Bayesian Divergence Time Estimation

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OUTLINE

Overview of divergence time estimation

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

break

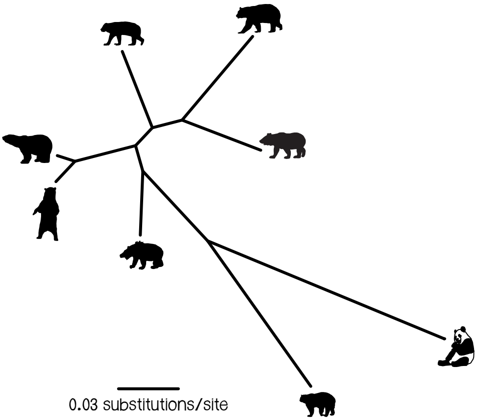
BEAST v2 Tutorial — Divergence-time estimation under birth-death processes

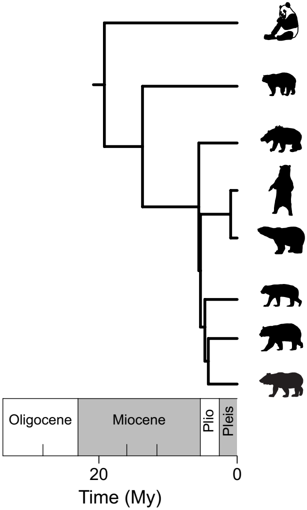
- Dating Bear Divergence Times with the Fossilized Birth-Death Process

dinner

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.





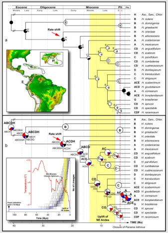
(silhouette images from `http://phylopic.org`)

A Time-Scale for Evolution

Phylogenetic divergence-time estimation

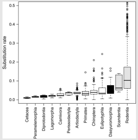
- What was the spacial and climatic environment of ancient angiosperms?
- How has mammalian body-size changed over time?
- How has the infection rate of HCV in Egypt changed over time?
- Is diversification in Caribbean anoles correlated with ecological opportunity?
- How has the rate of molecular evolution changed across the Tree of Life?

Historical biogeography



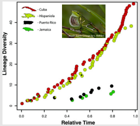
(Antonelli & Sanmartin. Syst. Biol. 2011)

Molecular evolution



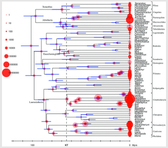
(Nabholz, Glemin, Galtier. MBE 2008)

Diversification



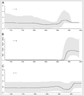
(Mahler, Revell, Glor, & Losos. Evolution 2010)

Trait evolution



(Lartillot & Delsuc. Evolution 2012)

Epidemiology



(Stadler et al. PNAS 2013)

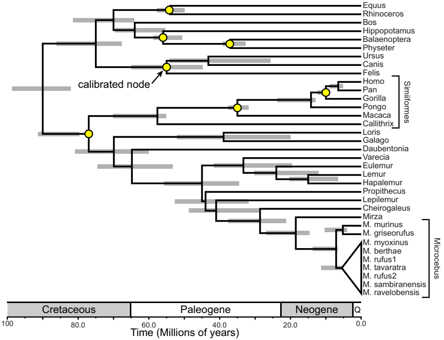
DIVERGENCE TIME ESTIMATION

Goal: Estimate the ages of interior nodes to understand the timing and rates of evolutionary processes

Model how rates are distributed across the tree

Describe the distribution of speciation events over time

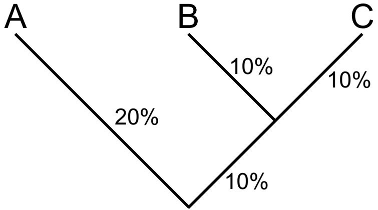
External calibration information for estimates of absolute node times



THE GLOBAL MOLECULAR CLOCK

Assume that the rate of evolutionary change is constant over time

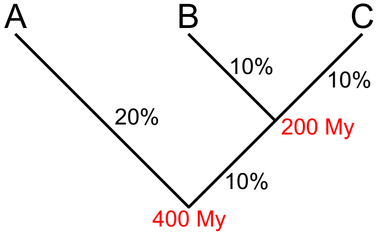
(branch lengths equal percent sequence divergence)



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

THE GLOBAL MOLECULAR CLOCK

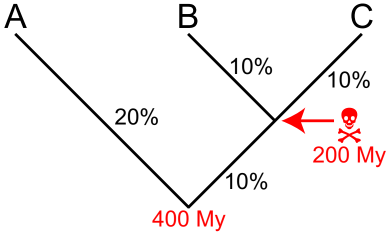
We can date the tree if we know the rate of change is 1% divergence per 10 My



(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)

REJECTING THE GLOBAL MOLECULAR CLOCK

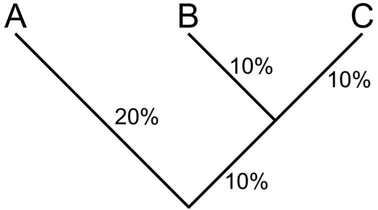
Rates of evolution vary across lineages and over time

Mutation rate:
Variation in

- metabolic rate
- generation time
- DNA repair

Fixation rate:
Variation in

- strength and targets of selection
- population sizes

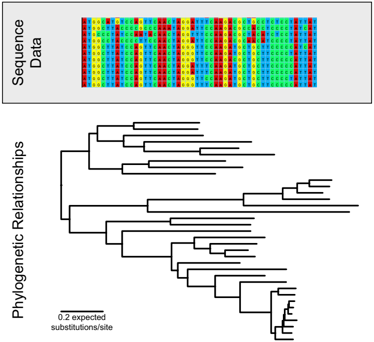


UNCONSTRAINED ANALYSIS

Sequence data provide information about **branch lengths**

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

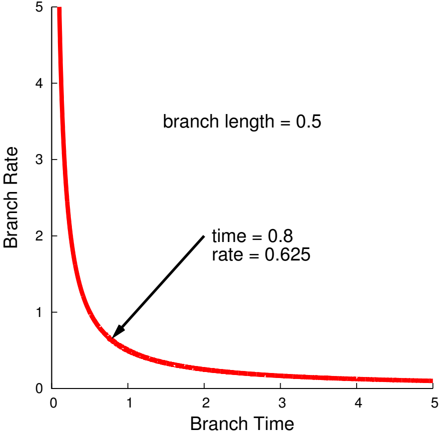
branch length = rate × time



RATE AND TIME

The sequence data provide information about branch length

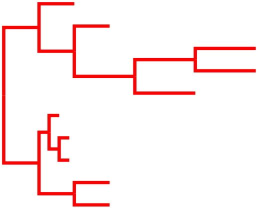
for any possible rate, there's a time that fits the branch length perfectly

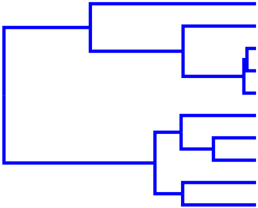


Methods for dating species divergences estimate the substitution rate and time separately

(based on Thorne & Kishino, 2005)

BAYESIAN DIVERGENCE TIME ESTIMATION


length = rate

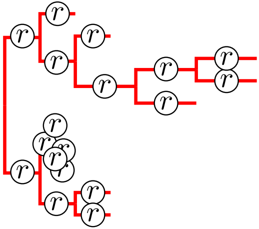

length = time

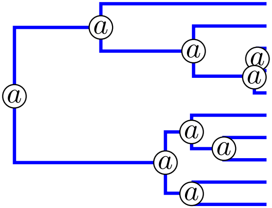
$$\mathcal{R} = (r_1, r_2, r_3, \ldots, r_{2N-2})$$

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

N = number of tips

BAYESIAN DIVERGENCE TIME ESTIMATION


length = rate


length = time

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N = number of tips

BAYESIAN DIVERGENCE TIME ESTIMATION

Posterior probability

$$f\left(\boldsymbol{\mathcal{R}}, \boldsymbol{\mathcal{A}}, \theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s \mid D, \Psi\right)$$

$\boldsymbol{\mathcal{R}}$	Vector of rates on branches
$\boldsymbol{\mathcal{A}}$	Vector of internal node ages
$\theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s$	Model parameters
D	Sequence data
Ψ	Tree topology

BAYESIAN DIVERGENCE TIME ESTIMATION

$$f(\boldsymbol{\mathcal{R}}, \boldsymbol{\mathcal{A}}, \theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s \mid D) \;=$$

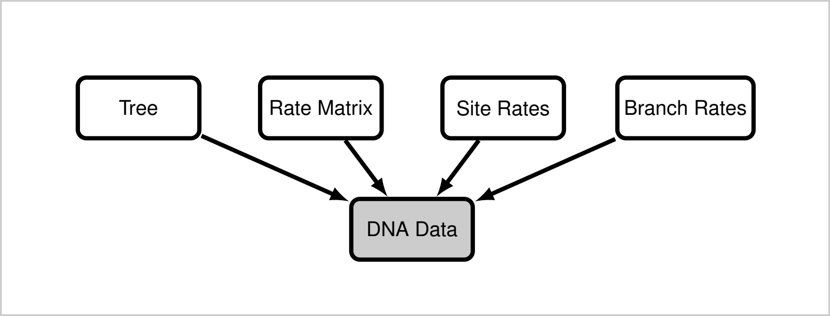
$$\frac{f\,(D \mid \boldsymbol{\mathcal{R}}, \boldsymbol{\mathcal{A}}, \theta_s)\; f(\boldsymbol{\mathcal{R}} \mid \theta_{\mathcal{R}})\; f(\boldsymbol{\mathcal{A}} \mid \theta_{\mathcal{A}})\, f(\theta_s)}{f(D)}$$

$f(D \mid \boldsymbol{\mathcal{R}}, \boldsymbol{\mathcal{A}}, \theta_{\mathcal{R}}, \theta_{\mathcal{A}}, \theta_s)$	Likelihood
$f(\boldsymbol{\mathcal{R}} \mid \theta_{\mathcal{R}})$	Prior on rates
$f(\boldsymbol{\mathcal{A}} \mid \theta_{\mathcal{A}})$	Prior on node ages
$f(\theta_s)$	Prior on substitution parameters
$f(D)$	Marginal probability of the data

BAYESIAN DIVERGENCE TIME ESTIMATION

Estimating divergence times relies on 2 main elements:

- Branch-specific rates: $f(\boldsymbol{\mathcal{R}} \mid \theta_{\mathcal{R}})$
- Node ages & Topology: $f(\boldsymbol{\mathcal{A}} \mid \theta_{\mathcal{A}})$



