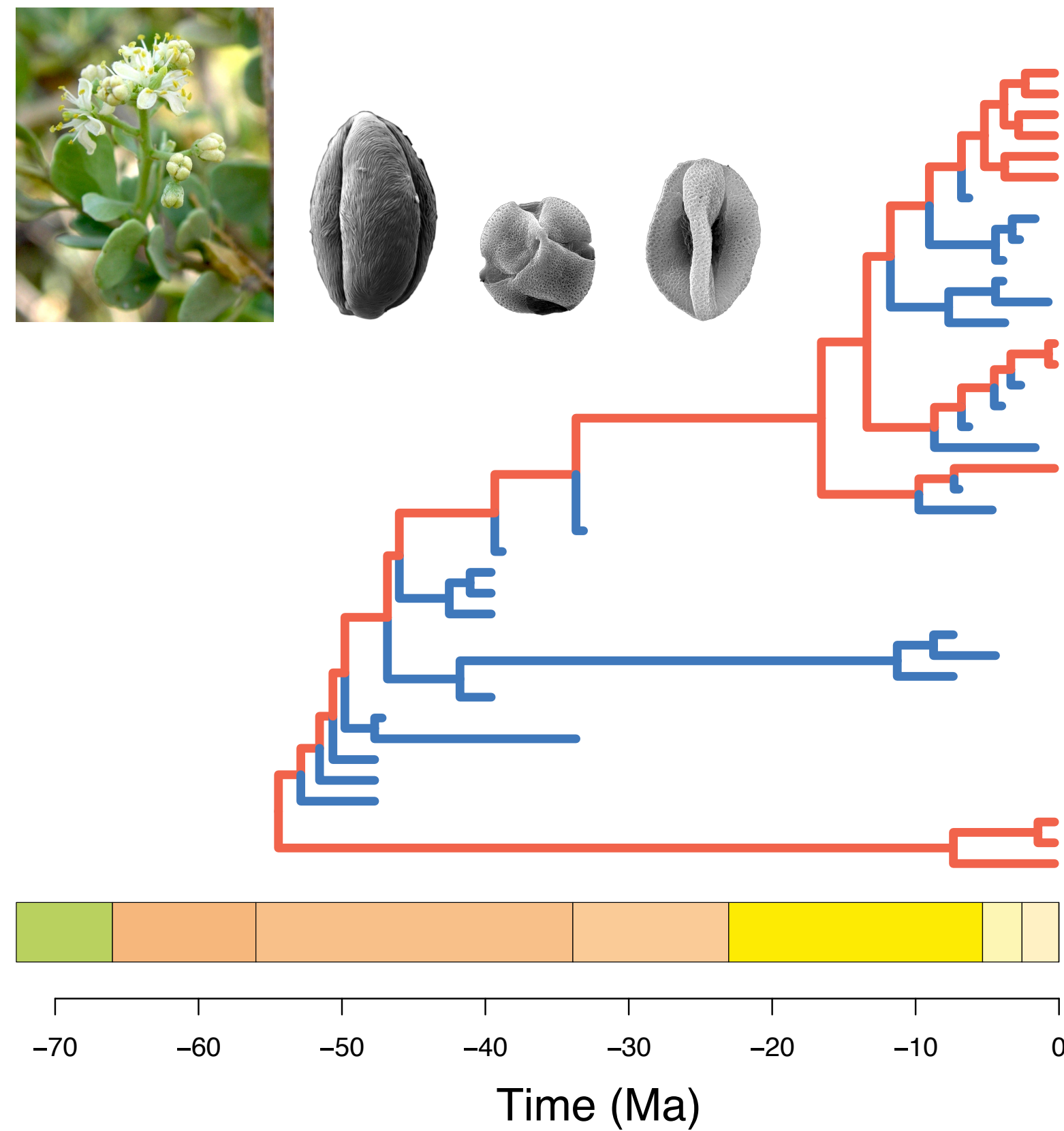


Challenges and potential of integrating fossil and molecular data in evolutionary analyses



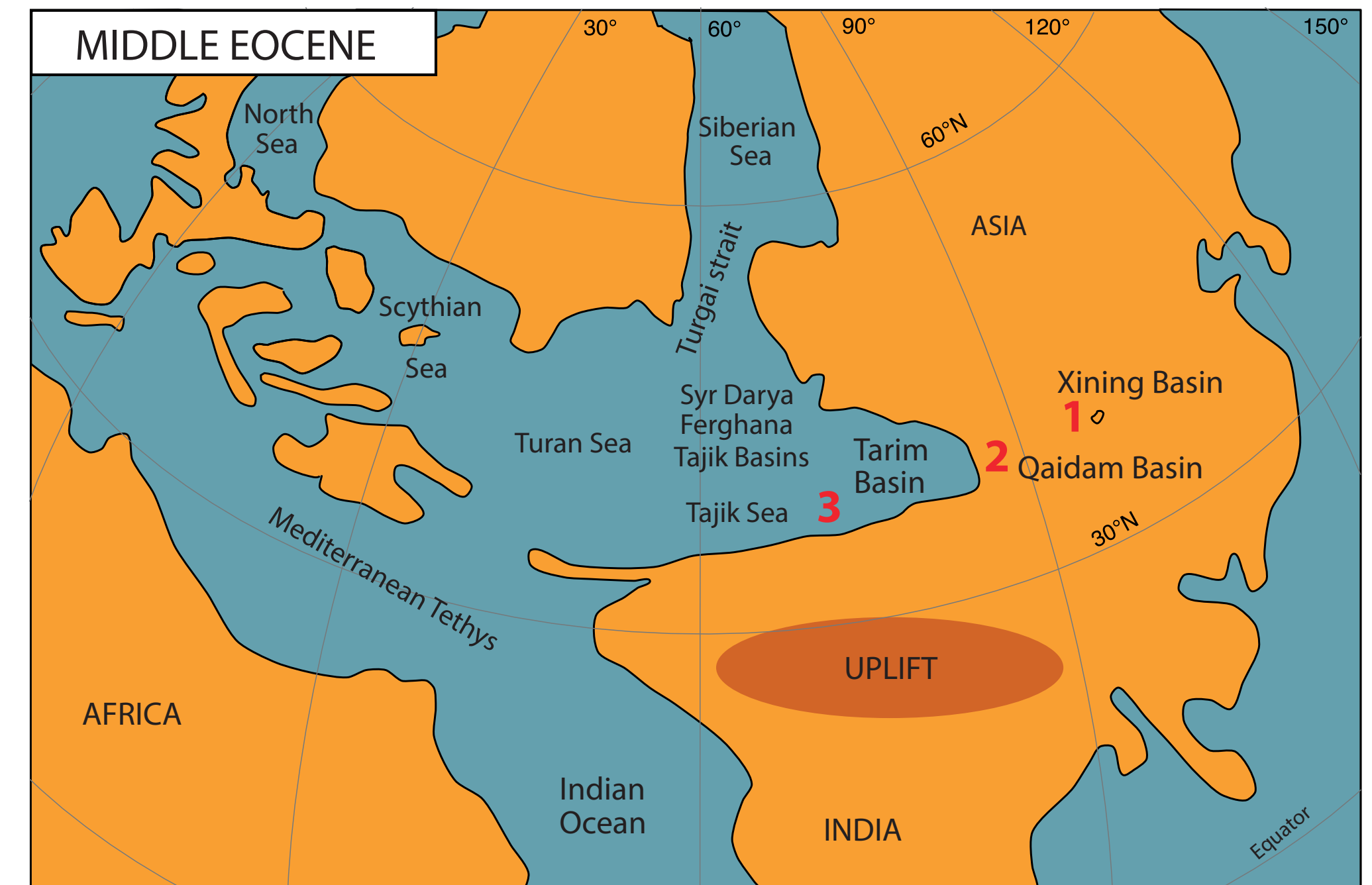
Macroevolutionary analyses: speciation, extinction, and trait evolution

Why are there plants adapted to brackish water in Tibet?



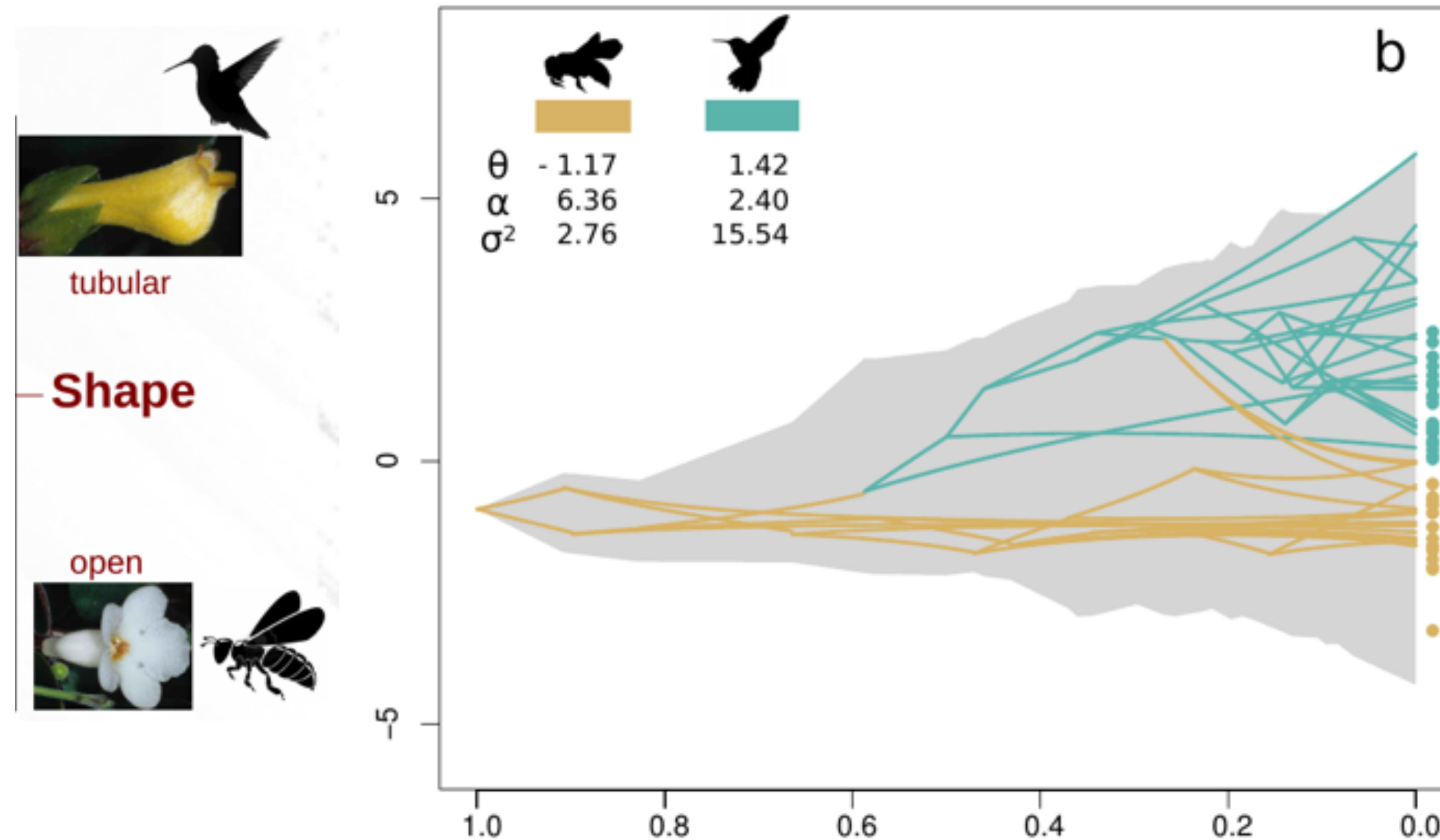
Diversification of Nitrariaceae

Woutersen et al. in prep.



Macroevolutionary analyses: speciation, extinction, and trait evolution

How do species interactions shape phenotypic evolution?

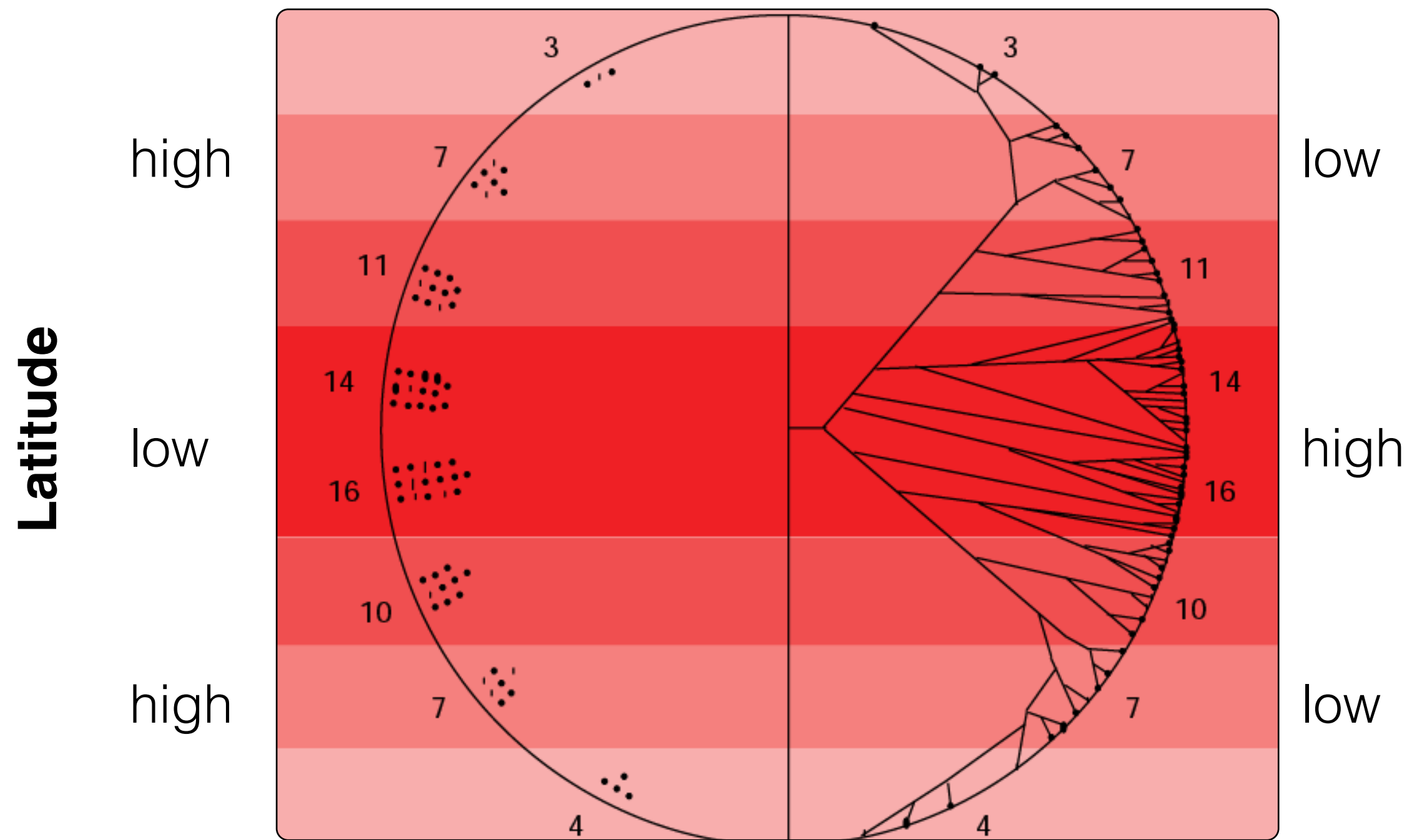


Floral evolution in Gesnariaceae

Serrano-Serrano et al. 2015 BMC Evol Biol

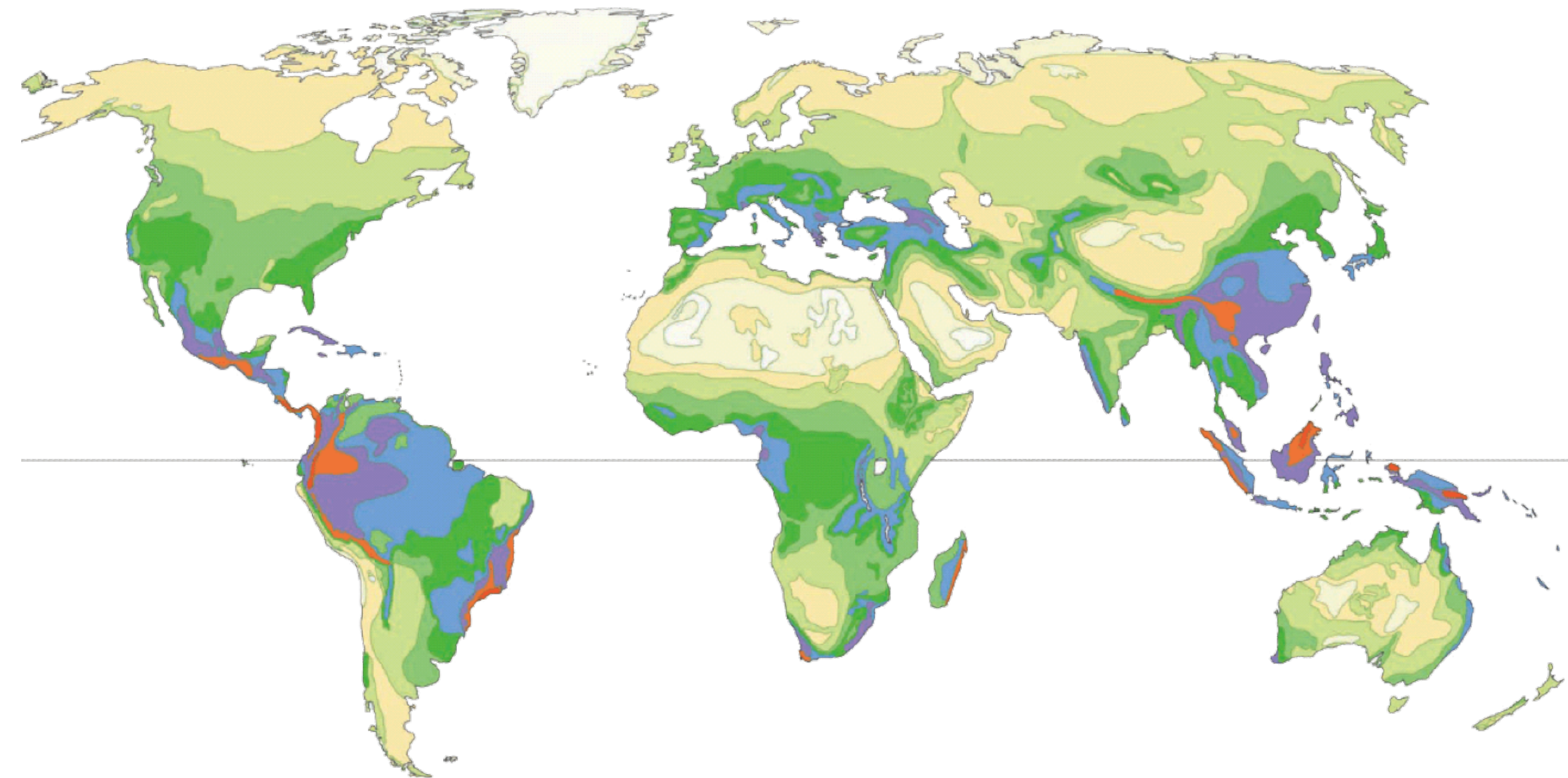
Macroevolutionary analyses: speciation, extinction, and trait evolution

Latitudinal Diversity Gradient (LDG)



Wiens and Donoghue, TREE 2004

Plant biodiversity hotspots

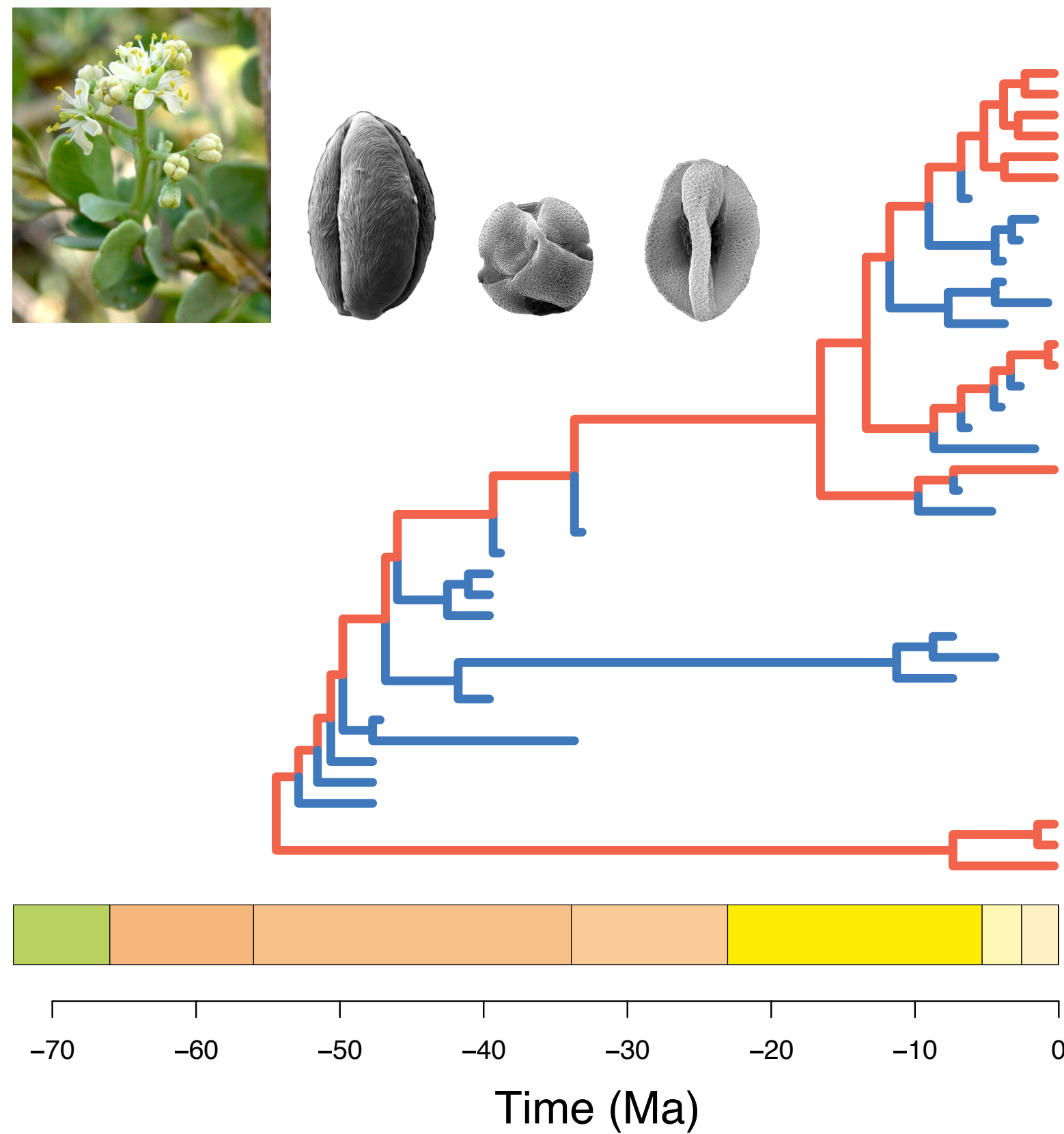


Barthlott et al . Erdkunde 2007

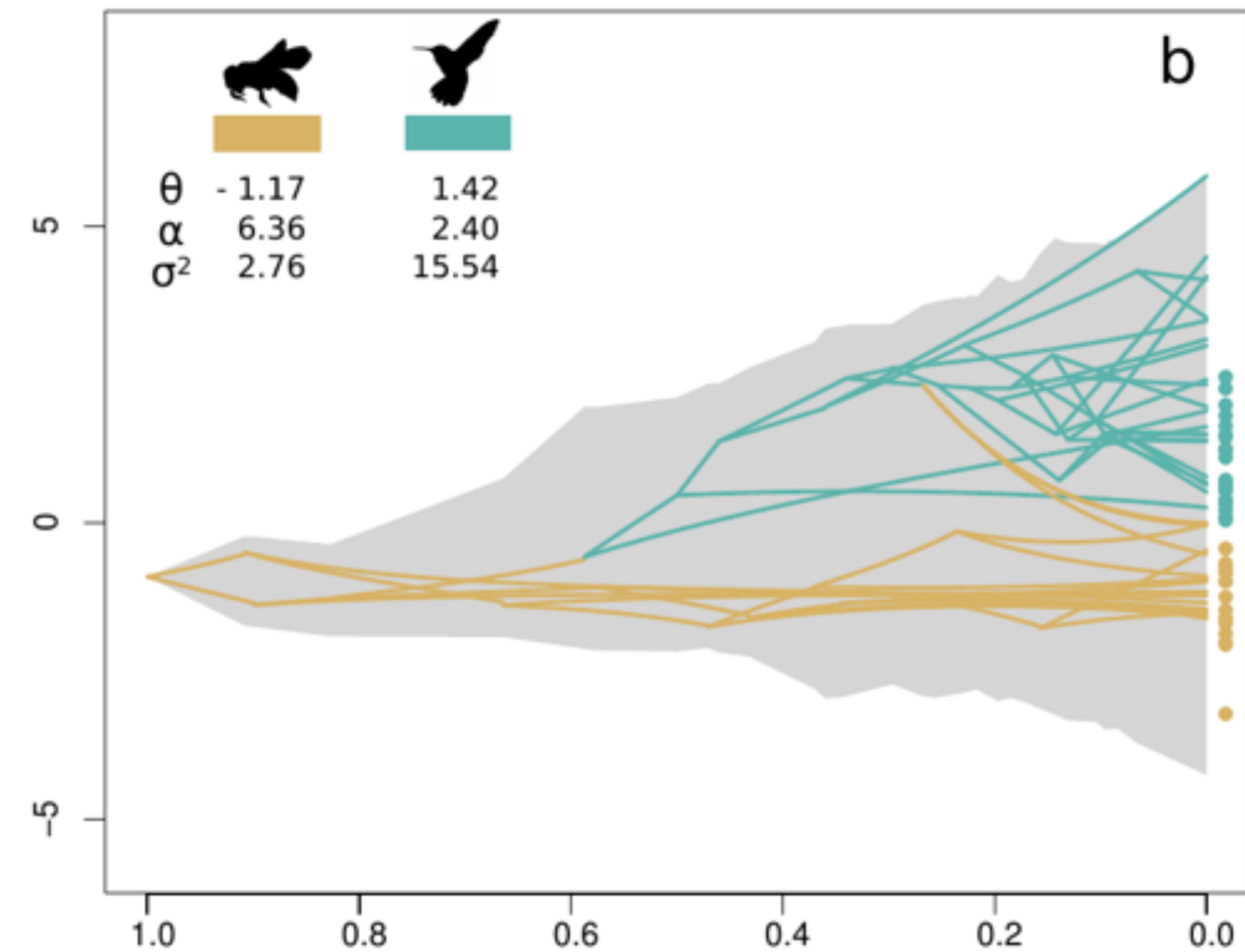
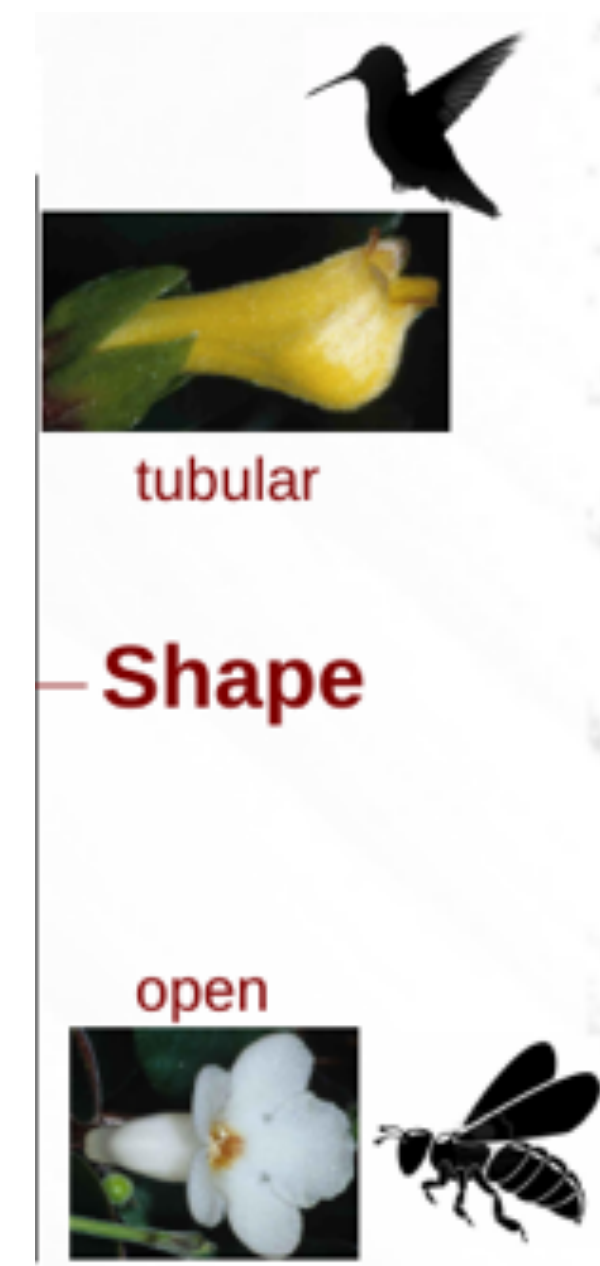
- Time to diversify
- Speciation and extinction rates
- Dispersal and migration rates

Macroevolutionary analyses: speciation, extinction, and trait evolution

Species diversification



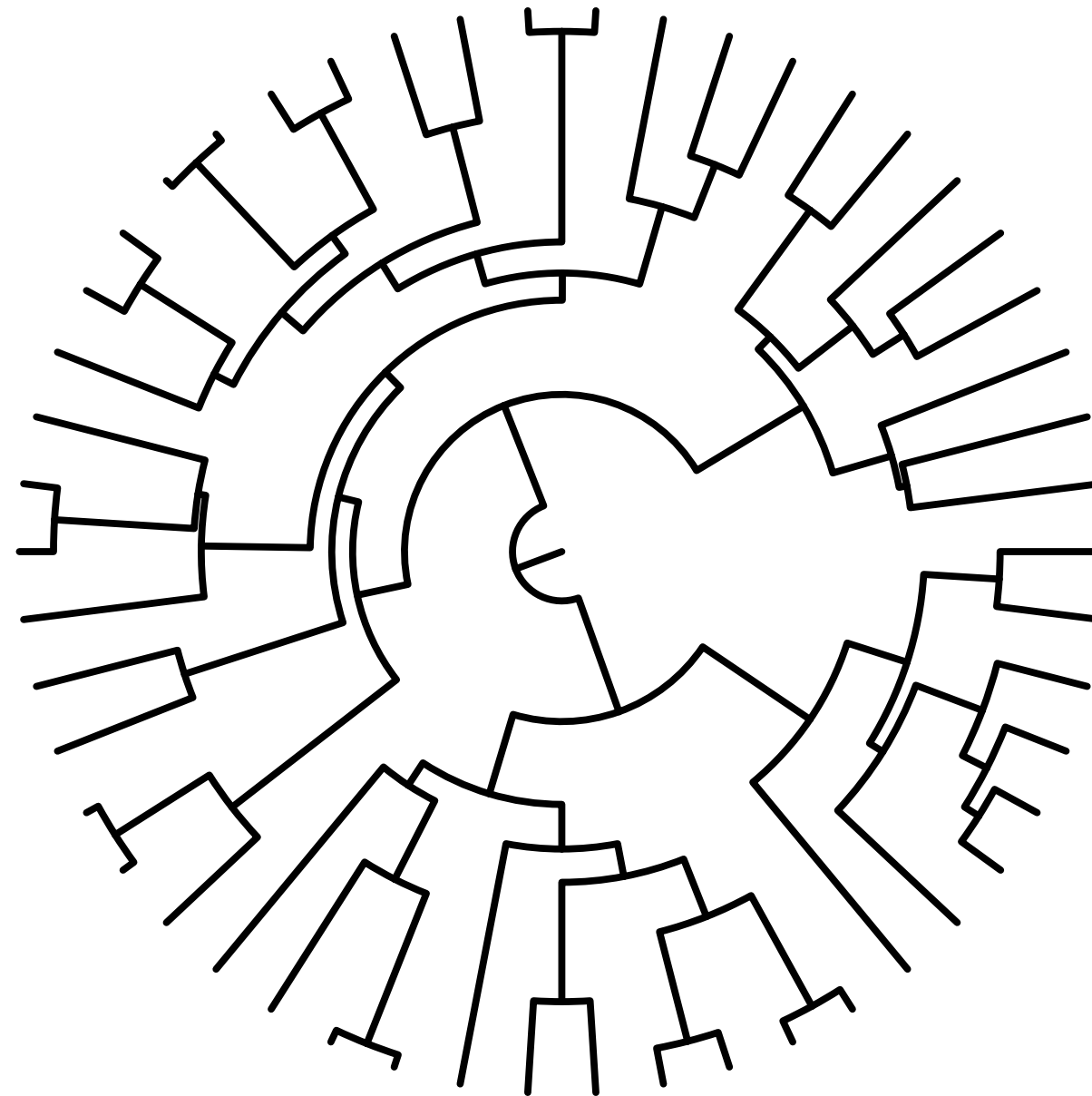
Trait evolution



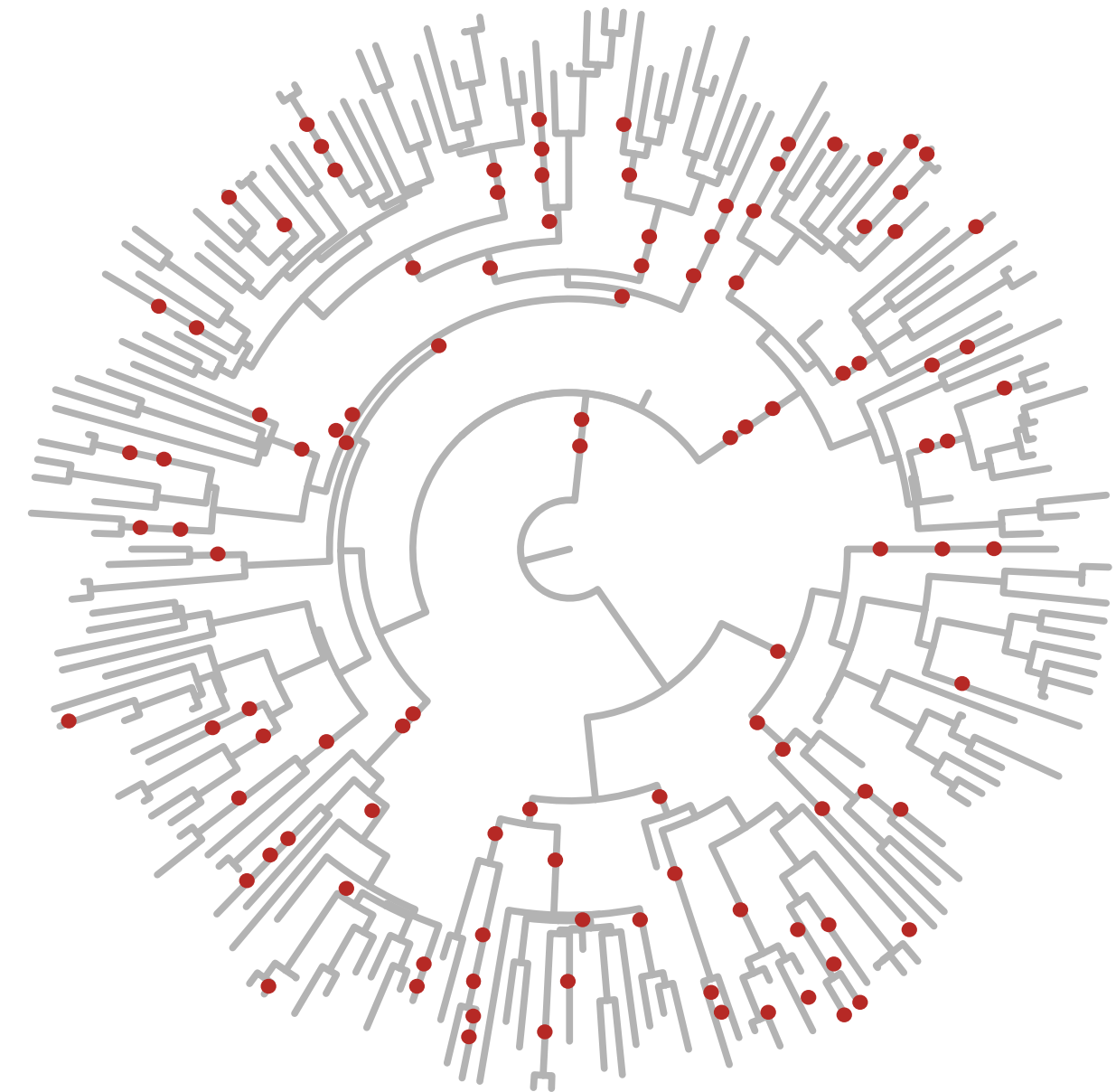
Extant-taxa phylogenies and the fossil record



**Complete
evolutionary history
of a clade**

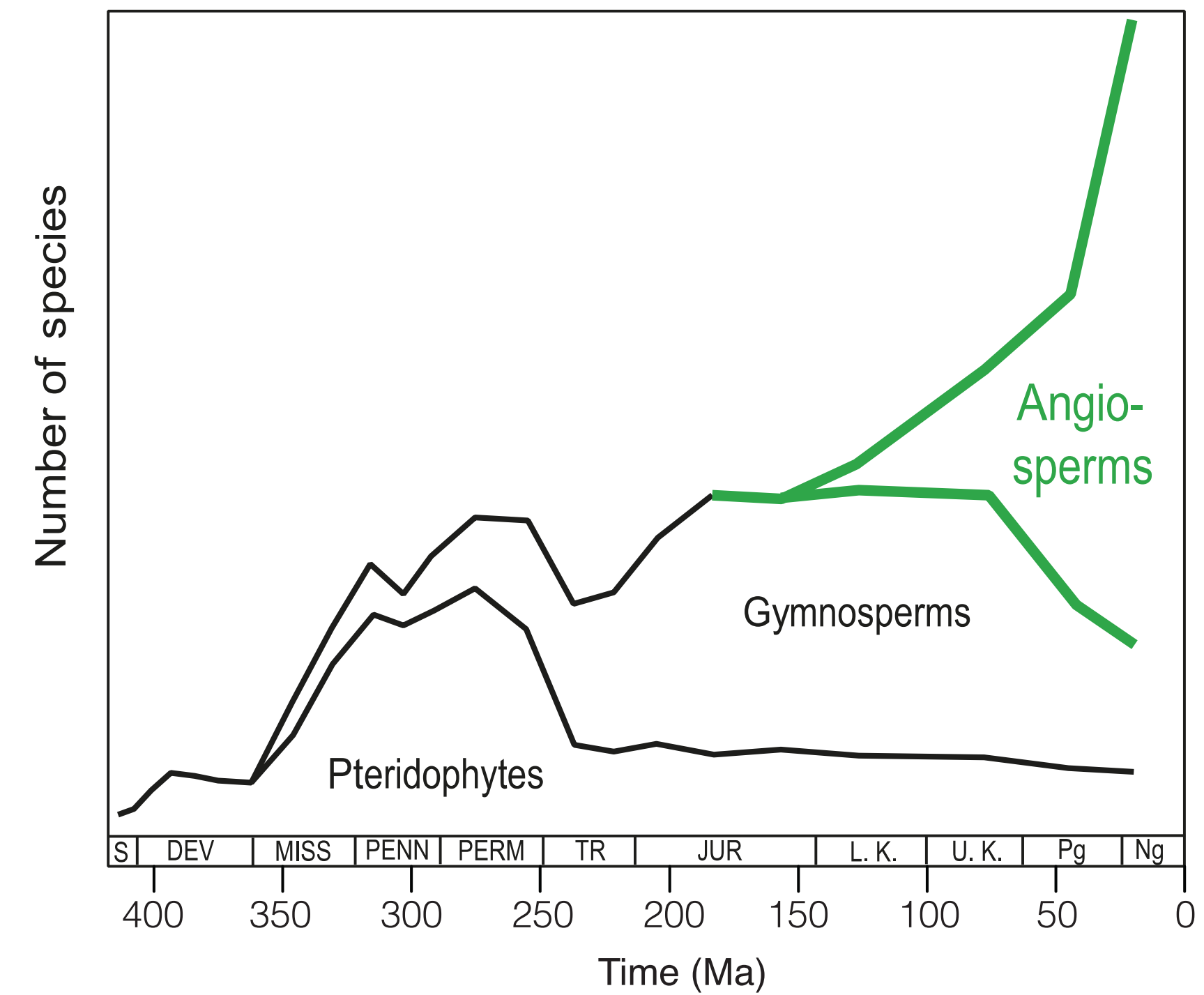
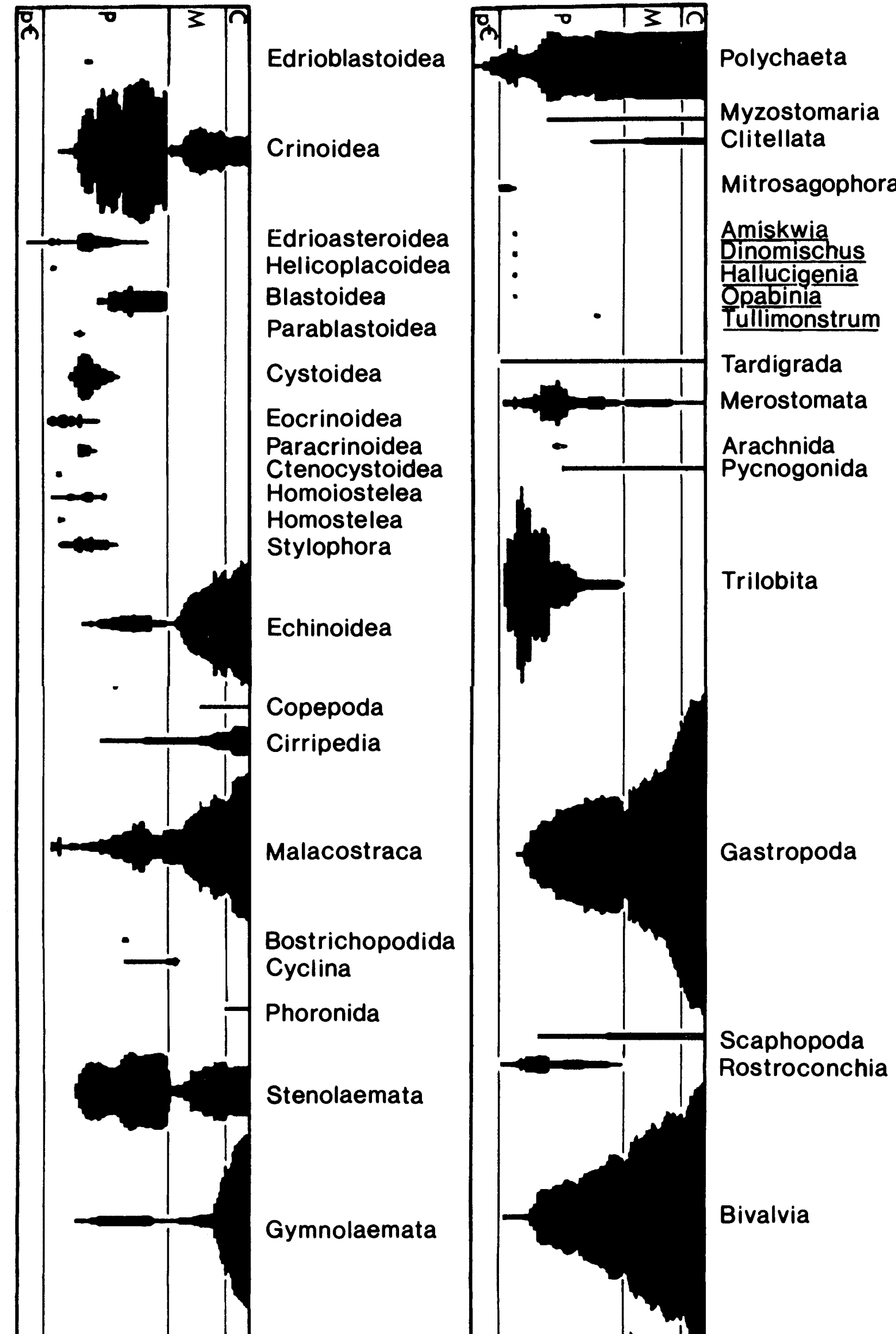


