

# BAYESIAN DIVERGENCE-TIME ESTIMATION

Tracy Heath

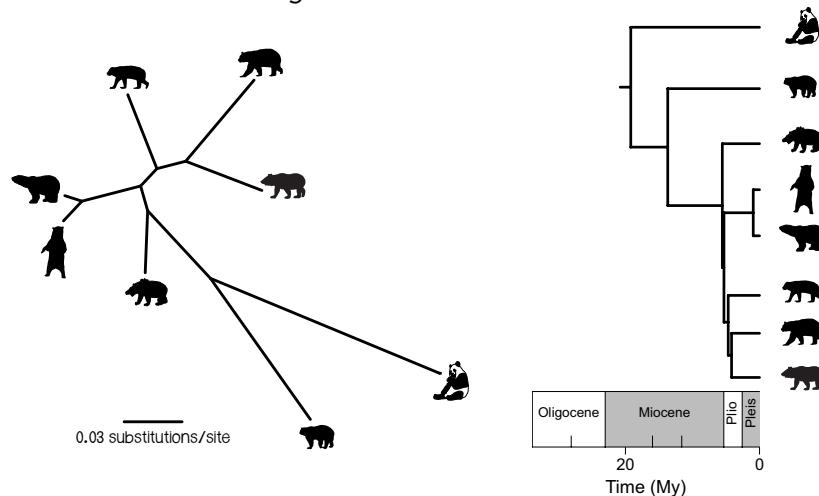
Ecology, Evolution, & Organismal Biology  
Iowa State University

 @tracy7  
<http://phyloworks.org>

2017 Phylogenetic Inference using RevBayes at NIMBioS

## A TIME-SCALE FOR EVOLUTION

Phylogenies with branch lengths proportional to time provide more information about evolutionary history than unrooted trees with branch lengths in units of substitutions/site.



(silhouette images from <http://phylopic.org>)

## OUTLINE

Theory: Divergence-time estimation

- Relaxed clock models – accounting for variation in substitution rates among lineages
- Tree models – lineage diversification and sampling

break

Practical: [Clock Models Tutorial](#) — Comparing clock models using Bayes factors

lunch

Theory: Total evidence analysis under the fossilized birth-death process

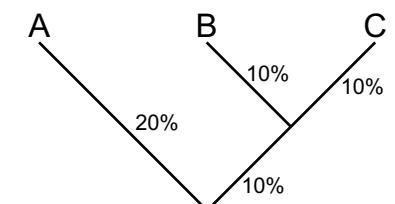
break

Practical: [Total Evidence FBD Tutorial](#) — analysis of fossil and molecular data under the FBD process

## THE GLOBAL MOLECULAR CLOCK

Assume that the rate of evolutionary change is constant over time

(branch lengths equal percent sequence divergence)

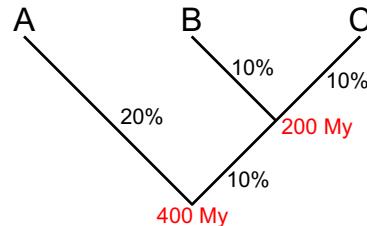


(Based on slides by Jeff Thorne; <http://statgen.ncsu.edu/thorne/compmolevo.html>)

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## THE GLOBAL MOLECULAR CLOCK

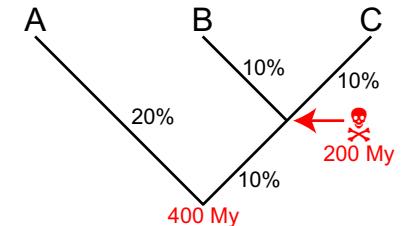
We can date the tree if we know the rate of change is 1% divergence per 10 My



(Based on slides by Jeff Thorne; <http://statgen.ncsu.edu/thorne/compmolevo.html>)

## THE GLOBAL MOLECULAR CLOCK

If we found a fossil of the MRCA of **B** and **C**, we can use it to calculate the rate of change & date the root of the tree



(Based on slides by Jeff Thorne; <http://statgen.ncsu.edu/thorne/compmolevo.html>)

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## REJECTING THE GLOBAL MOLECULAR CLOCK

Rates of evolution vary across lineages and over time

### Mutation rate:

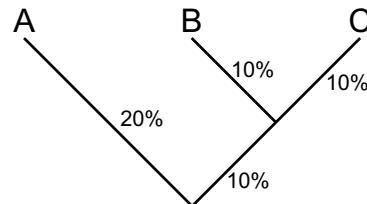
Variation in

- metabolic rate
- generation time
- DNA repair

### Fixation rate:

Variation in

- strength and targets of selection
- population sizes



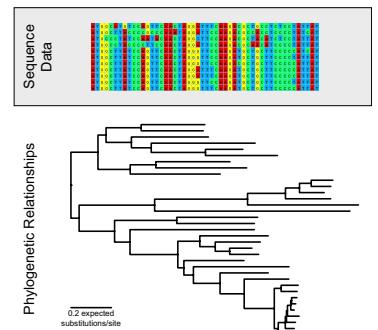
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## UNCONSTRAINED ANALYSIS

Sequence data provide information about **branch lengths**

In units of **the expected # of substitutions per site**

$$\text{branch length} = \text{rate} \times \text{time}$$

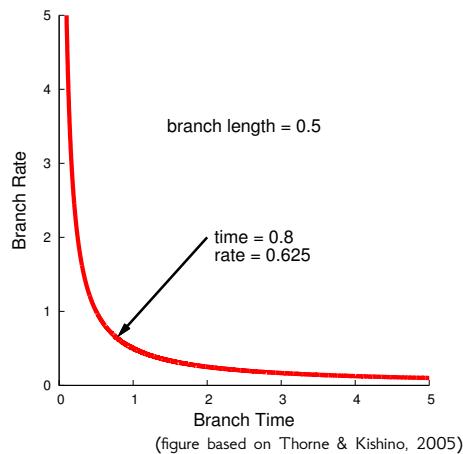


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## ESTIMATING RATE & TIME

The sequence data provide information about branch length

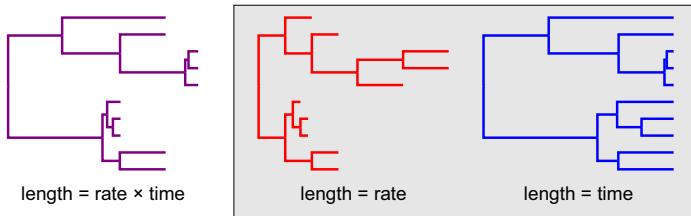
for any possible rate, there's a time that fits the branch length perfectly



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## ESTIMATING RATE & TIME

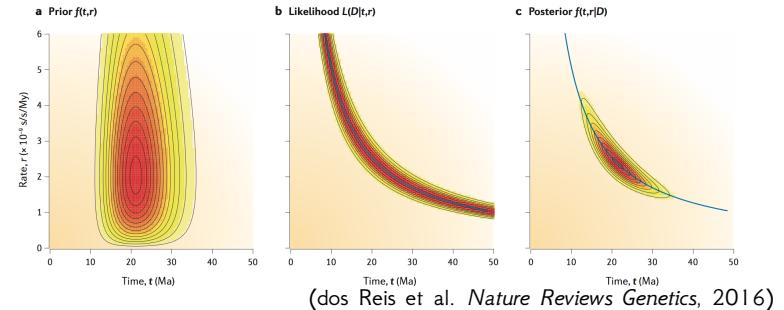
The expected # of substitutions/site occurring along a branch is the product of the substitution rate and time



Methods for dating species divergences estimate the substitution rate and time separately

## ESTIMATING RATE & TIME

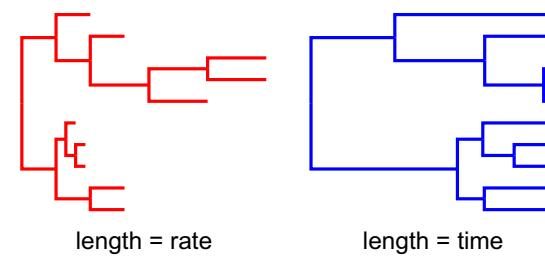
Methods for dating species divergences estimate the substitution rate and time separately



Tree-time priors for molecular phylogenies are only informative on a relative time scale

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## BAYESIAN DIVERGENCE TIME ESTIMATION



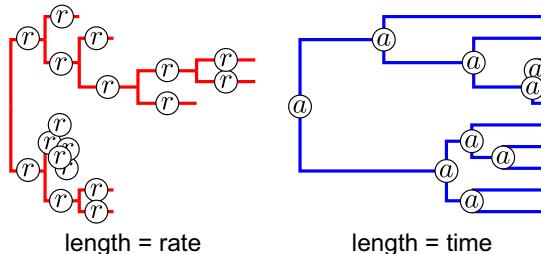
$$\mathcal{R} = (r_1, r_2, r_3, \dots, r_{2N-2})$$

$$\mathcal{A} = (a_1, a_2, a_3, \dots, a_{N-1})$$

$$N = \text{number of tips}$$

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## BAYESIAN DIVERGENCE TIME ESTIMATION



$$\mathcal{R} = (r_1, r_2, r_3, \dots, r_{2N-2})$$

$$\mathcal{A} = (a_1, a_2, a_3, \dots, a_{N-1})$$

$N$  = number of tips

## BAYESIAN DIVERGENCE TIME ESTIMATION

Posterior probability

$$f(\mathcal{R}, \mathcal{A}, \theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s, \mathcal{T} | D)$$

$\mathcal{R}$  Vector of rates on branches

$\mathcal{A}$  Vector of internal node ages

$\theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s$  Model parameters

$D$  Molecular or morphology data

$\mathcal{T}$  Tree topology

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## BAYESIAN DIVERGENCE TIME ESTIMATION

$$f(\mathcal{R}, \mathcal{A}, \theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s | D) =$$

$$\frac{f(D | \mathcal{R}, \mathcal{A}, \theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s)}{f(D)} \cdot f(\mathcal{R} | \theta_{\mathcal{R}}) \cdot f(\mathcal{A} | \theta_{\mathcal{A}}) \cdot f(\theta_s)$$

$f(D | \mathcal{R}, \mathcal{A}, \theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s)$

Likelihood

$f(\mathcal{R} | \theta_{\mathcal{R}})$

Prior on rates

$f(\mathcal{A} | \theta_{\mathcal{A}})$

Prior on node ages

$f(\theta_s)$

Prior on substitution parameters

$f(D)$

Marginal probability of the data

## MODELING RATE VARIATION

Some models describing lineage-specific substitution rate variation:

- **Global clock** (Zuckerkandl & Pauling, 1962)
- **Local clocks** (Hasegawa, Kishino & Yano 1989; Kishino & Hasegawa 1990; Yoder & Yang 2000; Yang & Yoder 2003, Drummond and Suchard 2010)
- **Punctuated rate change model** (Huelsenbeck, Larget and Swofford 2000)
- **Log-normally distributed autocorrelated rates** (Thorne, Kishino & Painter 1998; Kishino, Thorne & Bruno 2001; Thorne & Kishino 2002)
- **Mixture models on branch rates** (Heath, Holder, Huelsenbeck 2012)
- **Uncorrelated/independent rates models** (Drummond et al. 2006; Rannala & Yang 2007; Lepage et al. 2007)

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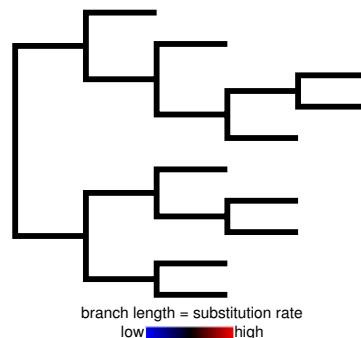
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## GLOBAL CLOCK

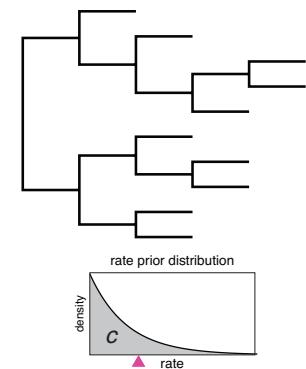
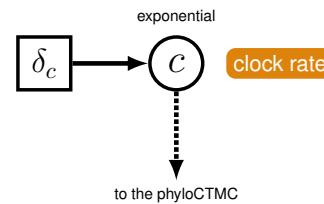
The substitution rate is constant over time

All lineages share the same rate

(Zuckerkandl & Pauling, 1962)



## GLOBAL CLOCK



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## RELAXED-CLOCK MODELS

To accommodate variation in substitution rates  
'relaxed-clock' models estimate lineage-specific substitution rates

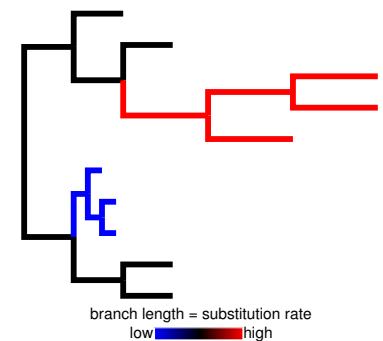
- Local clocks
- Punctuated rate change model
- Log-normally distributed autocorrelated rates
- Mixture models on branch rates
- Uncorrelated/independent rates models

## LOCAL MOLECULAR CLOCKS

Rate shifts occur infrequently over the tree

Closely related lineages have equivalent rates (clustered by sub-clades)

(Yang & Yoder 2003;  
Drummond & Suchard 2010)



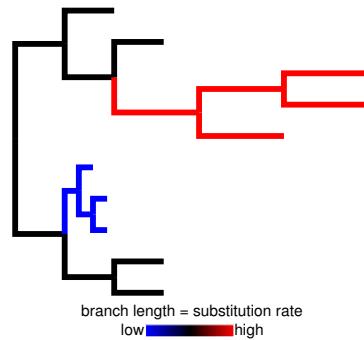
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## LOCAL MOLECULAR CLOCKS

Most methods for estimating local clocks required specifying the number and locations of rate changes *a priori*

Drummond and Suchard (2010) introduced a Bayesian method that samples over a broad range of possible *random local clocks*



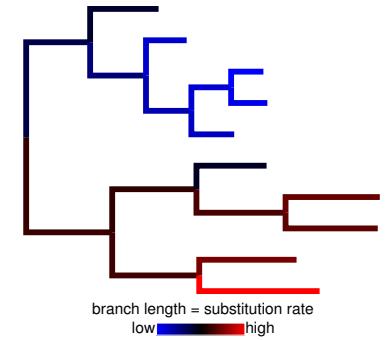
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## AUTOCORRELATED RATES

Substitution rates evolve gradually over time — closely related lineages have similar rates

The rate at a node is drawn from a lognormal distribution with a mean equal to the parent rate

Thorne, Kishino & Painter 1998;  
Kishino, Thorne & Bruno 2001



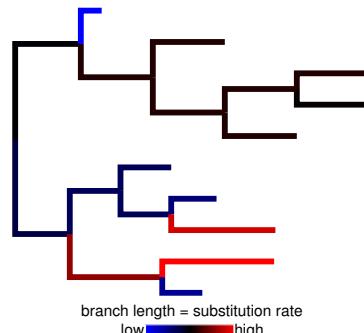
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## PUNCTUATED RATE CHANGE

Rate changes occur along lineages according to a point process

At rate-change events, the new rate is a product of the parent's rate and a  $\Gamma$ -distributed multiplier

(Huelsenbeck, Larget and Swofford 2000)



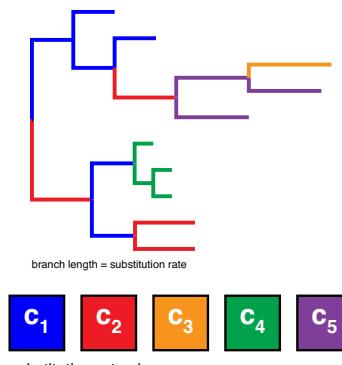
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## THE DIRICHLET PROCESS PRIOR (DPP)

A stochastic process that models data as a mixture of distributions and can identify latent classes present in the data

Random variables under the DPP informed by the data:

- the number of rate classes
- the assignment of branches to classes
- the rate value for each class



(Heath, Holder, Huelsenbeck. 2012)

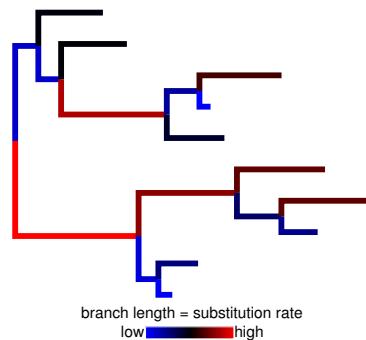


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## INDEPENDENT/UNCORRELATED RATES

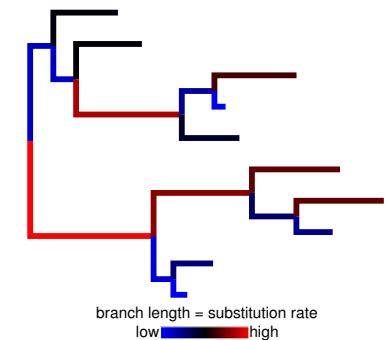
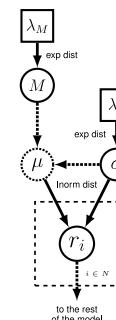
Lineage-specific rates are uncorrelated when the rate assigned to each branch is independently drawn from an underlying distribution

(Drummond et al. 2006; Rannala & Yang 2007;  
Lepage et al. 2007)



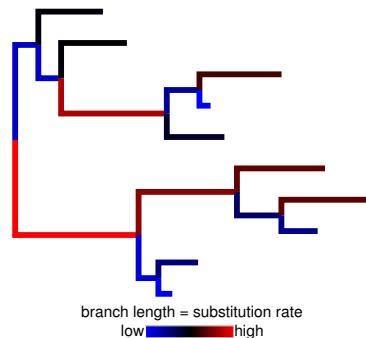
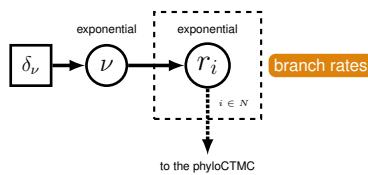
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## INDEPENDENT/UNCORRELATED RATES



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## INDEPENDENT/UNCORRELATED RATES



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## MODELING RATE VARIATION

These are only a subset of the available models for branch-rate variation

- Global clock
- Local clocks
- Punctuated rate change model
- Log-normally distributed autocorrelated rates
- Mixture models on branch rates
- Uncorrelated/independent rates models

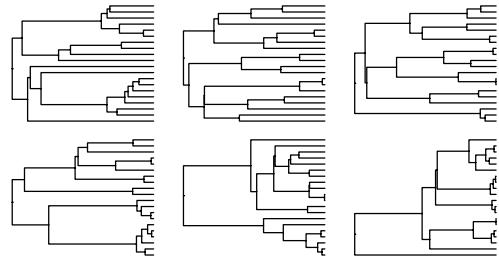
Considering model selection, uncertainty, & plausibility is **very** important for Bayesian divergence time analysis

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## PRIORS ON THE TREE AND NODE AGES

Relaxed clock Bayesian analyses require a prior distribution on time trees



Different node-age priors make different assumptions about the timing of divergence events

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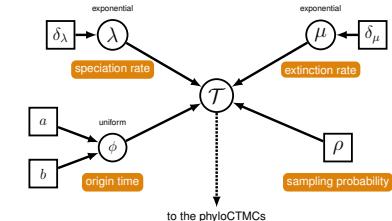
## STOCHASTIC BRANCHING PROCESSES

Node-age priors based on stochastic models of lineage diversification

### Birth-death-sampling process:

at any point in time a lineage can speciate at rate  $\lambda$  or go extinct with a rate of  $\mu$

Conditions on a probability of sampling a tip,  $\rho$  and the origin time of the process,  $\varphi$



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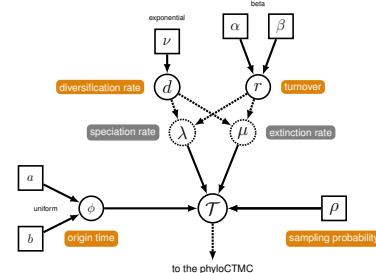
## STOCHASTIC BRANCHING PROCESSES

Node-age priors based on stochastic models of lineage diversification

### Birth-death-sampling

**process:** often the model is re-parameterized so that we are placing priors directly on the diversification rate ( $d$ ) and turnover ( $r$ ). And  $\lambda$  and  $\mu$  are deterministic nodes.

$$\lambda = \frac{d}{1-r}, \quad \mu = \frac{rd}{1-r}$$



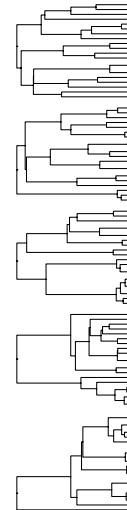
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## STOCHASTIC BRANCHING PROCESSES

Different values of  $\lambda$  and  $\mu$  lead to different trees

Bayesian inference under these models can be very sensitive to the values of these parameters

