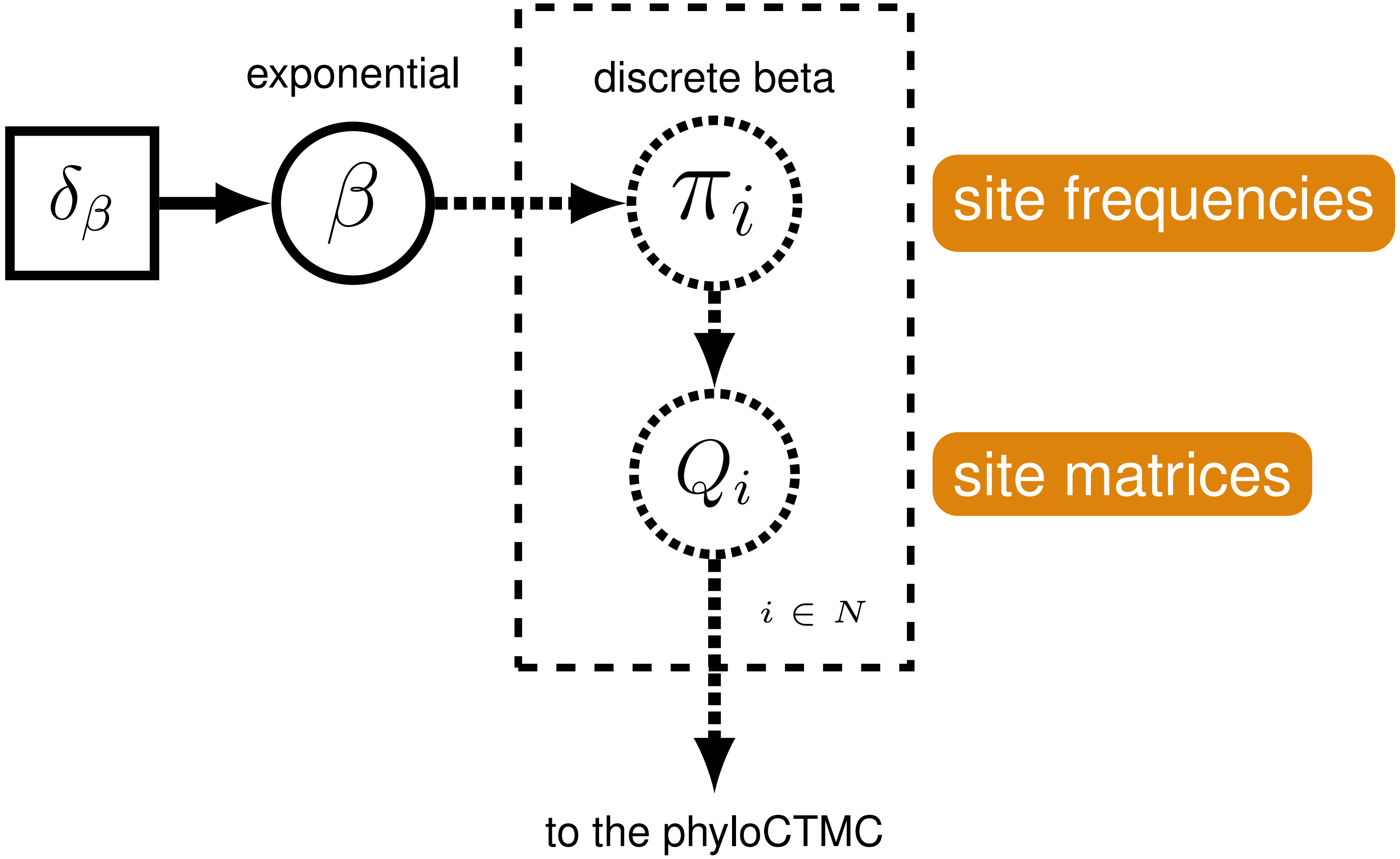
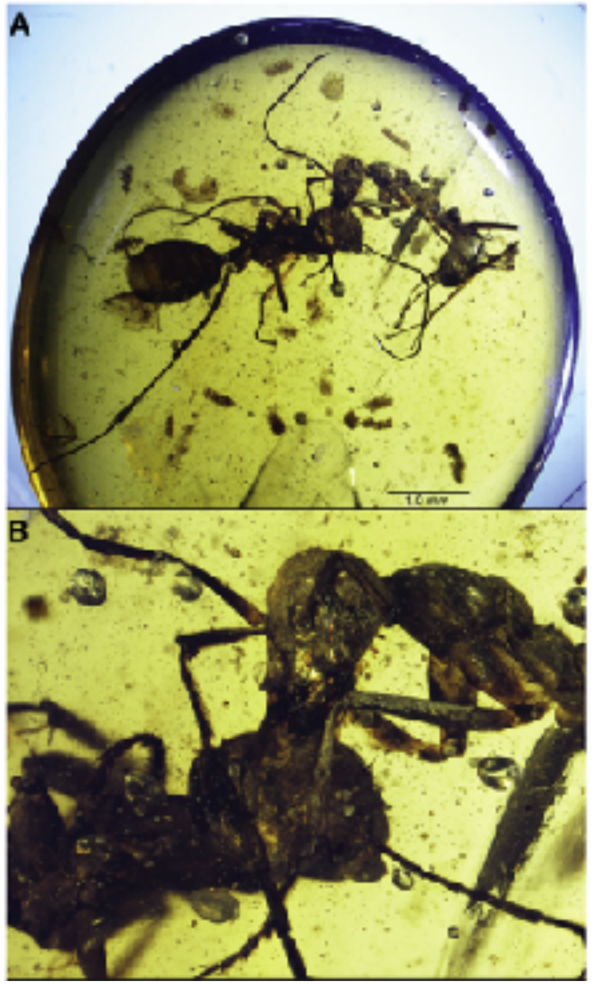
Discrete Morphology in RevBayes

April Wright
Iowa State University; The Field Museum

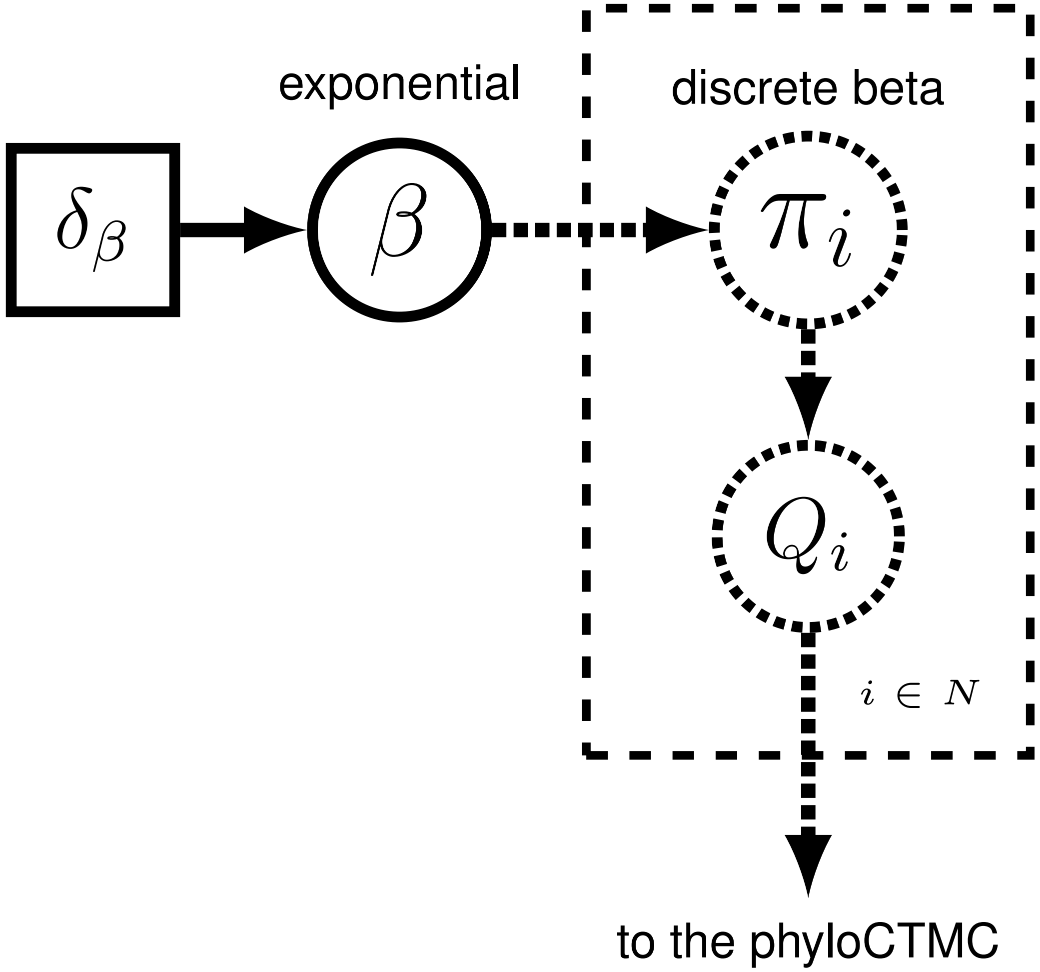
The Wright Lab - TBA



The Wright Lab - TBA



Barden and Grimaldi 2016



exponential

discrete beta

δ_β

β

π_i

Q_i

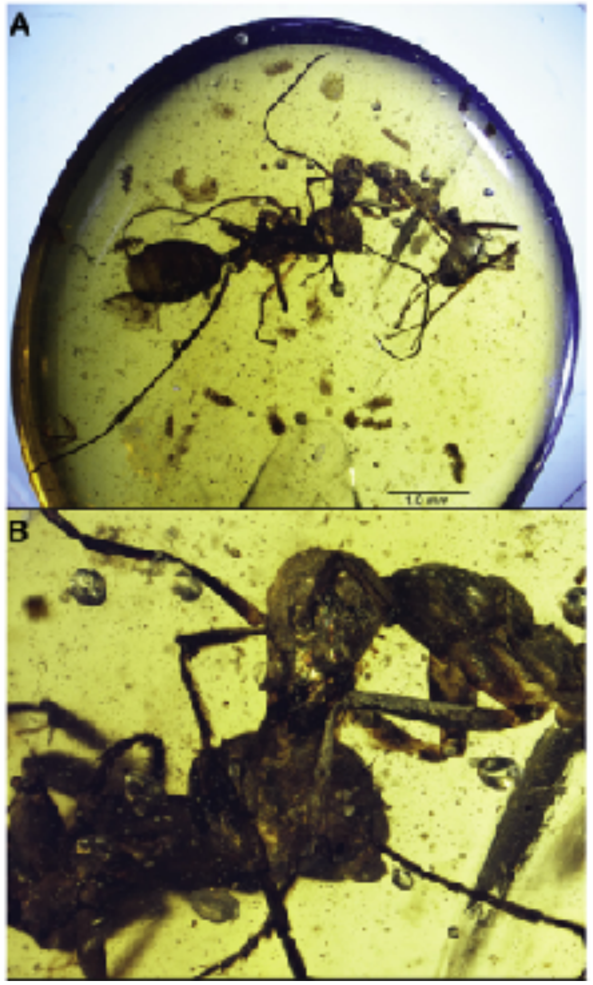
$i \in N$

to the phyloCTMC

site frequencies

site matrices

The Wright Lab - TBA



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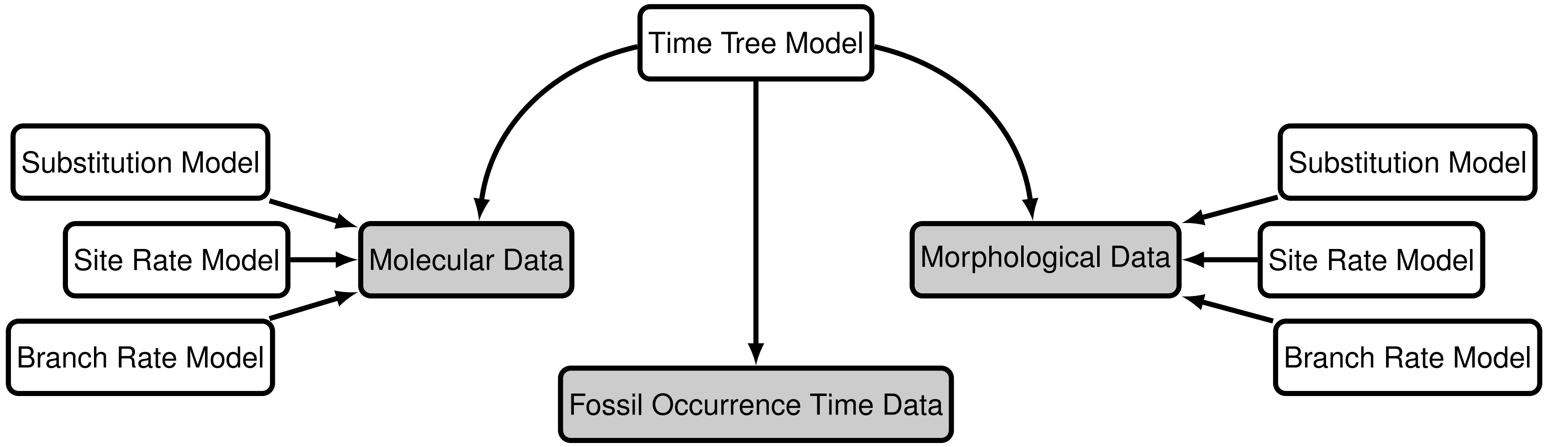


Time Tree Model

Substitution Model

Site Rate Model

Branch Rate Model

Molecular Data

Morphological Data

Substitution Model

Site Rate Model

Branch Rate Model

Fossil Occurrence Time Data

Outline

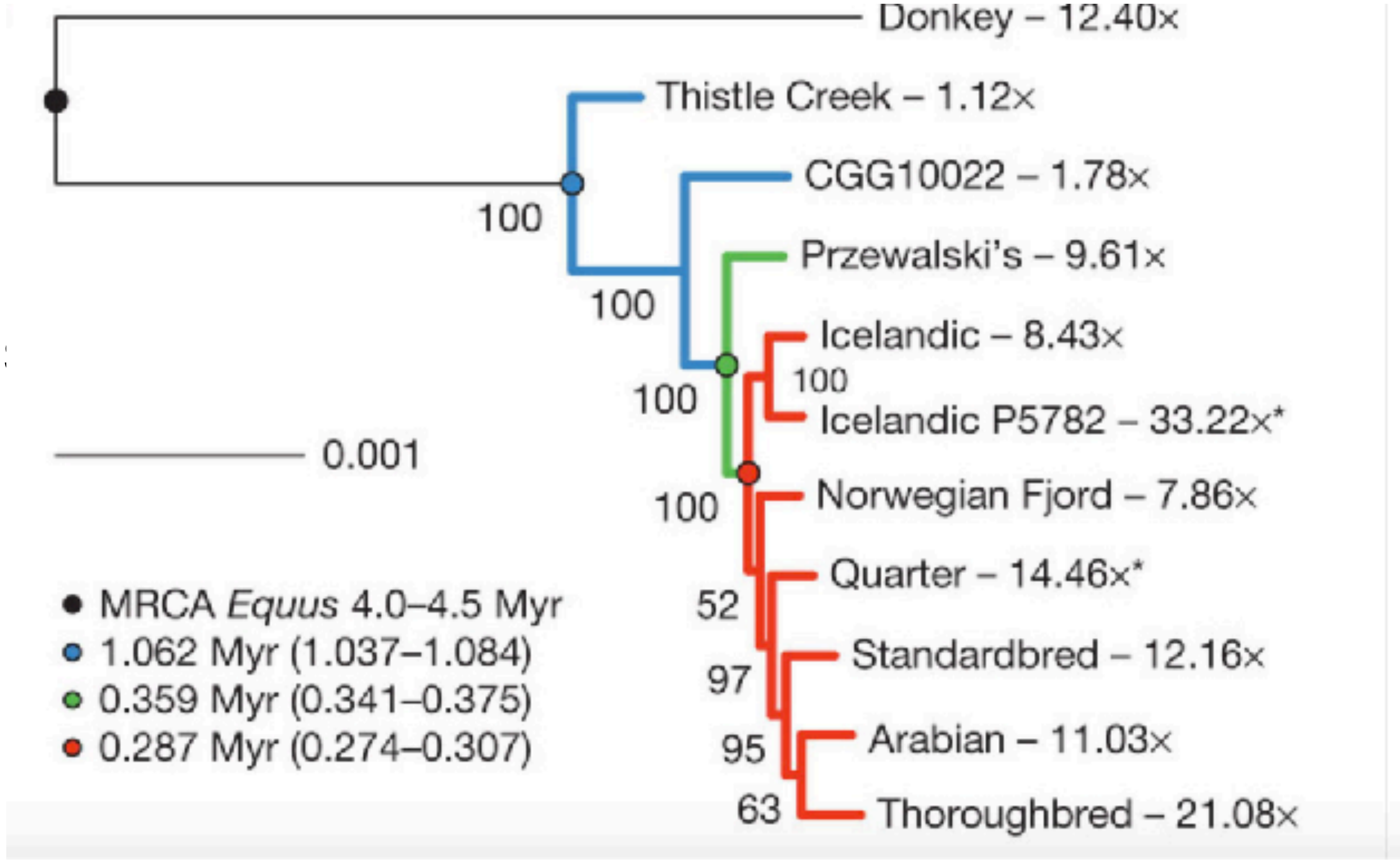
- An overview of morphology CTMCs in RevBayes
    - The Mk Model
    - Ascertainment Bias
    - Alternative Q-Matrices
    - State-Frequency heterogeneity models

Break

- Ancestral State Estimation in RevBayes
    - Sequential vs. Joint ancestral State Reconstruction
    - A few more fancy substitution matrices: Correlated characters, Covarion models