**Reconstructed
phylogeny of the
extant taxa**



Fossil record

Fossil-based estimates of species diversification

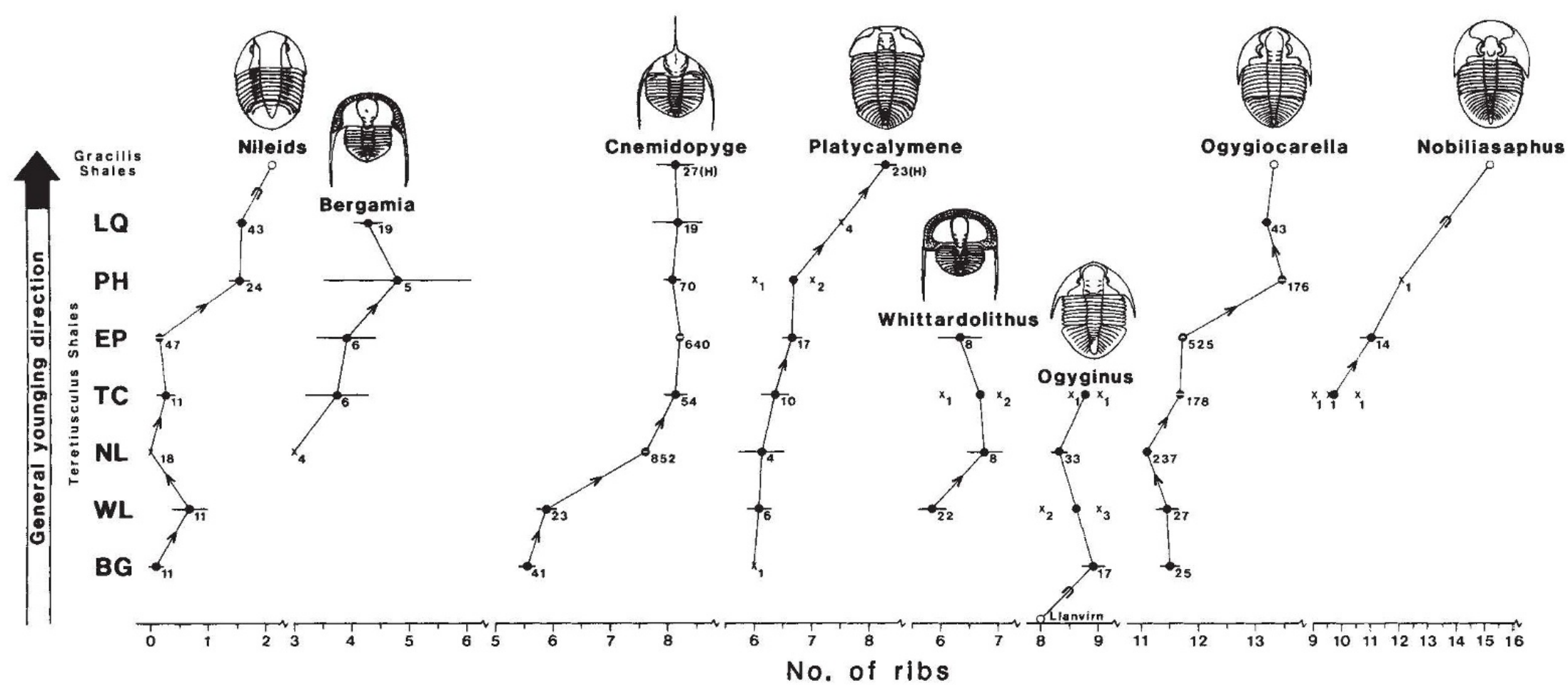


Spindle diagrams from fossil counts to understand broad diversification patterns in life history

Sepkoski 1981 Paleobiology; Niklas et al. 1983 Nature

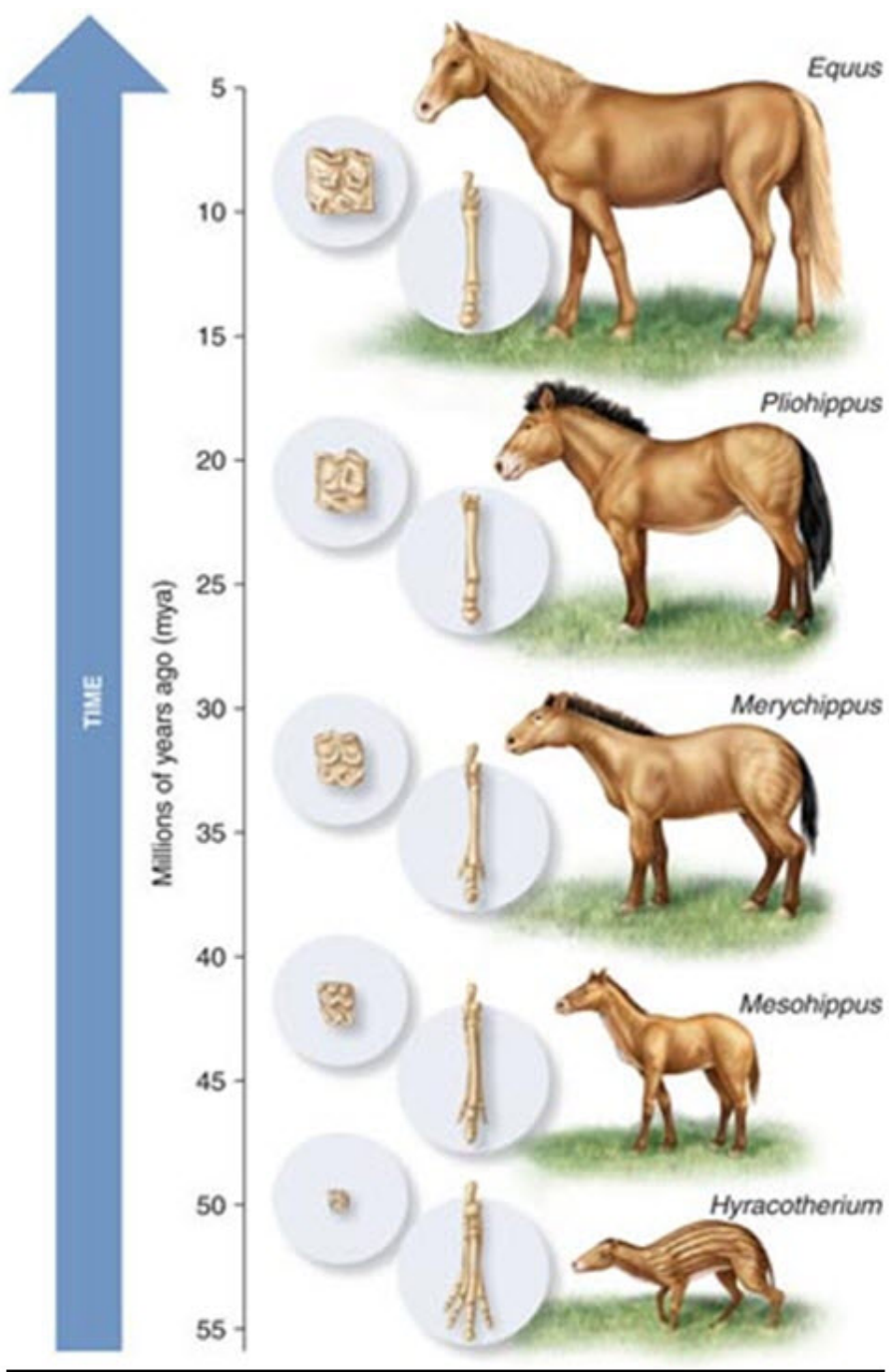
Fossil-based estimates of trait evolution

Random, gradual evolution

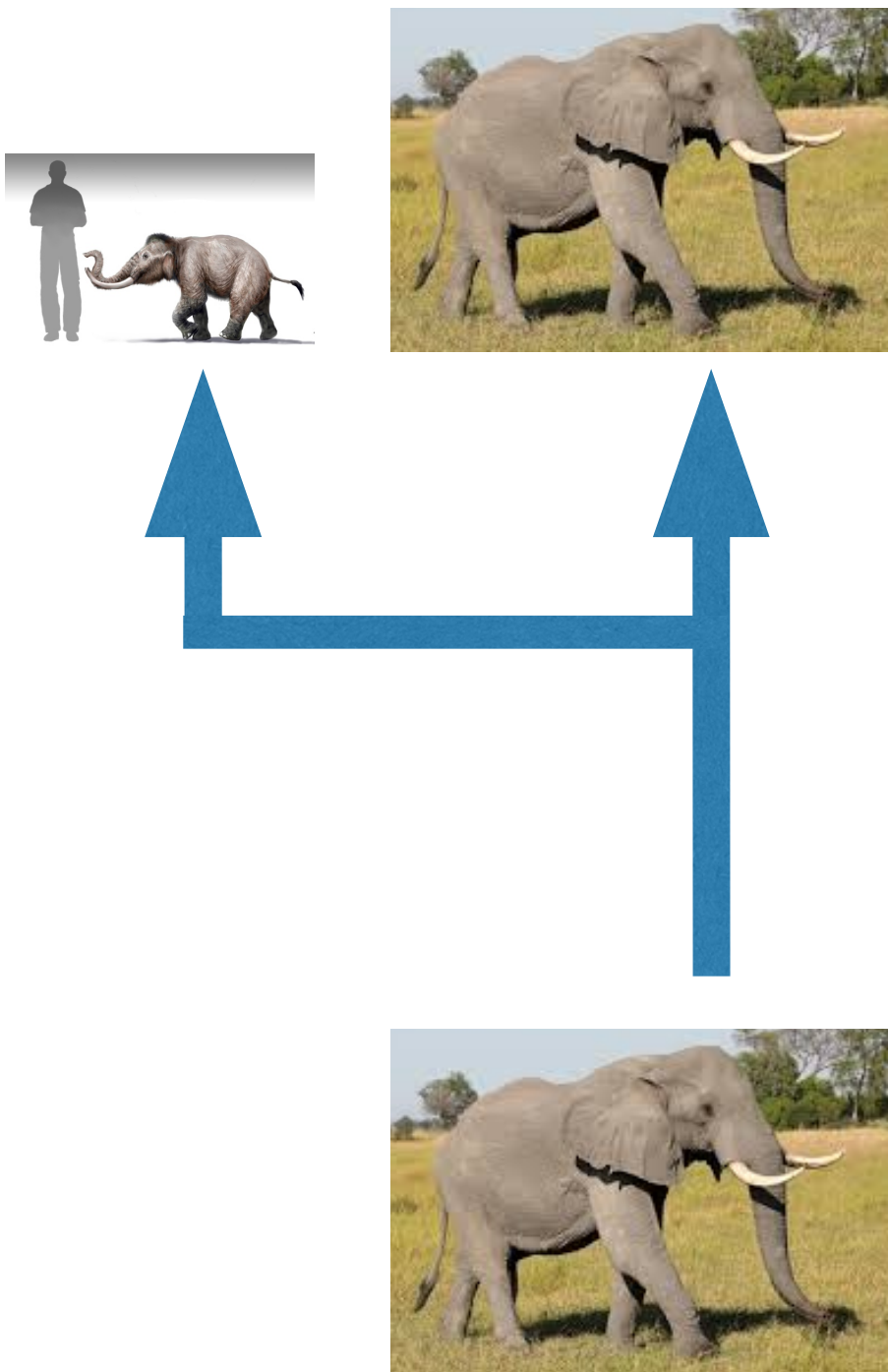


Sheldon 1987 Nature

Evolutionary trends

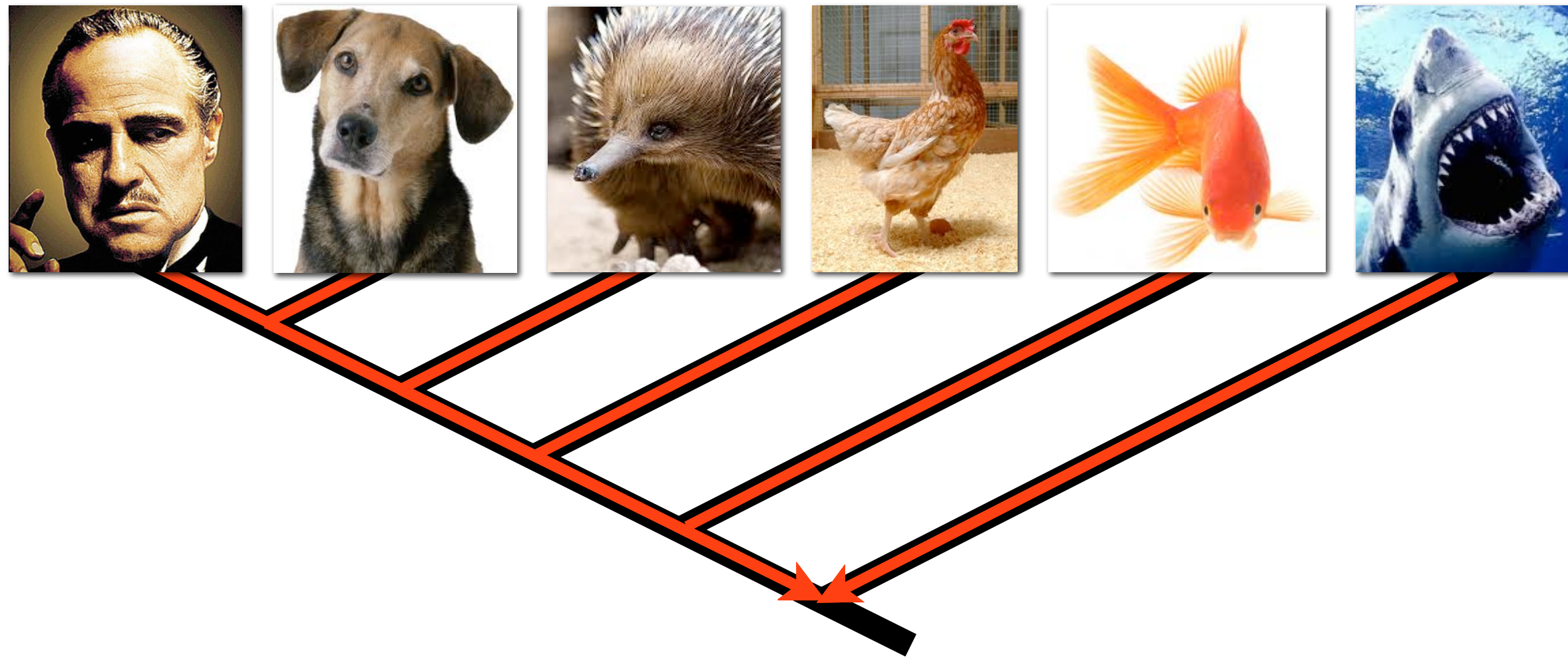


Phenotypic jumps

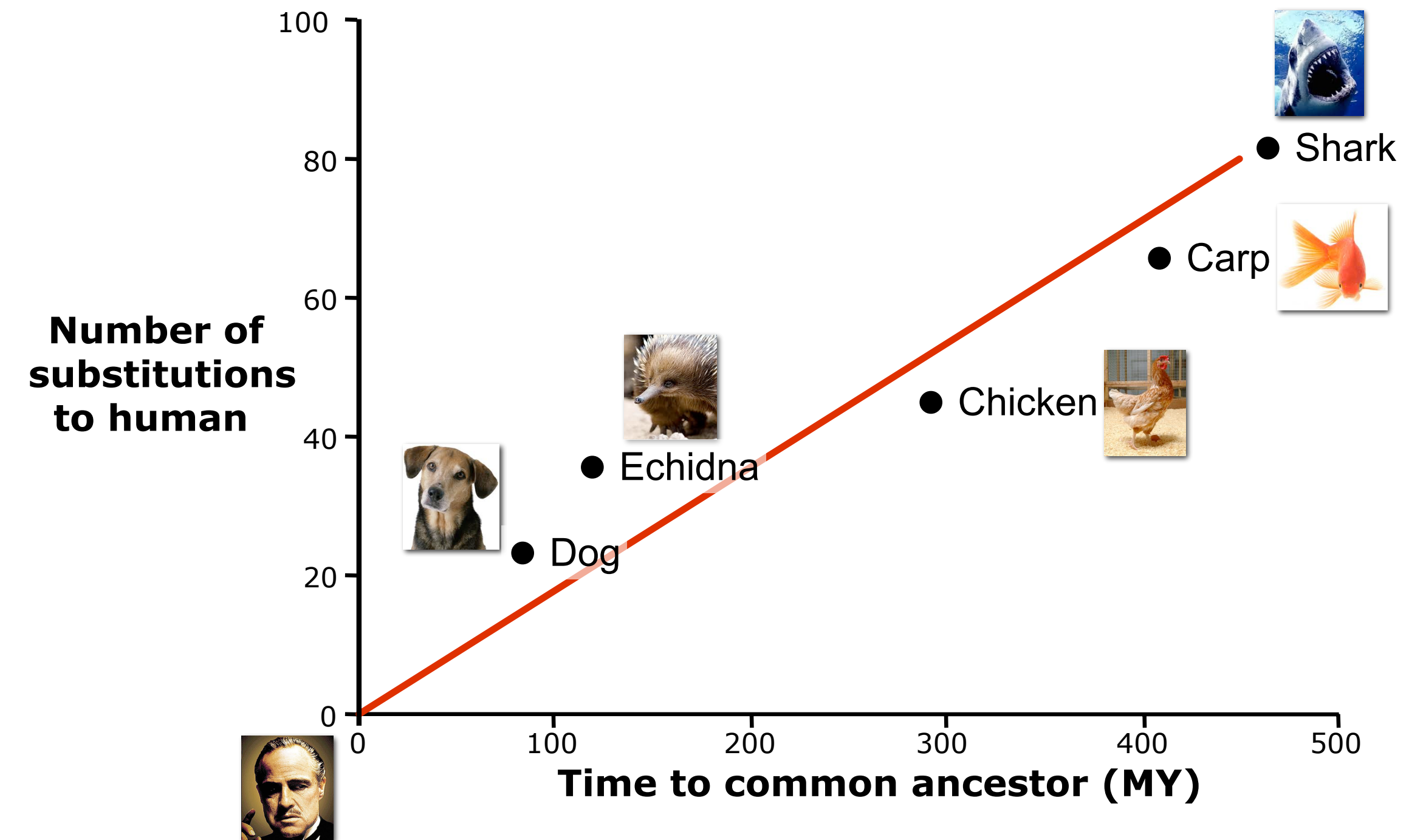


...meanwhile molecular phylogenetics started to take off

Theorizing the molecular clock

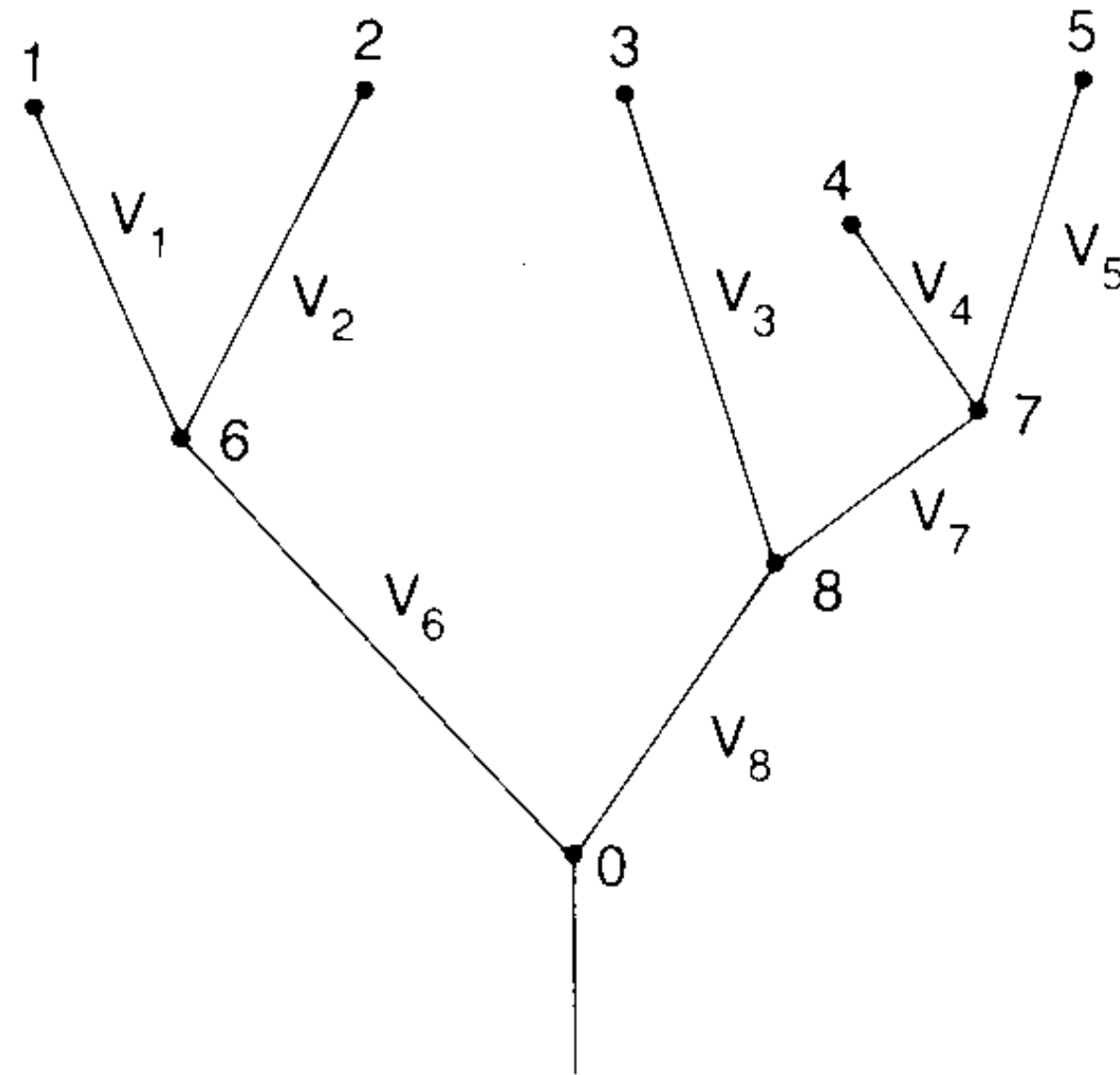


Neutral theory predicts that genetic distance between taxa will increase linearly with time



30 years of methodological, sequencing and computing progress

80s: Molecular phylogenetics gets started



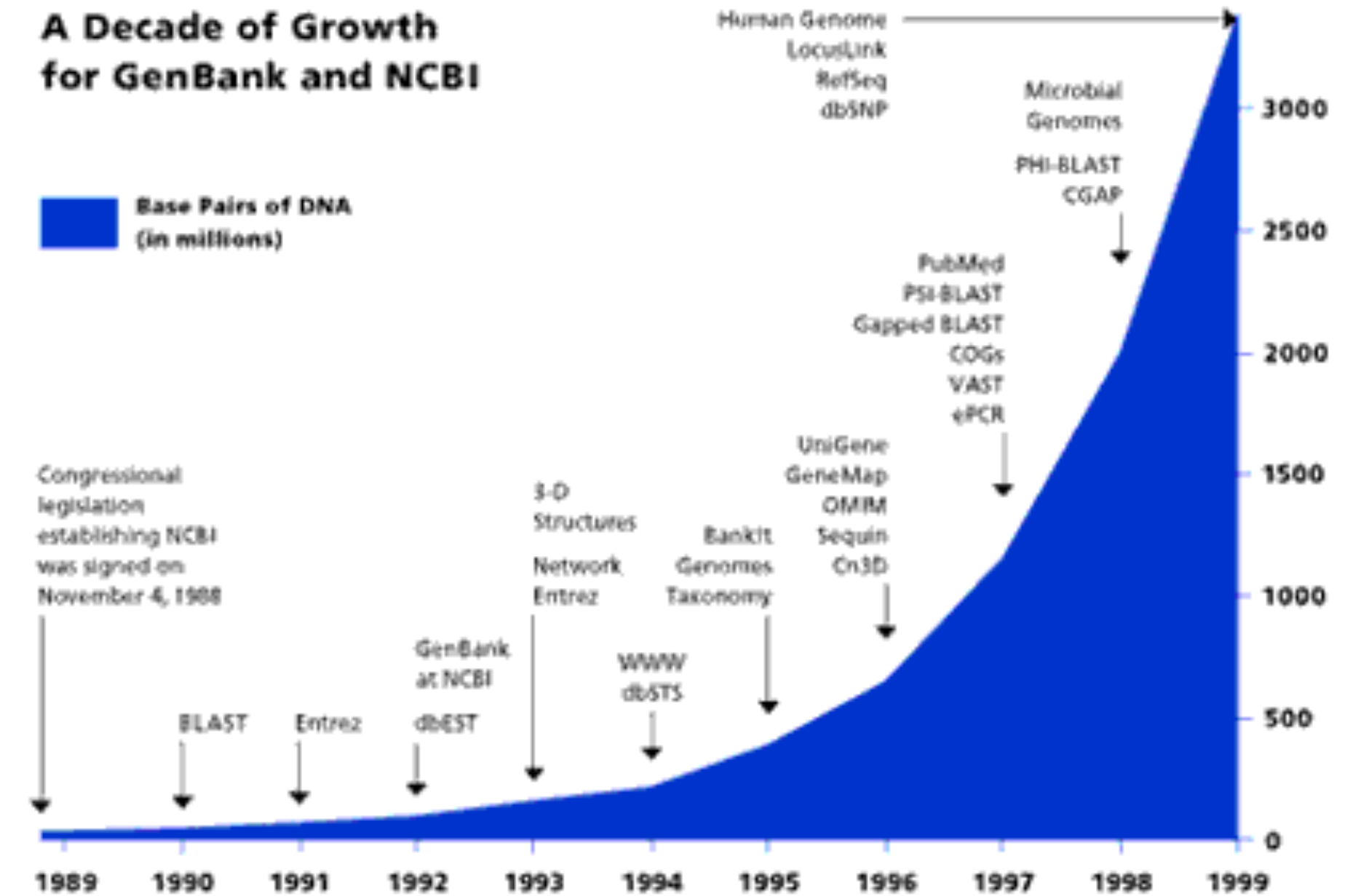
First likelihood-based estimation of phylogenetic trees

Felsenstein 1981 J Mol Evol

Open source software in the 80s

estimation of evolutionary trees. This package will be supplied on request, written in standard ANSI format on a magnetic tape supplied by the recipient. It must be acknowledged that this computer program is quite slow,

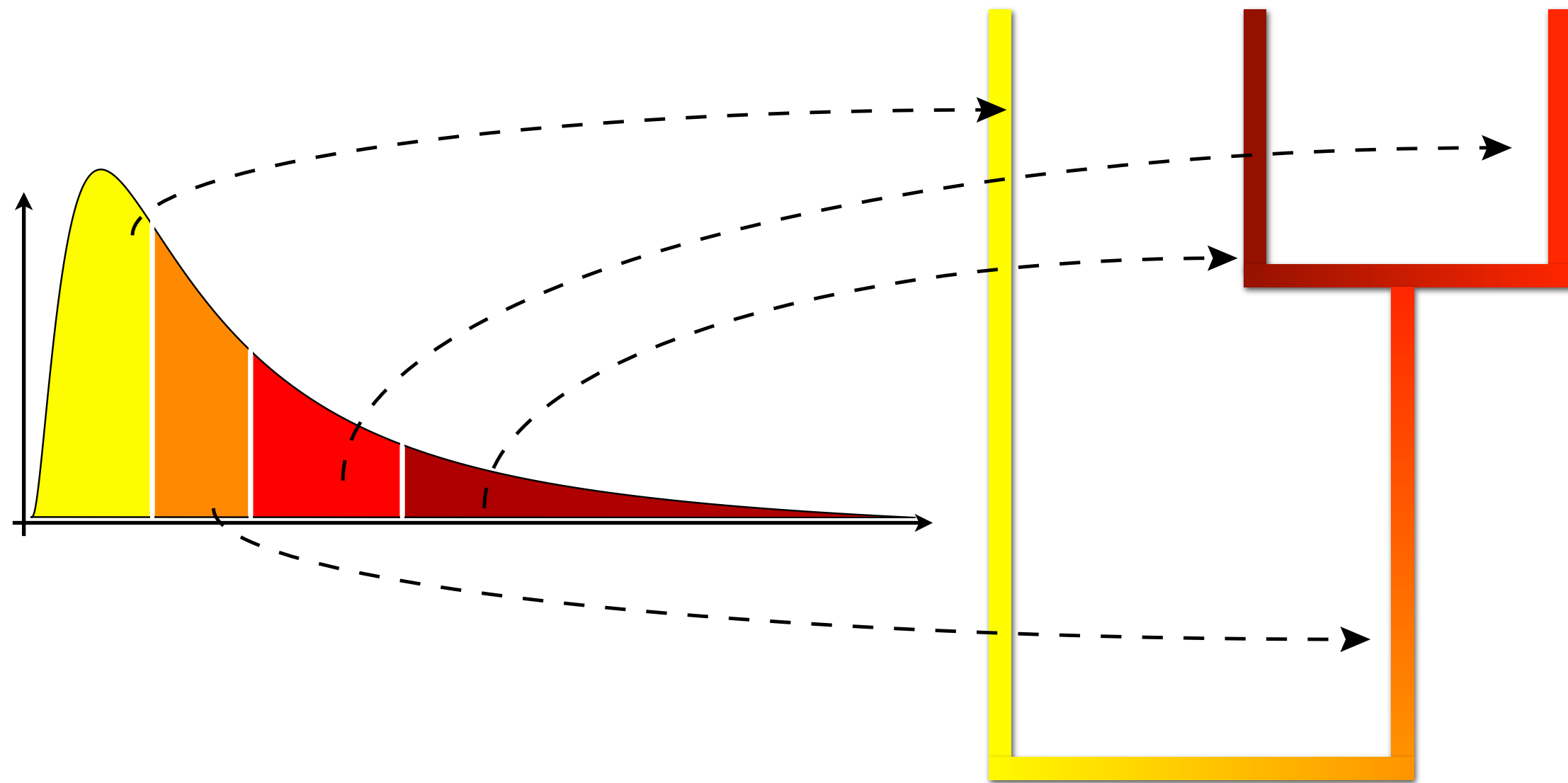
90s: “Big-data” era begins



30 years of methodological, sequencing and computing progress

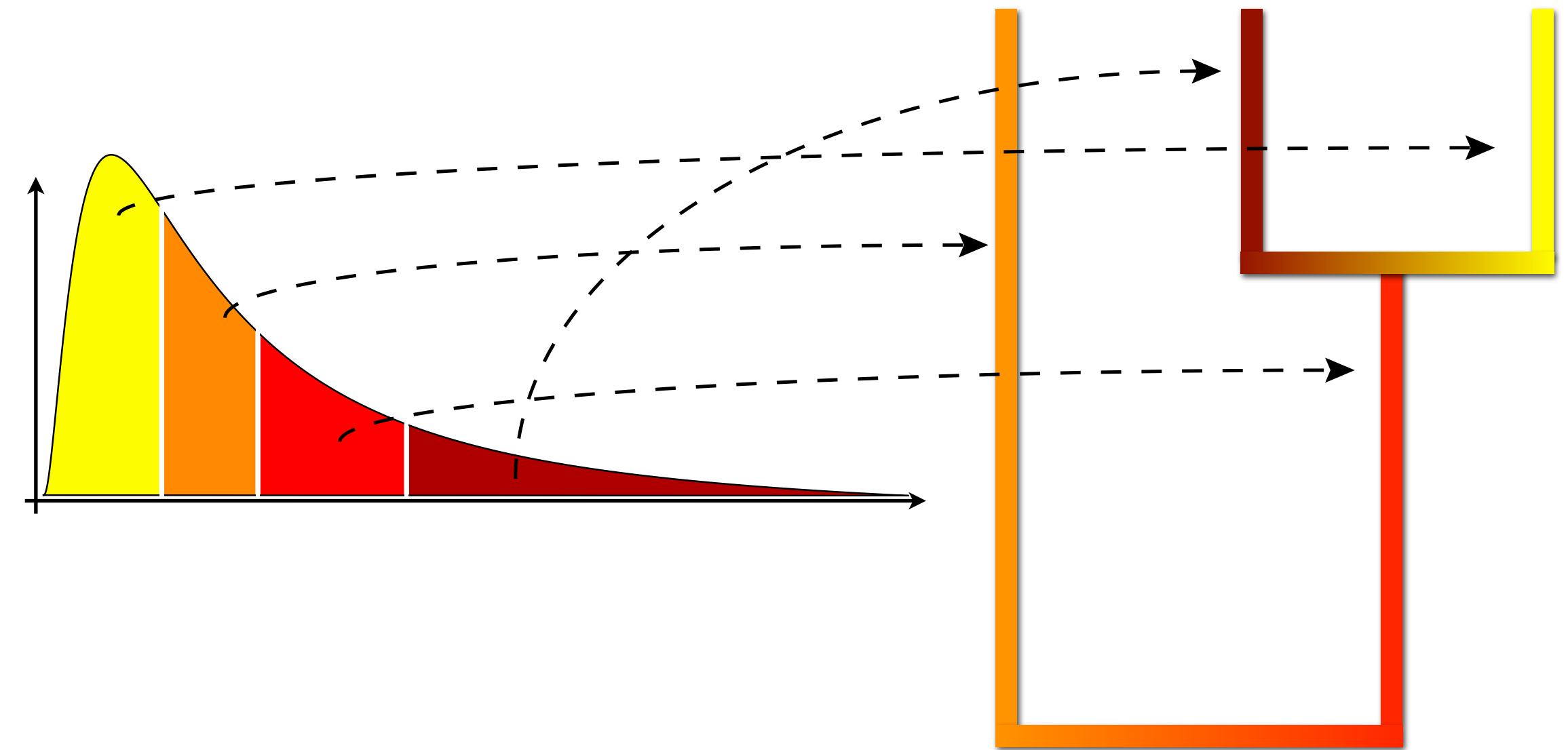
2000s: More realistic “relaxed” molecular clock models

Autocorrelated clocks



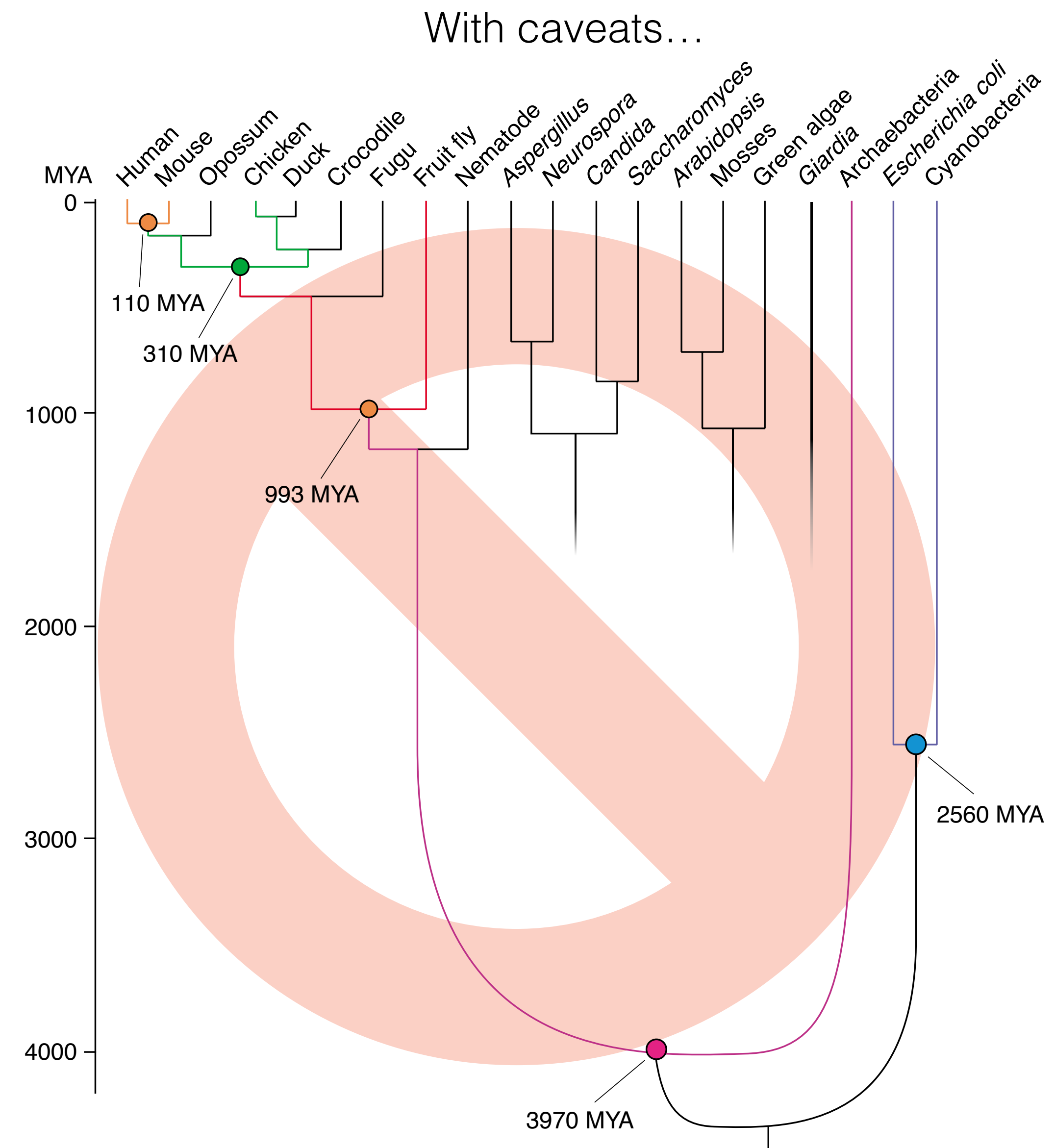
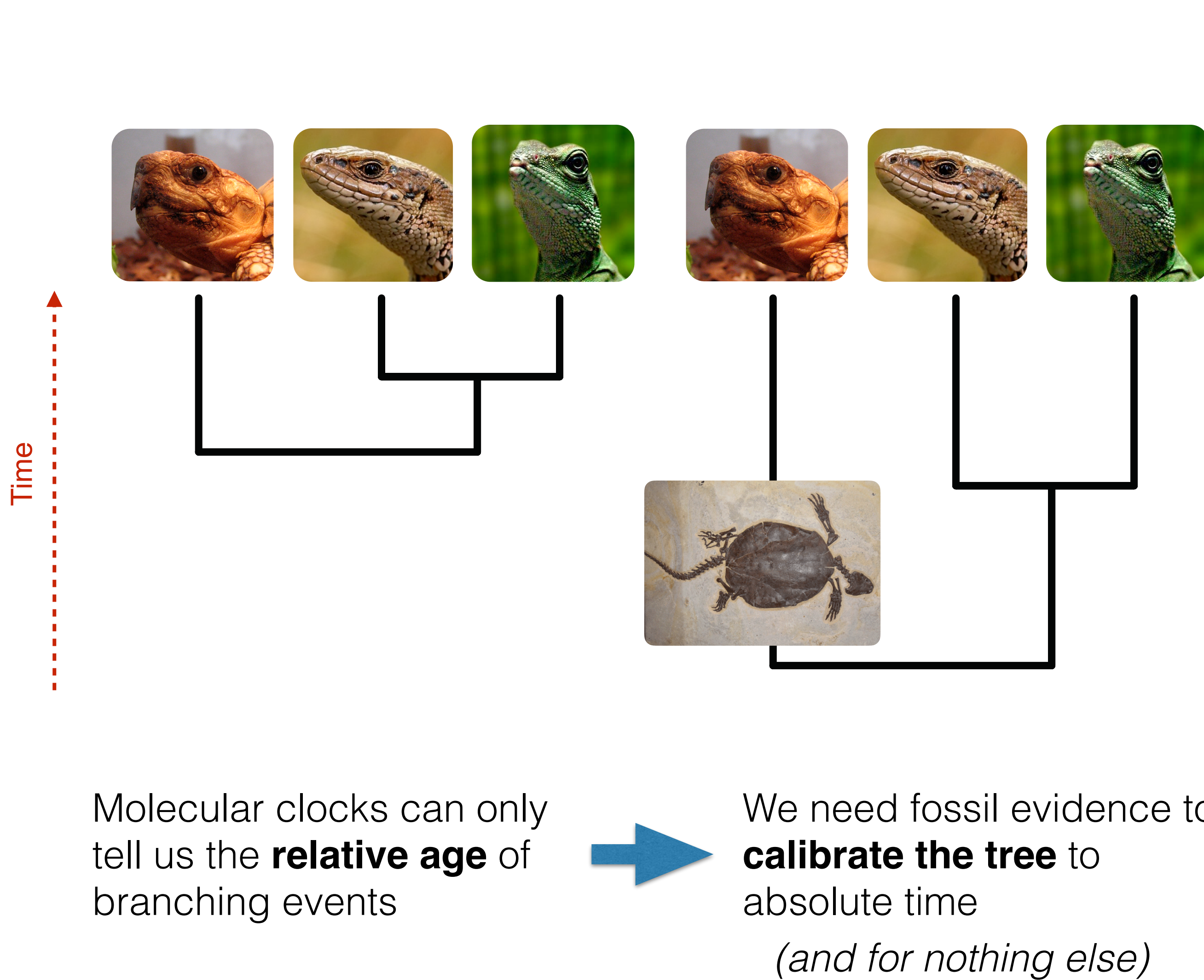
Thorne and Kishino 2002 Syst Biol

Uncorrelated clocks



Drummond et al. 2006 PLoS Biol

The era of fossils as *calibrations* (1990-2010)



Graur and Martin 2004 Trends Genetics

The era of fossils as *calibrations* (1990-2010)

Some issues still remain...



