Analytical paleo

The fossilised birth-death process

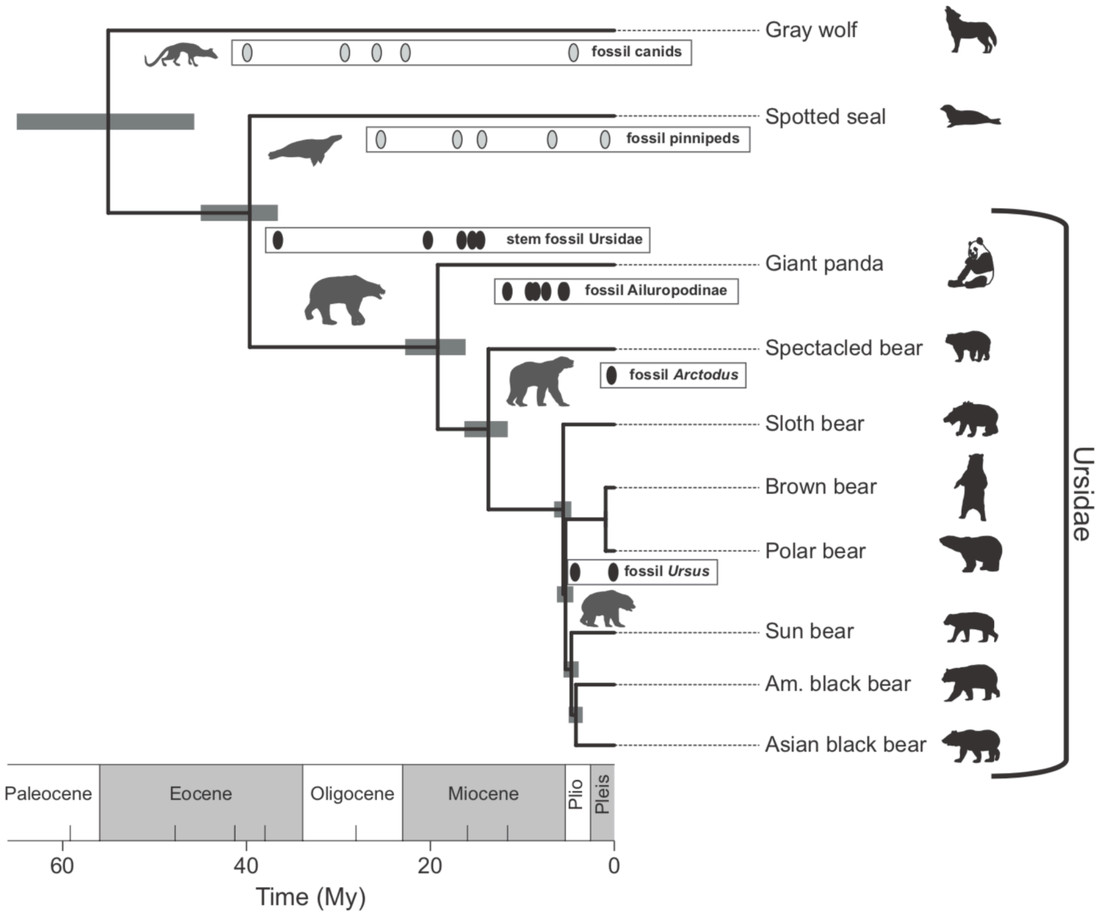
Rachel Warnock

20.08.2026



Next

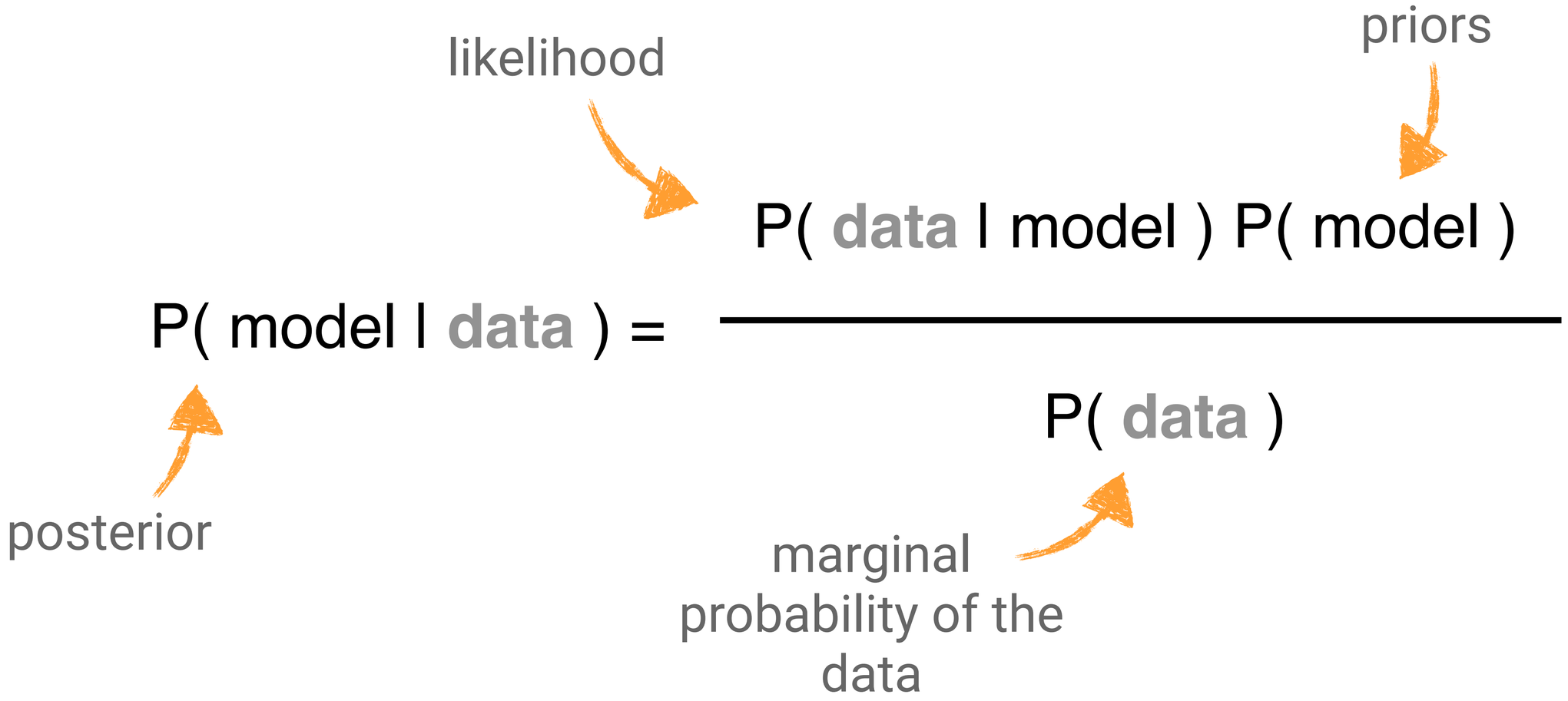
- **Recap**: tripartite framework
- The fossilised birth-death process
- Total-evidence dating



Bayesian divergence time estimation

Recap

We use a Bayesian framework



Bayesian divergence time estimation

The data

and / or

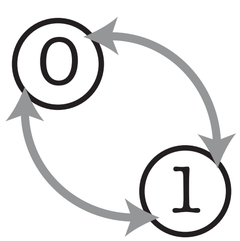
