



CALIBRATING SPECIES DIVERGENCE TIMES

Tracy A. Heath

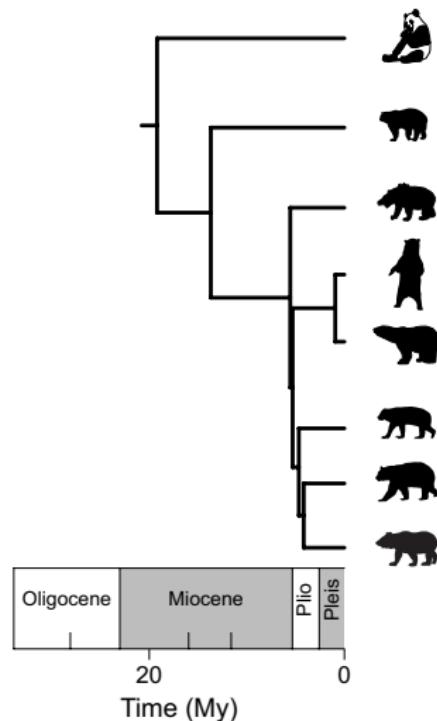
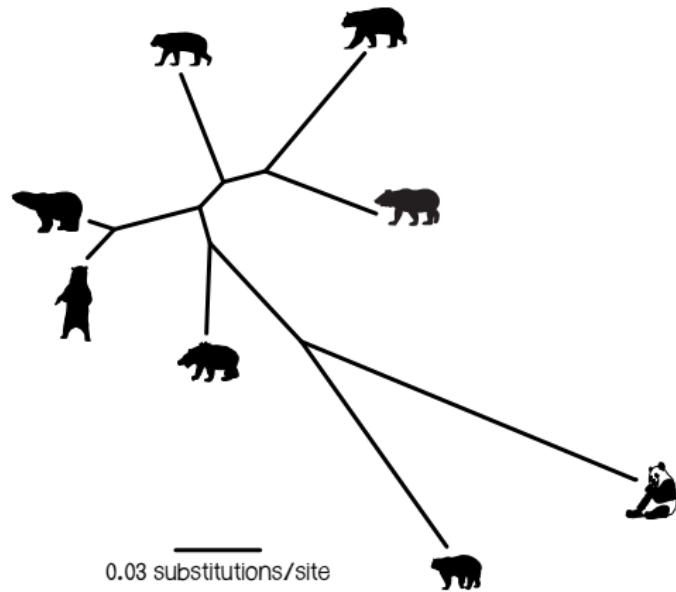
Ecology, Evolution, & Organismal Biology
Iowa State University

Taming the BEAST Workshop
Engelberg, Switzerland

July 1, 2016

A TIME-SCALE FOR MACROEVOLUTION

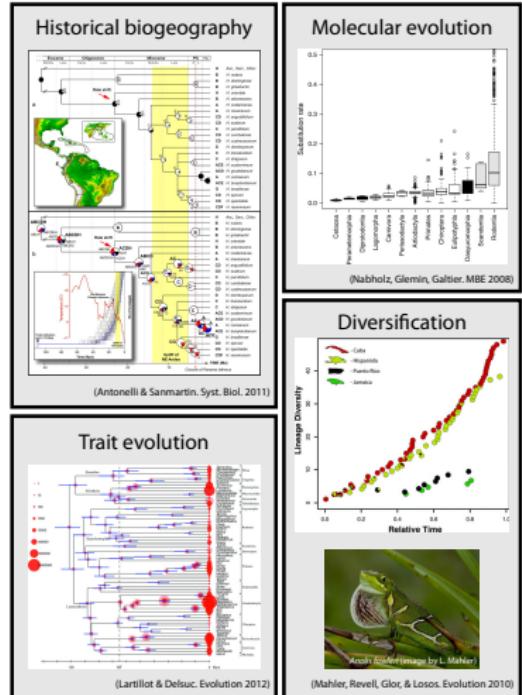
Phylogenies with branch lengths proportional to time provide more information about evolutionary history than unrooted trees with branch lengths in units of substitutions/site.



A TIME-SCALE FOR MACROEVOLUTION

Phylogenetic divergence-time estimation

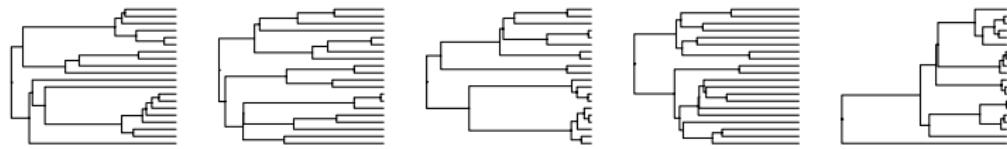
- What was the spacial and climatic environment of ancient angiosperms?
- How has mammalian body-size changed over time?
- Is diversification in Caribbean anoles correlated with ecological opportunity?
- How has the rate of molecular evolution changed across the Tree of Life?



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 *calibrate* or scale the tree to absolute time

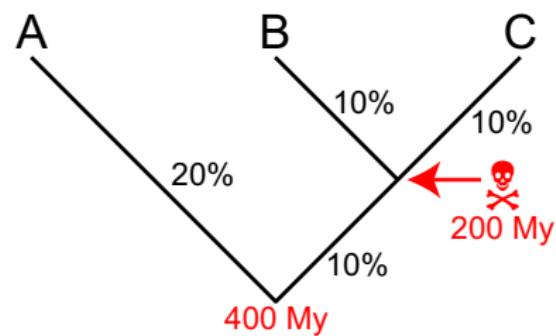


CALIBRATING DIVERGENCE TIMES

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

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

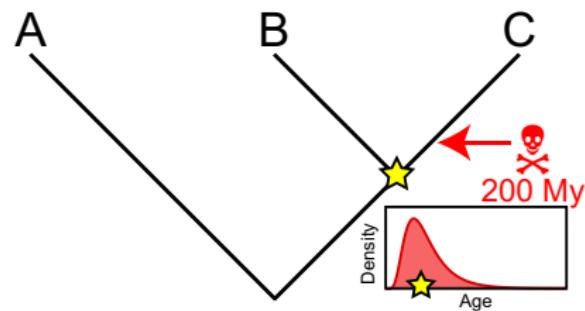
Uncertainty in the placement of fossils



CALIBRATION DENSITIES

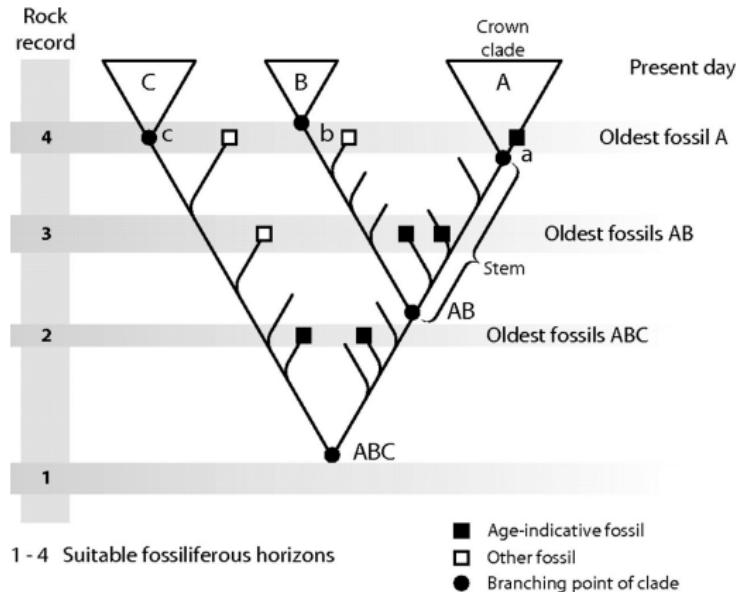
Bayesian inference is well suited to accommodating uncertainty in the age of the calibration node

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



ASSIGNING FOSSILS TO CLADES

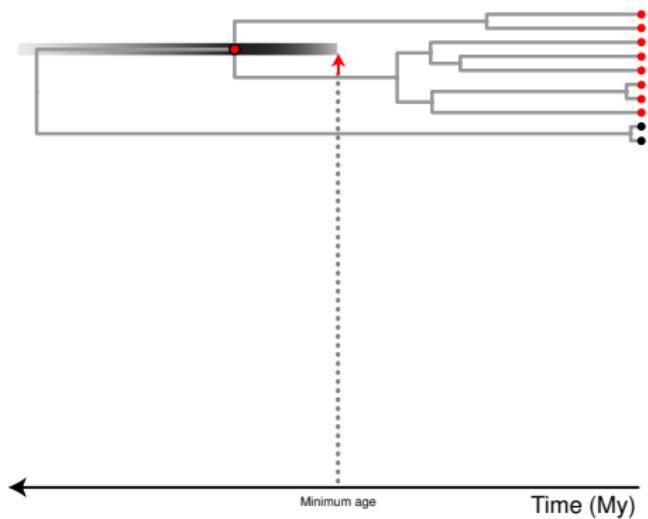
Misplaced fossils can affect node age estimates throughout the tree – if the fossil is older than its presumed MRCA