ARTICLES

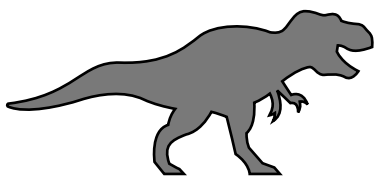
<https://doi.org/10.1038/s41477-019-0421-0>

Origin of angiosperms and the puzzle of the Jurassic gap

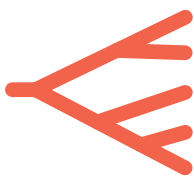
Hong-Tao Li^{1,15}, Ting-Shuang Yi^{1,15}, Lian-Ming Gao^{2,15}, Peng-Fei Ma^{1,15}, Ting Zhang^{1,15}, Jun-Bo Yang^{1,15}, Matthew A. Gitzendanner^{3,4,15}, Peter W. Fritsch⁵, Jie Cai¹, Yang Luo², Hong Wang², Michelle van der Bank⁶, Shu-Dong Zhang¹, Qing-Feng Wang^{1,7}, Jian Wang⁸, Zhi-Rong Zhang¹, Chao-Nan Fu^{2,9}, Jing Yang¹, Peter M. Hollingsworth¹⁰, Mark W. Chase^{11,12}, Douglas E. Soltis^{3,4,13,14}, Pamela S. Soltis^{3,13,14*} and De-Zhu Li^{1,2,9*}

Li et al. 2019 Nature Plants

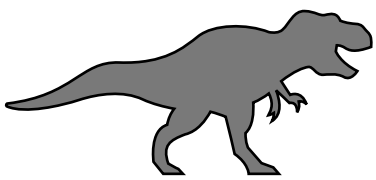
Origin of angiosperms



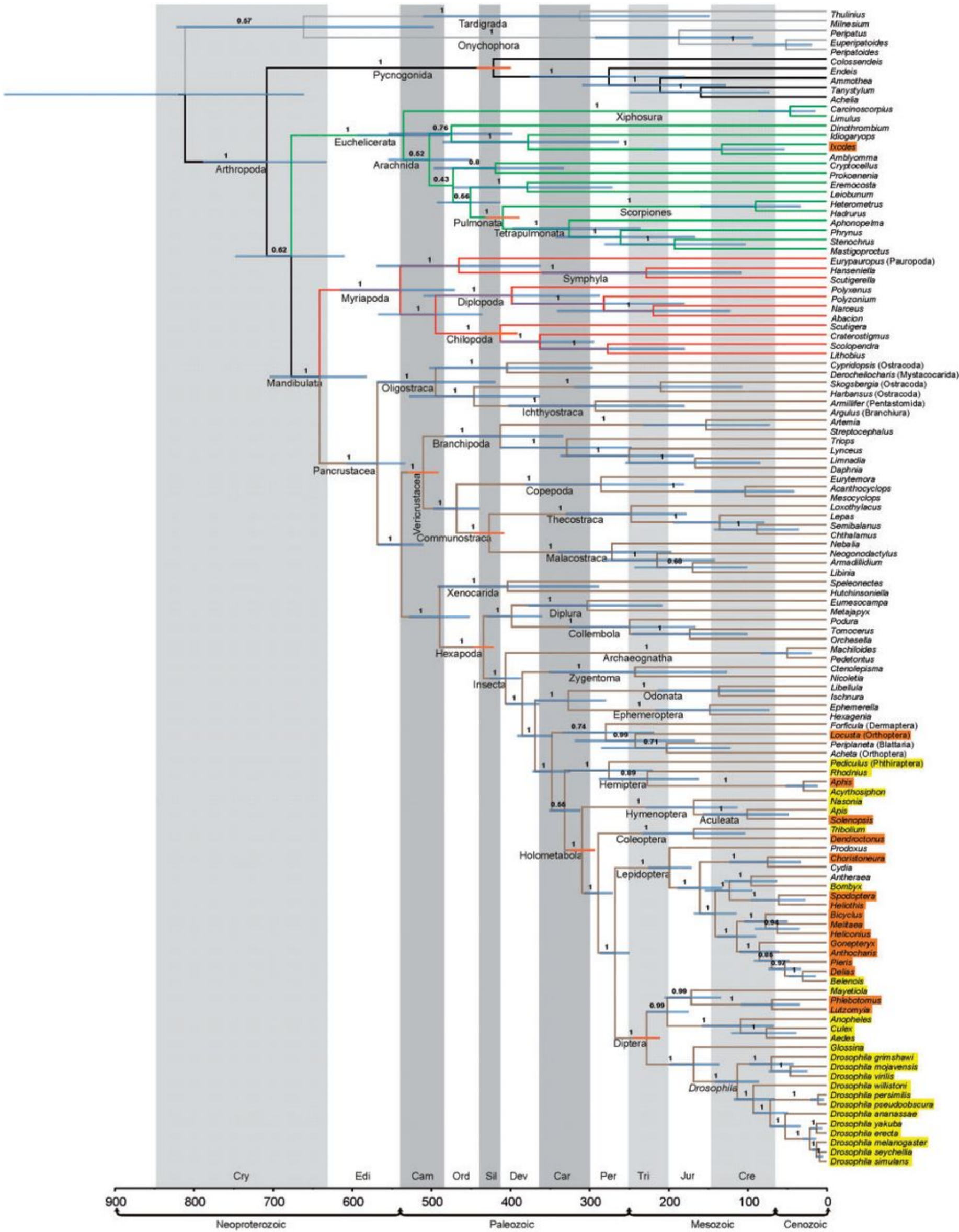
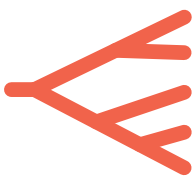
125 Ma vs >200 Ma



Origin of arthropods



540 Ma vs >800 Ma



Wheat and Wahlberg 2013 Syst Biol



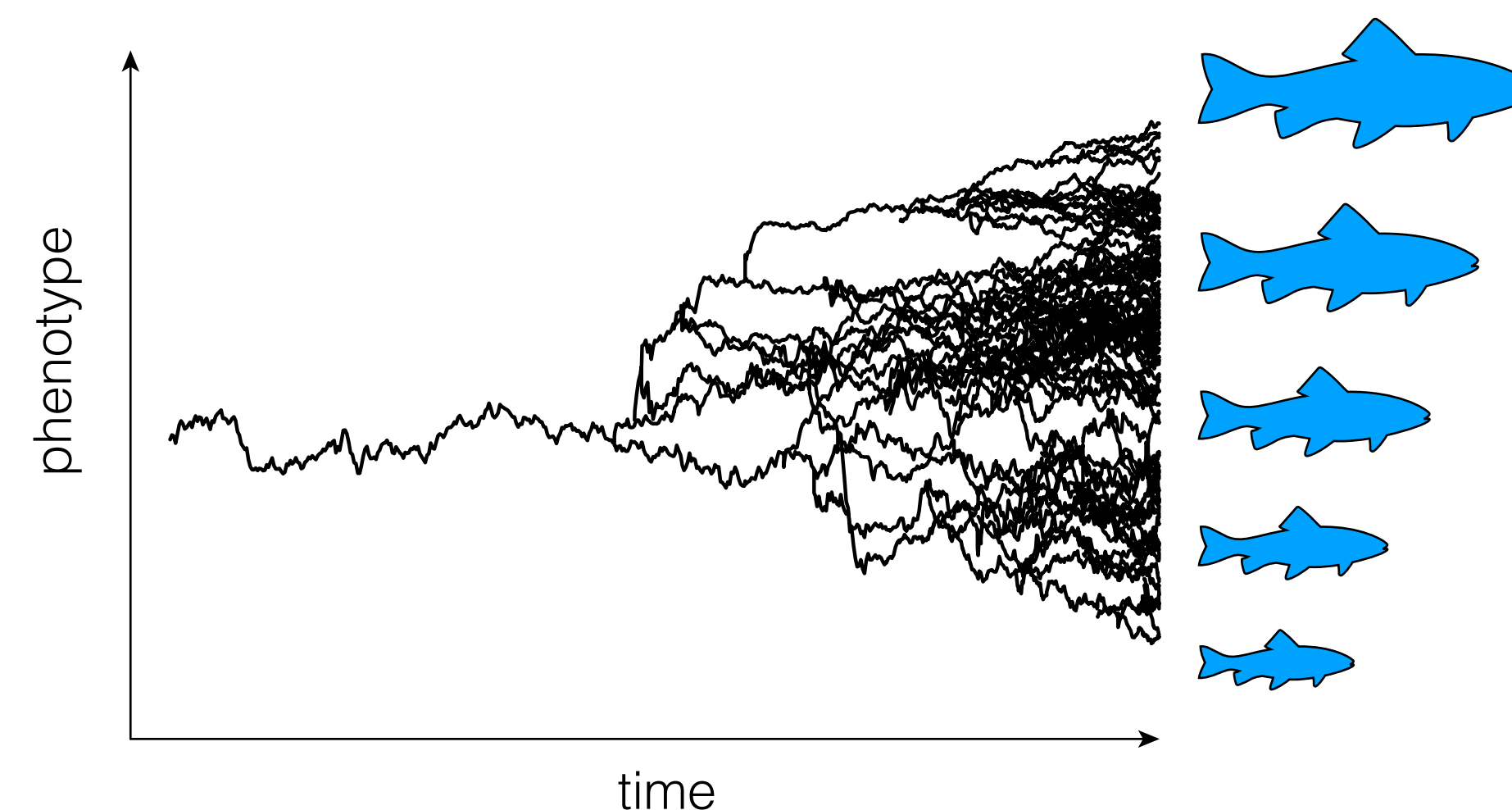
Phylogenetic comparative methods (1990-2010)

Methods to infer trait evolution and ancestral states

Brownian process: neutral stochastic evolution of a trait

$$dX(t) = \sigma dB(t)$$

Change in trait X by time t SD Random Noise by time t

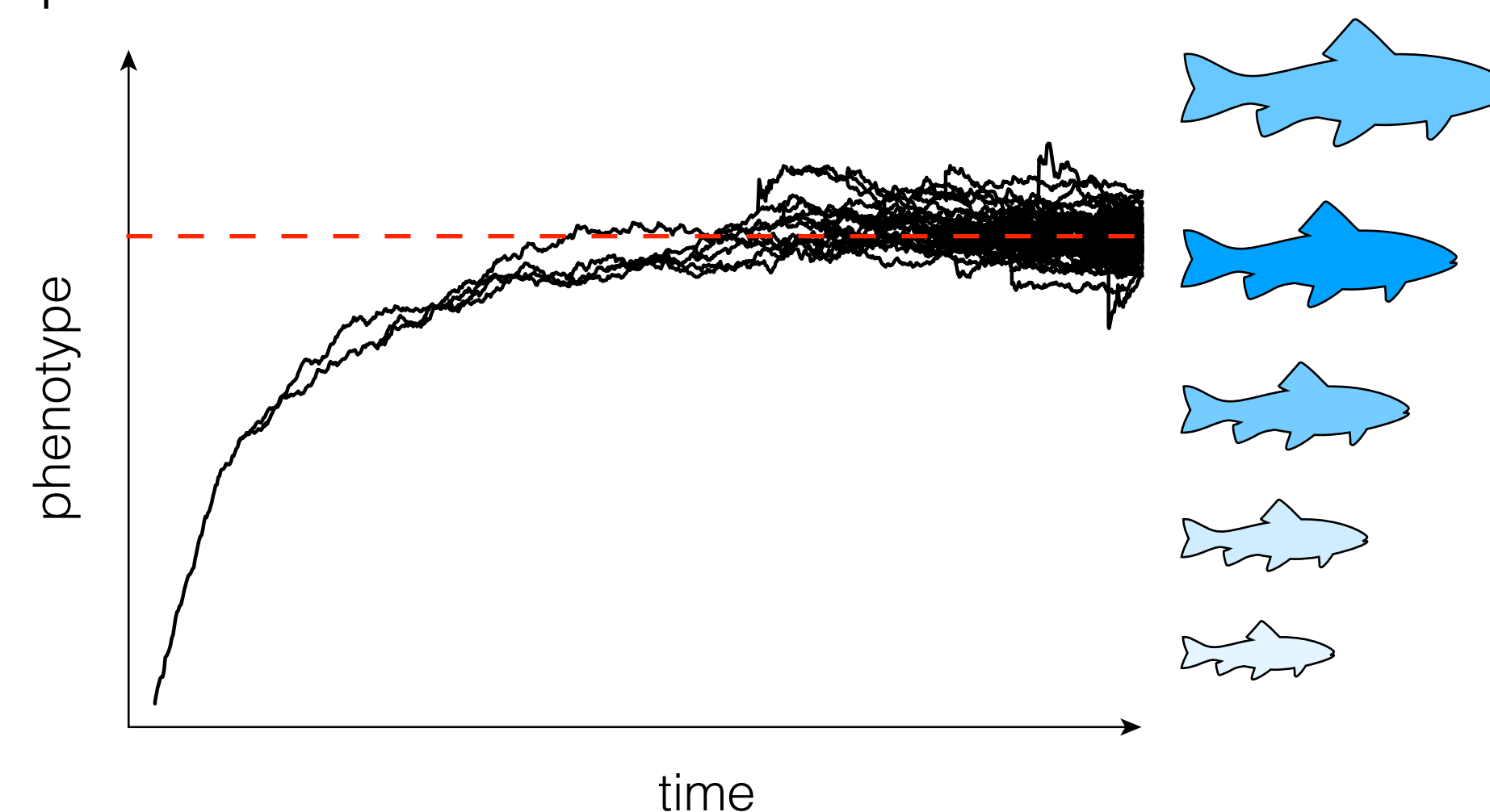


Ornstein-Uhlenbeck process: stochastic evolution pulled toward an optimum

$$dX(t) = \alpha[\theta - X(t)]dt + \sigma dB(t)$$

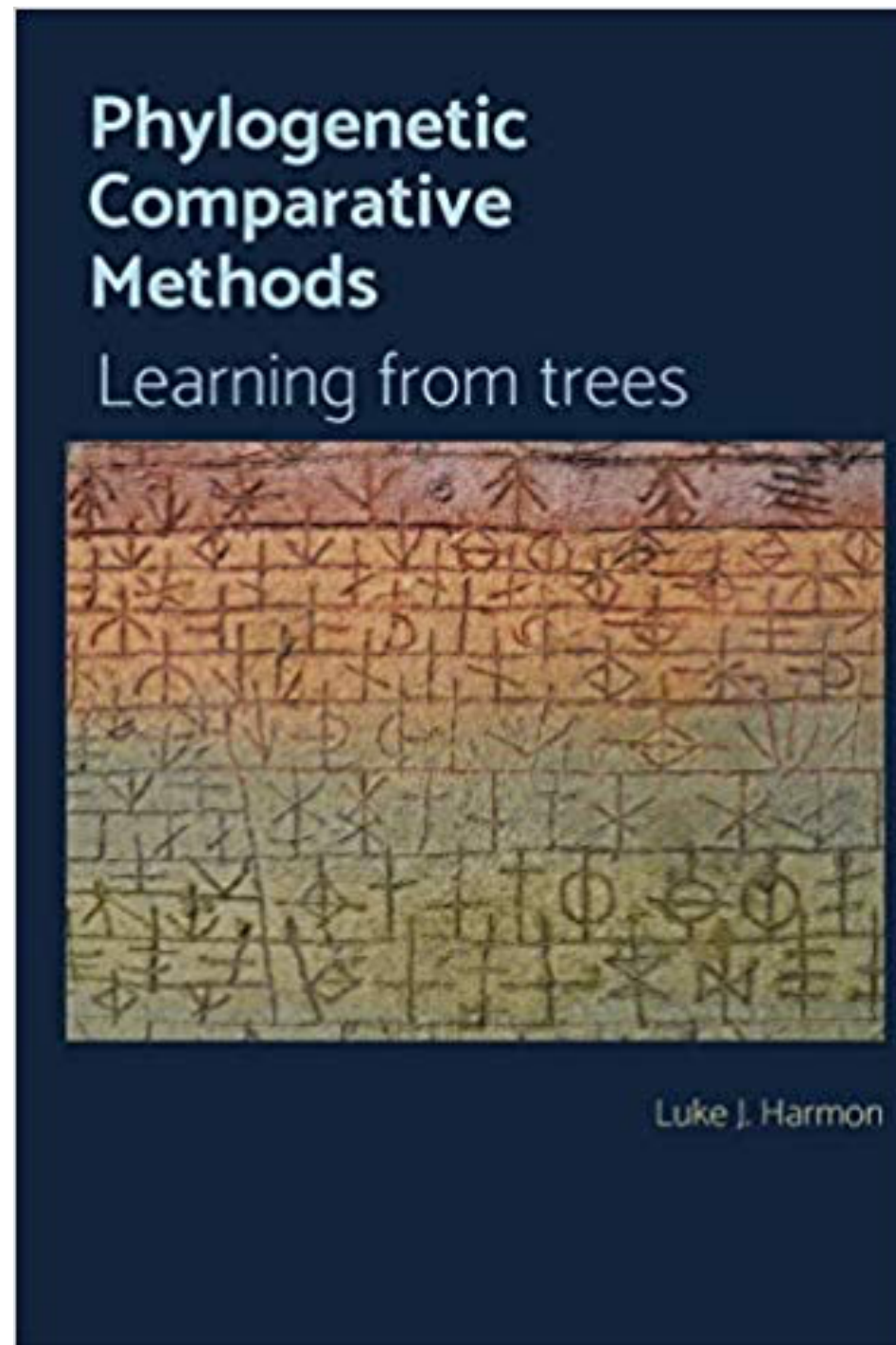
change in trait (X) over time (t) position of trait optimum value of trait (X) at time (t)

intensity of stabilizing selection towards optimum scales the variance of the random normal distribution random normal distribution



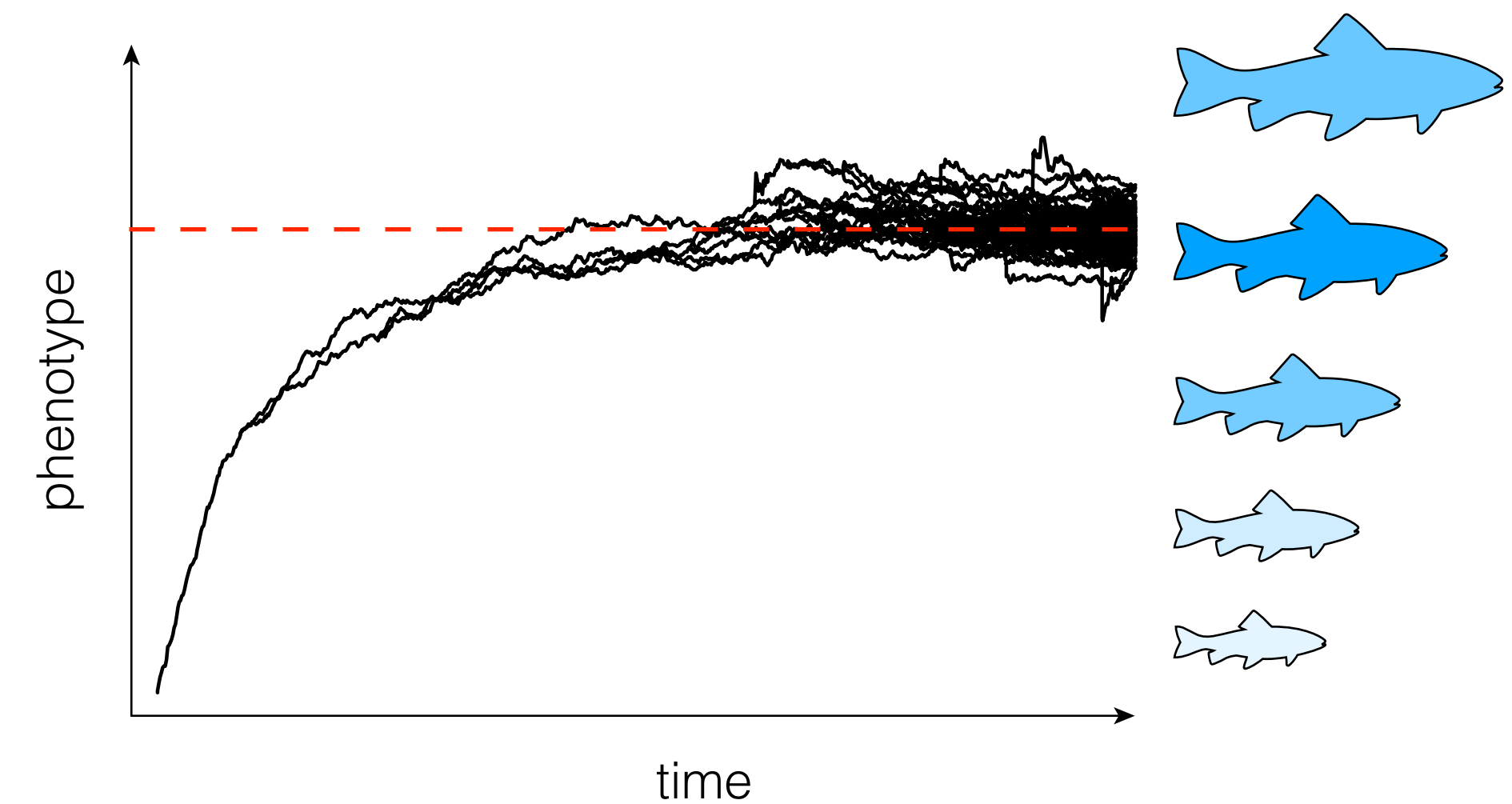
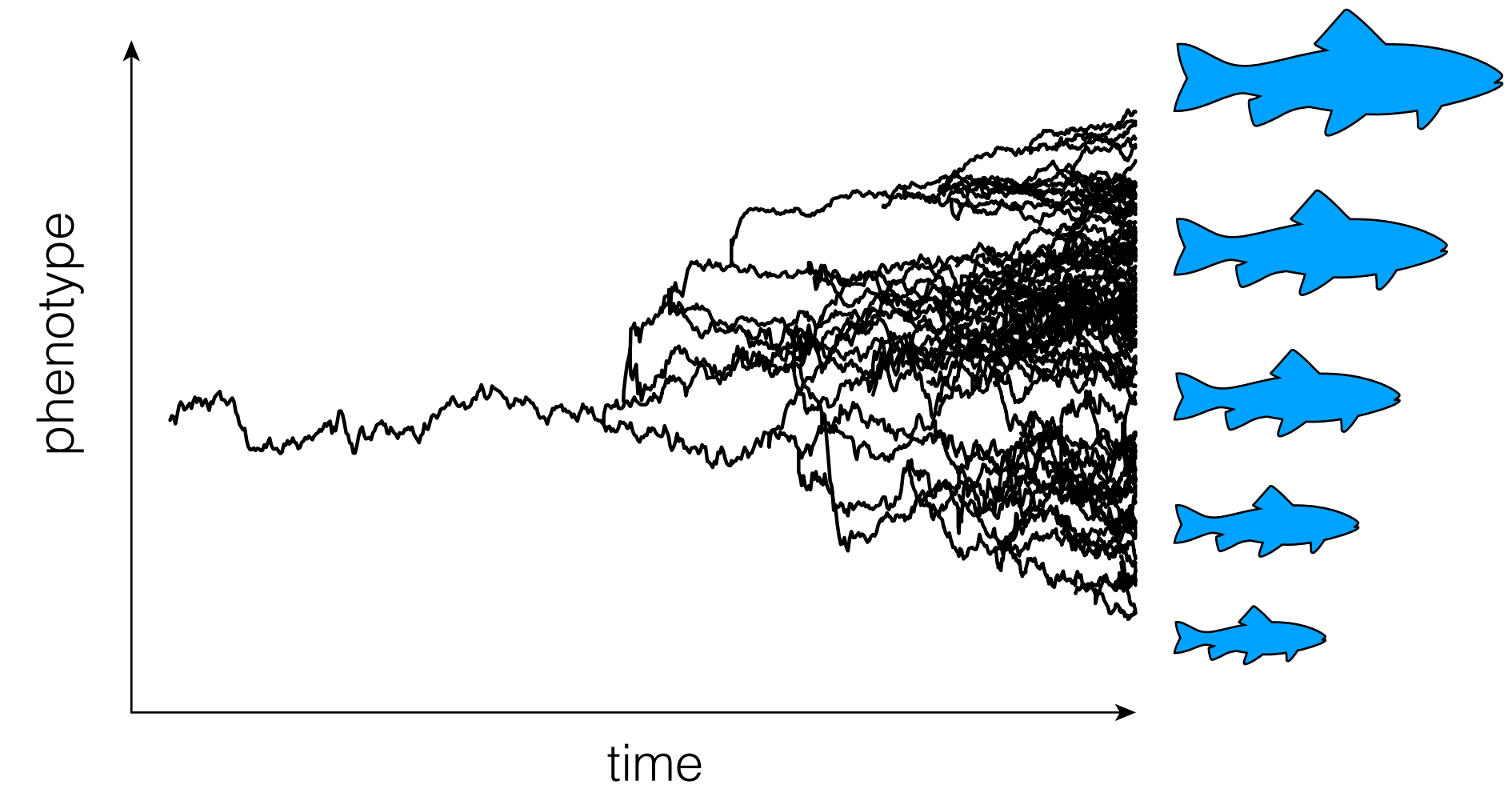
Phylogenetic comparative methods (1990-2010)

Methods to infer trait evolution and ancestral states



Luke Harmon

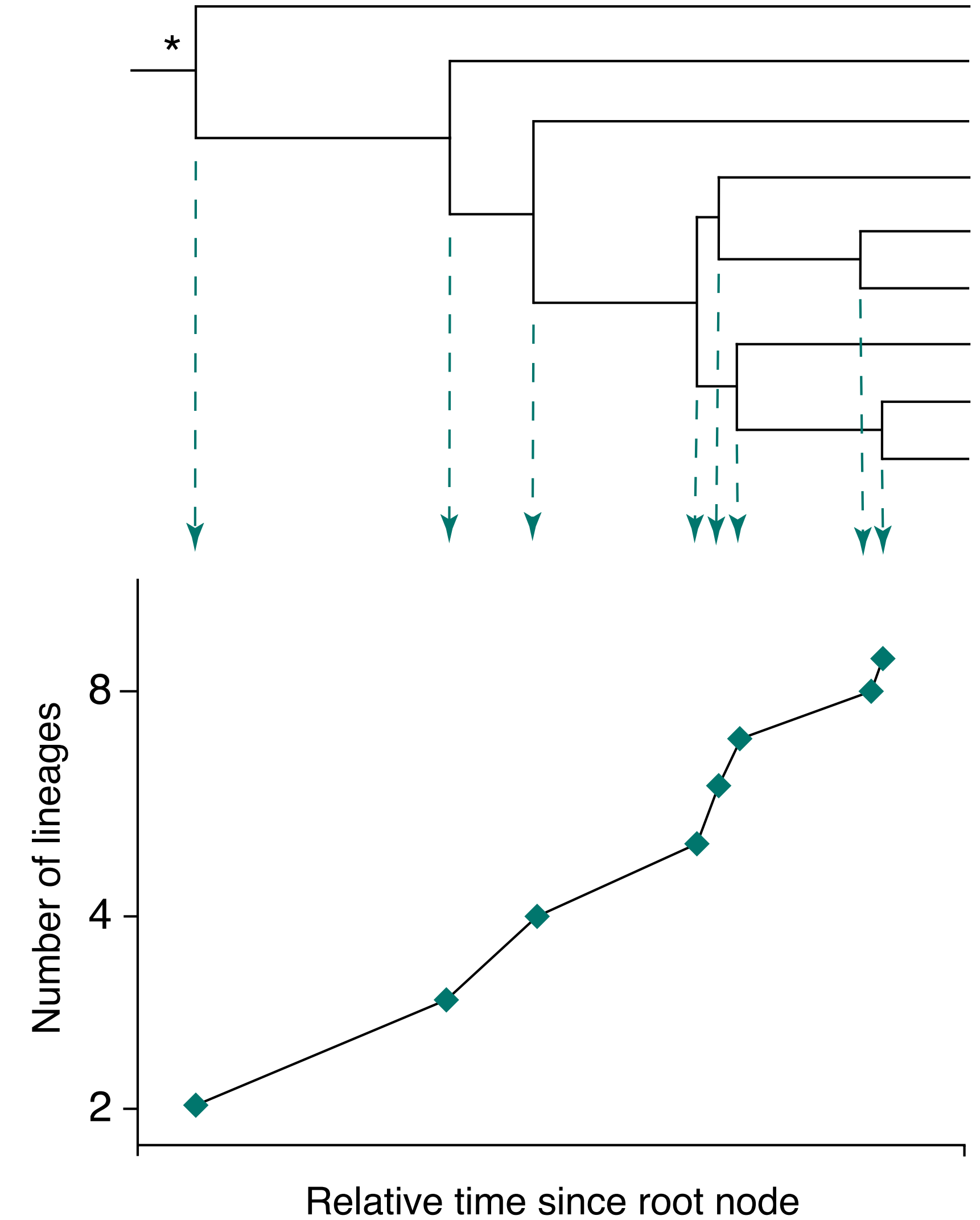
<https://lukejharmon.github.io/pcm/>



Using dated phylogenies to infer speciation and extinction rates

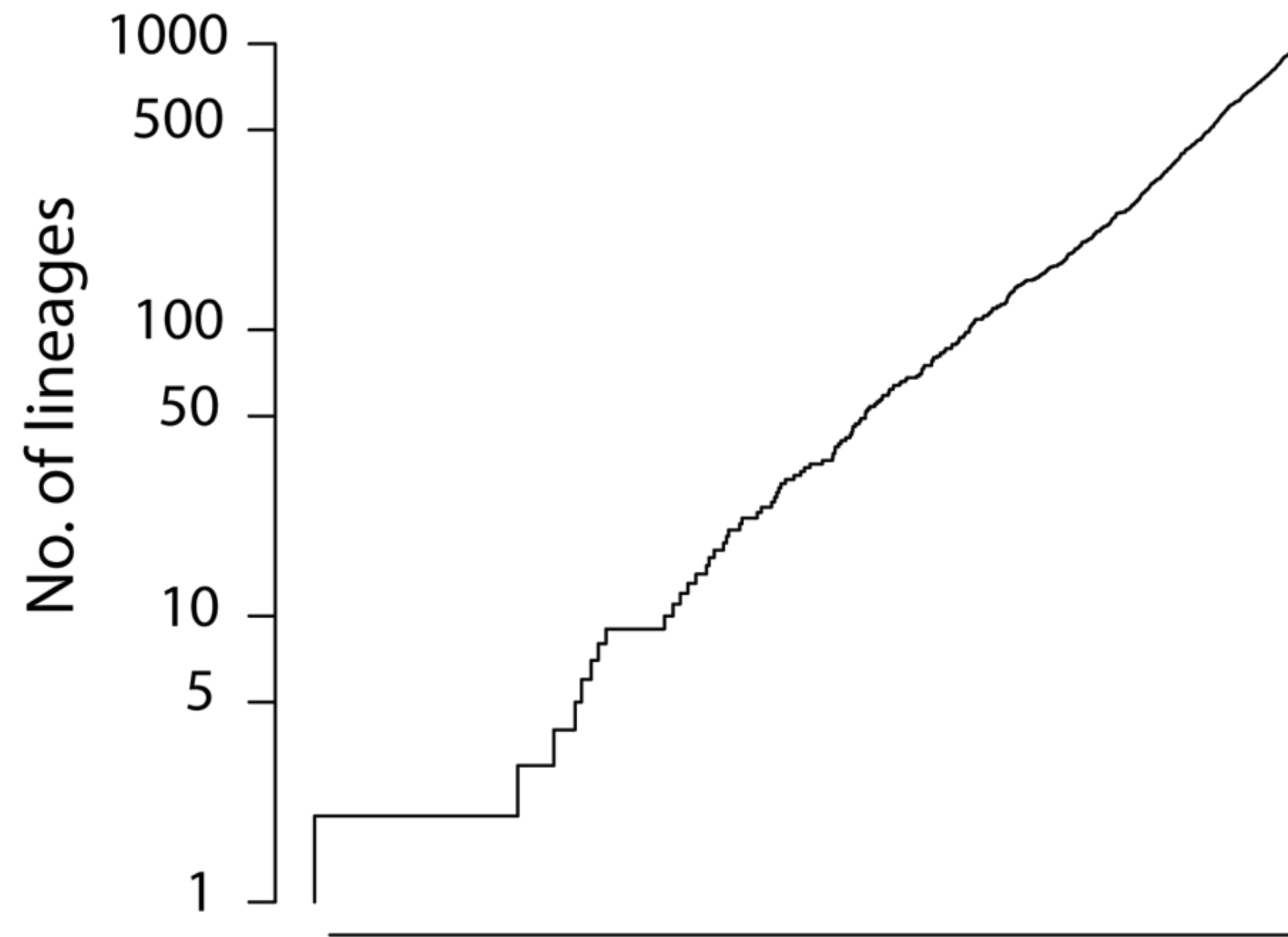
The 'reconstructed' birth-death process to infer speciation and extinction rates from a phylogeny of extant taxa.

**Lineage-through-time
plot**

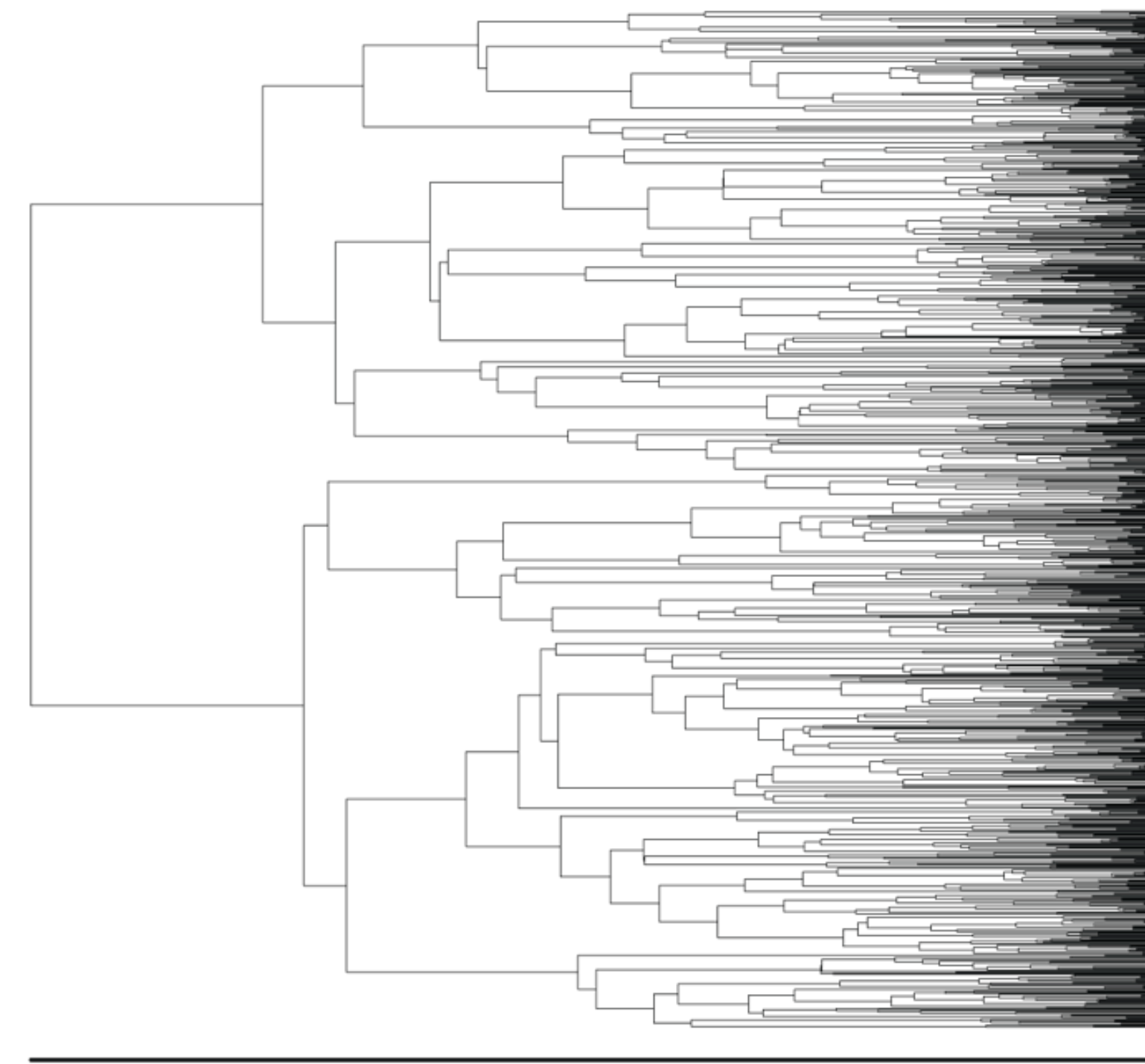


Temporal dynamics of species diversification: pure birth process

LTT plot

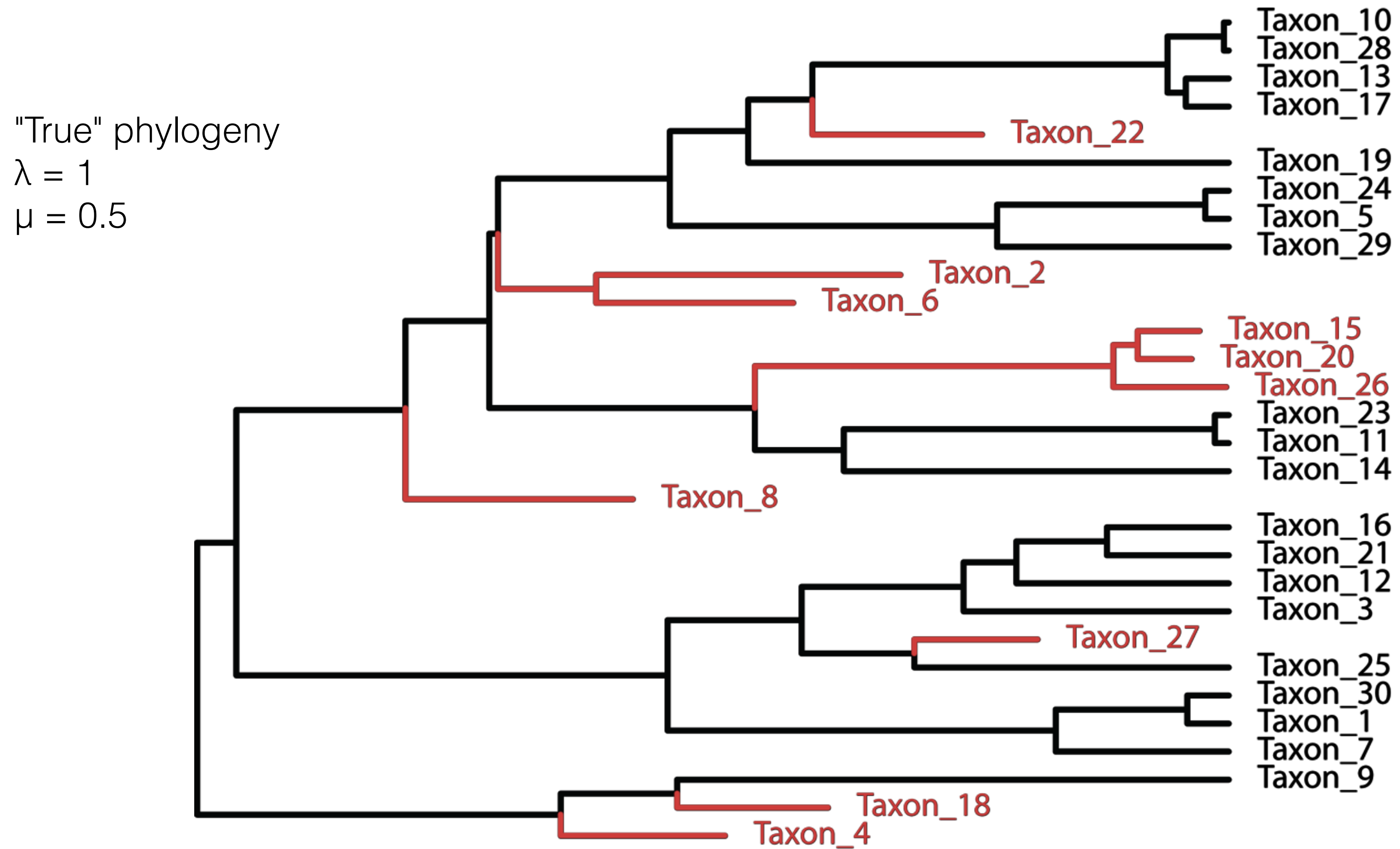


Phylogenetic tree

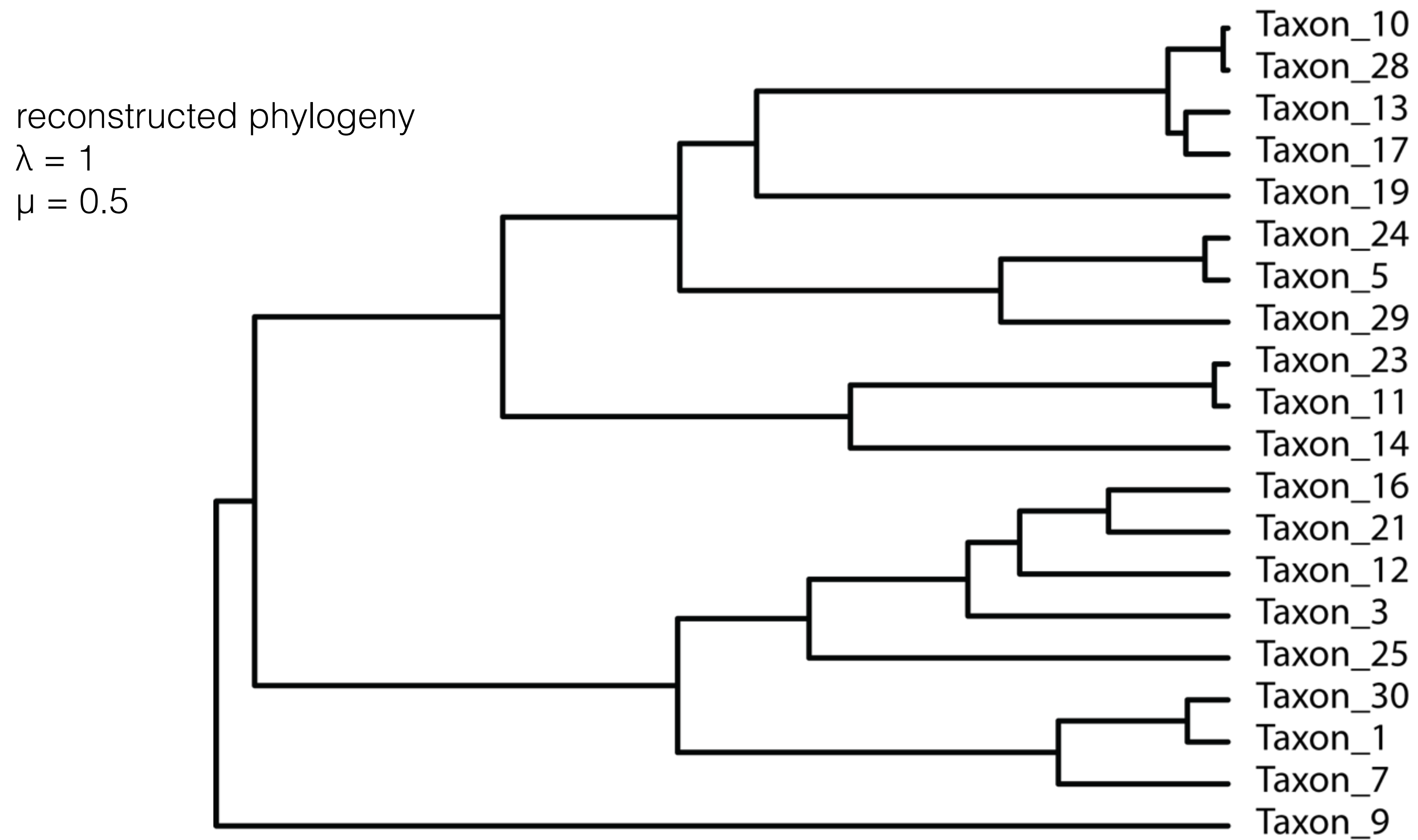


Time

What is the effect of extinction on an LTT plot?

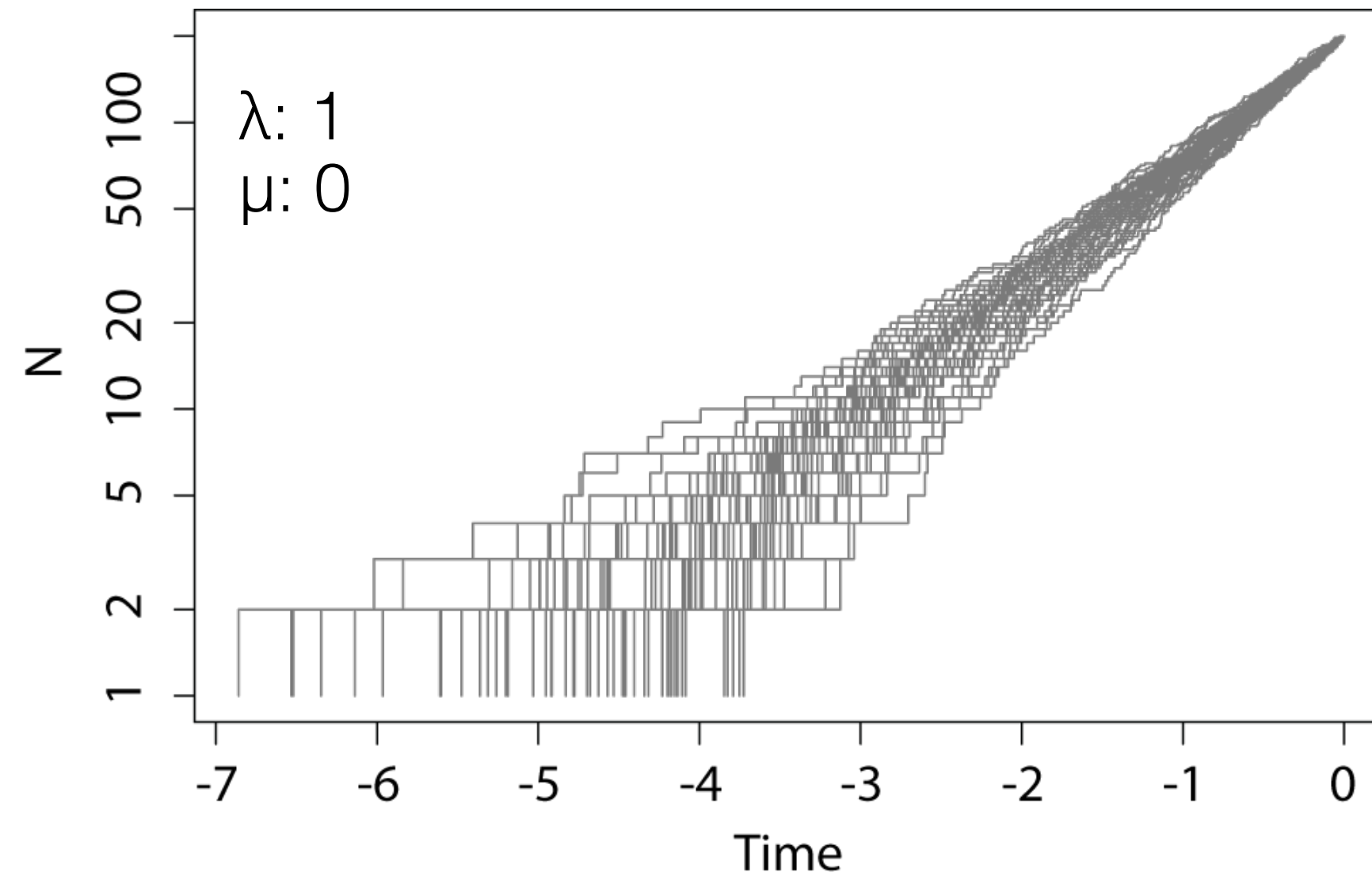


What is the effect of extinction on an LTT plot?