Incorporating Morphology in Phylogeny

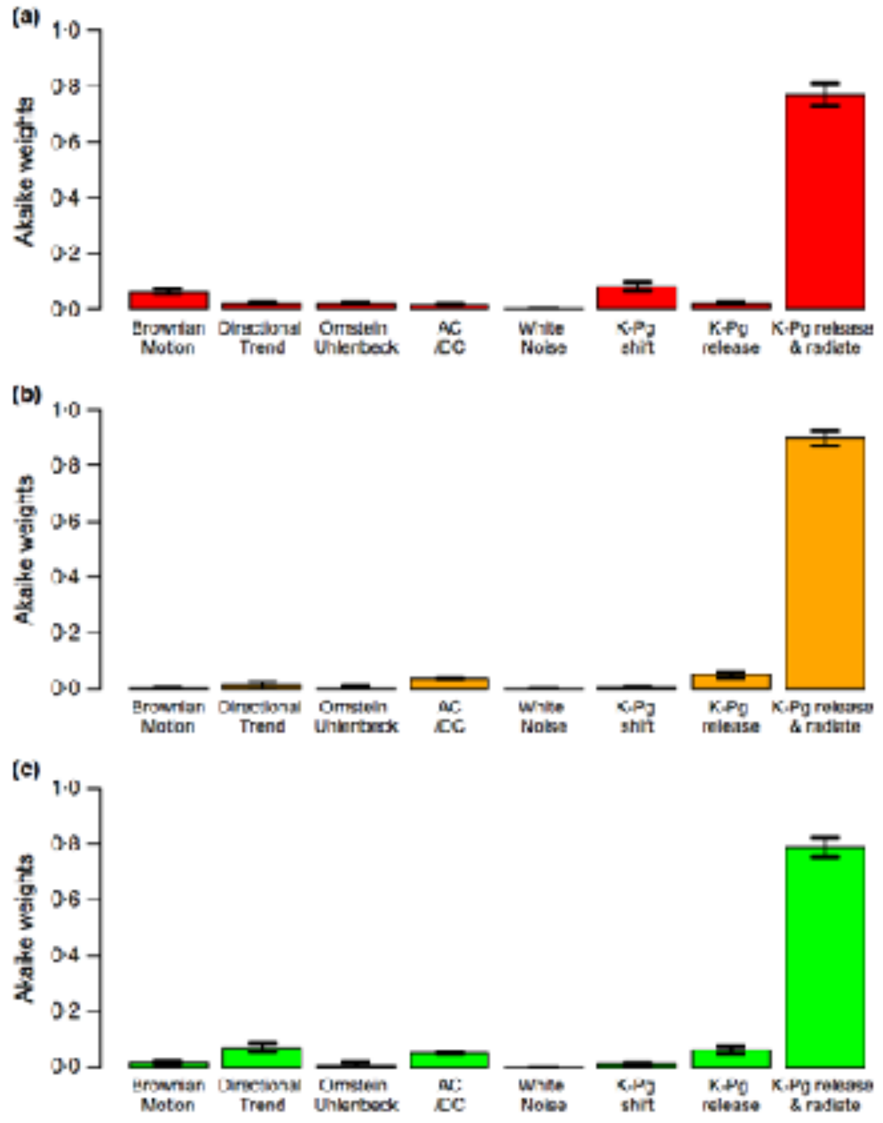
- Oldest DNA Sample
~700k years old



Orlando et al 2013

Incorporating Morphology in Phylogeny

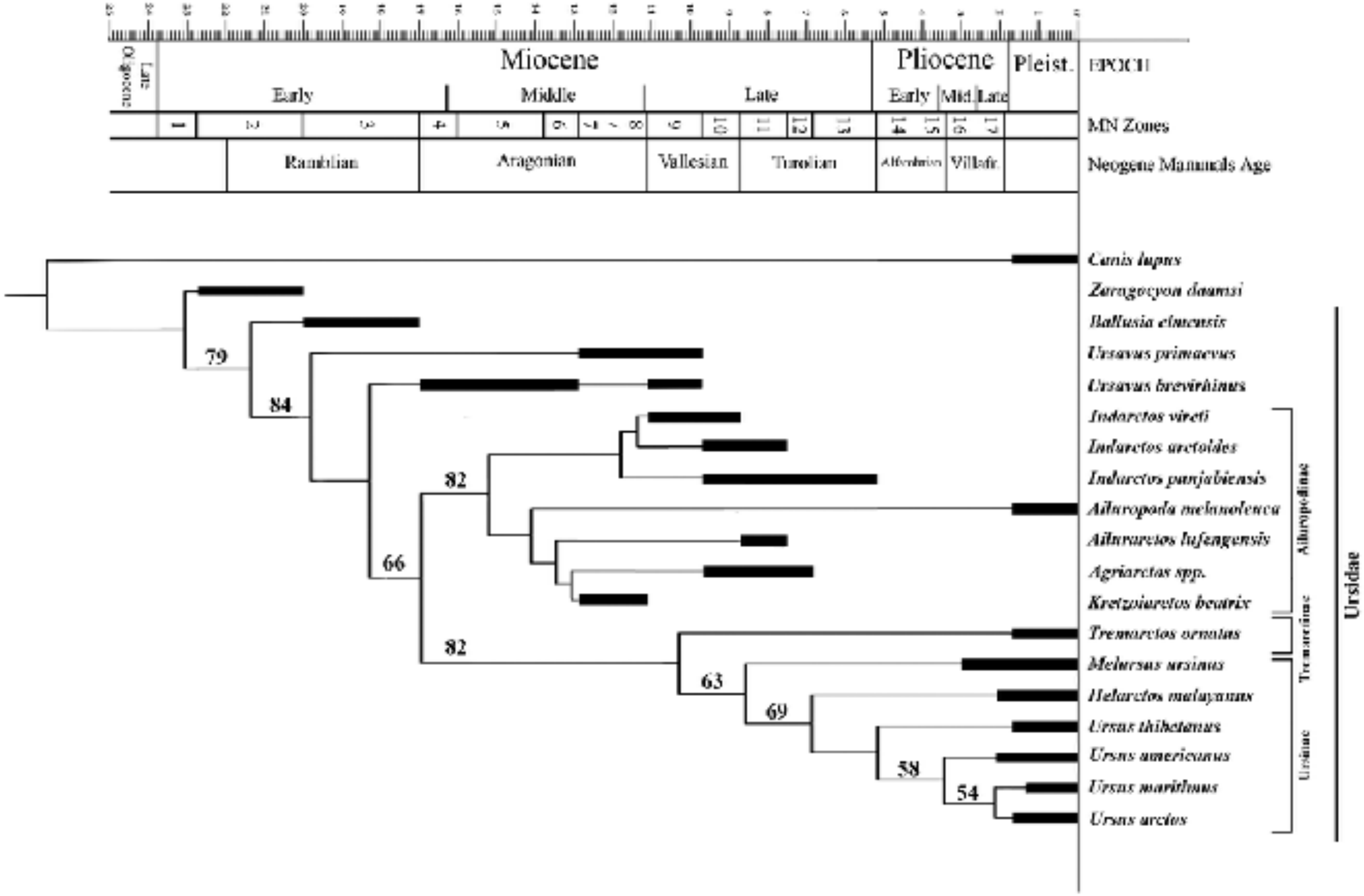
- Including paleontological specimens can help us make better inferences about comparative biology



Slater et al 2012

Fossils are the only direct observations of the past

Historically, phylogenetic trees estimated from morphological data have been inferred using maximum parsimony.



Abella et al. 2012

Incorporating Morphology in Phylogeny

- As neontologists, primarily working with molecular data have been interested in morphology, new methods were proposed

$$Q = \begin{pmatrix} -\mu_0 & \mu_{01} \\ \mu_{10} & -\mu_1 \end{pmatrix} ,$$

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The Mk model, Lewis, 2001

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$$Q = \begin{pmatrix} -\mu_0 & \mu & \mu & \mu \\ \mu & -\mu_1 & \mu & \mu \\ \mu & \mu & -\mu_2 & \mu \\ \mu & \mu & \mu & -\mu_3 \end{pmatrix} ,$$

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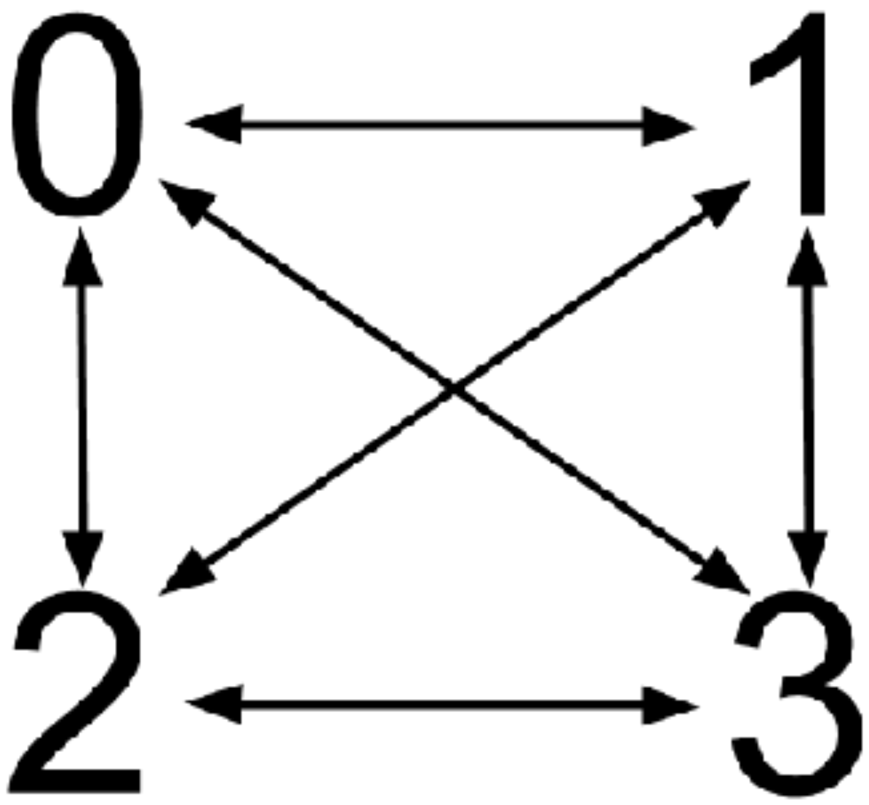
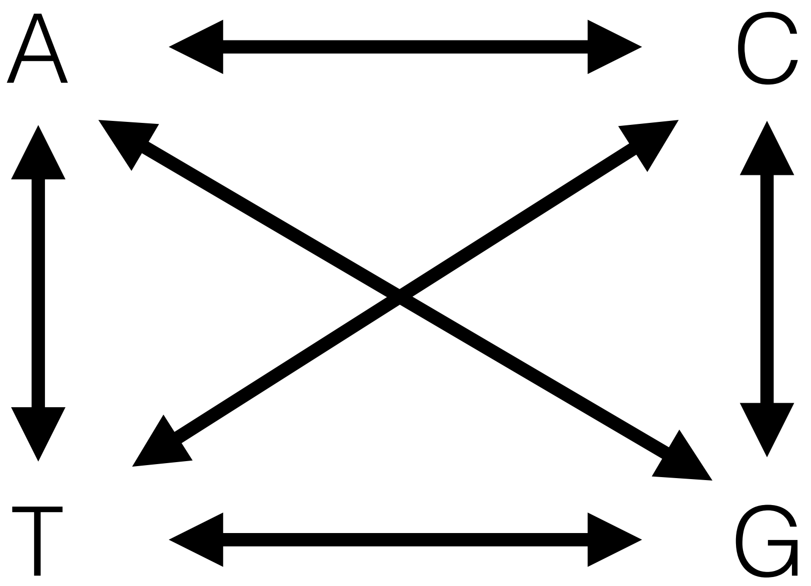


The Mk model, Lewis, 2001

Incorporating Morphology in Phylogeny



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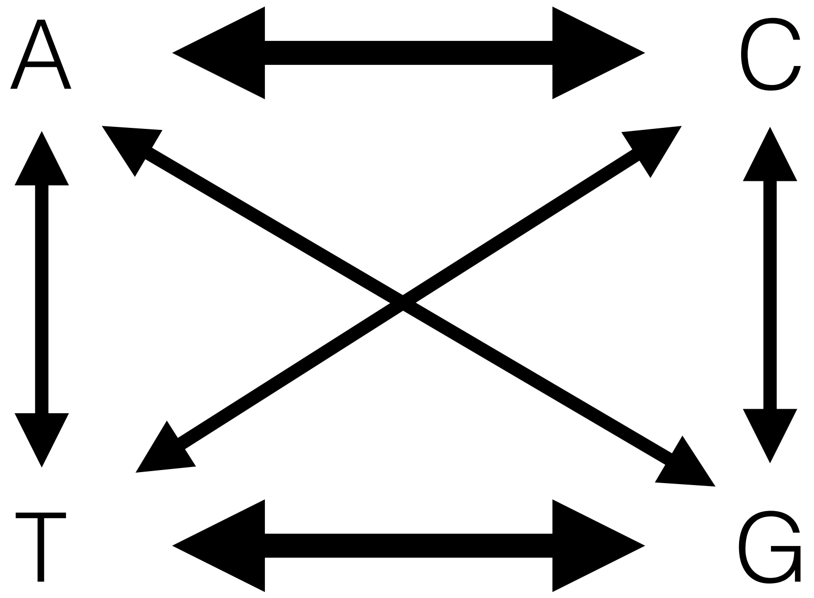
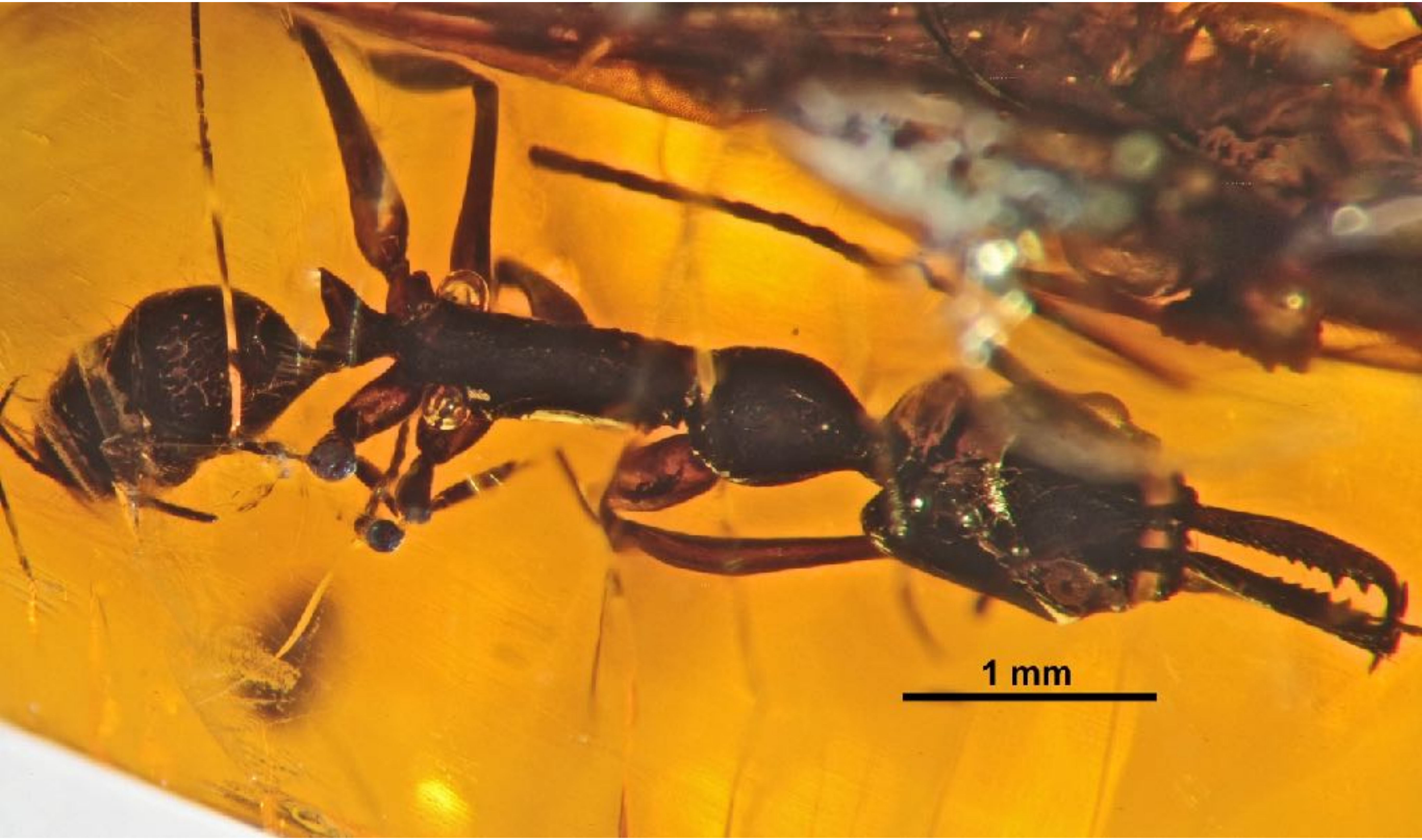
Incorporating Morphology in Phylogeny

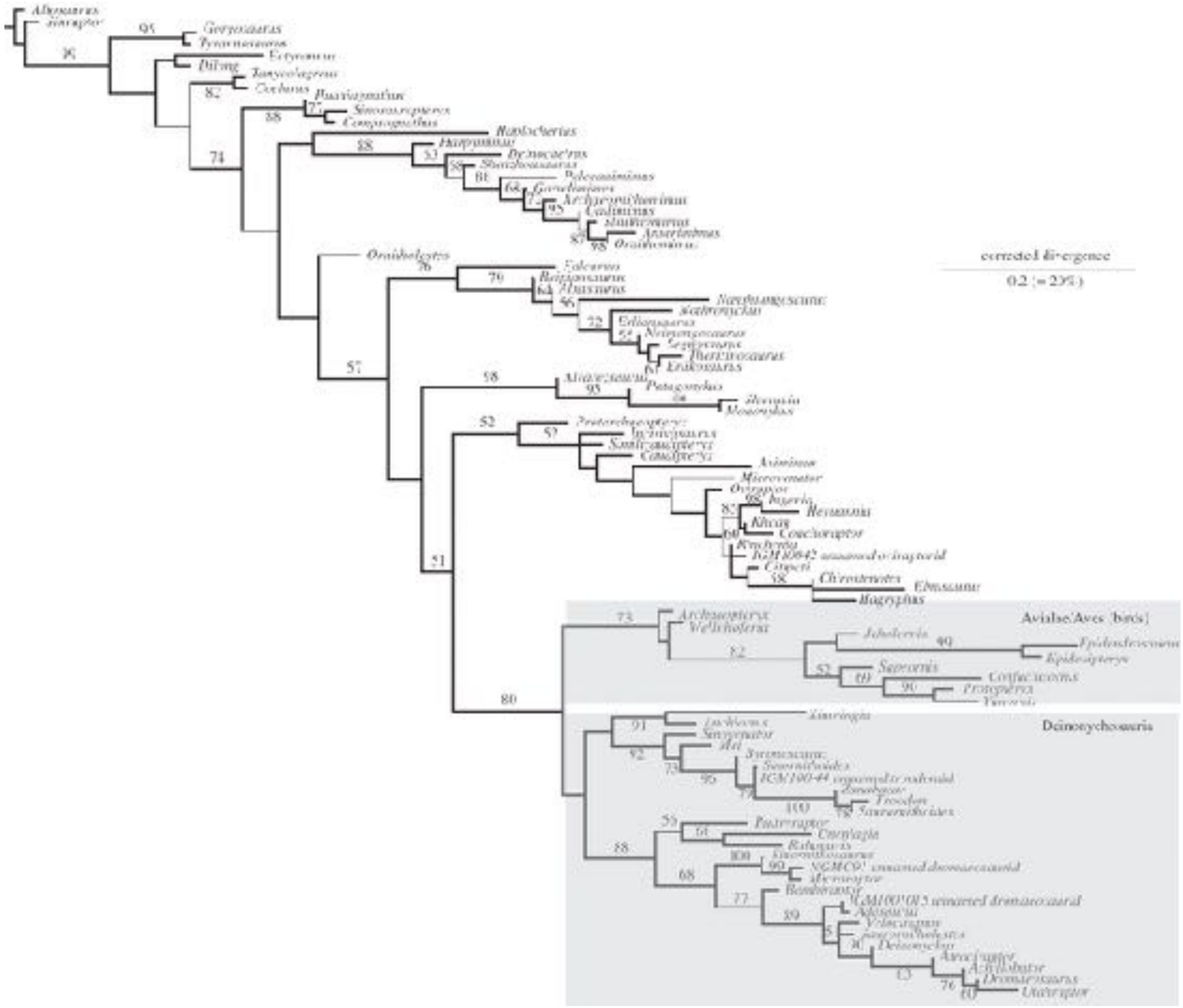


- As neontologists, primarily working with molecular data have been interested in morphology, new methods were proposed


1 mm

Incorporating Morphology in Phylogeny

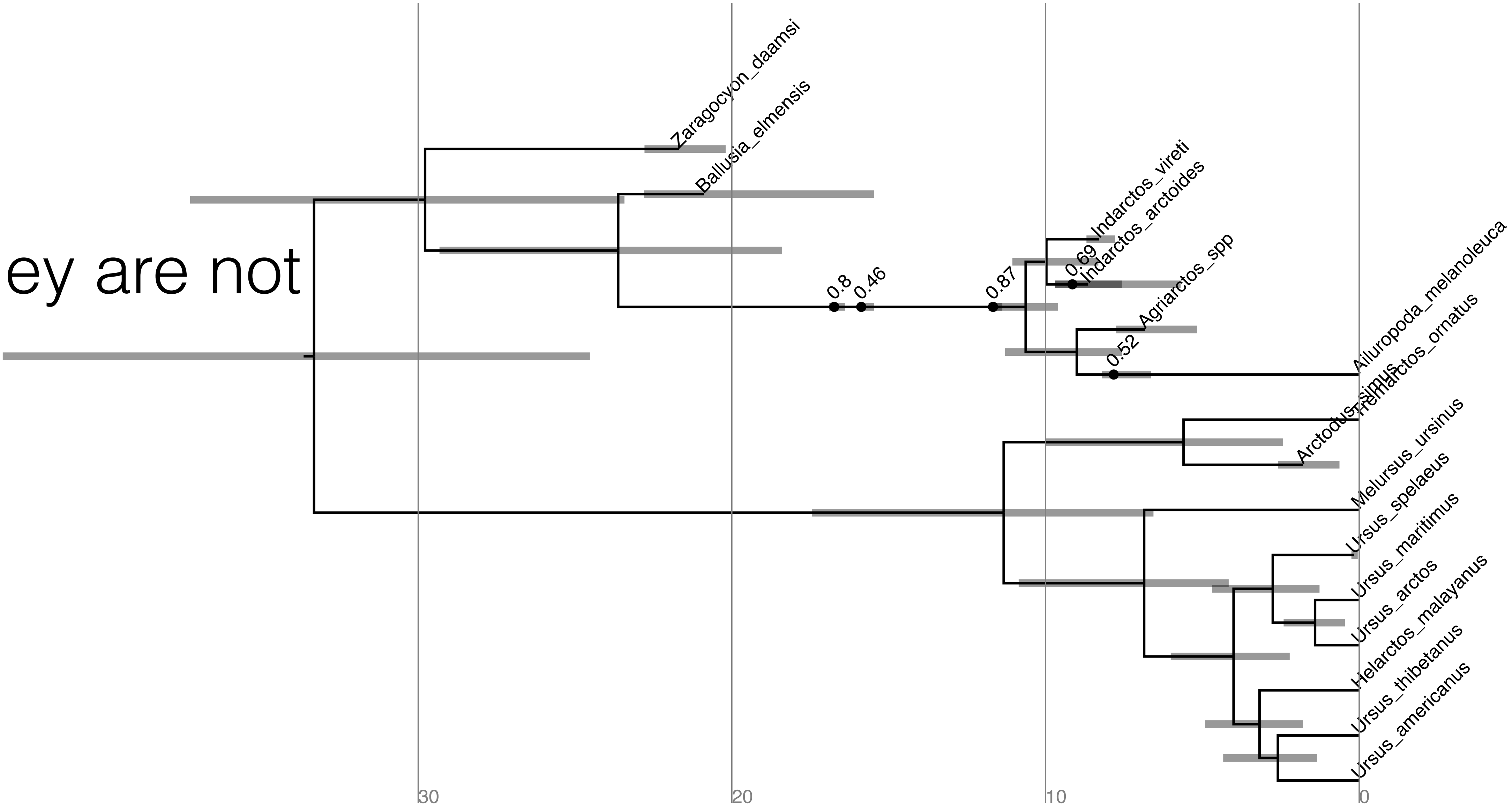
- Sometimes, use of a model-based method results in a different topology than a parsimony analysis