Fossil Calibration

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

Reliable **maximum** bounds are typically unavailable

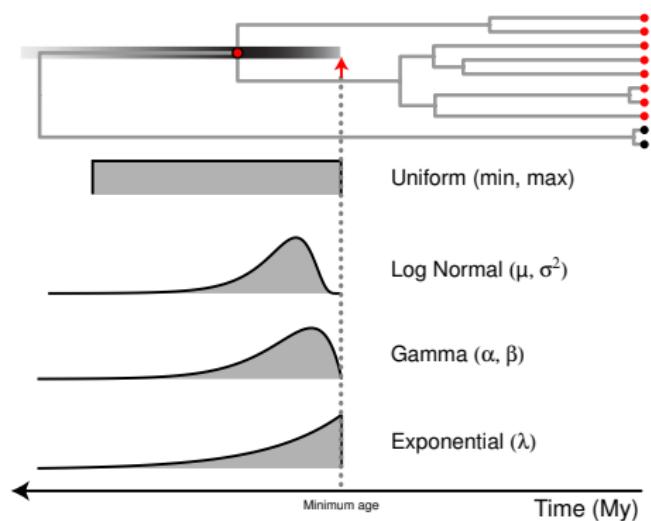


PRIOR DENSITIES ON CALIBRATED NODES

Common practice in Bayesian divergence-time estimation:

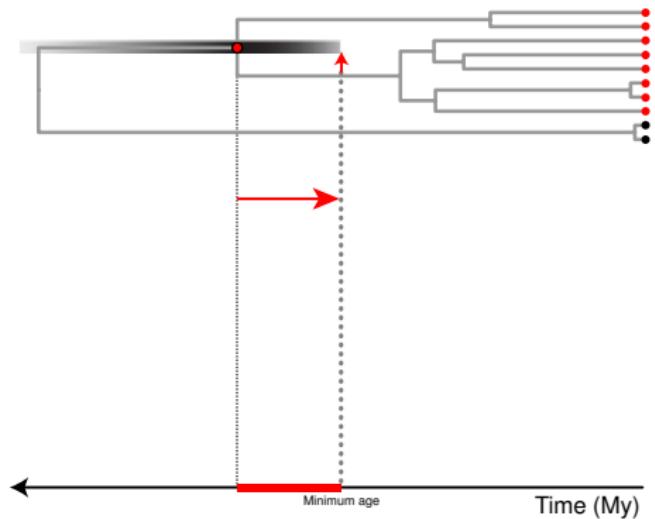
Parametric distributions are typically off-set by the age of the oldest fossil assigned to a clade

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



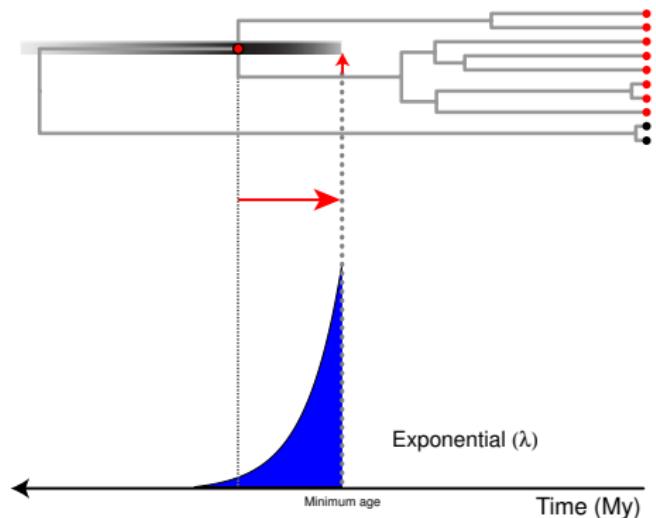
PRIOR DENSITIES ON CALIBRATED NODES

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



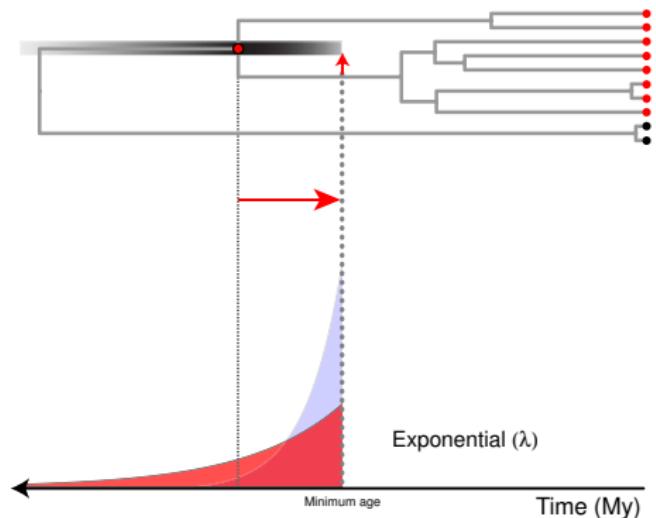
PRIOR DENSITIES ON CALIBRATED NODES

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 more **diffuse** prior densities

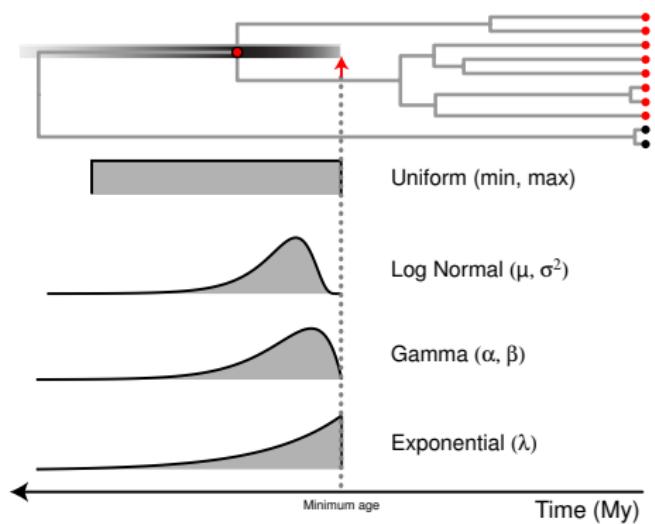


PRIOR DENSITIES ON CALIBRATED NODES

Common practice in Bayesian divergence-time estimation:

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

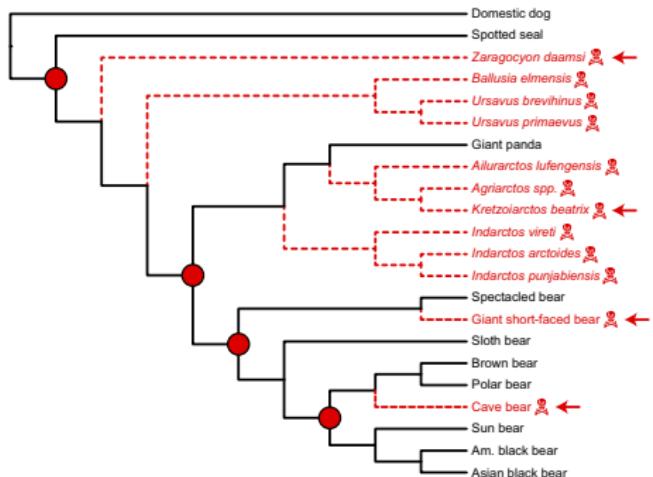
Specifying appropriate densities is a challenge for most molecular biologists



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

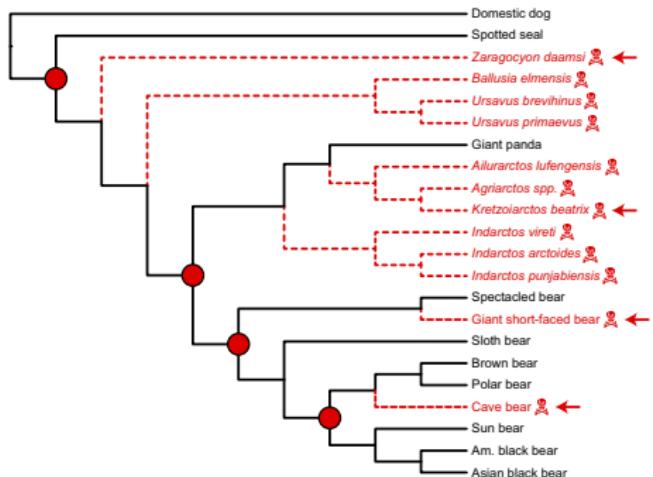


IMPROVING FOSSIL CALIBRATION

We want to use all of the available fossils

Example: Bears

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

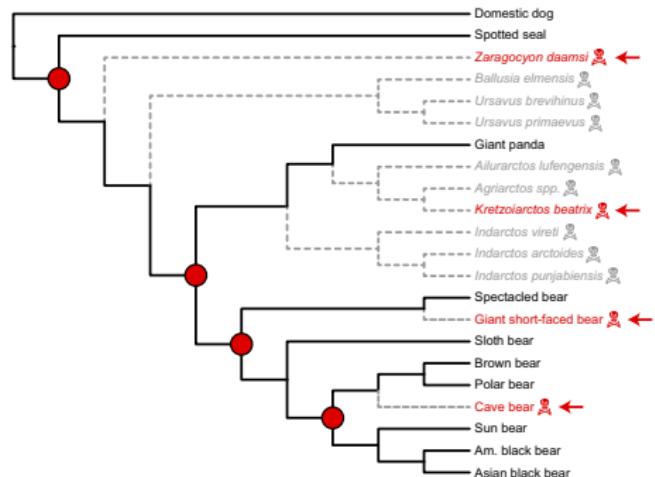


IMPROVING FOSSIL CALIBRATION

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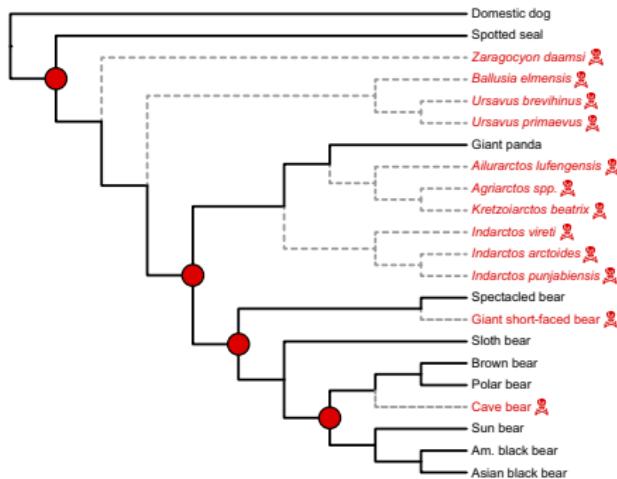
Example: Bears

