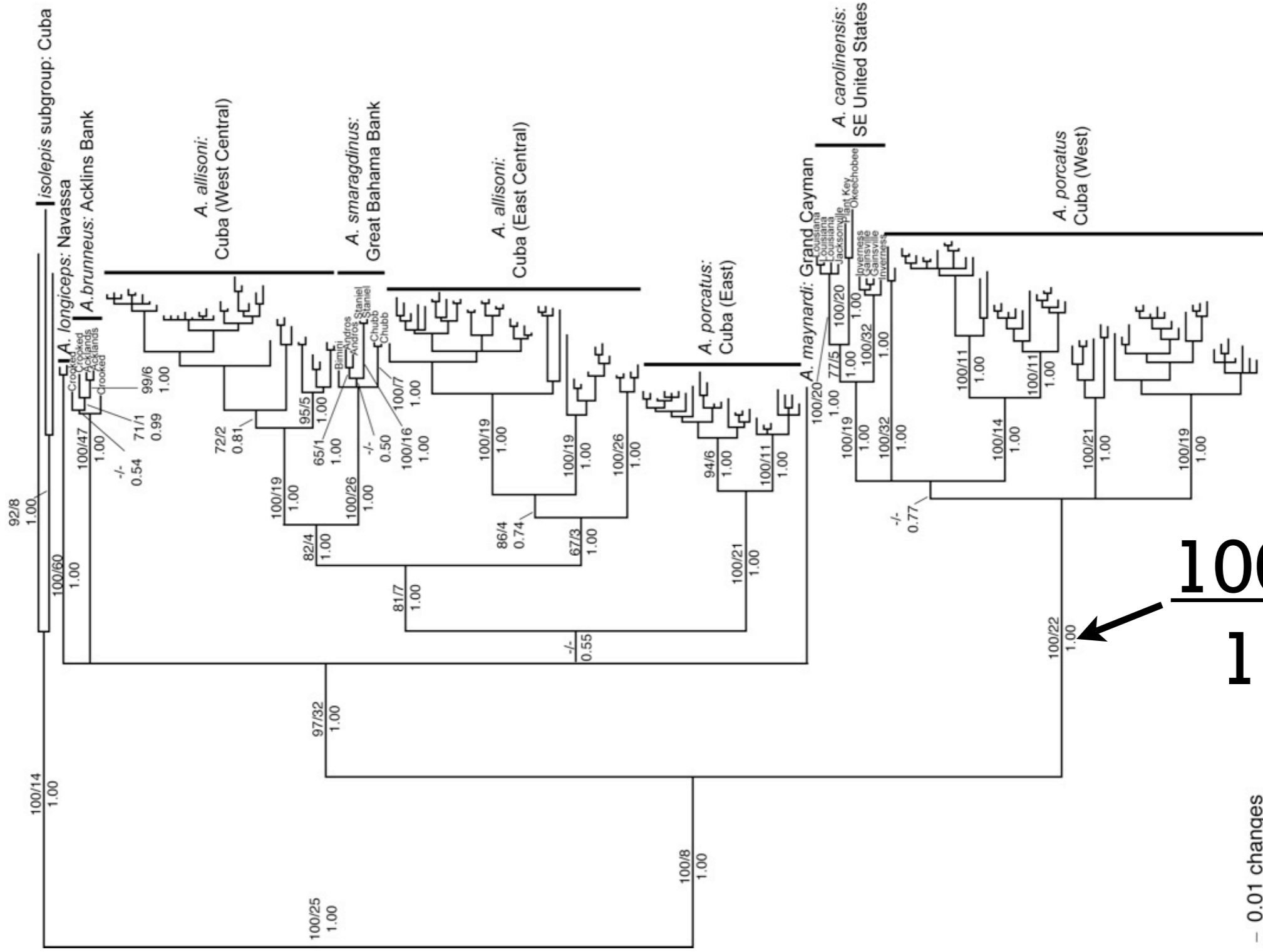


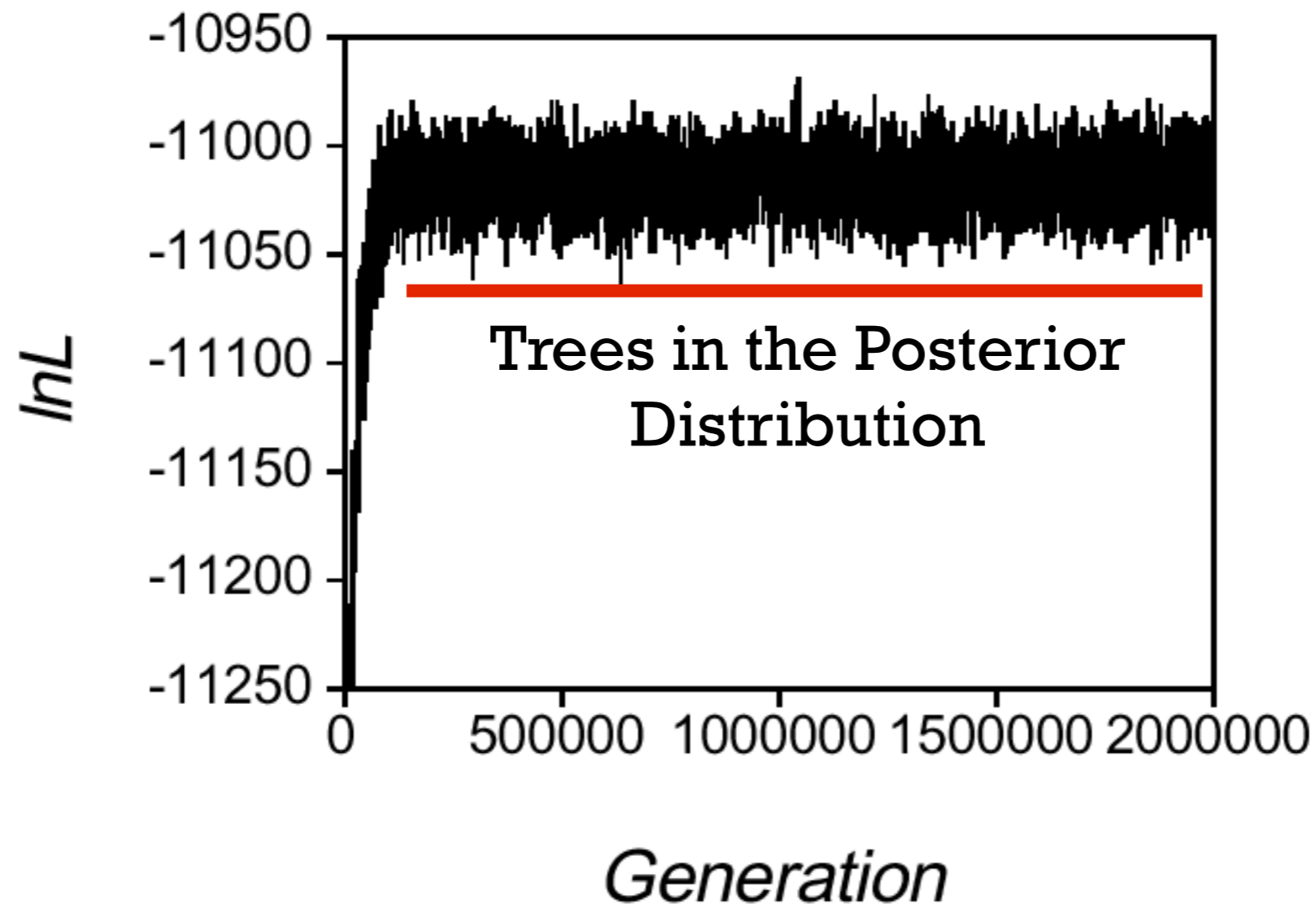
# Tree Support



# Measures of Tree Support

- **Heuristic Measures of Support**
  - Majority rule consensus trees
  - Posterior Probability (Bayesian only)
  - The Bootstrap
  - Decay Index
- **Hypothesis Testing**
  - Paired-sites tests (e.g., Templeton Test, KH Test)
  - Parametric bootstrap