Lee and Worthy, 2011

Incorporating Morphology in Phylogeny

- Often, they are not

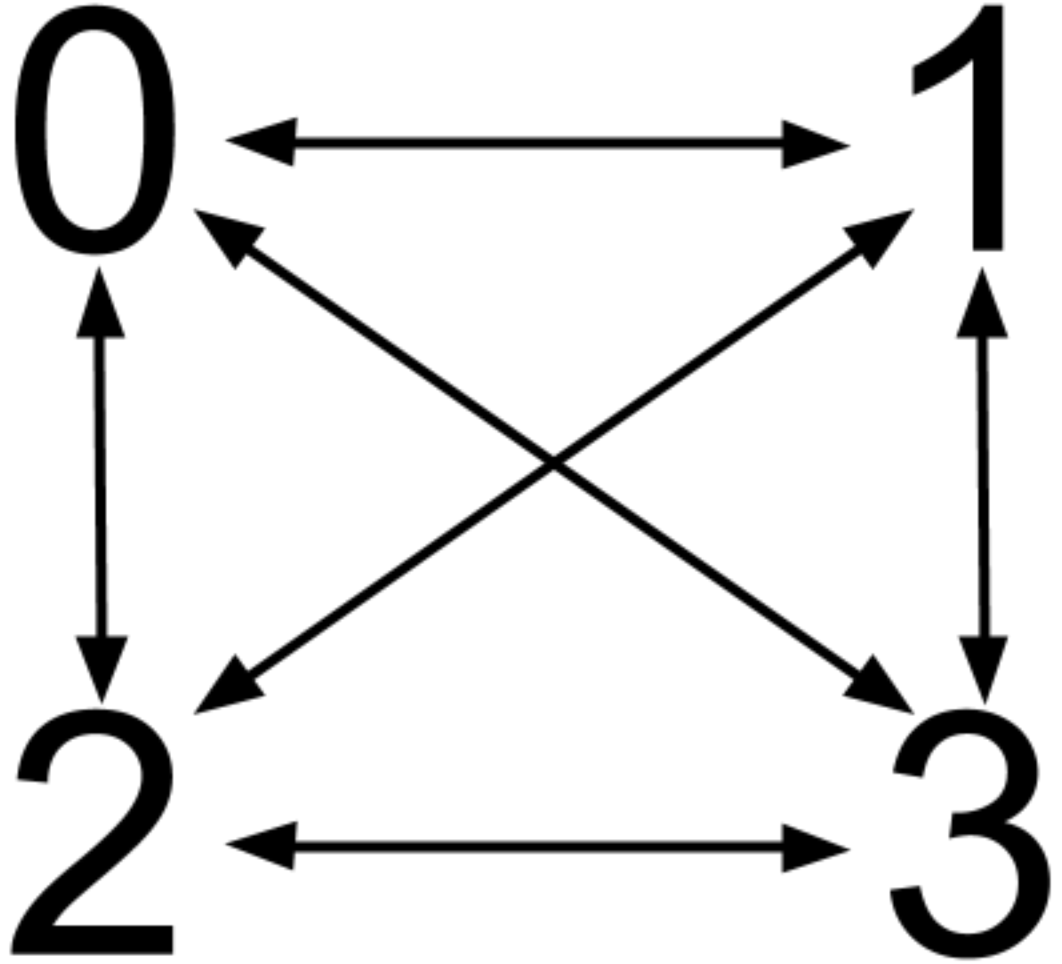



Percentage Topological Error
100
50
0
0
5
10
Evolutionary Rate
Parsimony: 75% missing data
Parsimony: No missing data
Mk: 75% missing data
Mk: No missing data

Incorporating Morphology in Phylogeny

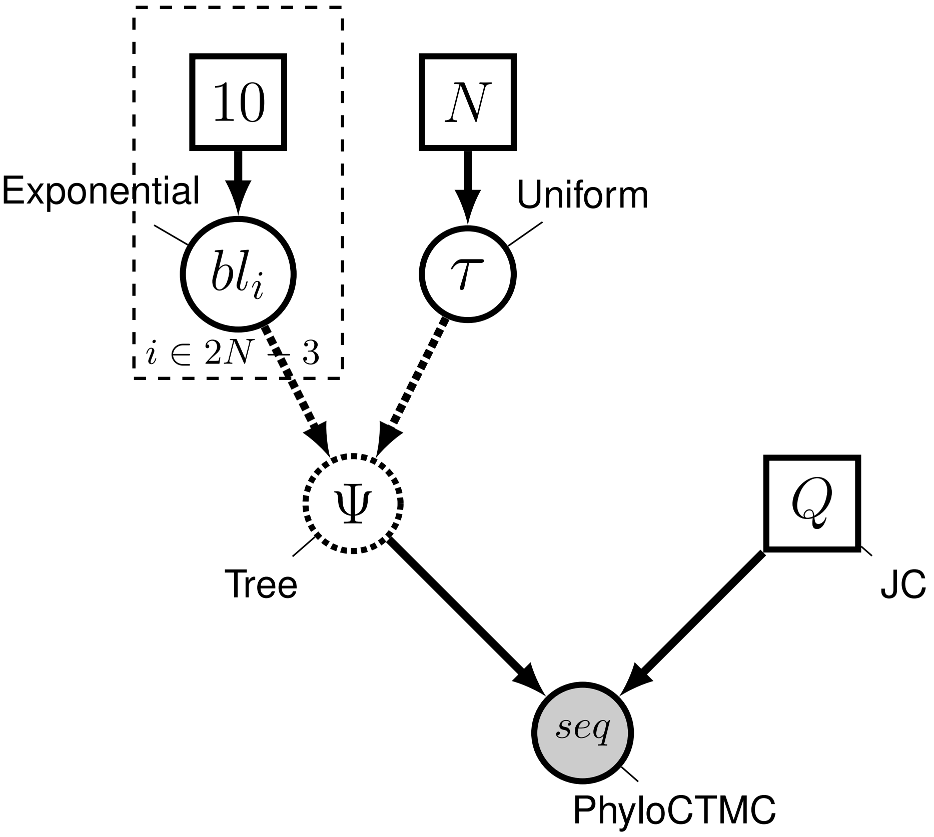
We will talk about how to relax this simplifying assumption in a bit

$$Q = \begin{pmatrix} -\mu_0 & \mu & \mu & \mu \\ \mu & -\mu_1 & \mu & \mu \\ \mu & \mu & -\mu_2 & \mu \\ \mu & \mu & \mu & -\mu_3 \end{pmatrix},$$



RevBayes

RevBayes implements the Mk Model
mcmc_simple.Rev



```
for (I in 1:n_branches) {
        bl[I] ~ dnExponential(10.0)
}
topology ~ dnUniformTopology(taxa)
psi := treeAssembly(topology, bl)


Q_morpho <- fnJC(2)


phyMorpho ~ dnPhyloCTMC( tree=psi,
siteRates=rates_morpho, Q=Q_morpho,
type="Standard", coding="variable" )

phyMorpho.clamp( data )
```

Adapted from Hohna, Landis, Heath

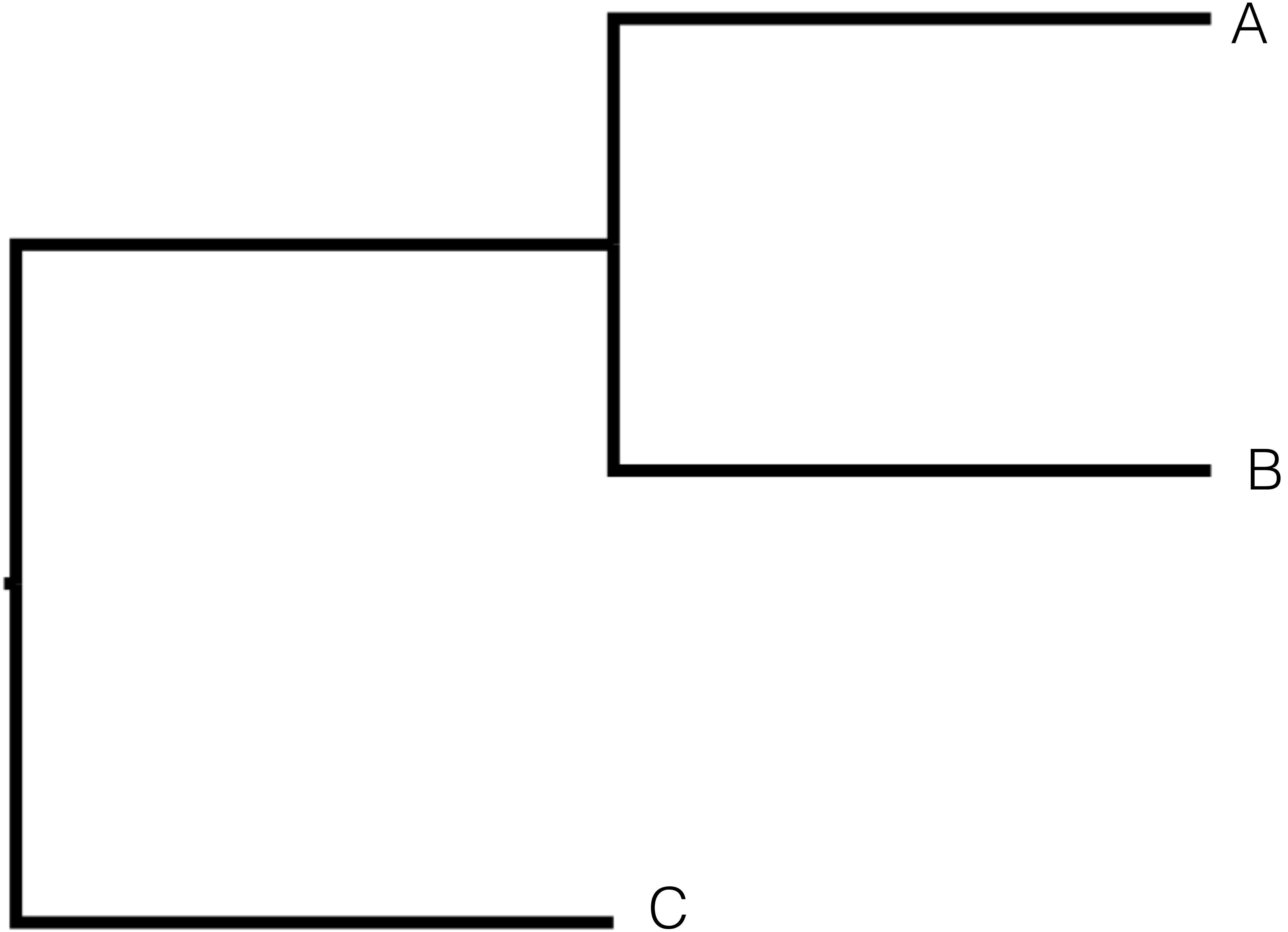
Ascertainment Bias

Systematic bias in the way the data are collected

Ascertainment Bias

	Char. 1	Char. 2	Char. 3
A	0	1	0
B	0	1	1
C	0	0	2

Ascertainment Bias



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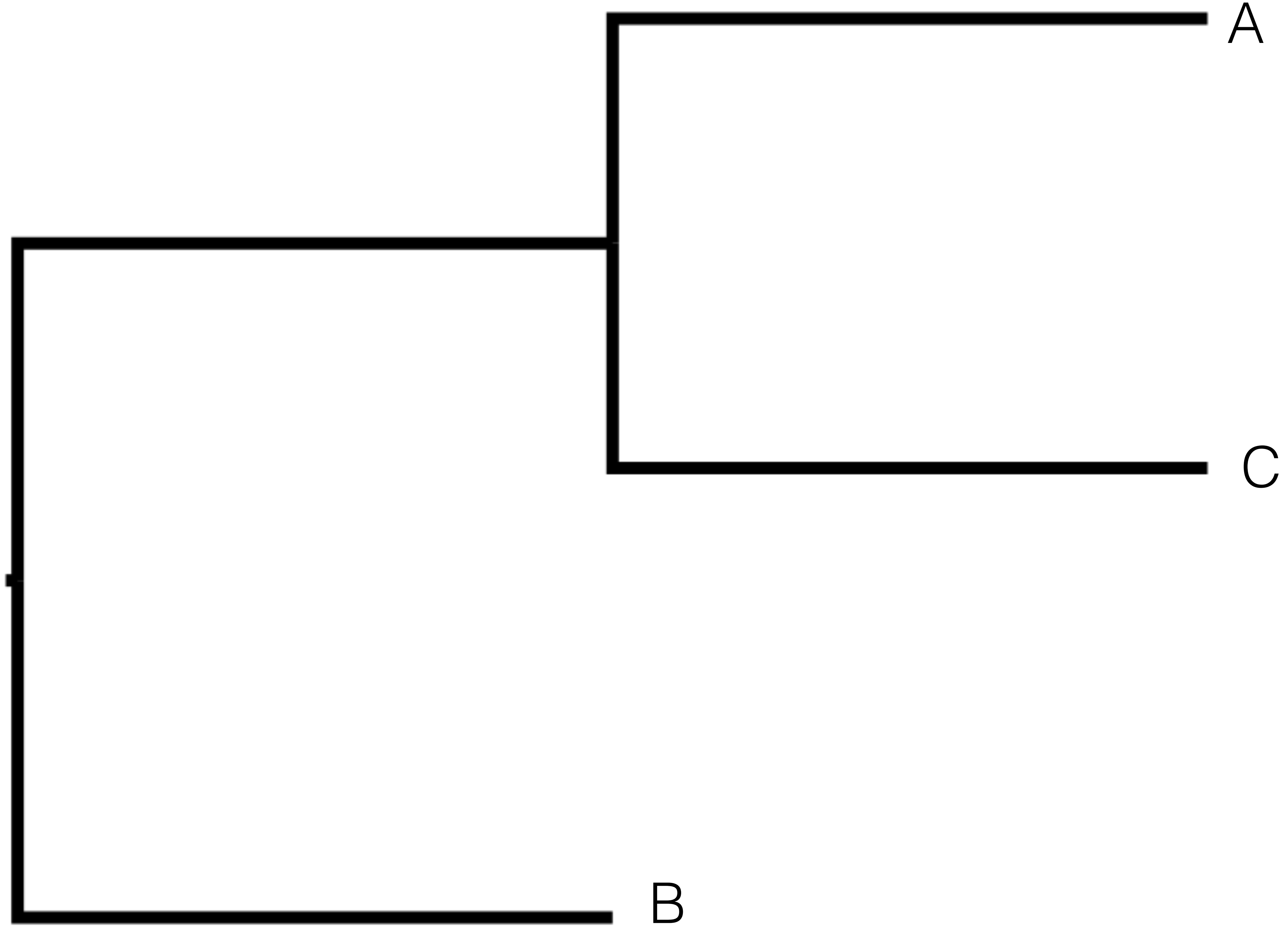

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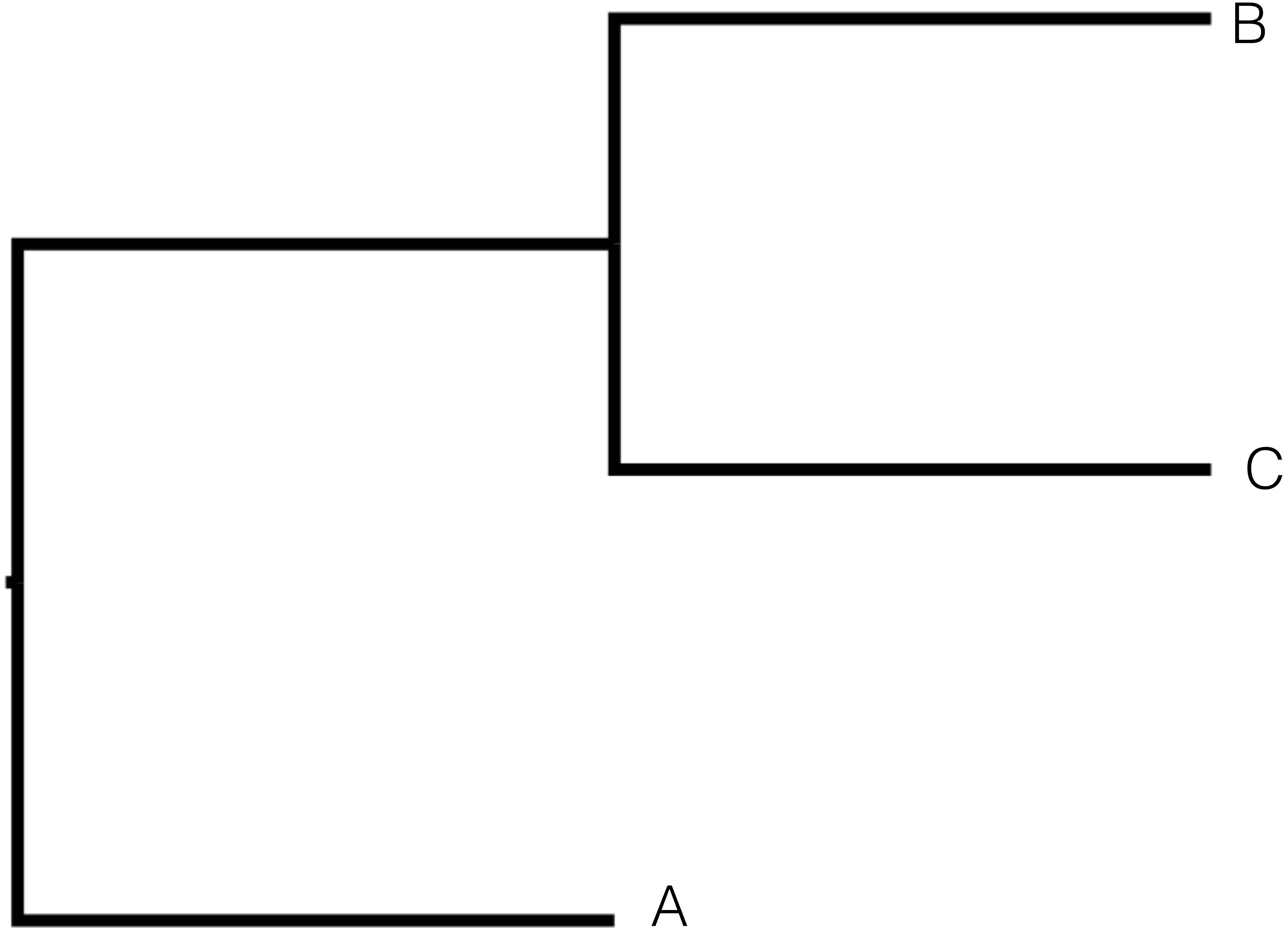
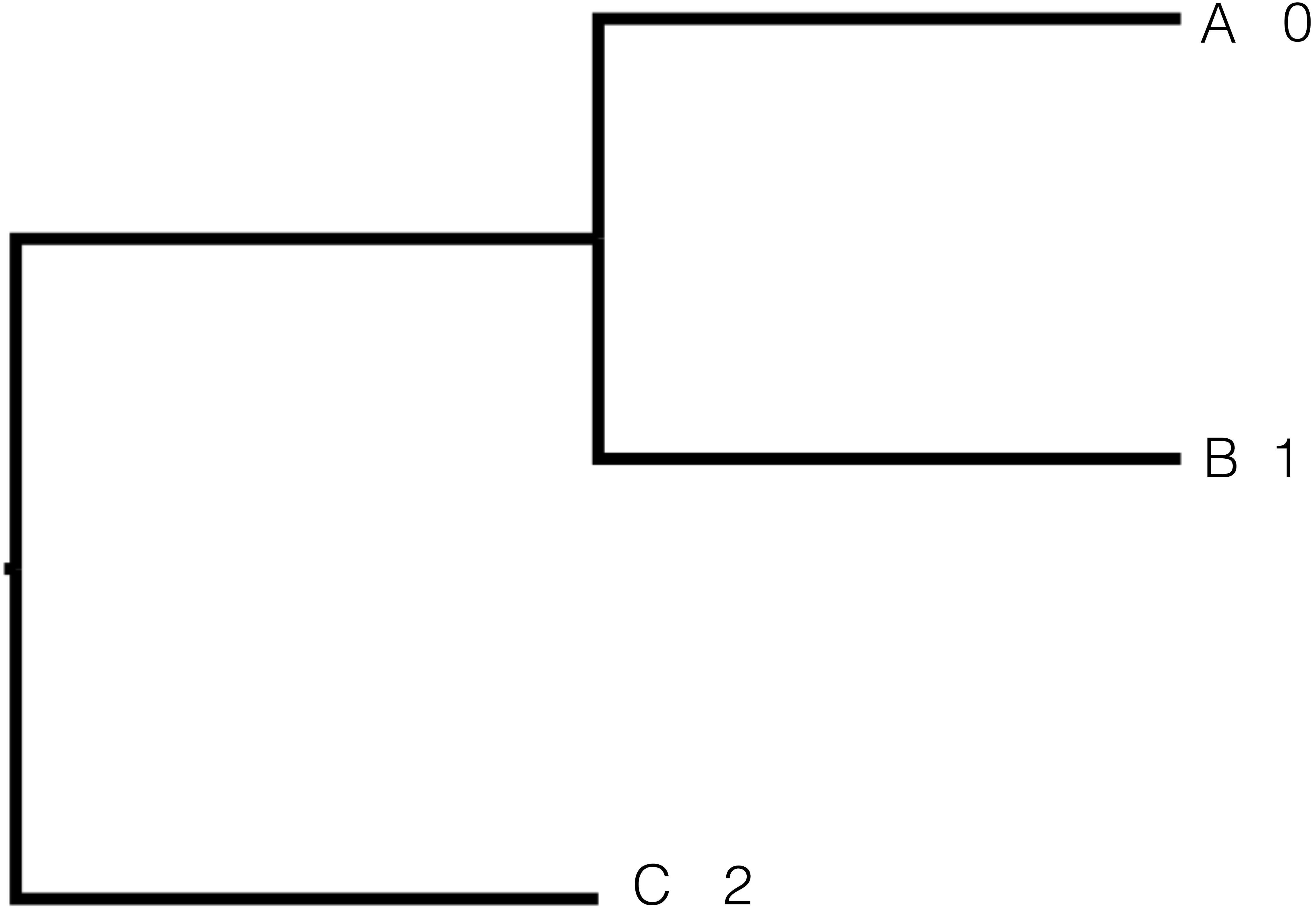