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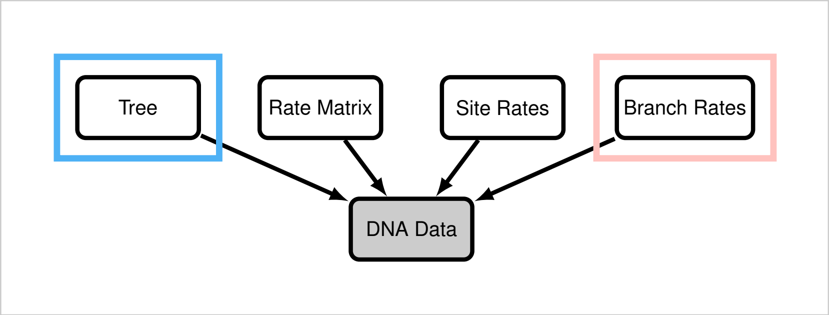


MODELING RATE VARIATION

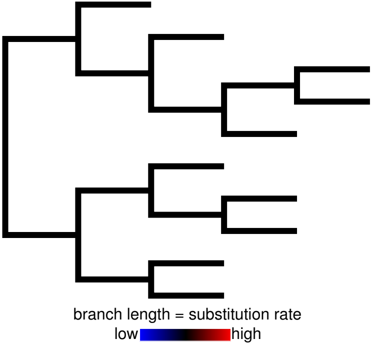
Some models describing lineage-specific substitution rate variation:

- **Global molecular clock** (Zuckerkandl & Pauling, 1962)
- **Local molecular 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)
- **Uncorrelated/independent rates models** (Drummond et al. 2006; Rannala & Yang 2007; Lepage et al. 2007)
- **Mixture models on branch rates** (Heath, Holder, Huelsenbeck 2012)

GLOBAL MOLECULAR CLOCK

The substitution rate is constant over time

All lineages share the same rate



(Zuckerkandl & Pauling, 1962)

RELAXED-CLOCK MODELS

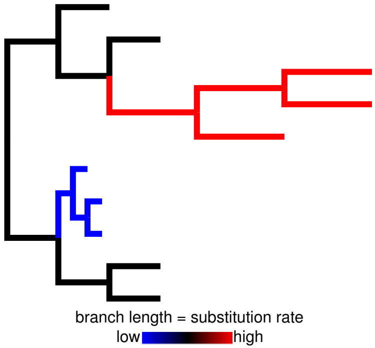
To accommodate variation in substitution rates 'relaxed-clock' models estimate lineage-specific substitution rates

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

LOCAL MOLECULAR CLOCKS

Rate shifts occur infrequently over the tree

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

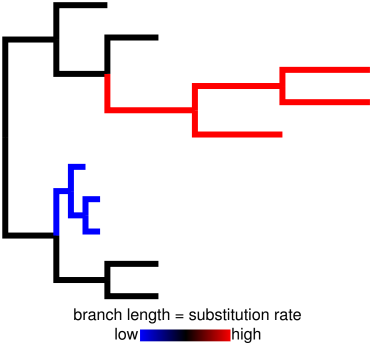


(Yang & Yoder 2003, Drummond and Suchard 2010)

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*

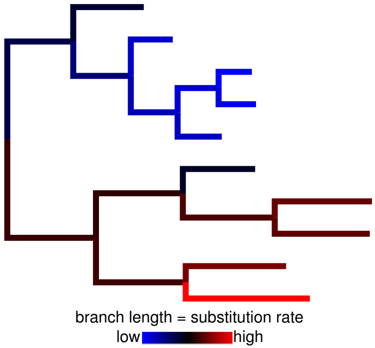


(Yang & Yoder 2003, Drummond and Suchard 2010)

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 (geometric brownian motion)

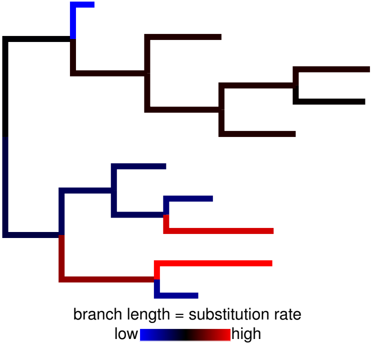


(Thorne, Kishino & Painter 1998; Kishino, Thorne & Bruno 2001)

PUNCTUATED RATE CHANGE

Rate changes occur along lineages according to a point process

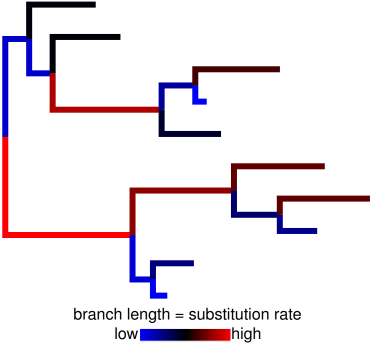
At rate-change events, the new rate is a product of the parent's rate and a Γ-distributed multiplier



(Huelsenbeck, Larget and Swofford 2000)

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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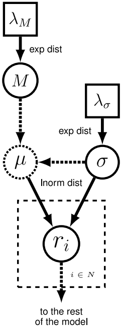
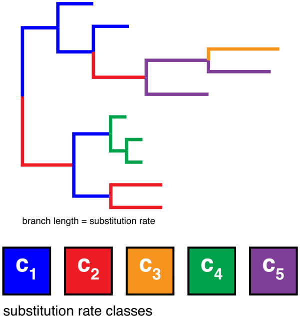


(Drummond et al. 2006; Rannala & Yang 2007; Lepage et al. 2007)

INFINITE MIXTURE MODEL

Dirichlet process prior: Branches are partitioned into distinct rate categories

The number of rate categories and assignment of branches to categories are random variables under the model



(Heath, Holder, Huelsenbeck. 2012 *MBE*)

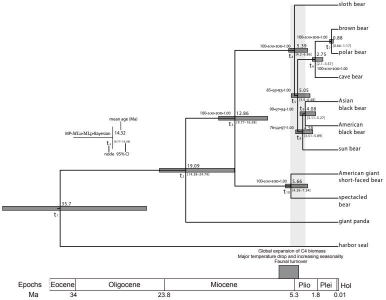
MODELING RATE VARIATION

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

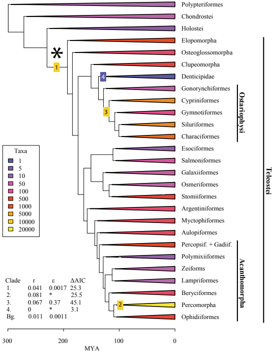
- **Global molecular clock**
- **Local molecular clocks**
- **Punctuated rate change model**
- **Log-normally distributed autocorrelated rates**
- **Uncorrelated/independent rates models**
- **Dirchlet process prior**

MODELING RATE VARIATION

Are our models appropriate across all data sets?



Krause et al., 2008. Mitochondrial genomes reveal an explosive radiation of extinct and extant bears near the Miocene-Pliocene boundary. BMC Evol. Biol. 8.



Clade	r	ε	ΔAIC
1.	0.041	0.0017	25.3
2.	0.081	*	25.5
3.	0.067	0.37	45.1
4.	0	*	3.1
Bg.	0.011	0.0011	

Santini et al., 2009. Did genome duplication drive the origin of teleosts? A comparative study of diversification in ray-finned fishes. BMC Evol. Biol. 9.

MODELING RATE VARIATION

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

- **Global molecular clock**
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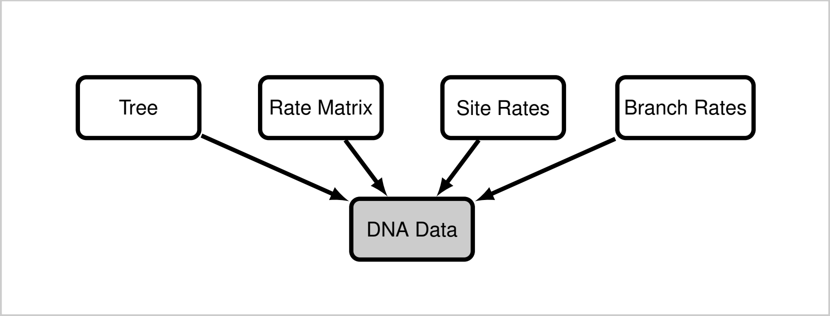
- **Dirchlet process prior**

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

BAYESIAN DIVERGENCE TIME ESTIMATION

Estimating divergence times relies on 2 main elements:

- Branch-specific rates: $f(\boldsymbol{\mathcal{R}} \mid \theta_{\mathcal{R}})$
- Node ages: $f(\boldsymbol{\mathcal{A}} \mid \theta_{\mathcal{A}})$



Tree

Rate Matrix

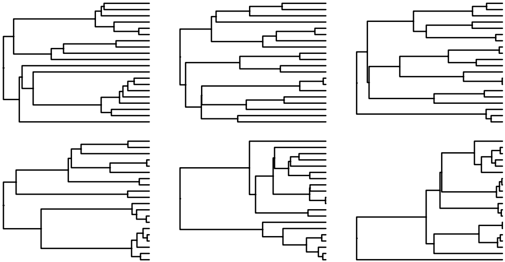
Site Rates

Branch Rates

DNA Data

PRIORS ON THE TREE AND NODE AGES

Relaxed clock Bayesian analyses require a prior distribution on time trees



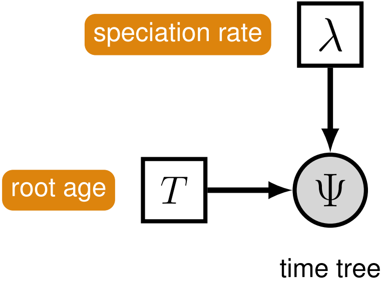
Different node-age priors make different assumptions about the timing of divergence events

Stochastic Branching Processes

Node-age priors based on stochastic models of lineage diversification

Yule process: assumes a constant rate of speciation, across lineages

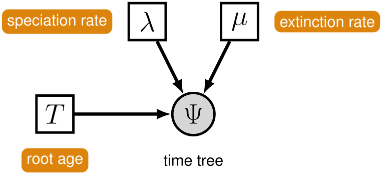
A pure birth process—every node leaves extant descendants (no extinction)



STOCHASTIC BRANCHING PROCESSES

Node-age priors based on stochastic models of lineage diversification

Constant-rate birth-death process: at any point in time a lineage can speciate at rate λ or go extinct with a rate of μ