```
0101... ATTG...
1101... TTGC...
0100... ATTC...
```

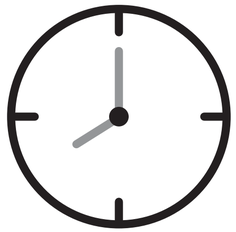


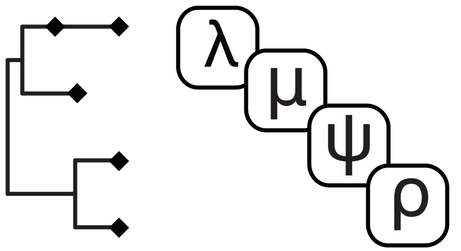
phylogenetics characters

sample ages

3 model components







substitution model

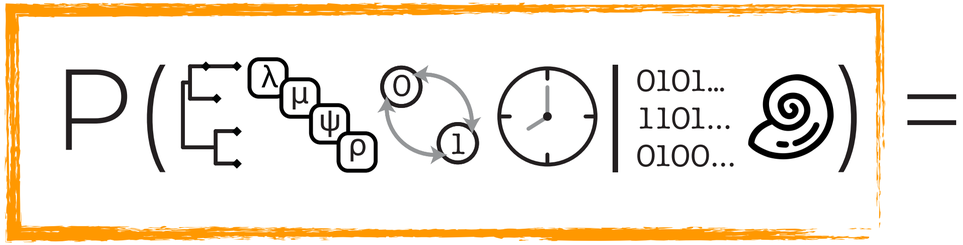
clock model

tree and tree model

Understanding the tripartite approach to Bayesian divergence time estimation
Warnock, Wright. (2020)