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



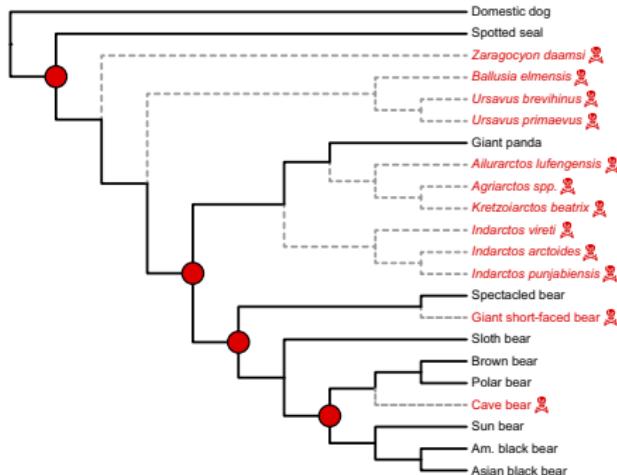
IMPROVING FOSSIL CALIBRATION

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



IMPROVING FOSSIL CALIBRATION

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



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.

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: 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

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E-mail: paul.lewis@uconn.edu

Syst. Biol. 61(6):973–999, 2012

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DOI:10.1093/sysbio/sys058

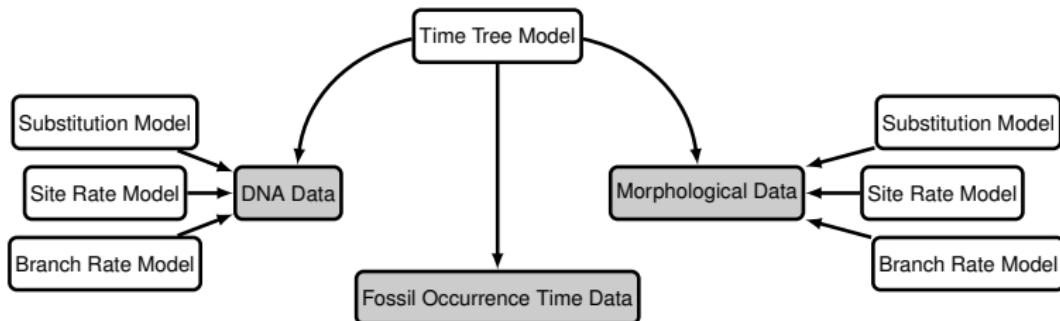
Advance Access publication on June 20, 2012

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

FREDRIK RONQUIST^{1,*}, SERAINA KLOPFSTEIN¹, LARS VILHELMSEN², SUSANNE SCHULMEISTER³, DEBRA L. MURRAY⁴, AND ALEXANDR P. RASNITSYN⁵

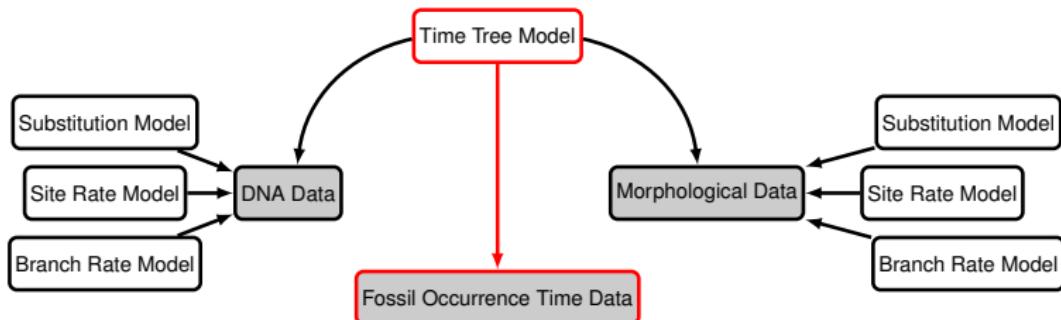
COMBINING FOSSIL & EXTANT DATA

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



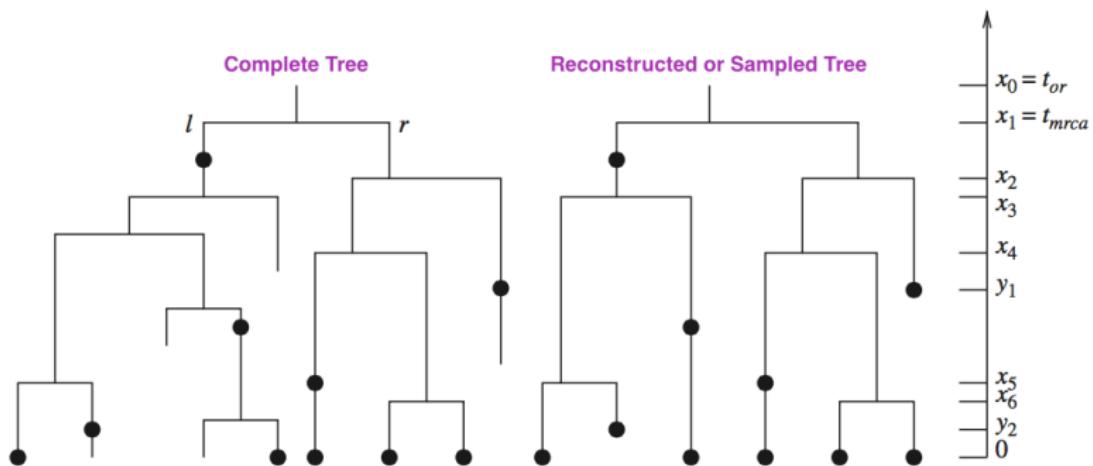
COMBINING FOSSIL & EXTANT DATA

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



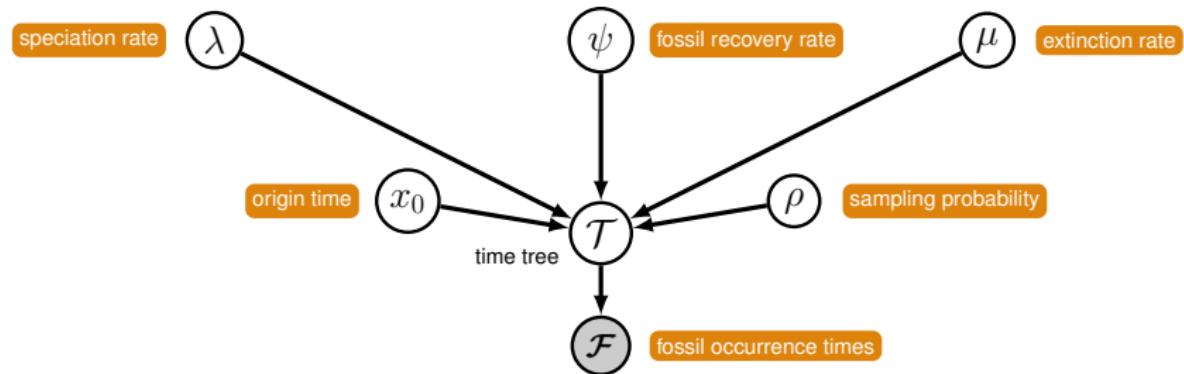
MODELING THE TREE & OCCURRENCE TIMES

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



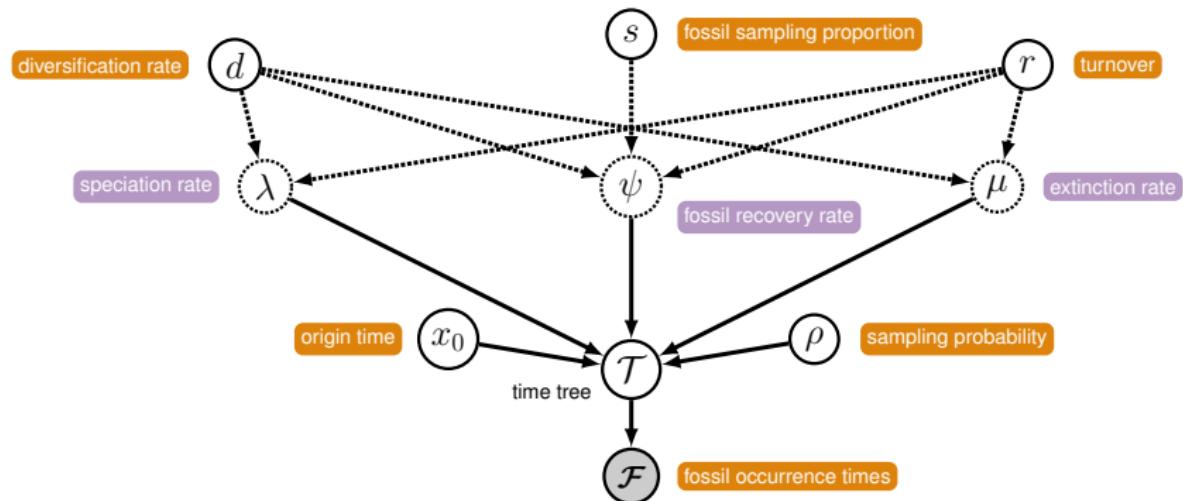
PARAMETERS OF THE FBD

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, turnover and fossil sampling proportion