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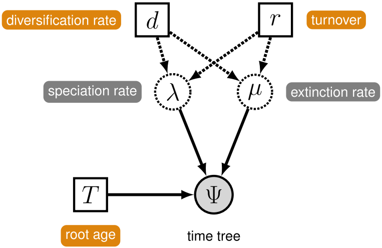
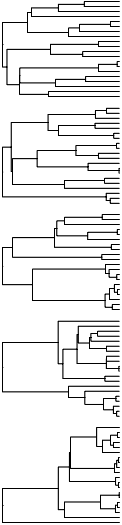


Stochastic Branching Processes

Different values of λ and μ lead to different trees

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

Using hyperpriors on λ and μ (or d and r) accounts for uncertainty in these hyperparameters

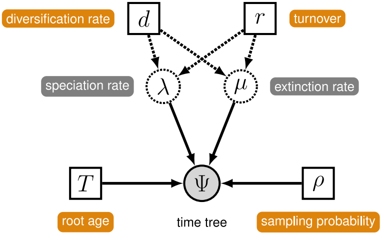


STOCHASTIC BRANCHING PROCESSES

Node-age priors based on stochastic models of lineage diversification

Birth-death-sampling process: an extension of the constant-rate birth-death model that accounts for random sampling of tips

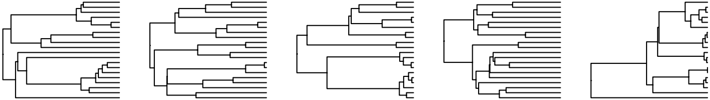
Conditions on a probability of sampling a tip, ρ



PRIORS ON NODE TIMES

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

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



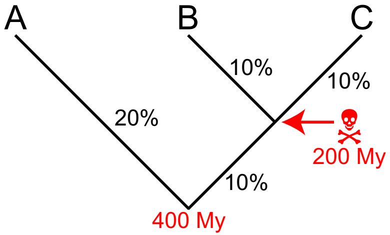
We need external information (like fossils) to provide absolute time scale

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

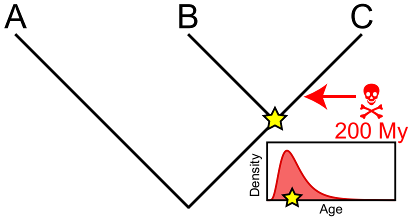
Uncertainty in the placement of fossils



CALIBRATION DENSITIES

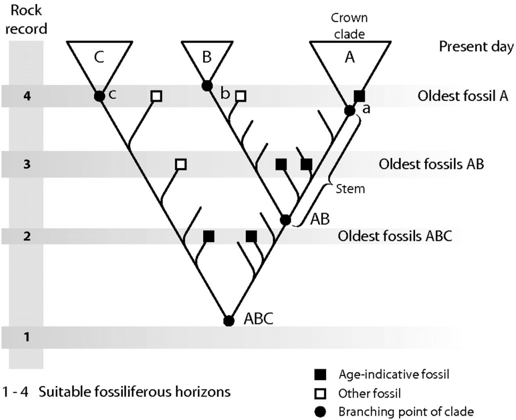
Bayesian inference is well suited to accommodating uncertainty in the age of the calibration node

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



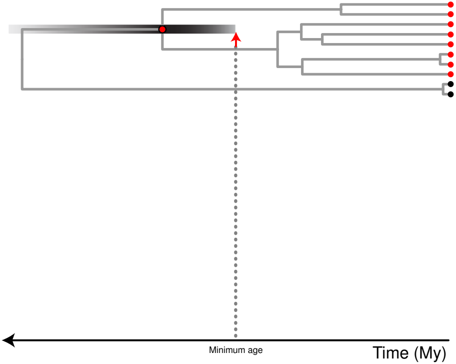
ASSIGNING FOSSILS TO CLADES

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)

FOSSIL CALIBRATION



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

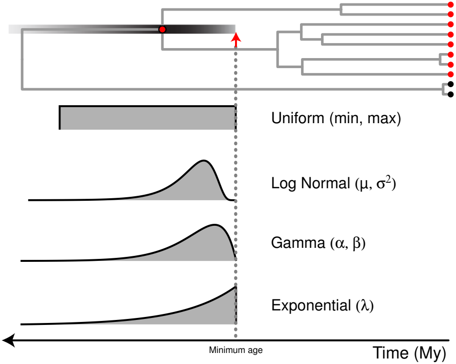
Reliable **maximum** bounds are typically unavailable

PRIOR DENSITIES ON CALIBRATED NODES

Common practice in Bayesian divergence-time estimation:

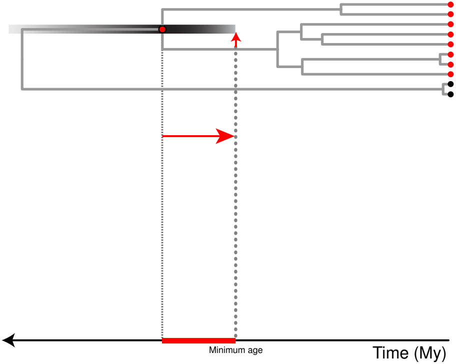
Parametric distributions are typically off-set by the age of the oldest fossil assigned to a clade

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



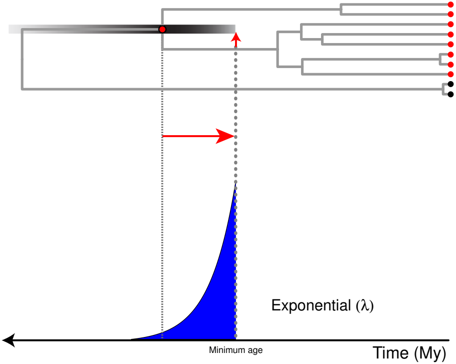
PRIOR DENSITIES ON CALIBRATED NODES

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



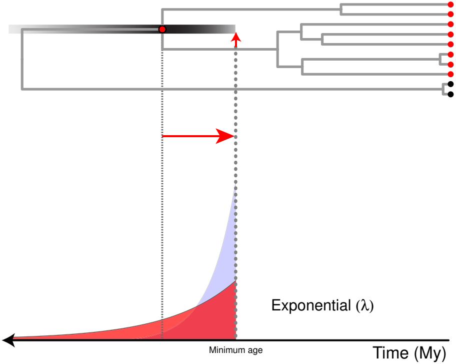
PRIOR DENSITIES ON CALIBRATED NODES

Overly **informative** priors can bias node age estimates to be too young



PRIOR DENSITIES ON CALIBRATED NODES

Uncertainty in the age of the MRCA of the clade relative to the age of the fossil may be better captured by **vague** prior densities

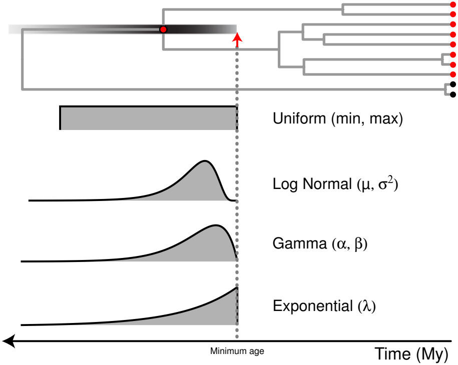


PRIOR DENSITIES ON CALIBRATED NODES

Common practice in Bayesian divergence-time estimation:

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

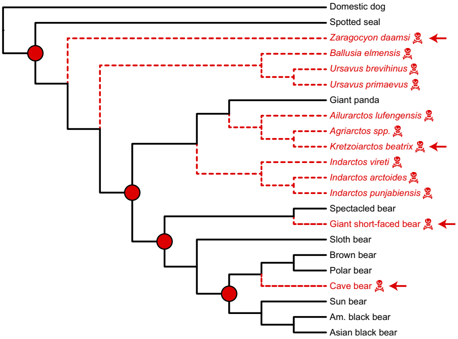
Specifying appropriate densities is a challenge for most molecular biologists



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

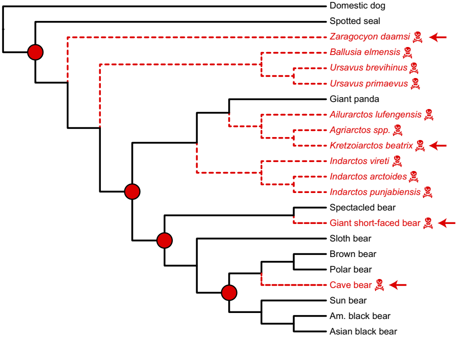


(Krause et al. *BMC Evol. Biol.* 2008; Abella et al. *PLoS ONE* 2012)

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

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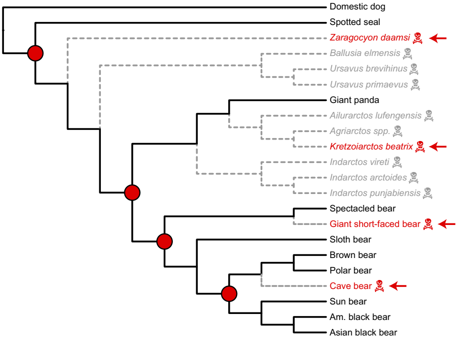
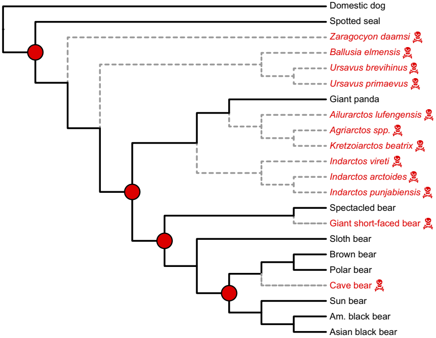


(Krause et al. *BMC Evol. Biol.* 2008; Abella et al. *PLoS ONE* 2012)

IMPROVING FOSSIL CALIBRATION

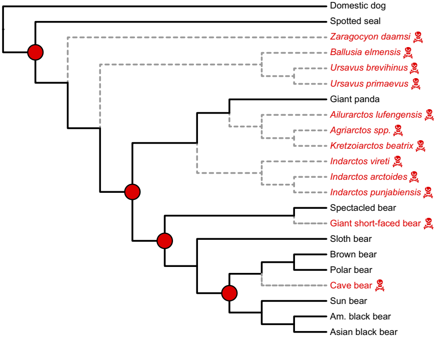
Because fossils are part of the diversification process, we can combine fossil calibration with birth-death models