Ascertainment Bias

	[redacted]	**Char. 2**	**Char. 3**
A	[redacted]	1	0
B	[redacted]	1	1
C	[redacted]	0	2

Ascertainment Bias



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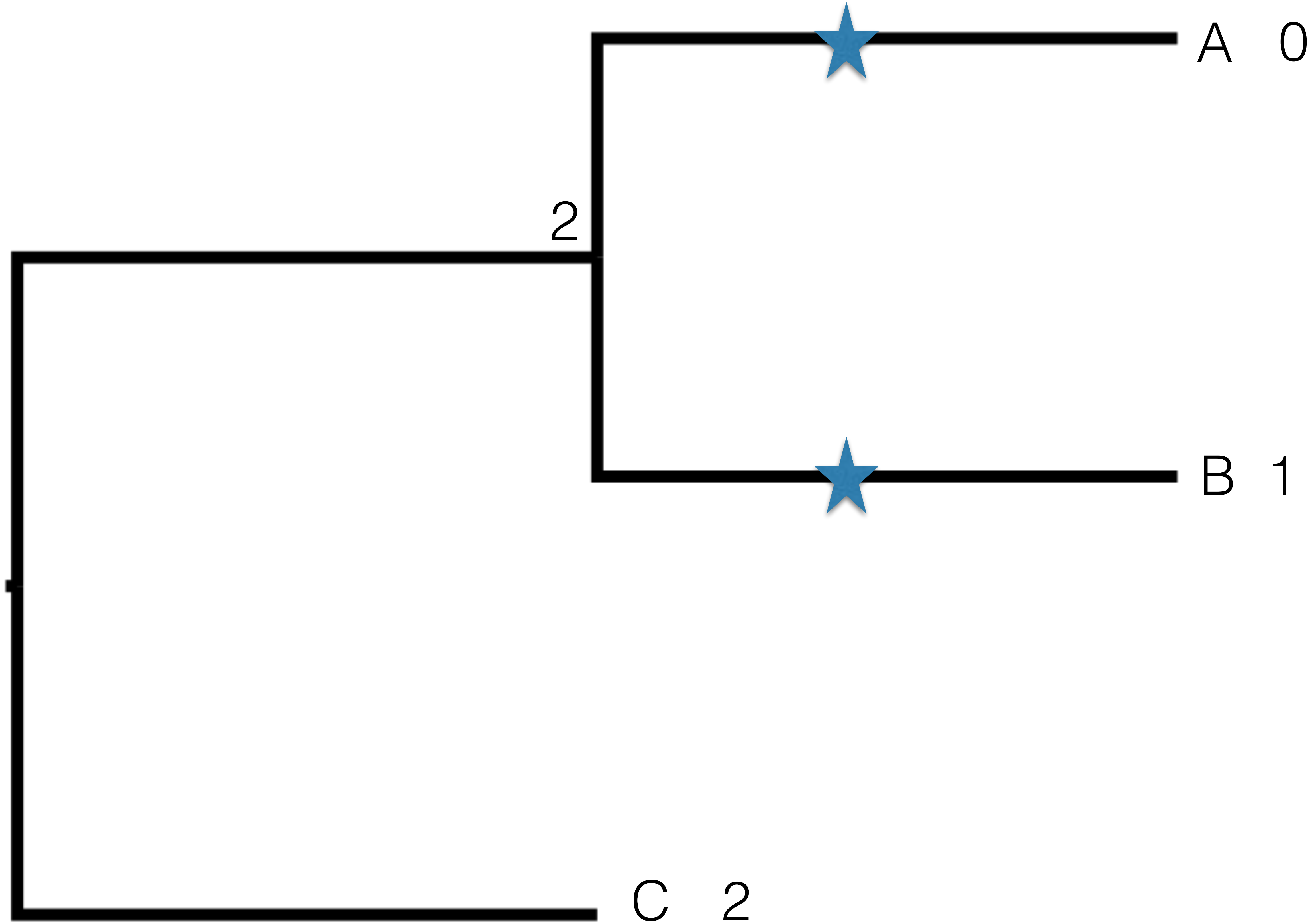

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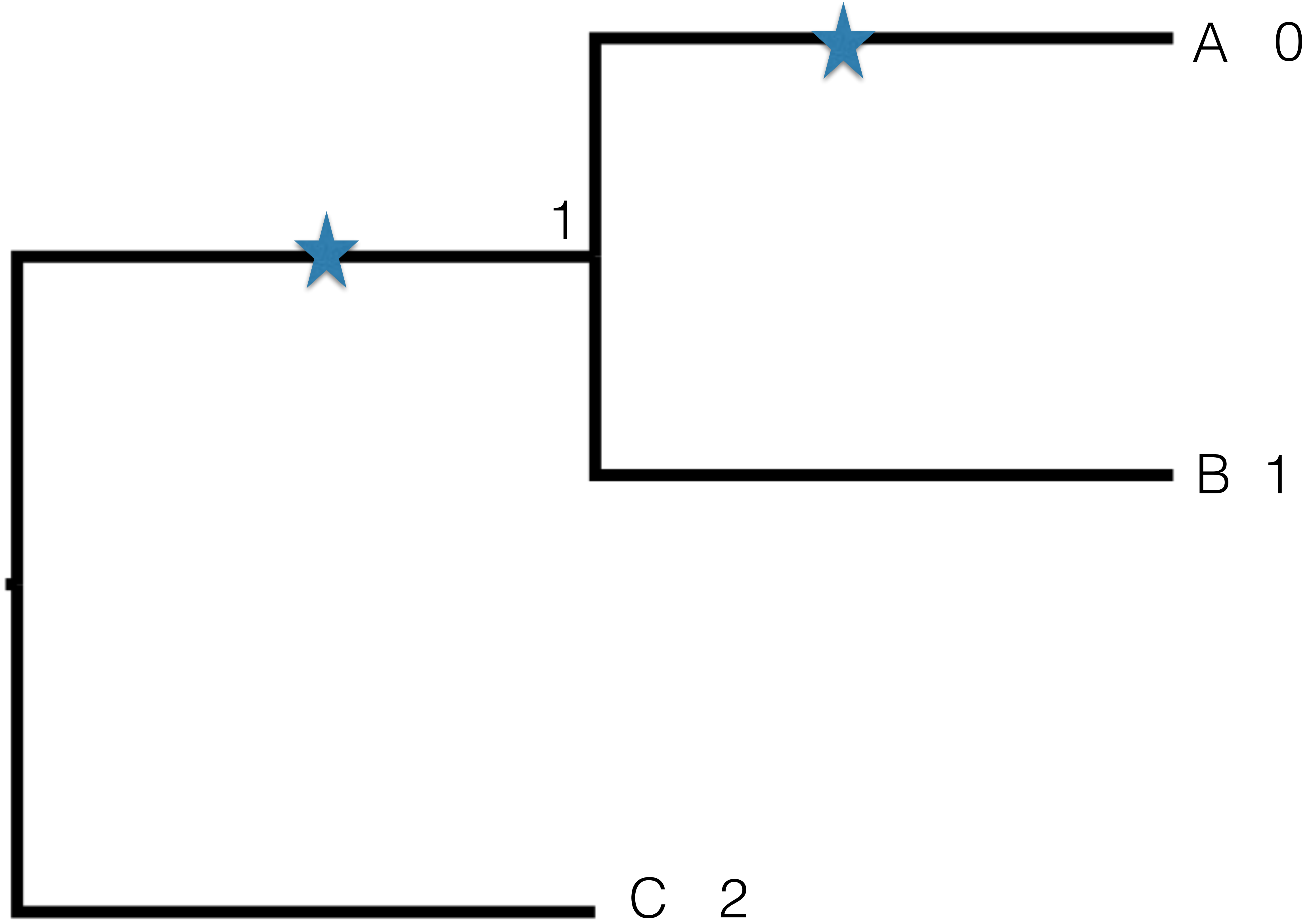

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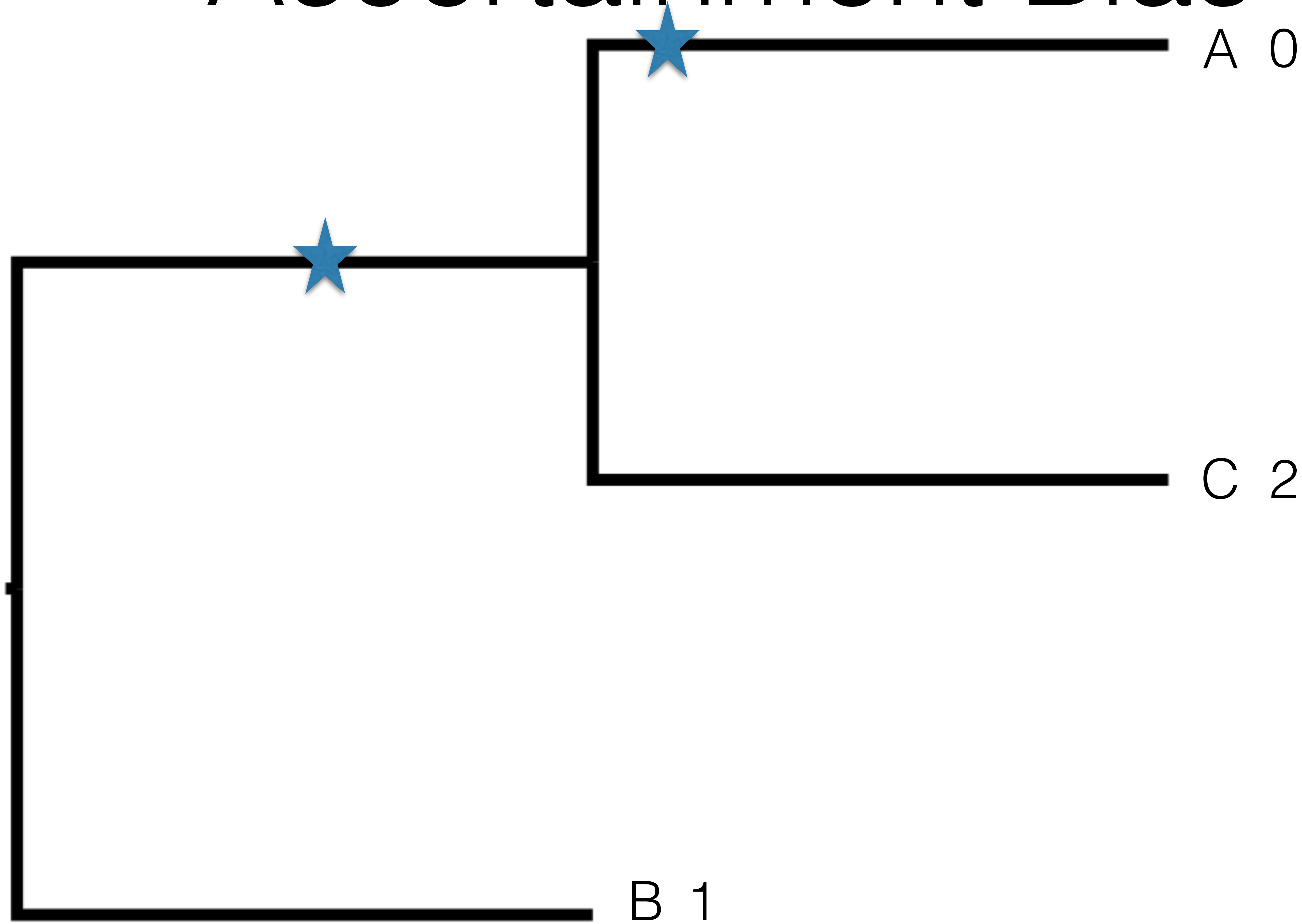

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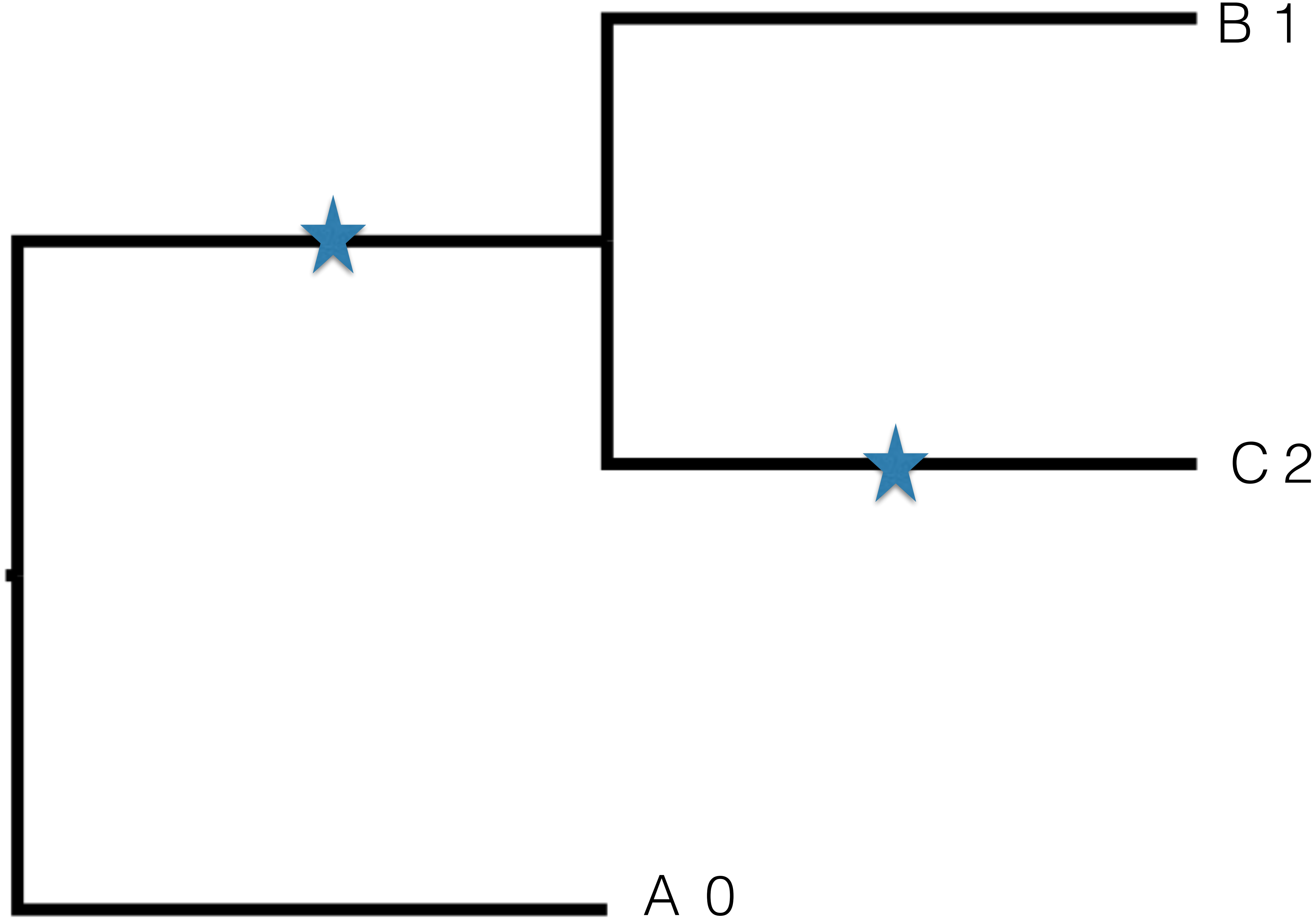
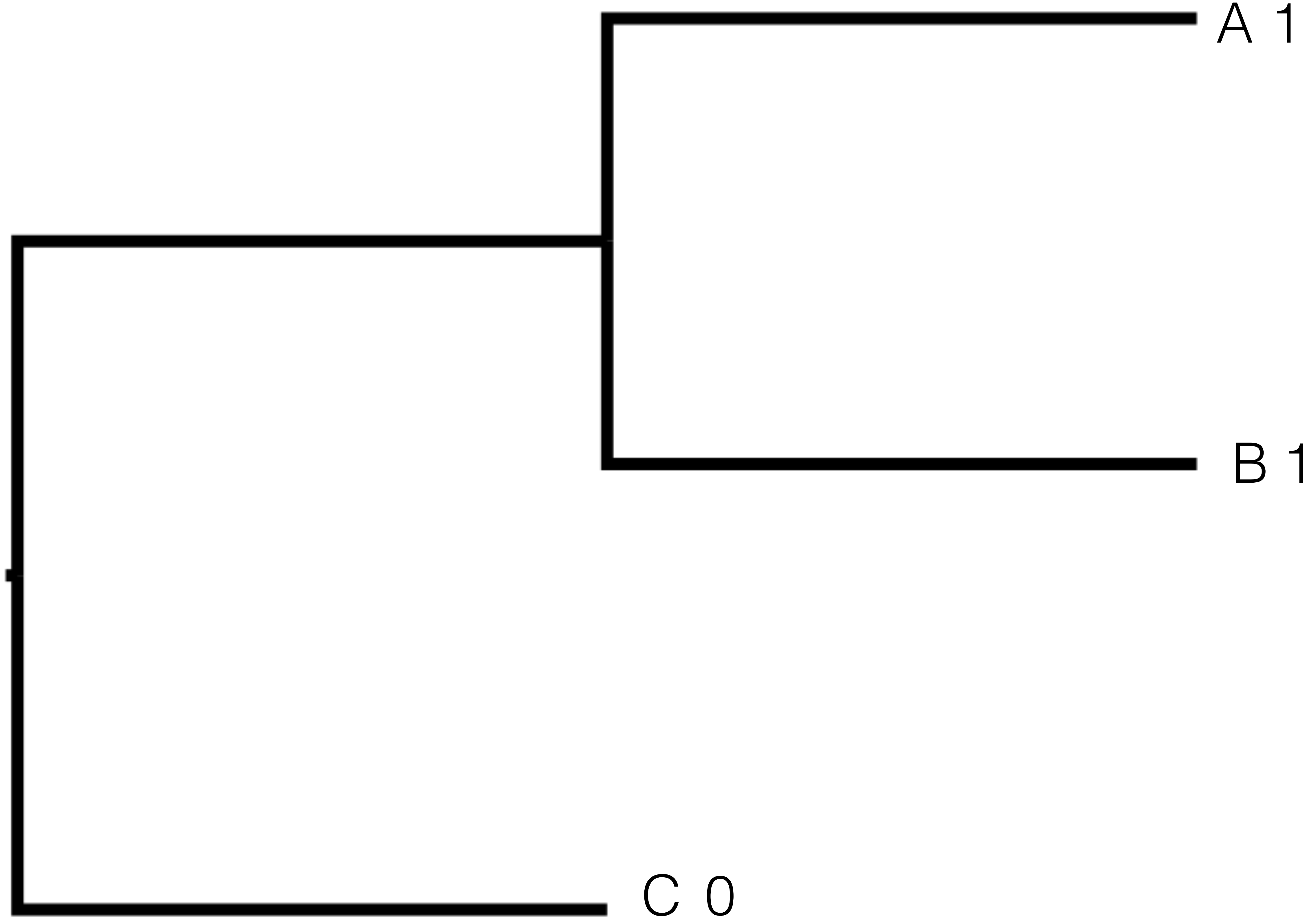