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

THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

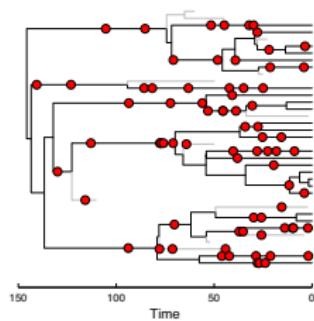
Improving statistical inference of absolute node ages

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

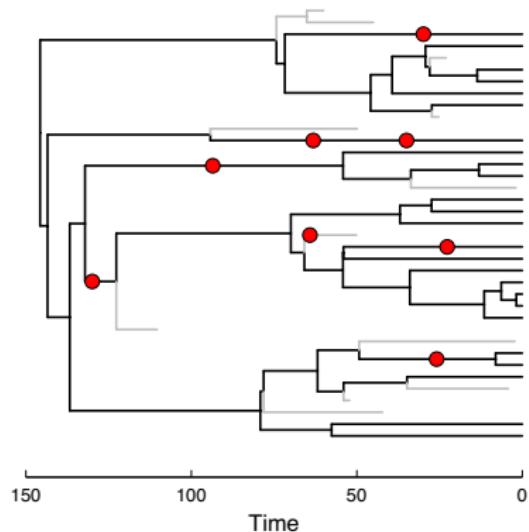


The fossilized birth–death process for coherent calibration of divergence-time estimates

Tracy A. Heath^{a,b}, John P. Huelsenbeck^{a,c}, and Tanja Stadler^{d,e,1}

THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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



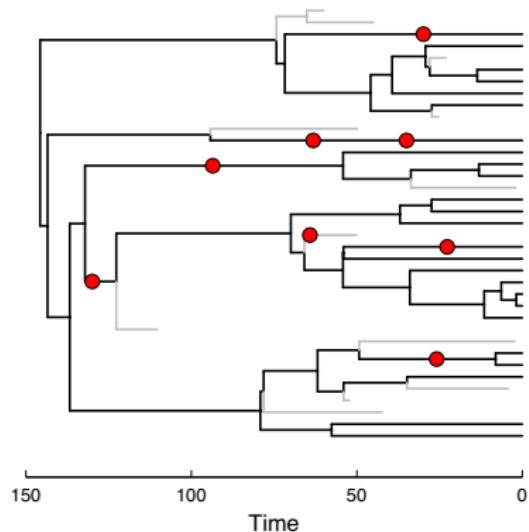
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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

λ = speciation

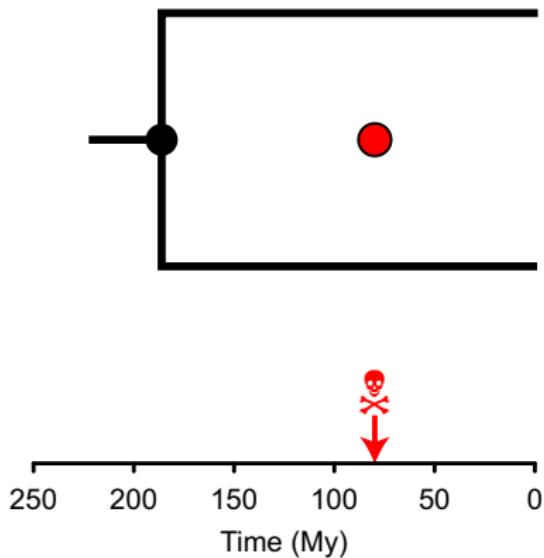
μ = extinction

ψ = fossilization/recovery



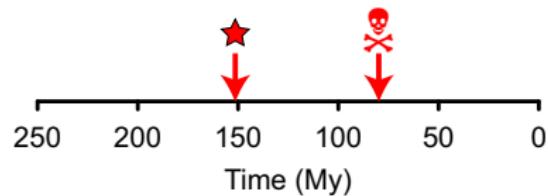
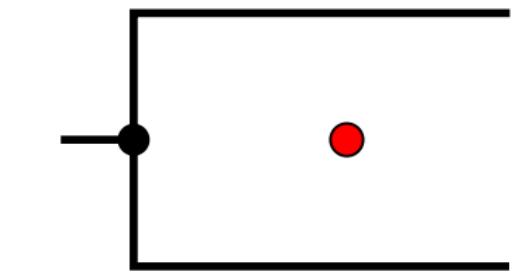
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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



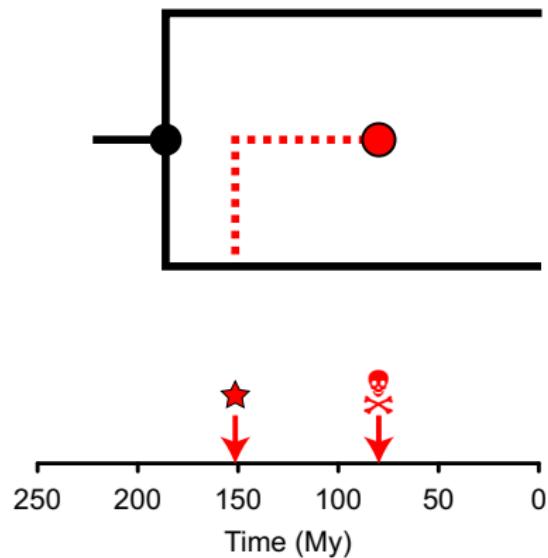
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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



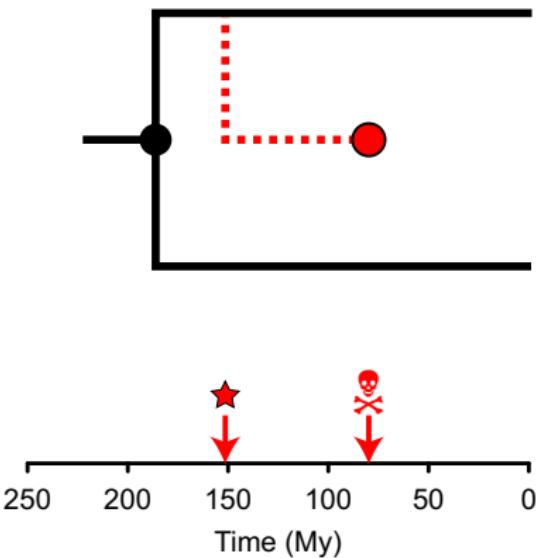
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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



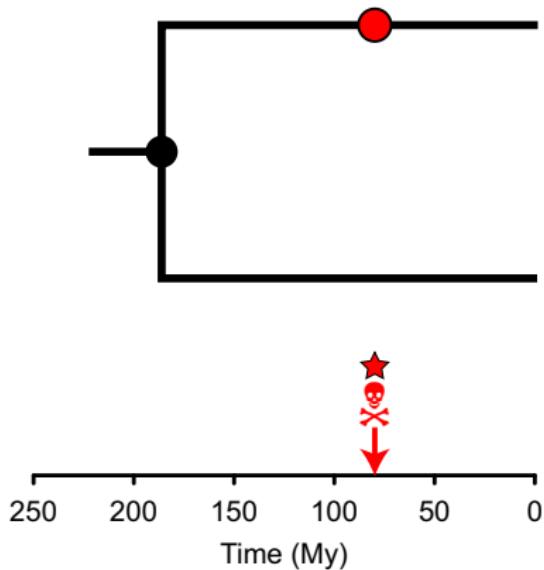
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

MCMC is used to propose new topological placements for the fossil



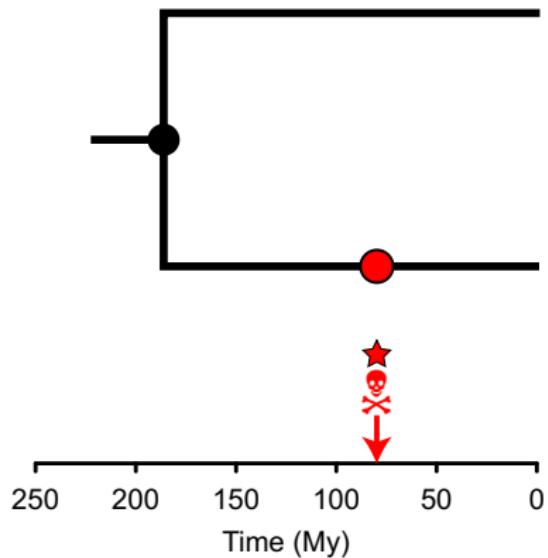
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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



THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

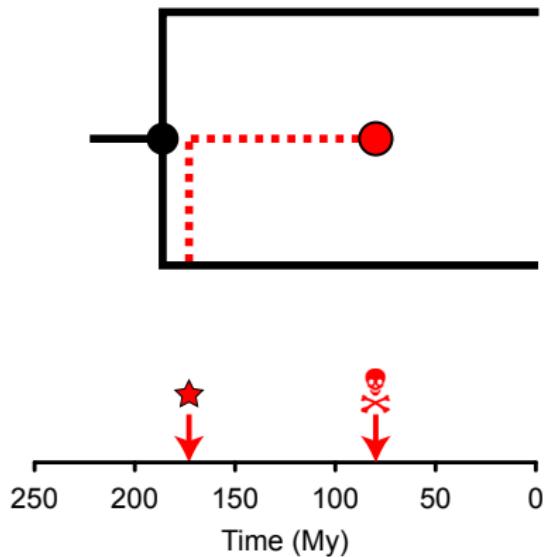
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THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

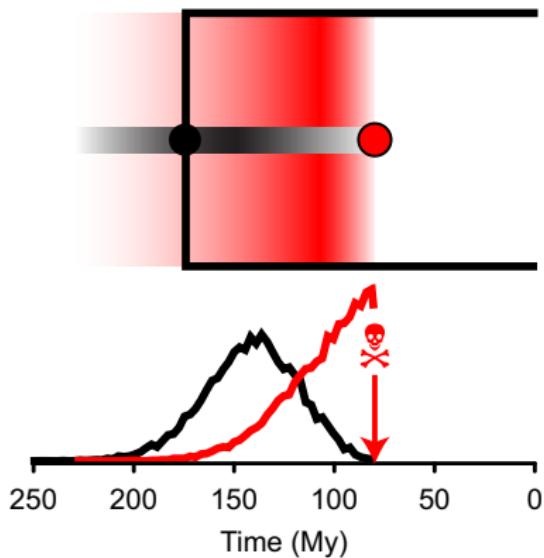
The probability of any realization of the diversification process is conditional on:

λ , μ , and ψ



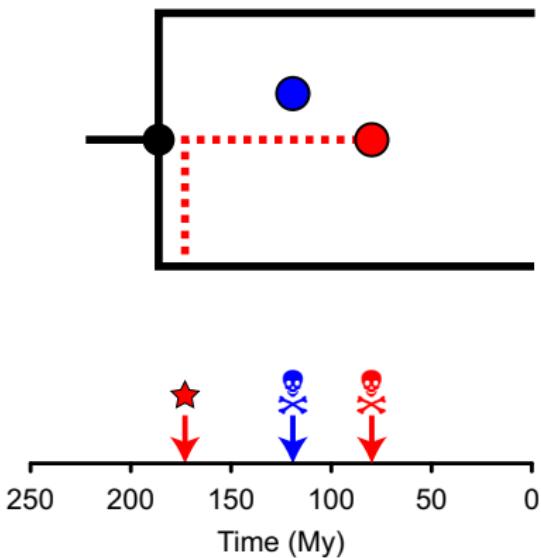
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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



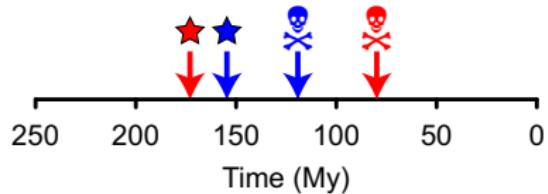
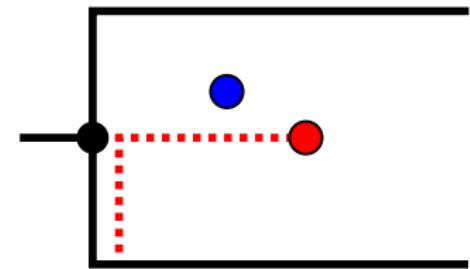
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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



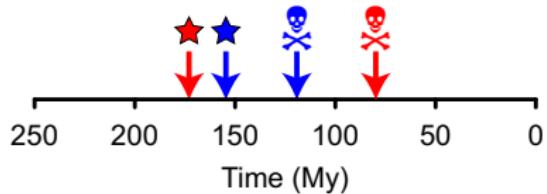
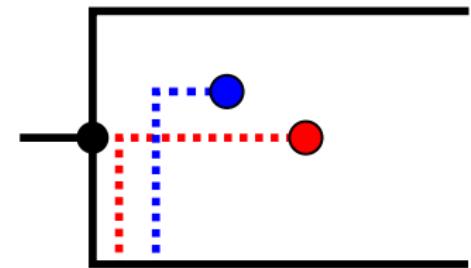
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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



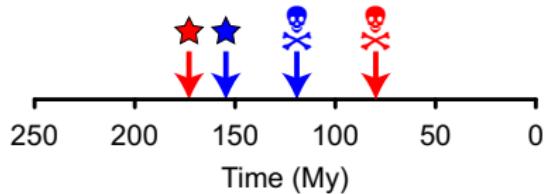
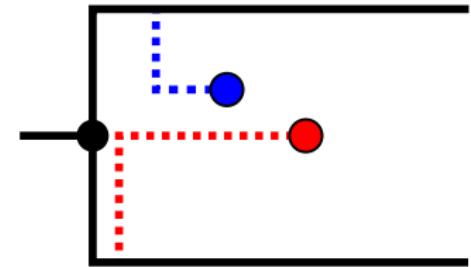
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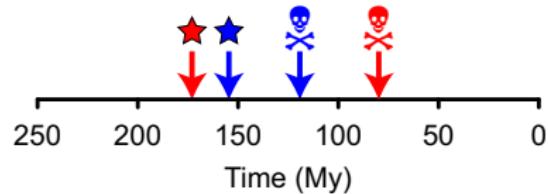
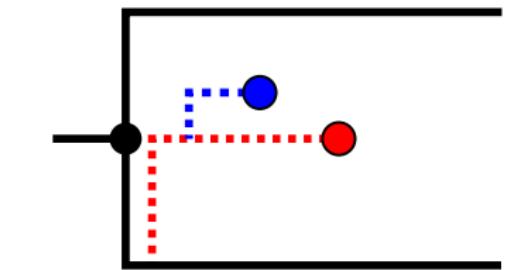
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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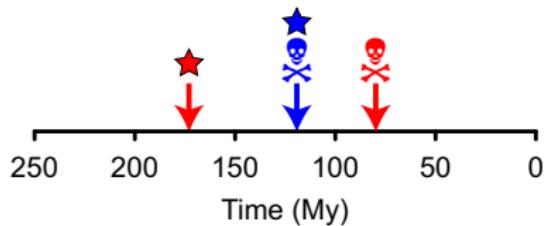
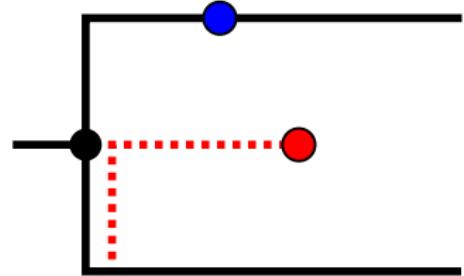
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

Or the unobserved branch leading to the other fossil



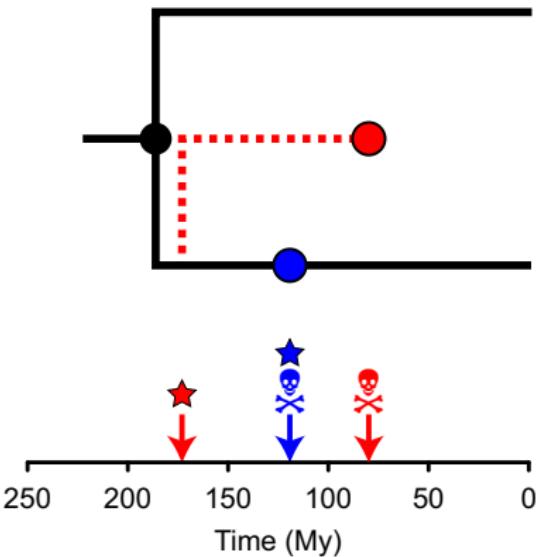
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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



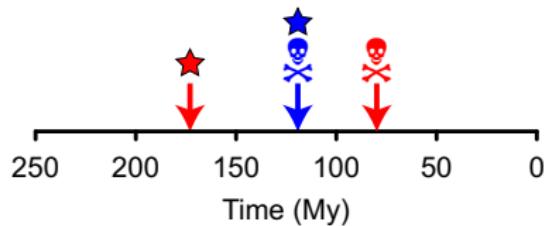
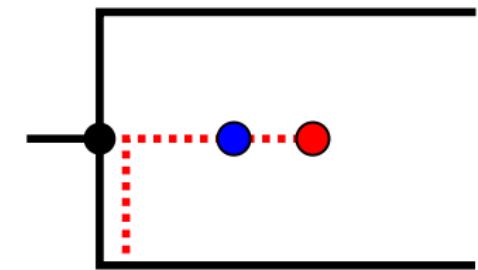
THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

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THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

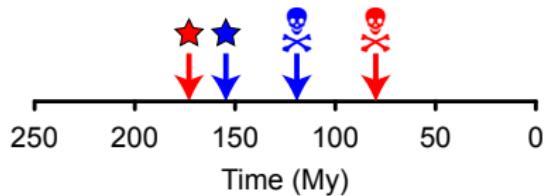
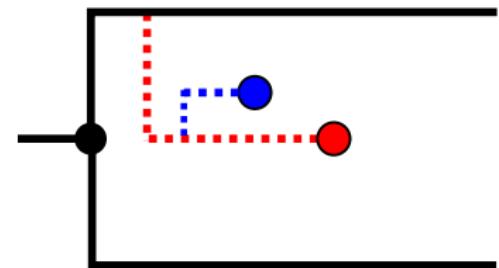
Or it is an ancestor of the other sampled fossil