Using hyperpriors on  $\lambda$  and  $\mu$  (or  $d$  and  $r$ ) accounts for uncertainty in these hyperparameters



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## OUTLINE

Theory: Divergence-time estimation

- Relaxed clock models — accounting for variation in substitution rates among lineages
- Tree models — lineage diversification and sampling

break

Practical: [Clock Models Tutorial](#) — Comparing clock models using Bayes factors

lunch

Theory: Total evidence analysis under the fossilized birth-death process

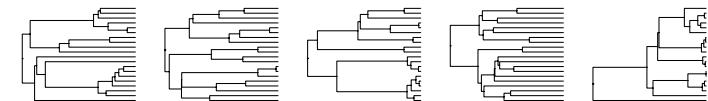
break

Practical: [Total Evidence FBD Tutorial](#) — analysis of fossil and molecular data under the FBD process

## PRIORS ON NODE TIMES

Sequence data are only informative on *relative* rates & times

Node-time priors cannot give precise estimates of *absolute* node ages



We need additional data (like fossils) to provide absolute time scale



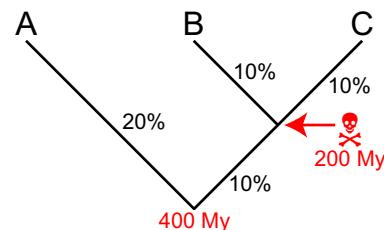
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## CALIBRATING DIVERGENCE TIMES

Fossils (or other data) are necessary to estimate *absolute* node ages

There is **no information** in the sequence data for absolute time

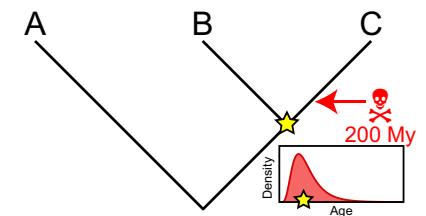
Uncertainty in the placement of fossils



## CALIBRATION DENSITIES

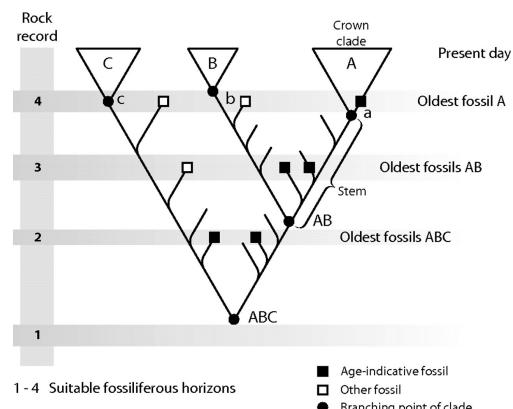
Bayesian inference is well suited to accommodating uncertainty in the age of the calibration node

Divergence times are calibrated by placing parametric densities on internal nodes offset by age estimates from the fossil record



## ASSIGNING FOSSILS TO CLADES

Misplaced fossils can affect node age estimates throughout the tree – if the fossil is older than its presumed MRCA



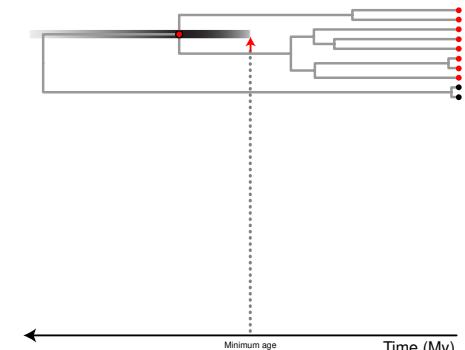
(figure from Benton & Donoghue *Mol. Biol. Evol.* 2007)

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## FOSSIL CALIBRATION

Age estimates from fossils can provide **minimum** time constraints for internal nodes

Reliable **maximum** bounds are typically unavailable



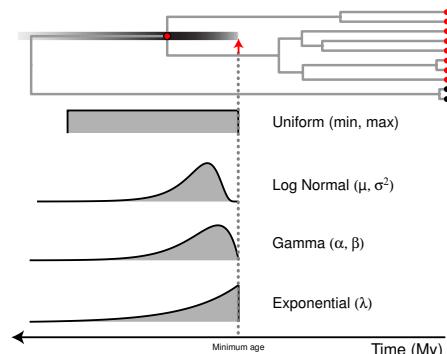
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## PRIOR DENSITIES ON CALIBRATED NODES

Common practice in Bayesian divergence-time estimation:

Parametric distributions are typically off-set by the age of the oldest fossil assigned to a clade

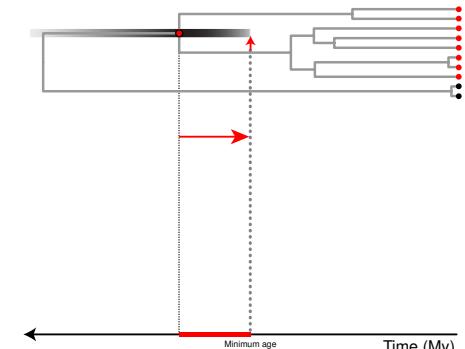
These prior densities do not (necessarily) require specification of maximum bounds



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## PRIOR DENSITIES ON CALIBRATED NODES

Describe the waiting time between the divergence event and the age of the oldest fossil



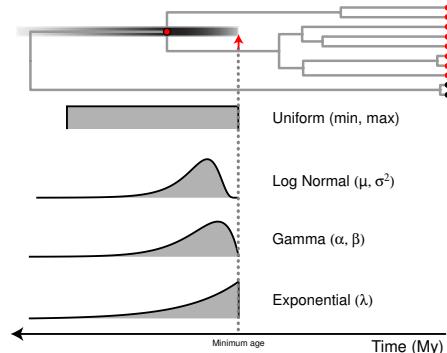
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## PRIOR DENSITIES ON CALIBRATED NODES

Common practice in Bayesian divergence-time estimation:

Estimates of absolute node ages are driven primarily by the calibration density

Specifying appropriate densities is a challenge for most molecular biologists

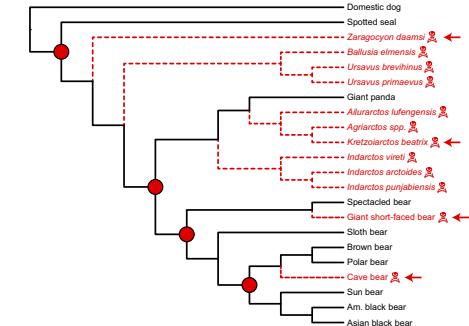


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## IMPROVING FOSSIL CALIBRATION

We would prefer to eliminate the need for *ad hoc* calibration prior densities

Calibration densities do not account for diversification of fossils



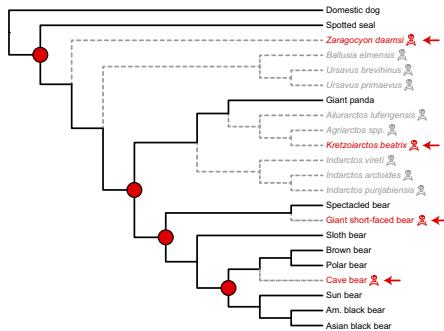
(Krause et al. BMC Evol. Biol. 2008; Abella et al. PLoS ONE 2012)

## IMPROVING FOSSIL CALIBRATION

We want to use all of the available fossils

**Example: Bears**

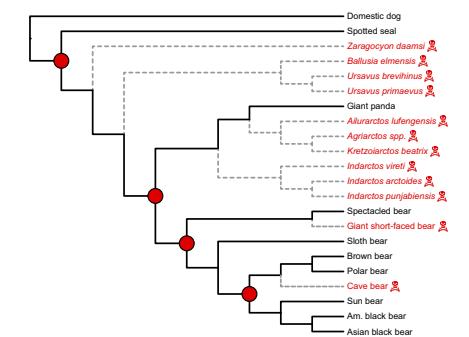
12 fossils are reduced to 4 calibration ages with calibration density methods



(Krause et al. BMC Evol. Biol. 2008; Abella et al. PLoS ONE 2012)

## IMPROVING FOSSIL CALIBRATION

Because fossils are part of the diversification process, we can combine fossil calibration with birth-death models



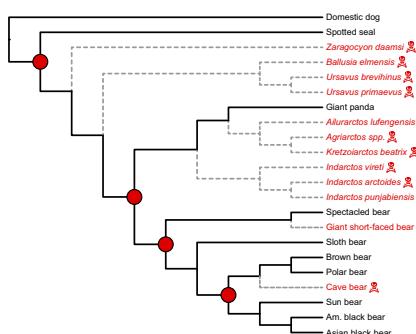
(Krause et al. BMC Evol. Biol. 2008; Abella et al. PLoS ONE 2012)

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## IMPROVING FOSSIL CALIBRATION

This relies on a branching model that accounts for **speciation, extinction, and rates of fossilization, preservation, and recovery**



(Krause et al. *BMC Evol. Biol.* 2008; Abella et al. *PLoS ONE* 2012)

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## PALEONTOLOGY & NEONTOLOGY

"Except during the interlude of the [Modern] Synthesis, there has been limited communication historically among the disciplines of evolutionary biology, particularly between students of evolutionary history (paleontologists and systematists) and those of molecular, population, and organismal biology. There has been increasing realization that barriers between these subfields must be overcome if a complete theory of evolution and systematics is to be forged."

Reaka-Kudla, M.L. & Colwell, R.: in E.C. Dudley (ed.), *The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic & Evolutionary Biology*, Discorides Press, Portland, OR, p. 16.