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

IMPROVING FOSSIL CALIBRATION

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



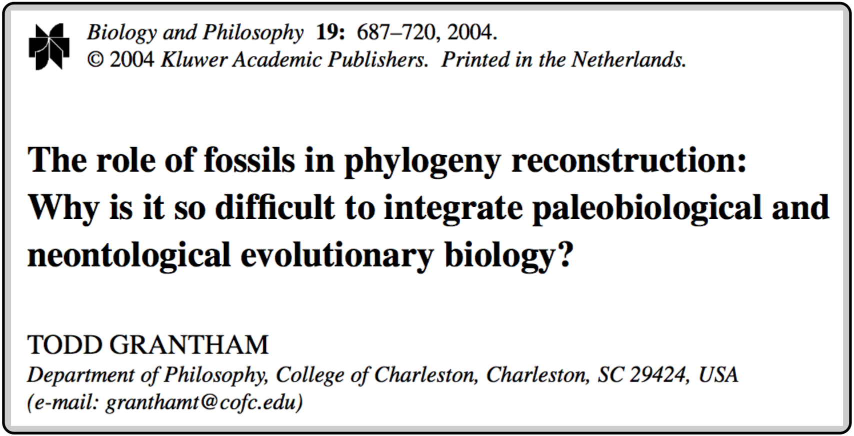
(Krause et al. *BMC Evol. Biol.* 2008; Abella et al. *PLoS ONE* 2012)

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 & Colwell: in Dudley (ed.), *The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic & Evolutionary Biology*, Discorides Press, Portland, OR, p. 16. (1994)

PALEONTOLOGY & NEONTOLOGY



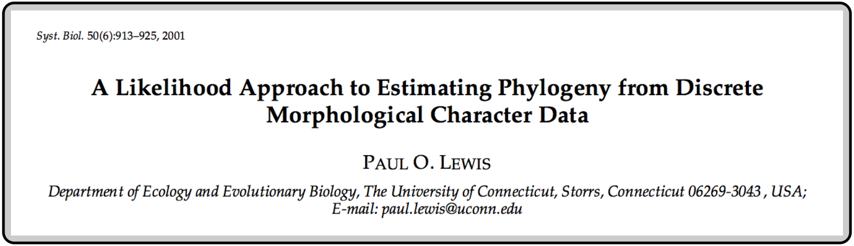
Biology and Philosophy **19:** 687–720, 2004.
© 2004 *Kluwer Academic Publishers. Printed in the Netherlands.*

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: granthamt@cofc.edu)

COMBINING FOSSIL & EXTANT DATA

Statistical methods provide a way to integrate paleontological & neontological data

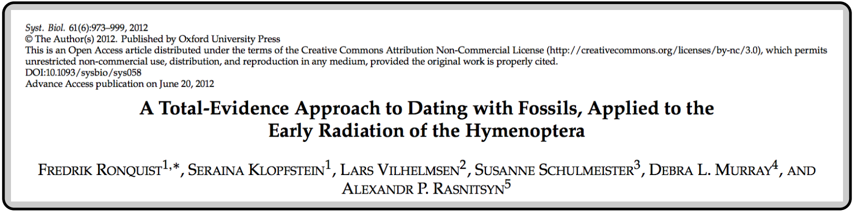


Syst. Biol. 50(6):913–925, 2001

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



Syst. Biol. 61(6):973–999, 2012
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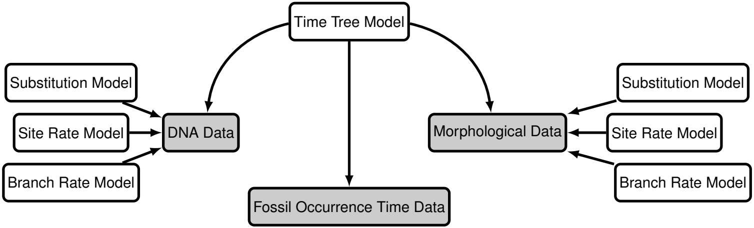
DOI:10.1093/sysbio/sys058
Advance Access publication on June 20, 2012

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

FREDRIK RONQUIST[1,*], SERAINA KLOPFSTEIN[1], LARS VILHELMSEN[2], SUSANNE SCHULMEISTER[3], DEBRA L. MURRAY[4], AND ALEXANDR P. RASNITSYN[5]

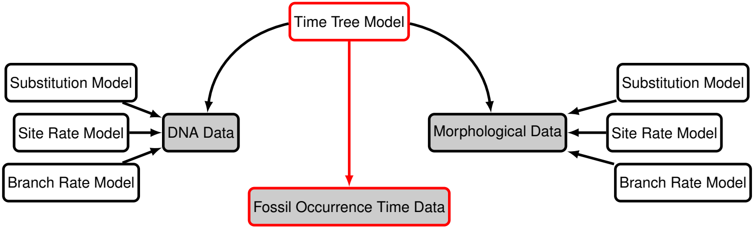
COMBINING FOSSIL & EXTANT DATA

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



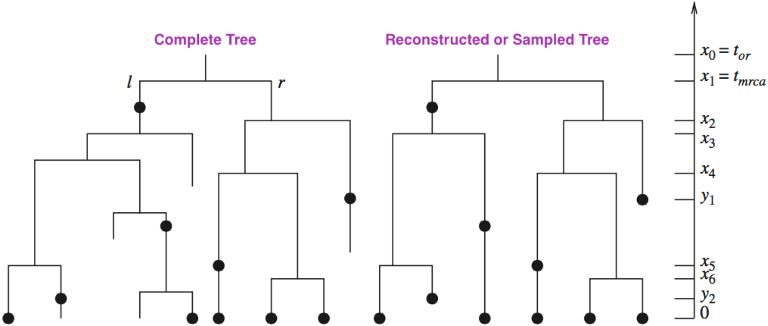
COMBINING FOSSIL & EXTANT DATA

Until recently, analyses combining fossil & extant taxa used simple or inappropriate models to describe the tree and fossil ages



Modeling the Tree & Occurrence Times

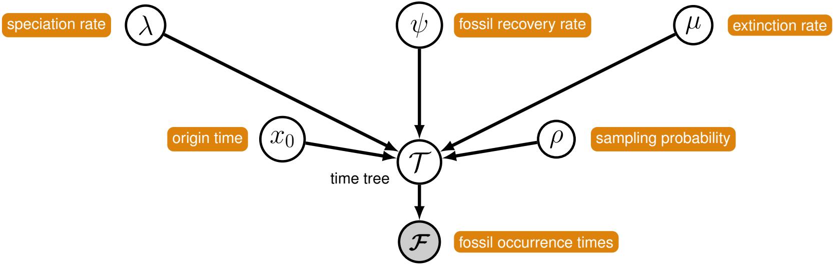
Stadler (2010) introduced a generating model for a serially sampled time tree — this is the *fossilized birth-death process*.



(Stadler. *Journal of Theoretical Biology* 2010)

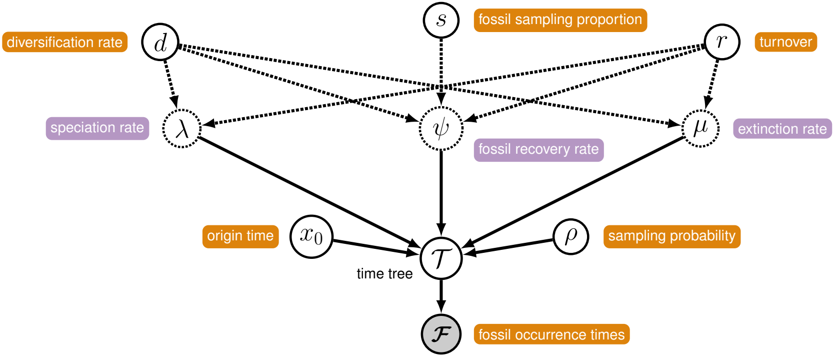
PARAMETERS OF THE FBD

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



PARAMETERS OF THE FBD

We re-parameterize the model so that we are directly estimating the diversification rate, turnonver and fossil sampling proportion



$$\lambda = \frac{d}{1-r} \qquad \mu = \frac{rd}{1-r} \qquad \psi = \frac{s}{1-s}\frac{rd}{1-r}$$

THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

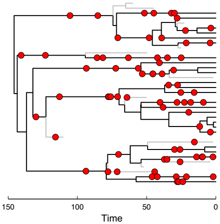
Improving statistical inference of absolute node ages

Eliminates the need to specify arbitrary calibration densities

Useful for 'total-evidence' analyses

Better capture our statistical uncertainty in species divergence dates

All reliable fossils associated with a clade are used



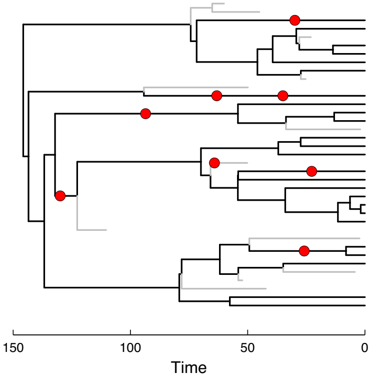
The fossilized birth–death process for coherent calibration of divergence-time estimates

Tracy A. Heath[a,b], John P. Huelsenbeck[a,c], and Tanja Stadler[d,e,1]

(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

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)

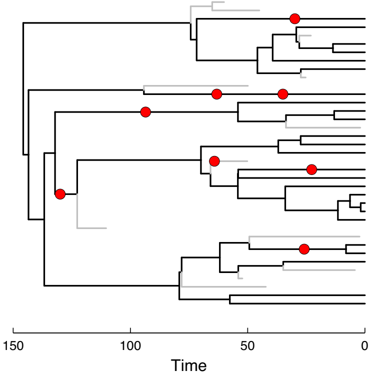
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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

$\lambda =$ speciation

$\mu =$ extinction

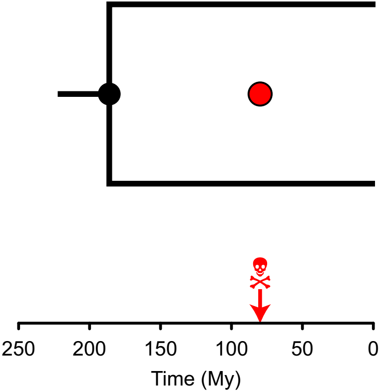
$\psi =$ fossilization/recovery



(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

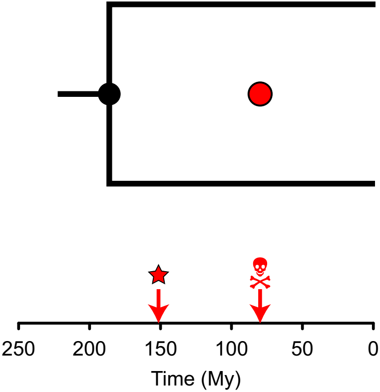
The occurrence time of the fossil ☠ indicates an observation of the birth-death process before the present



(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

The Fossilized Birth-Death Process (FBD)