THE FOSSILIZED BIRTH-DEATH PROCESS (FBD)

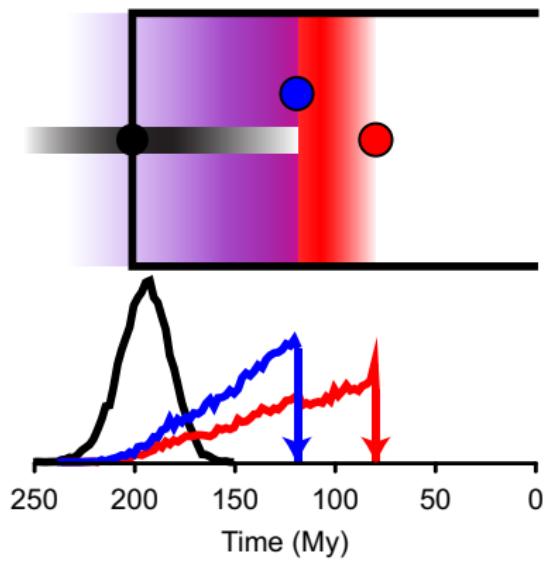
The probability of this realization of the diversification process is conditional on:

λ , μ , and ψ



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



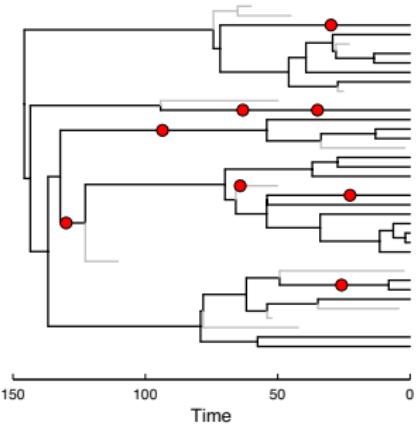
SAMPLED ANCESTORS

Sampled lineages with sampled descendants

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

On the probability of ancestors in the fossil record

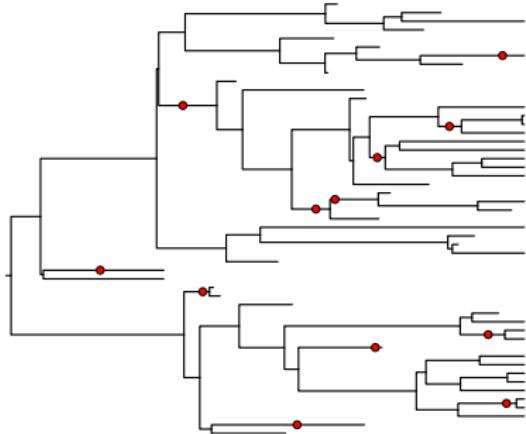
Mike Foote



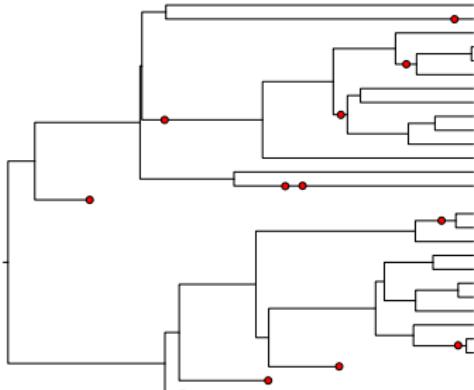
There is a non-zero probability of sampling ancestor-descendant relationships from the fossil record

SAMPLED ANCESTORS

Complete FBD Tree



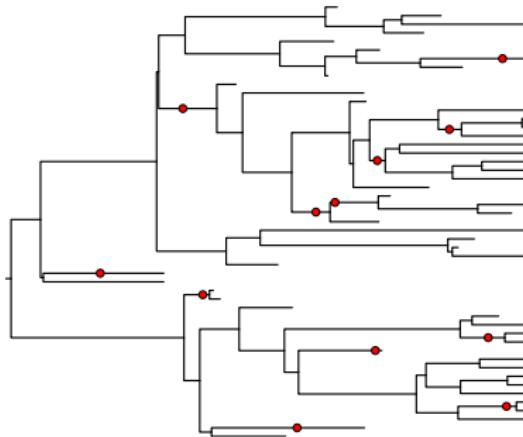
Reconstructed FBD Tree



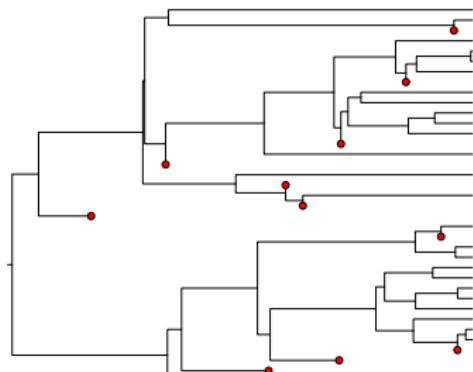
Because fossils & living taxa are assumed to come from a single diversification process, there is a non-zero probability of sampled ancestors

SAMPLED ANCESTORS

Complete FBD Tree

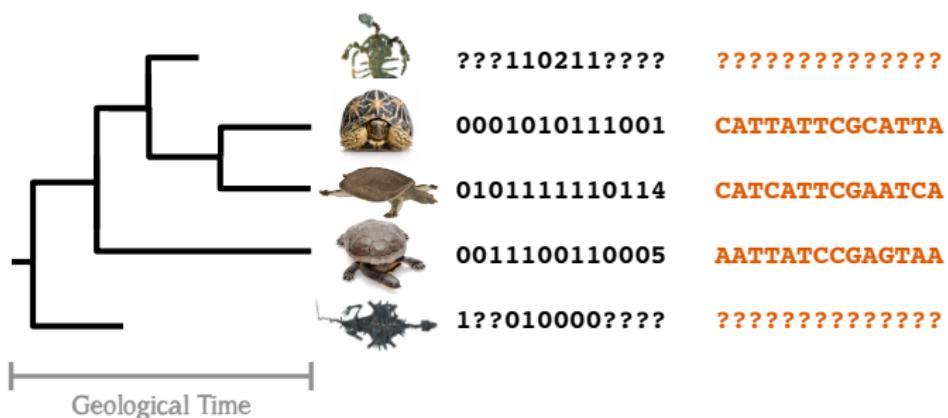
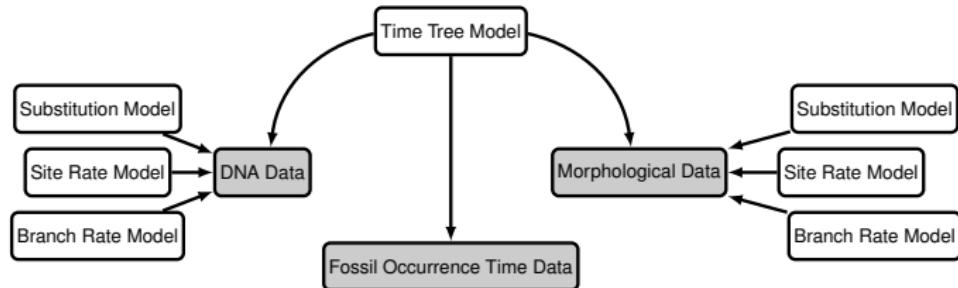


No Sampled Ancestor Tree

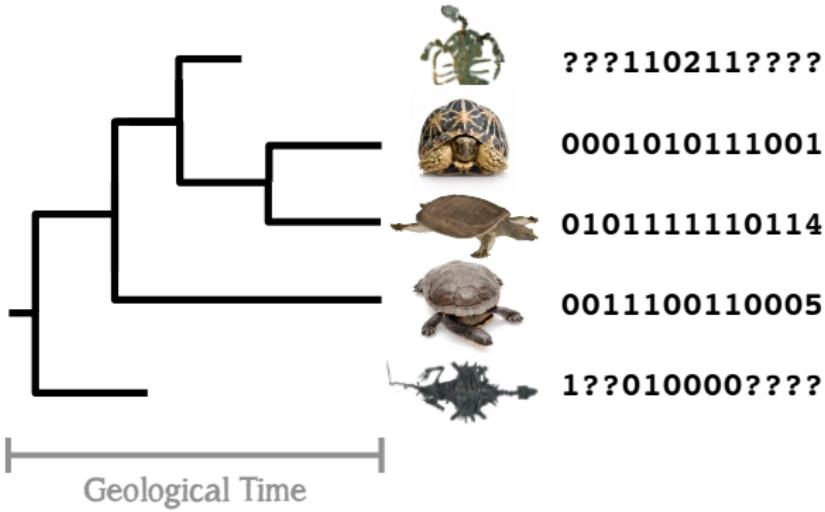


If all fossils are forced to be on separate lineages, this induces additional speciation events and will, in turn, influence rate & node-age estimates.