Ascertainment Bias

	[redacted]	**Char. 2**	[redacted]
A	[redacted]	1	[redacted]
B	[redacted]	1	[redacted]
C	[redacted]	0	[redacted]

Ascertainment Bias



Ascertainment Bias

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↑ Rate

Ascertainment Bias

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⬆ Rate

↓ Rate

RevBayes

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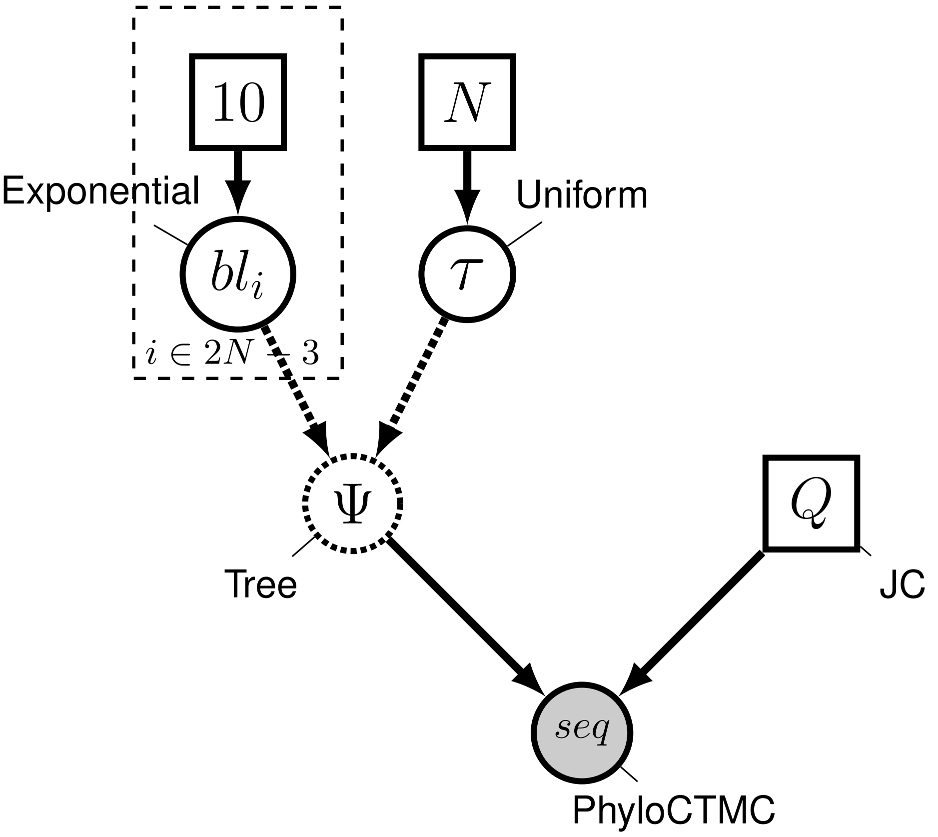

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Adapted from Hohna, Landis, Heath

RevBayes

Load both log files into Tracer

Morphology is complicated

Each morphological change may be underlain by multiple genetic changes

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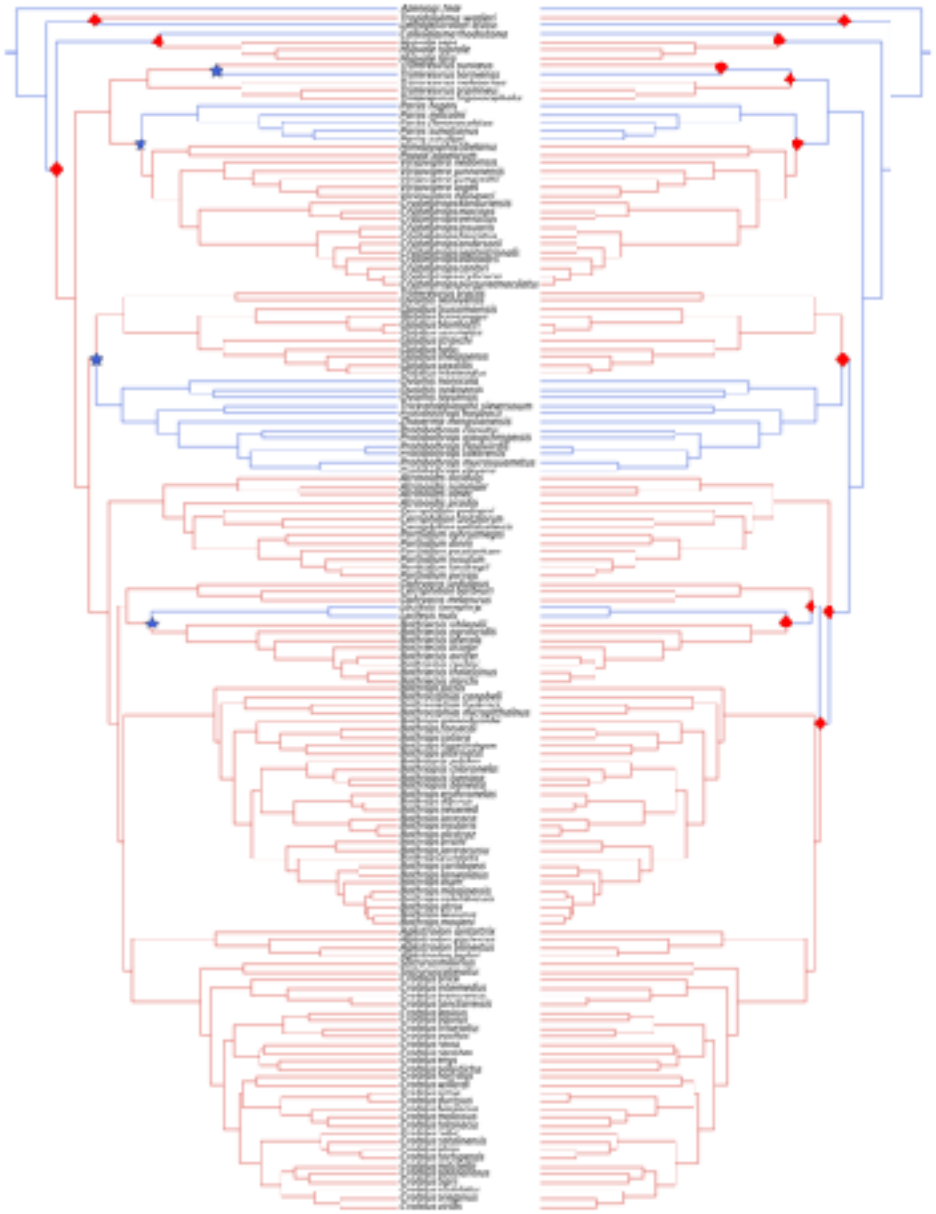

Wright et al. 2015

Studying parity mode evolution

Looked at multiple models that penalize changes in several ways

RevBayes 3.1

Morphology is complicated

We might expect that you have to go through one state to get to another

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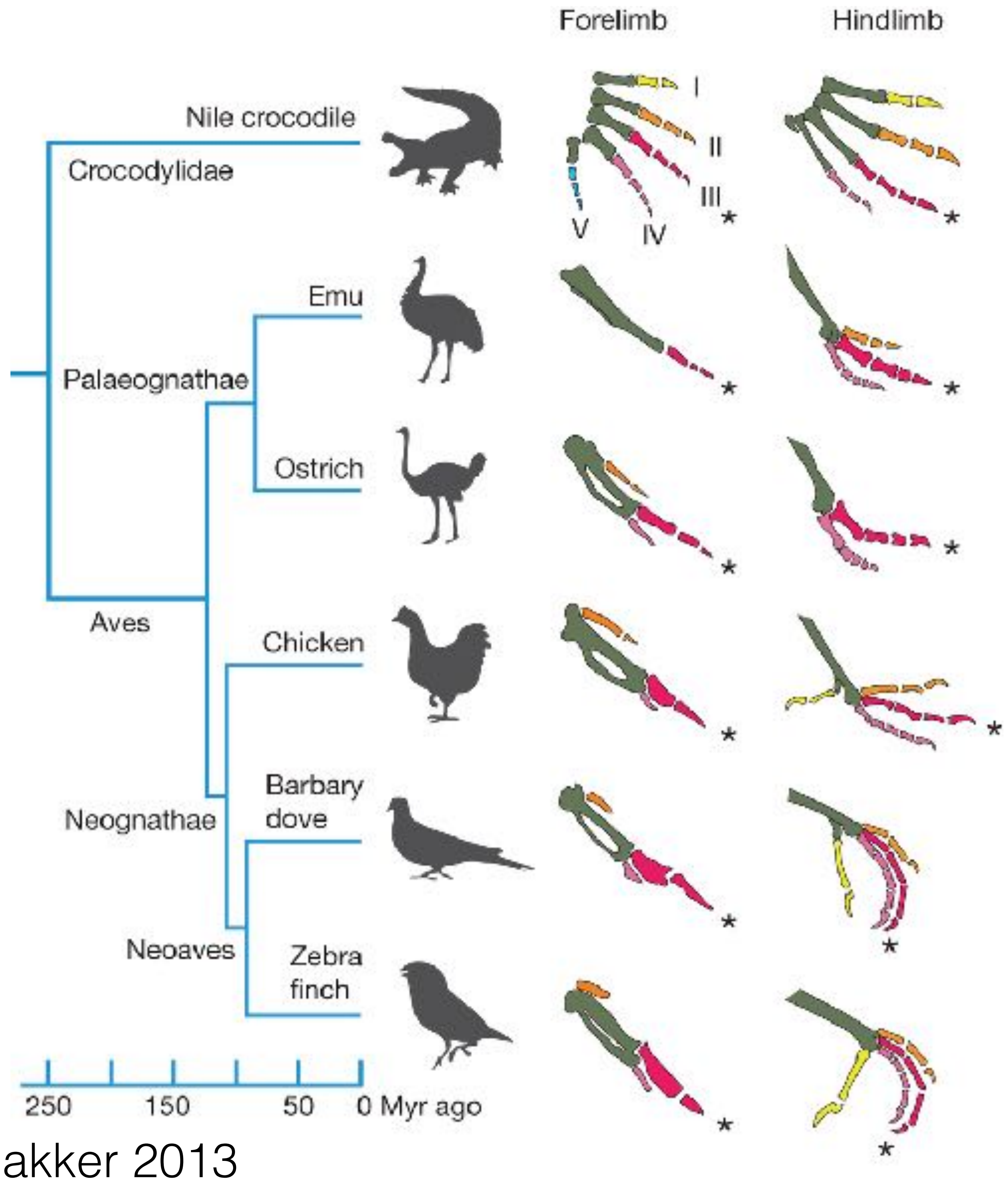
We might expect that you have to go through one state to get to another **(Wagner Parsimony)**

Morphology is complicated



de Bakker 2013

We might expect that you have to go through one state to get to another

RevBayes 3.2

These ways of getting around the assumption of equal transition rates require that we specify, *a priori* what we think our transition rates are and what characters we think evolve according to which matrix

We are going to do model comparisons between the Mk model and two ways of relaxing the assumption of equal rates using a prior on state frequencies

Each of you will run section 4 (mcmc_mk_discreitzed.Rev) of the RevBayes tutorial

We'll compare this to pre-cooked output from section 5.

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We'll compare this to pre-cooked output from section 5.

Start this now.

So what's in these two models?

$$\begin{tikzcd}
0 \arrow[r, shift left] & 1 \arrow[l, shift left]
\end{tikzcd}$$

Sphecomyrminae

Photo: Steve Shattuck

Sphecomyrminae

Photo: Steve Shattuck

- Presence of wasp-like features that are lost after divergence of Sphecomyrminae from the rest of the ants

Sphecomyrminae

Photo: Steve Shattuck

- Presence of wasp-like features that are lost after divergence of Sphecomyrminae from the rest of the ants

1 → 0

Sphecomyrminae

Photo: Steve Shattuck

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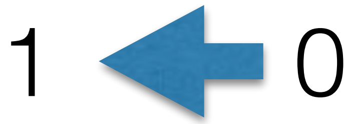
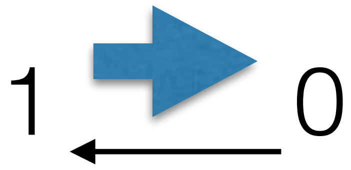


- Presence of ant apomorphies

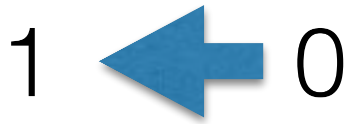


Sphecomyrminae

Photo: Steve Shattuck

Poor fit of character change symmetry assumption

- Presence of wasp-like features that are lost after divergence of Sphecomyrminae from the rest of the ants



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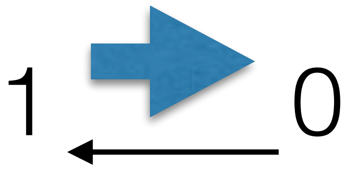
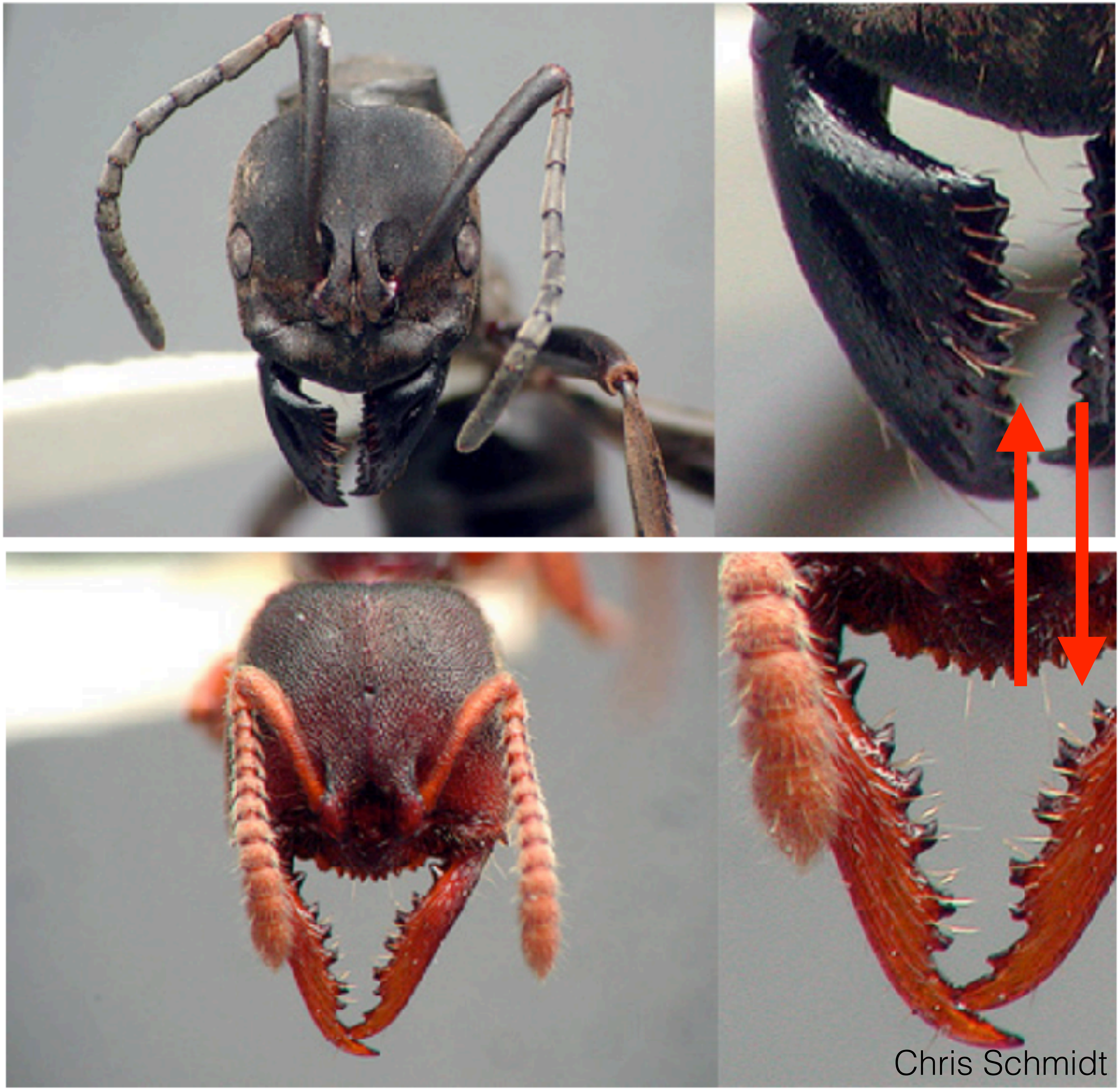


Chris Schmidt



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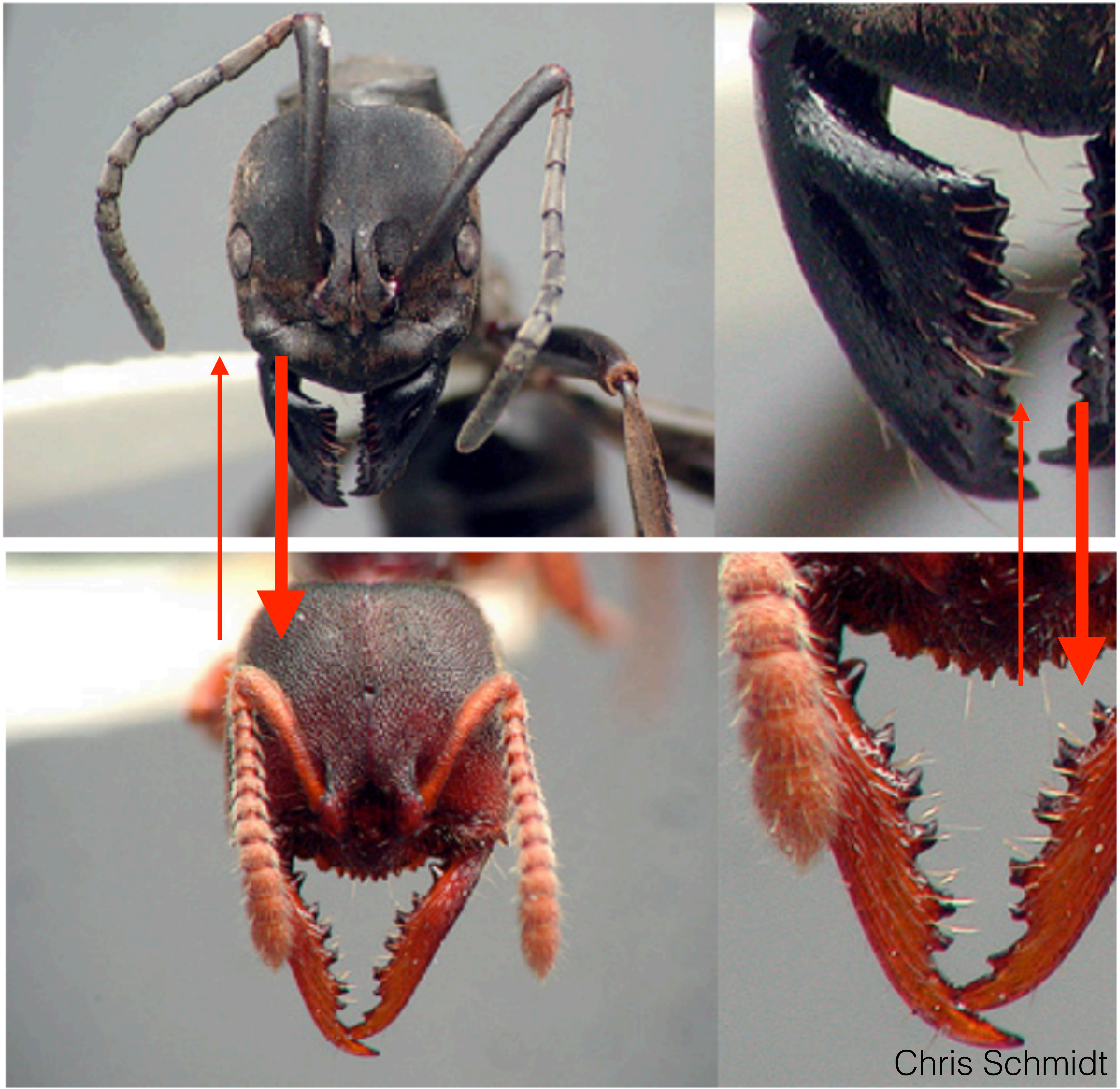

Chris Schmidt

Allowing asymmetrical transition rates

- We could come up with a new transition matrix

Allowing asymmetrical transition rates

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- We could also use a prior on state frequencies

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Probability of 0 to 1 change

0.75

Allowing asymmetrical transition rates

- We could come up with a new transition matrix
- We could also use a prior on state frequencies

Probability of 0 to 1 change
State Frequency of 0
0.75 x 0

Allowing asymmetrical transition rates

- We could come up with a new transition matrix
- We could also use a prior on state frequencies