# Bayesian Posterior Probability



# Consensus Trees

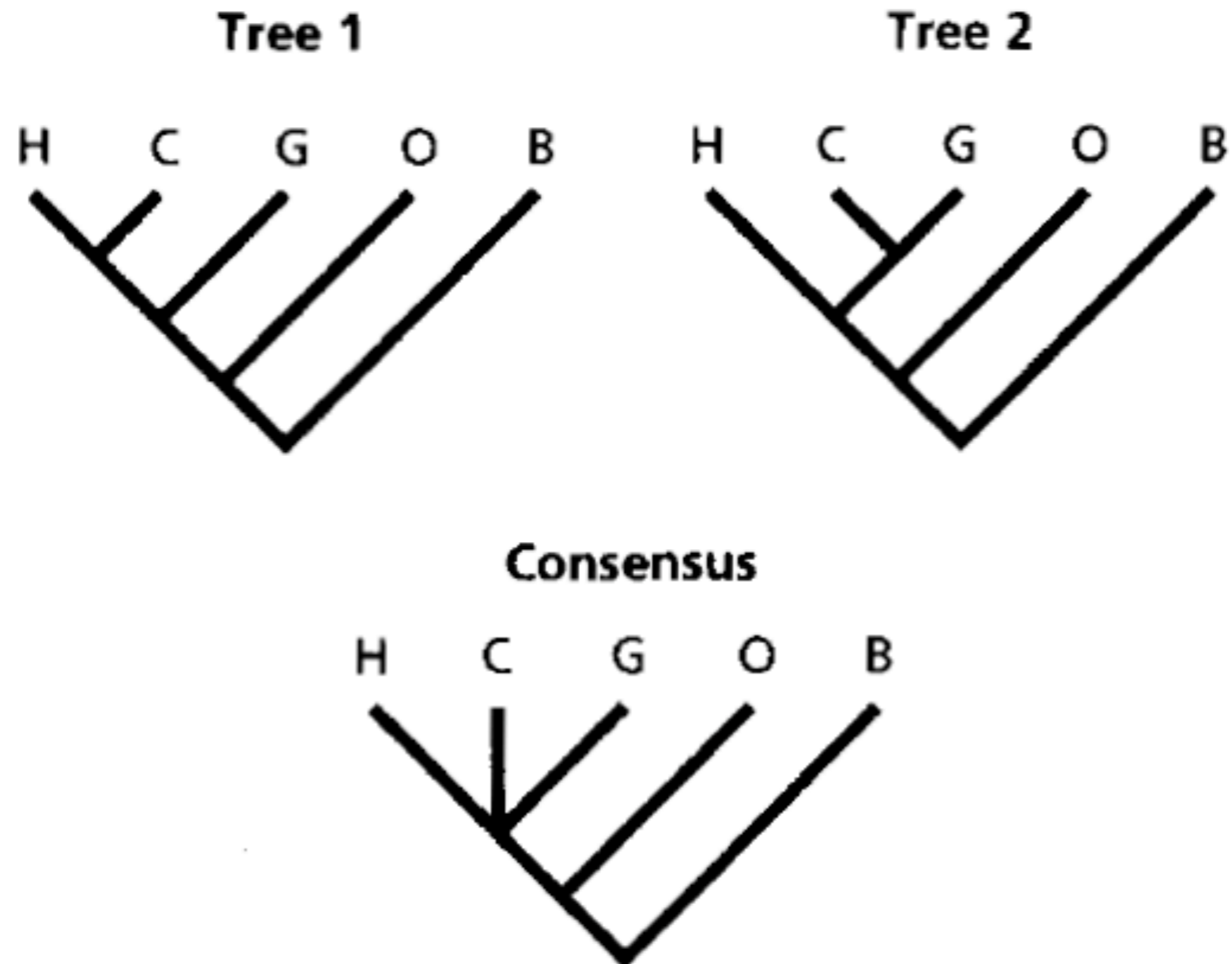
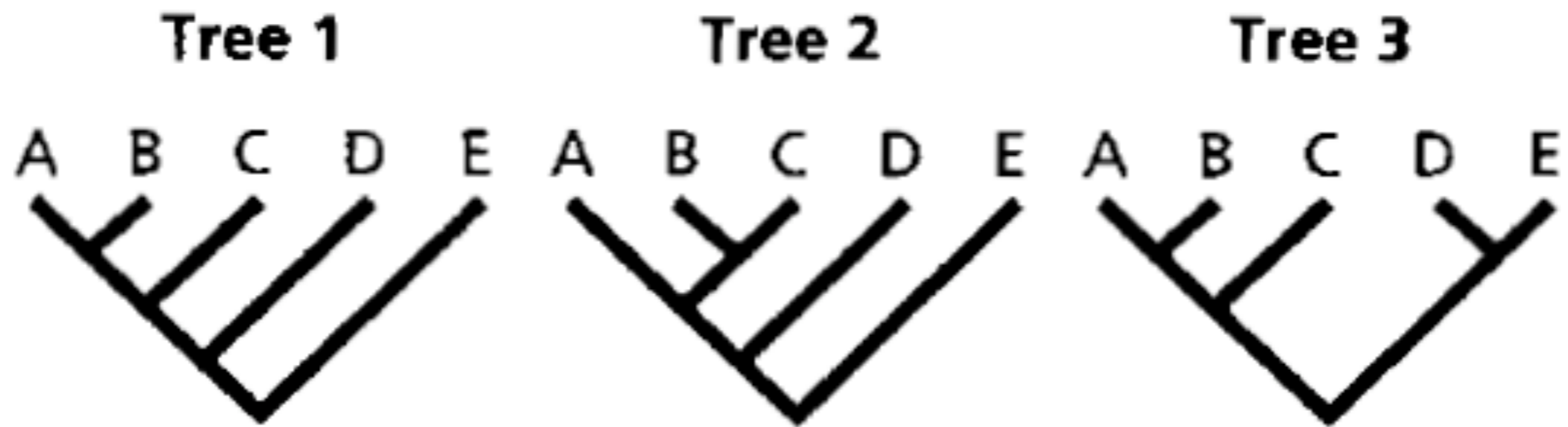
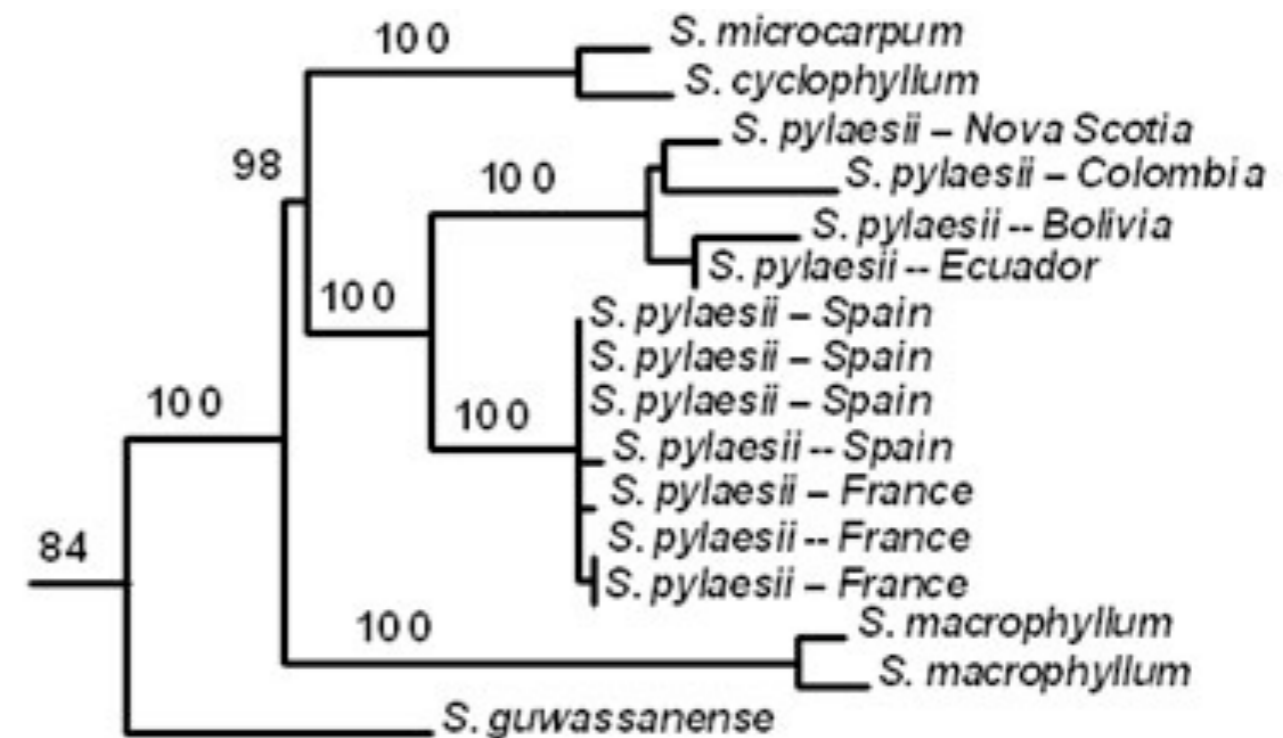
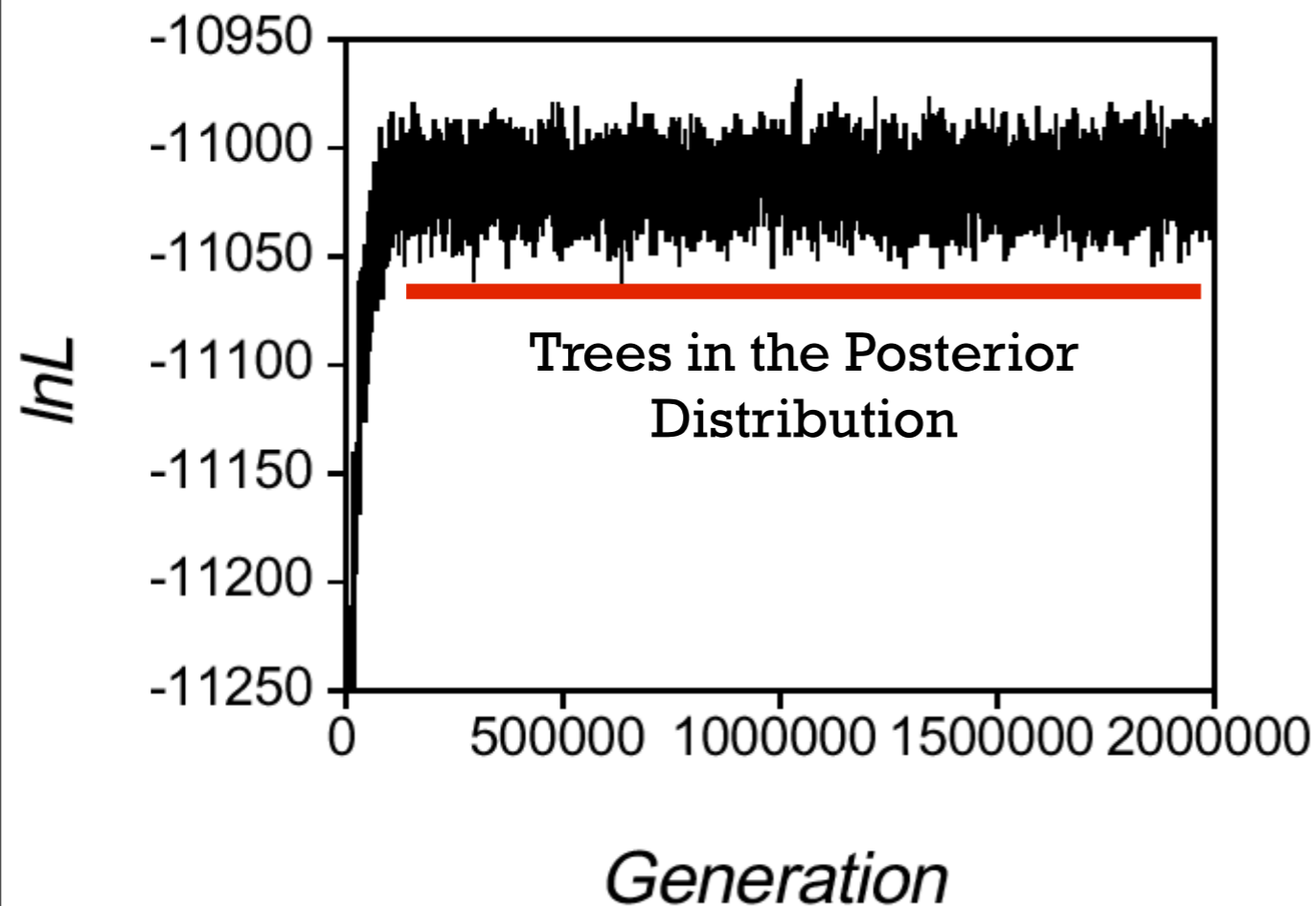


Figure 2.26 from Page and Holmes 1999

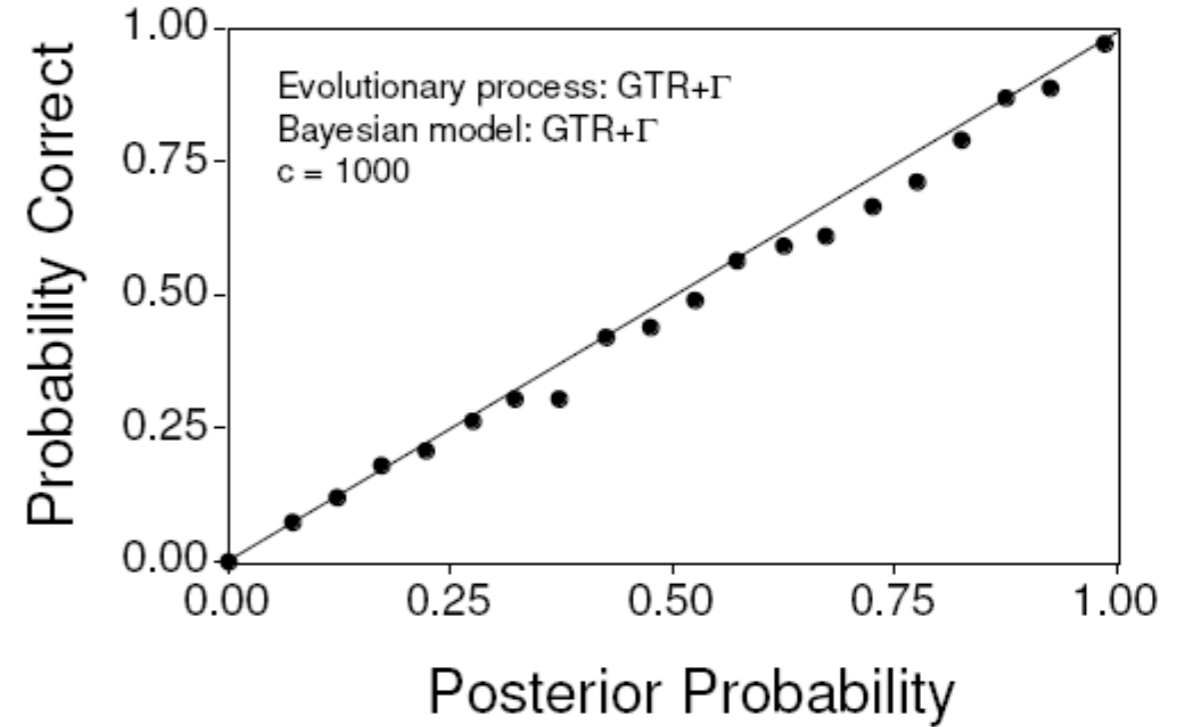
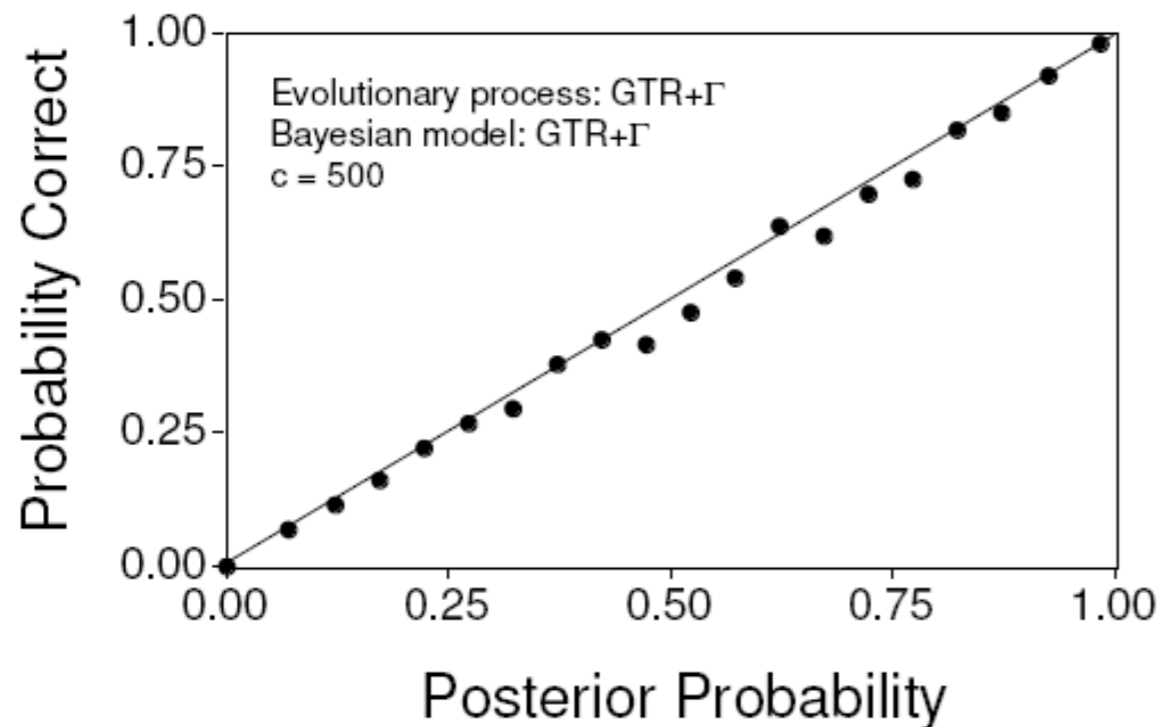
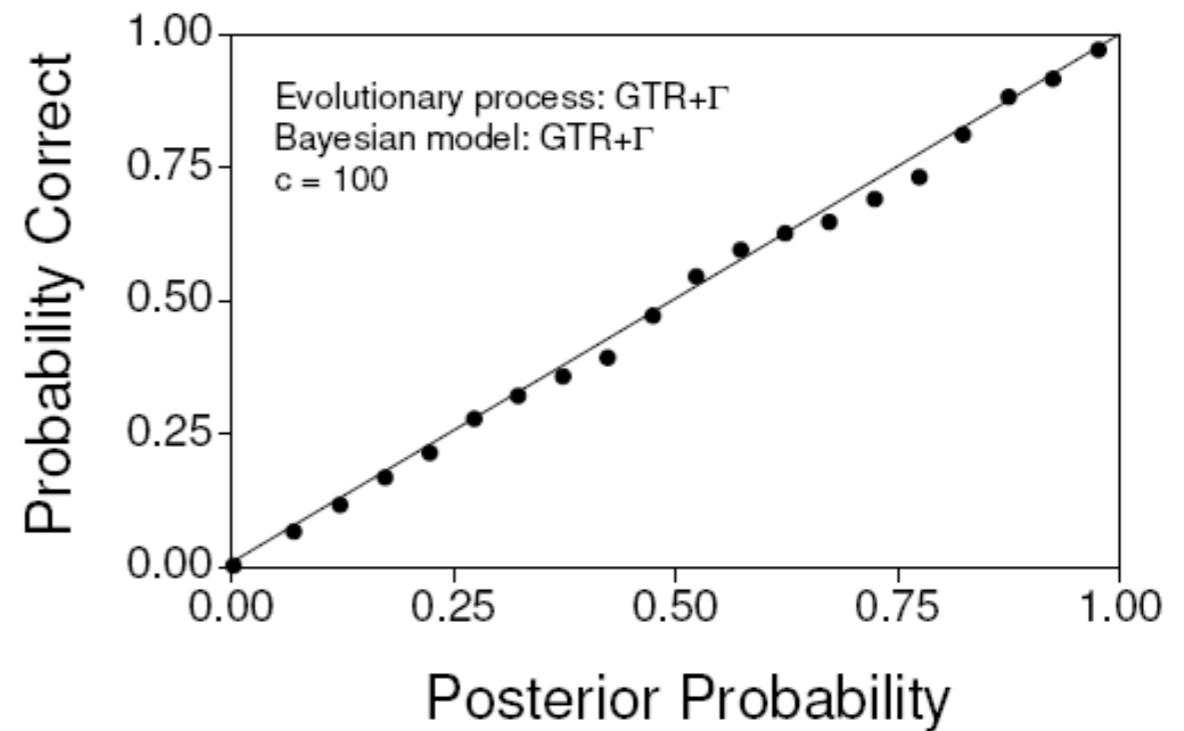
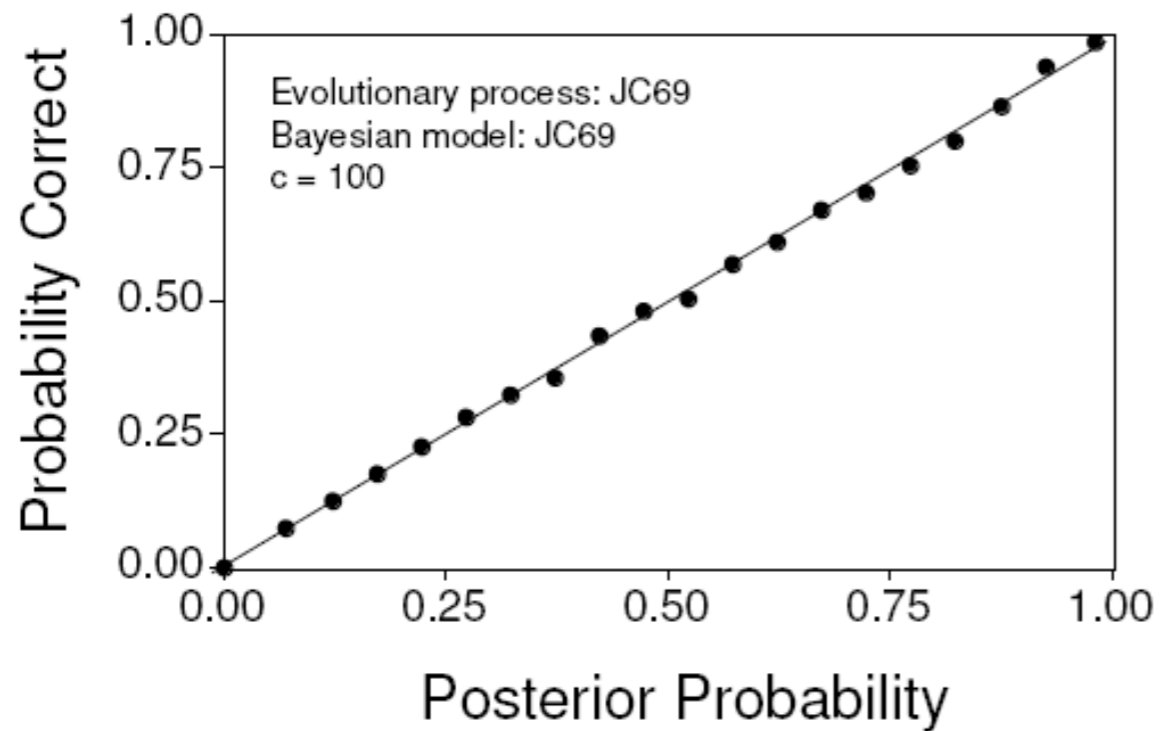
# Majority Rule Consensus