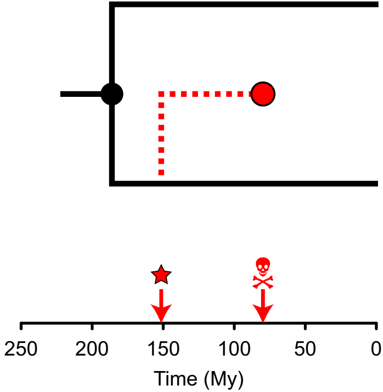
The fossil must attach to the tree at some time and to some branch: ★



(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

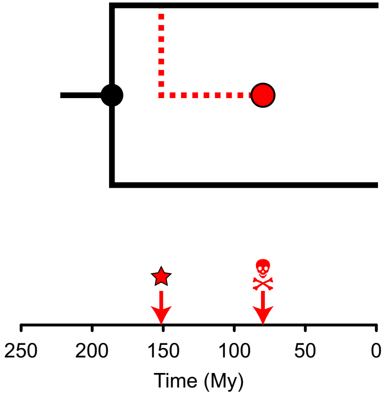
The Fossilized Birth-Death Process (FBD)

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



(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

The Fossilized Birth-Death Process (FBD)

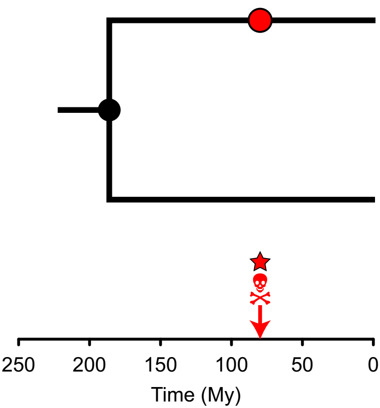


MCMC is used to propose new topological placements for the fossil

(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Using rjMCMC, we can propose ★ = ☠, which means that the fossil is a "sampled ancestor"



(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

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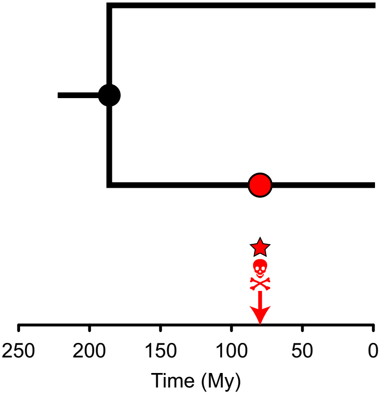
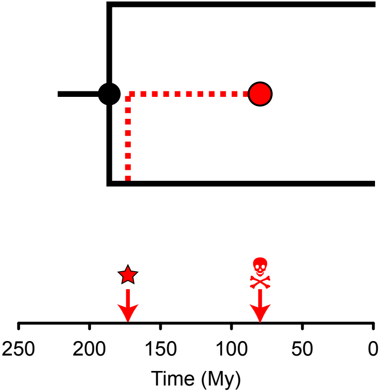


(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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

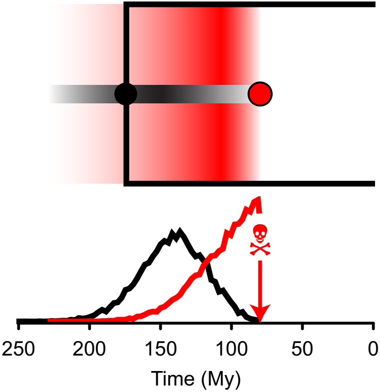
λ, μ, and ψ



(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

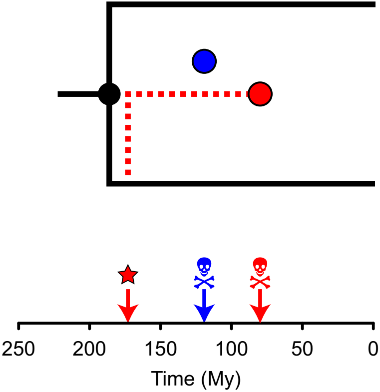
Using MCMC, we can sample the age of the MRCA ● and the placement and time of the fossil lineage



(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

The Fossilized Birth-Death Process (FBD)

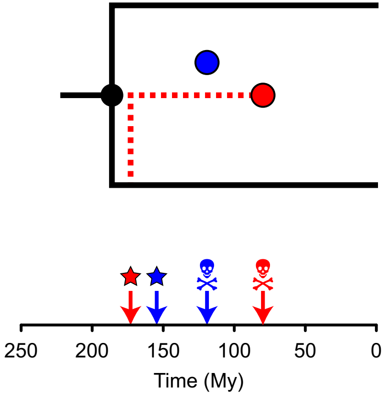
Under the **FBD**, multiple fossils are considered, even if they are descended from the same MRCA node in the extant tree



(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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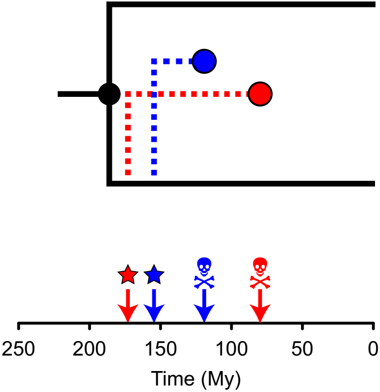

(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

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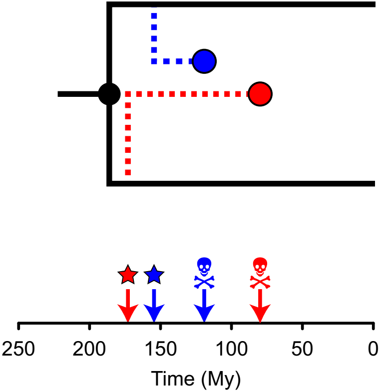
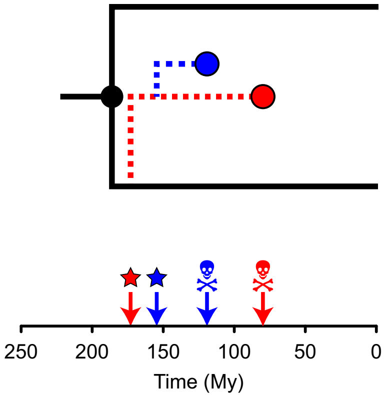


(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

The Fossilized Birth-Death Process (FBD)

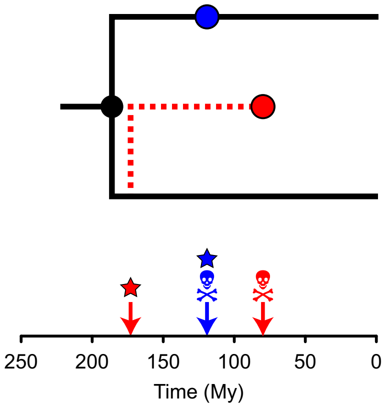
Or the unobserved branch leading to the other fossil



(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

The Fossilized Birth-Death Process (FBD)

If ★ = ☠, then the new fossil lies directly on a branch in the extant tree



(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

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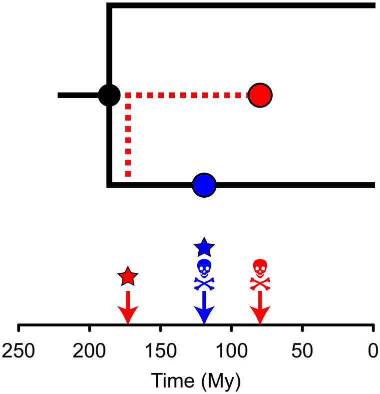
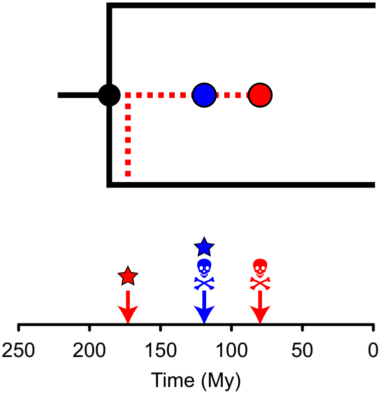


(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

The Fossilized Birth-Death Process (FBD)

Or it is an ancestor of the other sampled fossil

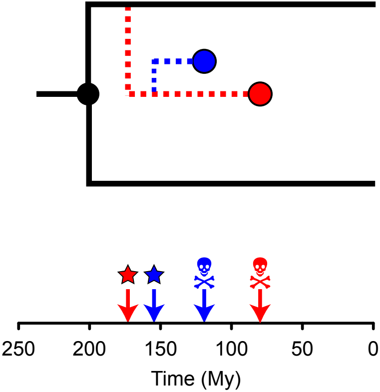


(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

The Fossilized Birth-Death Process (FBD)

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

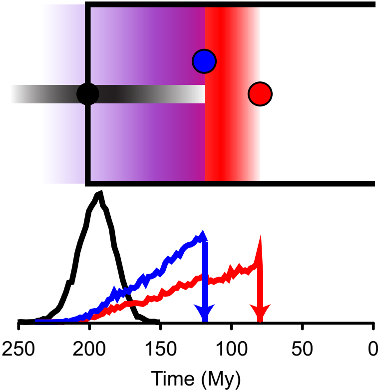
λ, μ, and ψ



(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

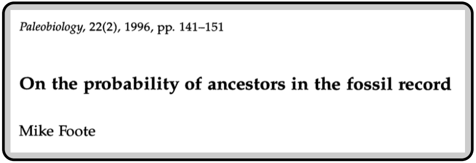
Using MCMC, we can sample the age of the MRCA ● and the placement and time of all fossil lineages



(Heath, Huelsenbeck, Stadler. *PNAS* 2014)

SAMPLED ANCESTORS

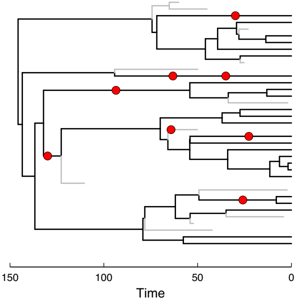
Sampled lineages with sampled descendants



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

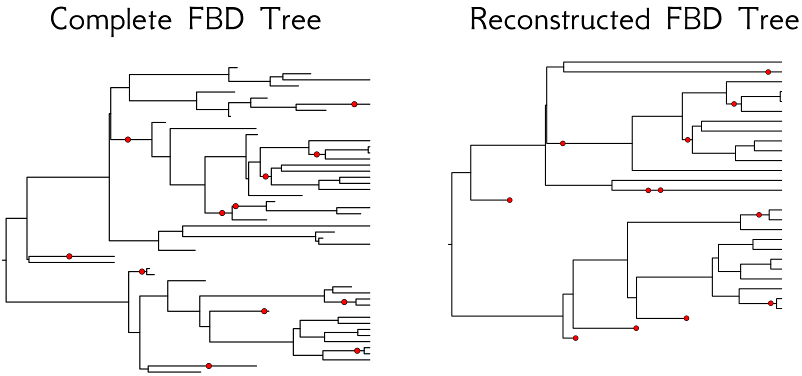
On the probability of ancestors in the fossil record