Probability of 0 to 1 change

State Frequency of 0

0.75 x 0 = 0.0

0

1

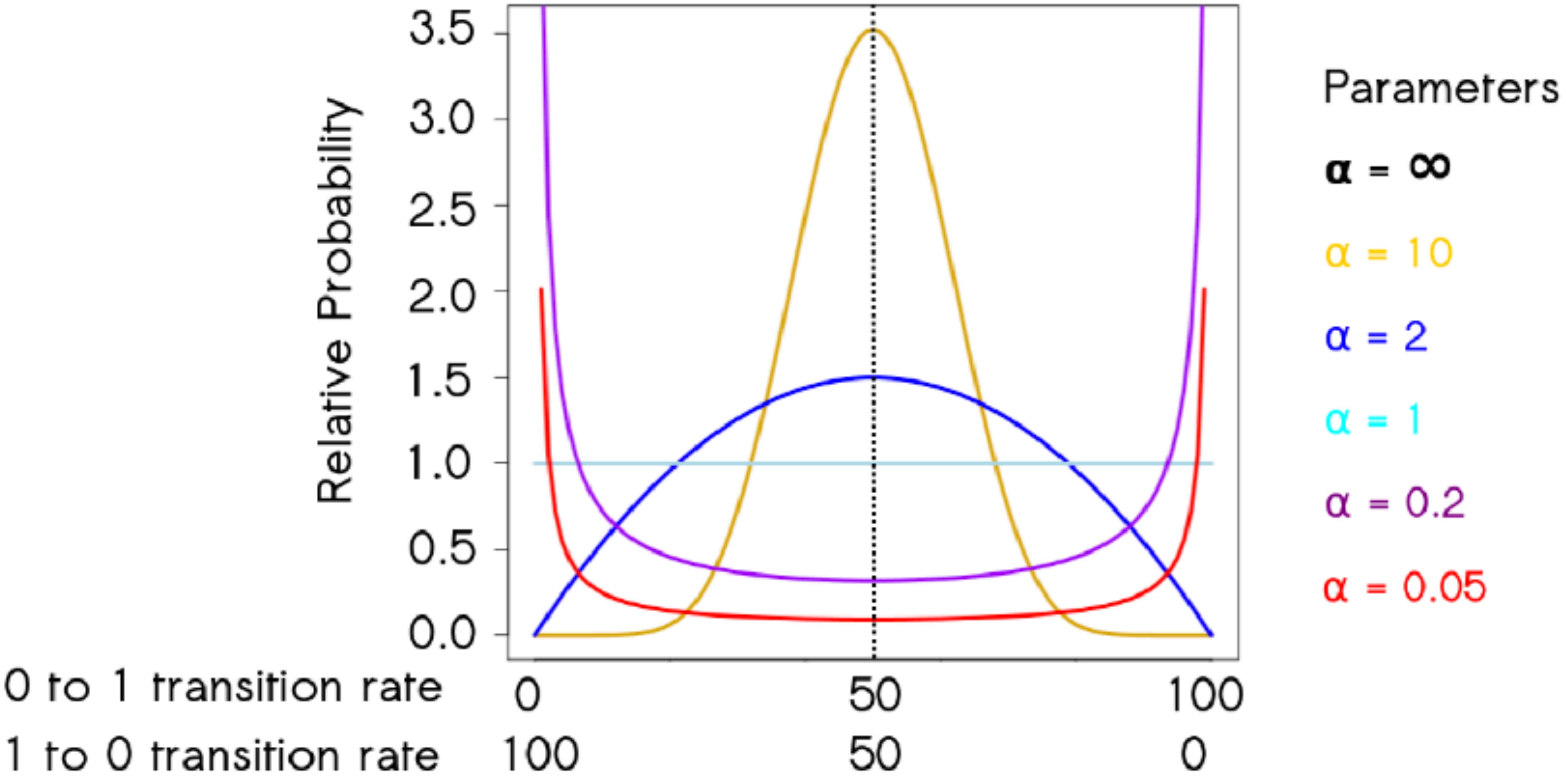
Allowing asymmetrical transition rates

- We could come up with a new transition matrix
- We could also use a prior on state frequencies

Probability of 0 to 1 change
State Frequency of 0
0.75 x 0.5 = 0.325

Symmetric Beta

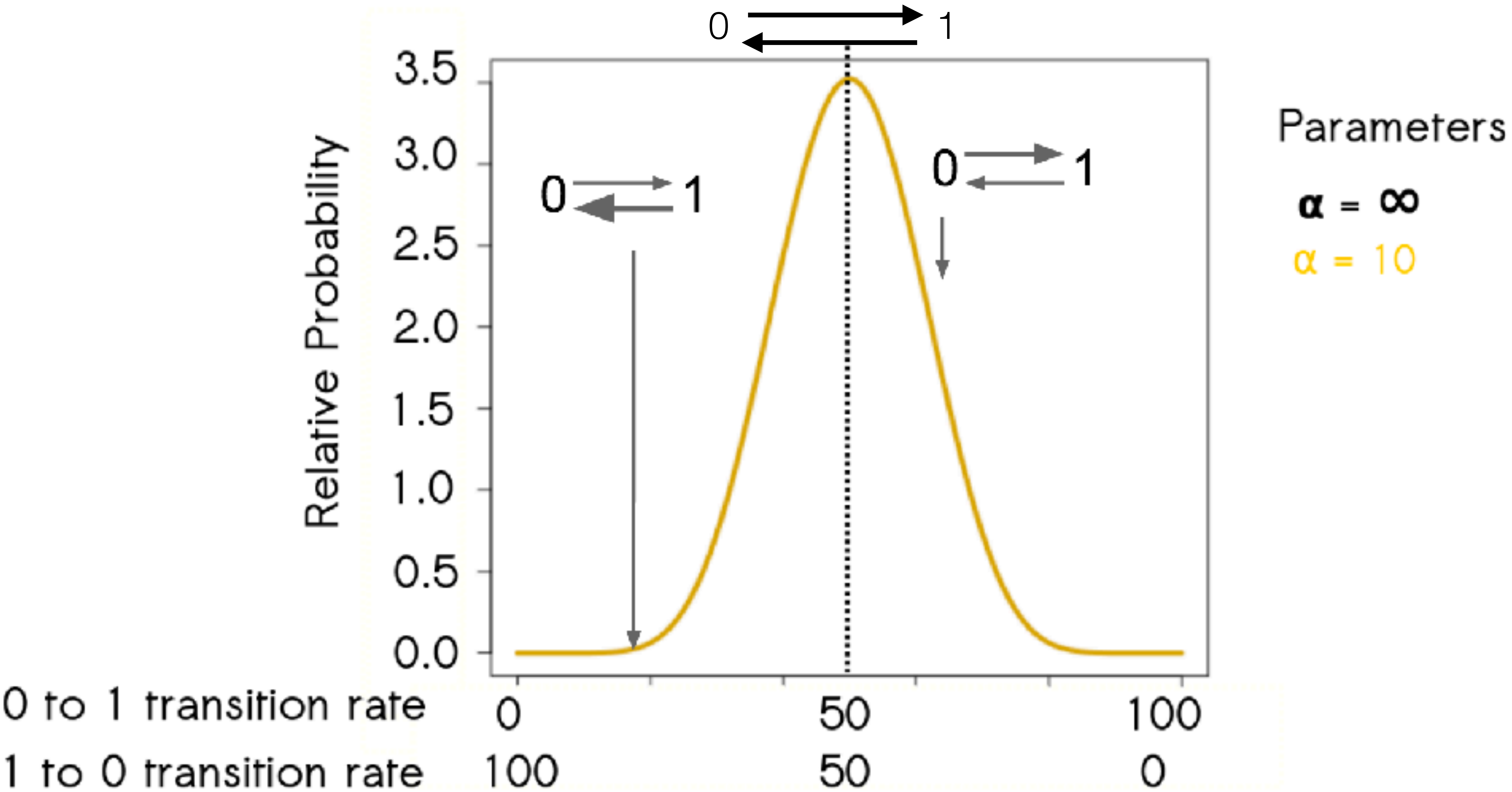
α ≠ β



Wright et al. 2016

Symmetric Beta

$$\alpha = \beta$$

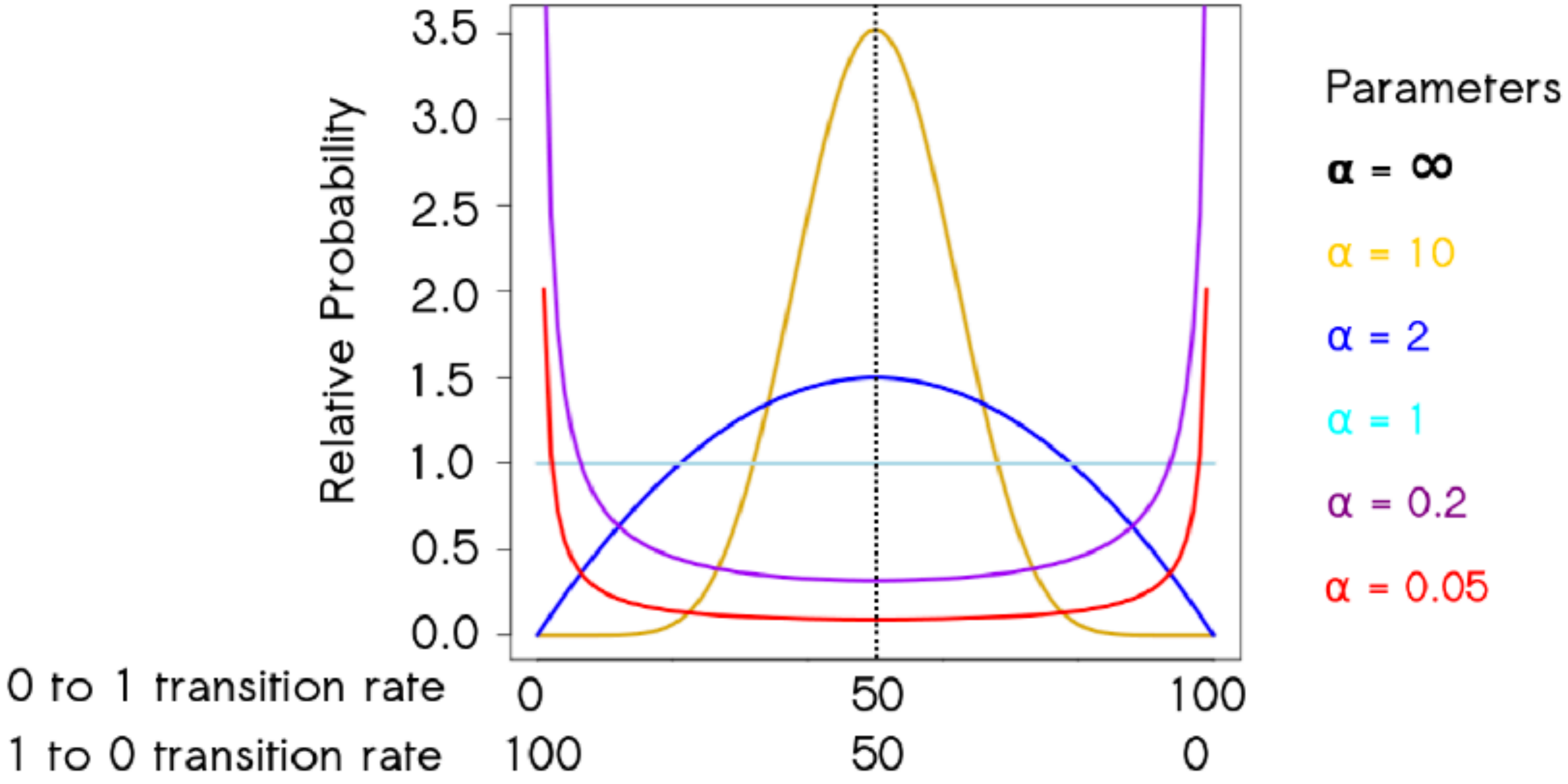


Wright et al. 2016

By allowing variation in state frequencies, we can allow asymmetrical transitions