# Bayesian Posterior Probabilities

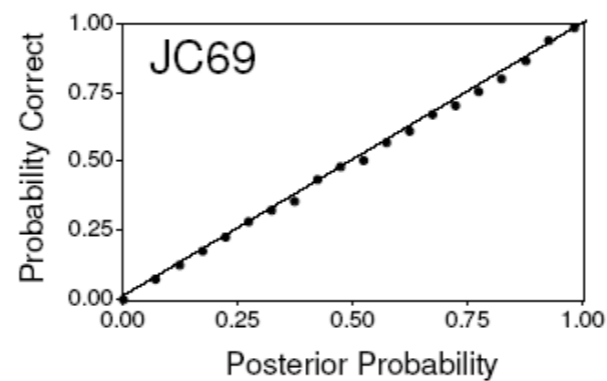
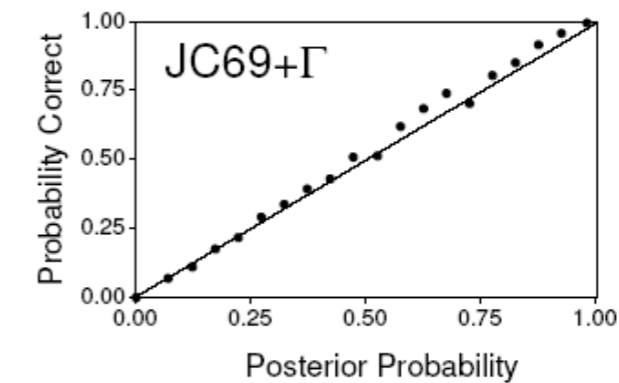
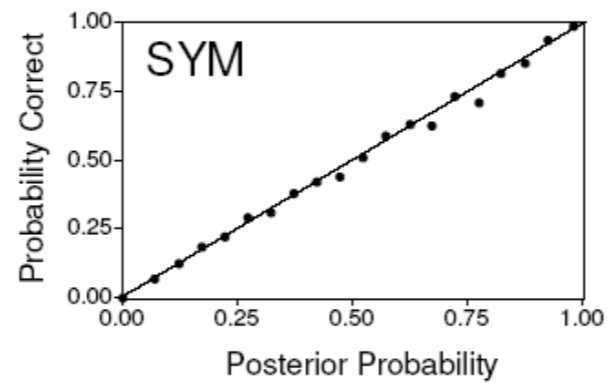
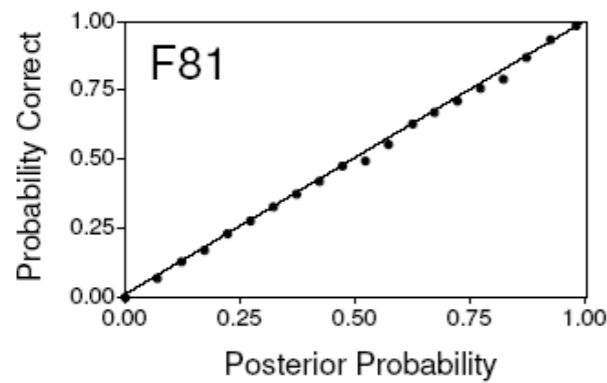
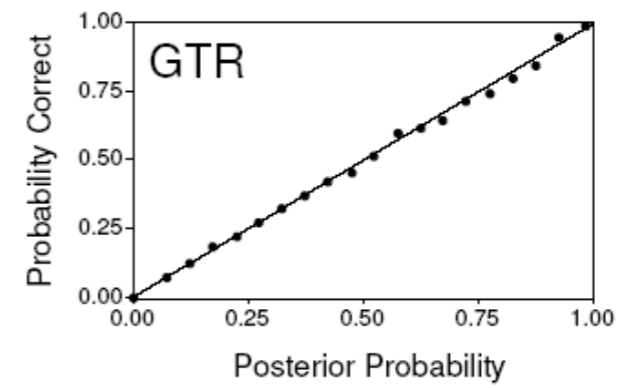
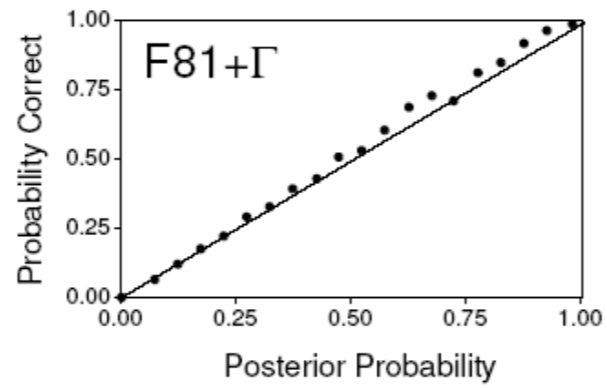
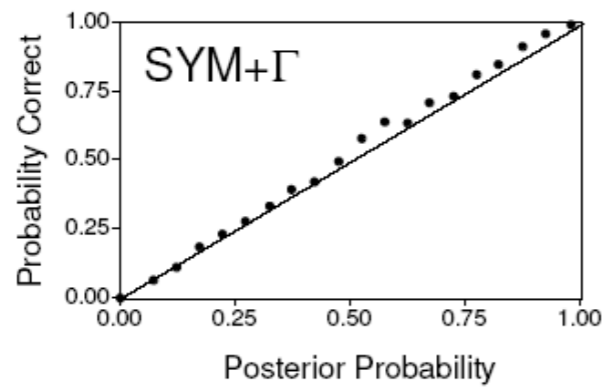
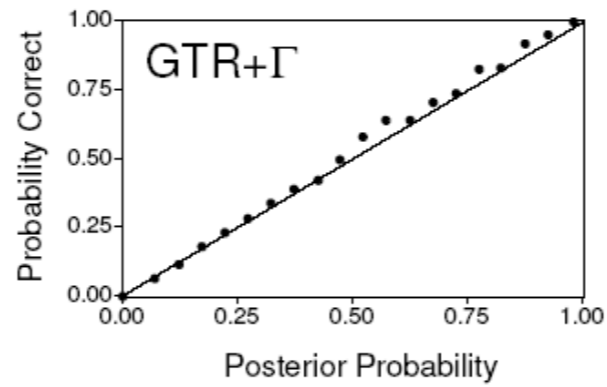