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## PALEONTOLOGY & NEONTOLOGY



*Biology and Philosophy* 19: 687–720, 2004.  
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**The role of fossils in phylogeny reconstruction:  
Why is it so difficult to integrate paleobiological and  
neontological evolutionary biology?**

TODD GRANTHAM

Department of Philosophy, College of Charleston, Charleston, SC 29424, USA  
(e-mail: [grantham@cofc.edu](mailto:grantham@cofc.edu))

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## COMBINING FOSSIL & EXTANT DATA

Statistical methods provide a way to integrate paleontological & neontological data

*Syst. Biol.* 50(6):913–925, 2001

### A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data

PAUL O. LEWIS

Department of Ecology and Evolutionary Biology, The University of Connecticut, Storrs, Connecticut 06269-3043, USA;  
E-mail: [paul.lewis@uconn.edu](mailto:paul.lewis@uconn.edu)

*Syst. Biol.* 61(3):973–999, 2012  
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DOI:10.1093/sysbio/sys058  
Advance Access publication on June 20, 2012

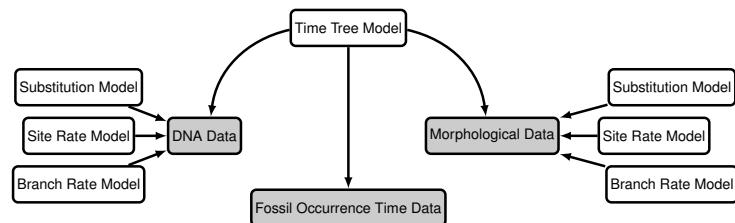
### A Total-Evidence Approach to Dating with Fossils, Applied to the Early Radiation of the Hymenoptera

FREDRIK RONQUIST<sup>1,\*</sup>, SERAINA KLOPFSTEIN<sup>1</sup>, LARS VILHELMSEN<sup>2</sup>, SUSANNE SCHULMEISTER<sup>3</sup>, DEBRA L. MURRAY<sup>4</sup>, AND ALEXANDR P. RASNITSYN<sup>5</sup>

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## COMBINING FOSSIL & EXTANT DATA

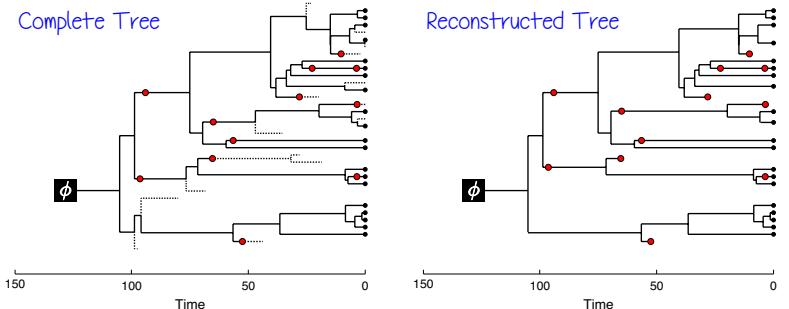
Combine models for sequence evolution, morphological change, & fossil recovery to jointly estimate the tree topology, divergence times, & lineage diversification rates



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## MODELING THE TREE & OCCURRENCE TIMES

Stadler (2010) introduced a generating model for a serially sampled time tree — this is the *fossilized birth-death process*.

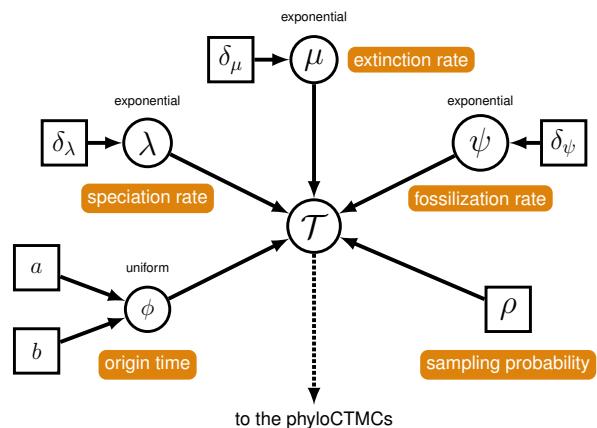


(Stadler. Journal of Theoretical Biology 2010)

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## PARAMETERS OF THE FBD

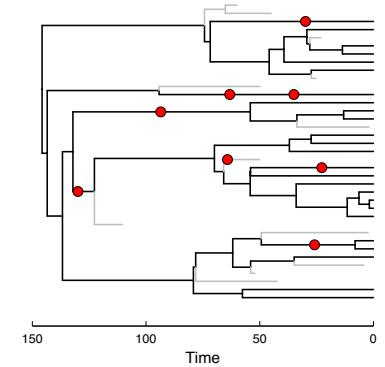
This graph shows the conditional dependence structure of the FBD model, which is a generating process for a sampled, dated time tree and fossil occurrences



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## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Recovered fossil specimens provide historical observations of the diversification process that generated the tree of extant species



(Heath, Huelsenbeck, Stadler. PNAS 2014)

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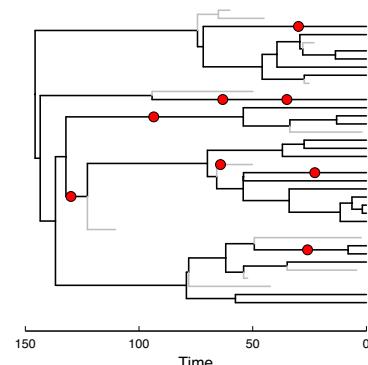
## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

The probability of the tree and fossil observations under a birth-death model with rate parameters:

$\lambda$  = speciation

$\mu$  = extinction

$\psi$  = fossilization/recovery

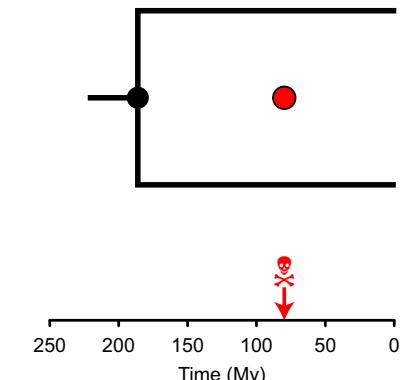


(Heath, Huelsenbeck, Stadler. PNAS 2014)

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## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

The occurrence time of the fossil indicates an observation of the birth-death process before the present

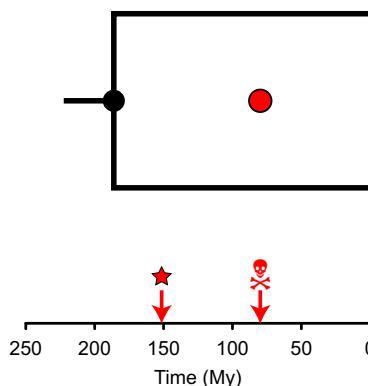


(Heath, Huelsenbeck, Stadler. PNAS 2014)

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## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

The fossil must attach to the tree at some time and to some branch:

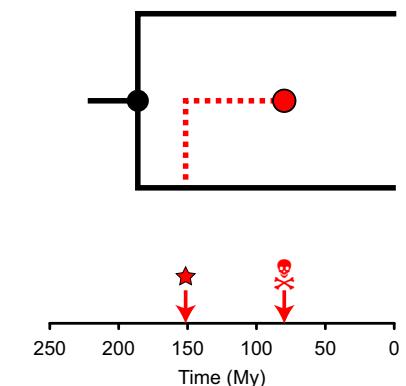


(Heath, Huelsenbeck, Stadler. PNAS 2014)

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## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

If it is the descendant of an unobserved lineage, then there is a speciation event at time

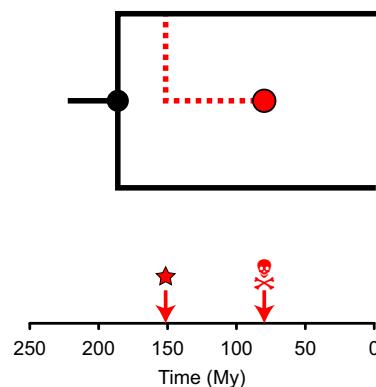


(Heath, Huelsenbeck, Stadler. PNAS 2014)

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## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

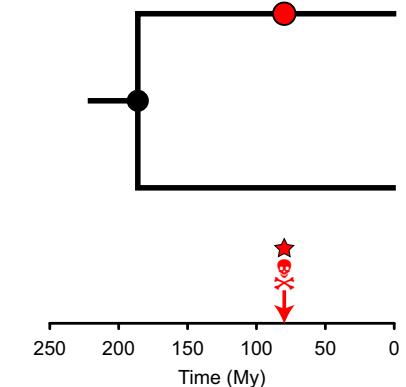
MCMC is used to propose new topological placements for the fossil



(Heath, Huelsenbeck, Stadler. PNAS 2014)

## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Using rjMCMC, we can propose  $\star = \text{💀}$ , which means that the fossil is a "sampled ancestor"



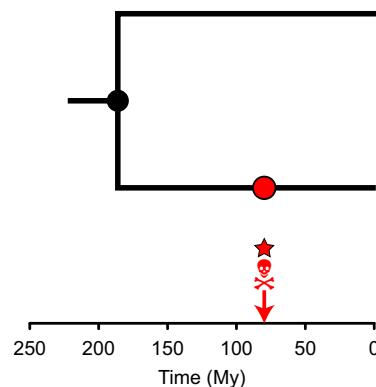
(Heath, Huelsenbeck, Stadler. PNAS 2014)

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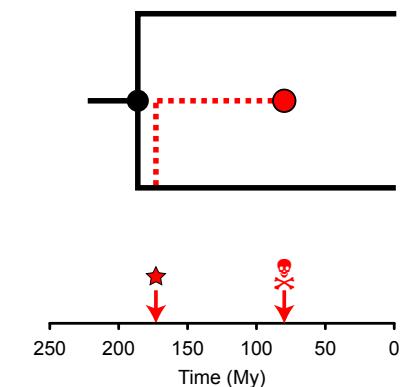
(Heath, Huelsenbeck, Stadler. PNAS 2014)

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## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

The probability of any realization of the diversification process is conditional on:

$\lambda$ ,  $\mu$ , and  $\psi$

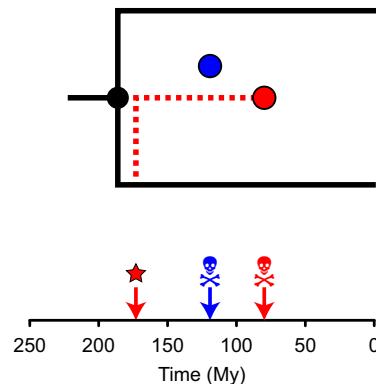


(Heath, Huelsenbeck, Stadler. PNAS 2014)

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## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

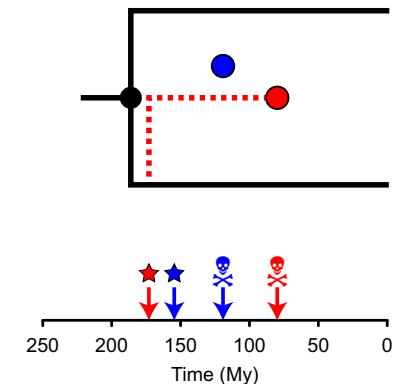
Under the **FBD**, multiple fossils are considered, even if they are descended from the same MRCA node in the extant tree



(Heath, Huelsenbeck, Stadler. PNAS 2014)

## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Given and , the new fossil can attach to the tree via speciation along either branch in the extant tree at time