Mike Foote



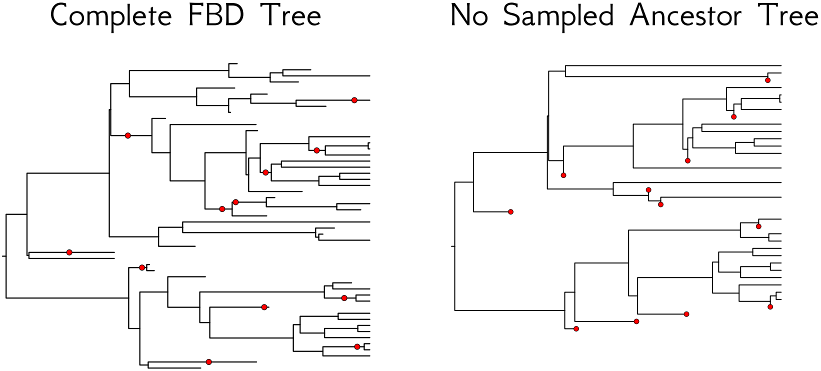
There is a non-zero probability of sampling ancestor-descendant relationships from the fossil record

SAMPLED ANCESTORS



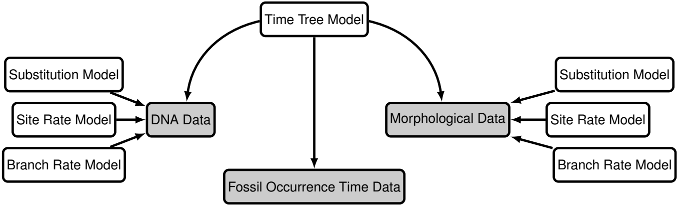
Because fossils & living taxa are assumed to come from a single diversification process, there is a non-zero probability of sampled ancestors

Sampled Ancestors



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

COMBINING FOSSIL & EXTANT DATA



Time Tree Model

Substitution Model

Site Rate Model

Branch Rate Model

DNA Data

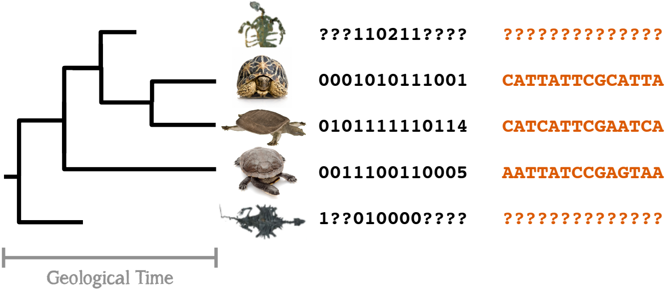
Morphological Data

Substitution Model

Site Rate Model

Branch Rate Model

Fossil Occurrence Time Data



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0001010111001 CATTATTCGCATTA

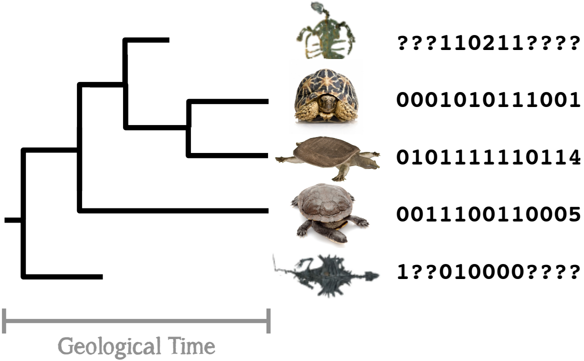
0101111110114 CATCATTCGAATCA

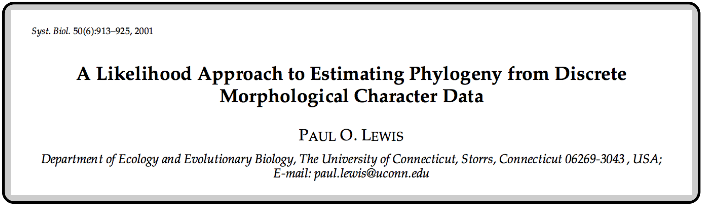
0011100110005 AATTATCCGAGTAA

1??010000???? ??????????????

(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

(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

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

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

(Lewis. *Systematic Biology* 2001)

MODELING MORPHOLOGICAL CHARACTER CHANGE

The Lewis Mkv model

Accounts for the ascertainment bias in morphological datasets by conditioning the likelihood on the fact that invariant characters are not sampled

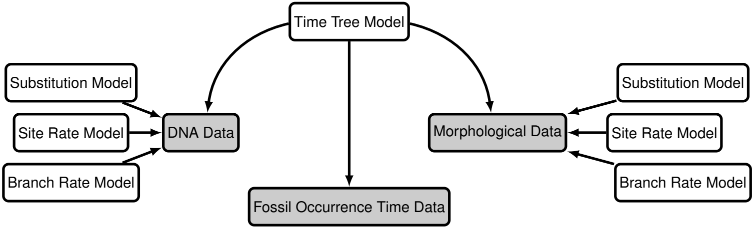
$$Q = \alpha \begin{bmatrix} 1-k & 1 & \dots & 1 \\ \vdots & 1-k & \dots & 1 \\ \vdots & \vdots & \ddots & \vdots \\ 1 & 1 & \dots & 1-k \end{bmatrix}$$

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

(Lewis. *Systematic Biology* 2001)

“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


Time Tree Model

Substitution Model

Site Rate Model

Branch Rate Model

DNA Data

Morphological Data

Substitution Model

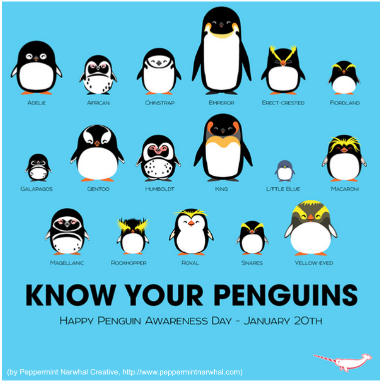
Site Rate Model

Branch Rate Model

Fossil Occurrence Time Data

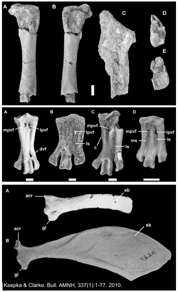
PENGUIN DIVERSITY IN DEEP TIME

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



(by Peppermint Narwhal Creative, http://www.peppermintnarwhal.com)

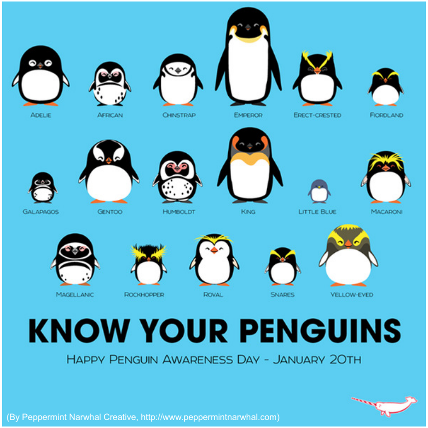
Photo of Daniel Ksepka and *Kairuku* specimen by R.E. Fordyce
(http://blogs.scientificamerican.com/observations/giant-prehistoric-penguin-was-bigger-than-an-emperor/)



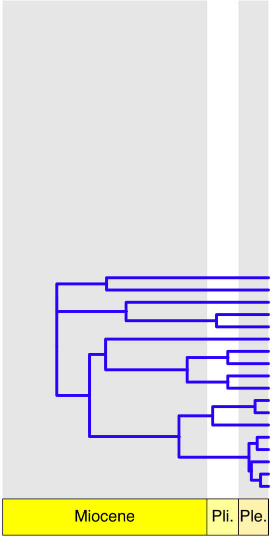
Ksepka & Clarke. Bull. AMNH, 337(1):1-77. 2010.

Artistic reconstructions by: Stephanie Abramowicz for Scientific American
Fordyce, R.E. and D.T. Ksepka. The Strangest Bird Scientific American 307, 56 – 61 (2012)

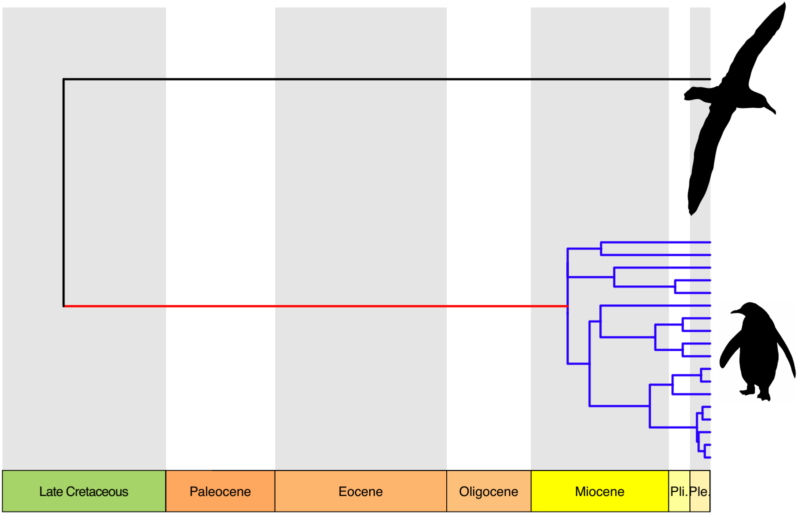
PENGUIN DIVERSITY



(By Peppermint Narwhal Creative, http://www.peppermintnarwhal.com)

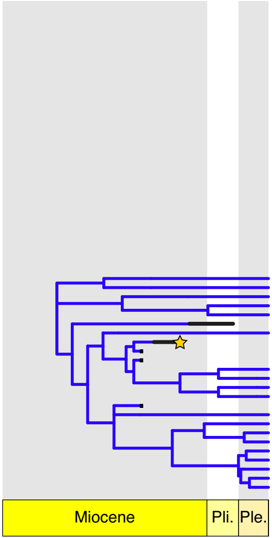


Penguin Diversity



(silhouette images from `http://phylopic.org`)

Fossil Penguin Diversity



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

PENGUINS IN THE OLIGOCENE

Kairuku

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

© Geology Museum of Otago (Chris Gaskin)