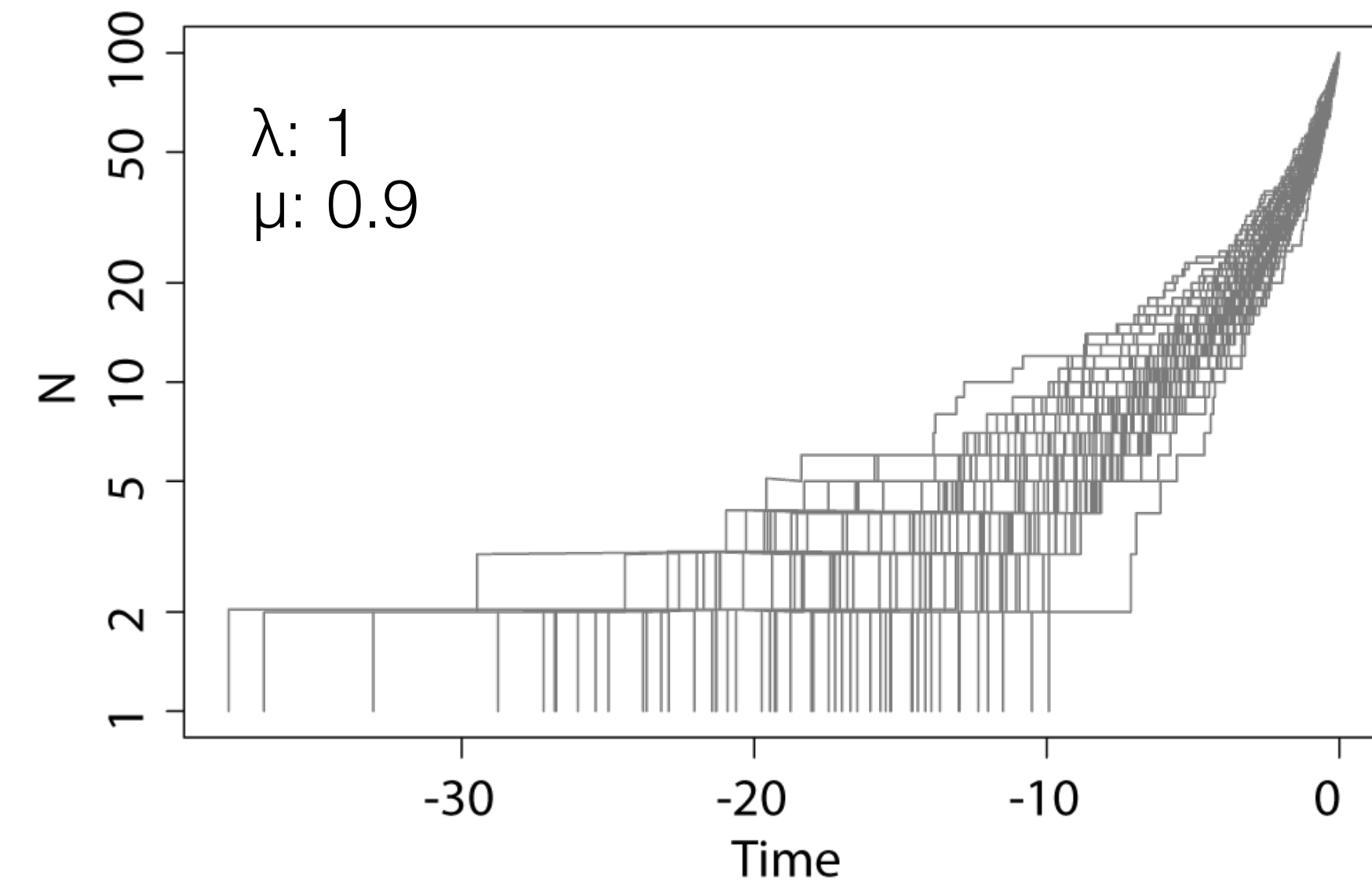
Birth-death processes in phylogenetics

pure-birth process (no extinction)



lineages accumulate linearly
through time in semi-log space

birth-death process



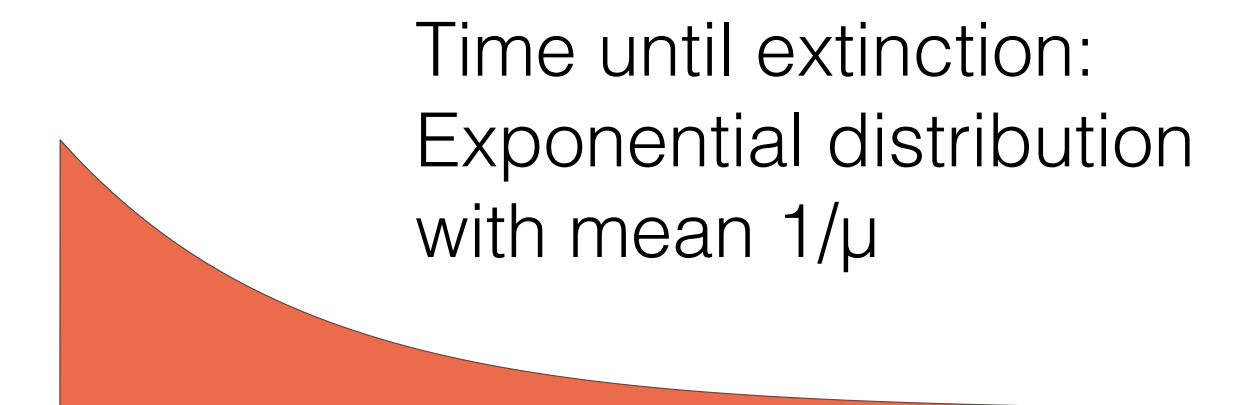
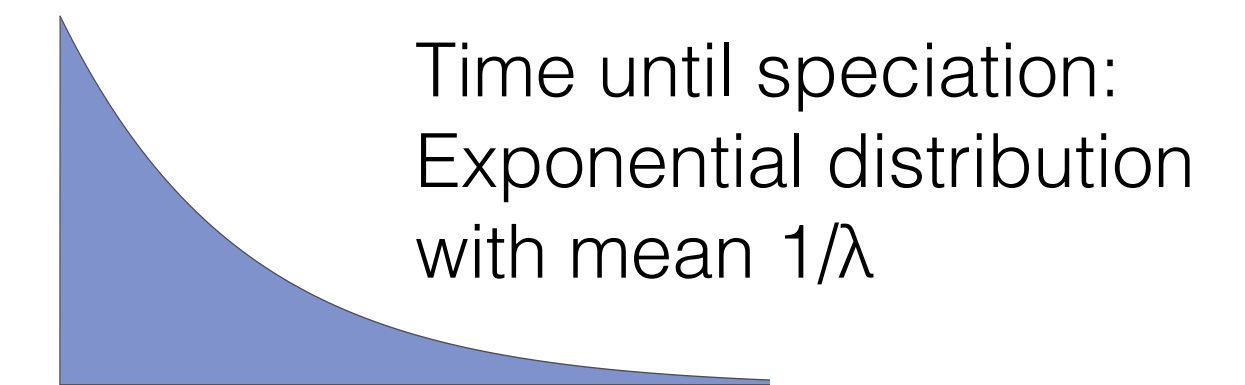
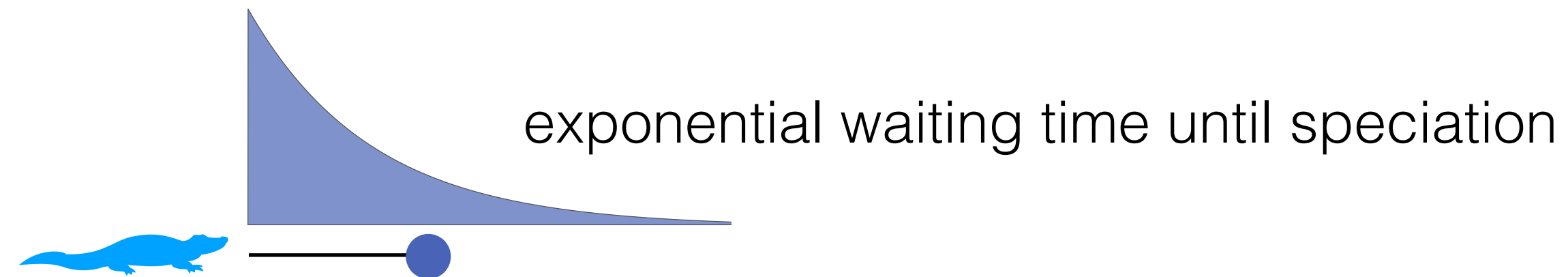
older lineages are more likely to
go extinct

Extinction leaves a signature in the temporal distribution of node ages

Species diversification as a birth-death stochastic process

λ : expected number of speciation events in 1 My per-lineage

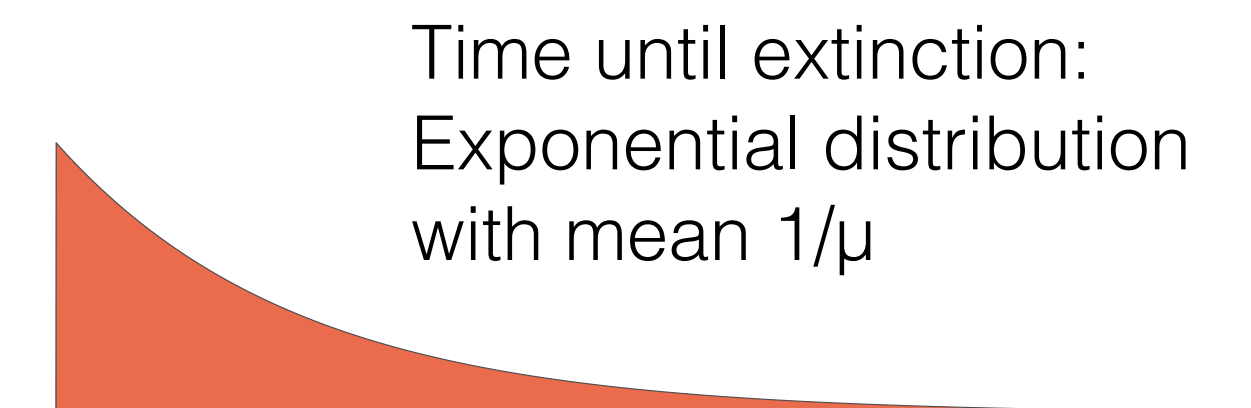
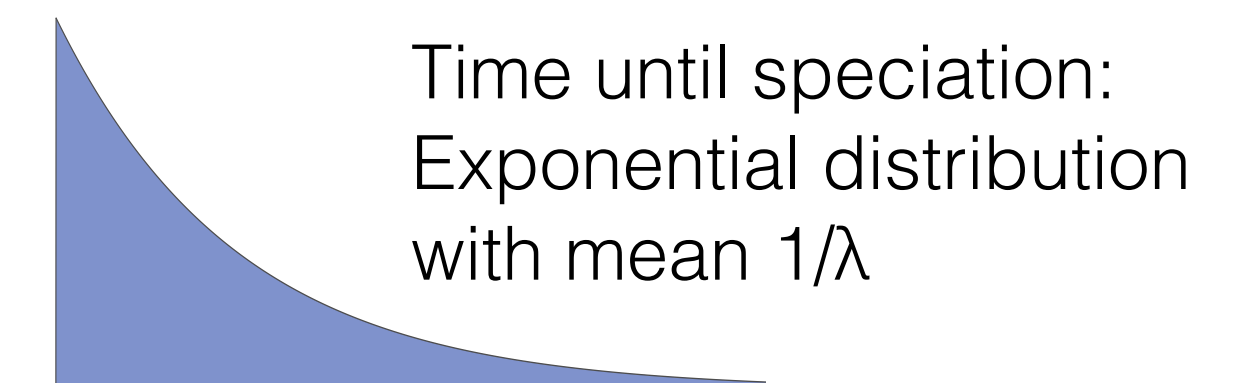
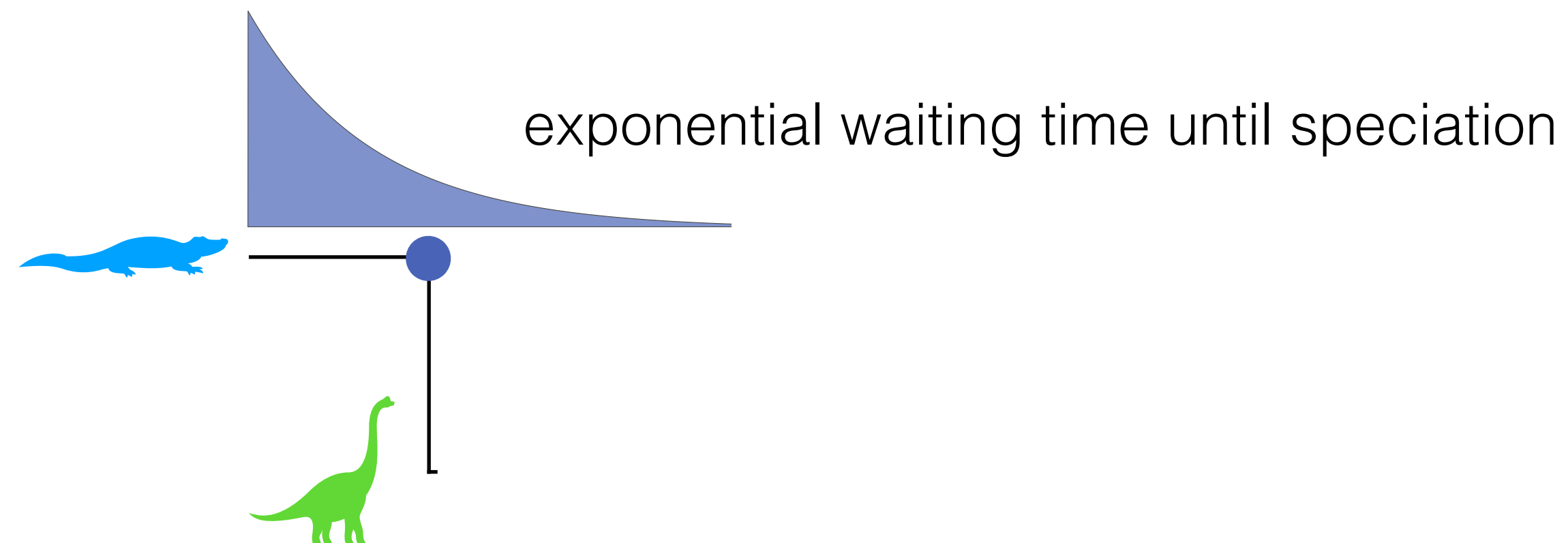
μ : expected number of extinction events in 1 My per-lineage



Parameters of the diversification process

λ : expected number of speciation events in 1 My per-lineage

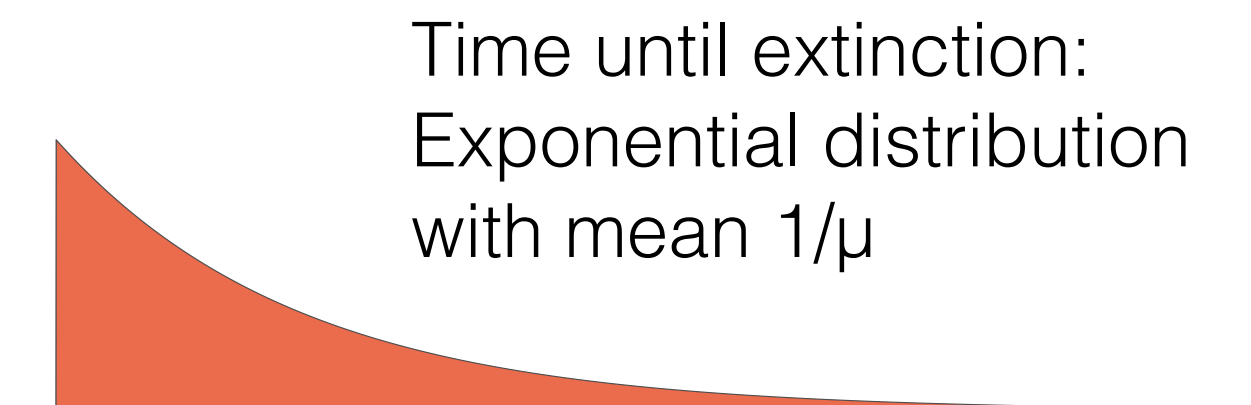
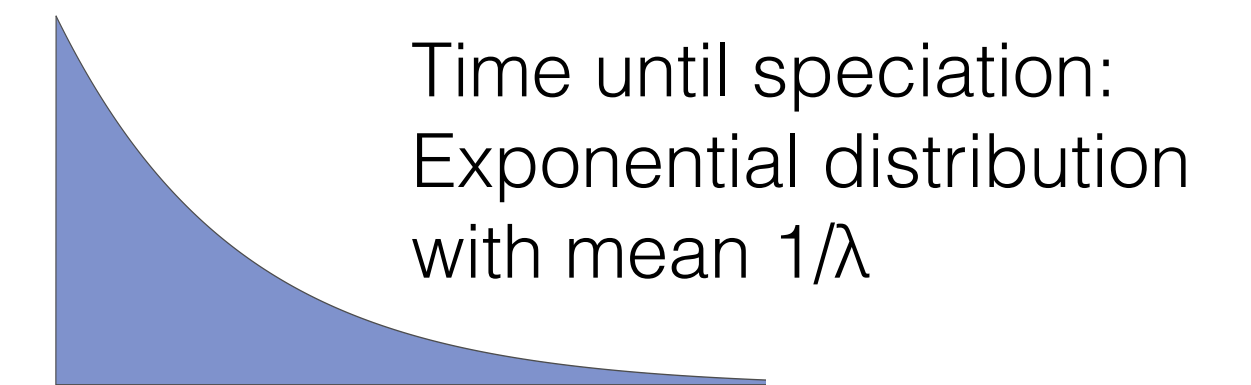
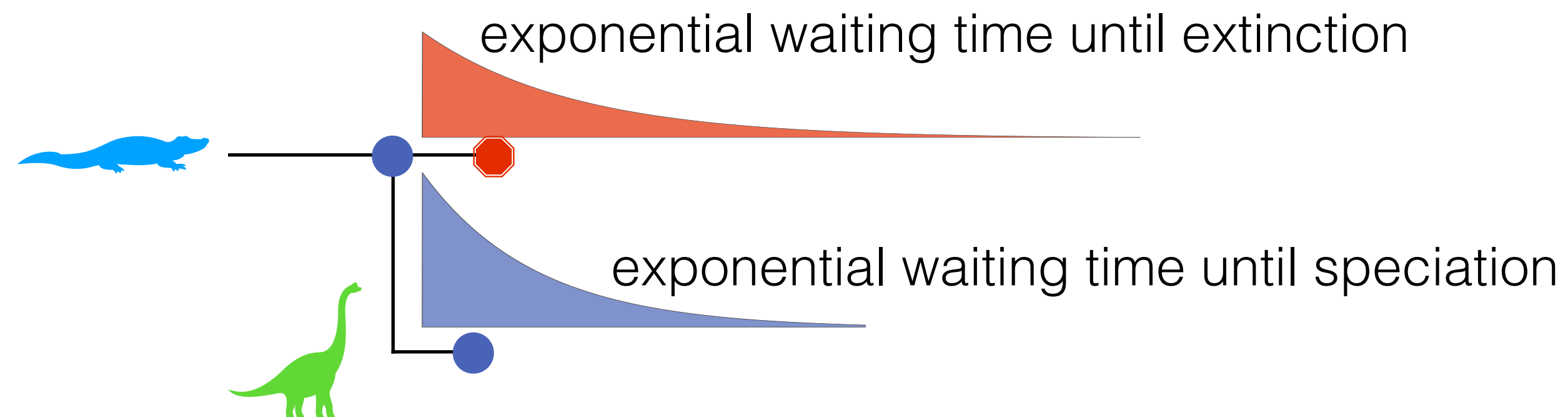
μ : expected number of extinction events in 1 My per-lineage



Parameters of the diversification process

λ : expected number of speciation events in 1 My per-lineage

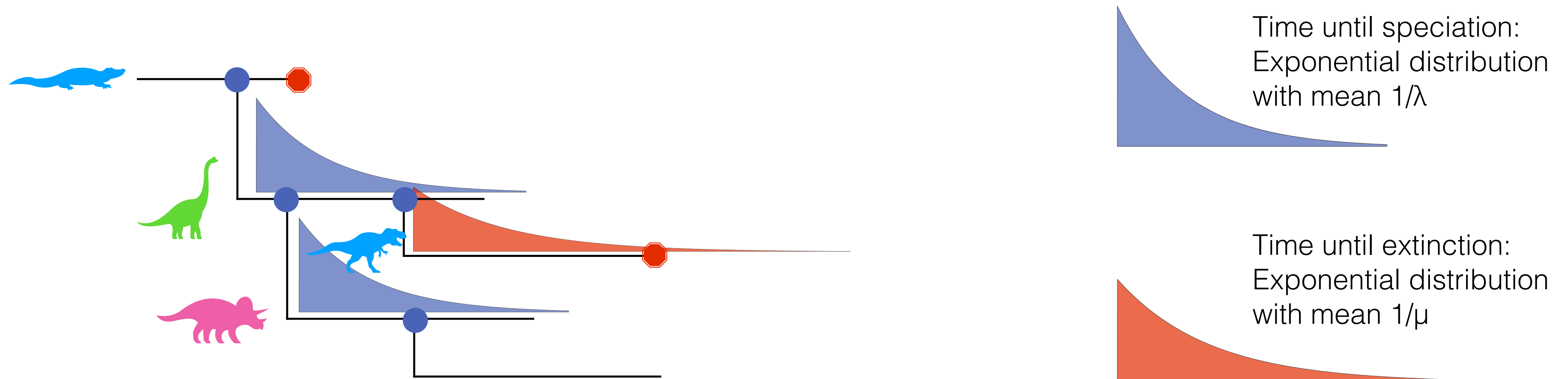
μ : expected number of extinction events in 1 My per-lineage



Parameters of the diversification process

λ : expected number of speciation events in 1 My per-lineage

μ : expected number of extinction events in 1 My per-lineage



Parameters of the diversification process

speciation rate λ (or p)

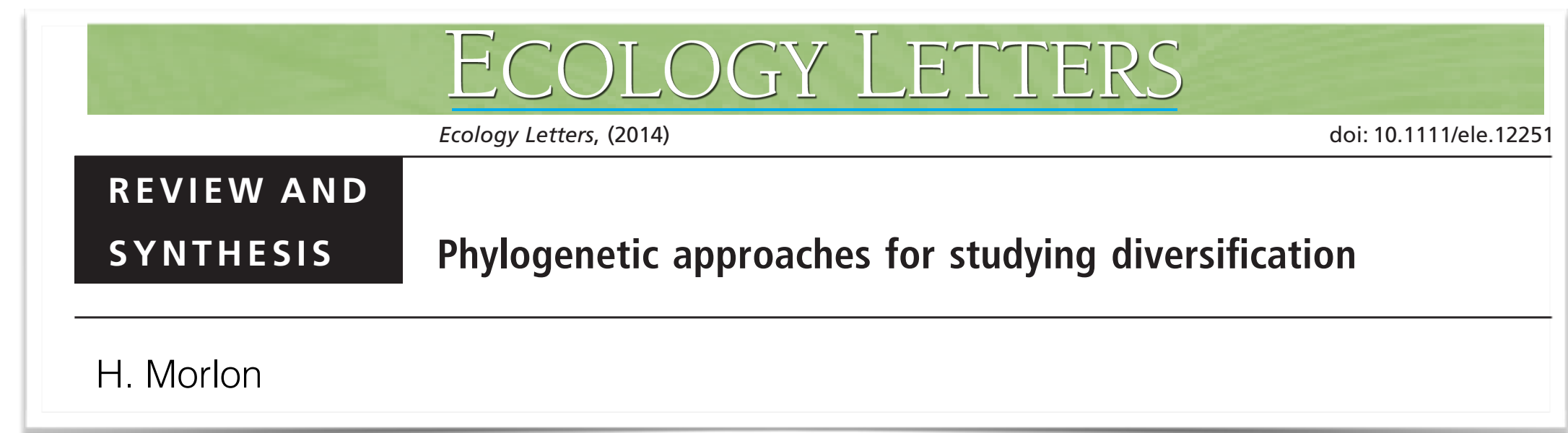
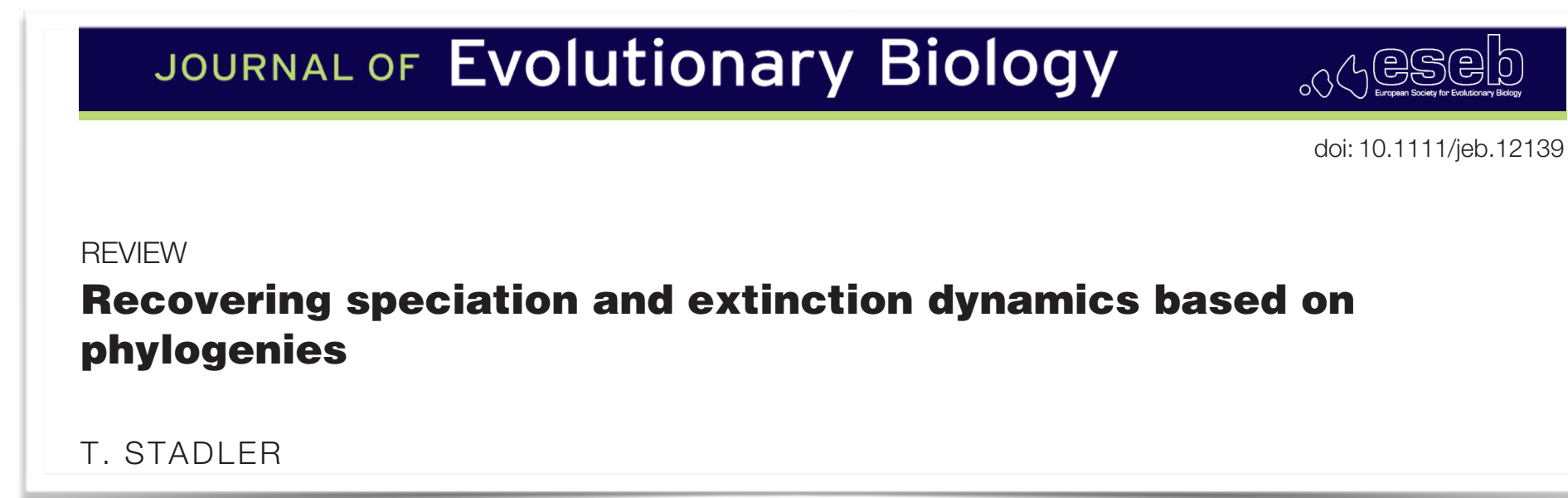
extinction rate μ (or q)

net diversification rate $r = \lambda - \mu$

extinction fraction $a = \mu / \lambda$

λ : expected number of speciation events in 1 My per-lineage

μ : expected number of extinction events in 1 My per-lineage



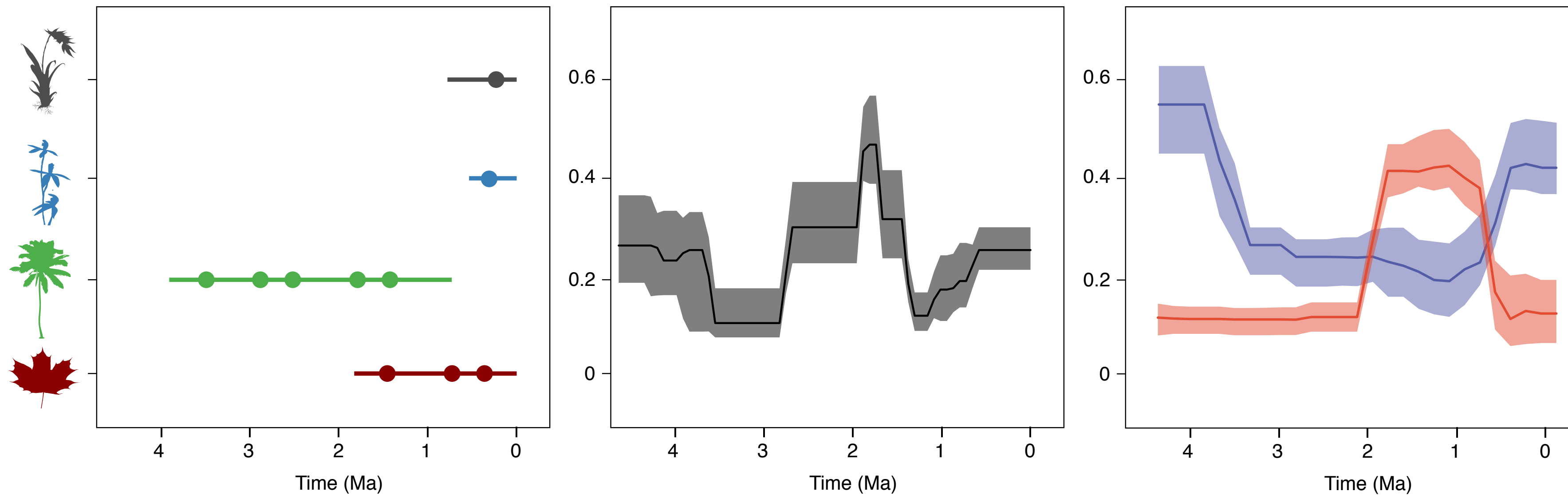
Estimating birth-death processes from the fossil record

$$\underbrace{P(q, \mathbf{s}, \mathbf{e}, \lambda, \mu | X)}_{\text{posterior}} \propto \underbrace{P(X | q, \mathbf{s}, \mathbf{e})}_{\text{likelihood}} \times \underbrace{P(\mathbf{s}, \mathbf{e} | \lambda, \mu)}_{\text{BD prior}} \times \underbrace{P(q)P(\lambda, \mu)}_{\text{other (hyper-)priors}}$$

Taxa duration

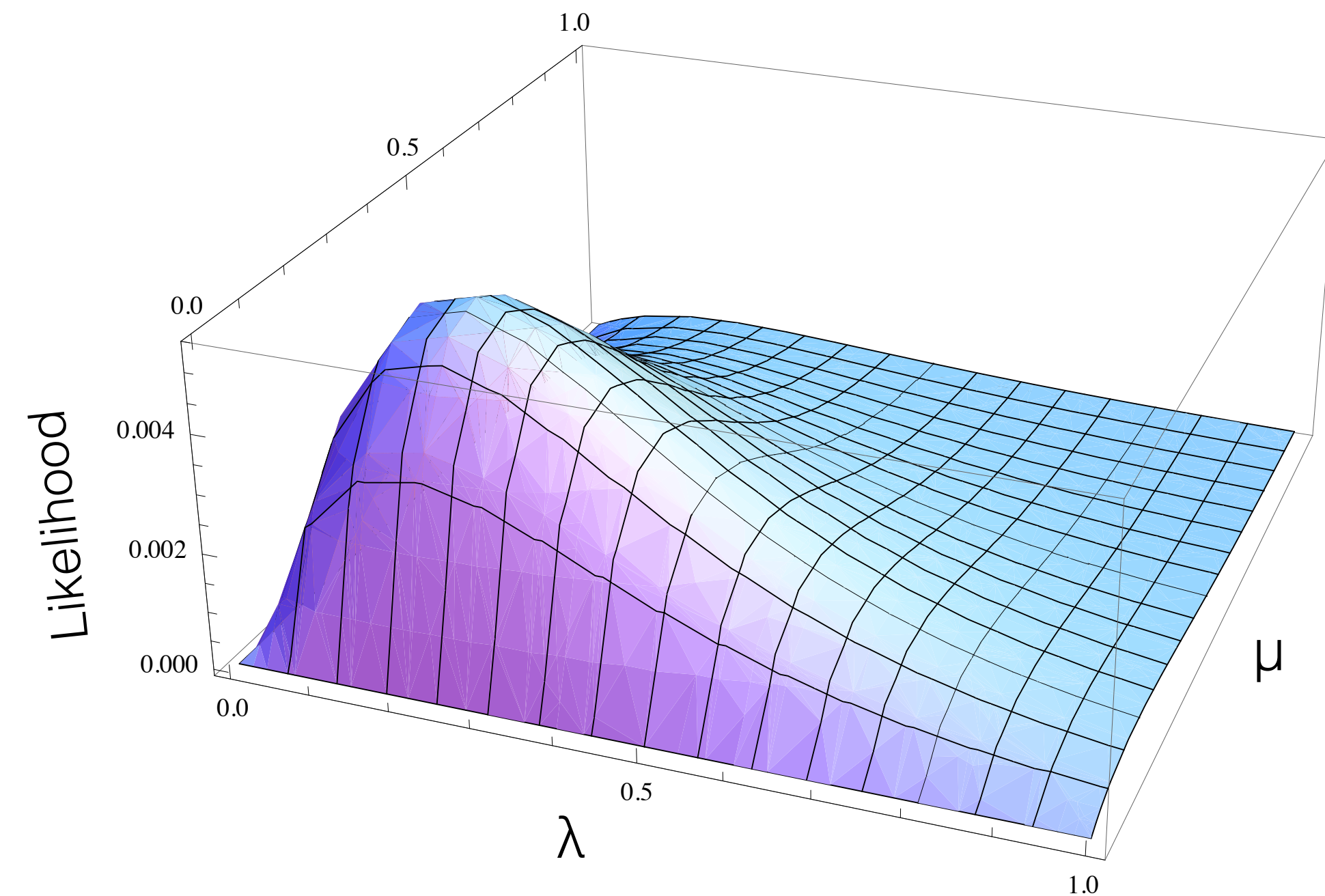
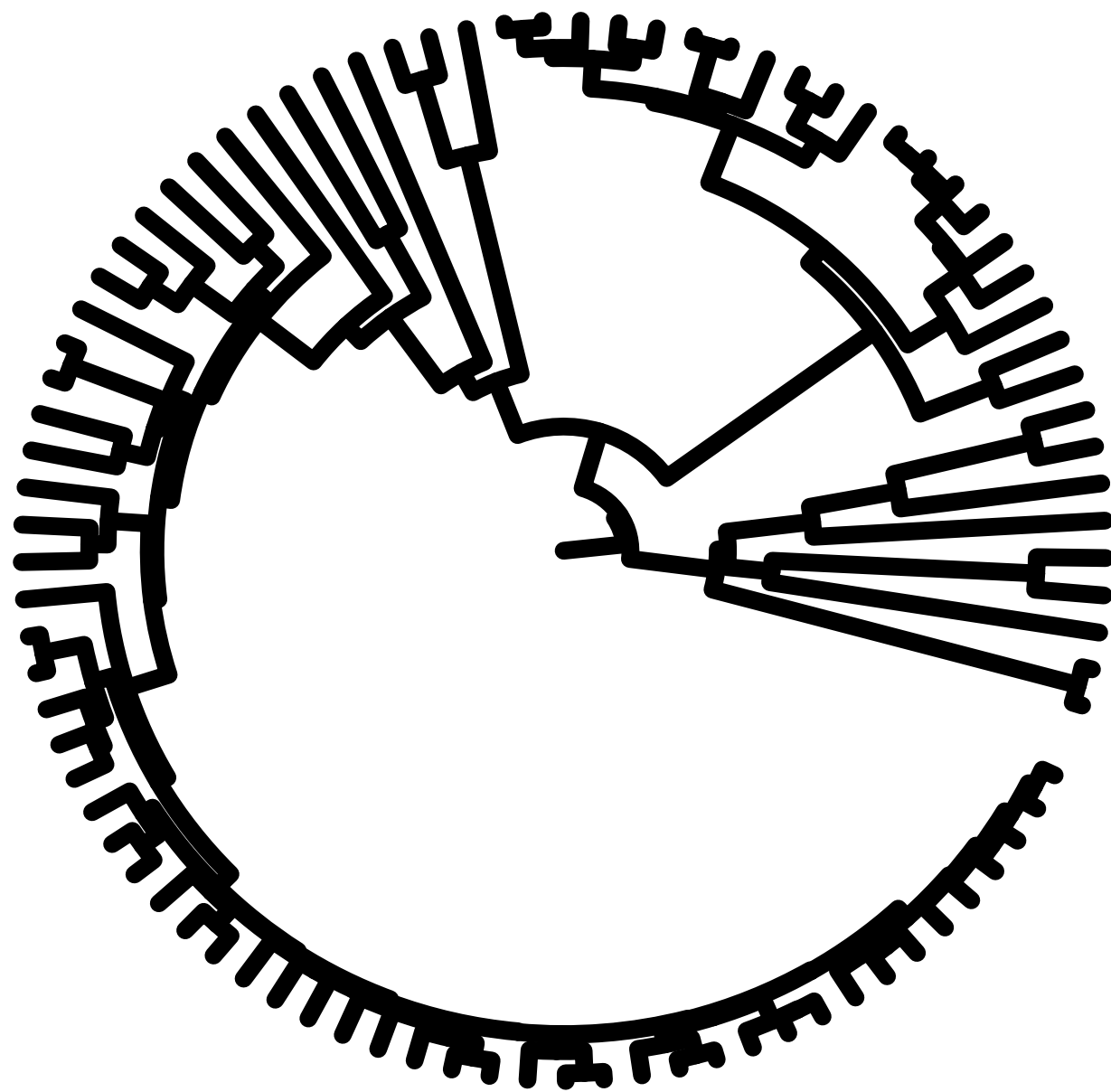
Preservation rates

Speciation & **extinction** rates

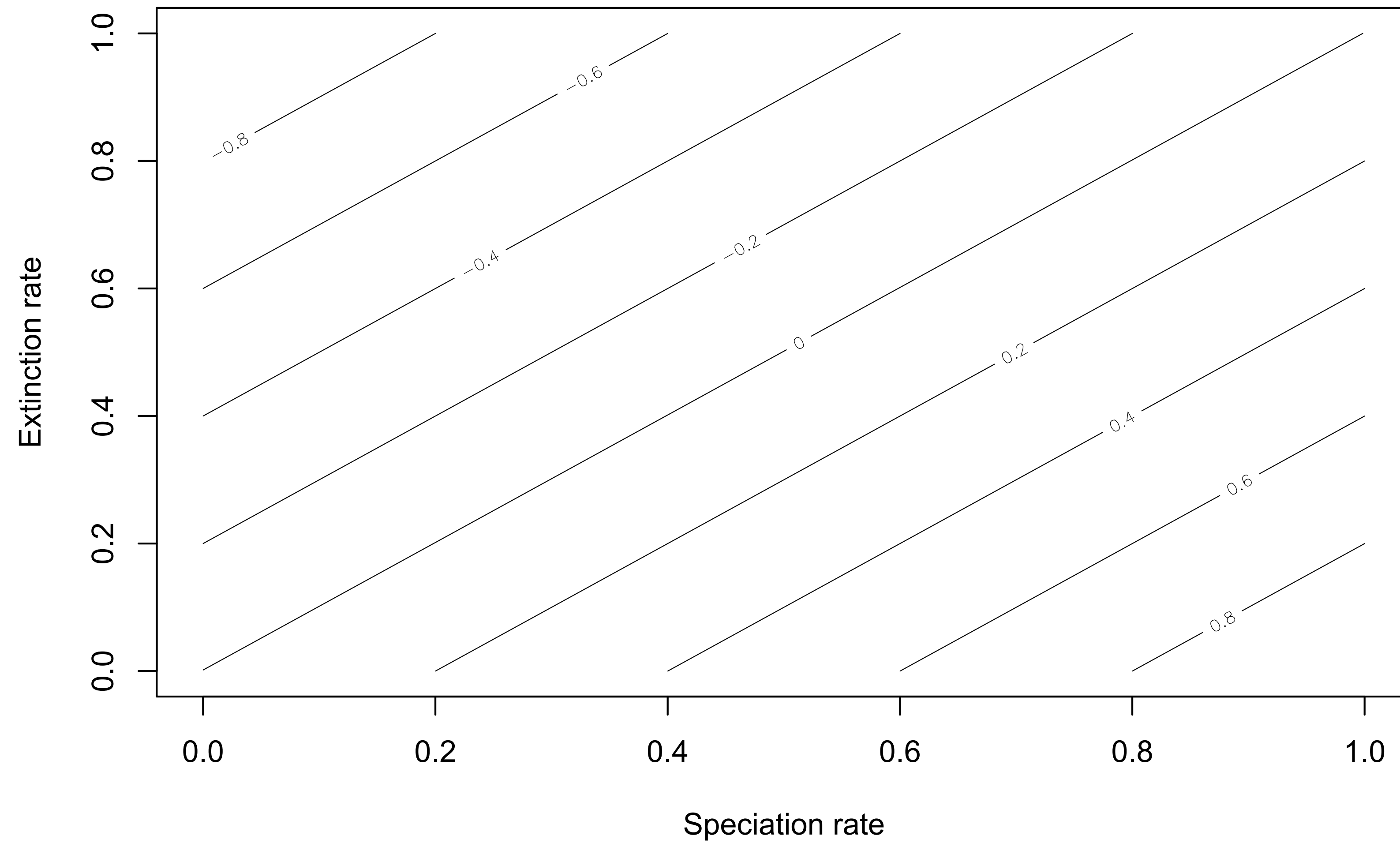


Estimating birth-death processes from phylogenies: the reconstructed birth-death process

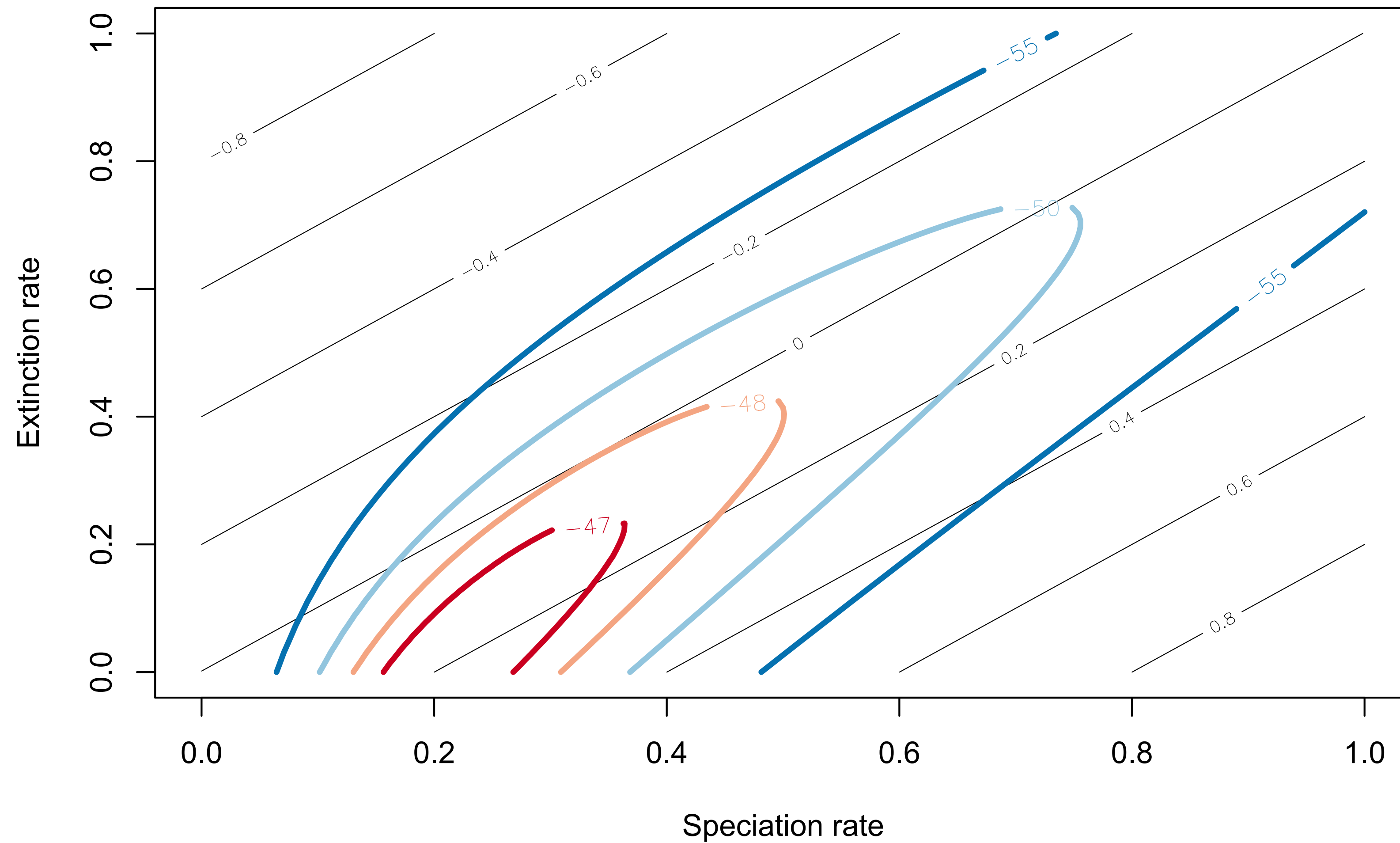
$$L(x; \lambda, \mu) = (s-1)! (\lambda - \mu)^{s-2} \exp \left((\lambda - \mu) \sum_{i=3}^s x_i \right) \times \left(1 - \frac{\mu}{\lambda} \right)^s \prod_{i=2}^s \left((\exp(\lambda - \mu) x_i) - \frac{\mu}{\lambda} \right)^{-2}$$