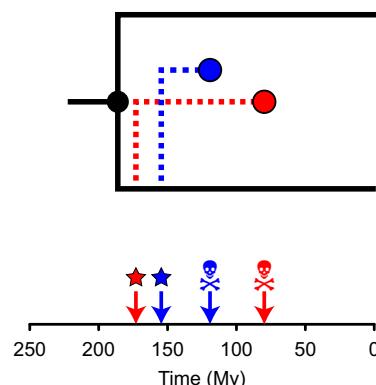


(Heath, Huelsenbeck, Stadler. PNAS 2014)

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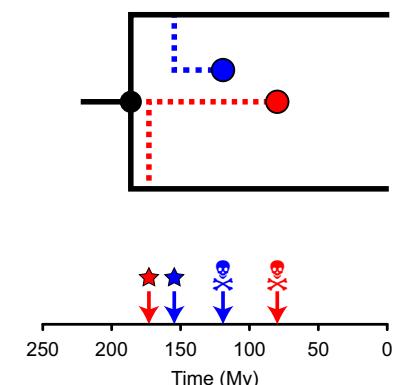


(Heath, Huelsenbeck, Stadler. PNAS 2014)

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## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Given and , the new fossil can attach to the tree via speciation along either branch in the extant tree at time

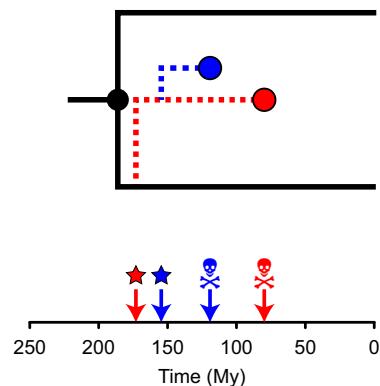


(Heath, Huelsenbeck, Stadler. PNAS 2014)

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## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

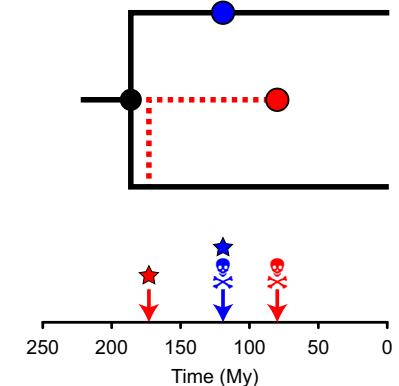
Or the unobserved branch leading to the other fossil



(Heath, Huelsenbeck, Stadler. PNAS 2014)

## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

If  $\star = \text{👤}$ , then the new fossil lies directly on a branch in the extant tree



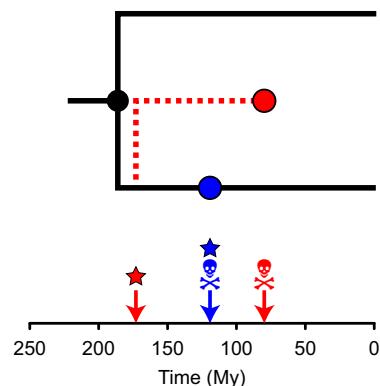
(Heath, Huelsenbeck, Stadler. PNAS 2014)

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## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

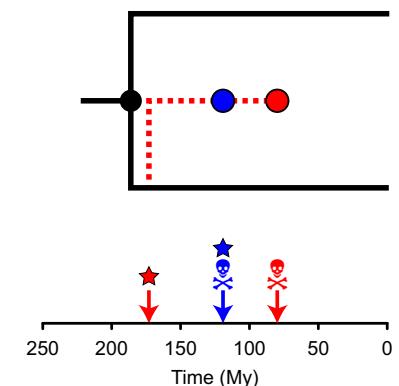
If  $\star = \text{👤}$ , then the new fossil lies directly on a branch in the extant tree



(Heath, Huelsenbeck, Stadler. PNAS 2014)

## THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Or it is an ancestor of the other sampled fossil



(Heath, Huelsenbeck, Stadler. PNAS 2014)

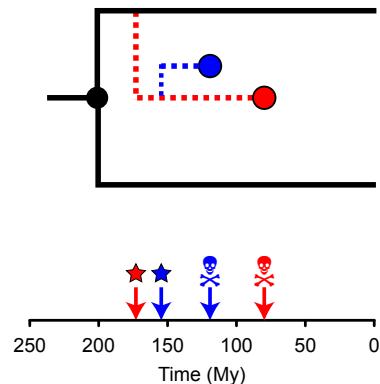
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# THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

The probability of this realization of the diversification process is conditional on:

$\lambda$ ,  $\mu$ , and  $\psi$



(Heath, Huelsenbeck, Stadler. PNAS 2014)

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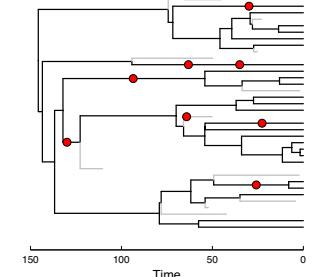
## SAMPLED ANCESTORS

Sampled lineages with sampled descendants

Paleobiology, 22(2), 1996, pp. 141–151

On the probability of ancestors in the fossil record

Mike Foote



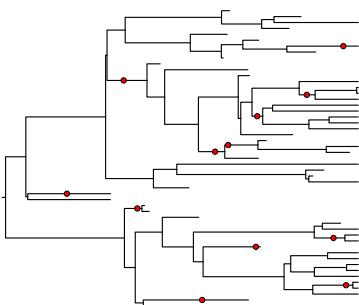
Time

There is a non-zero probability of sampling ancestor-descendant relationships from the fossil record

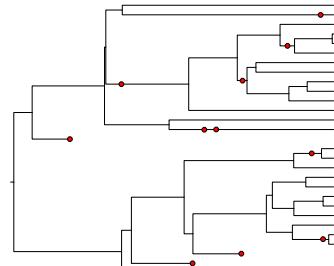
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## SAMPLED ANCESTORS

Complete FBD Tree



Reconstructed FBD Tree

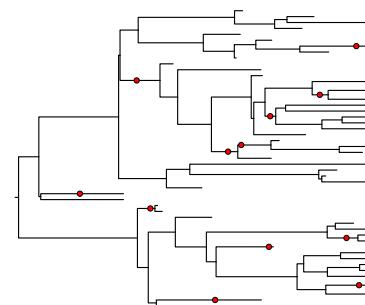


Because fossils & living taxa are assumed to come from a single diversification process, there is a non-zero probability of sampled ancestors

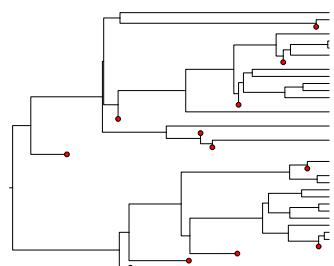
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## SAMPLED ANCESTORS

Complete FBD Tree



No Sampled Ancestor Tree

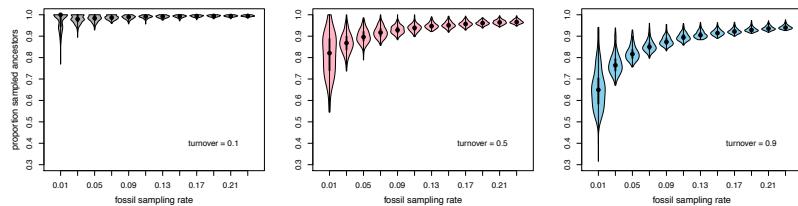


If all fossils are forced to be on separate lineages, this induces additional speciation events and will, in turn, influence rate & node-age estimates.

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## SAMPLED ANCESTORS

The proportion of sampled ancestors depends on the turnover rate, probability of sampling an extant tip, and rate of sampling fossils back in time

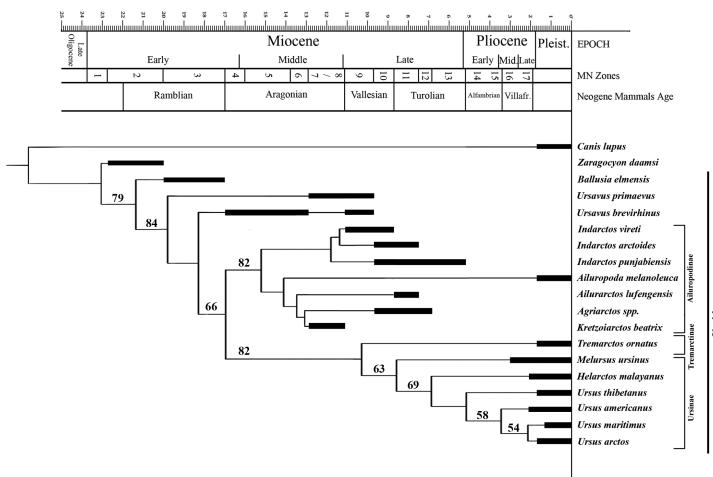


(Wright & Heath, unpublished)

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## FOSSIL RANGE DATA

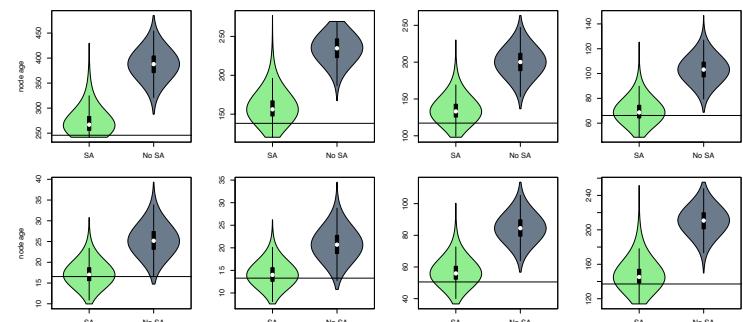
Fossil occurrence data are uncertain and are often given as stratigraphic ranges or intervals with uncertainty



(Abella et al. PLoS One 2012)

## FBD ACCOUNTS FOR SAMPLED ANCESTORS

Simulations: datasets simulated under the FBD & analyzed with or without accounting for sampled ancestors



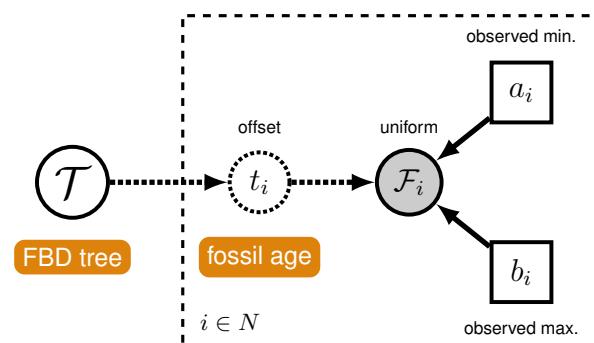
Node age estimates are too old when sampled ancestors are not allowed (and rates of diversification, turnover, and fossil recovery are also biased)