# Posterior Probabilities



# Posterior Probabilities

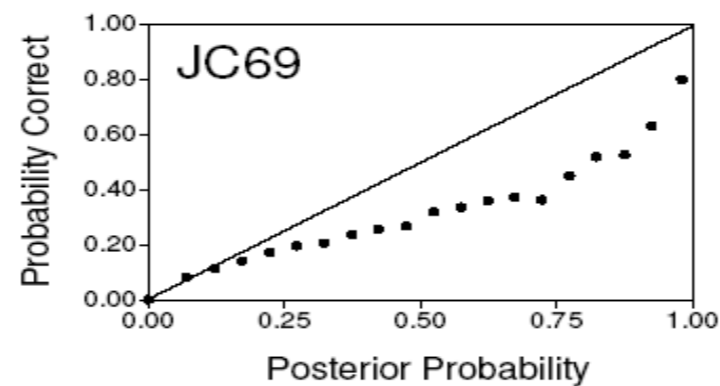
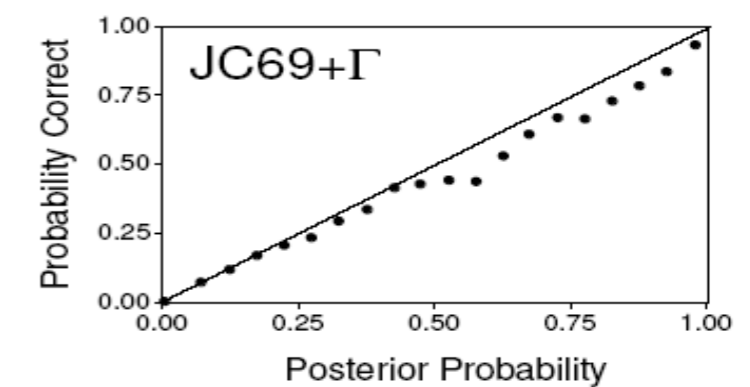
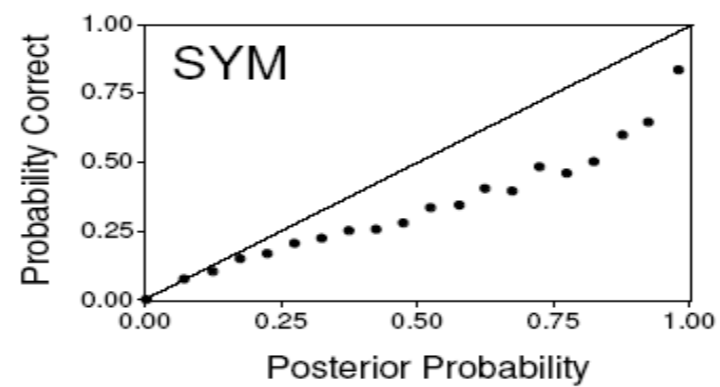
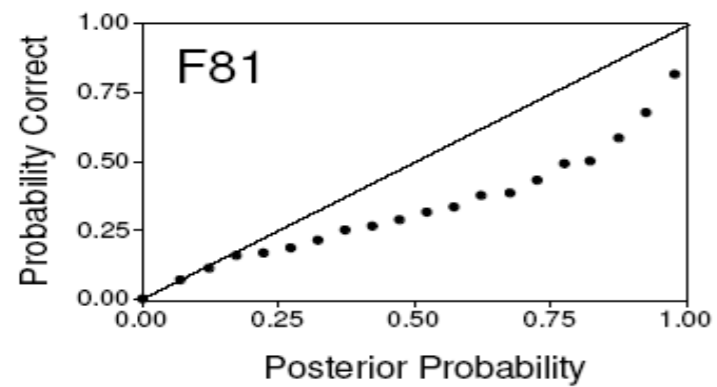
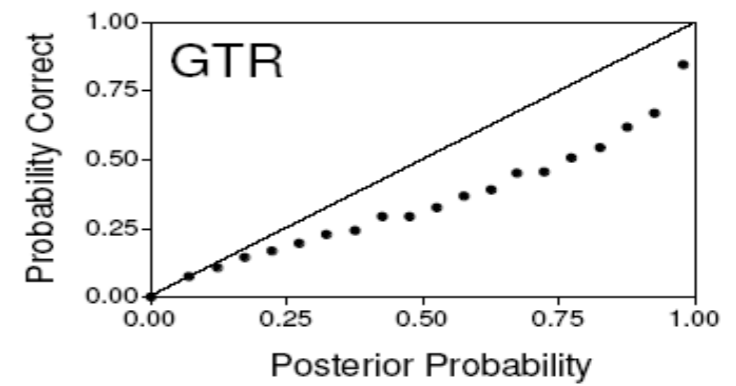
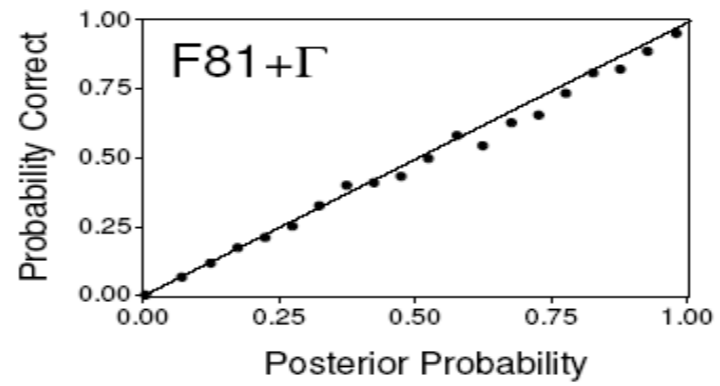
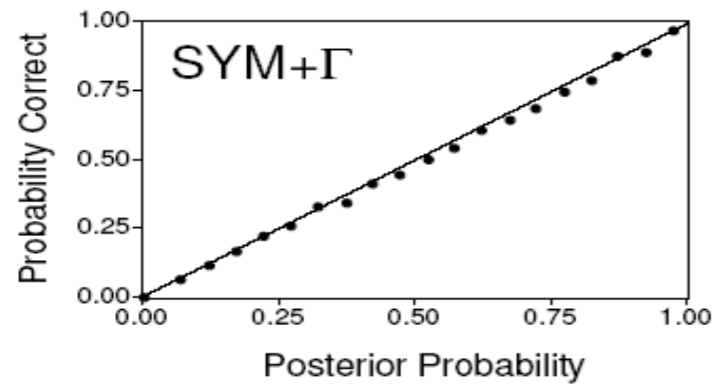
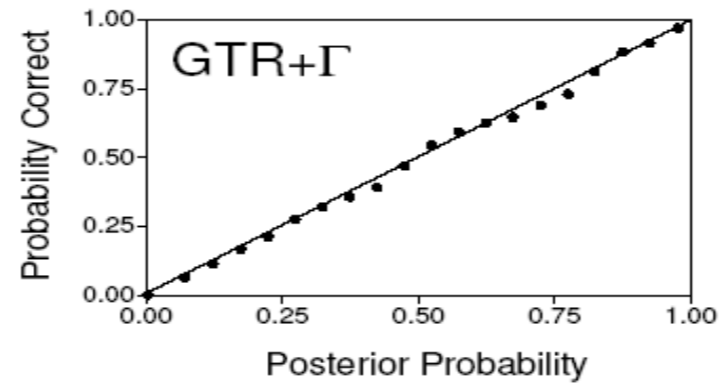
Evolutionary process: JC69  
100 Sites