Bayesian divergence time estimation

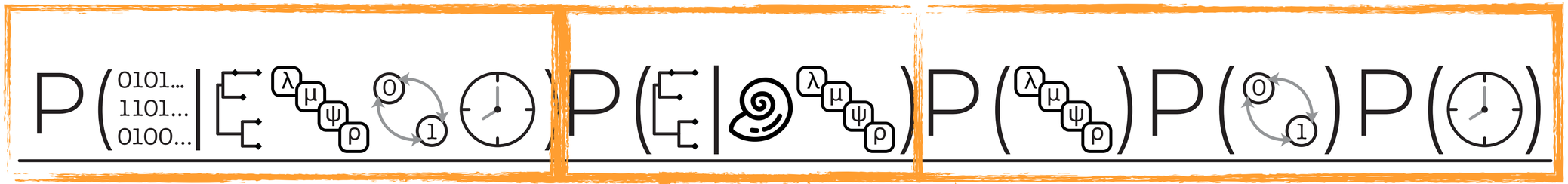
posterior

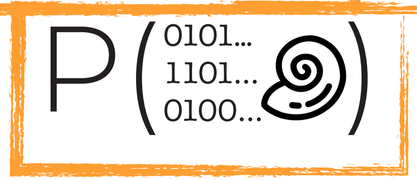


likelihood

probability of the time tree

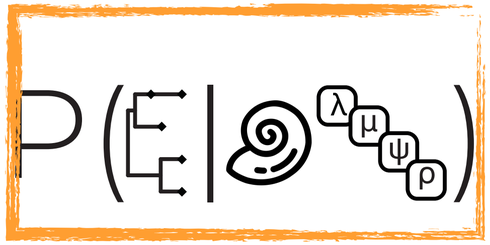
priors



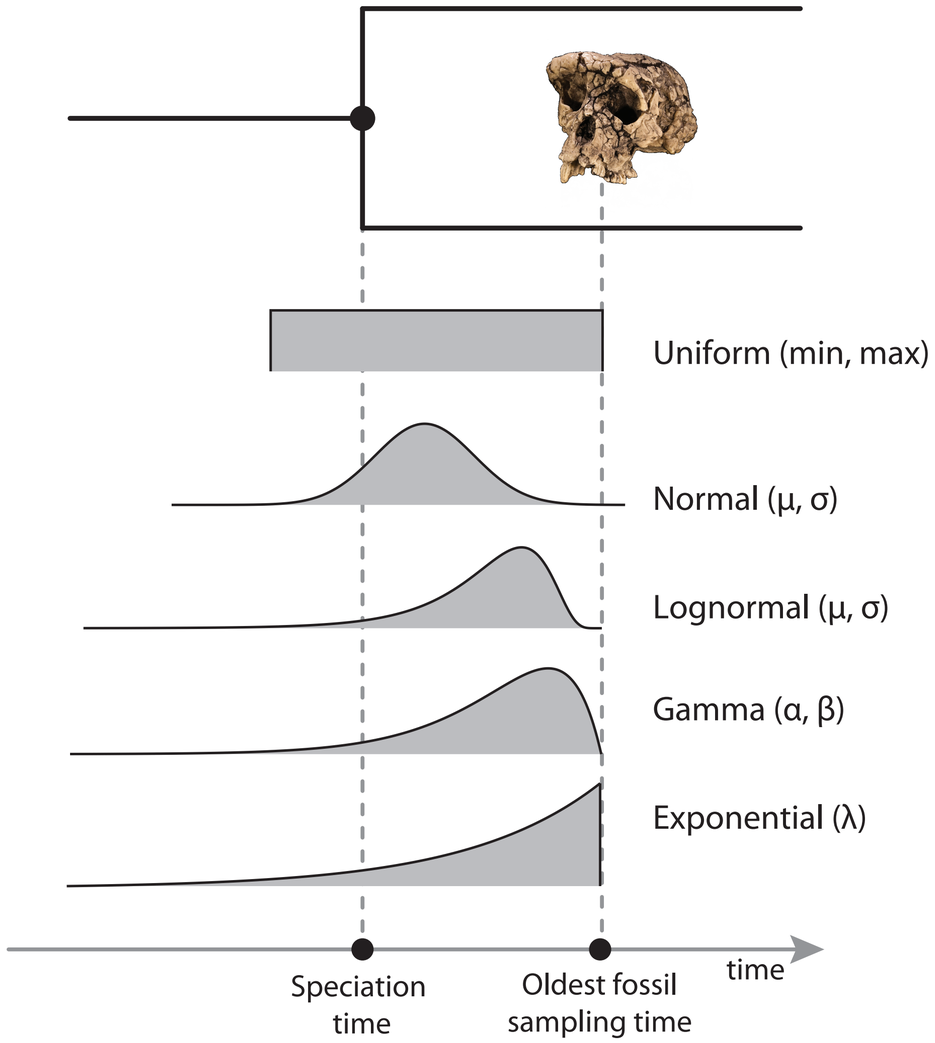


marginal pr of the data

probability of the time tree



Recap: Node dating



The tree includes extant (living) species only

We can use a calibration density to constrain internal node ages