Symmetric Beta

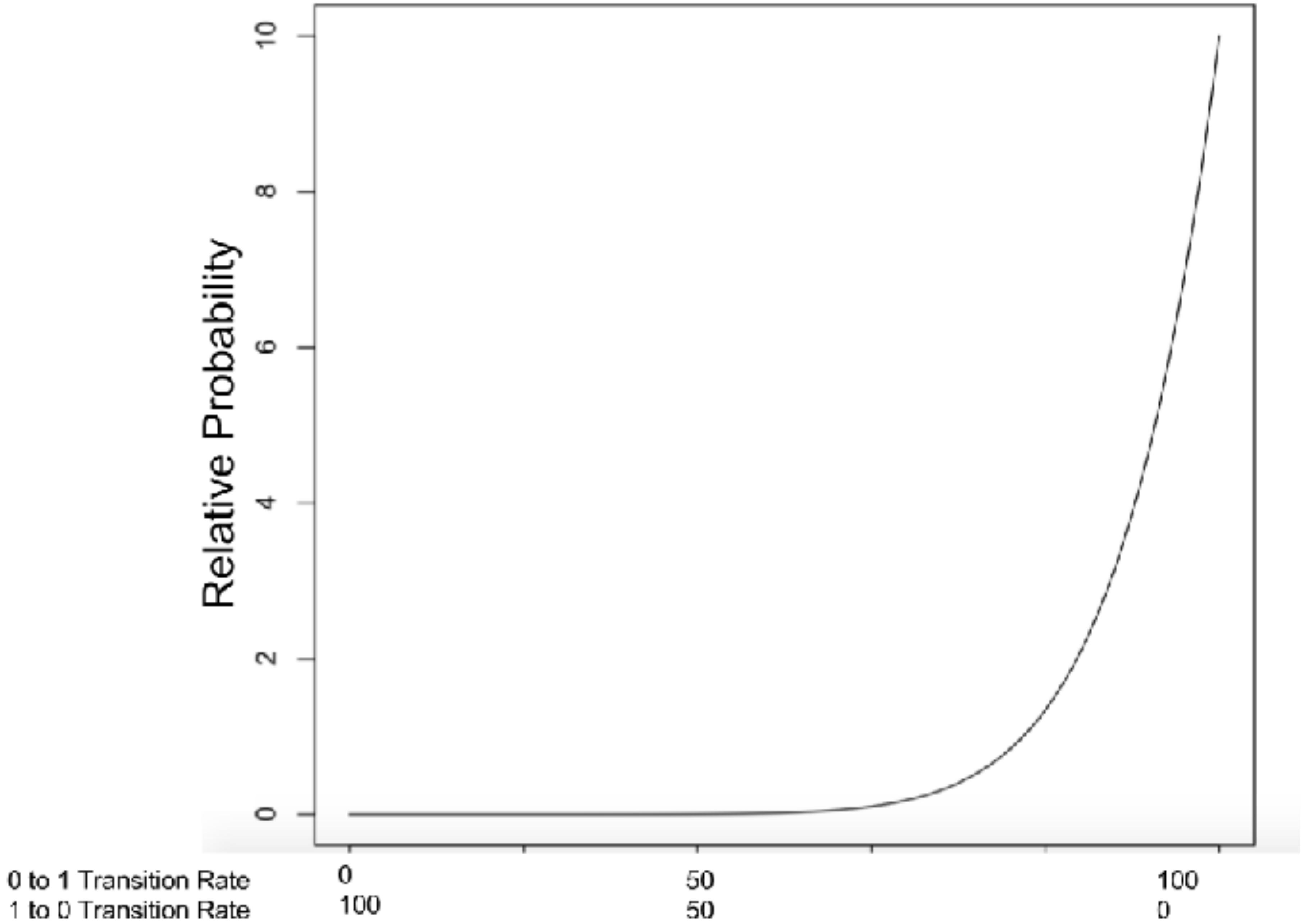
$\alpha = \beta$



Wright et al. 2016

Asymmetric Beta

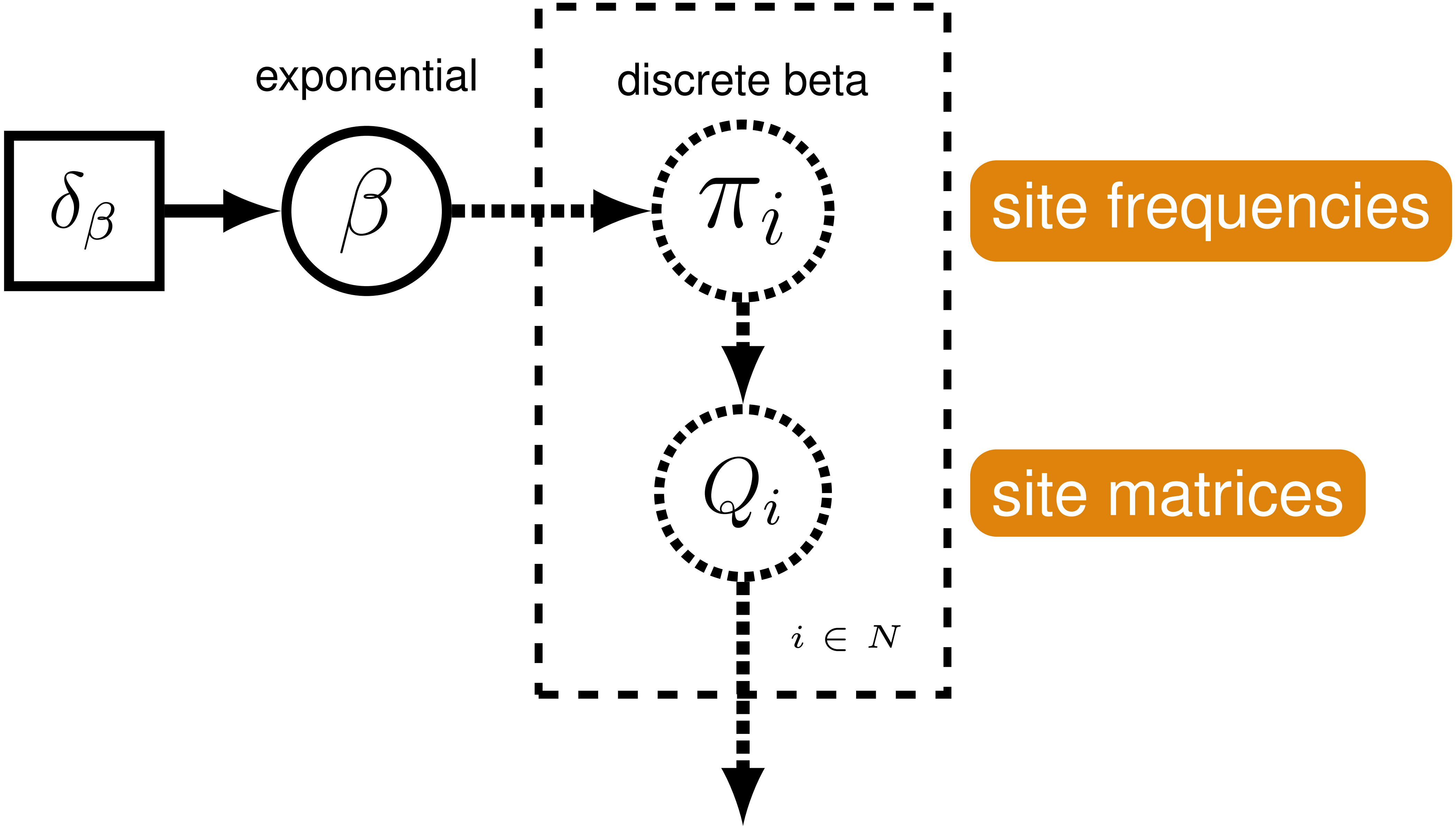
$\alpha \neq \beta$



Wright et al. in prep

Asymmetric Beta

α ≠ β



exponential

discrete beta

site frequencies

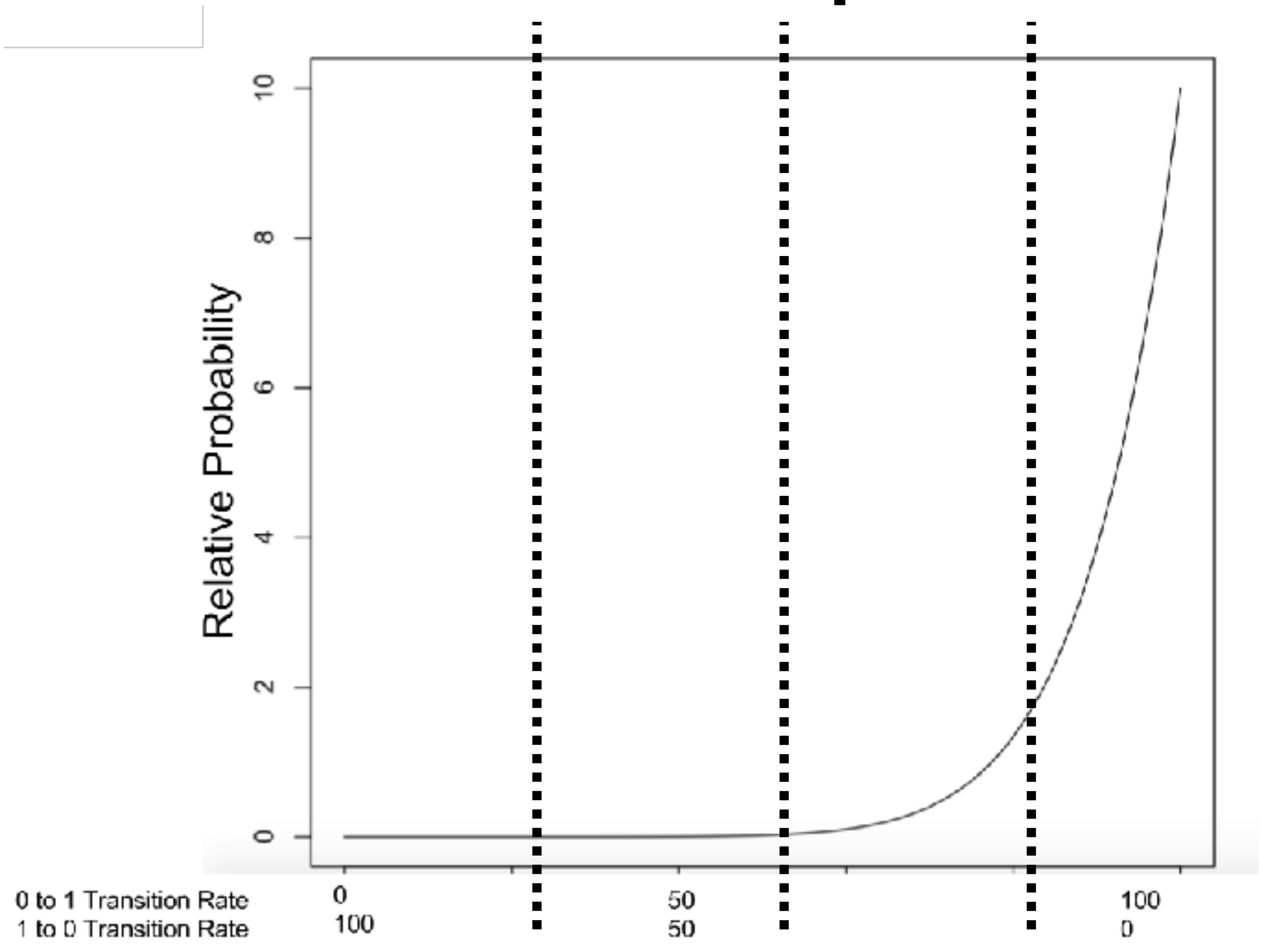
site matrices

to the phyloCTMC

Wright et al. in prep

Asymmetric Beta

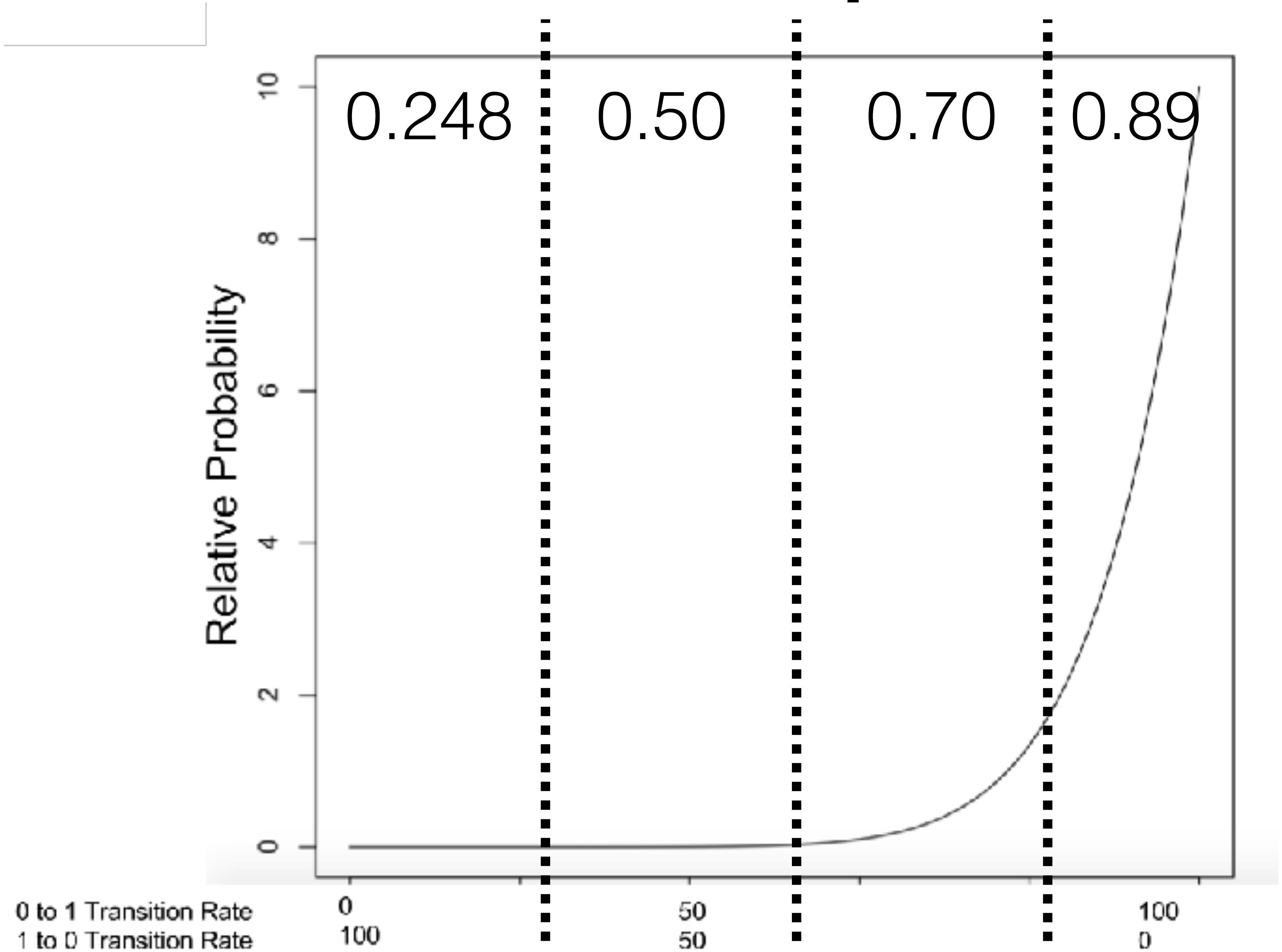
$\alpha \neq \beta$



Wright et al. in prep

Asymmetric Beta

α ≠ β



Wright et al. in prep

The previous model really only works for binary data

The previous model really only works for binary data

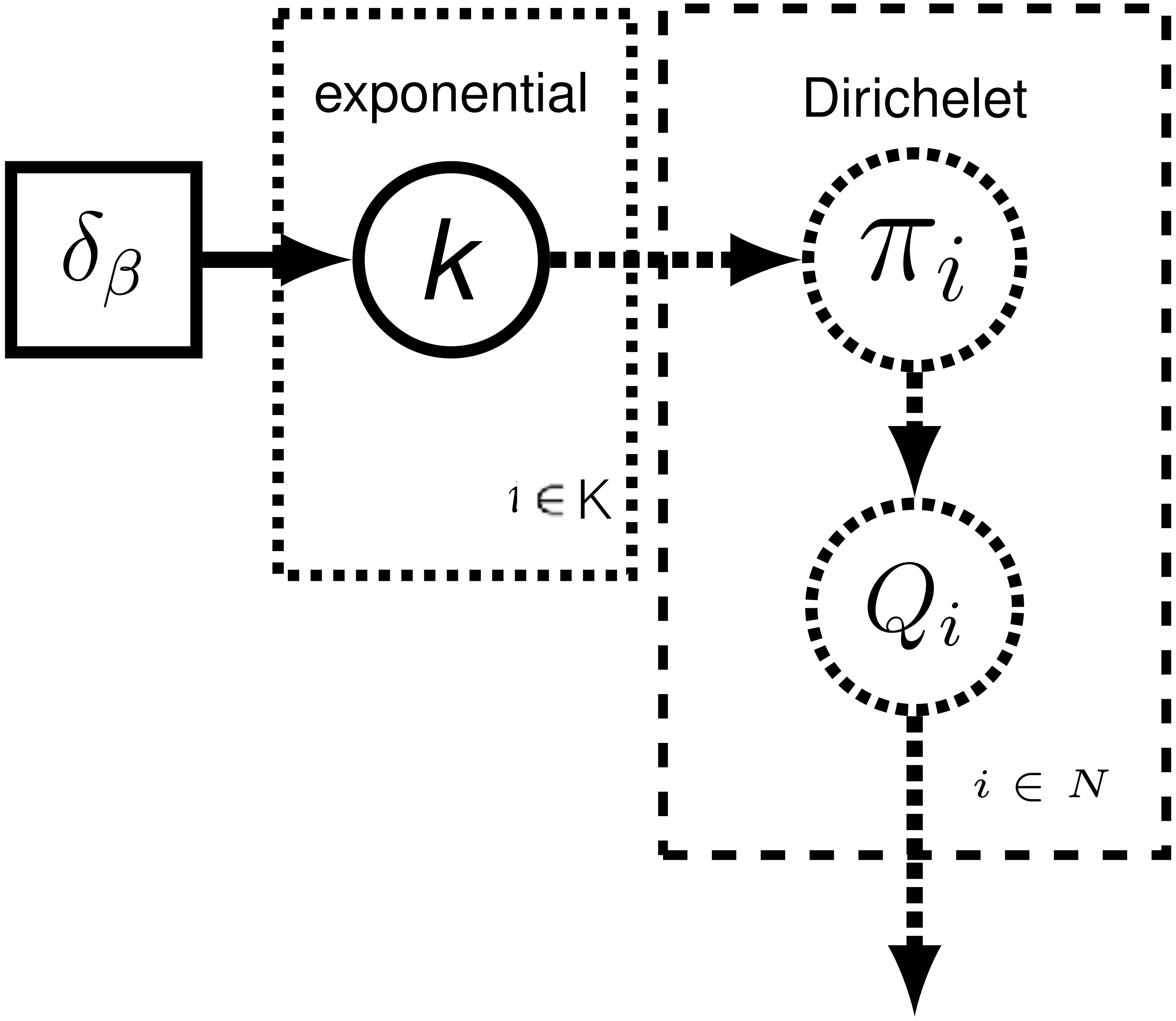
Maybe you don’t have binary data

Site Heterogenous Discrete Morphology Model

- The SDHM is similar to the CAT model

Site Heterogenous Discrete Morphology Model

- The SDHM is similar to the CAT model
- In this model, initialize our state frequencies from a Dirichlet prior, which allows us to expand the number of states beyond two

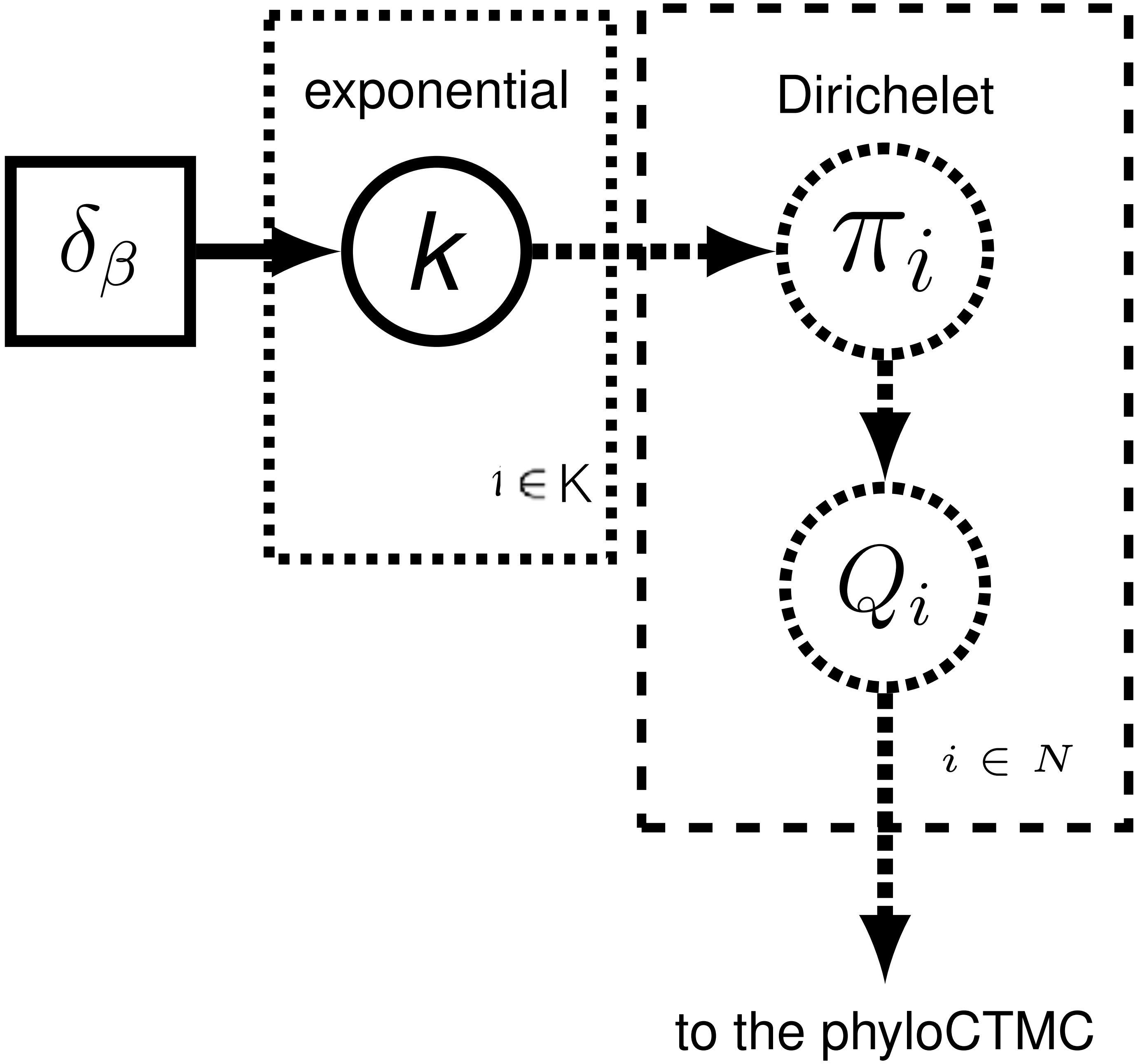


site frequencies

site matrices

to the phyloCTMC

[[0.651, 0.349]
[0.472, 0.528]
[0.548, 0.452]
[0.144, 0.856]]



site frequencies

site matrices

We're not going to focus further on this model

If you'd like to talk about it during open project hours, please come find me.

Load your output from your three inferences into Tracer. Also load hyperprior.log from output_examples

Break!

Ancestral State Estimation

- Marginalizing over unobserved character histories along a branch

Model, M
Parameters, Θ
Tip States, Xtip

Ancestral State Estimation

- Marginalizing over unobserved character histories along a branch

Model, M
Parameters, Θ
Tip States, Xtip

$$P(X_{tip}|\theta, M) = \sum_{X_{internal}} P(X_{internal}, X_{tip} \mid \theta, M)$$

Ancestral State Estimation

- Marginalizing over unobserved character histories along a branch

Model, M
Parameters, Θ
Tip States, Xtip

$$P(X_{tip}|\theta, M) = \textstyle\sum_{X_{internal}} P(X_{internal}, X_{tip} \mid \theta, M)$$

$$P(X_{internal}|\theta, M, X_{tip})$$

Joint estimation

- Somewhat confusing terminology
  - Historically, there has been joint and marginal estimation
    - **Joint:** finds the best probability combination of node states for the tree
    - **Marginal:** maximize probability at a node, not considering all other nodes in the tree

Joint estimation

- Somewhat confusing terminology
  - **Joint:** Treating both the tree and the ancestral state estimates as random variables

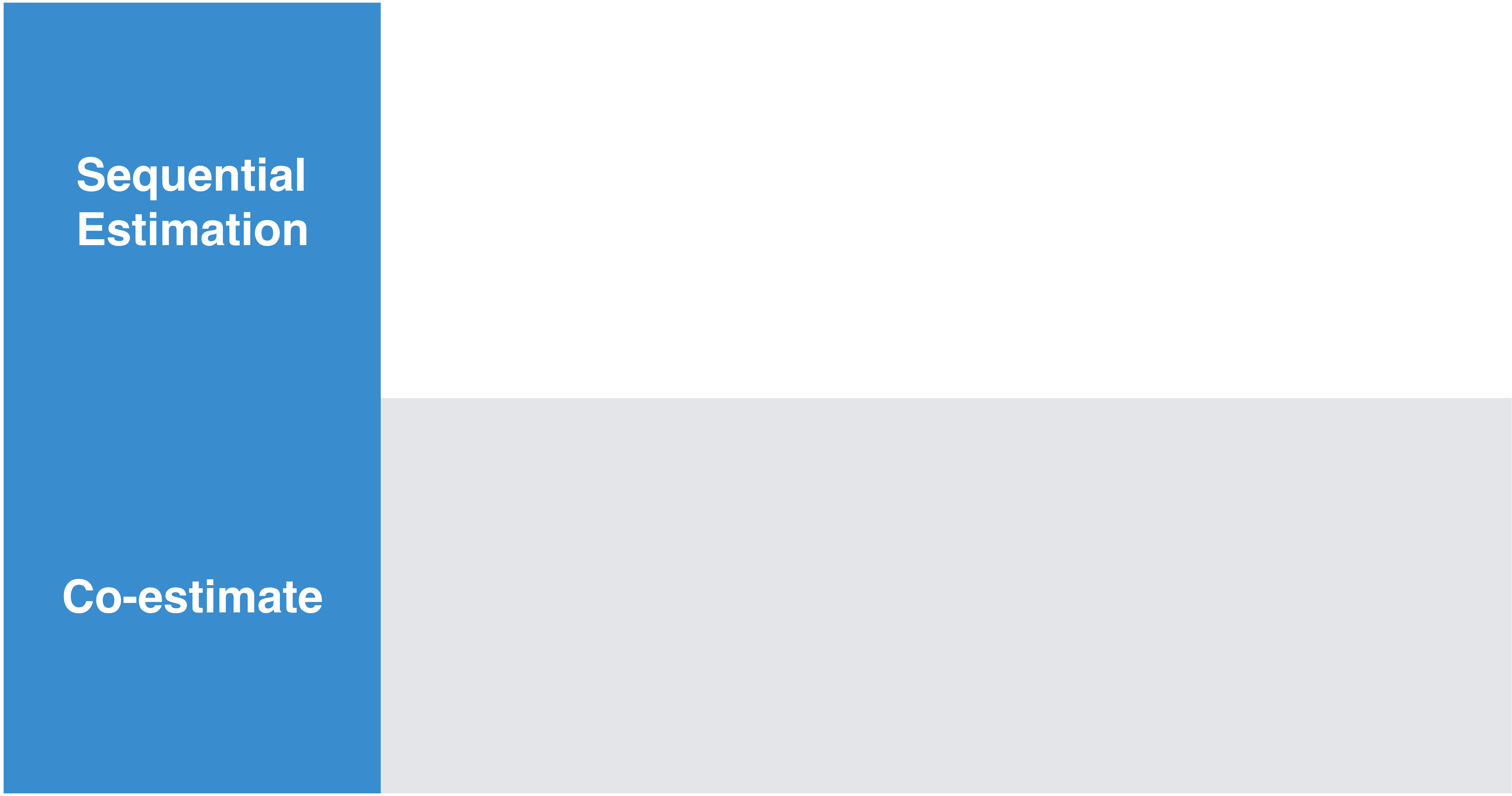
Joint estimation

- Somewhat confusing terminology
    - **Co-estimation:** Treating both the tree and the ancestral state estimates as random variables

Joint estimation

- Somewhat confusing terminology
  - **Sequential:** Infer the tree, then the ancestral states
  - **Co-estimate:** Treating both the tree and the ancestral state estimates as random variables