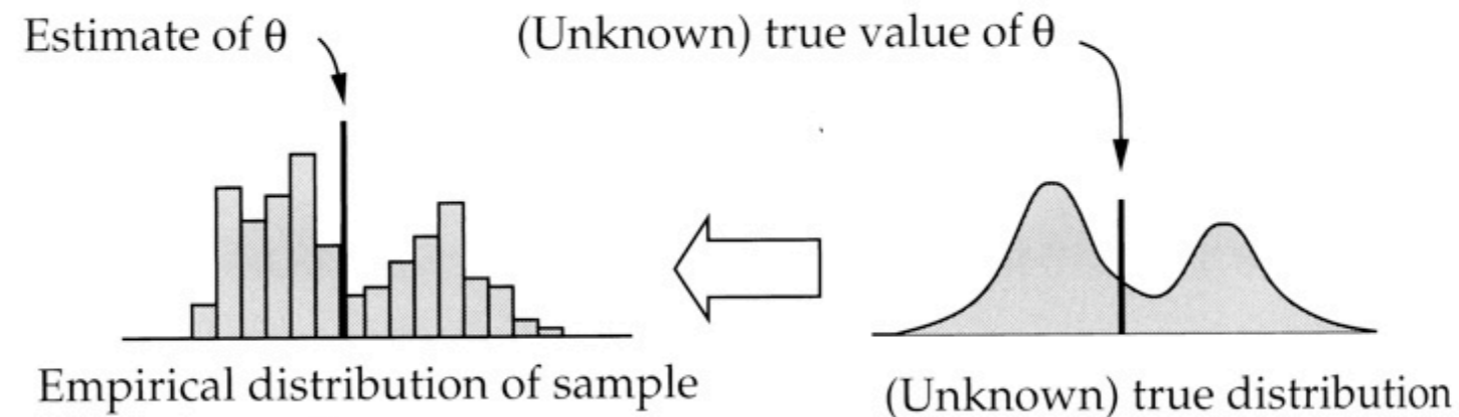
# Posterior Probabilities

Evolutionary process: GTR+ $\Gamma$   
100 Sites



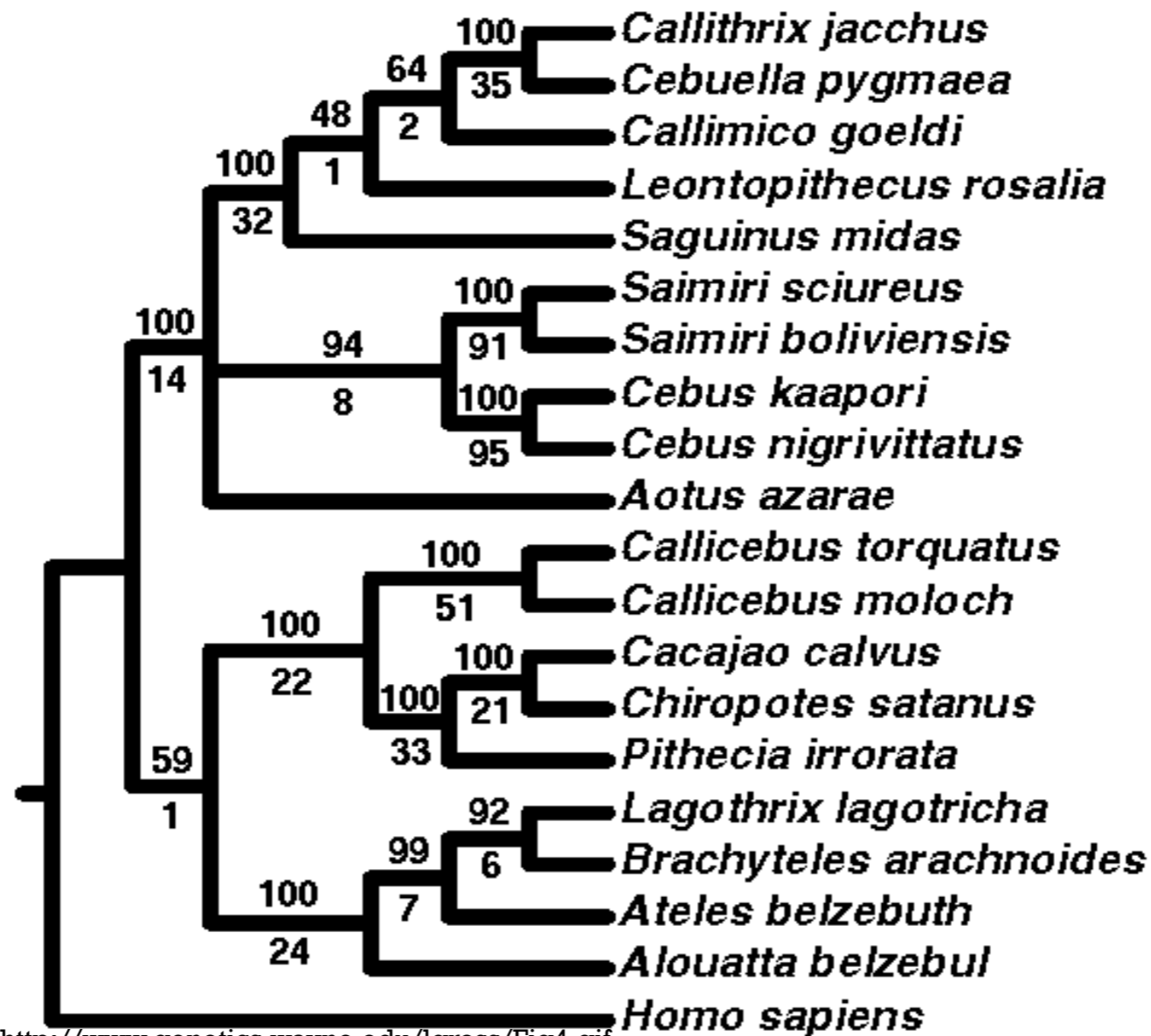
# Bootstrapping

- Sampling with replacement



# Bootstrapping a Phylogenetic Dataset

3. Ask which nodes are shared among analyses of bootstrapped datasets and construct consensus.

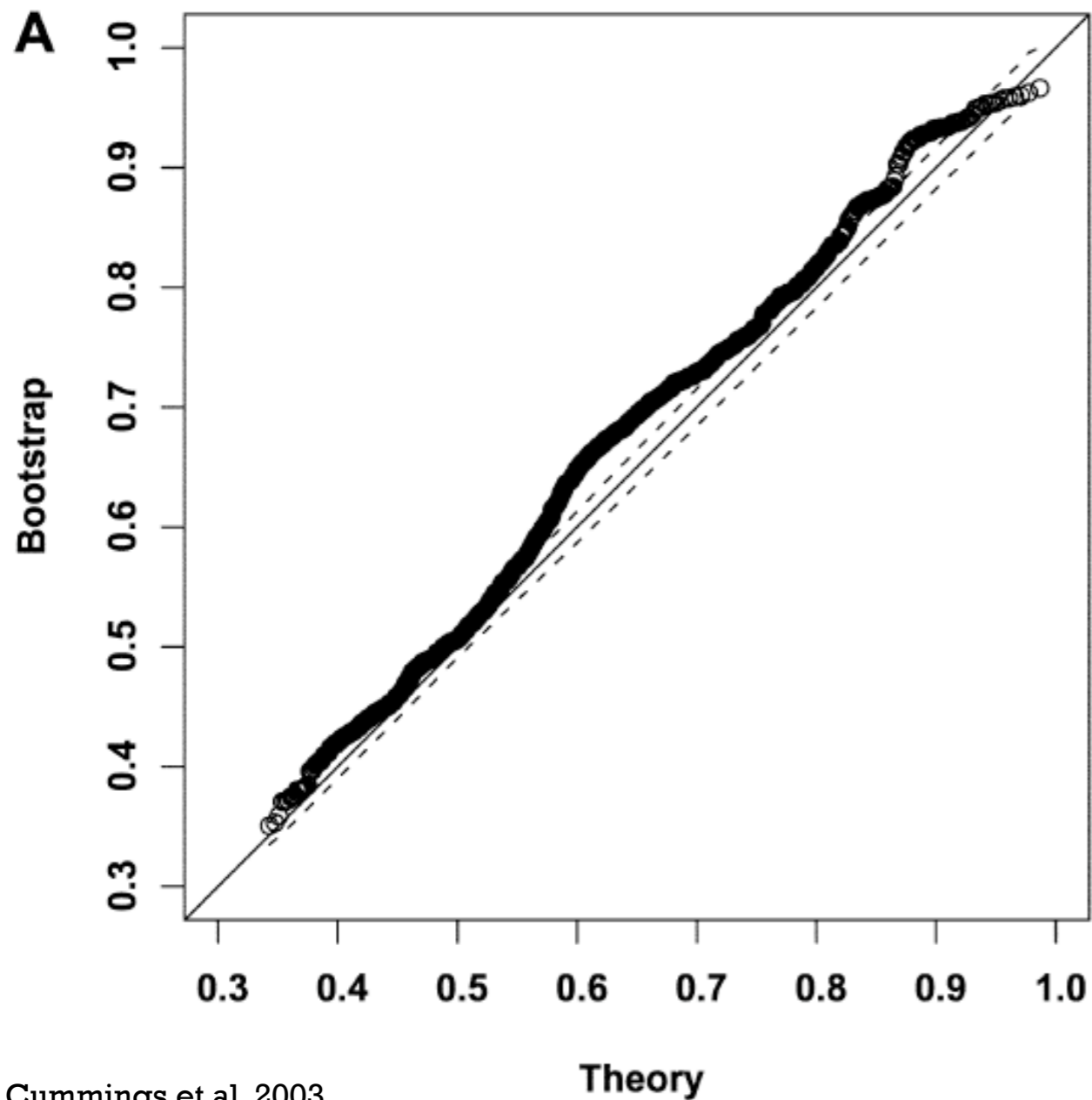


<http://www.genetics.wayne.edu/lgross/fig4.gif>

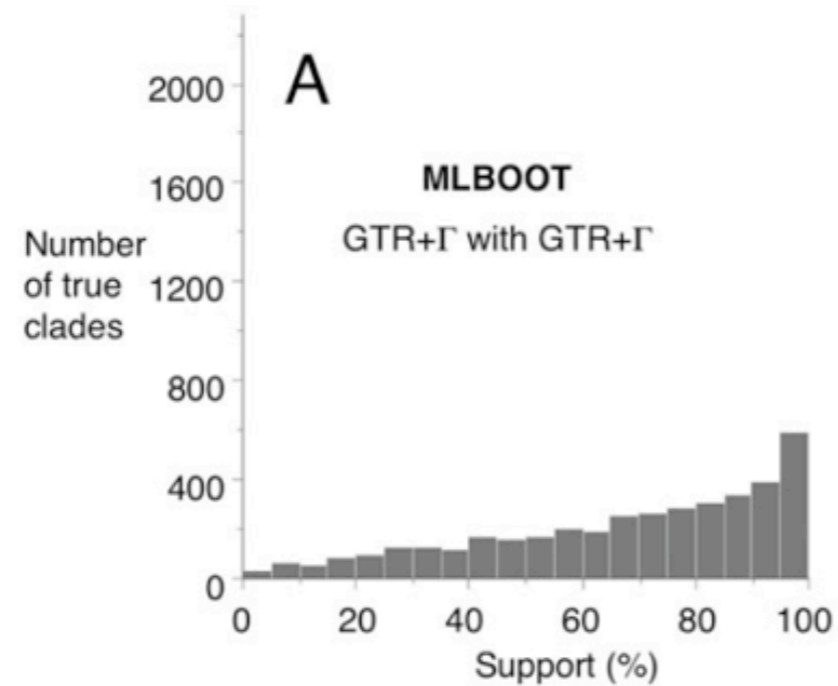
# Interpreting Bootstrap Values

- Value on each node = percent of bootstrapped datasets that support that node.
- What is a “significant” bootstrap?
  - Most studies indicate that bootstrap values are conservative.
  - Depending on who you talk to, values ranging from 70-100% are considered reliable (Hillis and Bull 1993)

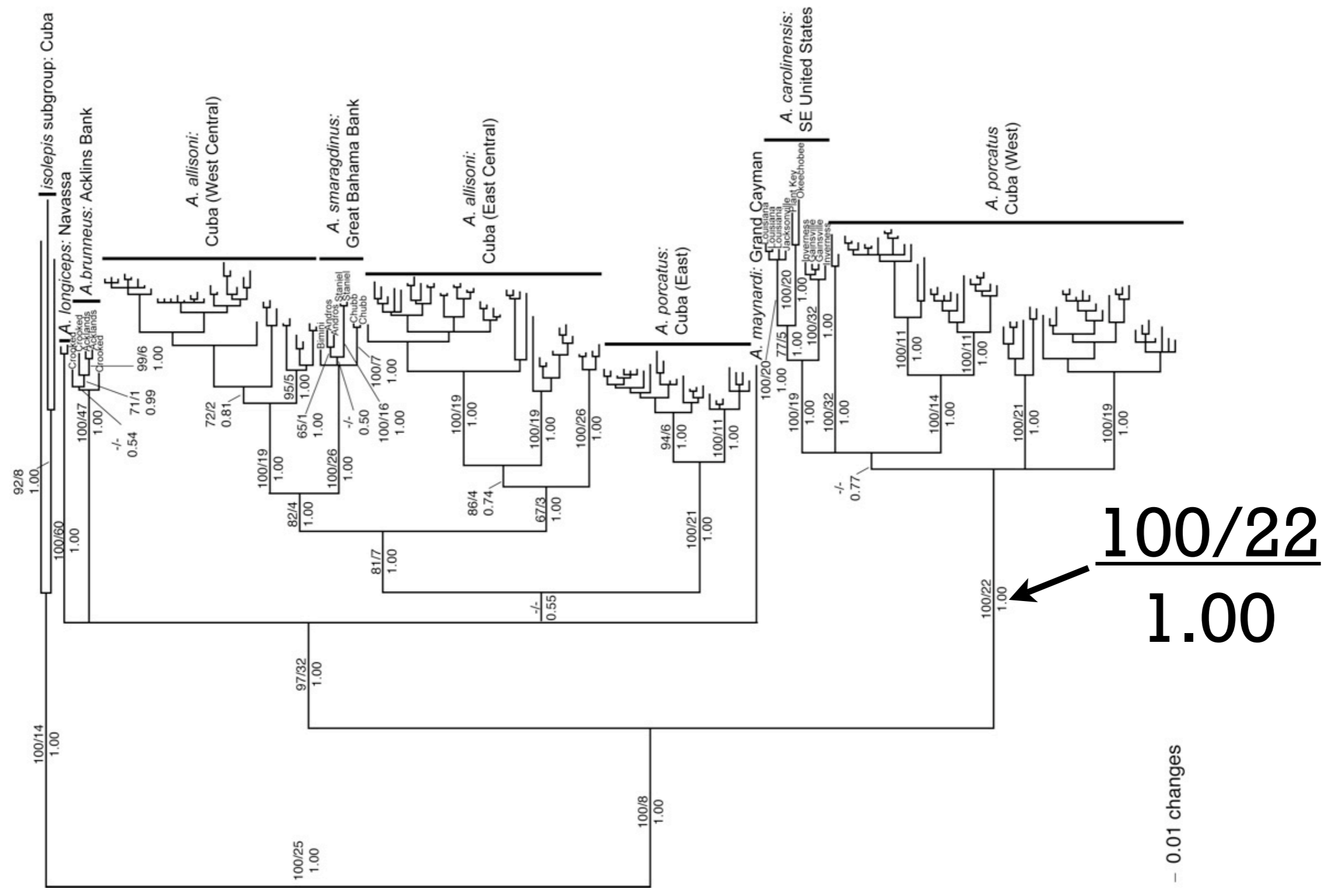
# Bayesian Posterior Probabilities Versus Bootstraps



# Bayesian Posterior Probabilities Versus Bootstraps



# Multiple Measures



- 0.01 changes

# Why Build Trees?

1. Framework for biodiversity information (systematics).  
Organizing system for biodiversity information.
2. Comparative hypotheses about adaptation, functional biology; ancestral state reconstruction (synthesizing ancestral molecules).
3. Predictions about unsampled taxa (bioprospecting, drug discovery). Few people are making predictions, but its been talked about. "An open niche" in phylogenetic inference.
4. Assays for "phylogenetic diversity" (conservation biology)

- M. Sanderson 2007



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- M. Sanderson 2007

# Outline

- **Importance of ancestral reconstruction.**
- **Characters used in ancestral reconstruction.**
- **Methods of reconstruction.**

# Evolution of Discrete Characters

- What are discrete characters?
- Evolution of discrete characters
  - Part I: Ancestral Reconstruction
    - Ancestral reconstruction with parsimony and likelihood
    - Testing phylogenetic signal
    - Incorporating phylogenetic uncertainty
  - Part II: Testing Hypotheses About Character Evolution
    - Testing alternative patterns of character evolution
    - Testing character correlation

# What are Discrete Characters & Why are They Used?

- Naturally discrete categories.
- Nucleotides in DNA sequence data (A, G, C, T).

anolis\_mt\_overlap\_040804\_NAMES

Taxa	Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	0	0	
1	P heteroderma	A	T	G	A	A	C	C	C	T	A	C	A	A	T	A	T	A	T	T	C	A	A	T	T	A	T	T	T	C	T	A	G	C	C	T	T	G	C	A	A	C	C	G	G	A	A	C	C	A	T	T	A	T	T	A	C	T	A	T	A	A	C	T	A	G	C	C	A	C	C	A	T	T	G	A	C	T	G	C	T	A	G	C	C	T	G	A	C	T	T	G	G	A	C	T	A	G	A	A			
2	P inderanae	A	T	G	A	G	C	C	C	T	A	C	A	G	T	A	T	T	C	A	A	T	T	A	T	T	T	C	T	A	G	T	A	T	T	G	C	A	A	C	C	G	G	A	A	C	C	A	T	T	A	T	T	A	C	T	A	T	A	A	C	C	A	G	C	C	A	C	C	A	T	T	G	A	C	T	G	T	T	A	G	C	C	T	G	A	C	T	T	G	G	A	C	T	G	G	A	A					
3	C barbatus	A	T	G	A	G	T	C	C	A	A	C	C	A	T	C	T	A	T	A	C	C	A	T	T	T	T	A	T	C	A	A	G	C	T	T	A	G	C	A	A	C	A	G	G	C	A	C	A	A	T	T	A	T	T	A	C	T	A	T	A	T	C	T	A	G	C	T	A	T	C	A	C	T	G	A	T	T	A	A	T	G	G	C	C	T	G	A	A	T	T	G	A	C	T	A	G	A	A				
4	C barbouri	A	T	G	A	G	C	C	C	A	A	T	T	A	T	A	C	A	T	A	C	A	A	T	T	T	T	A	T	C	A	A	G	C	C	T	A	G	C	A	A	C	A	G	G	C	A	C	A	A	T	T	A	T	T	A	C	T	A	T	A	A	C	T	A	G	C	T	T	T	C	A	C	T	G	A	C	T	A	A	T	A	G	C	A	T	G	A	A														
5	C porcus	A	T	G	A	G	T	C	C	A	A	C	C	A	T	A	T	A	T	A	C	T	A	T	T	T	T	A	T	C	A	A	G	C	T	T	A	G	C	A	A	C	A	G	G	C	A	C	A	A	T	T	A	T	T	A	C	C	A	T	A	T	C	T	A	G	C	T	A	T	C	A	C	T	G	A	T	T	A	A	T	A	G	C	C	T	G	A	A	T	C	G	G	A	C	T	A	G	A	A			
6	A ahli	A	T	G	A	G	C	C	C	A	A	T	A	T	A	T	A	T	A	C	A	C	A	A	T	T	A	T	A	C	T	A	T	C	A	A	G	C	C	T	A	G	C	A	A	C	A	G	G	C	A	C	A	A	T	T	A	T	T	A	C	T	A	T	A	A	C	C	A	G	C	C	A	C	C	A	T	T	G	A	C	T	T	A	T	A	G	C	C	T	G	G	T	T	G	G	C	C	T	A	G	A	A
7	A alayoni	A	T	G	A	G	C	C	C	A	A	T	T	A	T	T	A	T	T	A	C	A	A	C	T	A	T	T	C	T	T	T	C	A	A	G	C	C	T	A	G	C	A	A	C	A	G	G	C	A	C	A	A	T	T	A	T	T	A	C	T	A	T	A	A	C	C	A	G	C	C	A	C	C	A	T	T	G	A	C	T	T	A	T	A	G	C	C	T	G	G	T	T	G	G	C	C	T	A	G	A	A	
8	A alfaroi	A	T	G	A	G	T	C	C	A	G	C	A	A	T	T	T	A	T	A	C	A	A	T	T	T	C	T	A	A	C	C	A	G	C	C	T	A	G	C	A	C	C	G	G	C	A	C	A	A	T	T	A	T	T	A	C	T	A	T	A	A	C	T	A	G	C	T	T	T	C	A	C	T	G	A	T	T	A	A	T	A	G	C	C	T	G	A	A	T	C	G	G	A	C	T	A	G	A	A			

# What are Discrete Characters & Why are They Used?

- Naturally discrete categories.
- Discrete character states



Wings



No wings



# What are Discrete Characters & Why are They Used?

- Naturally discrete categories.
- Discrete ecological differences



**Aquatic**



**Terrestrial**

# What are Discrete Characters & Why are They Used?

- Simplification of continuous characters.



Small

Medium



Large



# Testing Hypotheses with Ancestral Reconstruction

- Examples from adaptive radiations.
  1. What did the ancestral Darwin's finch eat?
    - Basic methods and differences between parsimony and likelihood.