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(Wright & Heath, unpublished)

## FOSSIL AGE UNCERTAINTY

We can account for this by assuming each fossil can occur with uniform probability anywhere within a known time interval while conditioning on the FBD tree

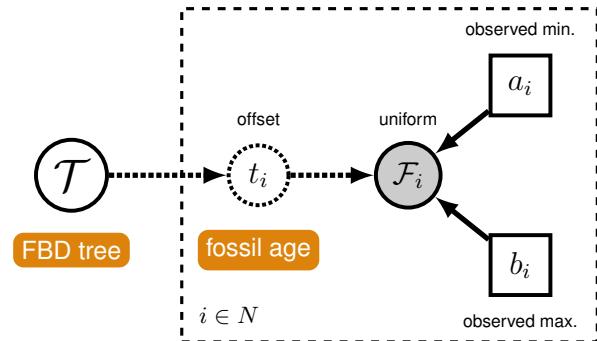


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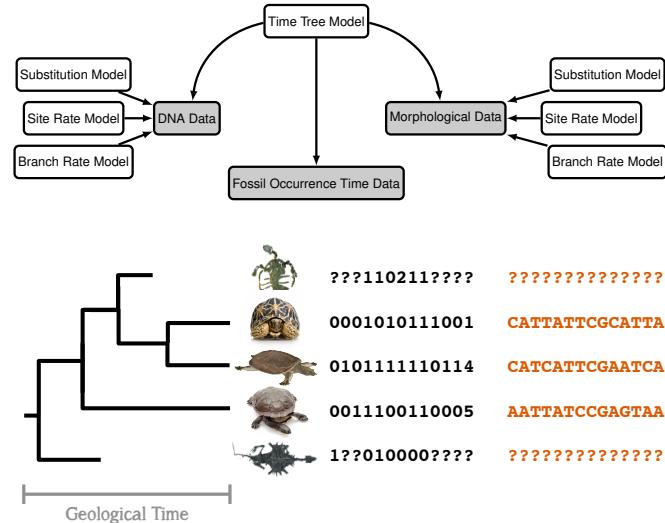
## Fossil Age Uncertainty

Here, we treat this part of the model as the *likelihood* of our fossil data given the tree parameter.



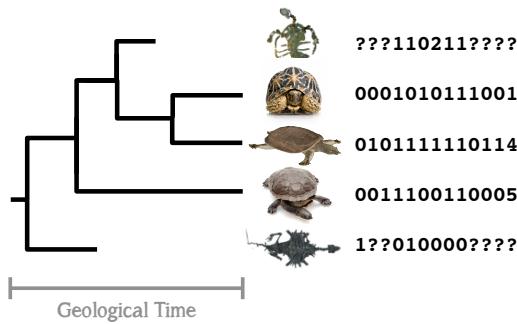
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## Combining Fossil & Extant Data



(turtle tree image by M. Landis)

## Modeling Morphological Character Change



*Syst. Biol.* 50(6):913–925, 2001

A Likelihood Approach to Estimating Phylogeny from Discrete Morphological Character Data

PAUL O. LEWIS

Department of Ecology and Evolutionary Biology, The University of Connecticut, Storrs, Connecticut 06269-3043, USA;  
E-mail: paul.lewis@uconn.edu

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(turtle tree image by M. Landis)

## Modeling Morphological Character Change

### The Lewis Mk model

Assumes a character can take  $k$  states

Transition rates between states are equal (symmetric)

T1	0
T2	0
T3	1
T4	2
T5	2
T6	1
T7	1

$$Q = \alpha \begin{bmatrix} 1-k & 1 & \dots & 1 \\ \vdots & 1-k & \dots & 1 \\ \vdots & \vdots & \ddots & \vdots \\ 1 & 1 & \dots & 1-k \end{bmatrix}$$

(Lewis. *Systematic Biology* 2001)

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# MODELING MORPHOLOGICAL CHARACTER CHANGE

## The Lewis Mk model

In the tutorial, all characters are binary, where  $k = 2$

$$Q = \alpha \begin{bmatrix} 1 - k & 1 \\ 1 & 1 - k \end{bmatrix}$$

This is a 'Jukes-Cantor' model on 2 states

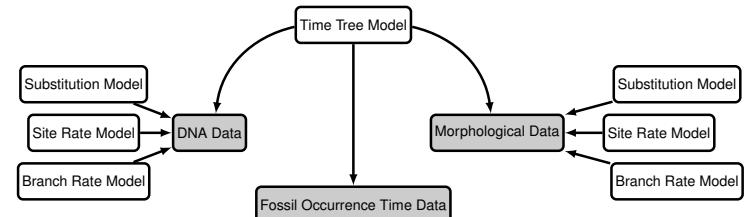
<b>T1</b>	<b>0</b>
<b>T2</b>	<b>1</b>
<b>T3</b>	<b>1</b>
<b>T4</b>	<b>1</b>
<b>T5</b>	<b>1</b>
<b>T6</b>	<b>0</b>
<b>T7</b>	<b>1</b>

(Lewis. *Systematic Biology* 2001)

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# "TOTAL-EVIDENCE" ANALYSIS

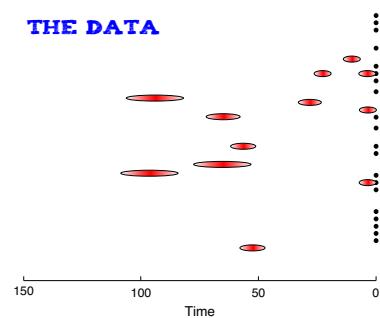
Integrating models of molecular and morphological evolution with improved tree priors enables joint inference of the tree topology (extant & extinct) and divergence times



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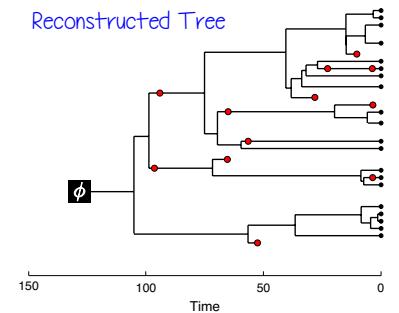
## "TOTAL-EVIDENCE" ANALYSIS

Allows us to estimate the reconstructed tree of our sampled fossils and extant taxa along with the diversification dynamics and rates of molecular and morphological evolution



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Allows us to estimate the reconstructed tree of our sampled fossils and extant taxa along with the diversification dynamics and rates of molecular and morphological evolution

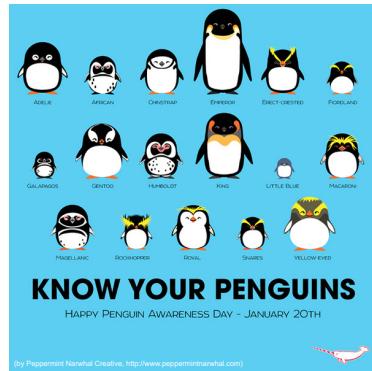


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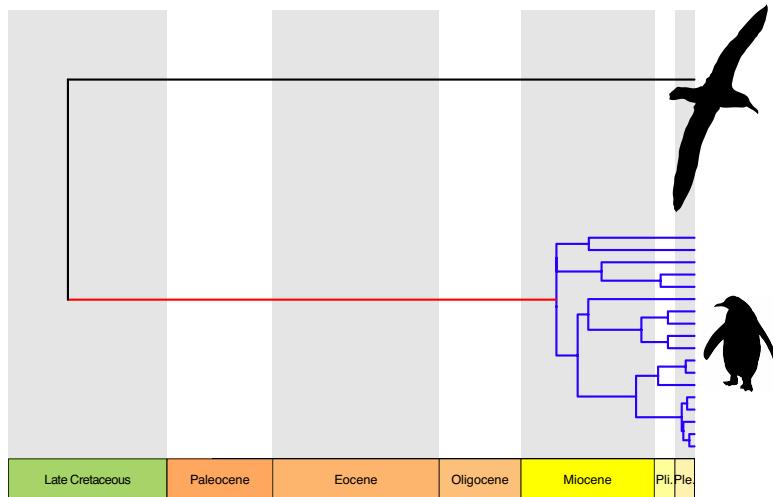
## PENGUIN DIVERSITY IN DEEP TIME

How does our understanding of penguin evolution improve when we consider both extant and fossil taxa?



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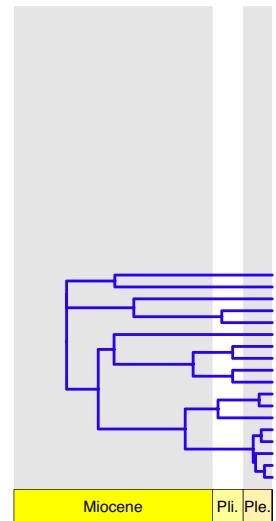
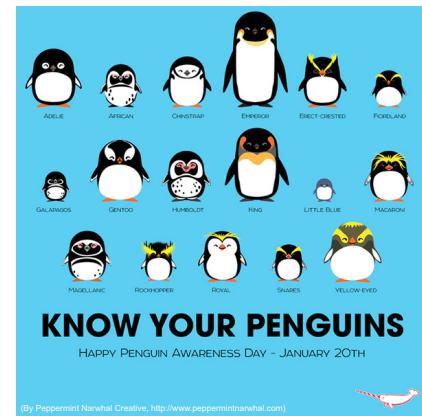
## PENGUIN DIVERSITY



(silhouette images from <http://phylopic.org>)

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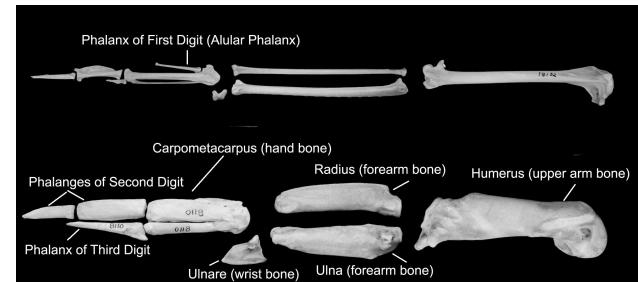
## PENGUIN DIVERSITY



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## WHAT MAKES A PENGUIN A PENGUIN?