Likelihood surface plot

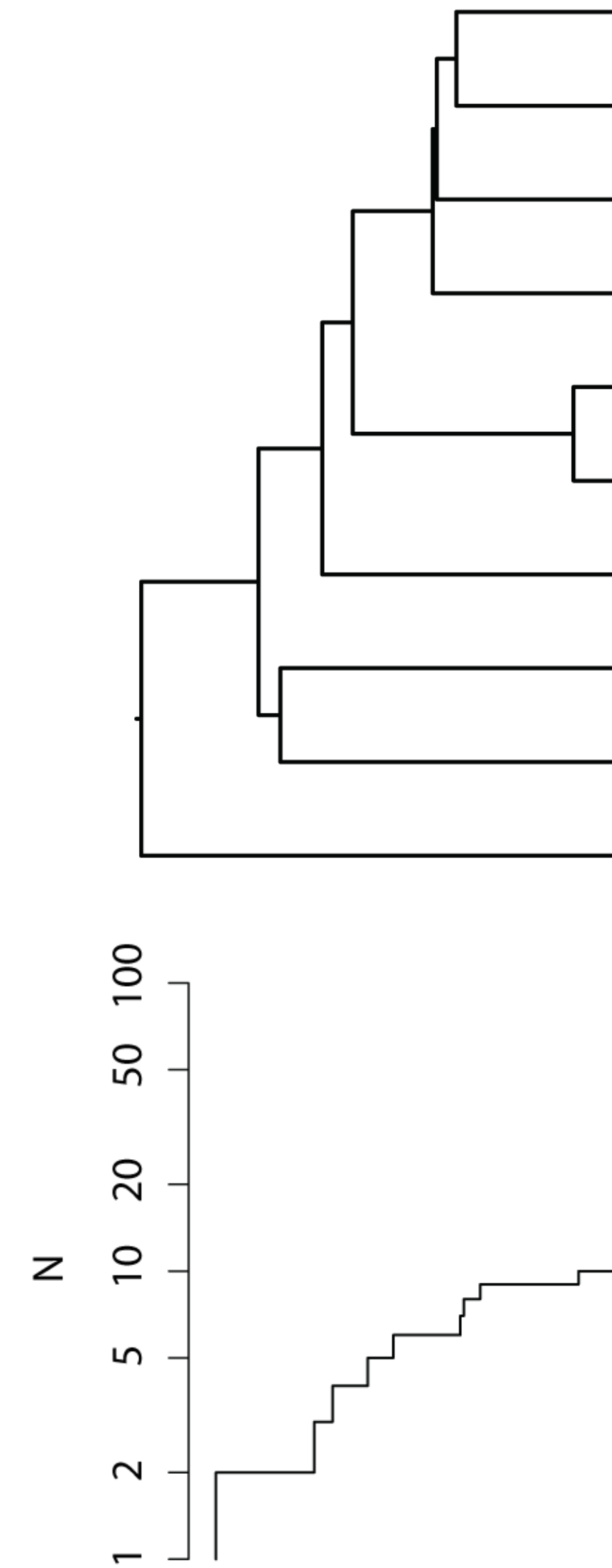
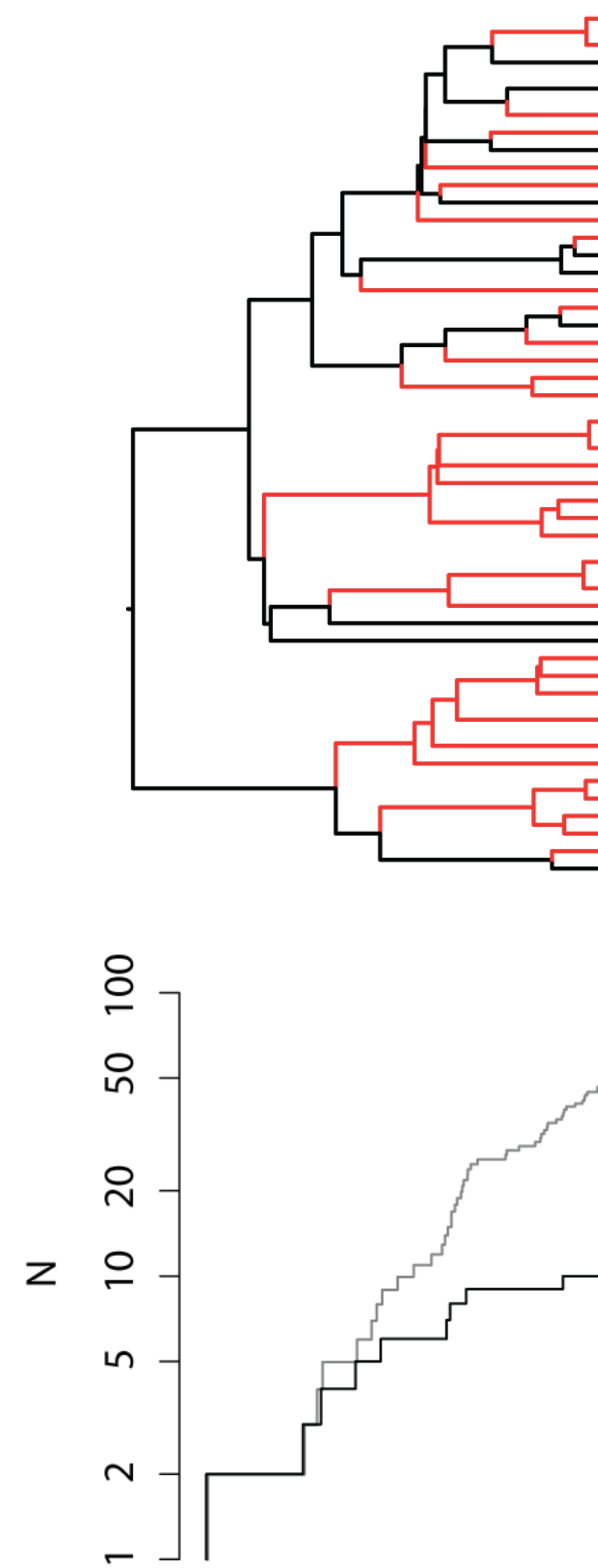
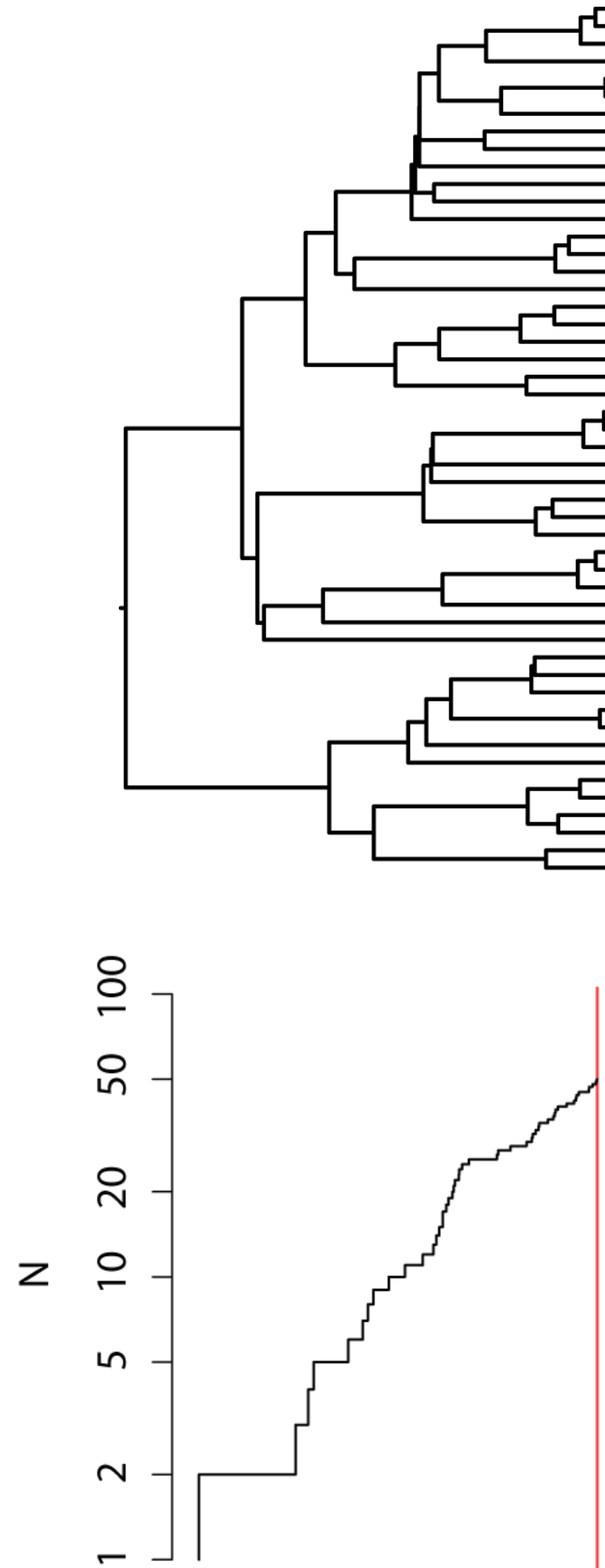


Likelihood surface plot



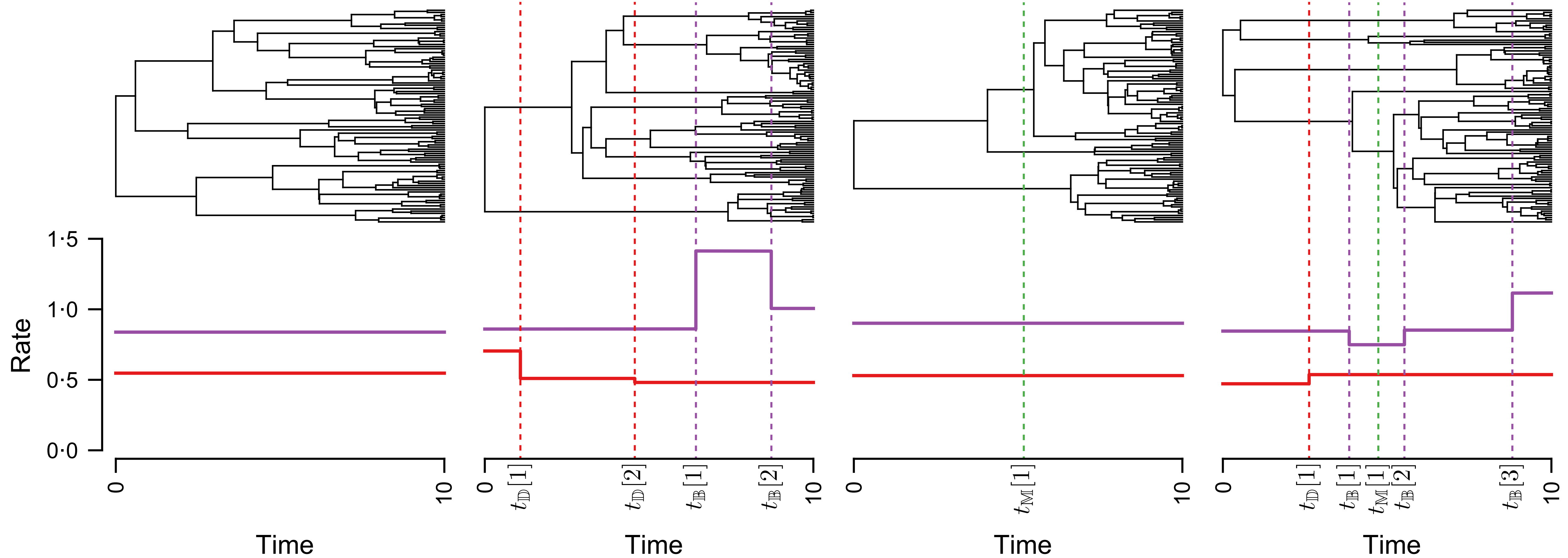
The effect of missing species (can be accounted for)

LTT

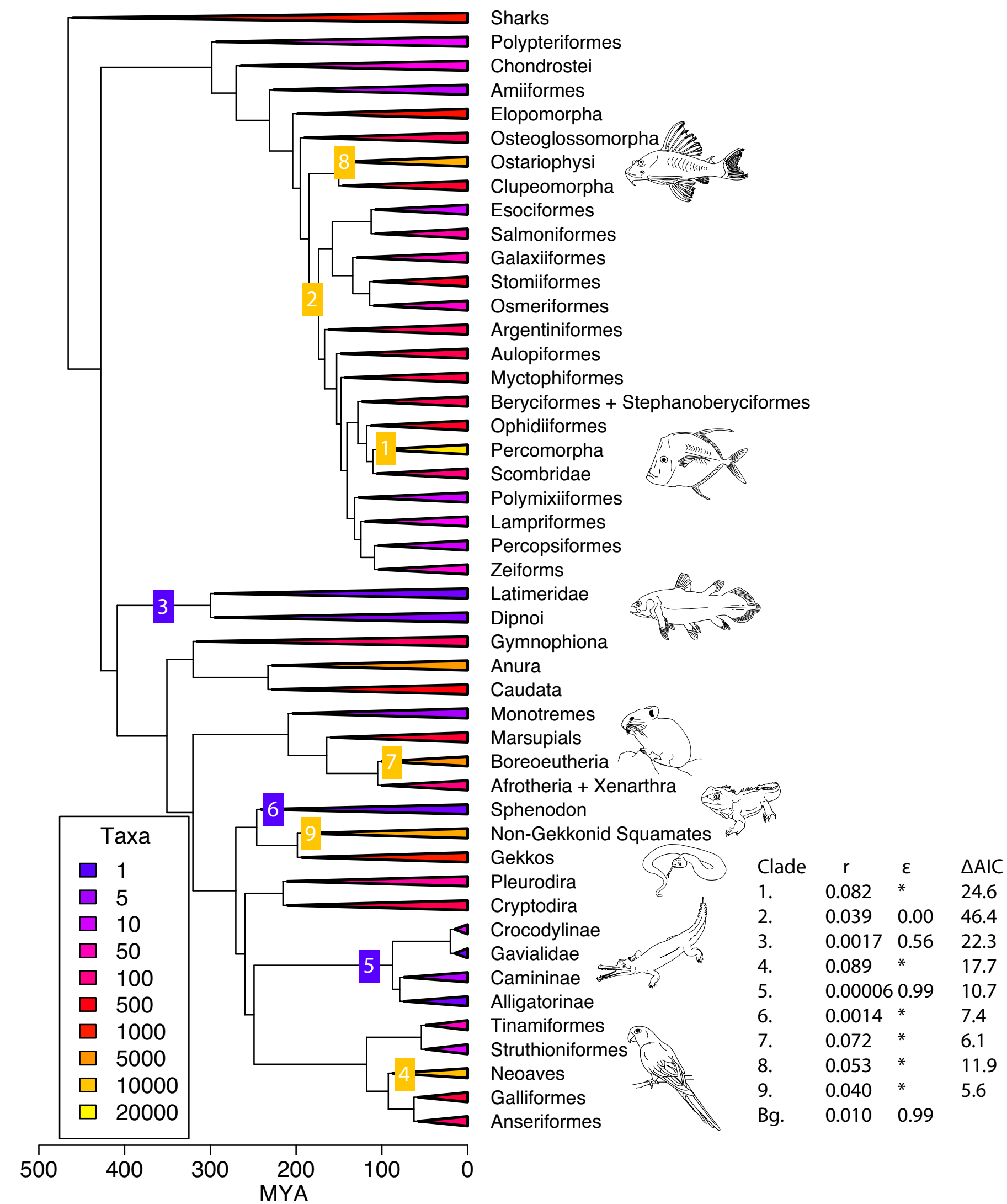
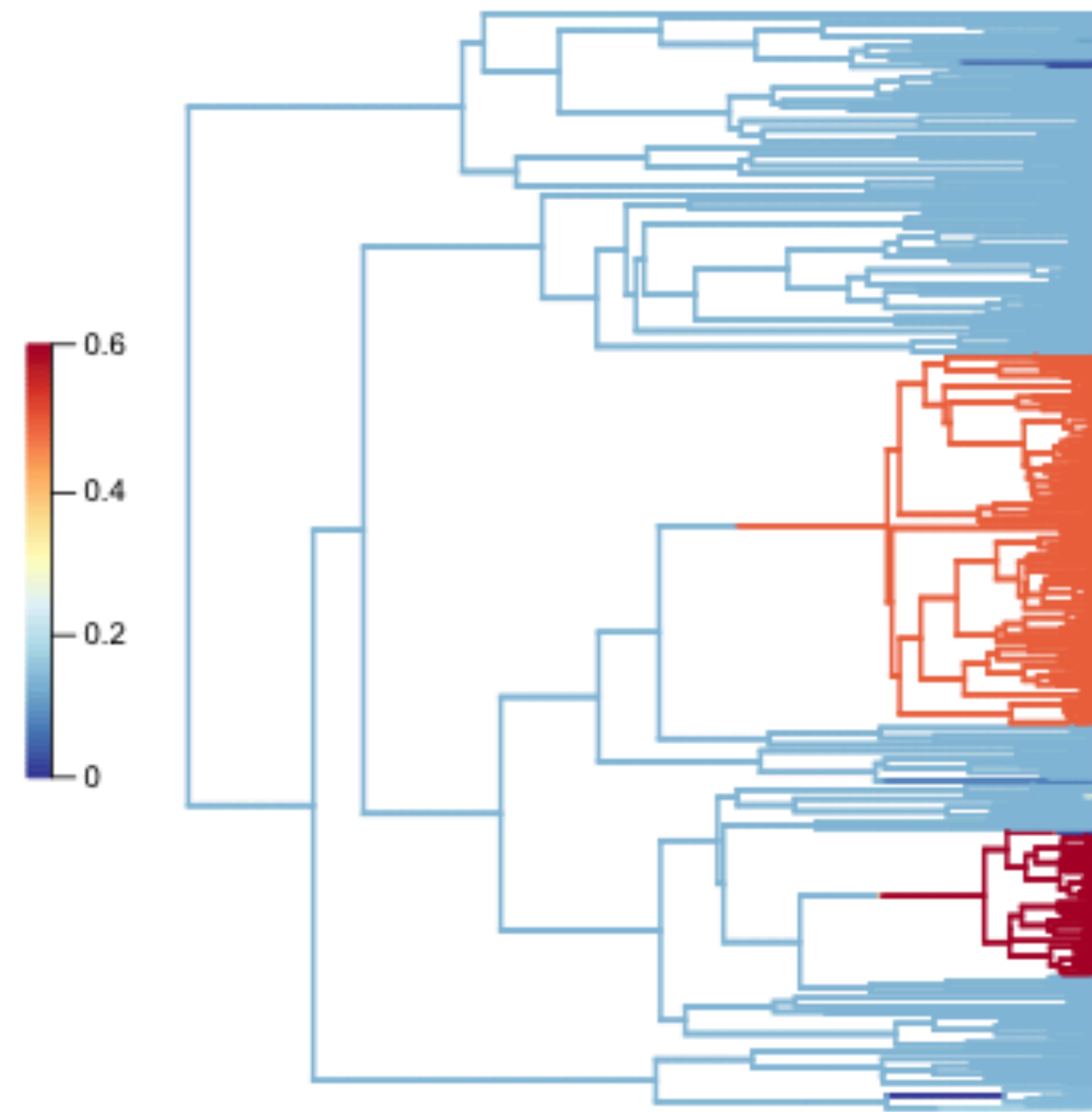


Yang & Rannala 1997 Mol Biol Evol; Stadler 2009 J Theor Biol

Skyline birth-death models

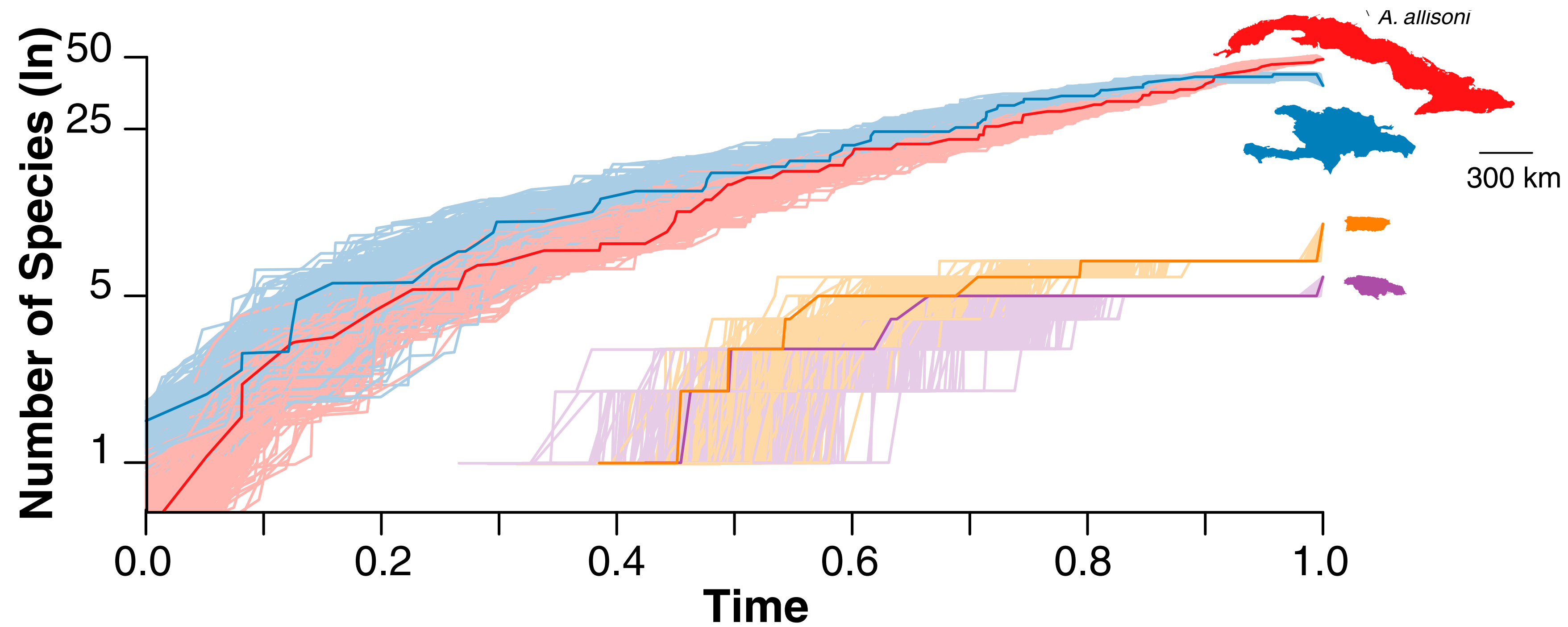


Birth-death models with rate variation across clades



Alfaro et al. 2009 PNAS; Rabosky et al. 2014 PLoS ONE

Birth-death models with diversity-dependence

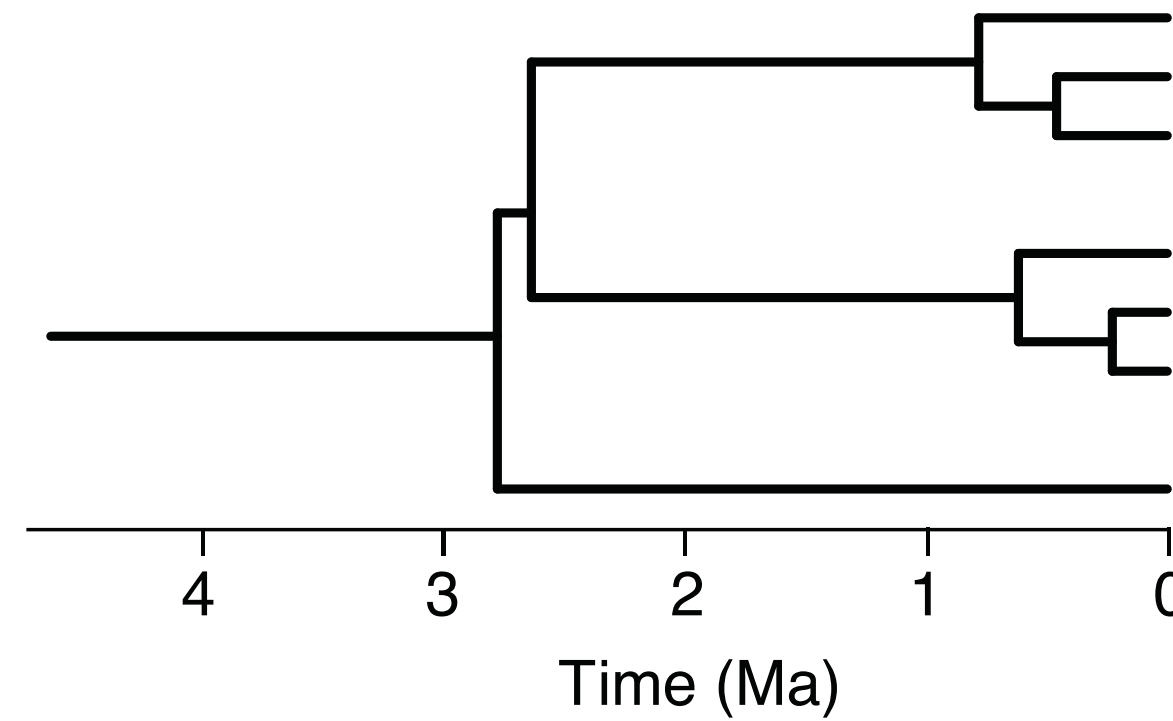


Non-exhaustive list of software implementing phylogenetic BD model

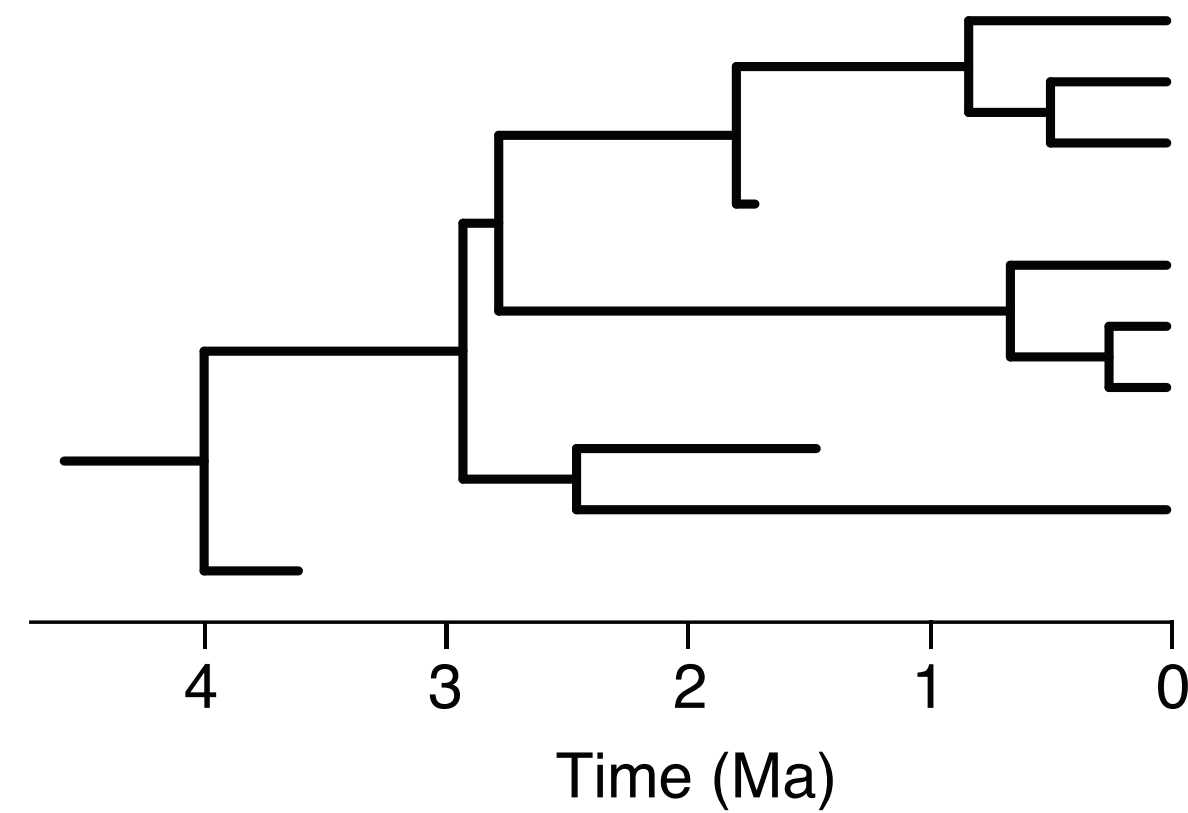
Program	Main developers	Methods
TreePar (R)	T. Stadler	Speciation and extinction rates through time
RPANDA (R)	H. Morlon	Speciation and extinction rates through time
TESS (R)	S. Hoehna, B. Moore	Speciation and extinction rates through time
DDD (R)	R. Etienne	Speciation and extinction rates under diversity dependence
Medusa (R)	M. Alfaro	Speciation and extinction rates across clades
BayesRate (Python)	D. Silvestro	Speciation and extinction rates across clades
BAMM (C++, R)	D. Rabosky	Speciation and extinction rates across clades (and through time)
RevBayes (C++)	D. Hoehna, M. Landis, T. Heath, J. Huelsenbeck	Speciation and extinction rates through time, fossilized birth-death models
diversiTree (R)	R. G. Fitzjohn	Trait-dependent speciation and extinction rates

Ideally fossils and phylogenies should tell the same story

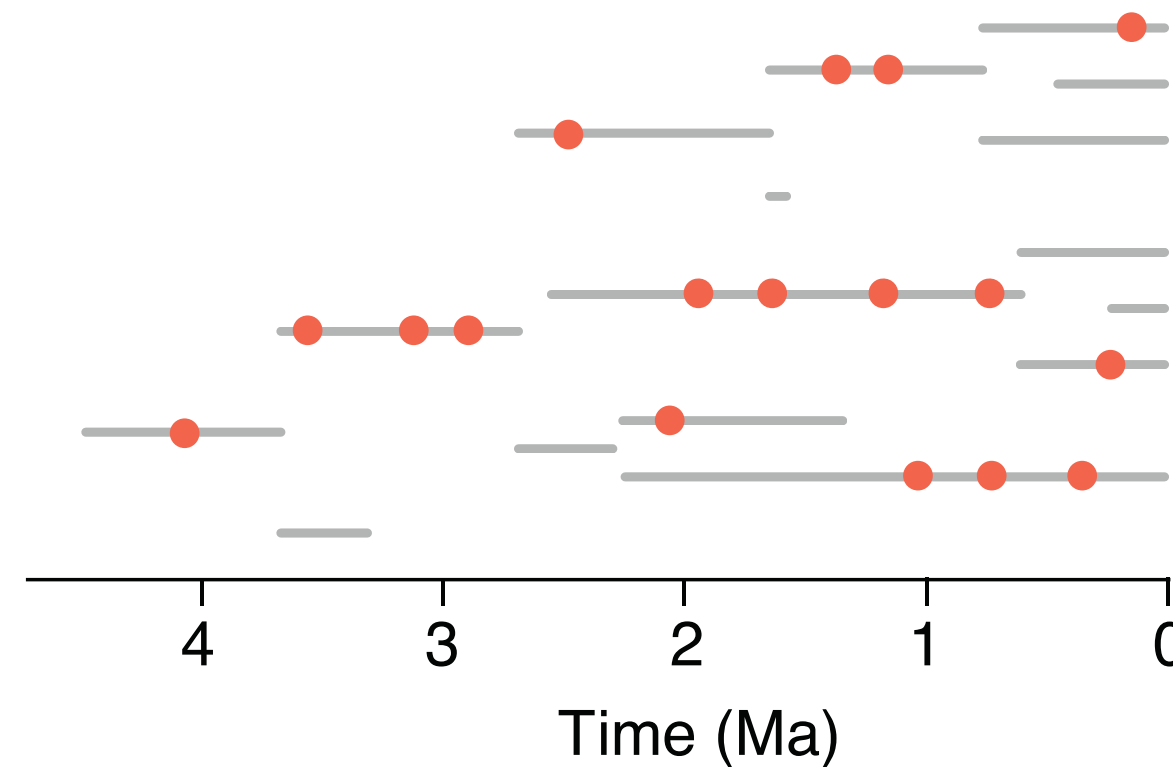
Phylogeny of extant species



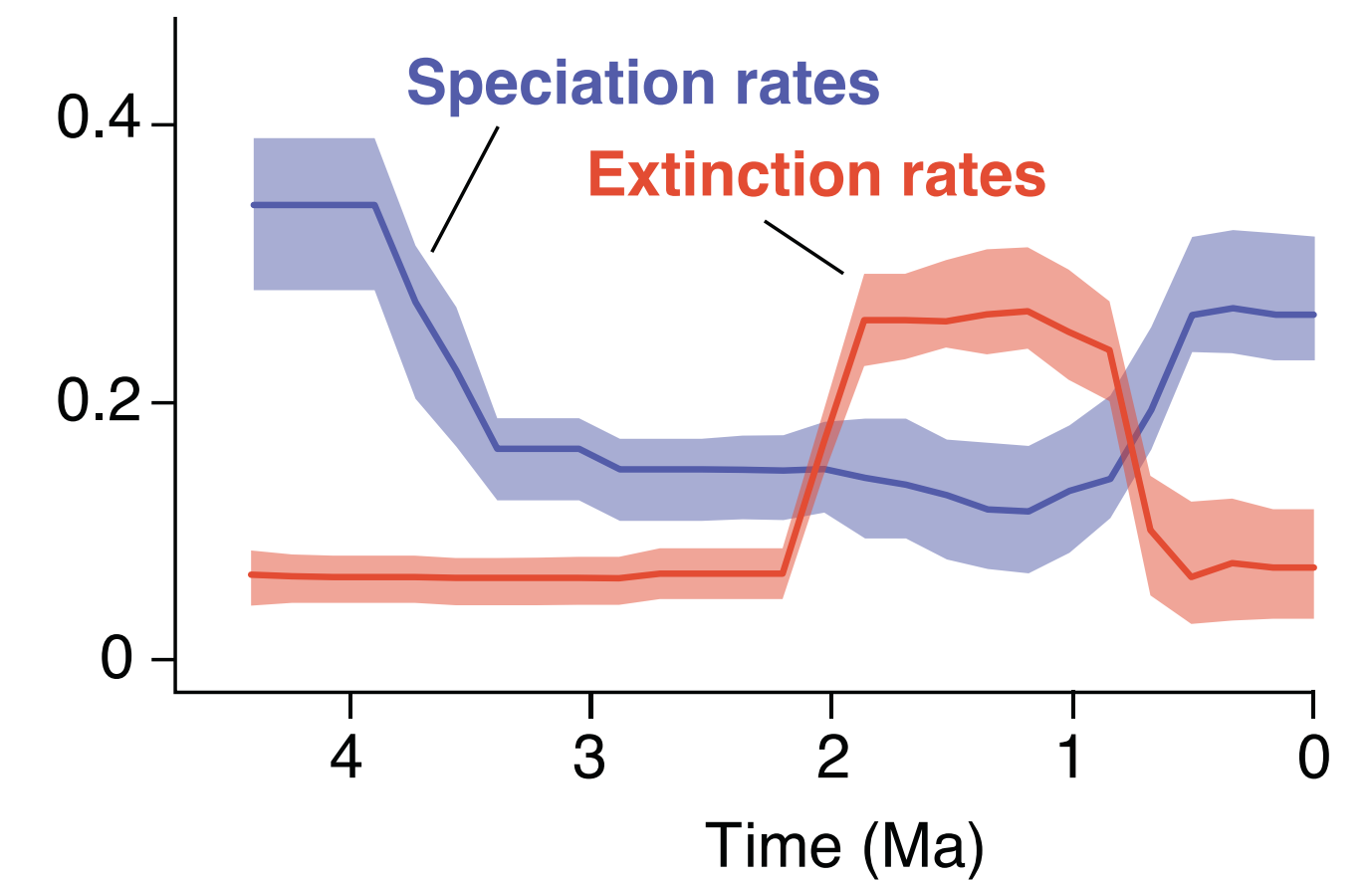
Complete evolutionary history



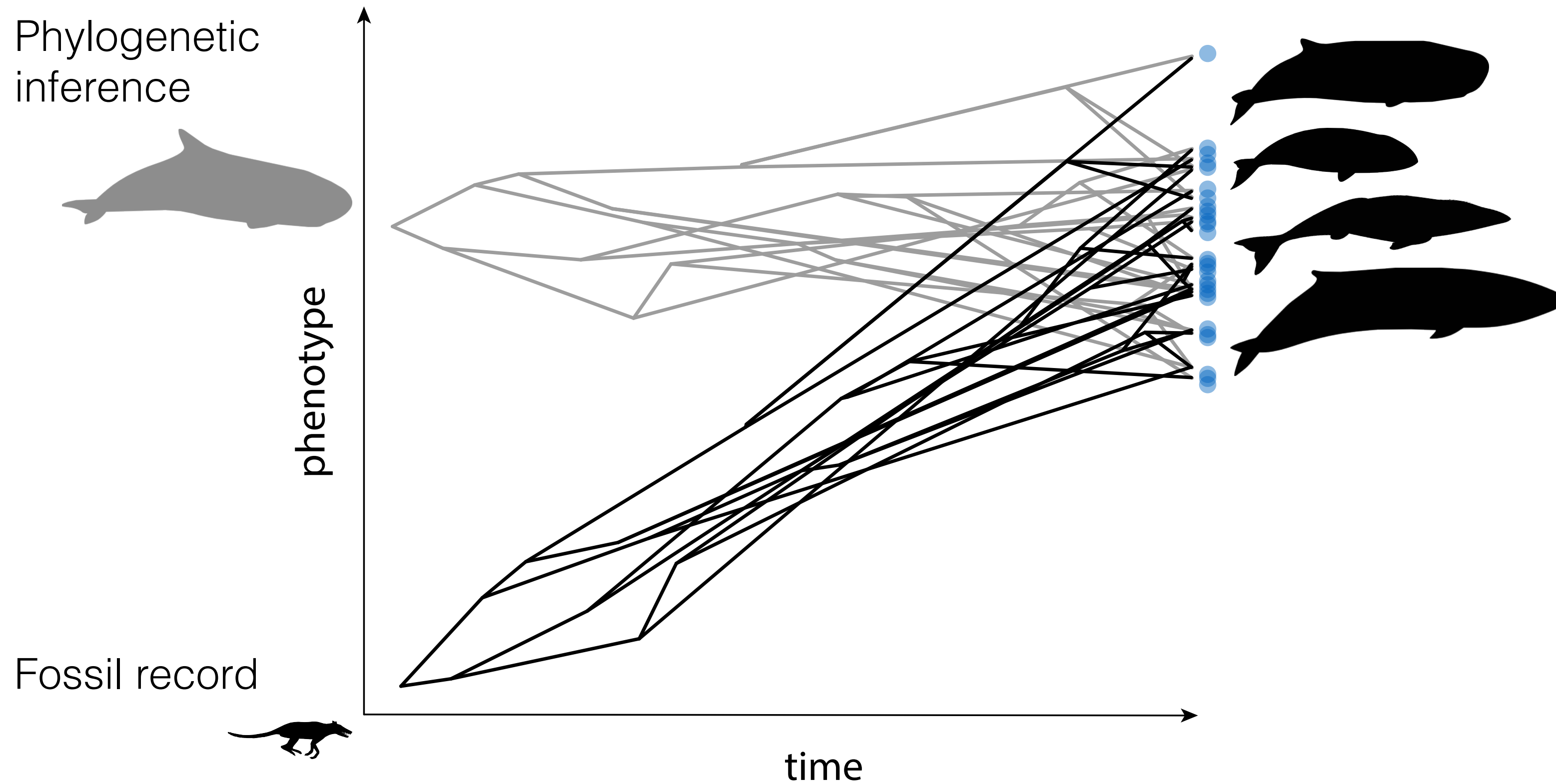
Fossil record



Diversification dynamics



Calls for integration of phylogenetic and fossil data – trait evolution



Opinion

Cell
PRESS

Diversity in time and space: wanted dead and alive

Susanne A. Fritz^{1*}, Jan Schnitzler^{1,2*}, Jussi T. Eronen^{1,3*}, Christian Hof^{1*},
Katrin Böhning-Gaese^{1,2*}, and Catherine H. Graham^{1,2,4*}

Methods in Ecology and Evolution

British Ecological Society

Methods in Ecology and Evolution 2013, **4**, 699–702

doi: 10.1111/2041-210X.12091

EDITORIAL

Unifying fossils and phylogenies for comparative analyses of diversification and trait evolution

Graham J. Slater^{1*} and Luke J. Harmon^{2,3}

Evolutionary Ecology Research, 2017, **18**: 187–200

Fossils matter – understanding modes and rates of trait evolution in Musteloidea (Carnivora)

Jan Schnitzler^{1,2*}, Christina Theis^{2,3*}, P. David Polly⁴ and Jussi T. Eronen^{5,6}



ANNUAL
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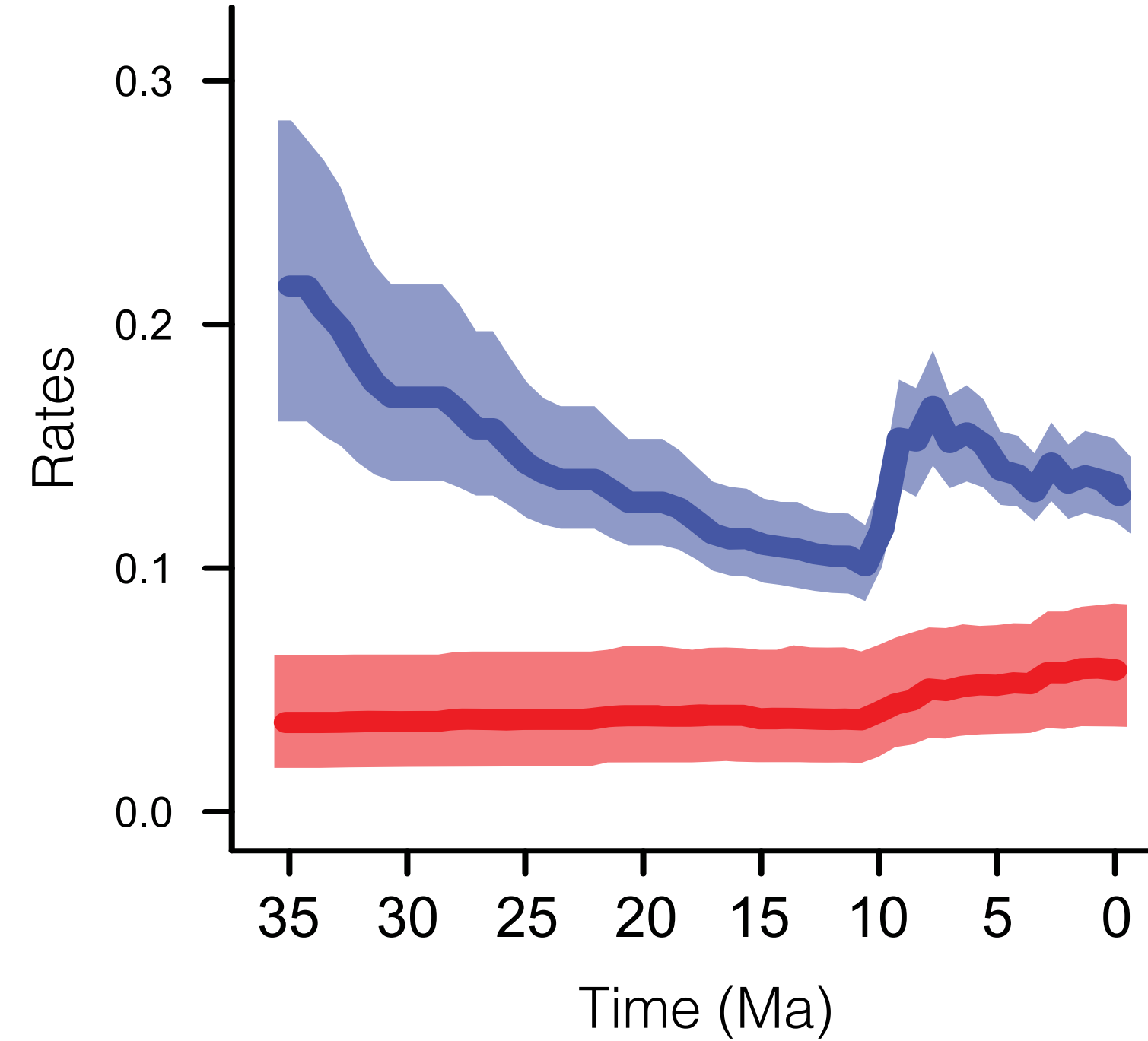
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Integrating Paleontological and Phylogenetic Approaches to Macroevolution