COMBINING FOSSIL & EXTANT DATA



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

T1 0

T2 0

T3 1

T4 2

T5 2

T6 1

T7 1

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

MODELING MORPHOLOGICAL CHARACTER CHANGE

The Lewis Mk ν model

Accounts for the ascertainment bias in morphological datasets

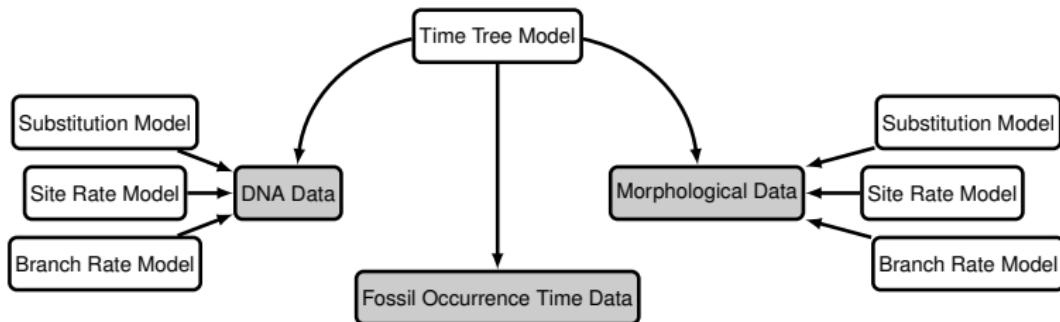
Adds a “dummy” character for each state to account for undersampling invariant characters

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

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

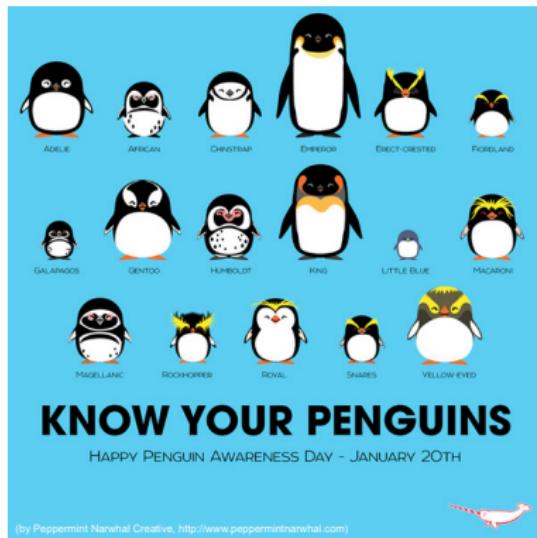
'TOTAL-EVIDENCE' ANALYSIS

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



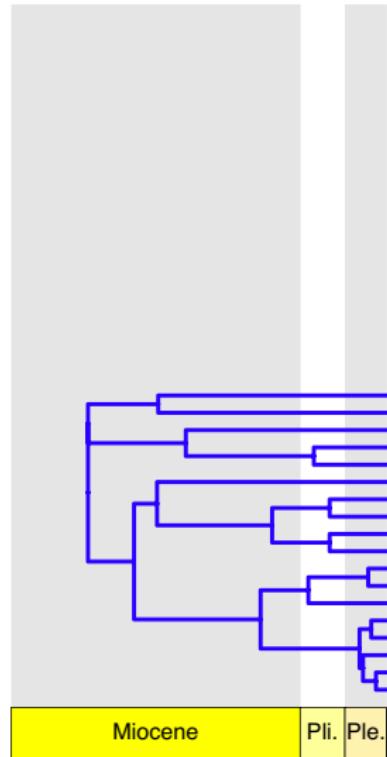
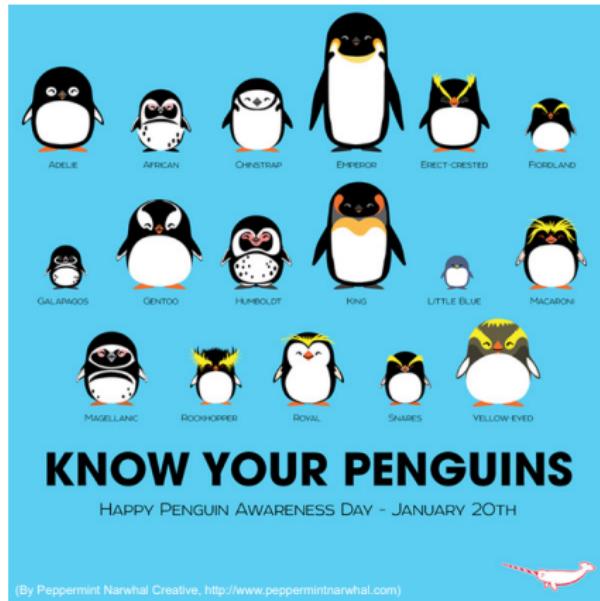
PENGUIN DIVERSITY IN DEEP TIME

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

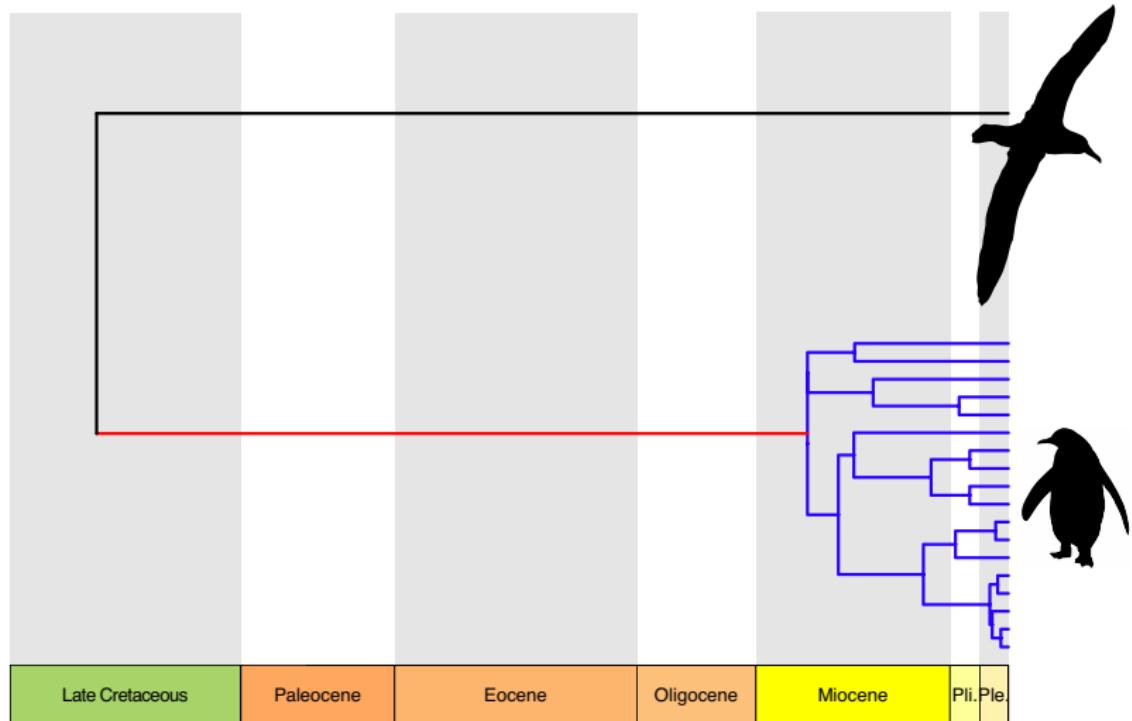


Artistic reconstructions by: Stephanie Abramowicz for Scientific American
Fonfroy, R.E. and D.T. Keayka. Bull. AMNH, 337(1):1-77 (2012)

PENGUIN DIVERSITY



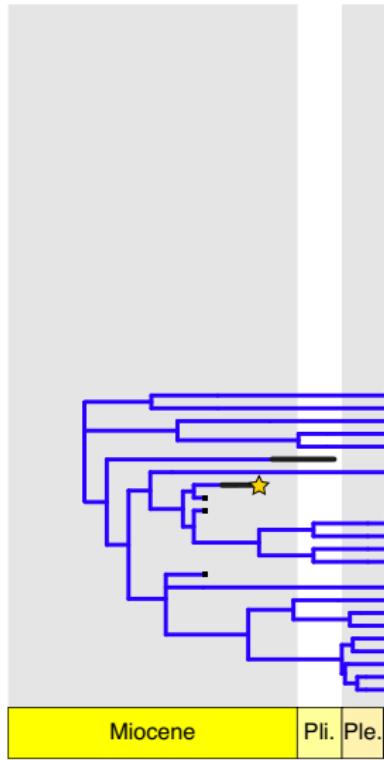
PENGUIN DIVERSITY



FOSSIL PENGUIN DIVERSITY



Martin Chávez



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

PENGUINS IN THE OLIGOCENE

Kairuku

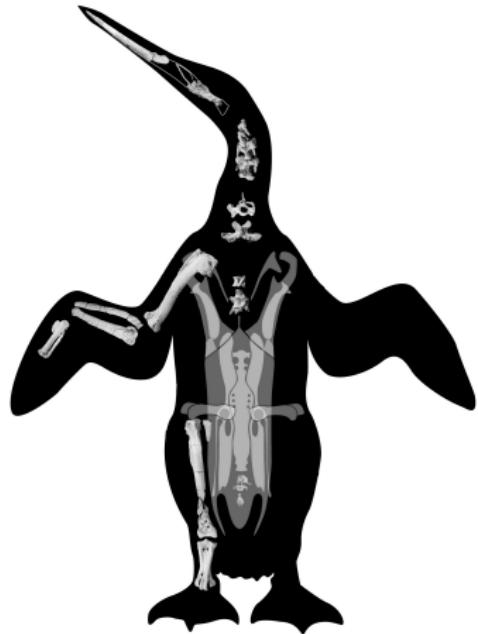
- ~1.5 m tall
- slender, with narrow bill
- scapula & pyostyle are more similar to non-penguins
- ~27 Mya