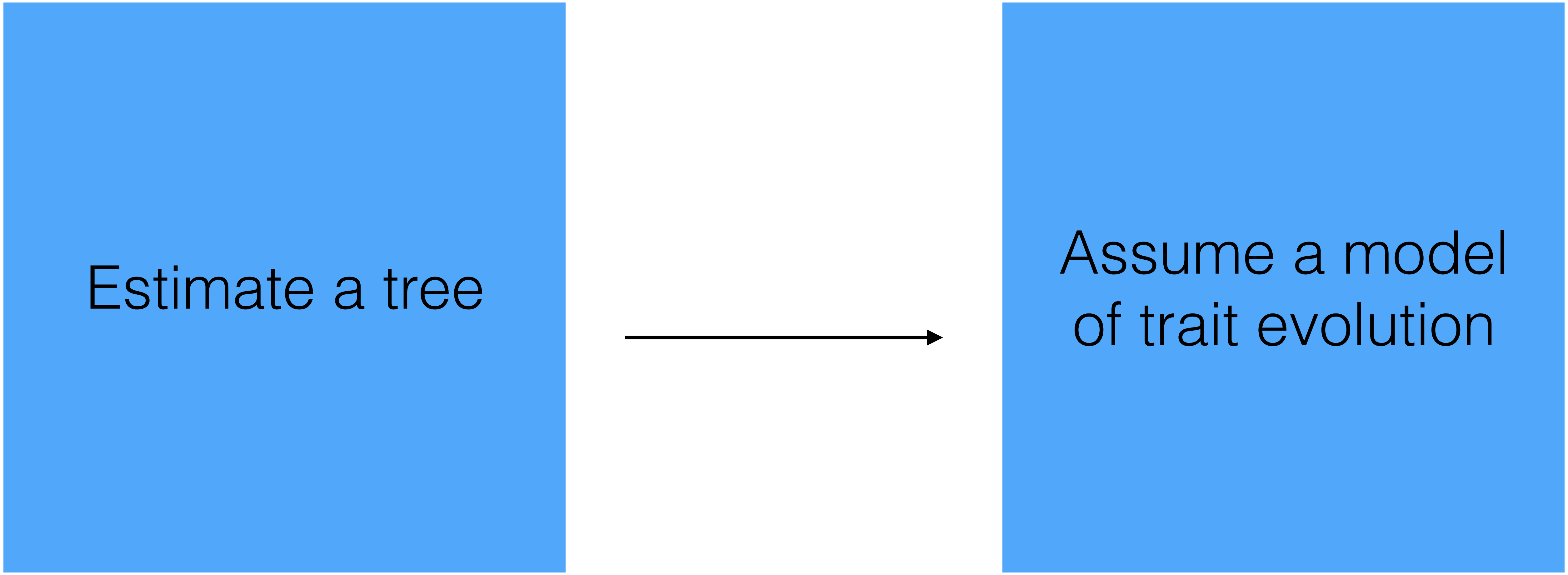
Ancestral State Estimation



Sequential Estimation

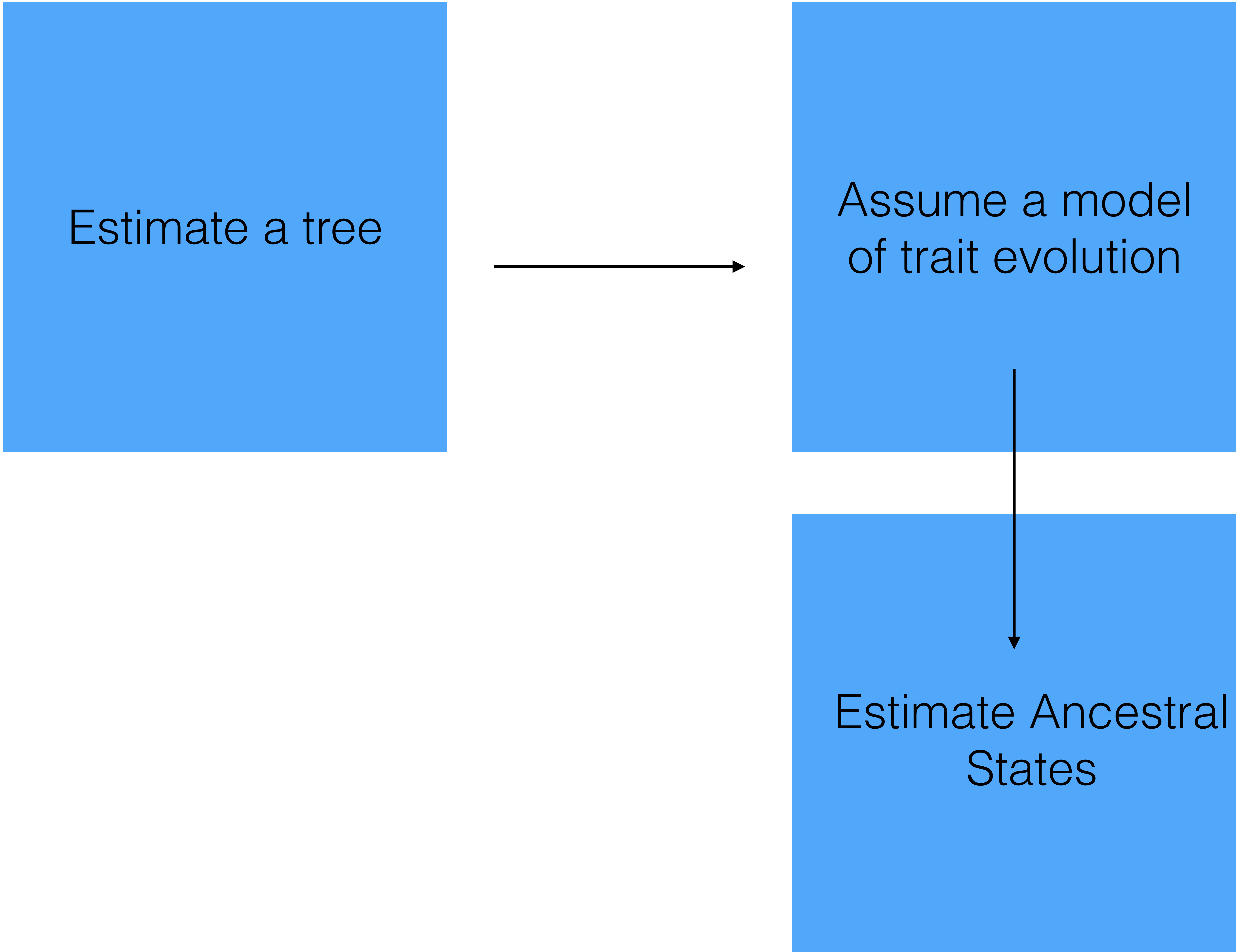
Co-estimate

Estimate a tree



Estimate a tree

Assume a model of trait evolution



Estimate a tree

Assume a model of trait evolution

Estimate Ancestral States

Ancestral State Estimation

Sequential Estimation	Quick
Co-estimate	

Ancestral State Estimation

Sequential Estimation	Quick Fairly intuitive
Co-estimate Estimation	

Ancestral State Estimation

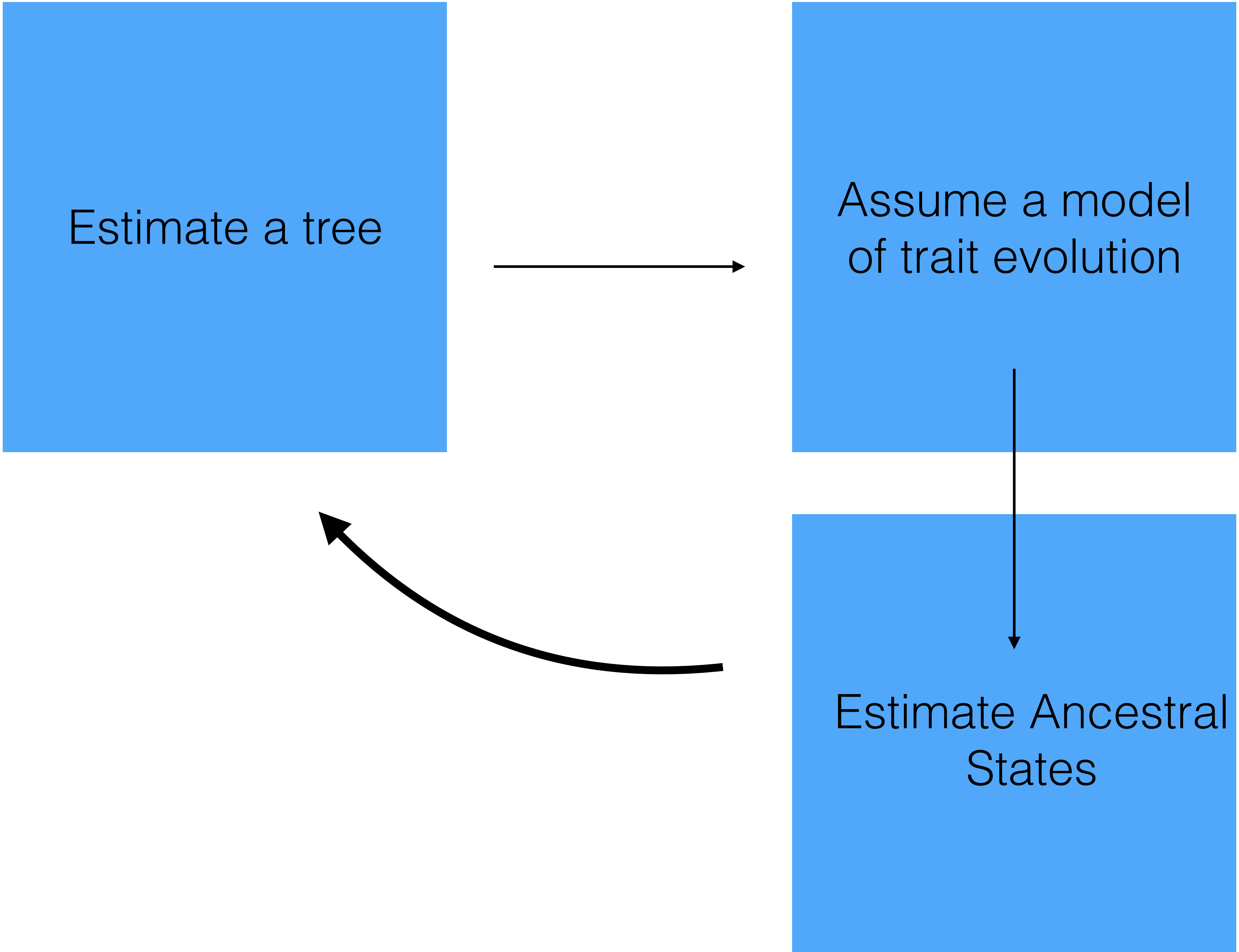
Sequential Estimation

Quick
Fairly intuitive
Easy-to-use implementations

Co-estimate

Ancestral State Estimation

Sequential Estimation	Quick Fairly intuitive Easy-to-use implementations	Ignores tree uncertainty
Co-estimate		



Estimate a tree

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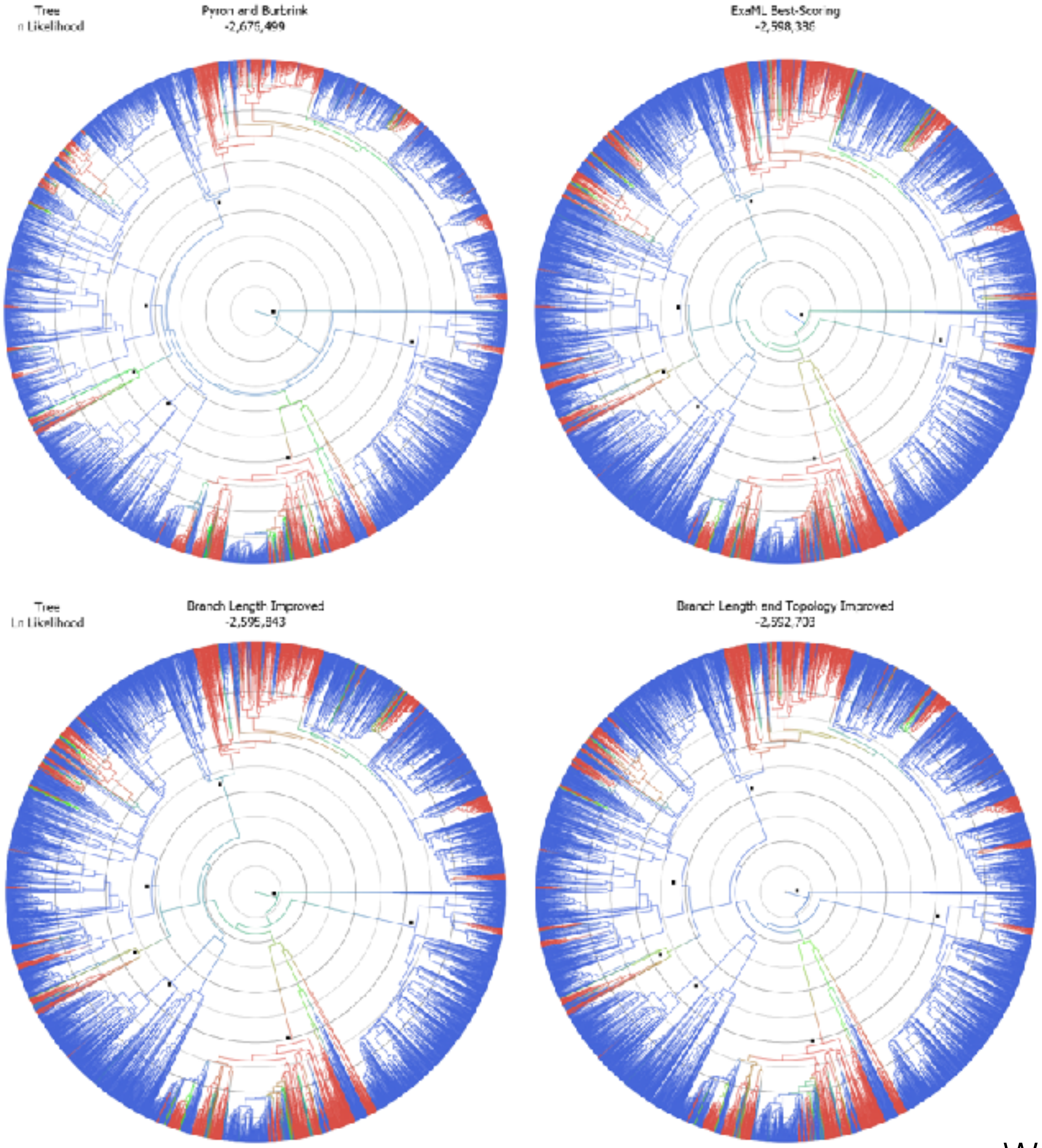
Estimate Ancestral States



Pyron and Burbrink
-2,675,499

ExaML Best-Scoring
-2,598,336

Branch Length Improved
-2,595,843

Branch Length and Topology Improved
-2,592,703

Wright et al 2015

Ancestral State Estimation

Sequential Estimation	Quick Fairly intuitive Easy-to-use implementations	Ignores tree uncertainty Hard to see uncertainty across trees
Co-estimate		

Ancestral State Estimation

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Ancestral State Estimation

Sequential Estimation	Quick Fairly intuitive Easy-to-use implementations	Ignores tree uncertainty Hard to see uncertainty across trees Partitioning uncertainty
Co-estimate	Doesn’t redouble effort Can visualize the uncertainty in ancestral states more naturally Doesn’t reduce dataset size	There hasn’t been a really great implementation of this

Ancestral State Estimation in RevBayes

Ancestral State Estimation in RevBayes

- In the simplest format, we can simply add a monitor for ancestral states to our model.

Ancestral State Estimation in RevBayes

- In the simplest format, we can simply monitor that ancestral states for our model.

- In fact, we have already done this.

Ancestral State Estimation in RevBayes

mcmc_mk.Rev, mcmc_simple.Rev

Ancestral State Estimation in RevBayes

- By adding this monitor, we call a second set of computations that conditions the node state on the tip state
- Co-estimates the most likely set of ancestral states **(joint estimation)**

Ancestral State Estimation in RevBayes

We will now look at how we can visualize our data nicely

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RevGadgets is an R package for visualizing output from some of the analyses that RevBayes can put out

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RevGadgets is an R package for visualizing output from some of the analyses that RevBayes can put out

(Did you have trouble getting RevGadgets to work?)

Ancestral State Estimation in RevBayes

First we annotate the MAP tree with our ancestral states (including their uncertainty)

Ancestral State Estimation in RevBayes

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(make_anc_state.R)

Ancestral State Estimation in RevBayes

First we annotate the MAP tree with our ancestral states (including their uncertainty)

Then, we decorate!

Ancestral State Estimation in RevBayes

First we annotate the MAP tree with our ancestral states (including their uncertainty)

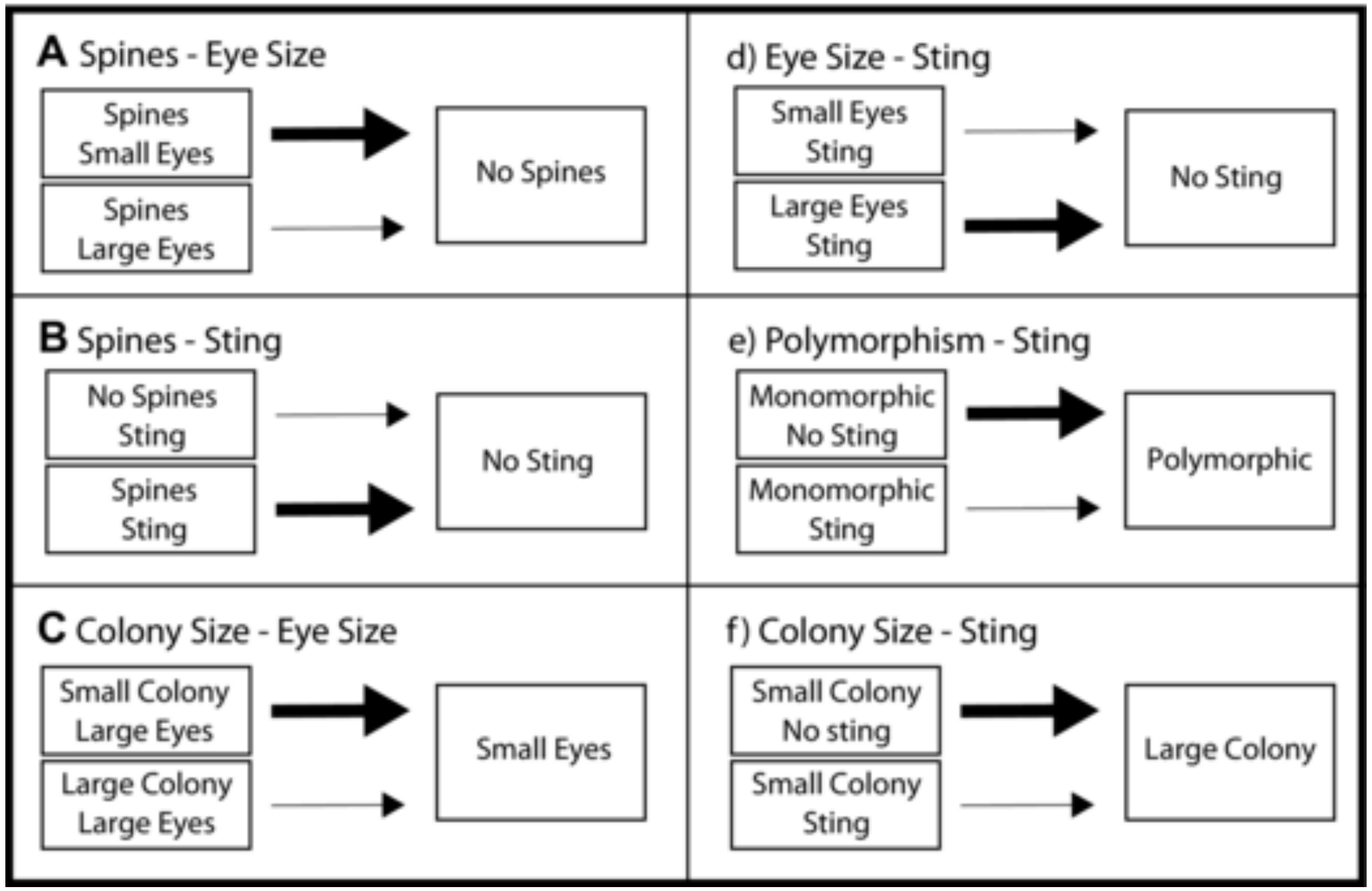
Then, we decorate!

(plot_anc_state.R)

Character Correlation

Character Correlation

- We might have some reason to believe that two characters are correlated



Blanchard and Moreau 2016

Character Correlation

- We might have some reason to believe that two characters are correlated
- We can accommodate this in a Q-matrix

$$Q = \begin{pmatrix} - & \mu_{00\to10} & \mu_{00\to01} & 0 \\ \mu_{10\to00} & - & 0 & \mu_{10\to11} \\ \mu_{01\to00} & 0 & - & \mu_{01\to11} \\ 0 & \mu_{11\to10} & \mu_{11\to01} & - \end{pmatrix}$$

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- Only one event occurs at a time
- Probability of X changing depends on Y, and vice versa

RevBayes 3.3

Covarion Models

- We’ve talked at a few points about models that rely on an unobserved state

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- We’ve talked at a few points about models that rely on an unobserved state
- Covarion models are structurally similar to correlated trait models
  - Have a ‘hidden’ state
  - Originally proposed for nucleotide evolution

Covarion Models

$$Q = \left(\begin{array}{cc|cc} - & r_1 q_{01}^{(1)} & s_{12} & 0 \\ r_1 q_{10}^{(1)} & - & 0 & s_{12} \\ \hline s_{21} & 0 & - & r_2 q_{01}^{(2)} \\ 0 & s_{21} & r_2 q_{10}^{(2)} & - \end{array}\right)$$

RevBayes 3.4

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If you just want to see the transition probabilities and calculate a transition probability, follow the PDF

RevBayes 3.4

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If you would like to run this, mcmc_mk_covarion.Rev