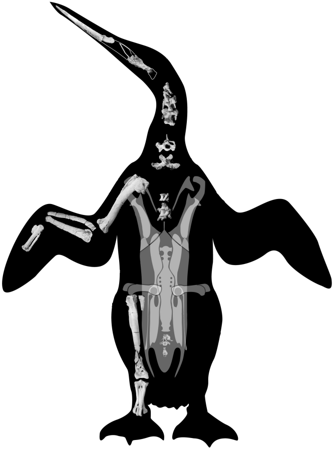
Image courtesy of Daniel Ksepka

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

PENGUINS IN THE PALEOCENE

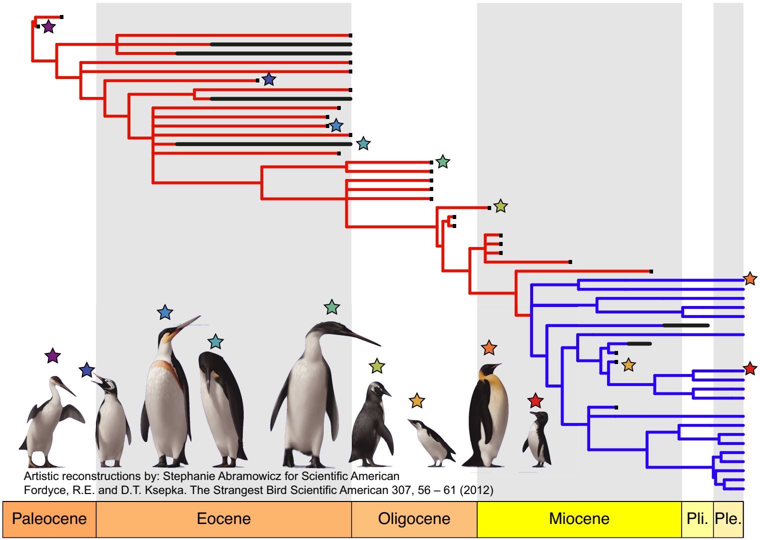
Waimanu

- oldest known penguin species
- intermediate wing morphology
- $\sim$58–61.6 Mya



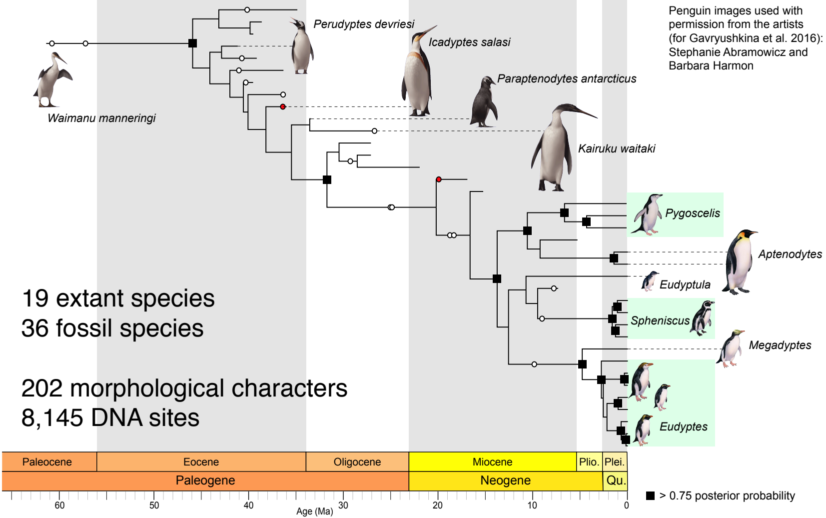
(Slack et al., *Mol. Biol. Evol.* 2006)

Penguin Diversity in Deep Time



Artistic reconstructions by: Stephanie Abramowicz for Scientific American
Fordyce, R.E. and D.T. Ksepka. The Strangest Bird Scientific American 307, 56 – 61 (2012)

PENGUIN DIVERSITY IN DEEP TIME



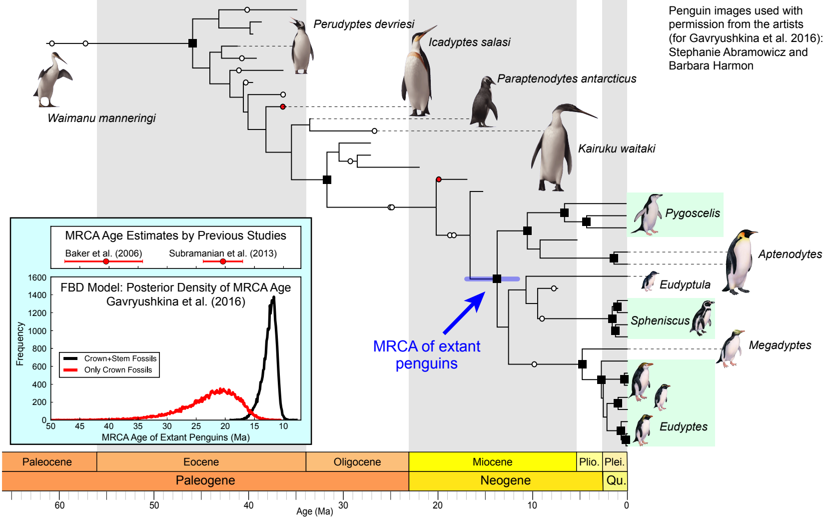
Penguin images used with
permission from the artists
(for Gavryushkina et al. 2016):
Stephanie Abramowicz and
Barbara Harmon

19 extant species
36 fossil species

202 morphological characters
8,145 DNA sites

(Gavryushkina, Heath, Ksepka, Welch, Stadler, Drummond. *Syst. Biol.*, in press. `http://arxiv.org/abs/1506.04797`)

PENGUIN DIVERSITY IN DEEP TIME



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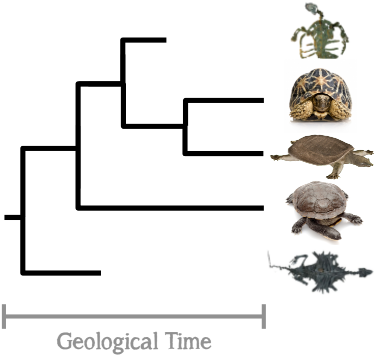
(Gavryushkina, Heath, Ksepka, Welch, Stadler, Drummond. *Syst. Biol.*, in press. `http://arxiv.org/abs/1506.04797`)

MOLECULES + MORPHOLOGY + FOSSILS



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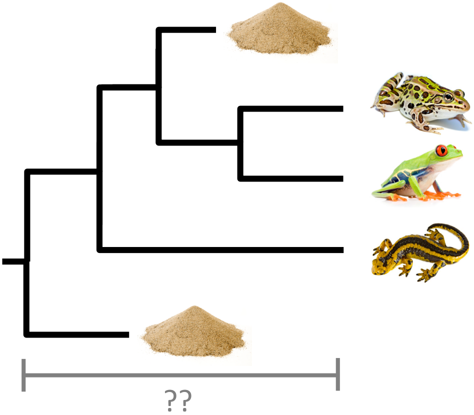
1??010000????	??????????????

(based on slides by M. Landis)

...but I study amphibians...



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CCGA	1101
CTCA	0001
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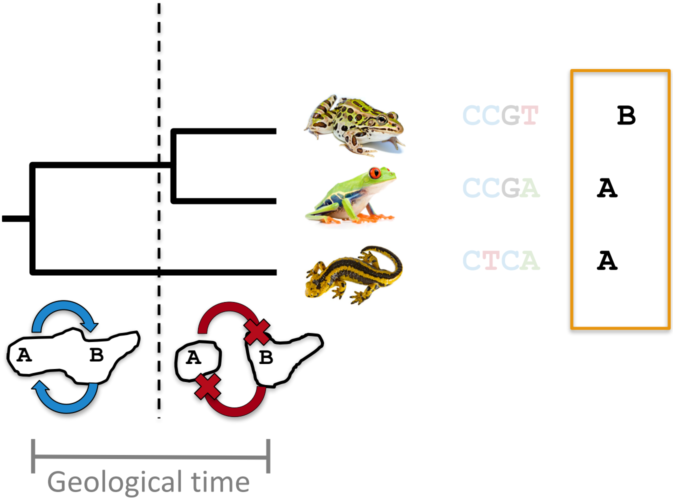
(slides courtesy of M. Landis; http://bit.ly/2alHqB4)

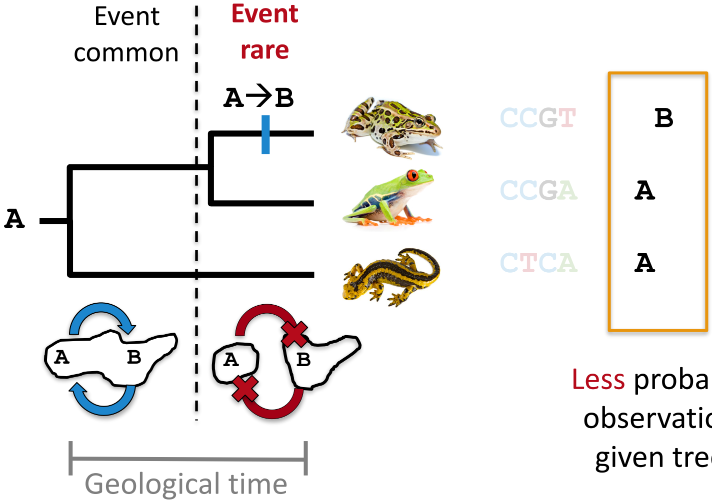
Molecules + biogeography + paleogeography



+ Paleogeography Landis, 2016

(slides courtesy of M. Landis; http://bit.ly/2alHqB4)

Events should occur *before areas split*

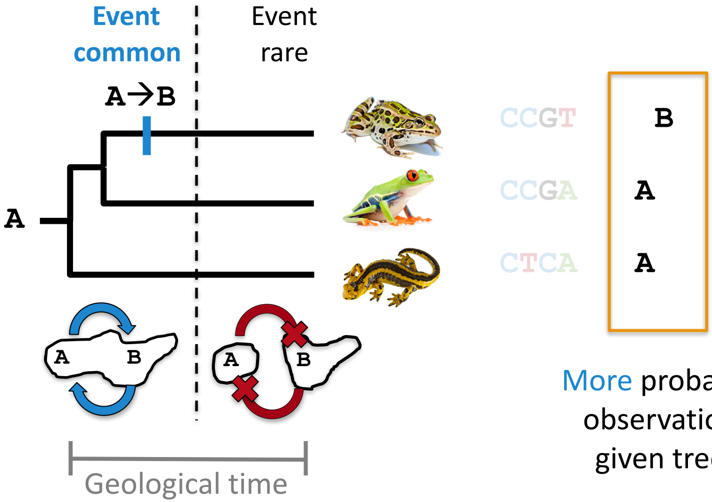


Less probable observation given tree

+ Paleogeography Landis, 2016

(slides courtesy of M. Landis; http://bit.ly/2alHqB4)