# Problems with Ancestral Reconstruction

1999

POINTS OF VIEW

665

*Syst. Biol.* 48(3):665–674, 1999

## Some Limitations of Ancestral Character-State Reconstruction When Testing Evolutionary Hypotheses

CLIFFORD W. CUNNINGHAM

*Zoology Department, Duke University, Durham, North Carolina 27708-0325, USA; E-mail: cliff@duke.edu*



### COMMENTARIES

Uncertainty in the reconstruction of ancestral character states and limitations on the use of phylogenetic comparative methods

JONATHAN B. LOSOS

Department of Biology, Washington University, St Louis

*(Received 14 January 1999; initial acceptance 24 May 1999;  
final acceptance 19 July 1999; MS. number: AS-1236)*

# Testing Hypotheses with Ancestral Reconstruction

- What did the ancestral Darwin's finch eat?
  - Basic methods and differences between parsimony and likelihood.



# Ancestral Reconstruction

- Information needed:

1. Trait values for taxa of interest.

2. Underlying phylogeny for those taxa.



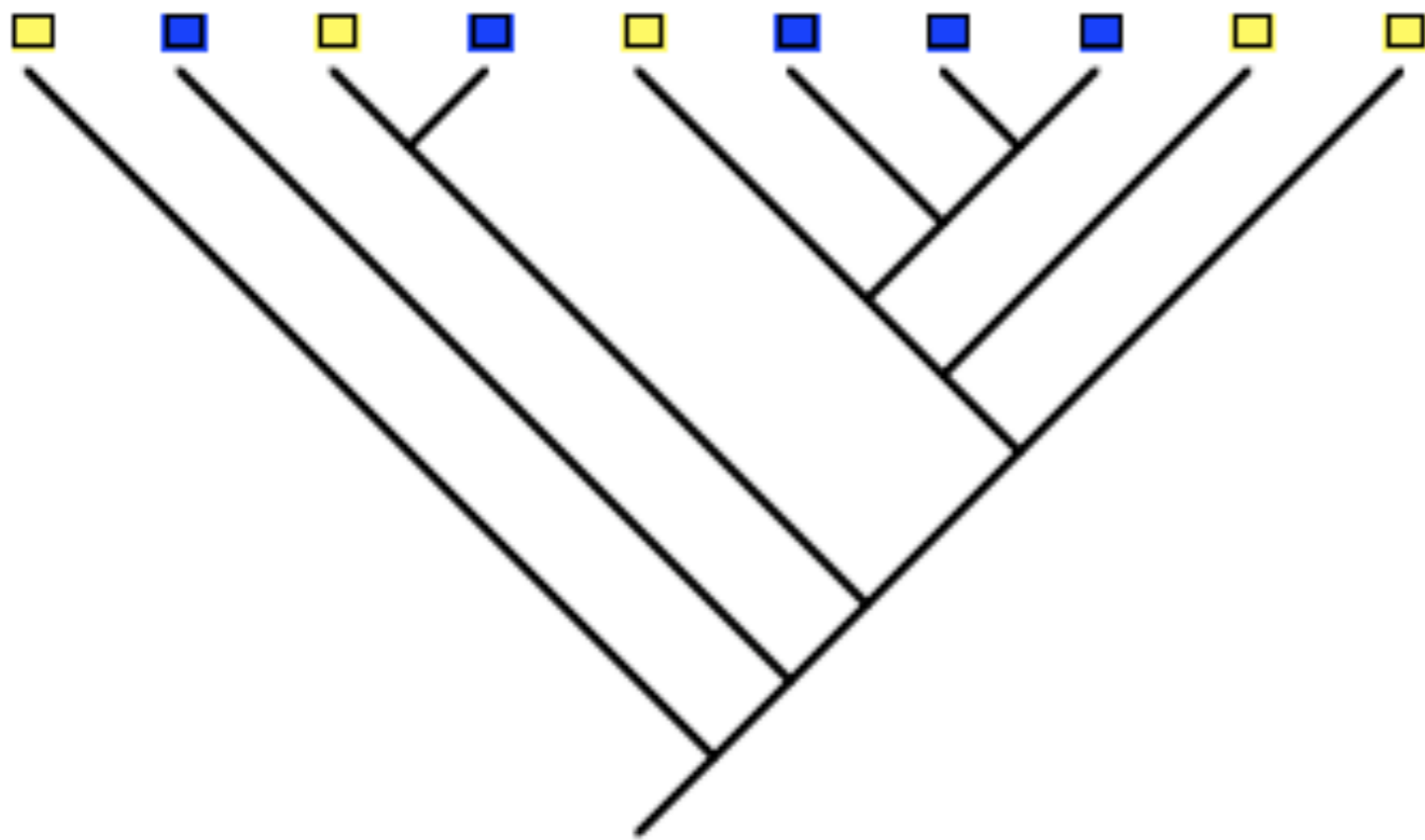
# Alternative Reconstructions



- 9 internal nodes and two possible states for each node means there are  $2^9$  or 512 possible reconstructions.
- Which reconstructions are best and how do we find them?

# Ancestral Reconstruction

- Information needed:
  1. Trait values for taxa of interest.
  2. Underlying phylogeny for those taxa.
  3. Model that describes trait evolution.



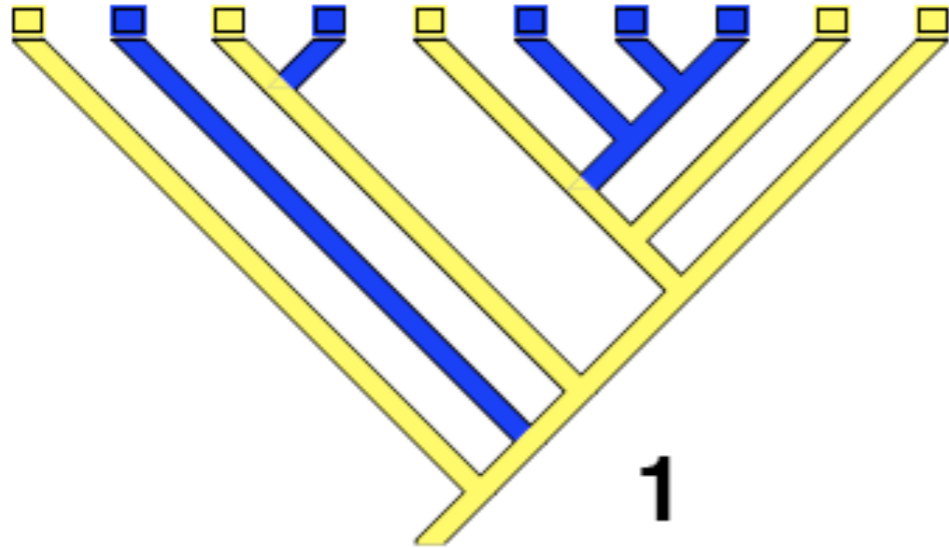
*To:*

	□	■
<i>From:</i> □	0	$G$
■	$L$	0

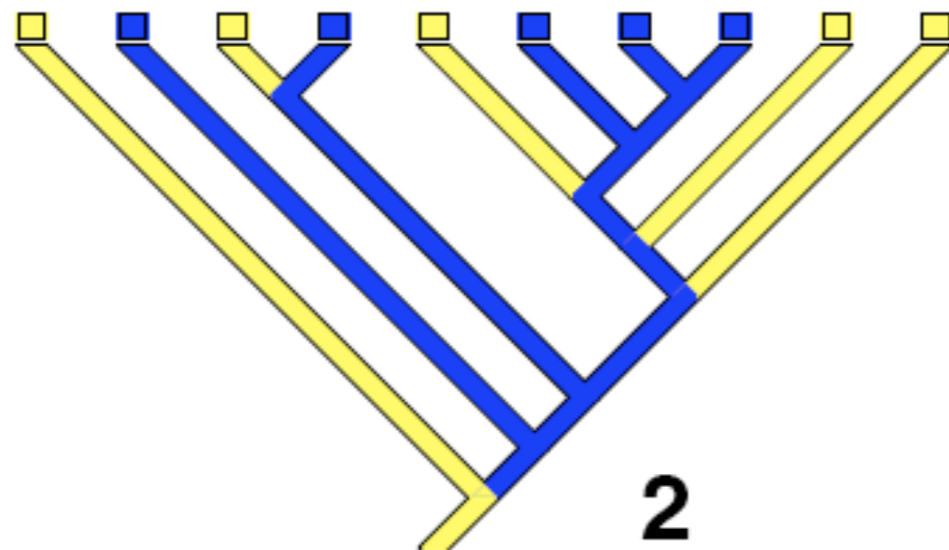
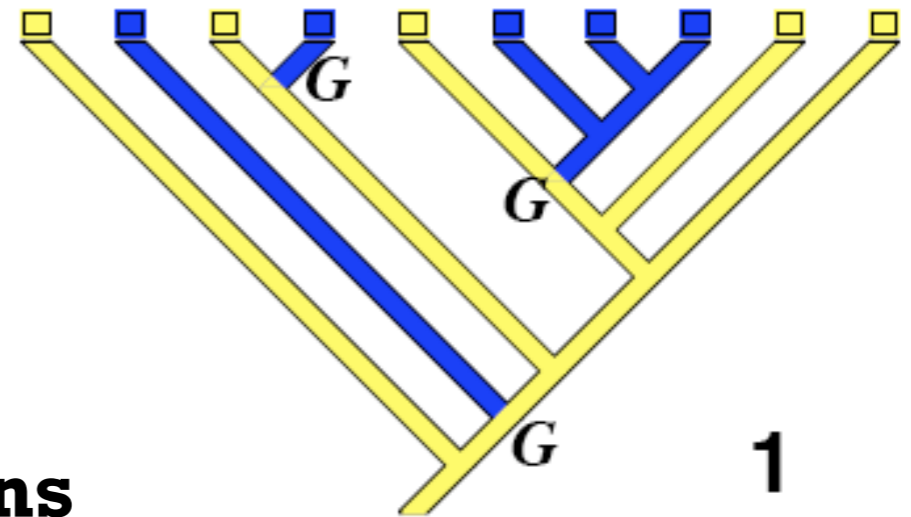
A cost or step matrix



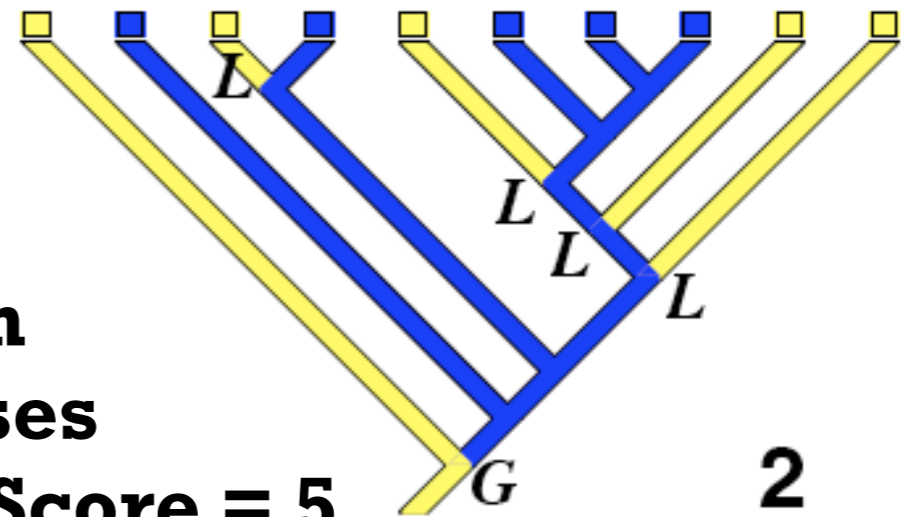
# Reconstructing Ancestral States



**3 Gains**  
**Total Score = 3**



**1 Gain**  
**4 Losses**  
**Total Score = 5**



# Testing Hypotheses with Ancestral Reconstruction

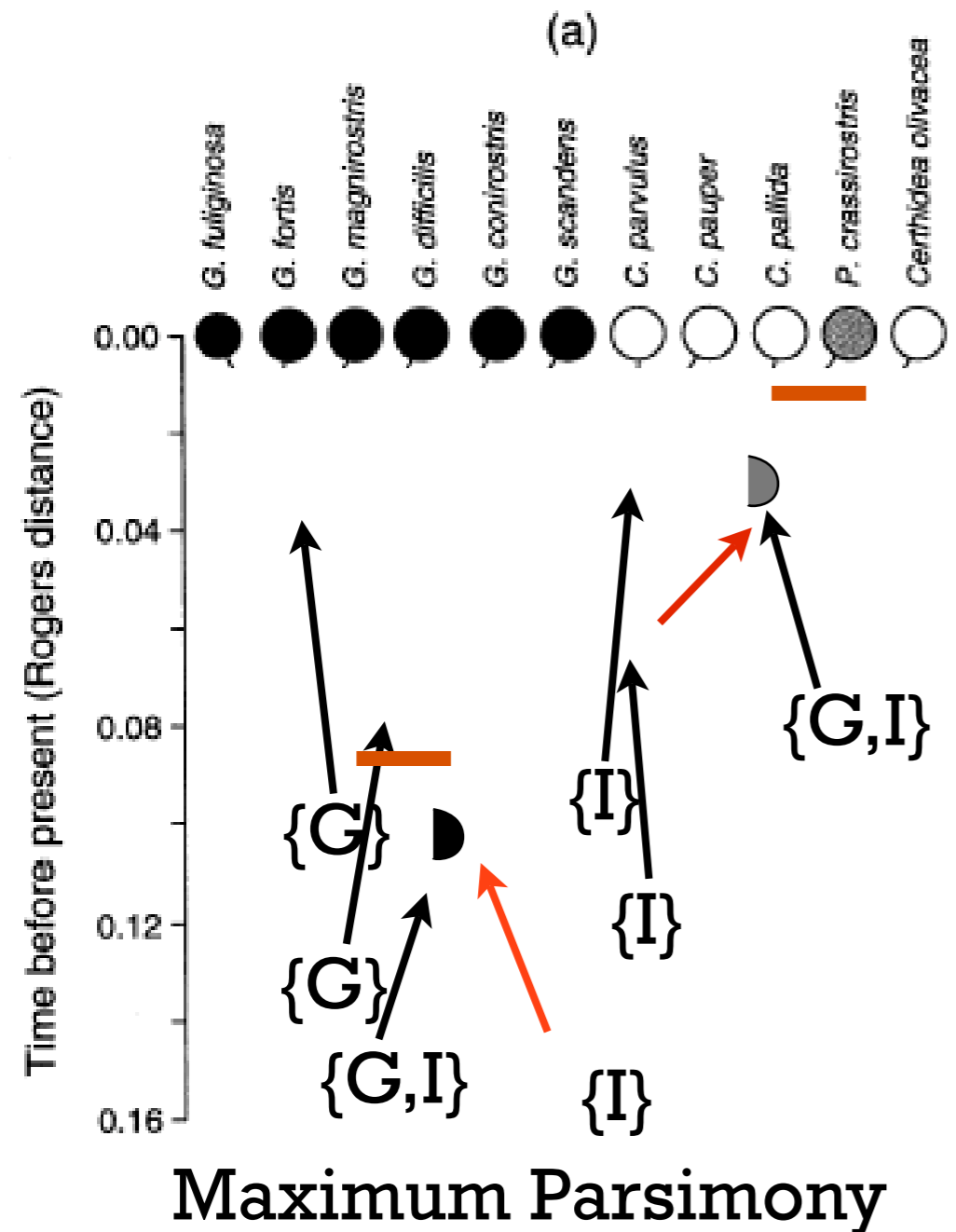
- What did the ancestral Darwin's finch eat?
  - Basic methods and differences between parsimony and likelihood.