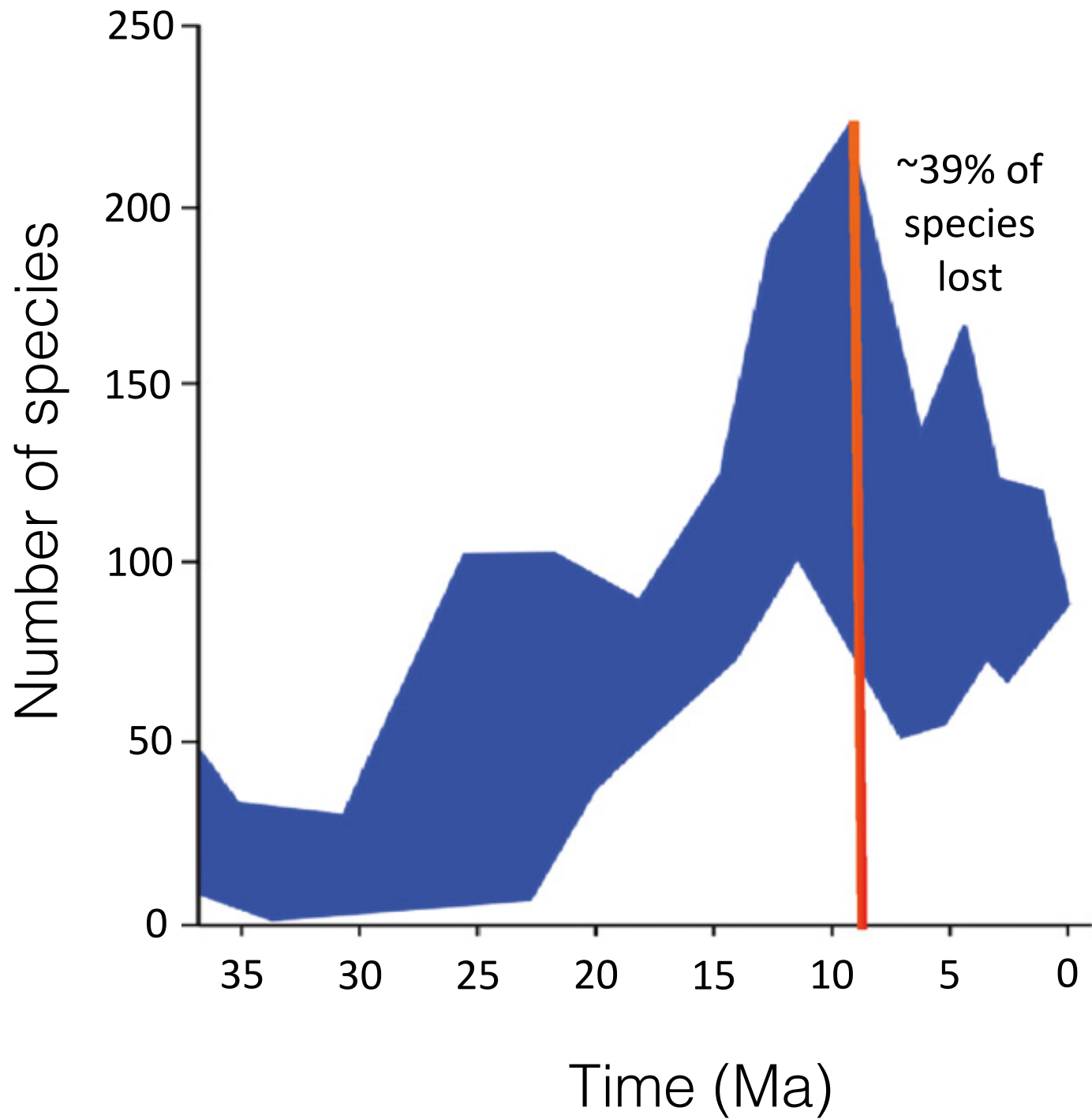
Gene Hunt¹ and Graham Slater²

Calls for integration of phylogenetic and fossil data – diversification rates

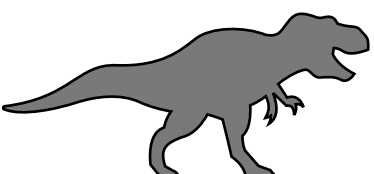
Phylogenetic inference



Fossil data



Rabosky 2014 PLoS One



Quental and Marshall 2010 TREE

nature
ecology & evolution

PERSPECTIVE

PUBLISHED: 23 MAY 2017 | VOLUME: 1 | ARTICLE NUMBER: 0165

Five palaeobiological laws needed to understand the evolution of the living biota

Charles R. Marshall

Opinion

Cell
PRESS

Diversity dynamics: molecular phylogenies need the fossil record

Tiago B. Quental and Charles R. Marshall

ORIGINAL ARTICLE

doi:10.1111/j.1558-5646.2009.00926.x

EXTINCTION RATES SHOULD NOT BE ESTIMATED FROM MOLECULAR PHYLOGENIES

Daniel L. Rabosky^{1,2,3,4}

doi:10.1111/



Extinction can be estimated from moderately sized molecular phylogenies

Jeremy M. Beaulieu^{1,2} and Brian C. O'Meara³

Building phylogenetic trees with fossils (2012–today)

Combining molecular and morphological data (molecular and morphological clocks)

Molecular matrix

66 extant taxa
7 genes
~5kb

Morphological matrix

61 extant taxa
343 characters
(77% complete)

Morphological matrix

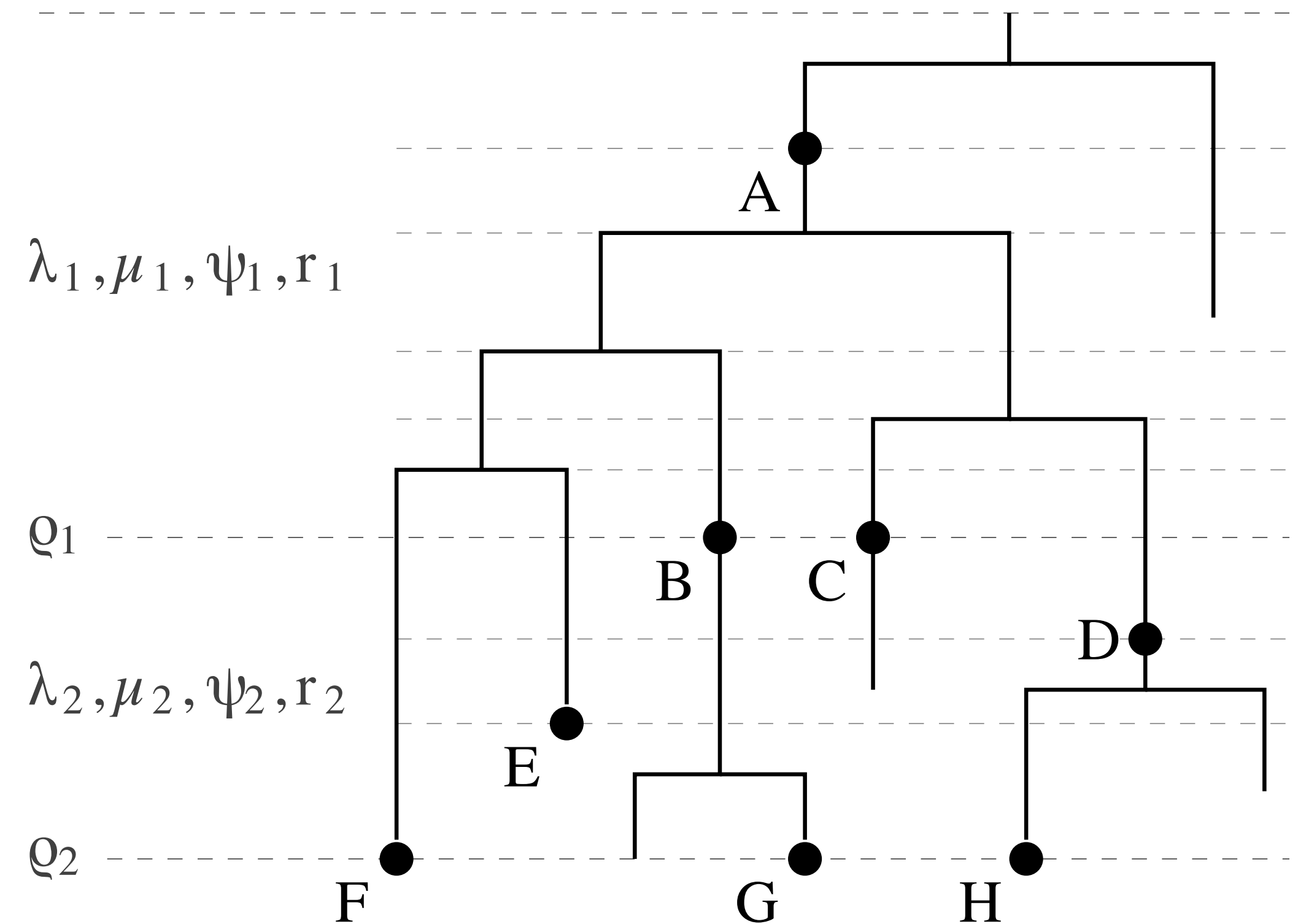
45 fossil taxa
343 characters
(12% complete)

Combined matrix

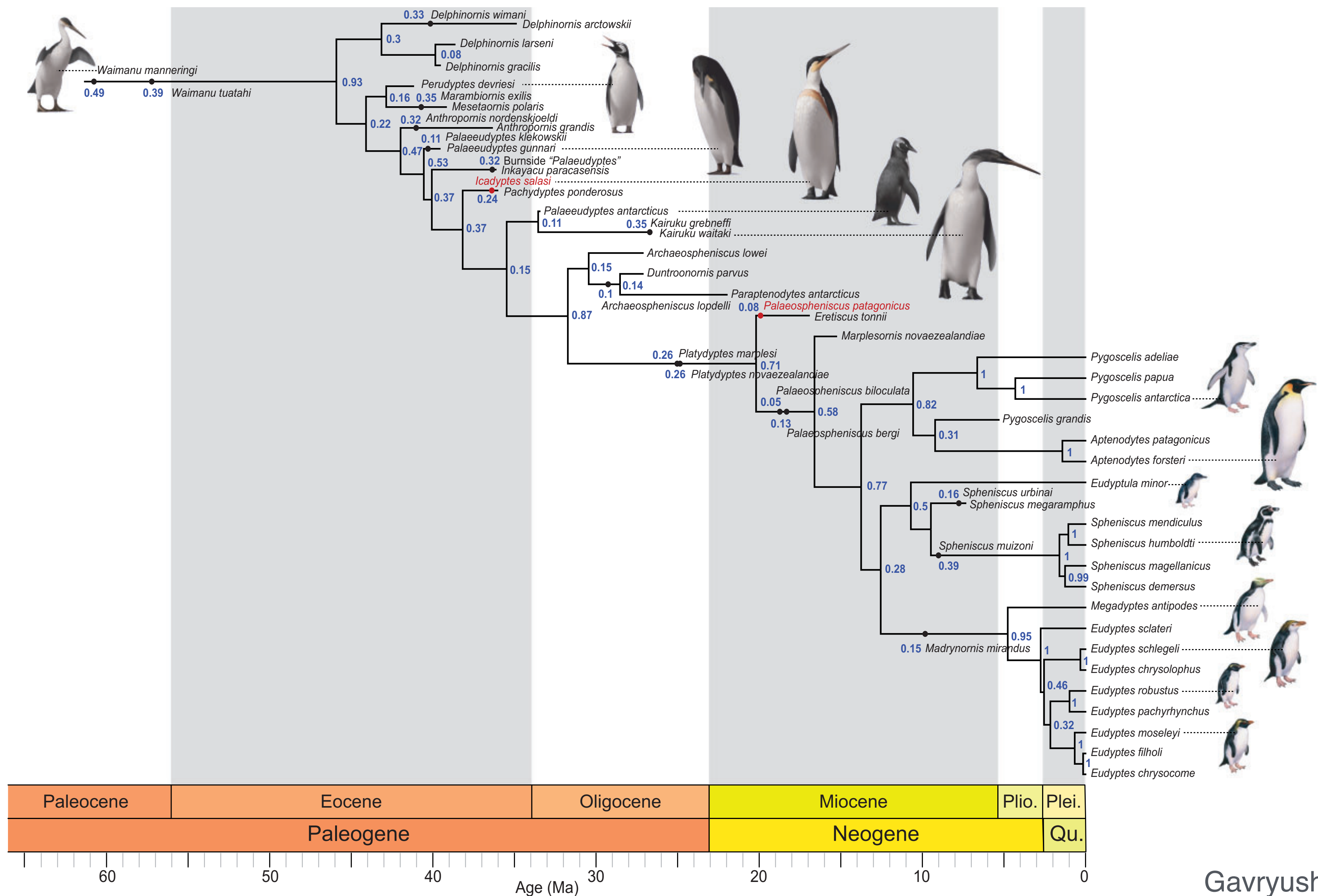
113 extant and
fossil taxa

Total-evidence analysis

The fossilized birth-death process

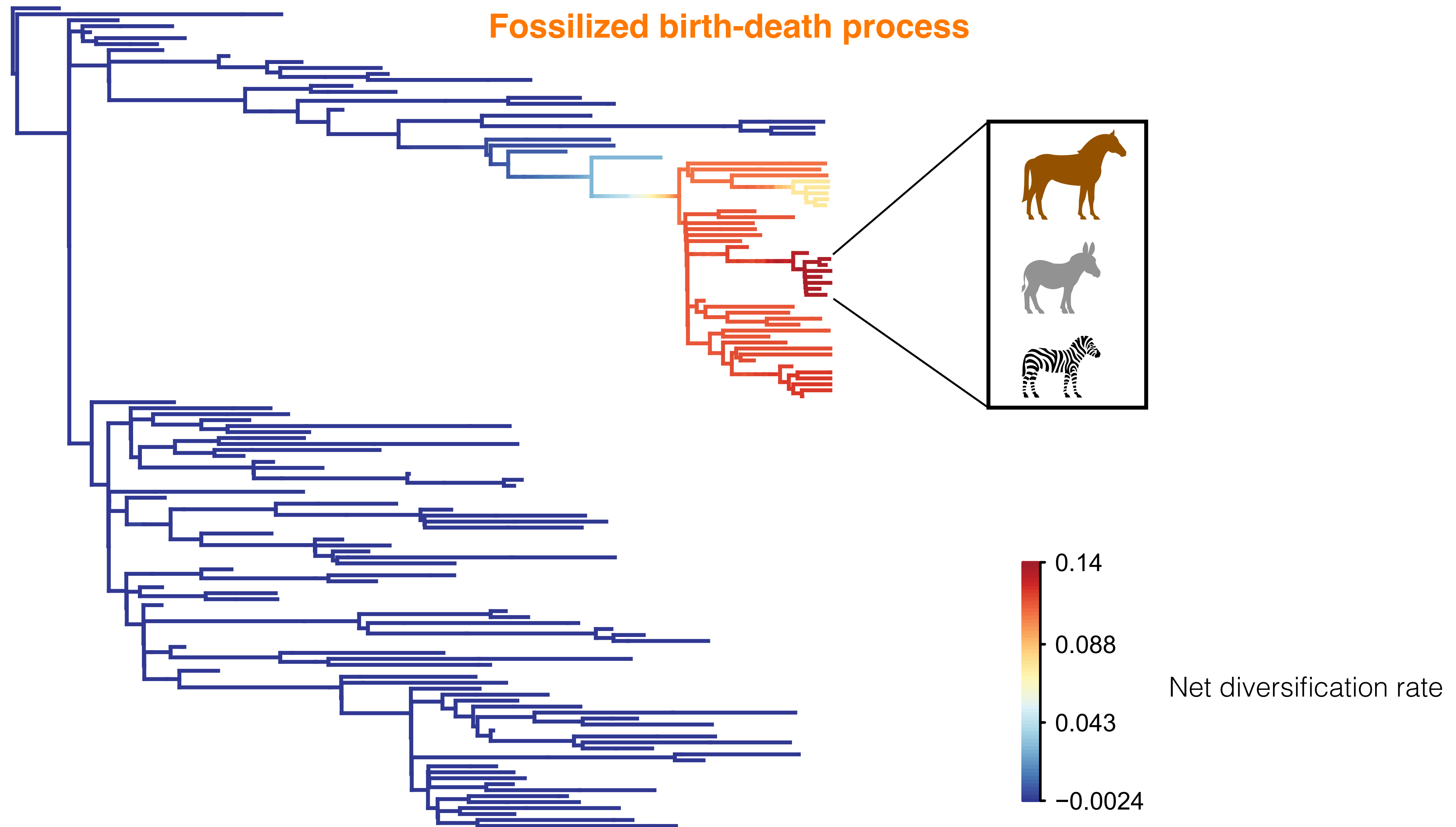


Building phylogenetic trees with fossils (2012–today)



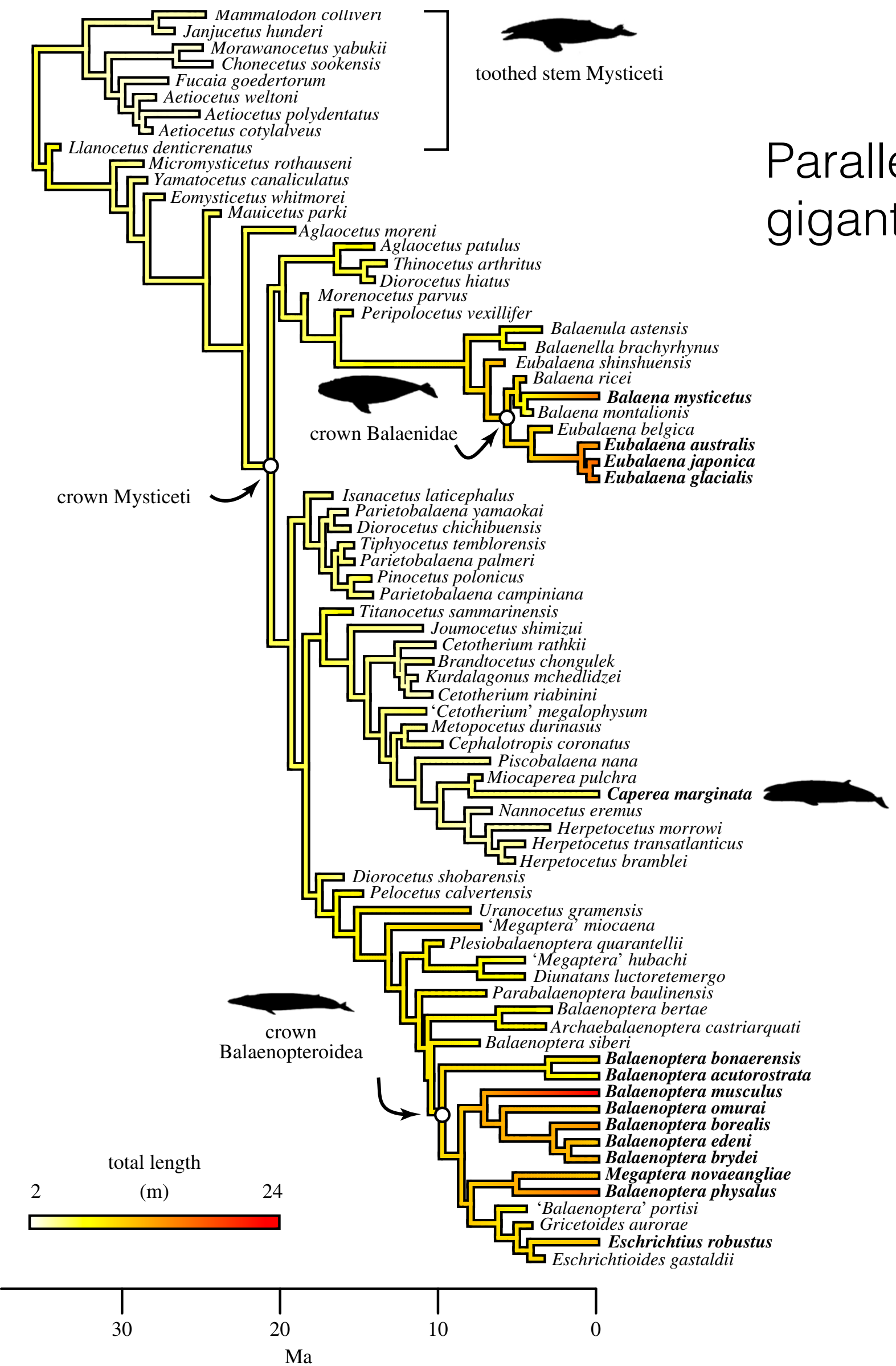
Gavryushkina 2016 Syst Biol

Speciation and extinction rates from phylogenies with fossils



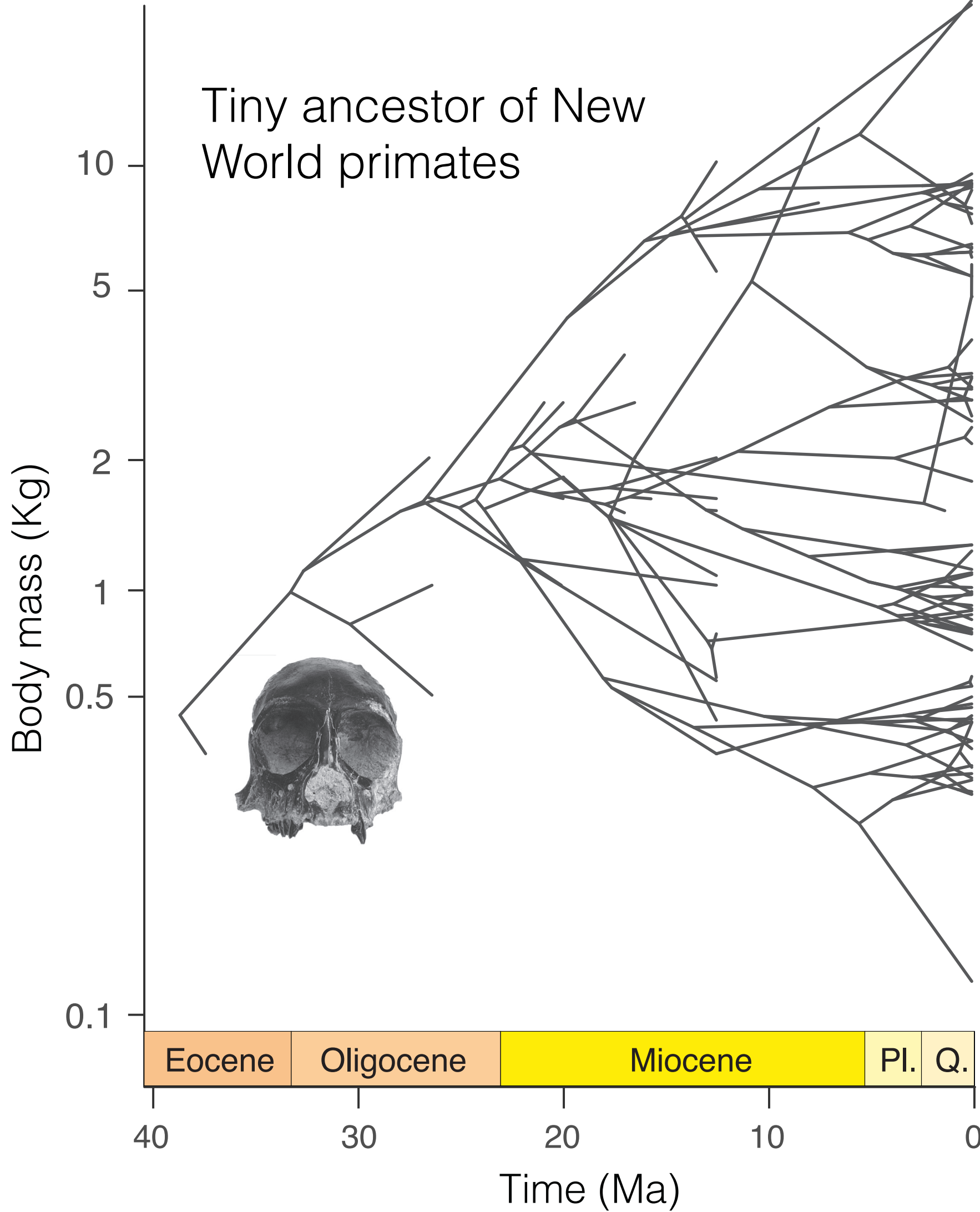
Cantalapiedra et al. 2017 Science; Mitchell et al. 2018 Syst Biol

Inferring trait evolution from phylogenies with fossils



Parallel evolution of gigantism in whales

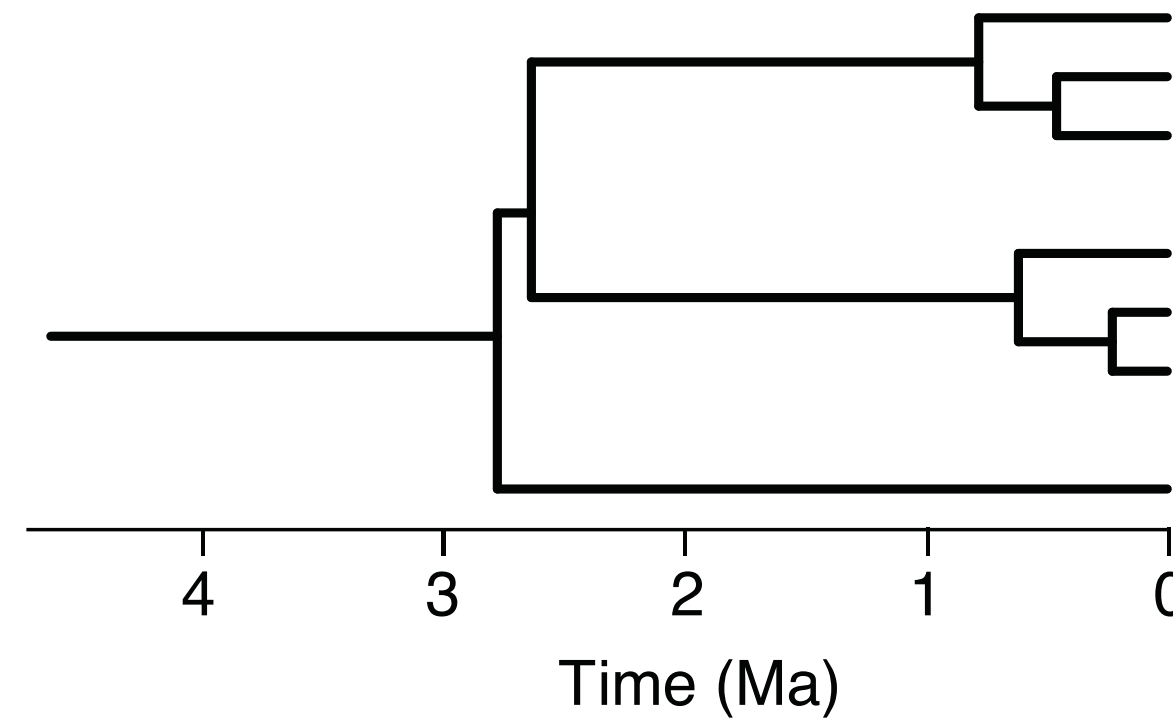
Fossilized Brownian process



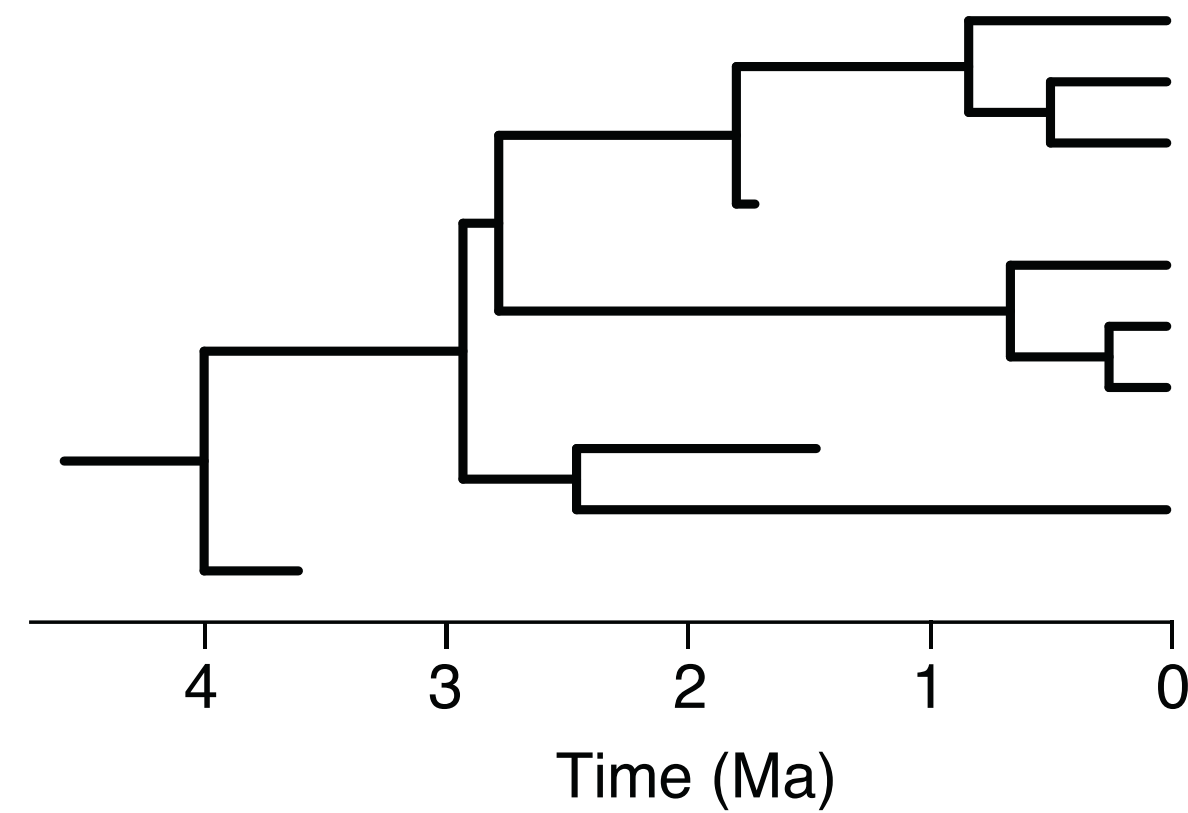
Slater et al. 2012 MEE; 2017 Proc Roy Soc B; Silvestro et al. 2018 Syst Biol

Ideally fossils and phylogenies should tell the same story

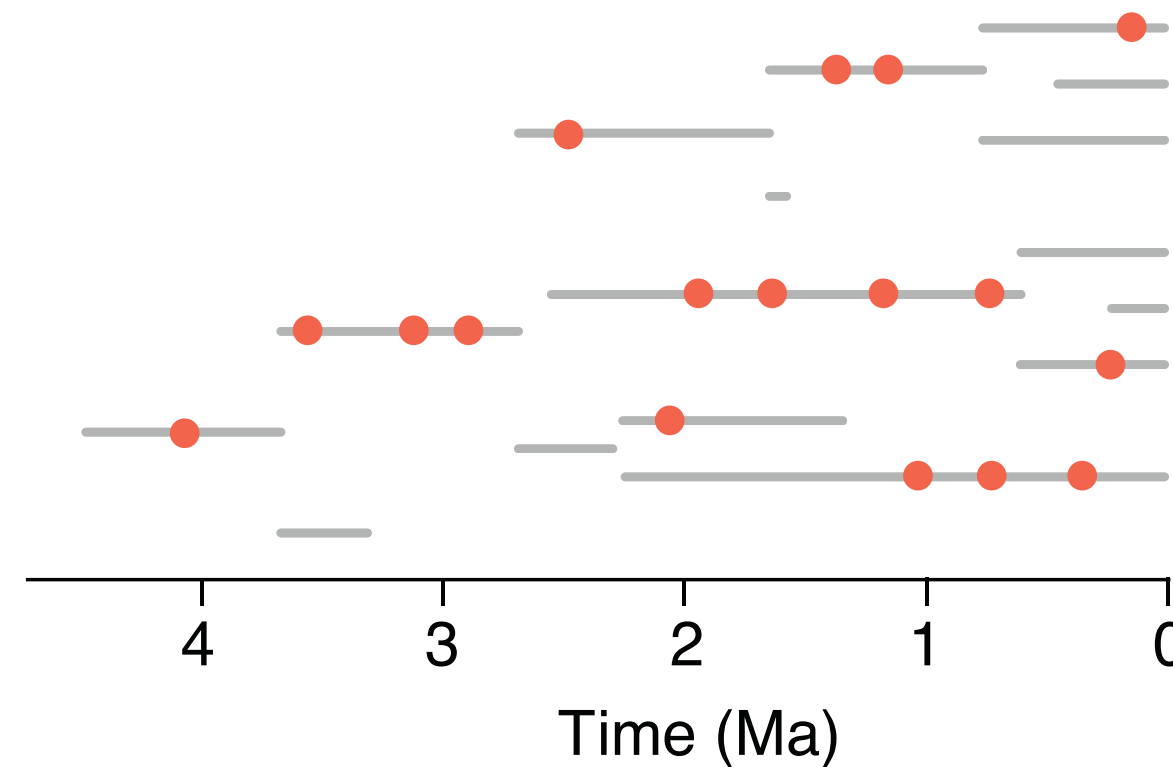
Phylogeny of extant species



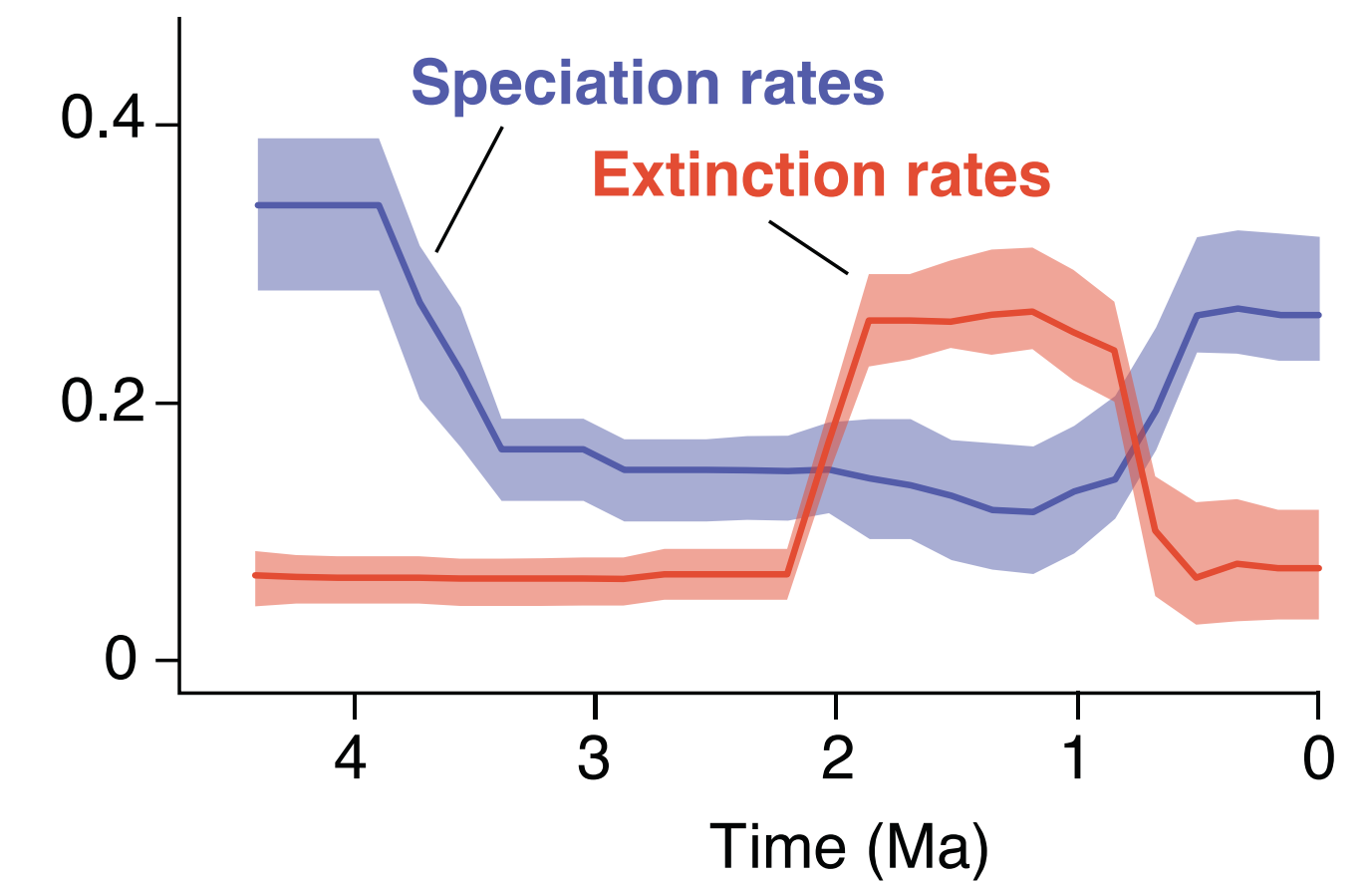
Complete evolutionary history



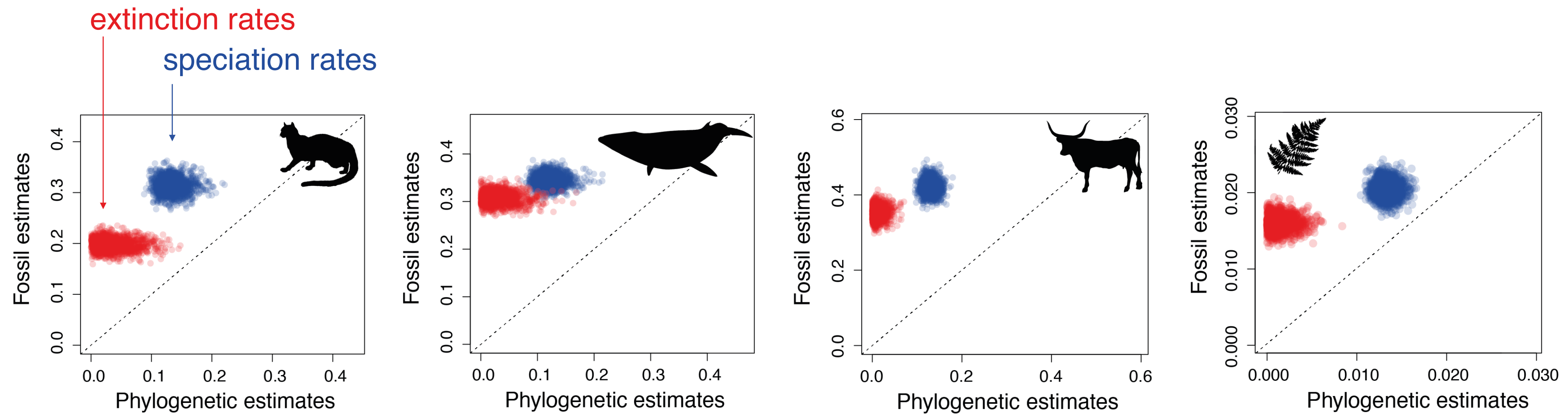
Fossil record



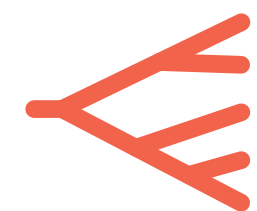
Diversification dynamics



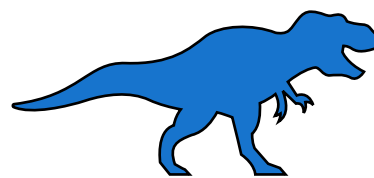
Why are fossil-based and phylogenetic rate estimates almost always different?