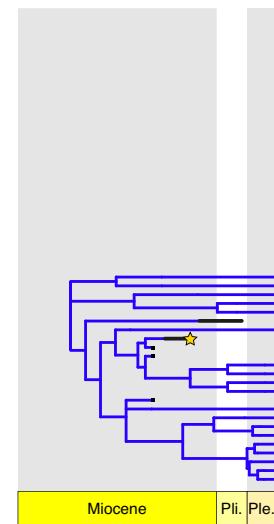
Flattened, solid wing-bones



(image courtesy of D. Ksepka <https://fossilpenguins.wordpress.com>)

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## Fossil Penguin Diversity



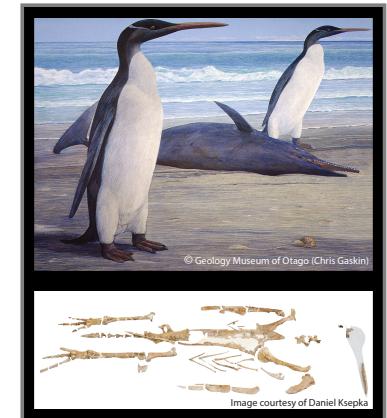
(*S. urbinai* holotype fossil, 5–7 MYA, image by Martin Chávez)

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## Penguins in the Oligocene

### Kairuku

- ~1.5 m tall
- slender, with narrow bill
- scapula & pygostyle are more similar to non-penguins
- ~27 Mya



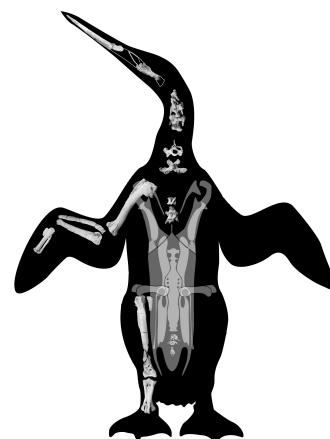
(Ksepka, Fordyce, Ando, & Jones, *J. Vert. Paleo.* 2012)

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## Penguins in the Paleocene

### Waimanu

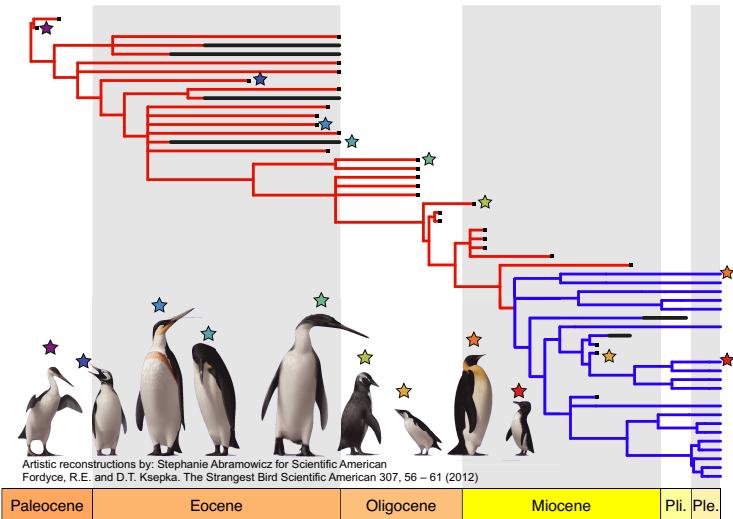
- oldest known penguin species
- intermediate wing morphology
- ~58–61.6 Mya



(Slack et al., *Mol. Biol. Evol.* 2006)

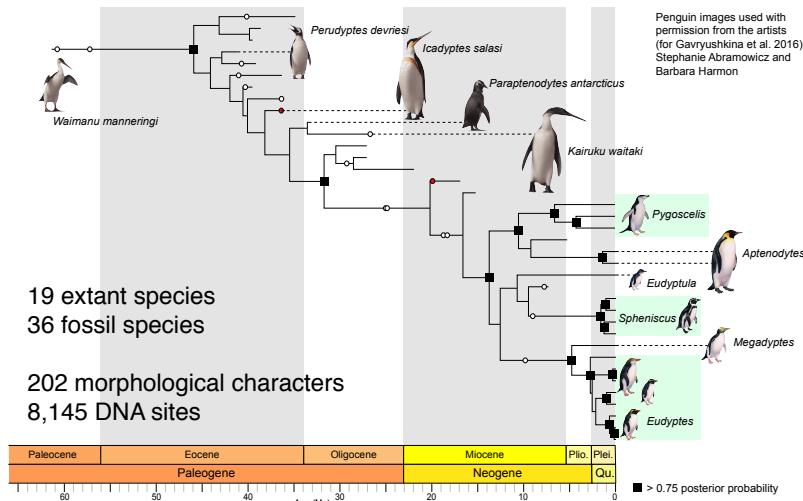
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## Penguin Diversity in Deep Time



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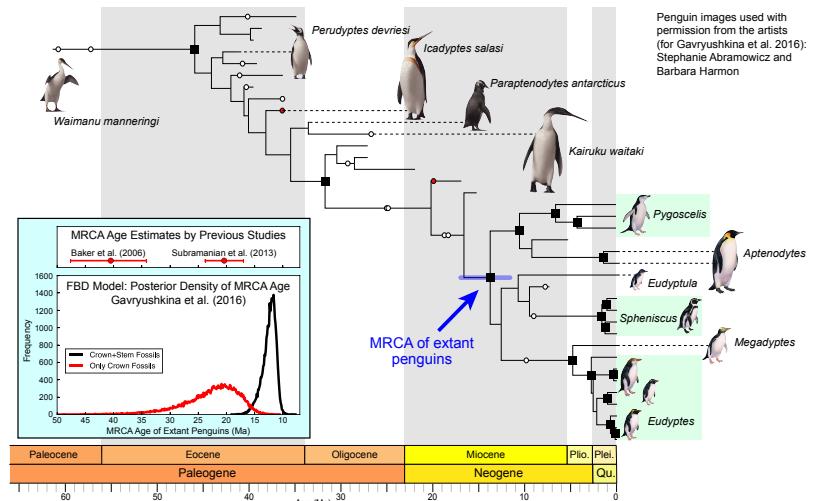
## PENGUIN DIVERSITY IN DEEP TIME



(Gavryushkina, Heath, Ksepka, Welch, Stadler, Drummond. *Syst. Biol.*, in press. doi:10.1093/syb060)

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## PENGUIN DIVERSITY IN DEEP TIME

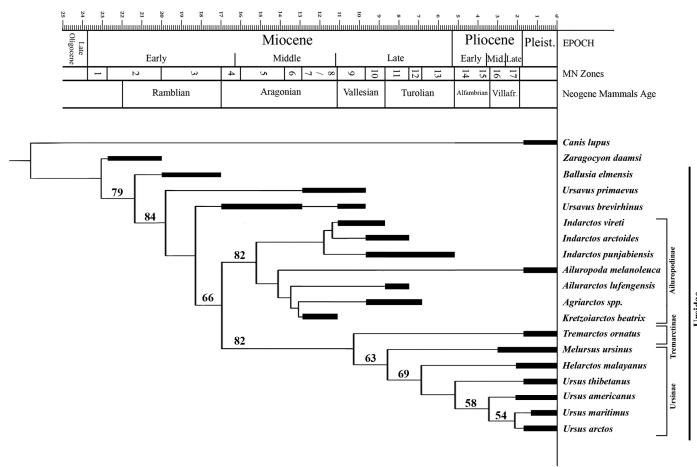


(Gavryushkina, Heath, Ksepka, Welch, Stadler, Drummond. *Syst. Biol.*, in press. doi:10.1093/syb060)

Tracy A. Heath (2017 RevBayes Workshop at NIMBioS, Knoxville, TN)

## STRATIGRAPHIC RANGE DATA & PHYLOGENIES

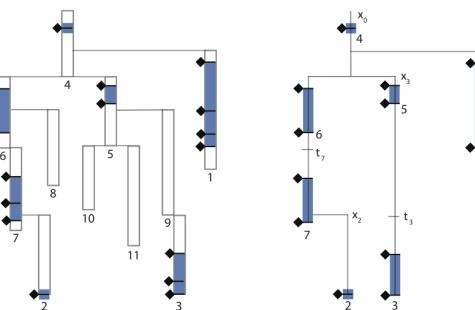
For many clades, data for fossil lineages are stratigraphic ranges representing multiple occurrences over time



(Abella et al. PLoS One 2012)

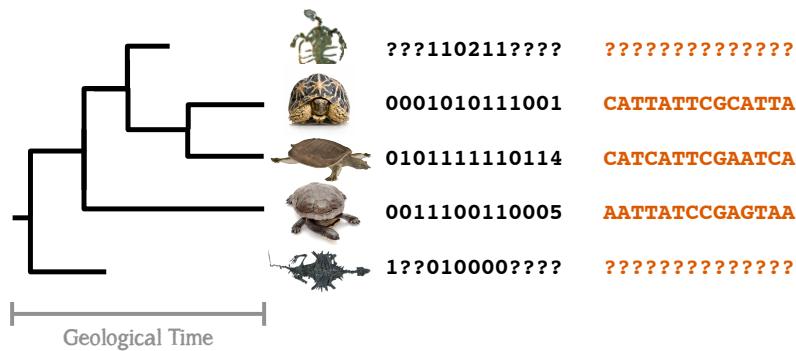
## STRATIGRAPHIC RANGE DATA & PHYLOGENIES

We are developing models to account for the structure of the fossil record and the nature of paleontological data



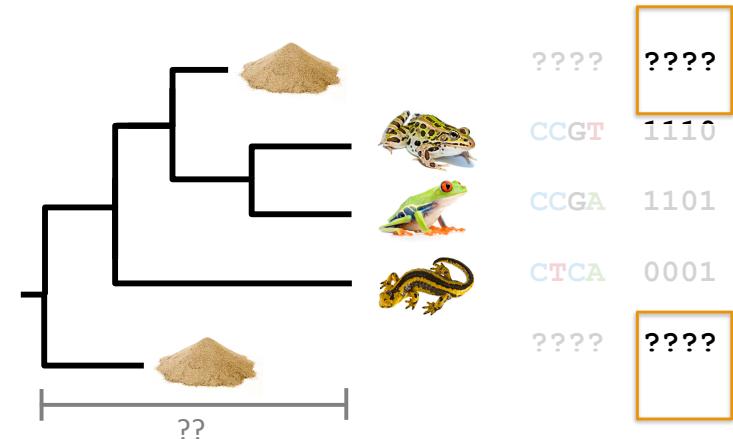
Stadler, Gavryushkina, Warnock, Drummond, Heath  
arXiv preprint: <https://arxiv.org/abs/1706.10106>

## MOLECULES + MORPHOLOGY + FOSSILS



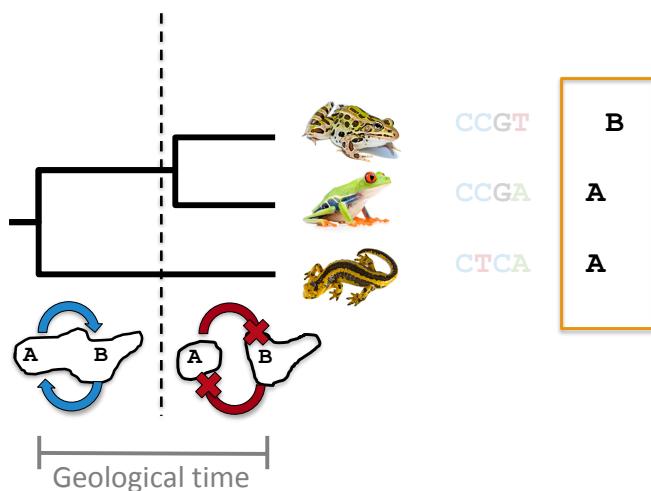
(based on slides by M. Landis)

...but I study amphibians...



