea lion	G	T	A	A	A	G	C	G	T	C	T	G	C	C	T

Parsimony: Molecular Data

	Positions in DNA sequence														
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Mole	G	T	T	A	A	-	C	T	T	C	T	C	A	C	T
Cat	G	T	T	G	A	-	C	C	T	C	T	T	A	C	T
Hyena	G	T	T	G	A	-	C	C	T	C	T	C	A	C	T
Civet	G	T	T	G	A	-	C	C	T	C	T	C	A	C	T
Dog	G	T	T	A	A	G	C	A	T	C	T	G	C	C	T
Raccoon	G	T	T	A	A	G	G	G	T	C	T	G	C	C	T
Bear	C	T	T	A	A	G	T	G	T	C	T	G	C	C	T
Otter	G	T	T	A	A	G	G	G	T	C	T	G	C	C	T
Seal	G	T	A	A	A	G	C	G	T	C	T	G	C	C	T
Walrus	G	T	A	A	A	G	C	G	T	C	T	G	C	C	T
Sea lion	G	T	A	A	A	G	C	G	T	C	T	G	C	C	T



Parsimony: Molecular Data

Taxon A:	G	T	A	T	T	G	A	C	C	A	C	T	G	A	C	T	A	G	C	A	T
Taxon B:	G	C	A	T	T	A	A	C	C	A	T	T	G	T	C	T	A	G	C	A	A

Ancestor	G	T	A	T	T	G	A	C	C	A	C	T	G	A	C	T	A	G	C	A	T
Descendant	G	C	A	T	T	-	-	-	-	-	T	T	G	T	C	T	A	G	C	A	A

Deletion

Ancestor	G T A T T G A C C - - A C T G A C T A G C A T
Descendant	G C A T T A A C C A C C A T T G T C T A G C A A

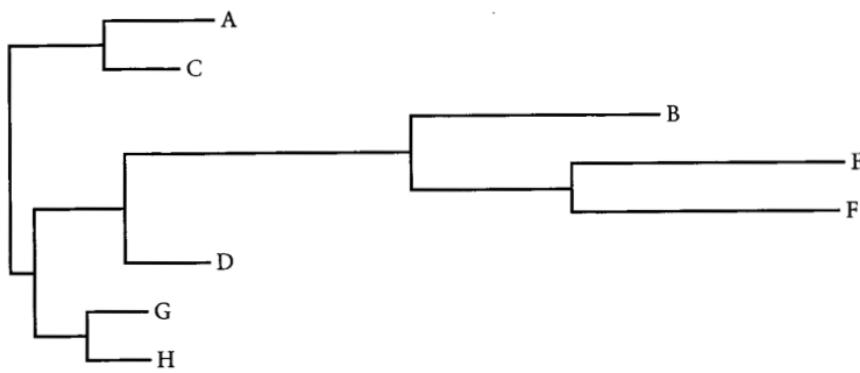
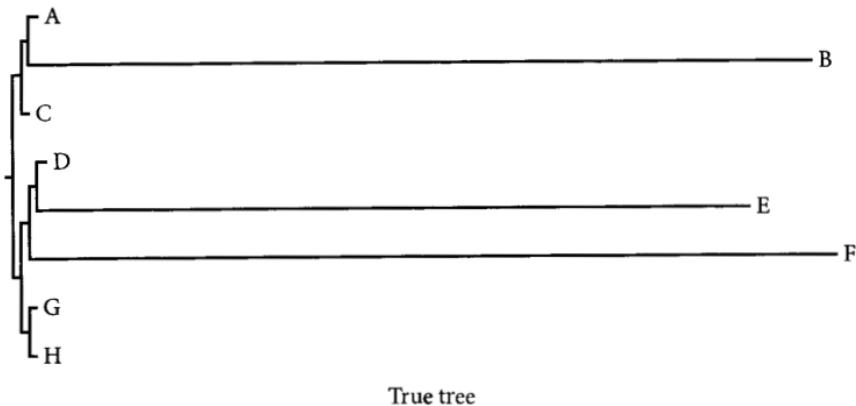
Insertion

We do not necessarily know *a priori* about ancestor/descendant relationships. So insertions and deletions are generally referred to as **indels**.

How many events does an indel represent?

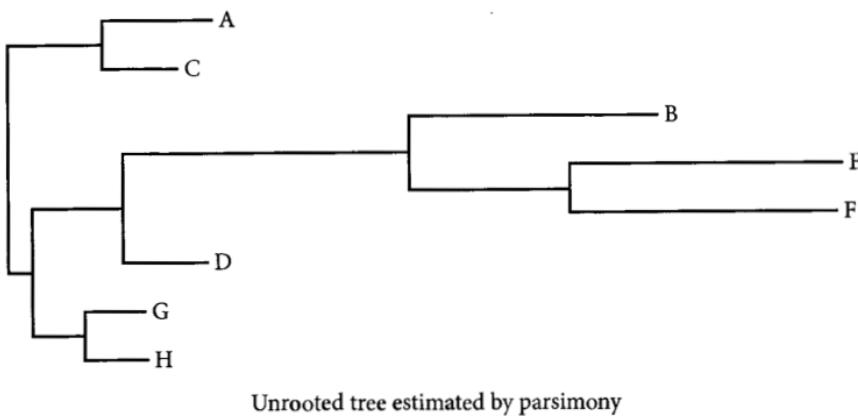
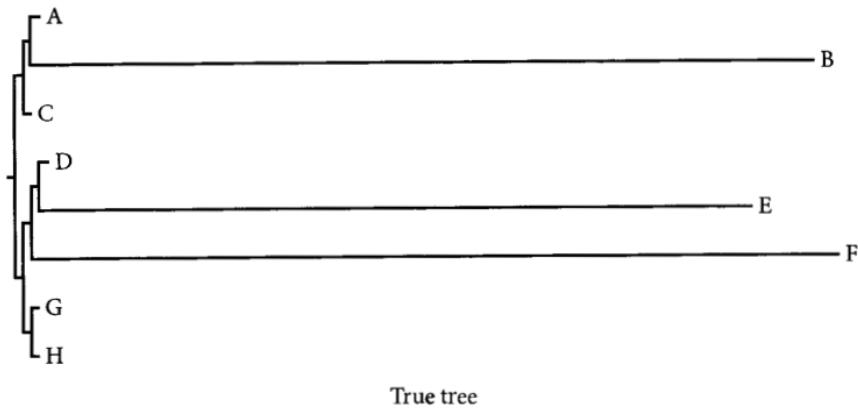
Problems of Parsimony

Parsimony does not take branch lengths into account. High rates of evolution, especially in different parts of the tree can lead to inference of wrong tree



Problems of Parsimony

Parsimony does not take branch lengths into account. High rates of evolution, especially in different parts of the tree can lead to inference of wrong tree



Character weighing may alleviate the issue but there is no formal way of testing weighting schemes in the parsimony framework.

Markov models in phylogenetics