# Assigning Ancestral States:

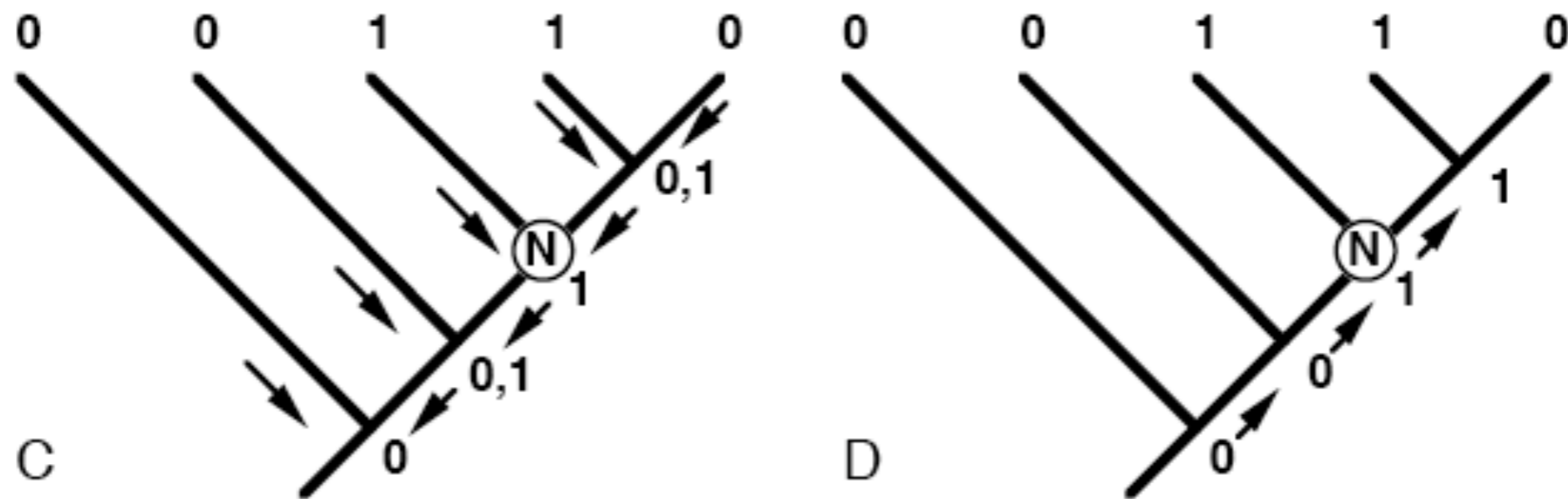
- The Simple Down-pass/Up-pass Method with Darwin's Finches



**2 Changes**



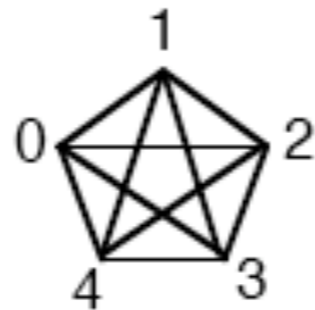
# Problems with Simple Farris Method



Both MPRs (A and B)  
and Farris's (1970) method (C and D)

# Alternative Models

## 1. Unordered (Fitch parsimony)



# Alternative Models

## 2. Ordered (Wagner parsimony)

0 — 1 — 2 — 3 — 4

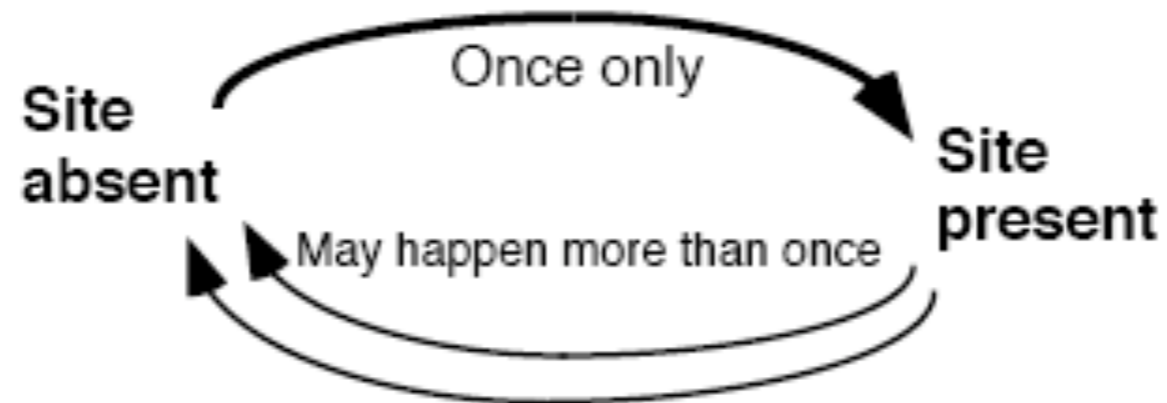
# Alternative Models

3. Irreversible (Camin-Sokal parsimony)

0 → 1 → 2 → 3 → 4

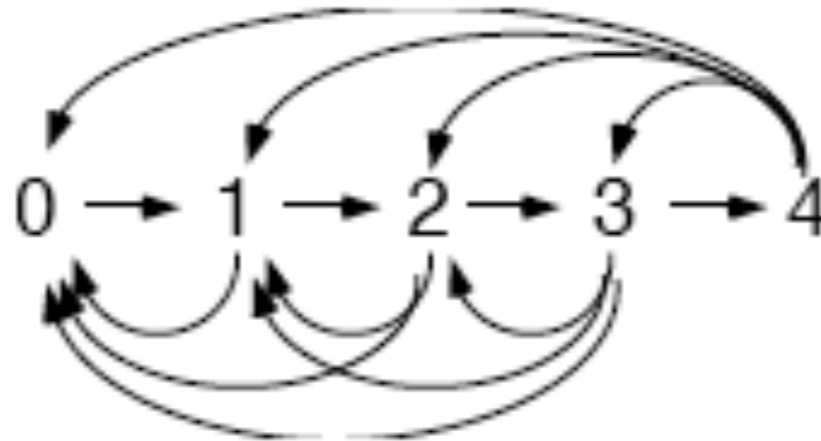
# Alternative Models

## 4.Dollo



# Alternative Models

## 5.Step Matrix



# Alternative Models

1. Unordered (Fitch parsimony)
2. Ordered (Wagner parsimony)
3. Irreversible (Camin-Sokal parsimony)
4. Dollo
5. Step Matrix

# Unweighted Parsimony





# Weighted Parsimony

**From**

	Yellow	Blue
Yellow	0	1
Blue	3	0

Yellow
--------

0

1

**To**

Blue
------

3

0

# Limitations of Parsimony

- Limited to one change per branch, regardless of how long (branch length data not considered).
- Underestimates variance of ancestral states and doesn't provide error estimates for ancestral reconstructions.
- Performs poorly with rapidly evolving characters, tending to push divergence events toward the tips.

# Maximum Likelihood Methods

Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters

MARK PAGEL

*School of Mathematical Sciences, Queen Mary and Westfield College, University of London, London E1 4NS, U.K.*

Pagel 1994. Proc. Royal Soc.

## EVOLUTION

*INTERNATIONAL JOURNAL OF ORGANIC EVOLUTION*

PUBLISHED BY

THE SOCIETY FOR THE STUDY OF EVOLUTION

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Vol. 51

December 1997

No. 6

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*Evolution*, 51(6), 1997, pp. 1699–1711

### LIKELIHOOD OF ANCESTOR STATES IN ADAPTIVE RADIATION

DOLPH SCHLUTER,<sup>1,2</sup> TREVOR PRICE,<sup>3</sup> ARNE Ø. MOOERS<sup>1,4</sup> AND DONALD LUDWIG<sup>1,5</sup>

<sup>1</sup>*Department of Zoology and Centre for Biodiversity Research, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada*

<sup>2</sup>*E-mail: schluter@zoology.ubc.ca*

<sup>3</sup>*Biology Department O-116, University of California—San Diego, La Jolla, California 92093*

*E-mail: tprice@ucsd.edu*

<sup>4</sup>*E-mail: mooers@bio.uva.nl*

<sup>5</sup>*E-mail: ludwig@zoology.ubc.ca*

Schluter et al. 1997

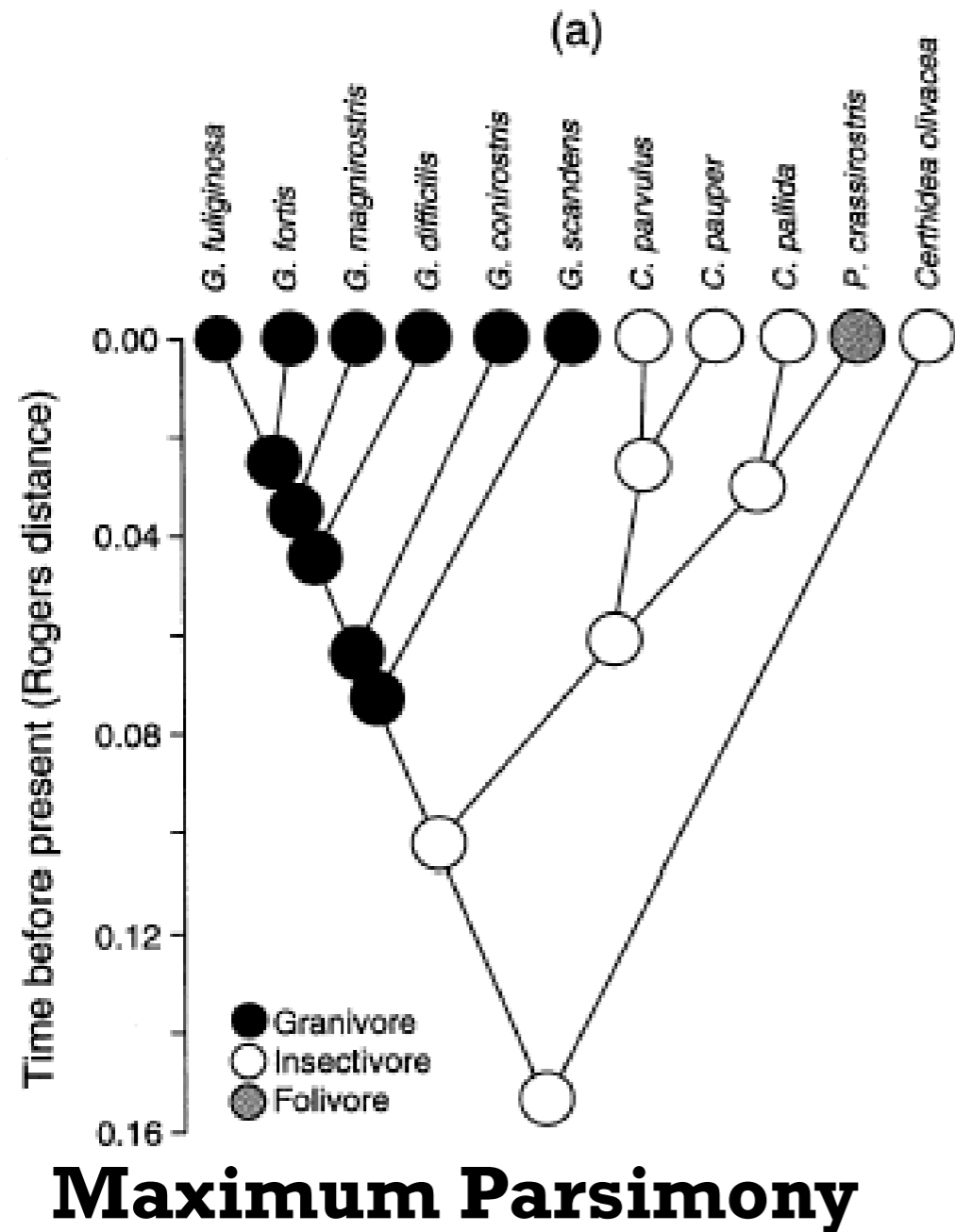
# **Advantages of Maximum Likelihood**

- **Incorporates branch length information.**
- **Permits multiple changes along a single branch.**
- **Provides estimate of uncertainty in ancestral reconstructions.**