(slides courtesy of M. Landis, <http://bitly/2alHqB4>)

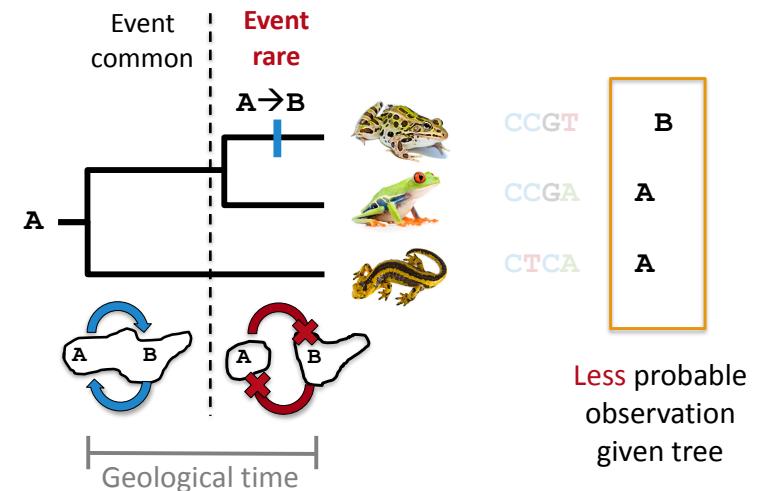
## Molecules + biogeography + paleogeography



+ Paleogeography Landis, 2016

(slides courtesy of M. Landis; <http://bitly/2alHqB4>)

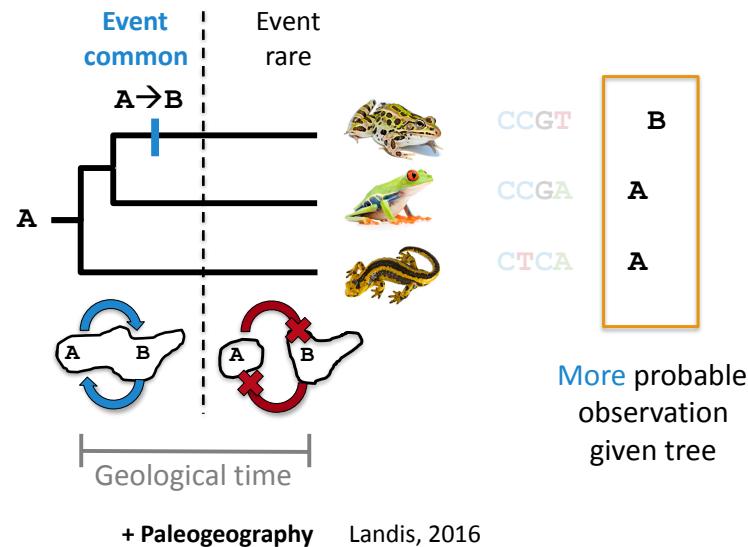
Events should occur *before* areas split



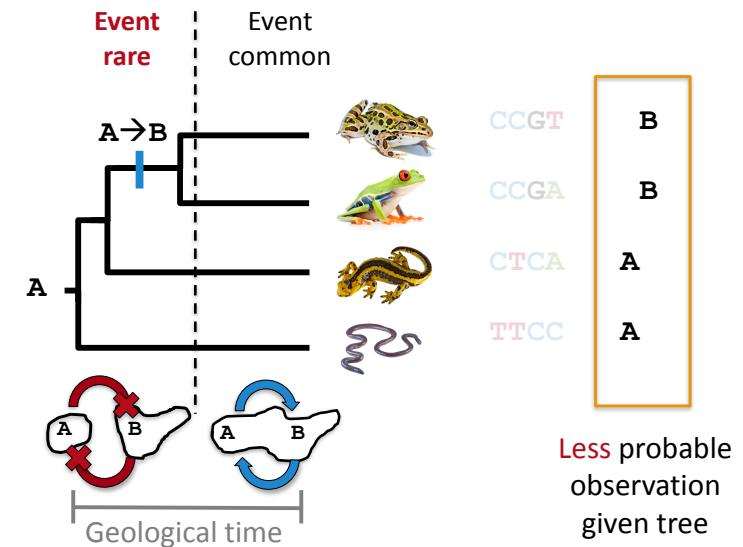
+ Paleogeography Landis, 2016

(slides courtesy of M. Landis; <http://bitly/2alHqB4>)

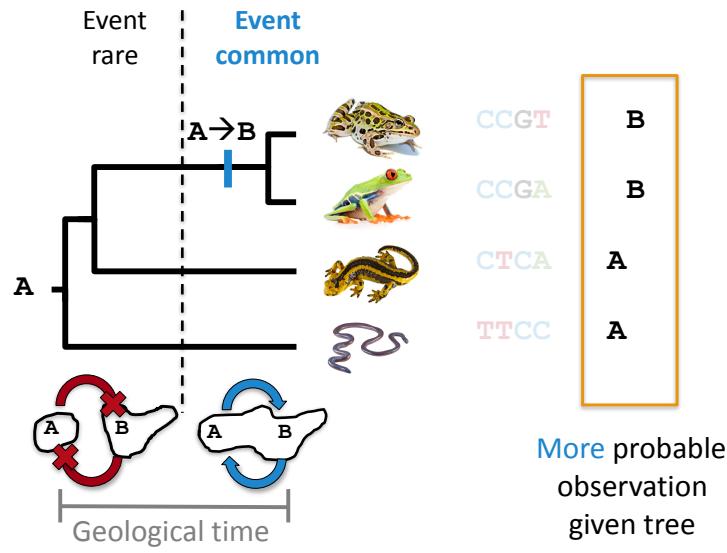
## Events should occur *before areas split*



## Events should occur *after areas merge*



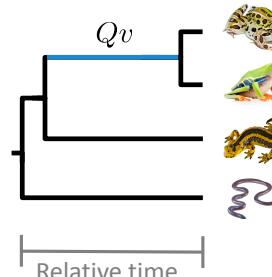
## Events should occur *after areas merge*



## BIOGEOGRAPHIC DATING

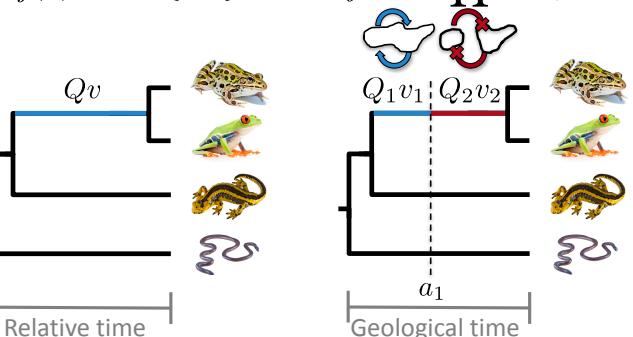
### Constant Model

$$P_{ij}(v) = \exp\{Qv\}$$



### Epoch Model

$$P_{ij}(v) = \prod \exp\{Q_k v_k\}$$



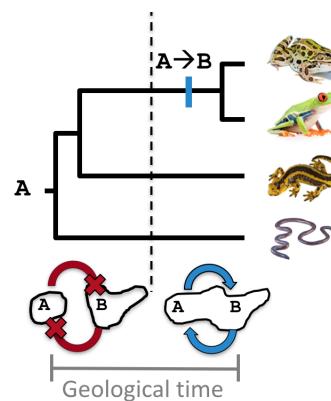
**Epoch model**    Ree et al., 2005  
Bielejec et al., 2014

(image by M. Landis)

## BIOGEOGRAPHIC DATING

### Fossil-free calibration

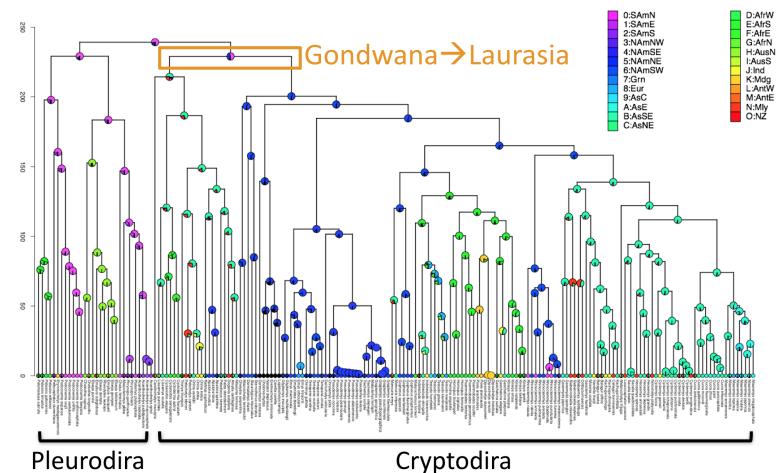
- data: molecular sequences
- data: biogeographic ranges
- empirical paleogeographic model that alters the rates of biogeographic change over time



Landis. 2017. "Biogeographic Dating of Speciation Times Using Paleogeographically Informed Processes". *Systematic Biology*  
doi: [10.1093/sysbio/syw040](https://doi.org/10.1093/sysbio/syw040).

## DATING + ANCESTRAL AREA RECONSTRUCTION

### Ancestral area estimates (+G)



(image by M. Landis)

## OUTLINE

Theory: Divergence-time estimation

- Relaxed clock models — accounting for variation in substitution rates among lineages
- Tree models — lineage diversification and sampling

break

Practical: [Clock Models Tutorial](#) — Comparing clock models using Bayes factors

lunch

Theory: Total evidence analysis under the fossilized birth-death process

break

Practical: [Total Evidence FBD Tutorial](#) — analysis of fossil and molecular data under the FBD process