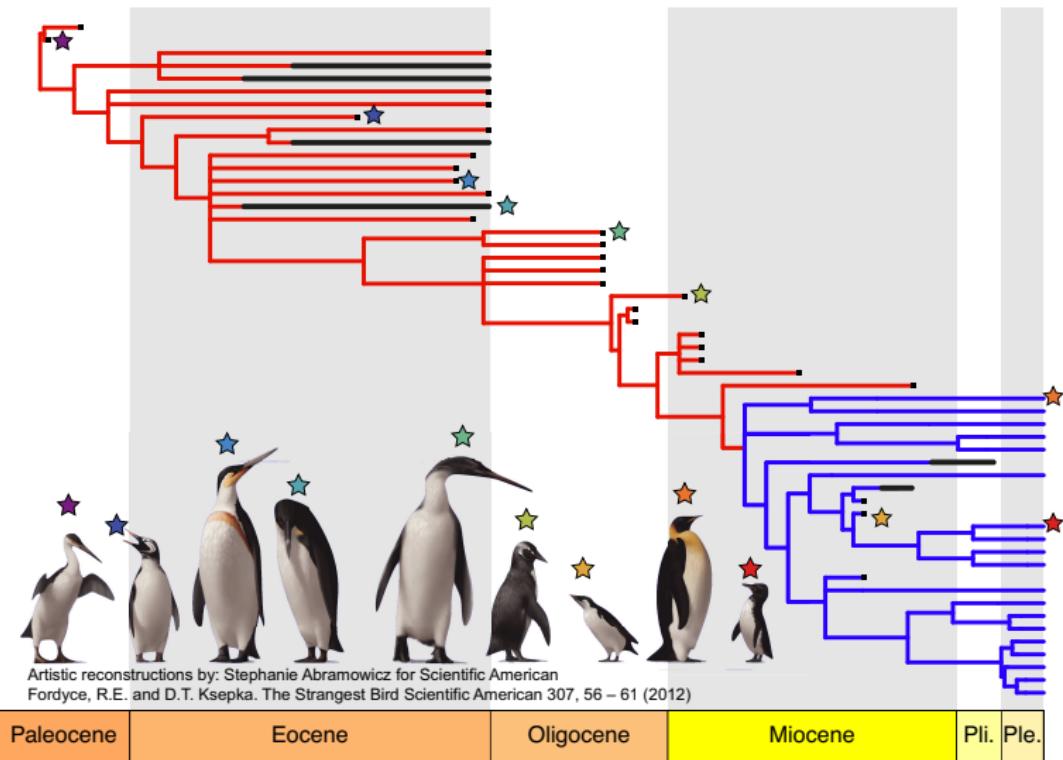
PENGUINS IN THE PALEOCENE

Waimanu

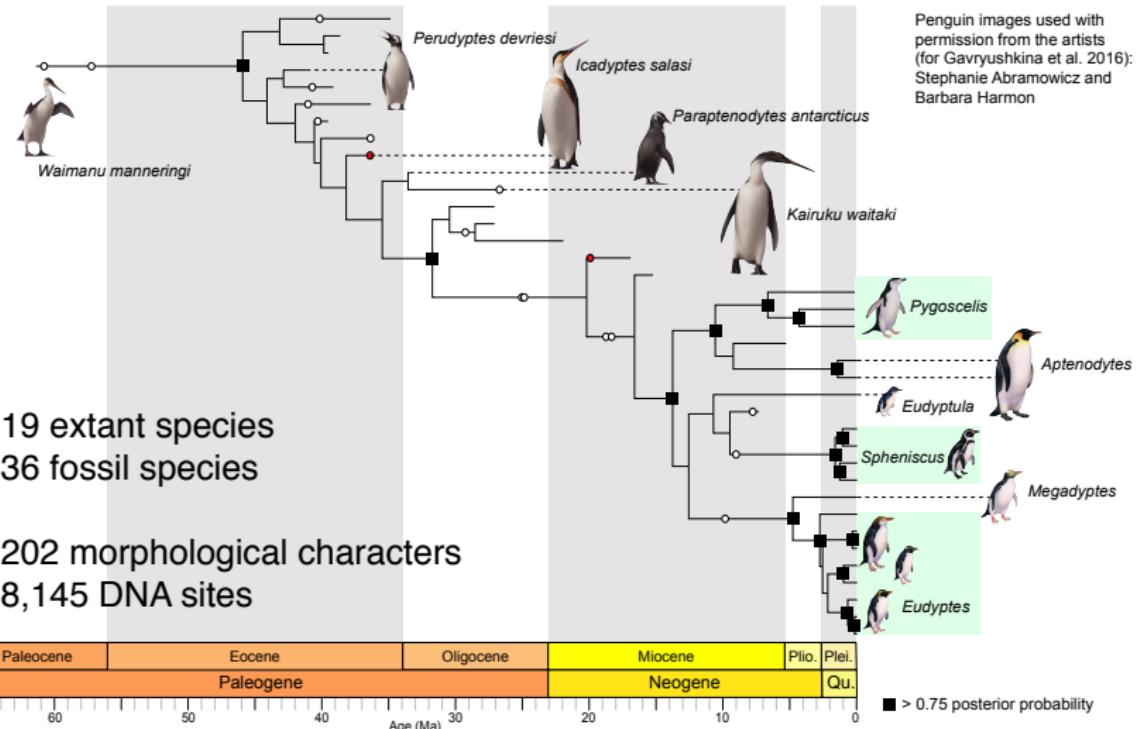
- oldest known penguin species
- intermediate wing morphology
- ~58–61.6 Mya



PENGUIN DIVERSITY IN DEEP TIME

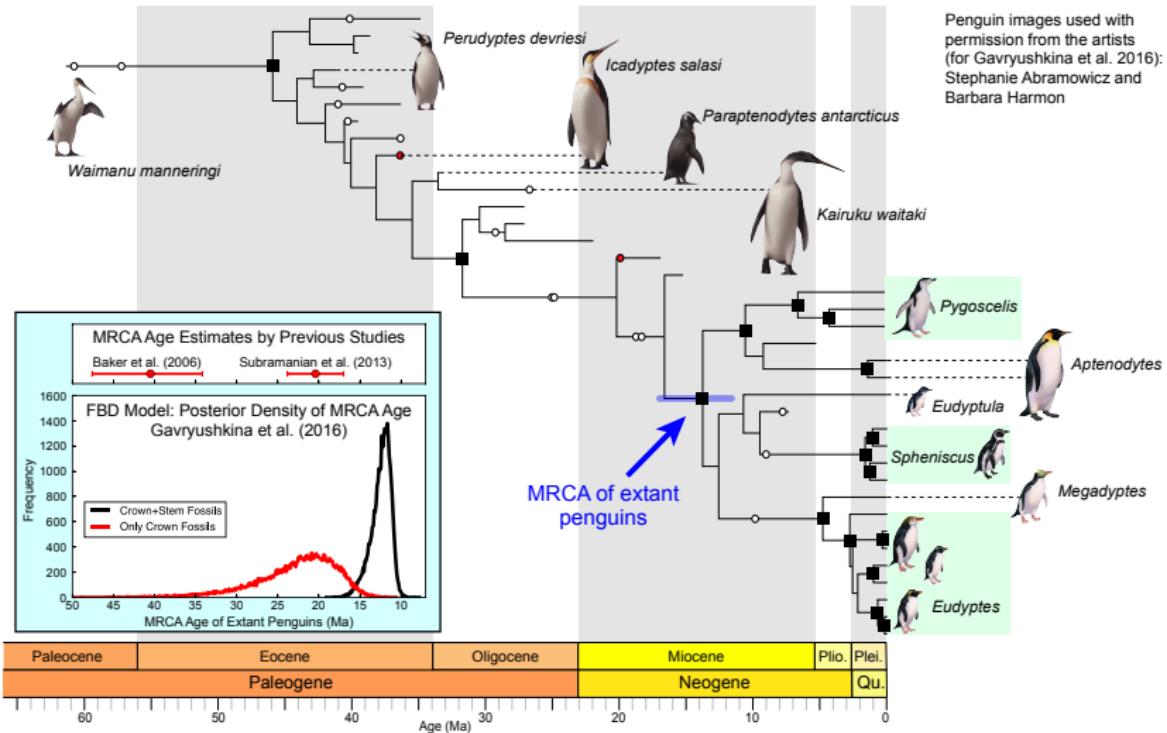


PENGUIN DIVERSITY IN DEEP TIME



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

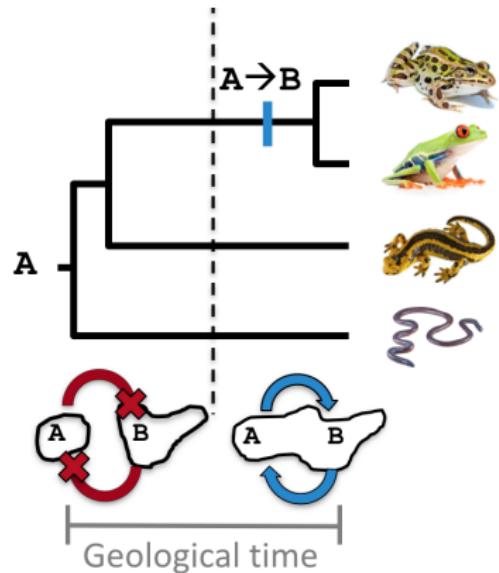
PENGUIN DIVERSITY IN DEEP TIME



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.

DATING + ANCESTRAL AREA RECONSTRUCTION

See Michael Landis' talk:

<https://www.youtube.com/watch?v=H0CFjMrvLsQ>