Estimated mean longevity of carnivore species



phylogenetic
estimate: 7 Myr



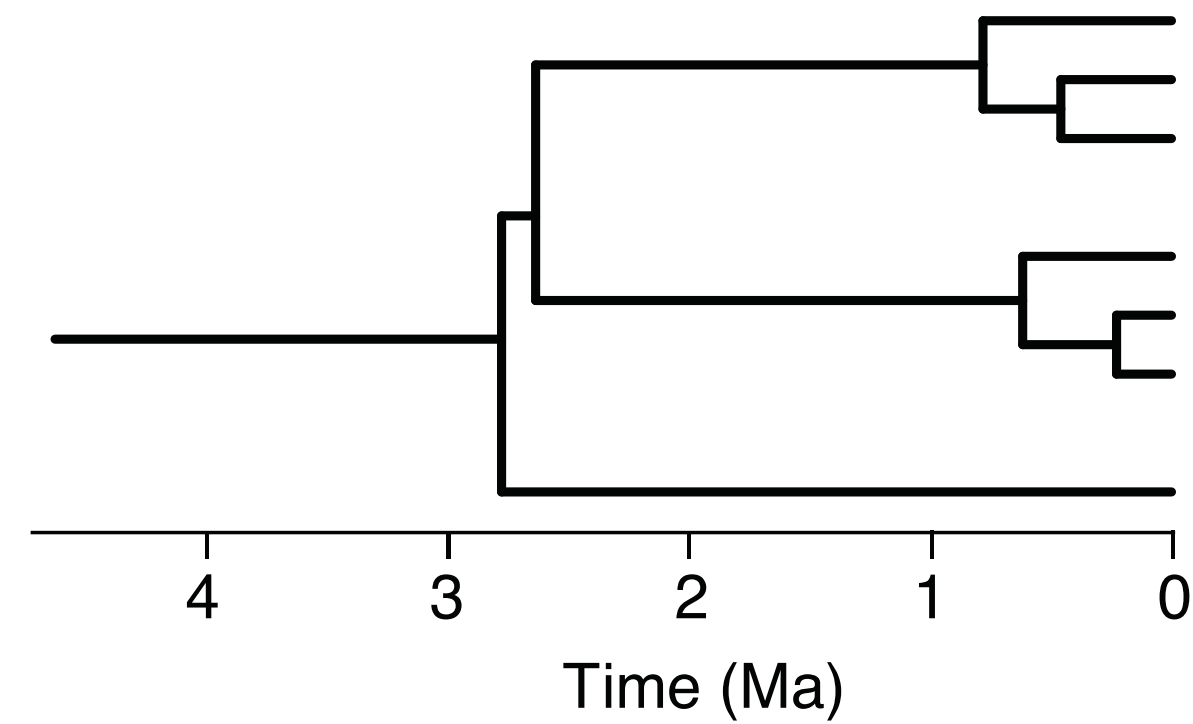
fossil estimate:
2.1 Myr

Hagen et al. 2017 Syst Biol

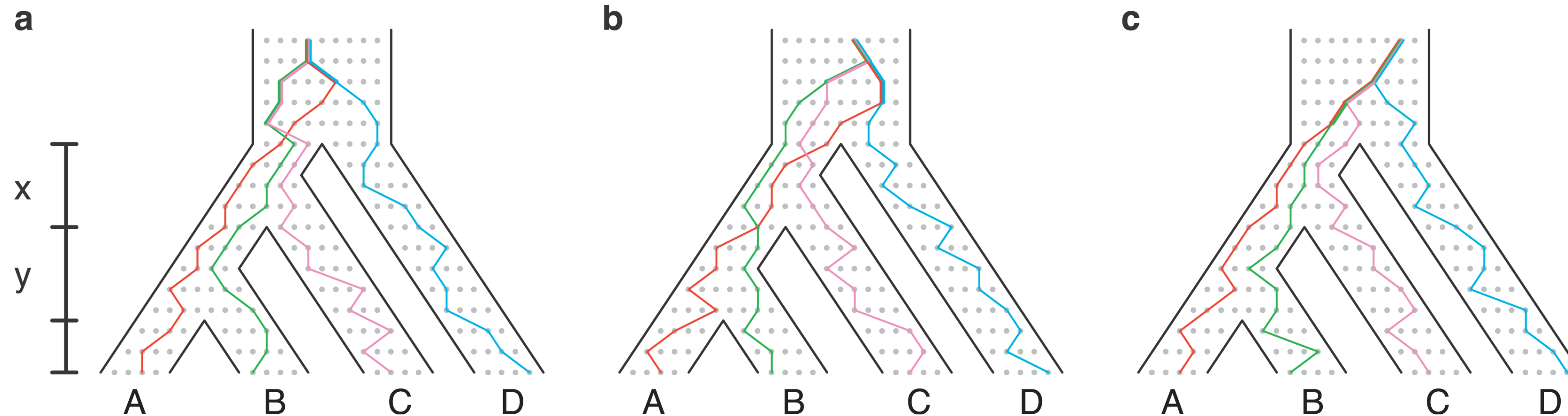
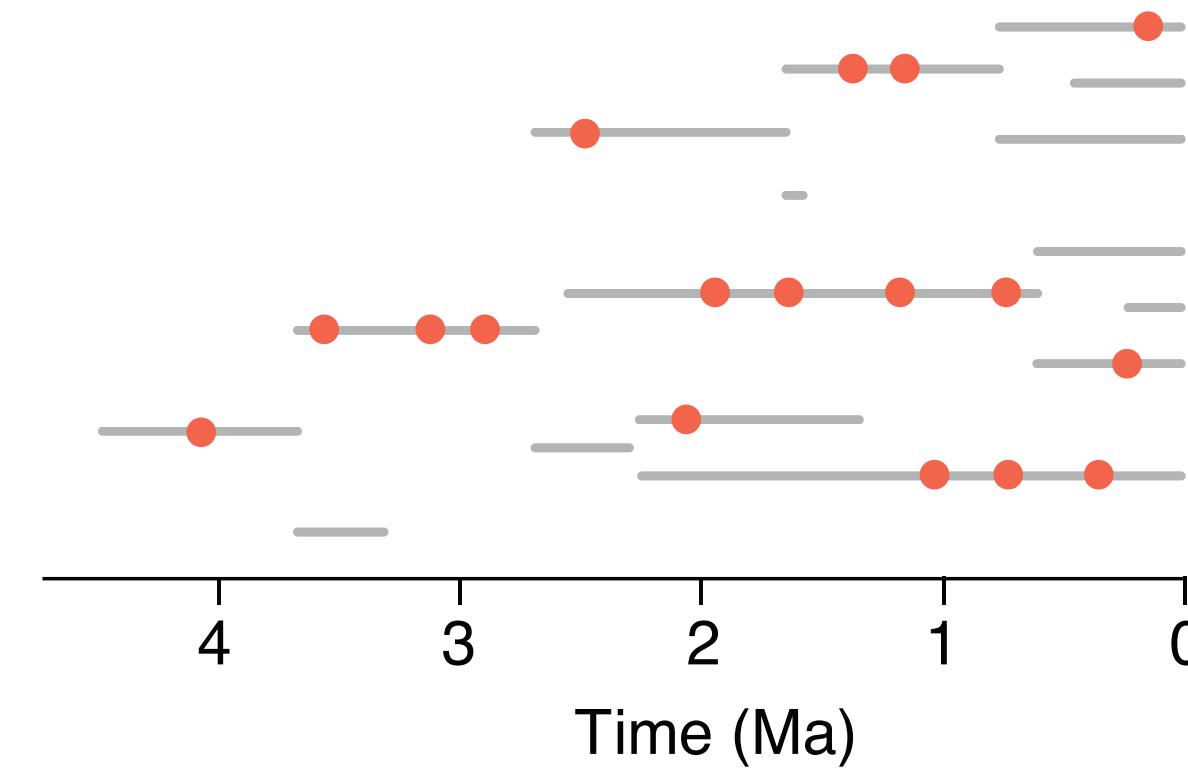


Maybe “integrating” fossils and phylogenies is like concatenating genes ignoring discordance among gene trees

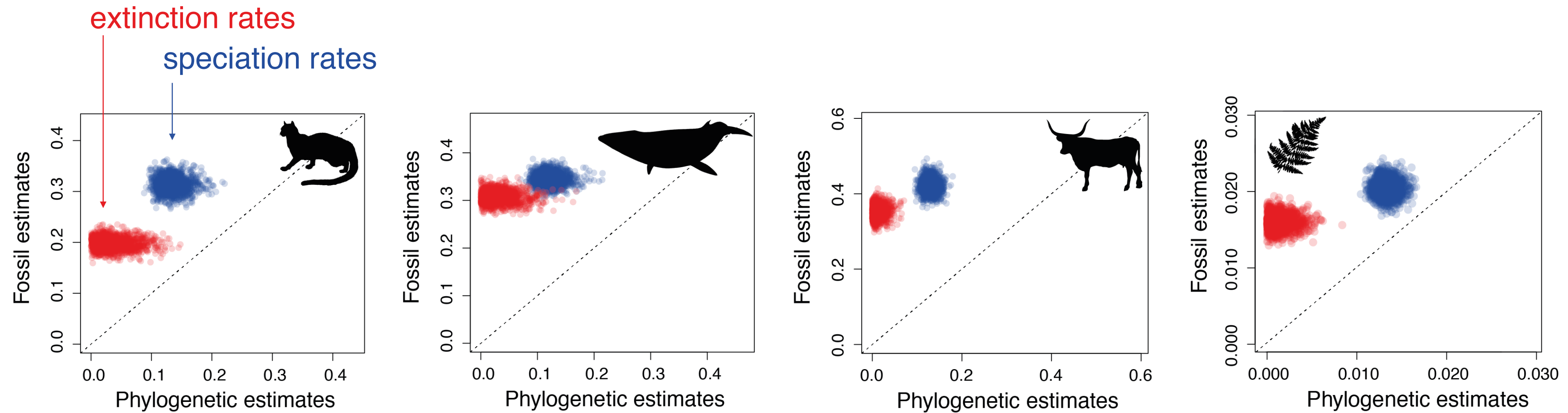
Phylogeny of extant species



Fossil record



Why are fossil-based and phylogenetic rate estimates almost always different?

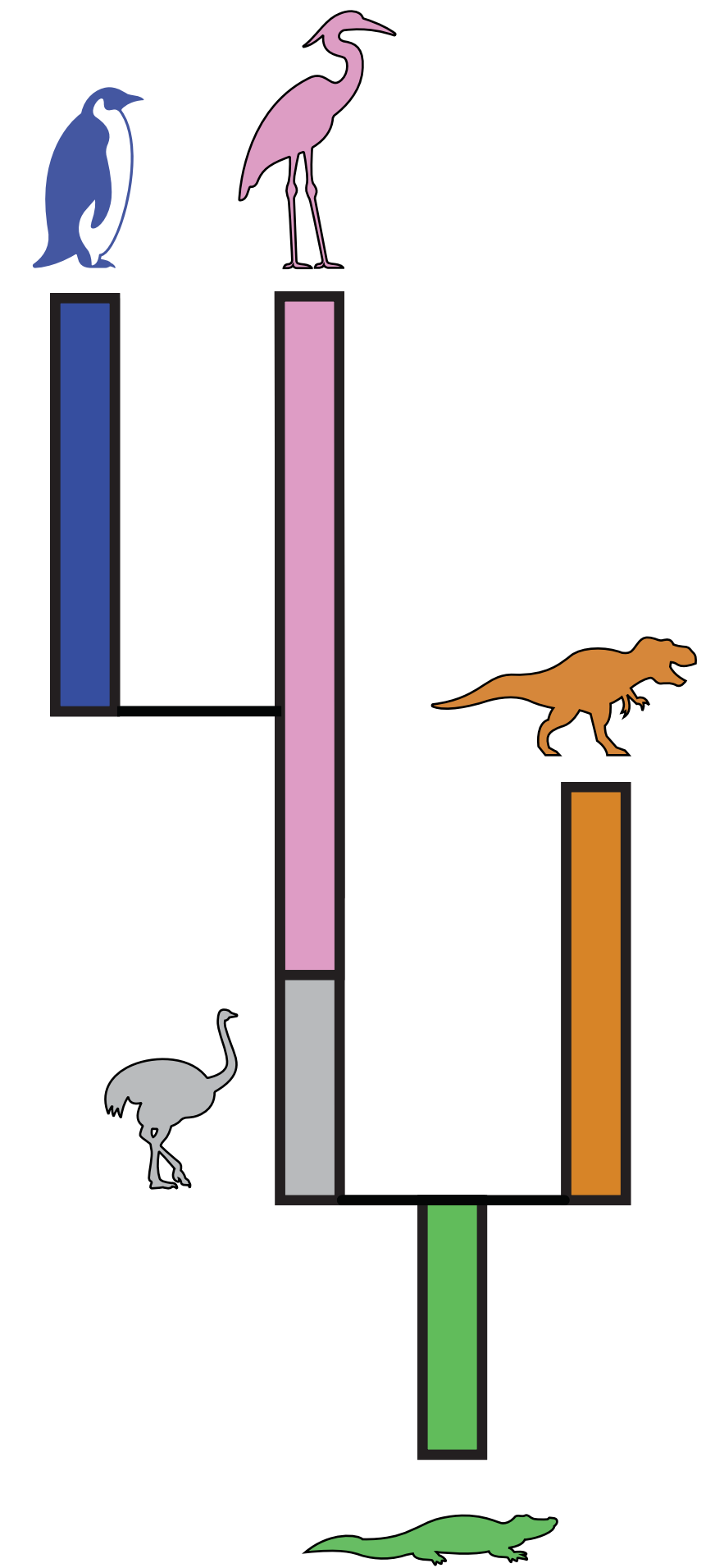
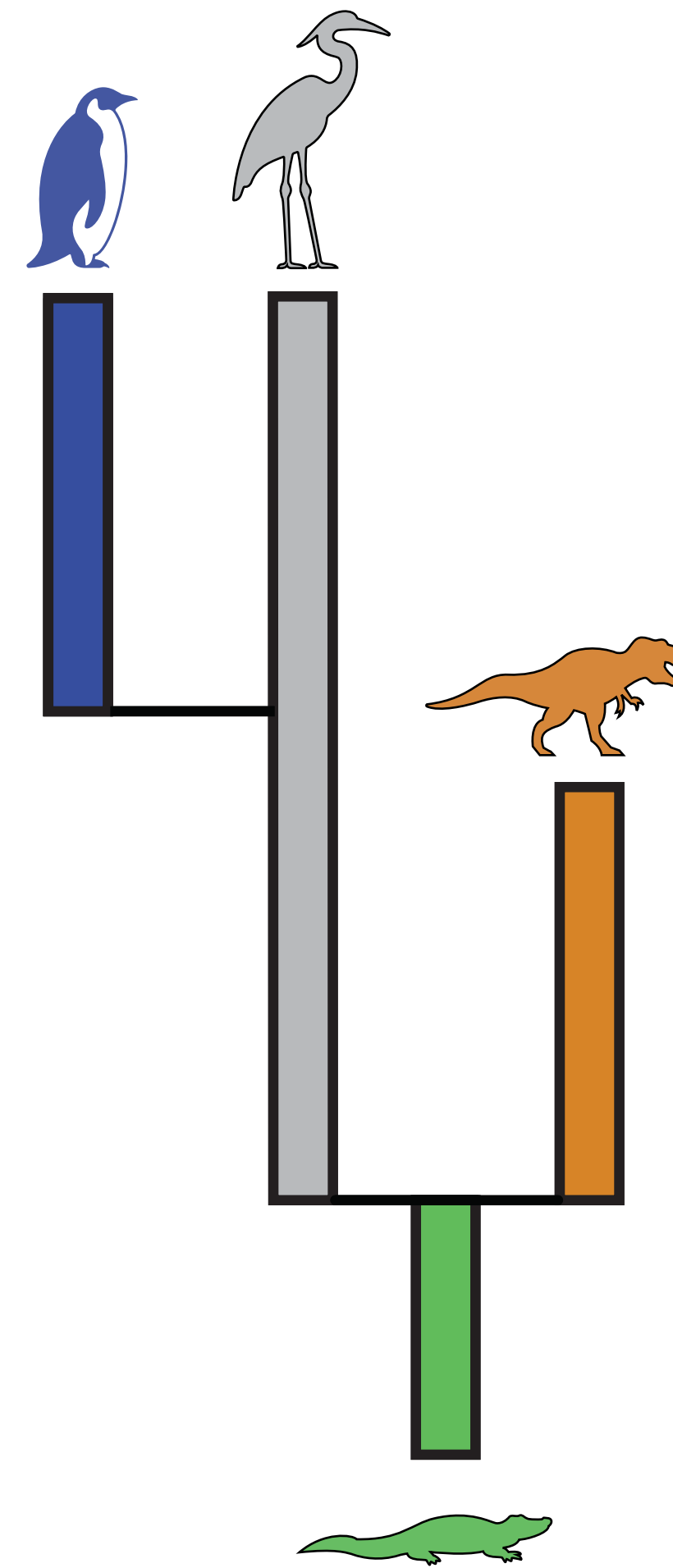
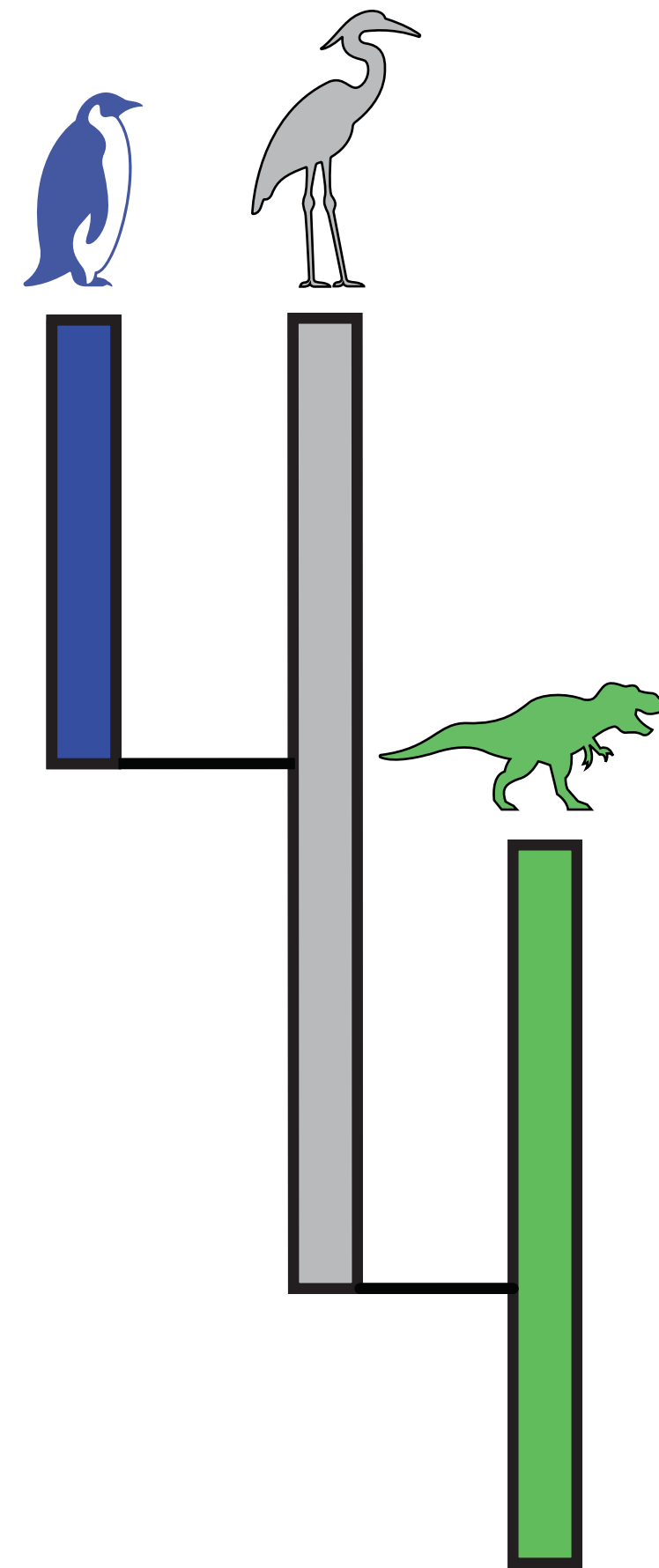


Fossils and phylogenies are the result of the same evolutionary history

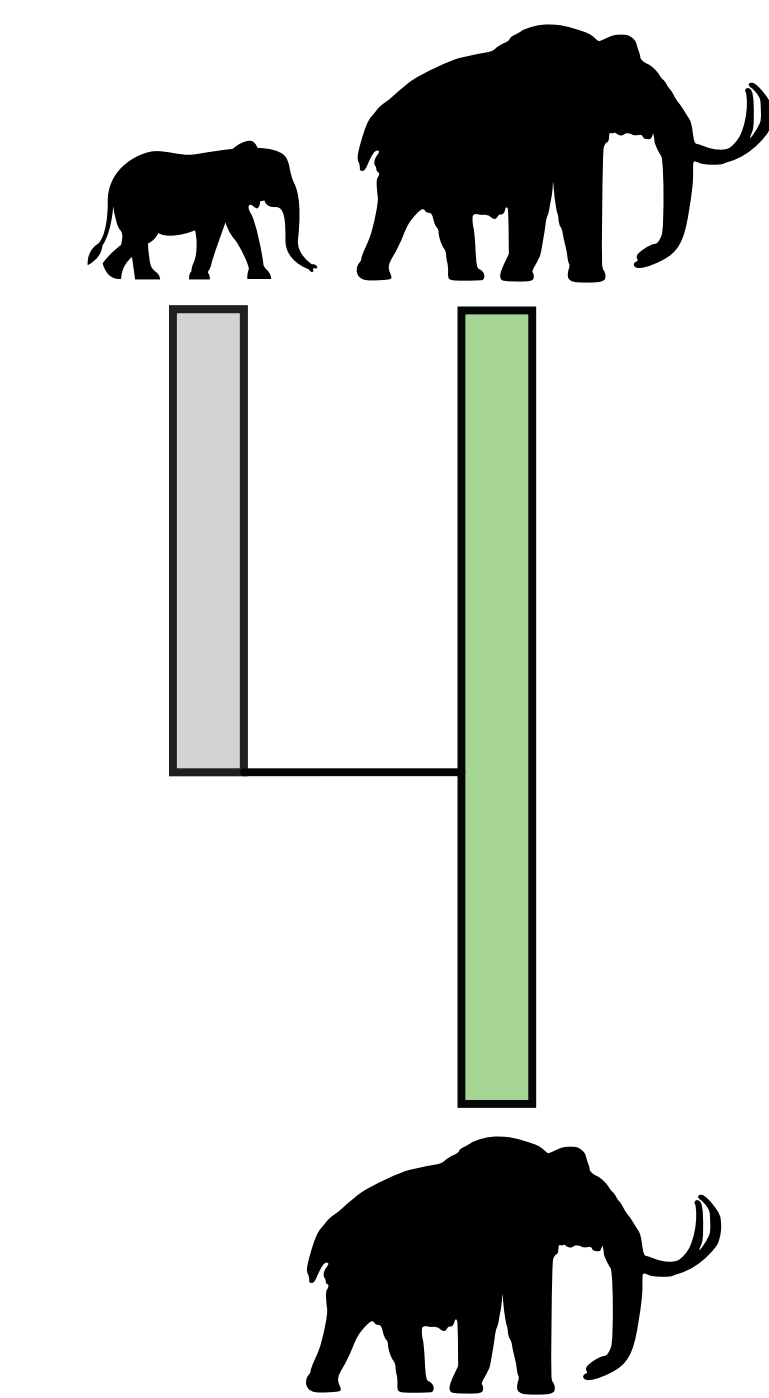


There are no obvious theoretical flaws to explain the discrepancy

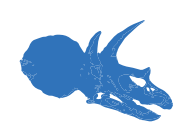
How many speciation and extinction events?



Different species concepts and speciation modes change how we interpret speciation and extinction rates



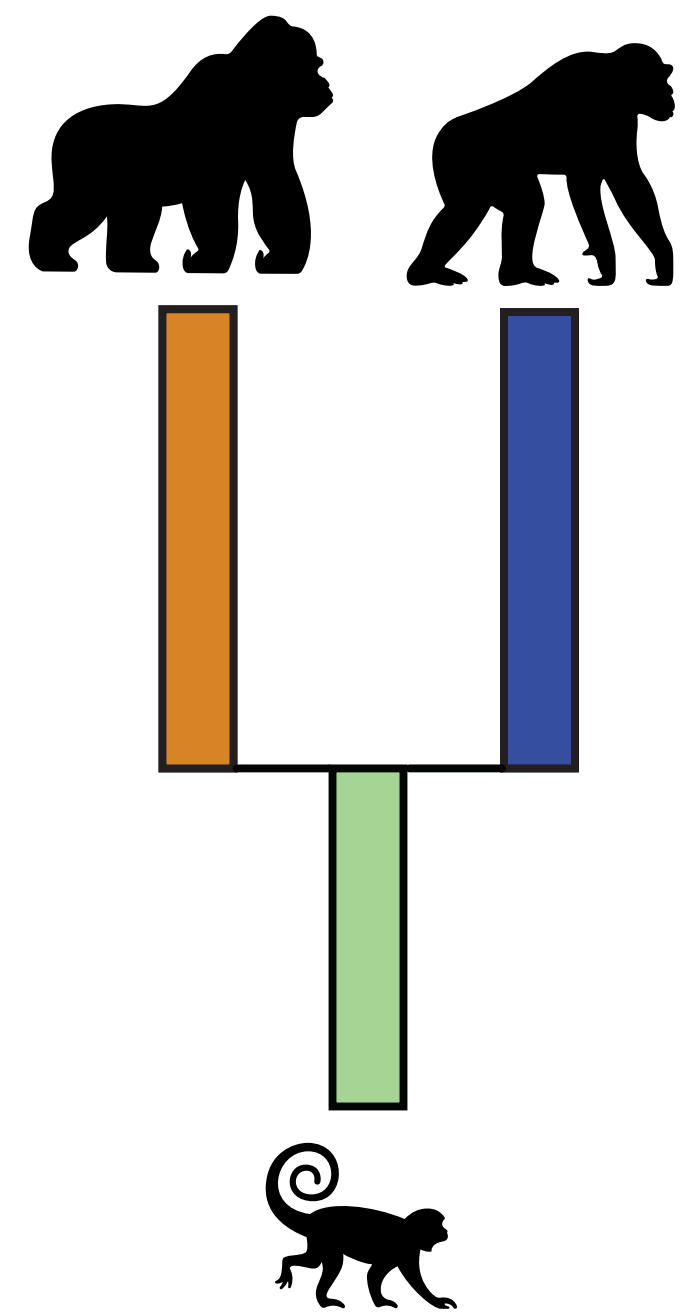
Budding speciation



1 speciation



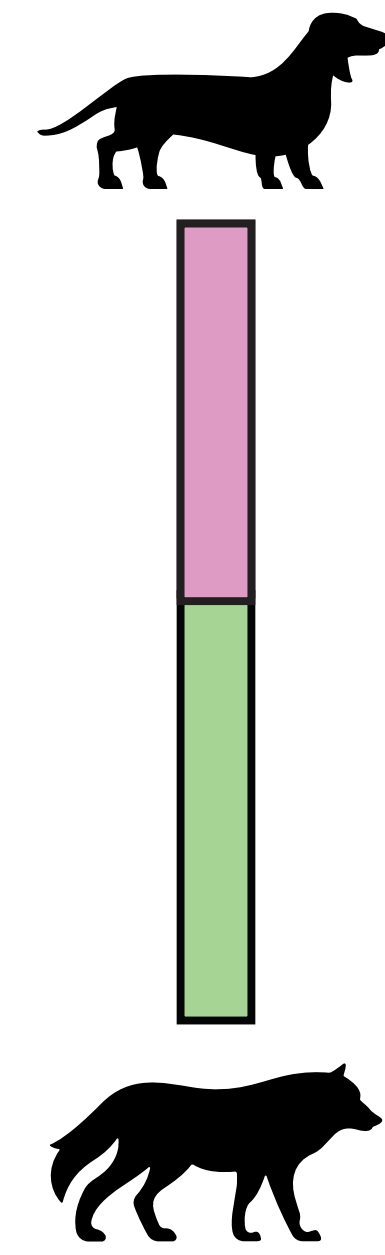
1 speciation



Bifurcation

2 speciations, 1 extinction

1 speciation



Anagenetic speciation

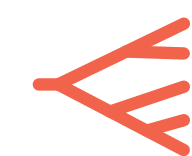
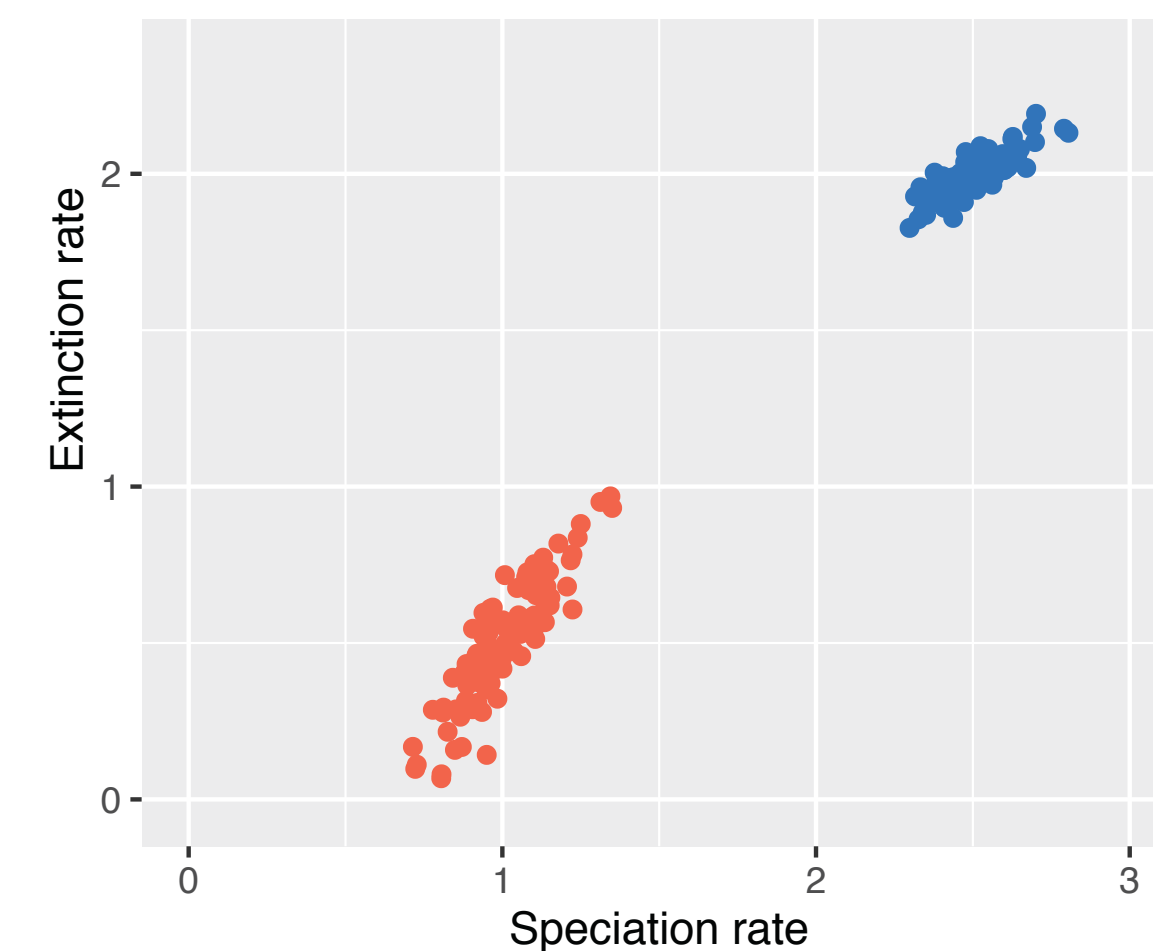
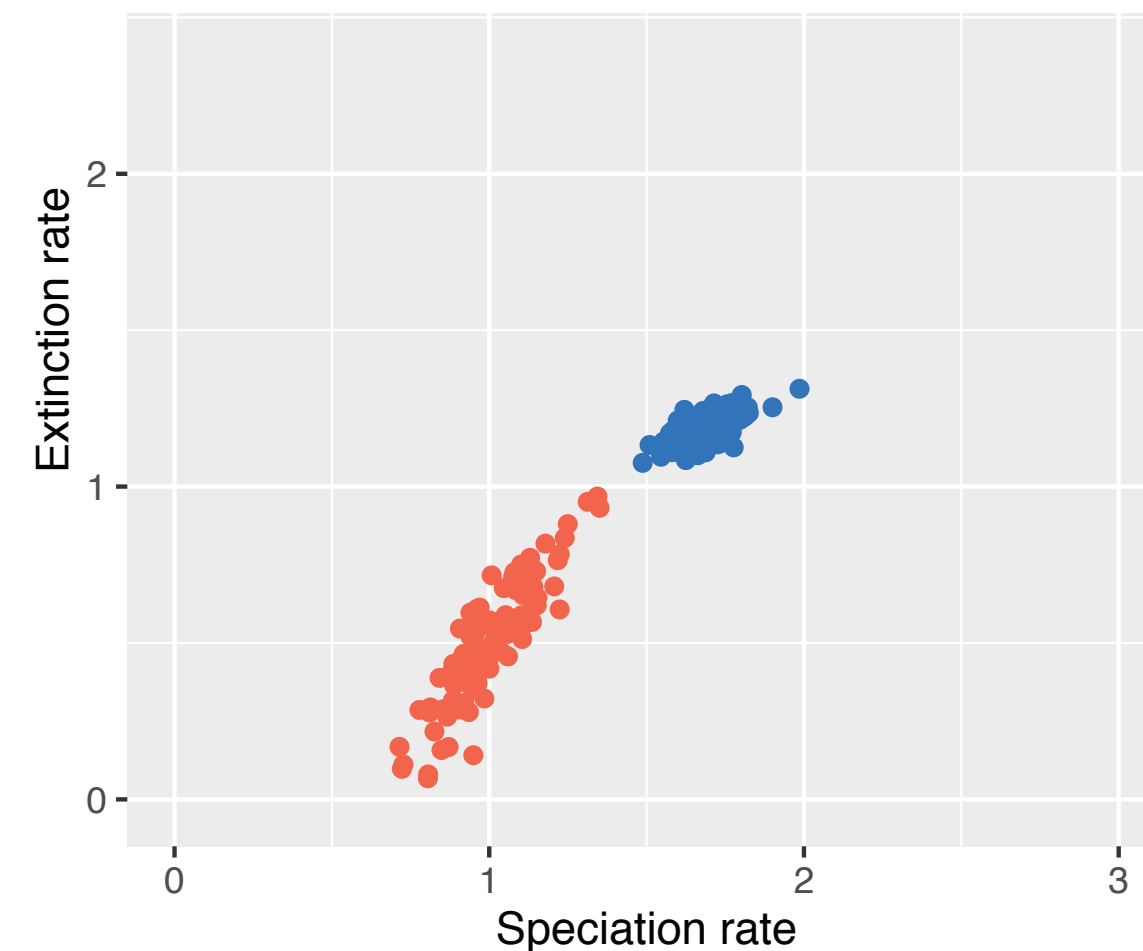
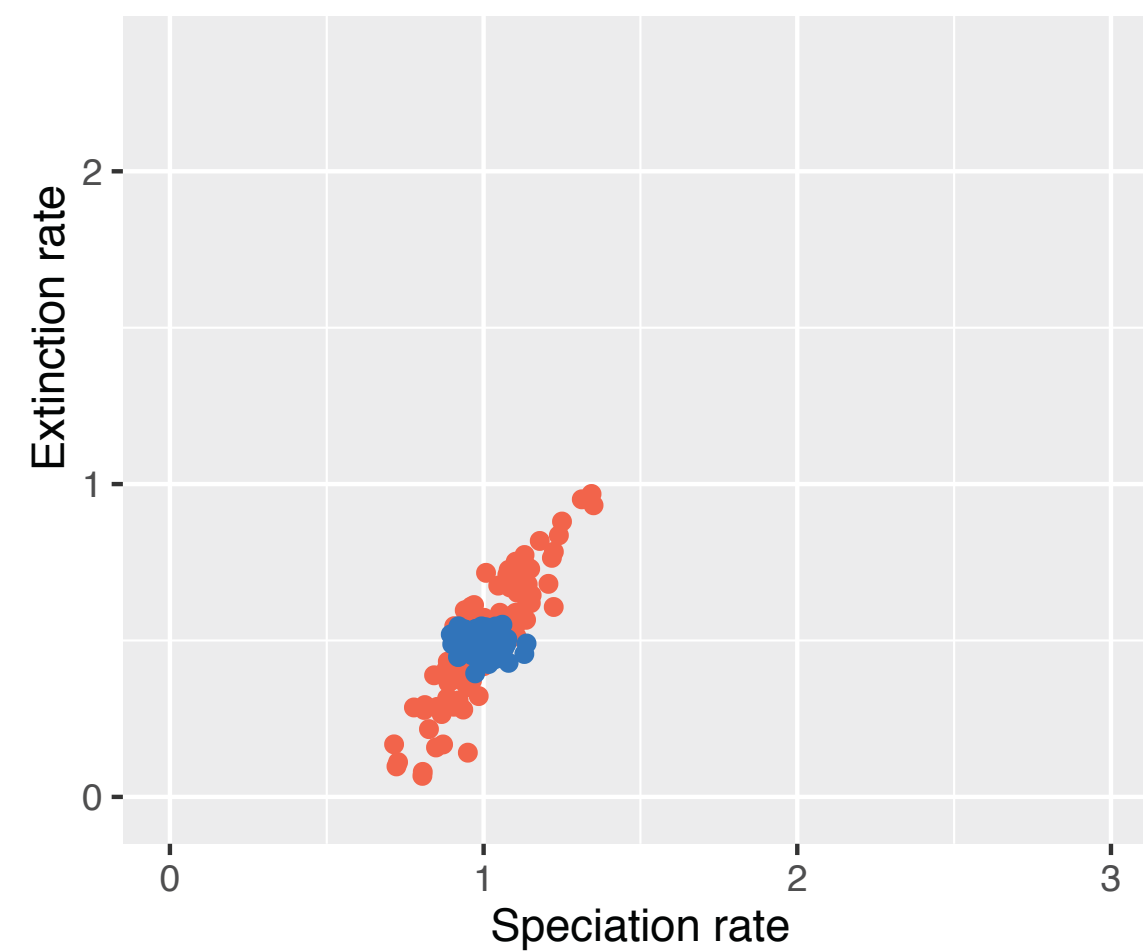
1 speciation, 1 extinction

No events

Foote 1996 Paleobiology; Ezard et al. 2012 Biol Lett

Are fossil and phylogenetic rate estimates *expected* to be equal?

Increasing levels of speciation by bifurcation or anagenesis →



phylogenetic estimates



fossil estimates



R Warnock



A Gavryushkina

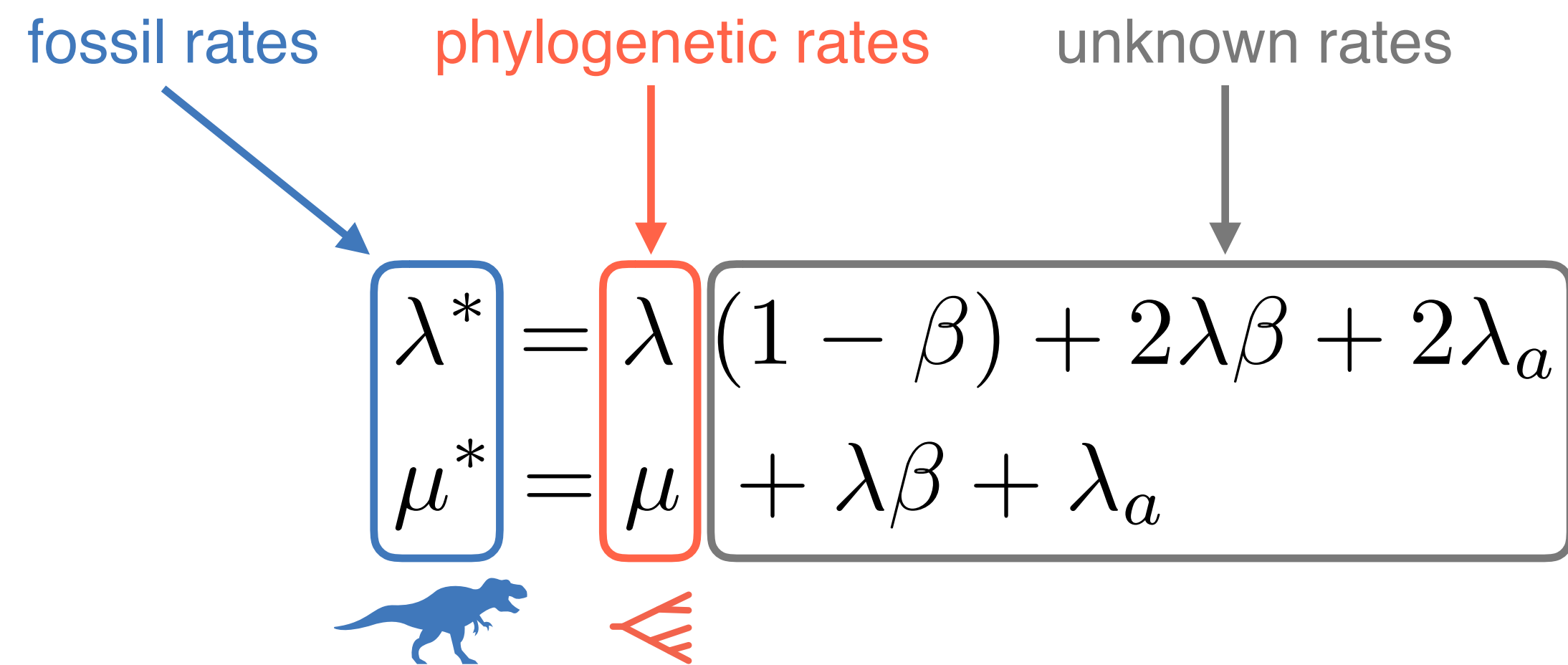


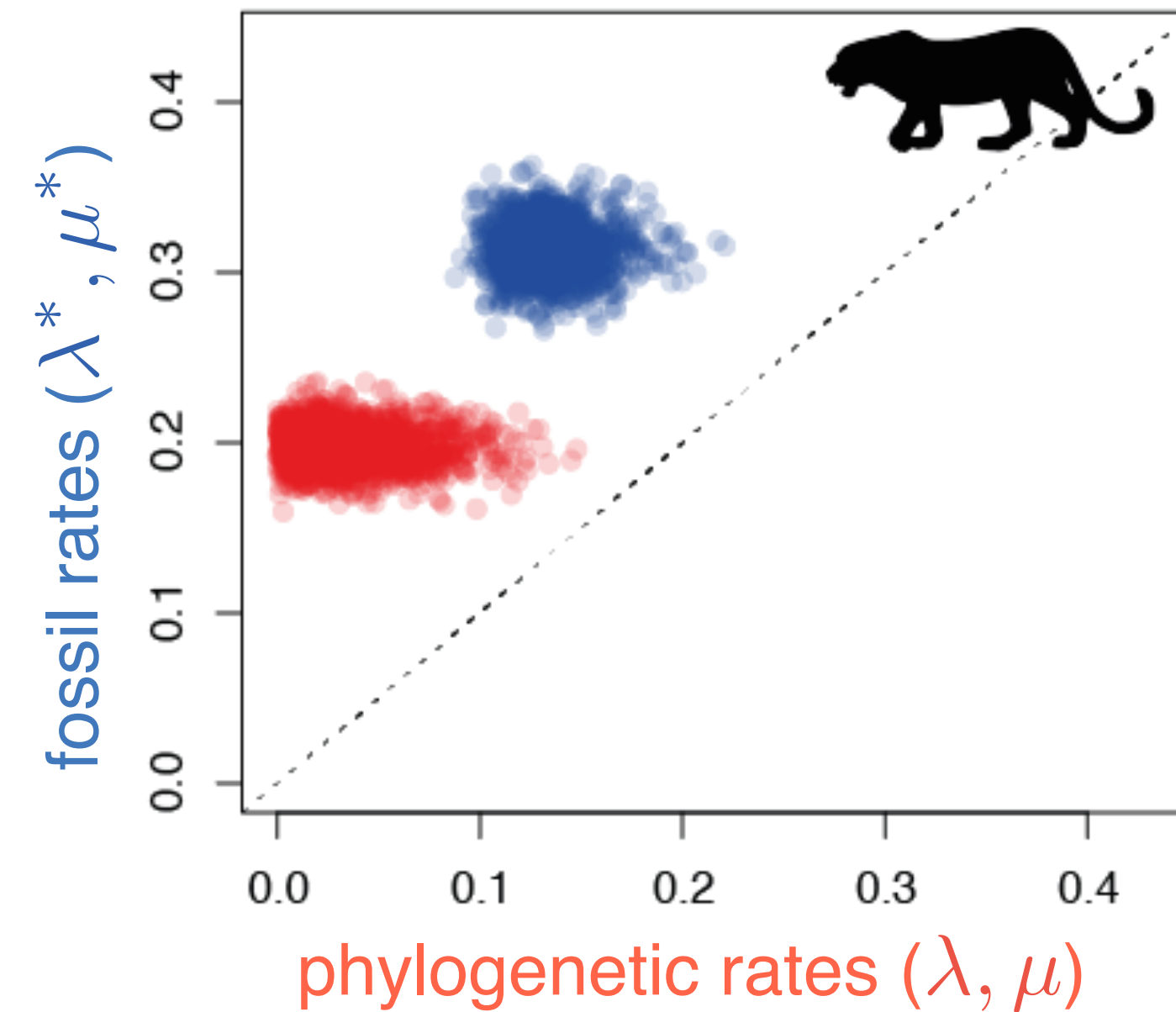
T Stadler

Introducing the birth-death chrono-species model

Predicting the discrepancy between phylogenetic and fossil rate estimates

fossil rates phylogenetic rates unknown rates

$$\begin{aligned} \lambda^* &= \lambda (1 - \beta) + 2\lambda\beta + 2\lambda_a \\ \mu^* &= \mu + \lambda\beta + \lambda_a \end{aligned}$$