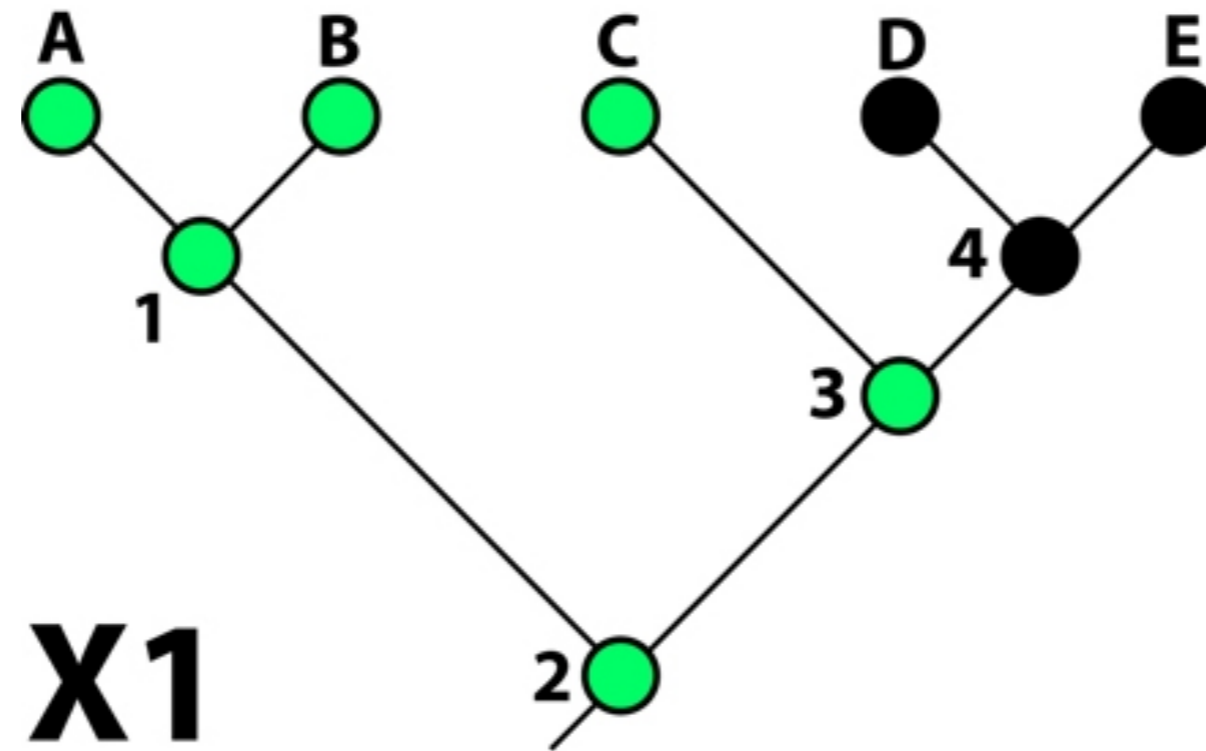
# Parsimony v. Likelihood

	<b>Optimization</b>	<b>Rate Estimate</b>	<b>Key Assumption(s)</b>
<b>Parsimony</b>	Number of changes	Number of changes	(1) Character change rare. (2) No more than 1 change per branch.
<b>Likelihood</b>	Likelihood score	Instantaneous rate of change	(1) Rate of change constant over time. (2) Prob. change proportional to branch length

# What Did the Ancestor of Darwin's Finches Eat?



# Step 1: Assessing the Likelihood of Specific Scenario(s)

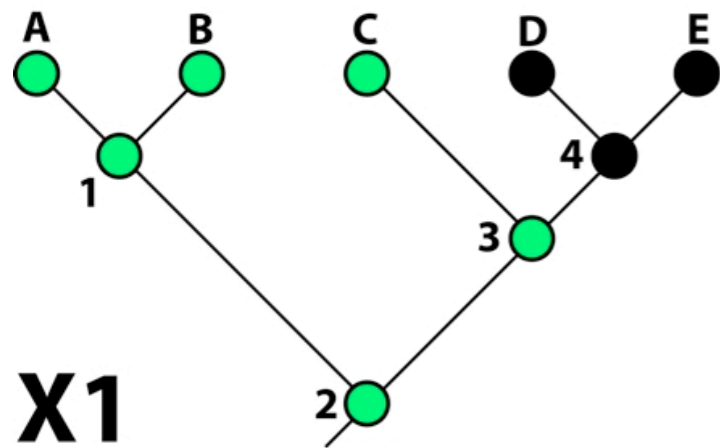


- **Parameters for Likelihood Estimation**
  - $q_l$  = rate of character evolution
  - $X$  ( $X$ ) = state of ancestral node (set of possible character states at all nodes)
  - $p_{ij}$  = probability of transition from state  $i$  to state  $i'$
  - $P(X) = \prod_{i,i'} p_{ii'}$  = probability of set of ancestral states



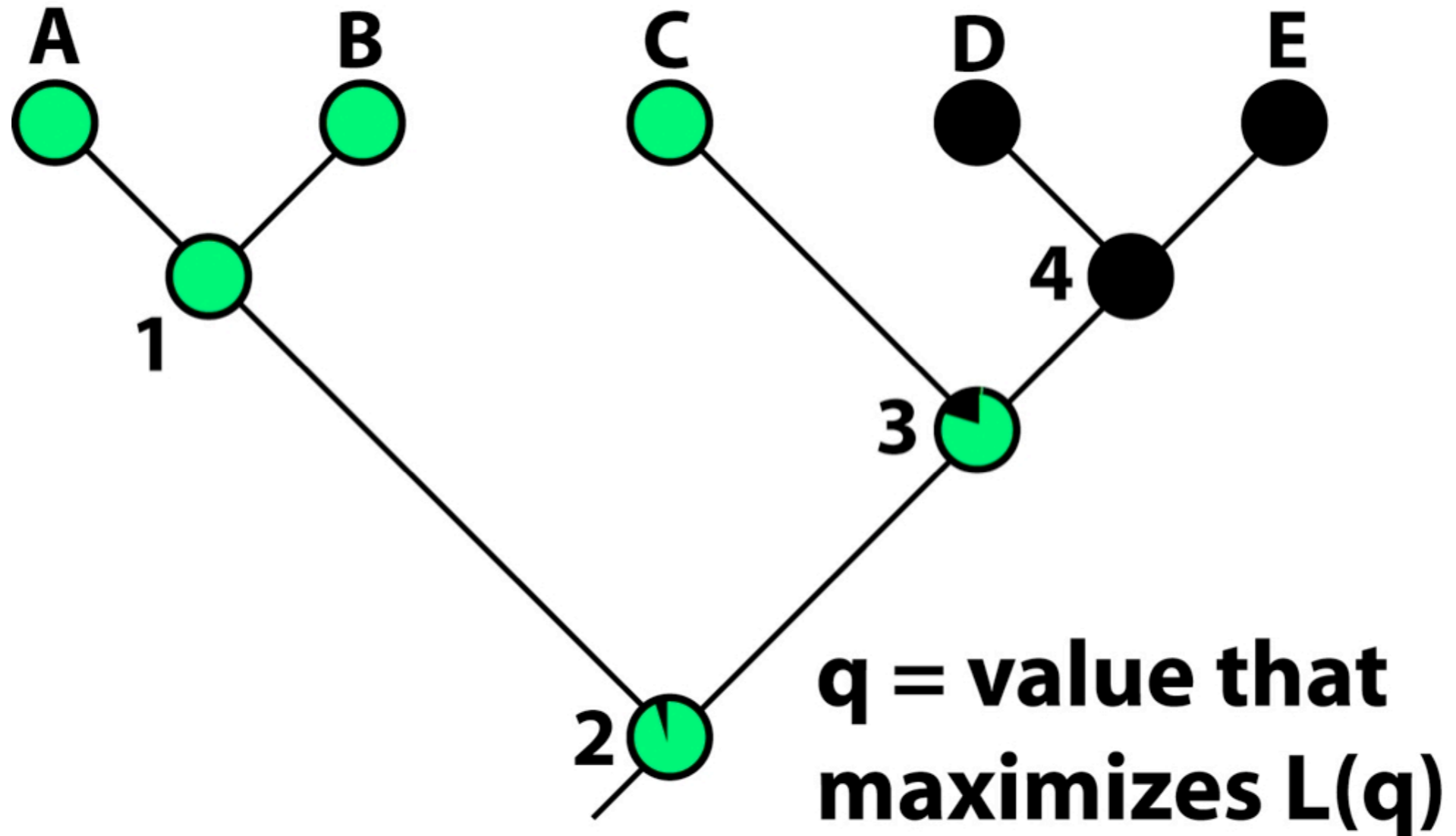
# Step 1: Estimating the 'Global' Rate Parameter

- Generate a likelihood score for each possible value of  $q$  by summing across all possible ancestral reconstructions.
- Rate with best likelihood score over all possible reconstructions is the 'global' rate estimate.



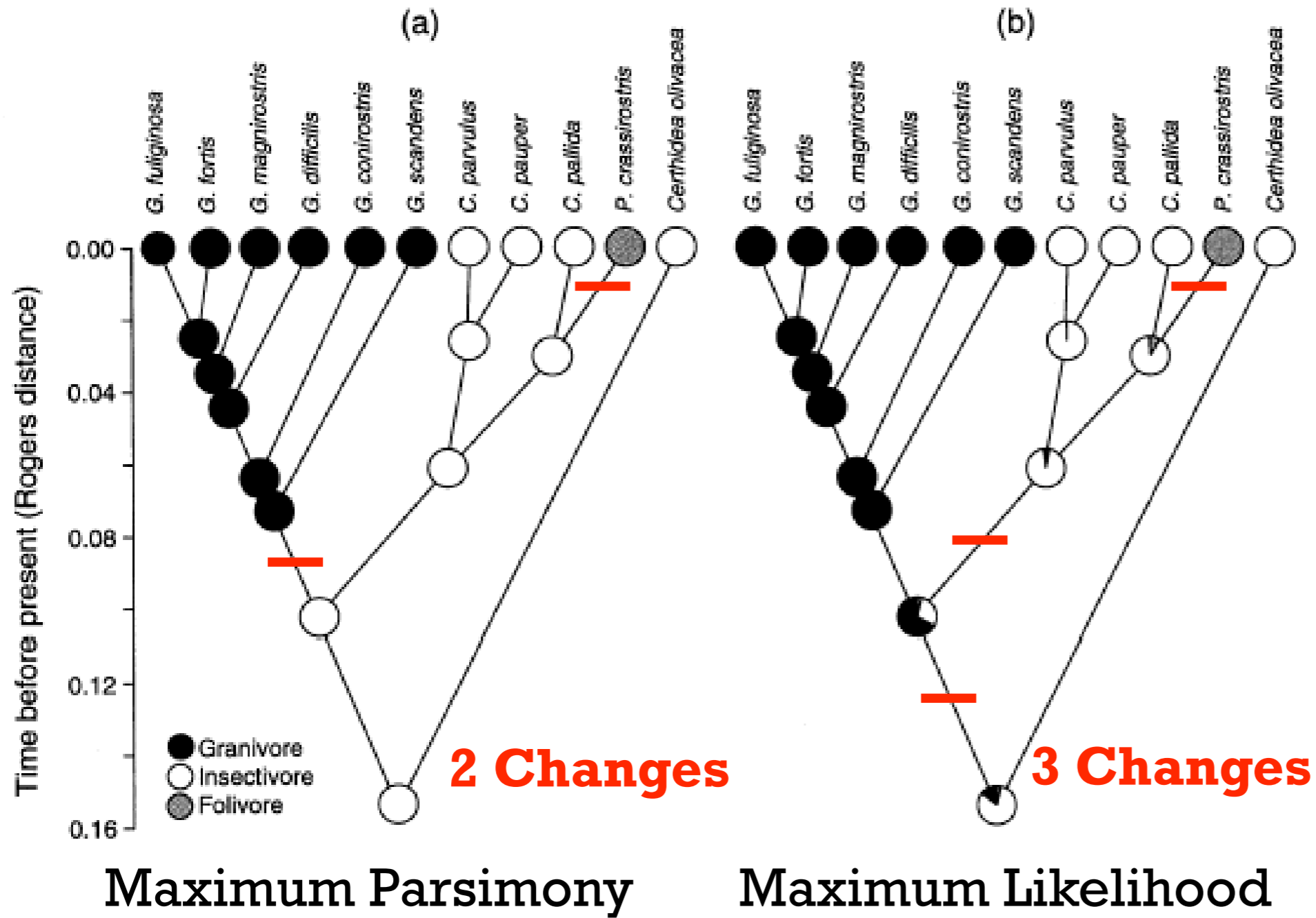
$$L(q) = \sum_{X_1, X_2 \dots X_N} P(X_1, X_2 \dots X_N)$$

# Step II: Estimate Likelihood of Ancestral States



$$L(u_1 | q) = \sum_{X_2, X_3, \dots, X_N} P(u_1, X_2, X_3, \dots, X_N)$$

# What Did the Ancestor of Darwin's Finches Eat?



# Estimating Multiple Rate Parameters