Events should occur *before areas split*

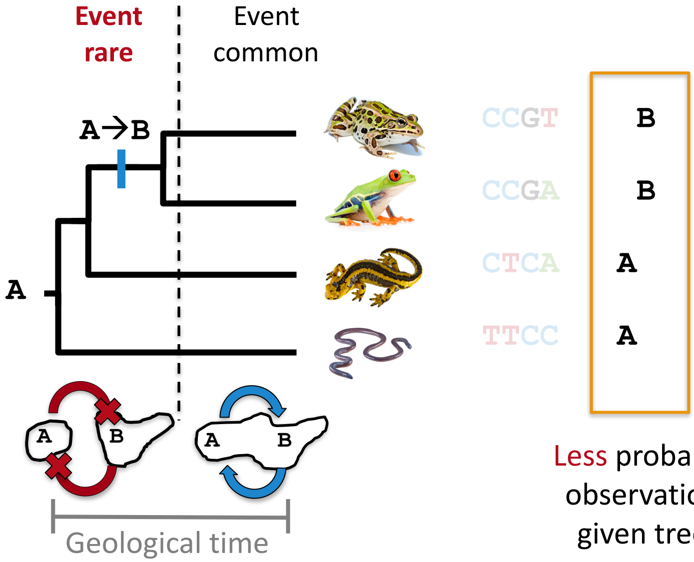


More probable observation given tree

+ Paleogeography Landis, 2016

(slides courtesy of M. Landis; http://bit.ly/2alHqB4)

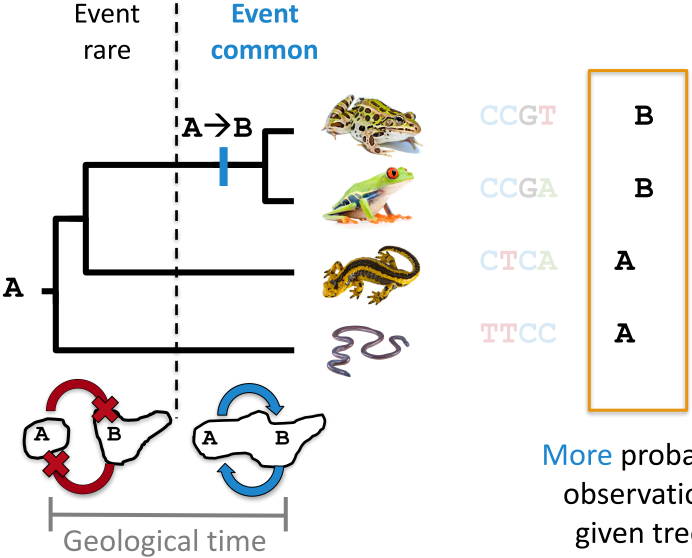
Events should occur *after areas merge*



Less probable observation given tree

(slides courtesy of M. Landis; http://bit.ly/2alHqB4)

Events should occur *after areas merge*



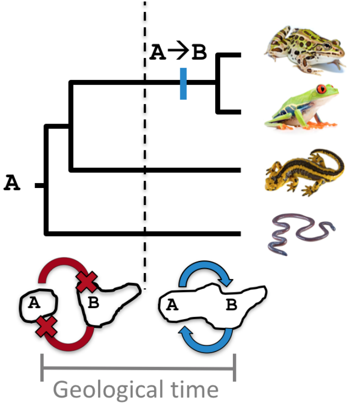
More probable observation given tree

(slides courtesy of M. Landis; http://bit.ly/2alHqB4)

BIOGEOGRAPHIC DATING

Fossil-free calibration

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



Landis. In Press. "Biogeographic Dating of Speciation Times Using Paleogeographically Informed Processes". *Systematic Biology*, doi: 10.1093/sysbio/syw040.

(image by M. Landis; `http://bit.ly/2alHqB4`)

Biogeographic Dating

25 areas, 26 time-slices, 540–0Ma

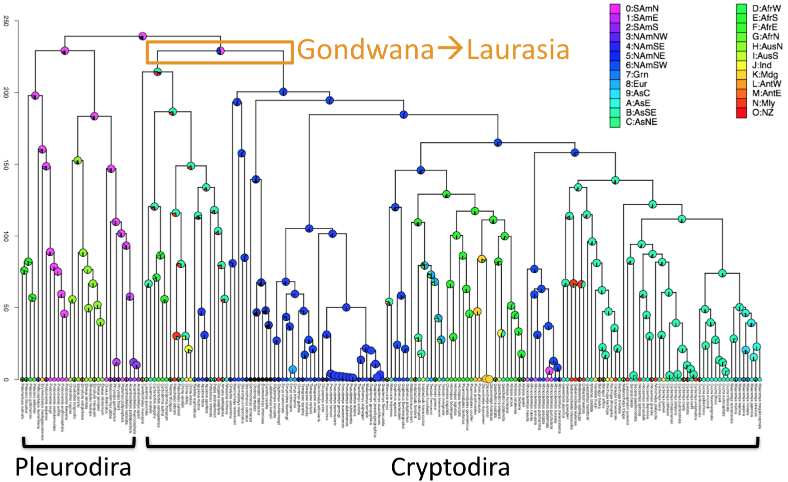
strong=share land, weak=nearby land, none=all pairs

Connectivity model constructed using literature review and GPlates (`http://www.gplates.org/`)

(model & animation courtesy of M. Landis; `http://bit.ly/2alHqB4`)

Dating + Ancestral Area Reconstruction

Ancestral area estimates (+G)



Gondwana→Laurasia

Pleurodira

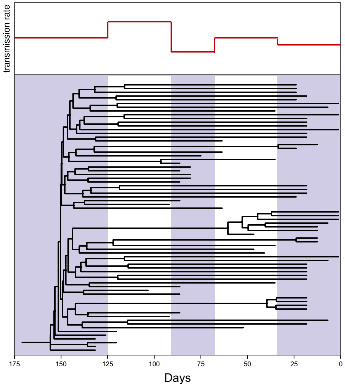
Cryptodira

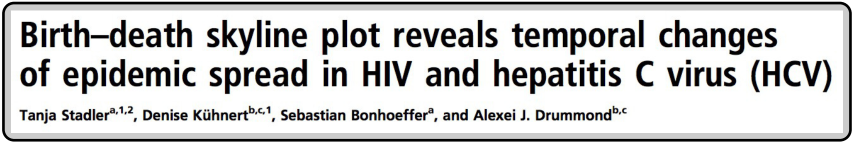
(image by M. Landis; http://bit.ly/2alHqB4)

SKYLINE BIRTH-DEATH PROCESS

A piecewise shifting model where parameters change over time

Used to estimate epidemiological parameters of an outbreak





Birth–death skyline plot reveals temporal changes of epidemic spread in HIV and hepatitis C virus (HCV)

Tanja Stadler[a,1,2], Denise Kühnert[b,c,1], Sebastian Bonhoeffer[a], and Alexei J. Drummond[b,c]

(see Stadler et al. *PNAS* 2013 and Stadler et al. PLoS Currents Outbreaks 2014)

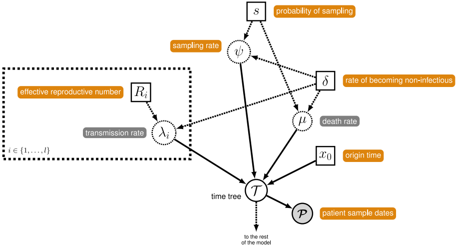
SKYLINE BIRTH-DEATH PROCESS

l is the number of parameter intervals

R_i is the effective reproductive number for interval $i \in l$

δ is the rate of becoming non-infectious

s is the probability of sampling an individual after becoming non-infectious



$$R_i = \frac{\lambda_i}{\mu + \psi}, \quad \delta = \mu + \psi, \quad s = \frac{\psi}{\mu + \psi}$$

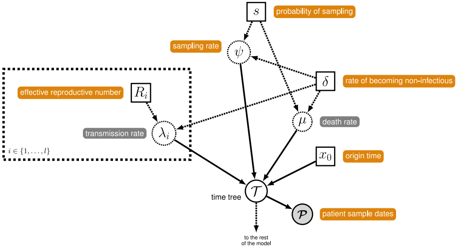
SKYLINE BIRTH-DEATH PROCESS

l is the number of parameter intervals

λ_i is the transmission rate for interval $i \in l$

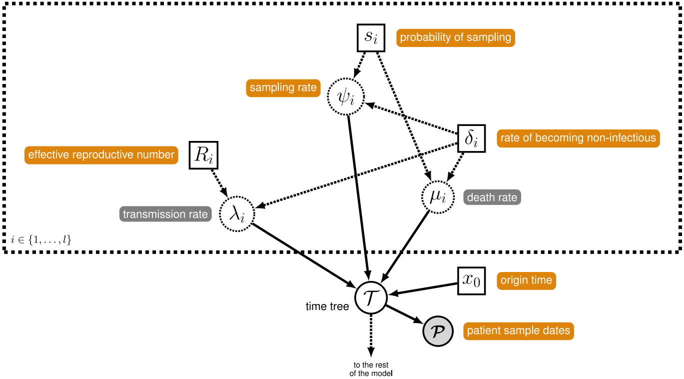
μ is the viral lineage death rate

ψ is the rate each individual is sampled



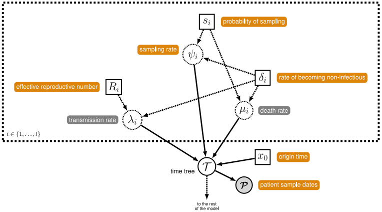
$$\lambda_i = R_i \delta, \quad \mu = \delta - s\delta, \quad \psi = s\delta$$

SKYLINE BIRTH-DEATH PROCESS

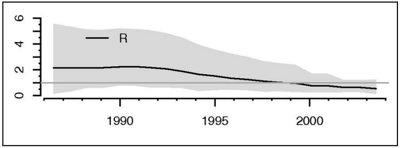


SKYLINE BIRTH-DEATH PROCESS

A decline in *R* over the history of HIV-1 in the UK is consistent with the introduction of effective drug therapies



After 1998 *R* decreased below 1, indicating a declining epidemic



(Stadler et al. *PNAS* 2013)

EXERCISE IN BEAST2

This tutorial uses sequence data and fossil occurrence times to date species divergences using a relaxed-clock model and the fossilized birth-death process