New Speciation Model Challenges Evolution, Supports Creation

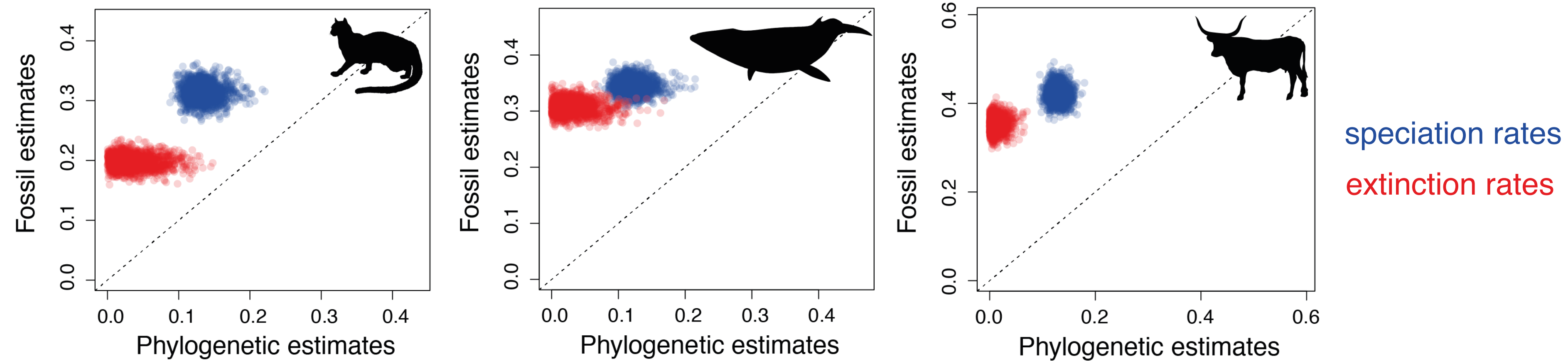
AUGUST 19TH, 2019



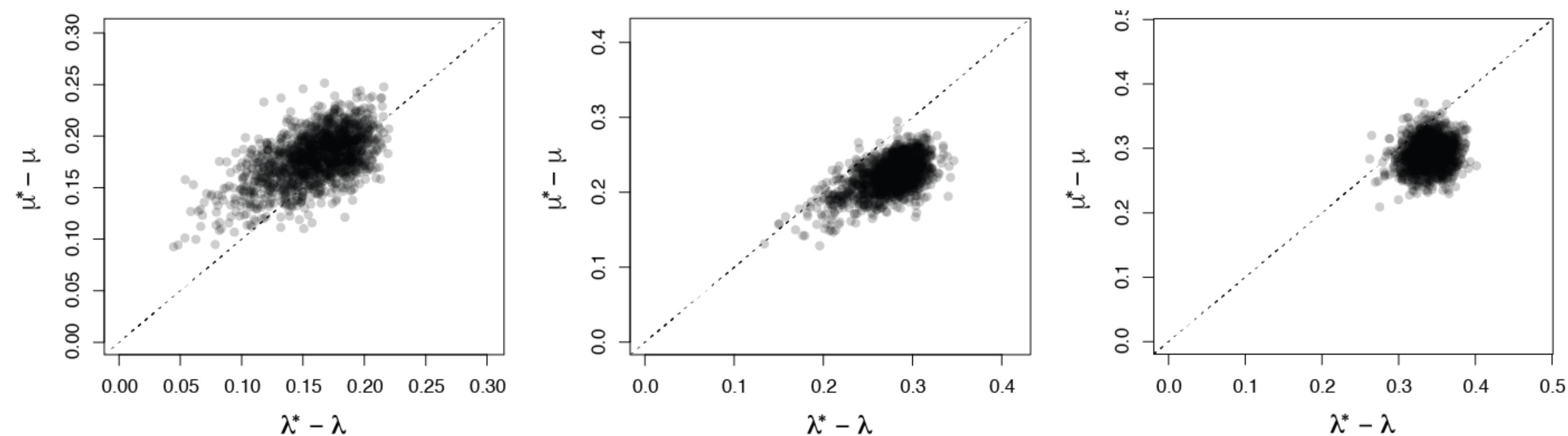
DR. HUGH ROSS *Science and Faith Brief*

Silvestro et al. 2018, Nature Comm

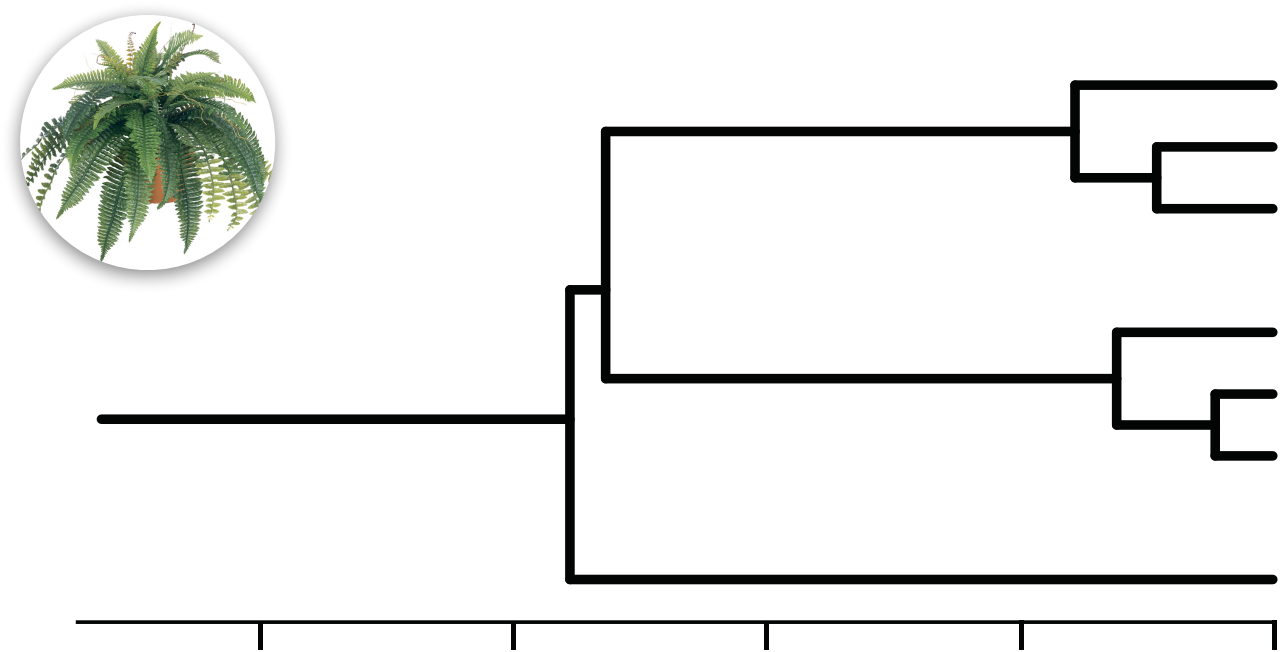
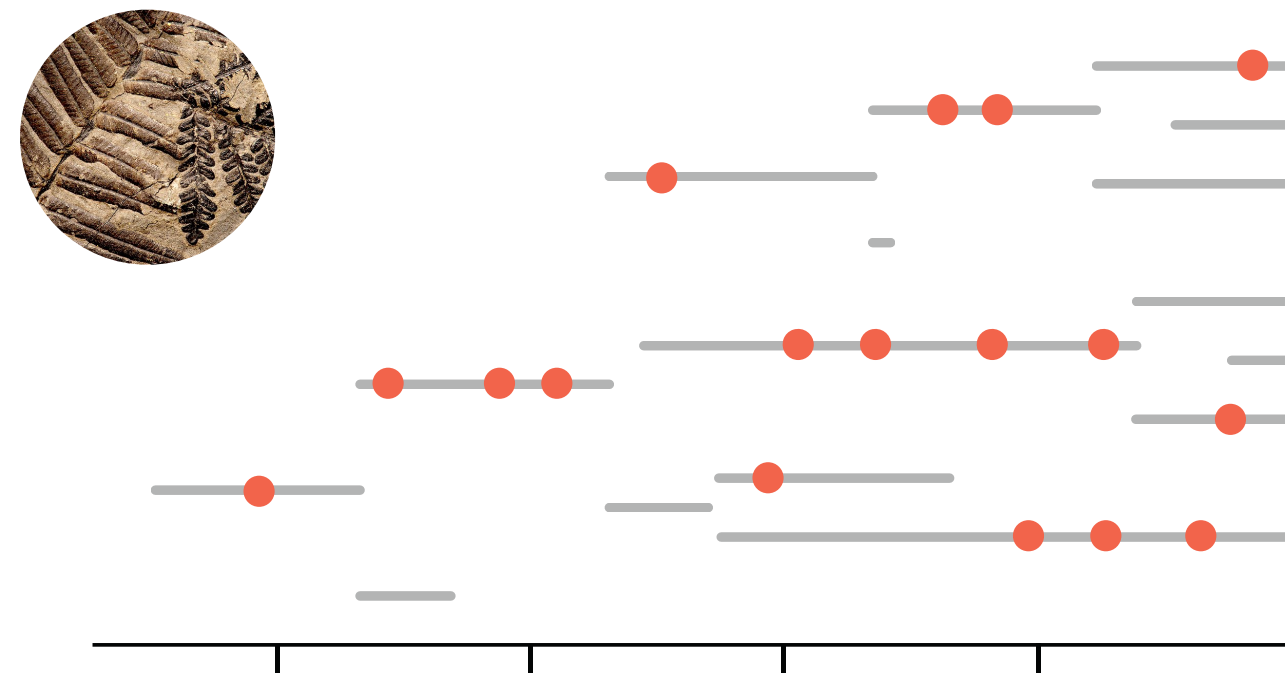
Introducing the birth-death chrono-species model



Rate differences are compatible with the BDC model

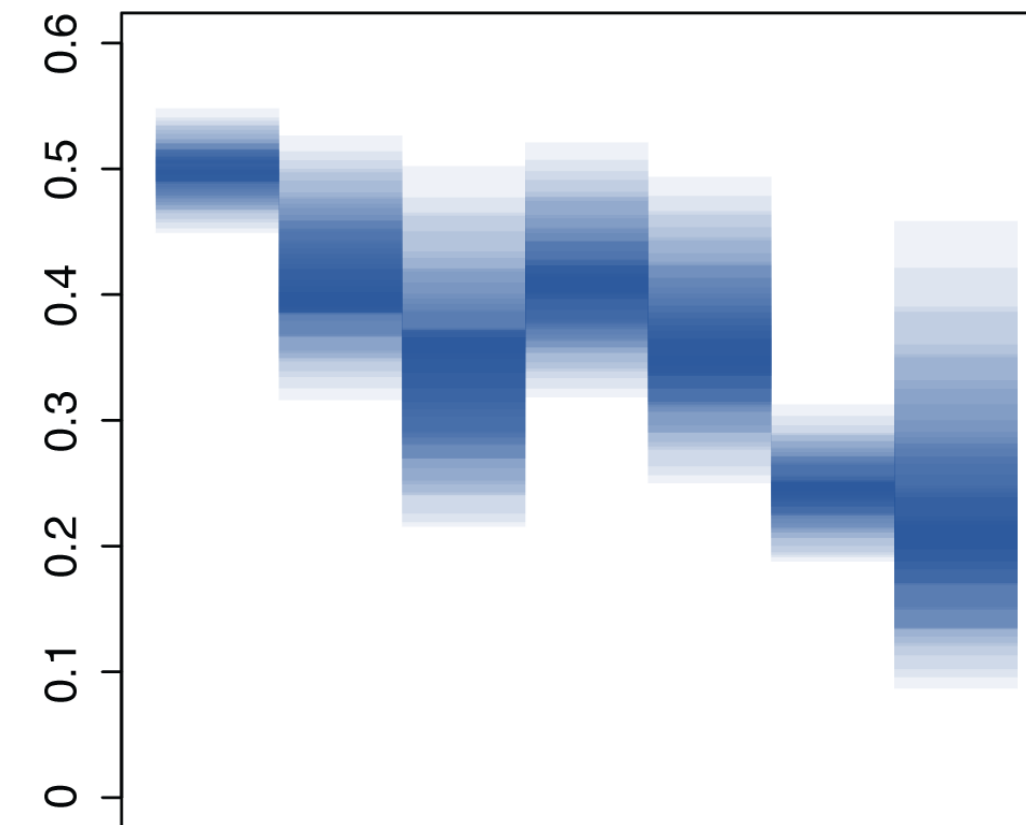


Allowing for rate variation: The BDC skyline model



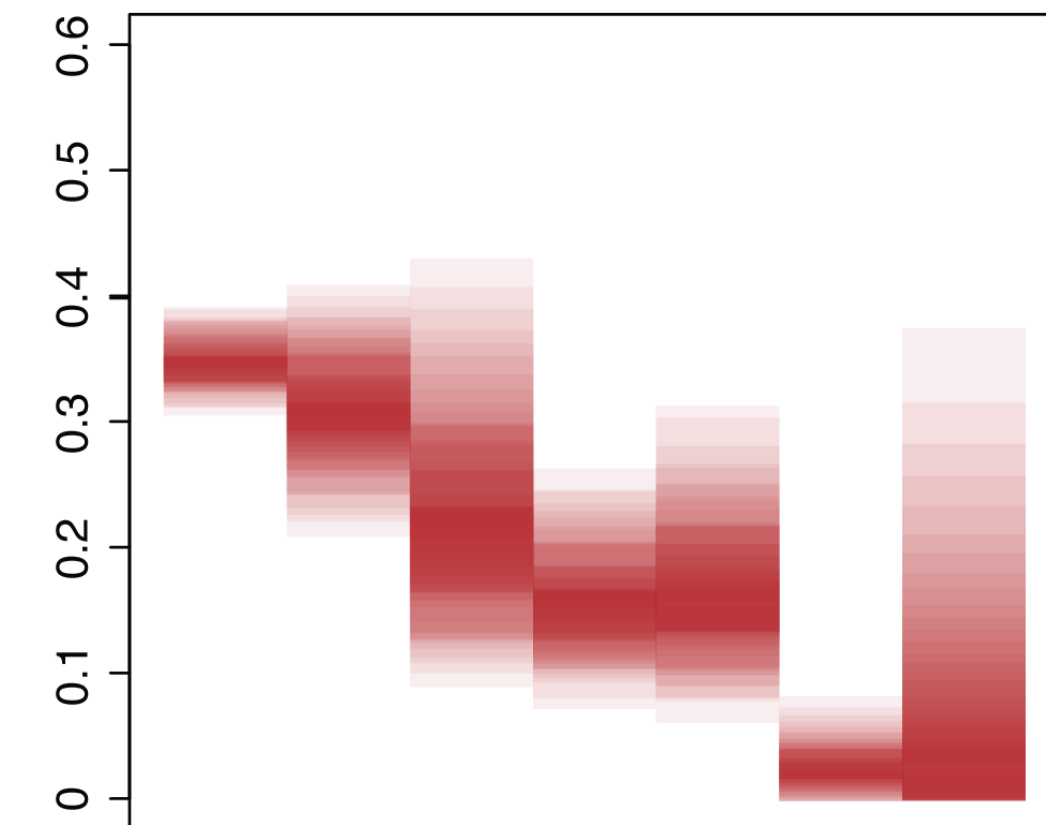
Time (Ma)

speciation rates

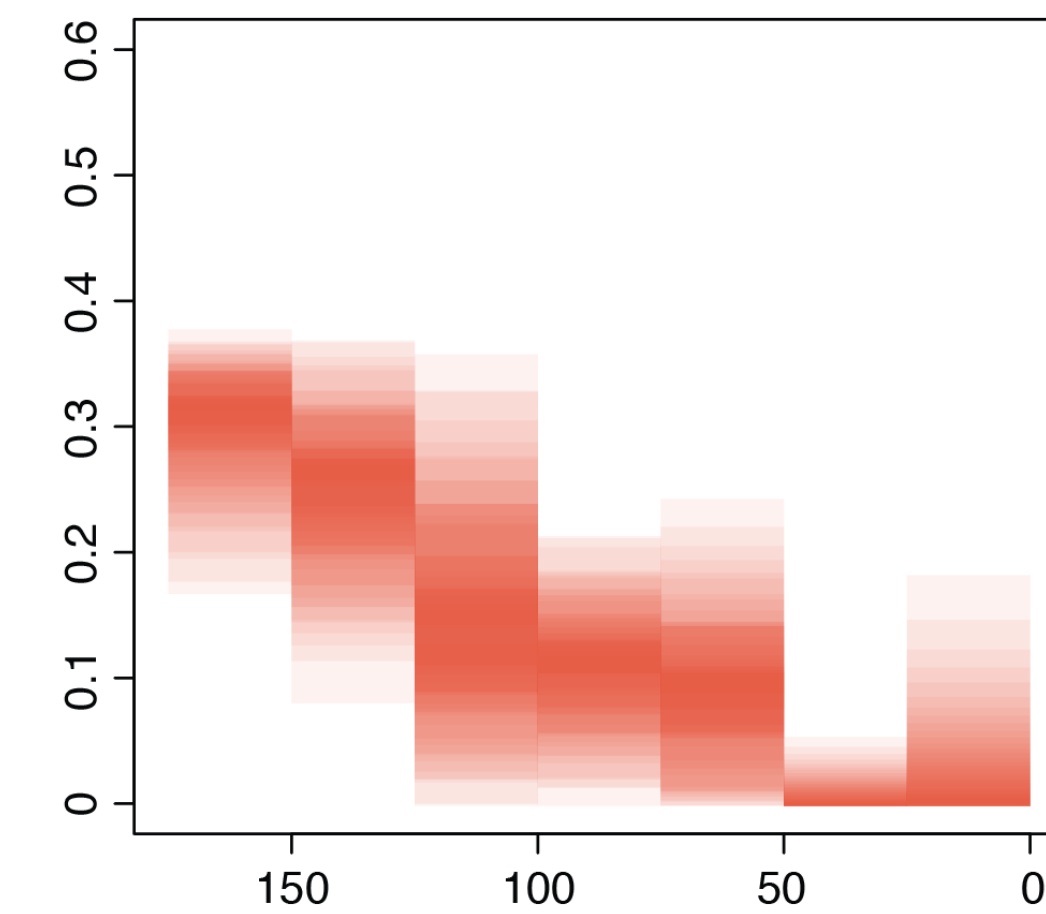
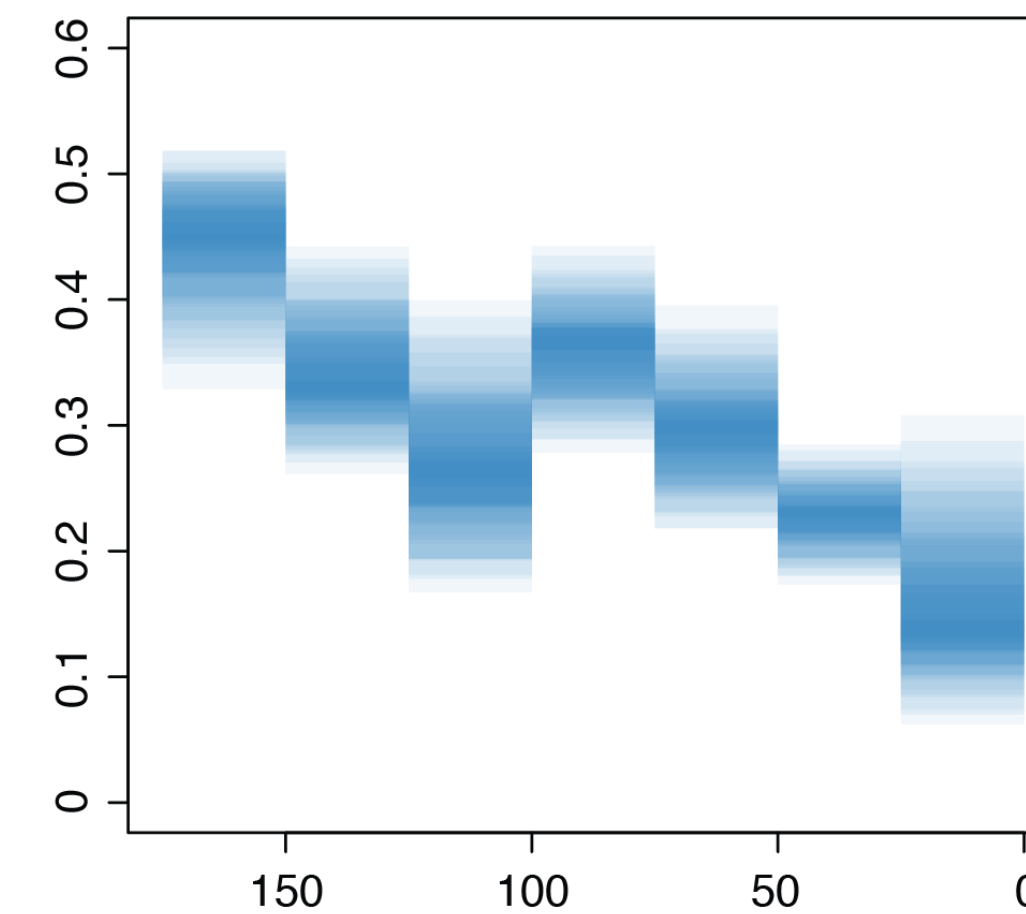


Time (Ma)

extinction rates



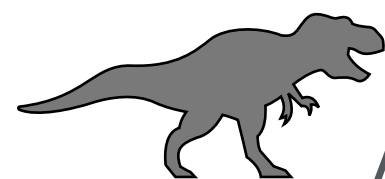
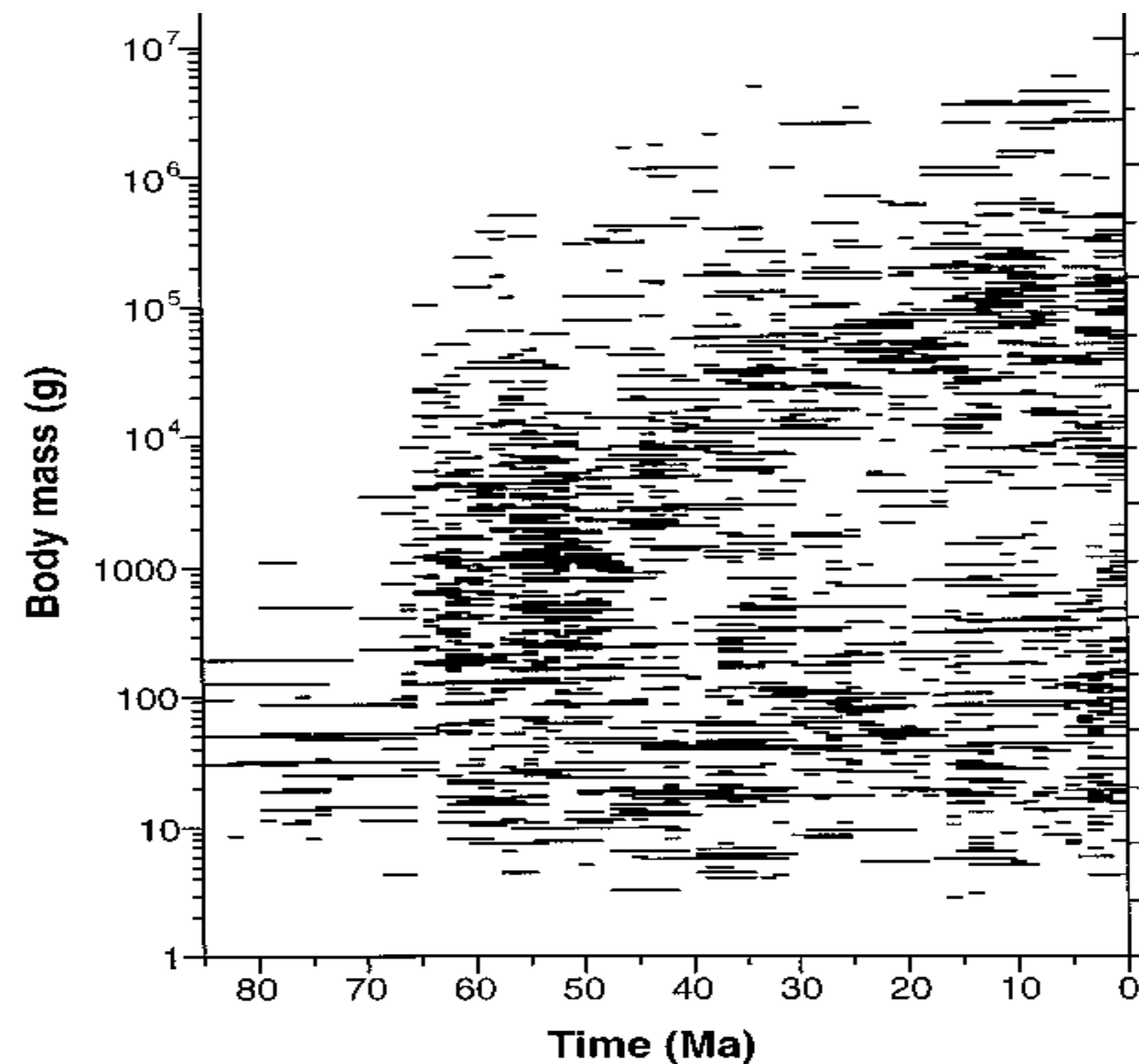
Time (Ma)



For a long time paleo- and neo- evolutionary biologists have happily ignored one another

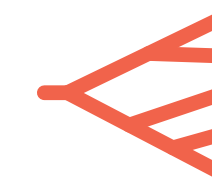
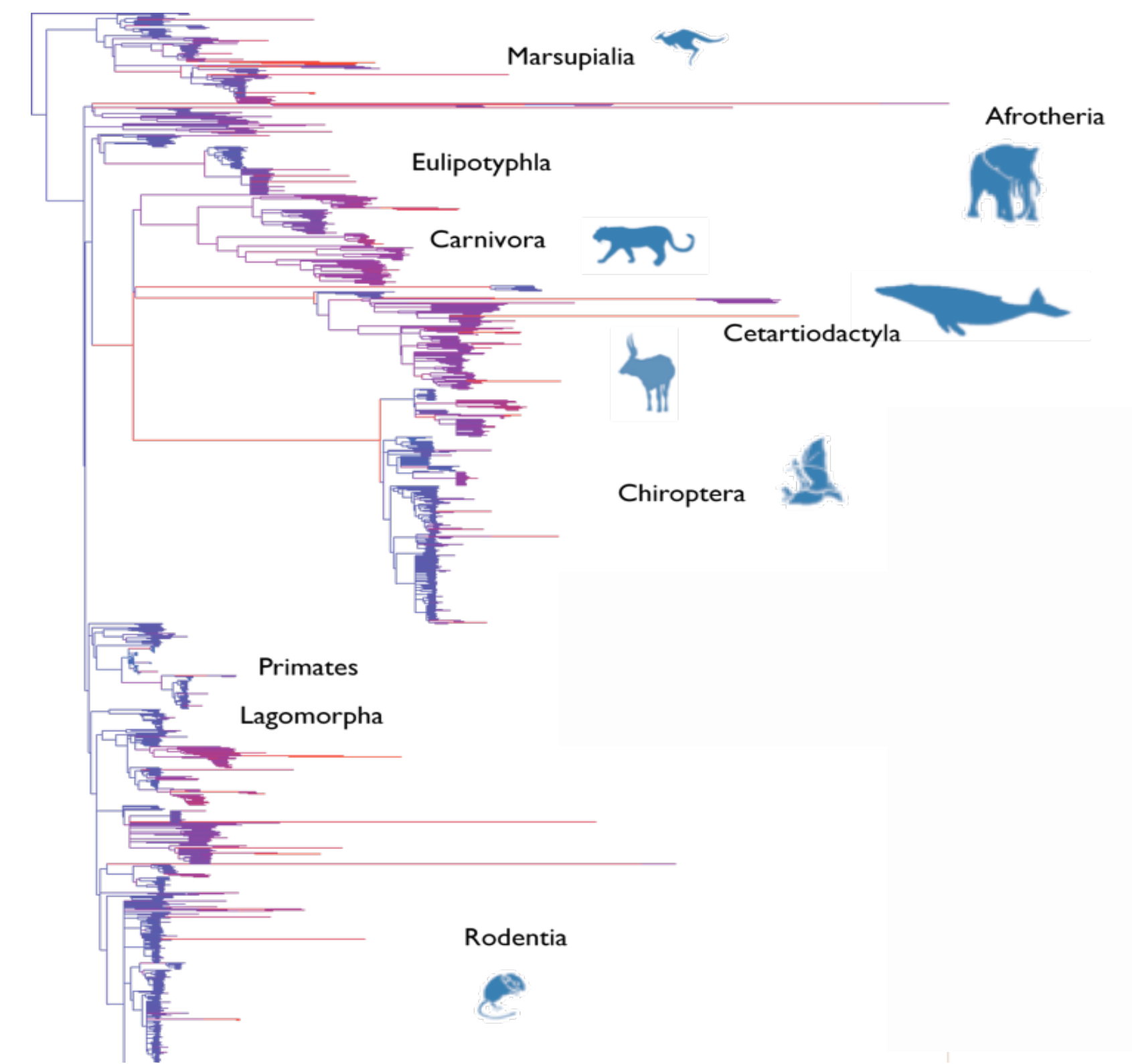
Models of trait evolution

Trends in mammalian body size evolution



Alroy 1998, Science

Rates of mammalian body size evolution

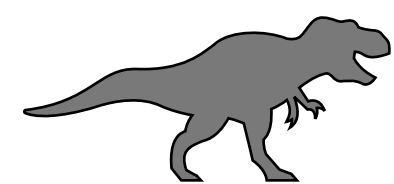
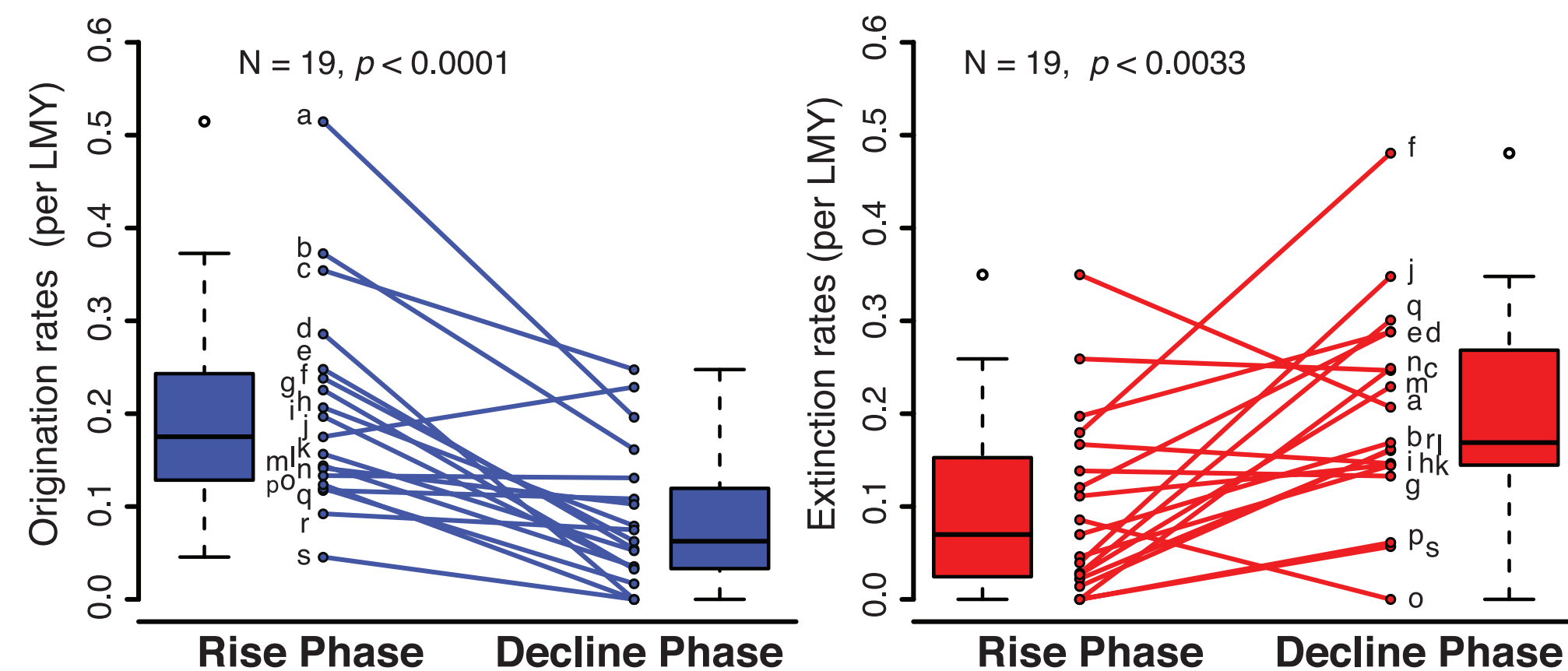


Venditti et al. 2011, Nature
Cooper and Purvis 2010 Am Nat

For a long time paleo- and neo- evolutionary biologists have happily ignored one another

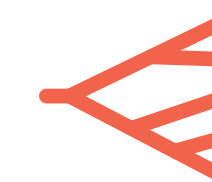
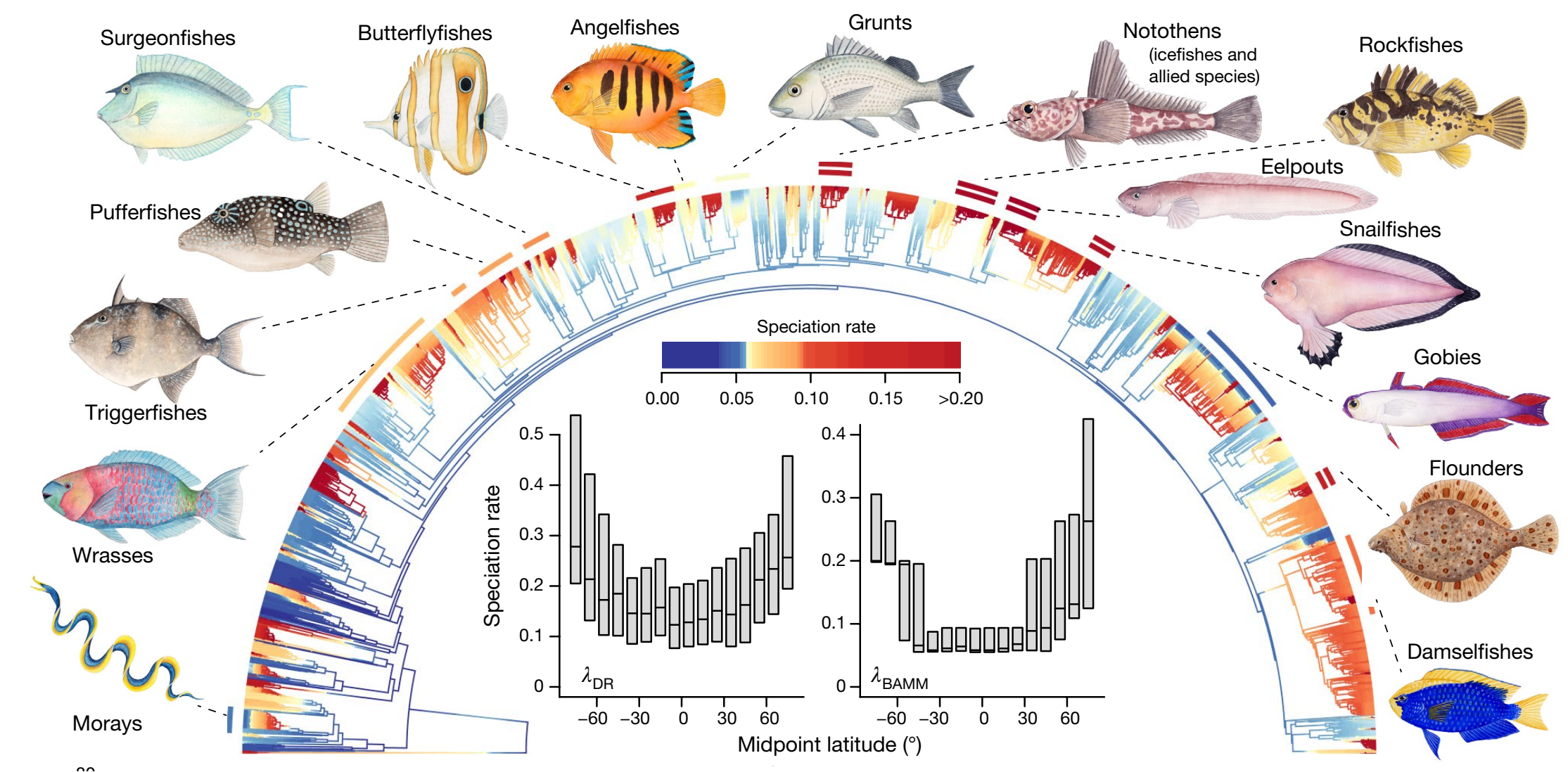
Models of species speciation and extinction

Speciation and extinction in mammalian families



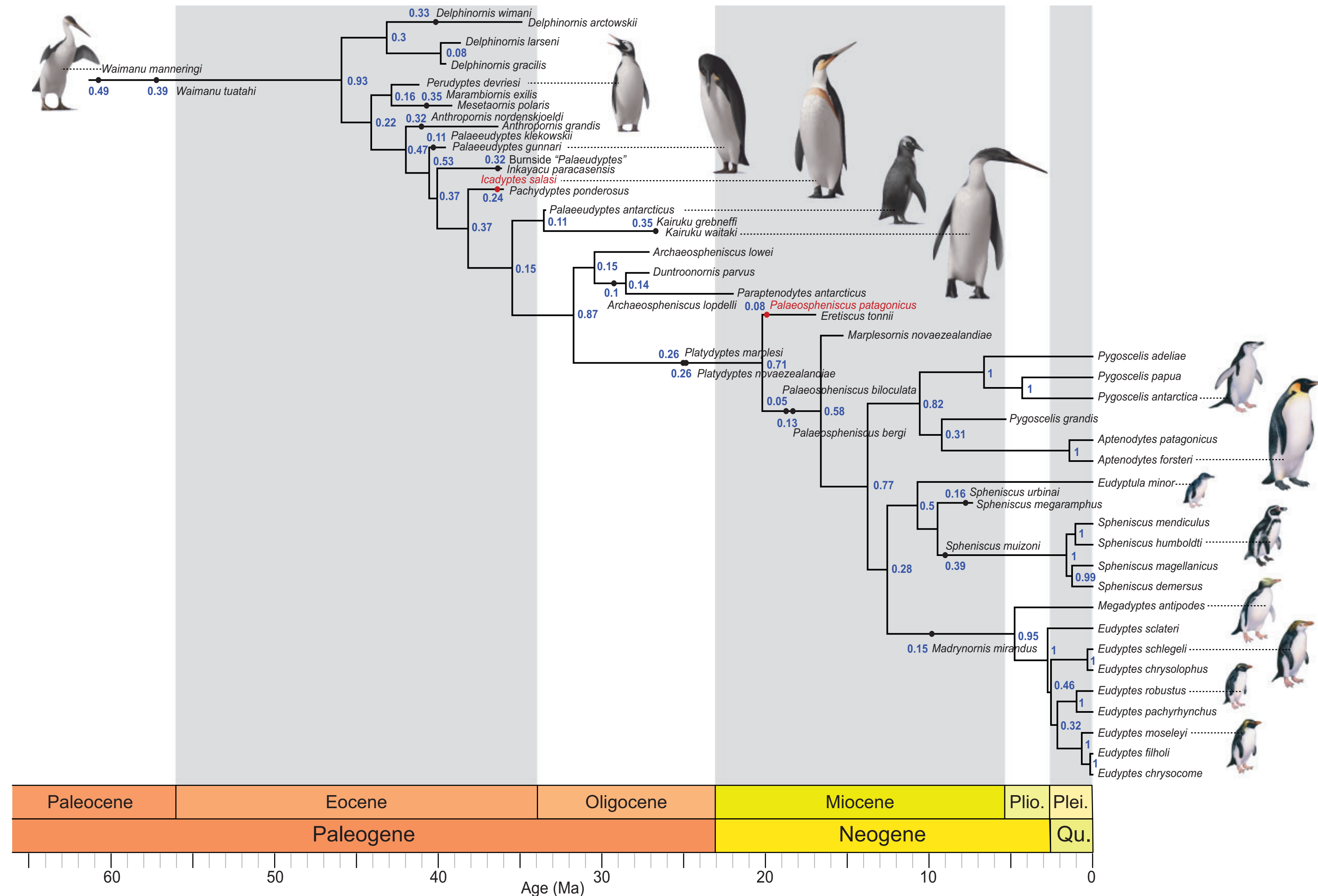
Quental and Marshall 2010 Science

Patterns of speciation rates in marine fish

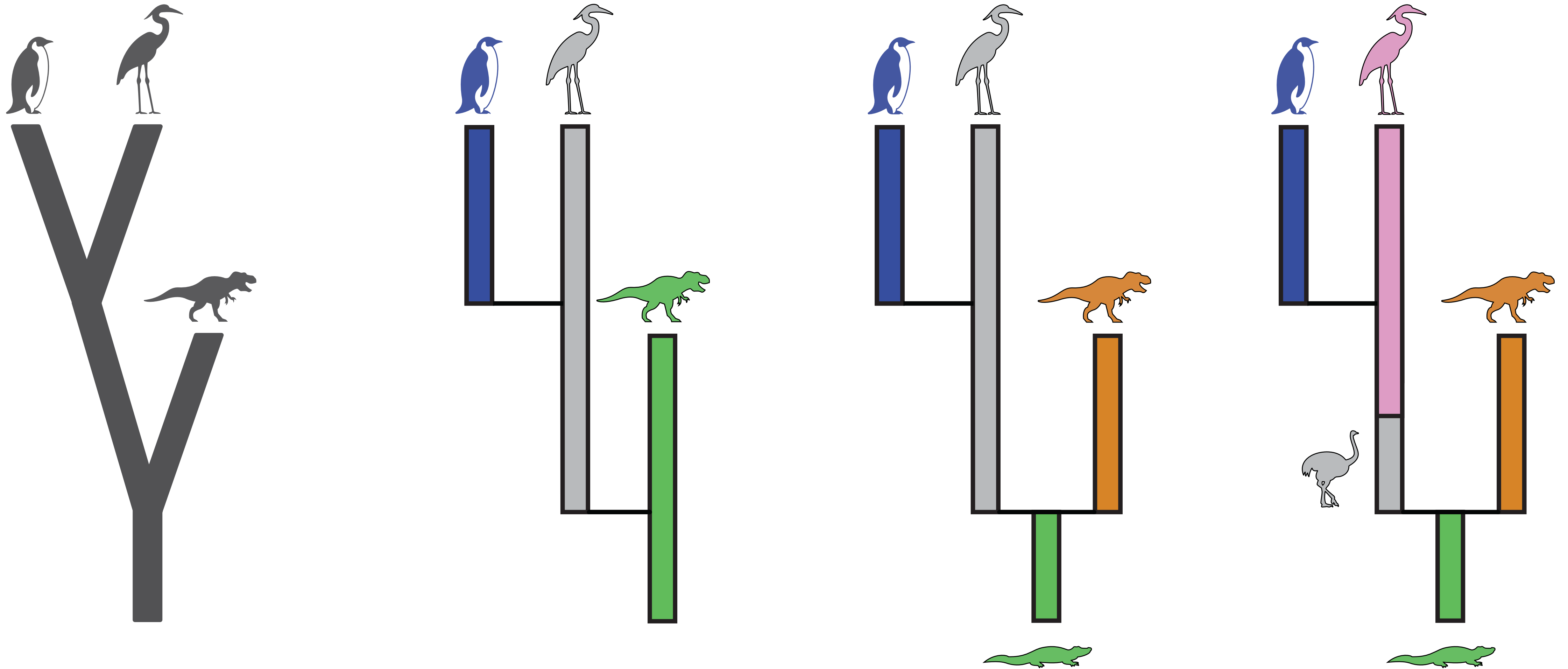


Rabosky et al. 2018, Nature

Now we are seeing an increased integration between paleobiology and phylogenetics



Do we need to re-think the integration between fossils and phylogenies?



Thank you for listening

If you are interested in learning more about Bayesian stats



www.transmittingscience.org

3rd Edition

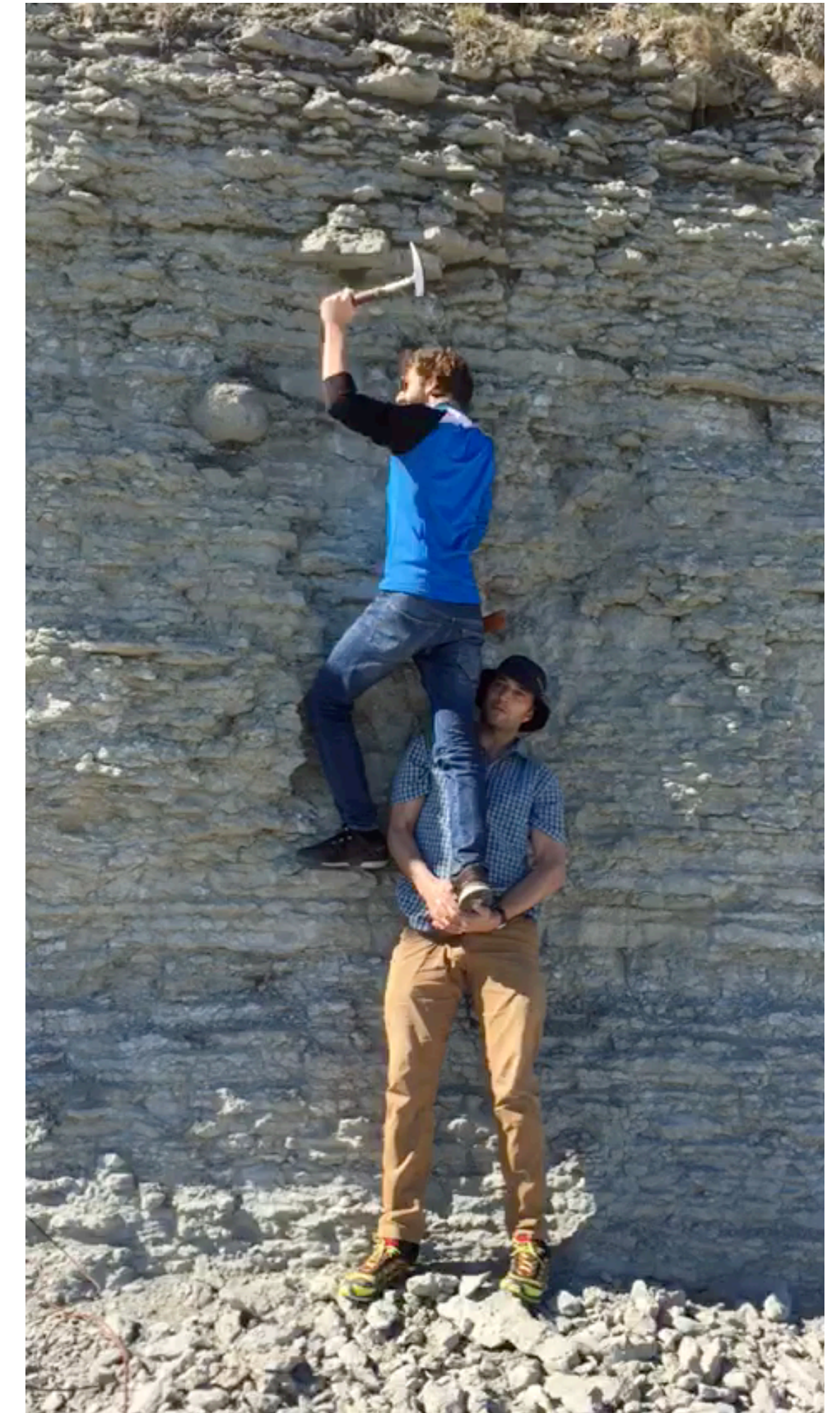
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Silurian coral reef in Gotland 🇸🇪
(playing paleontologist with A. Antonelli)



daniele.silvestro@bioenv.gu.se
<https://github.com/dsilvestro>



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