We typically use a birth-death process model to describe the tree generating process

Adapted from *Heath* (2012) Sys Bio

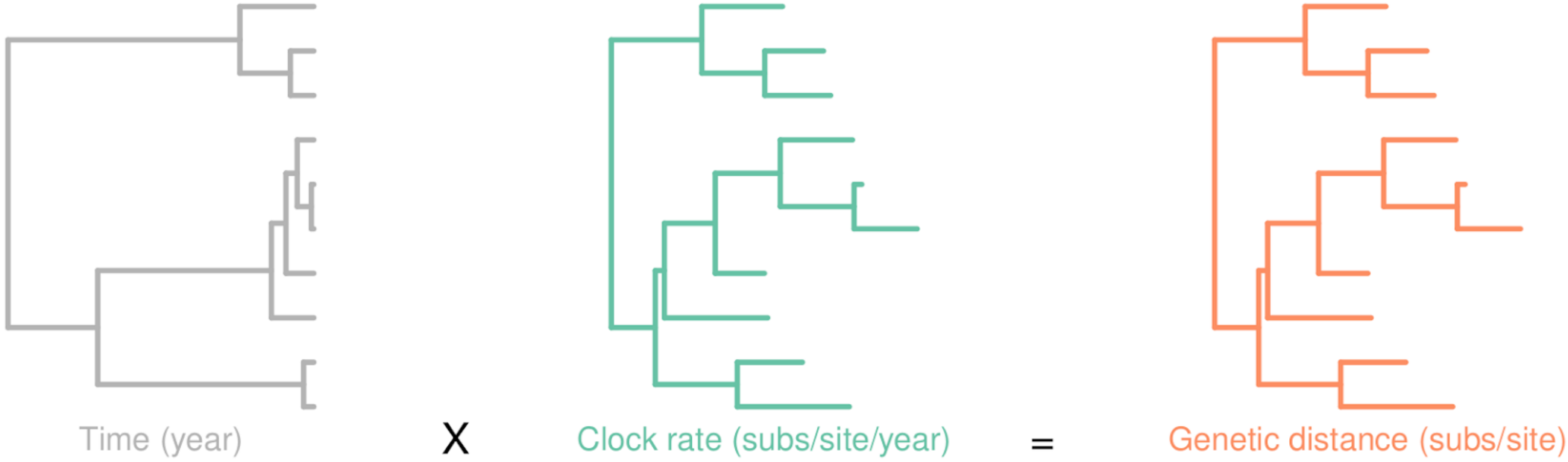
Issues with node dating

Summary

1. Rate and time is non-identifiable
2. Calibrations are hard to define objectively
3. The “effective priors” do not match the user specified priors
4. We’re potentially excluding a lot of information

The priors will always influence our results

Rate and time are not identifiable - not a conventional Bayesian problem



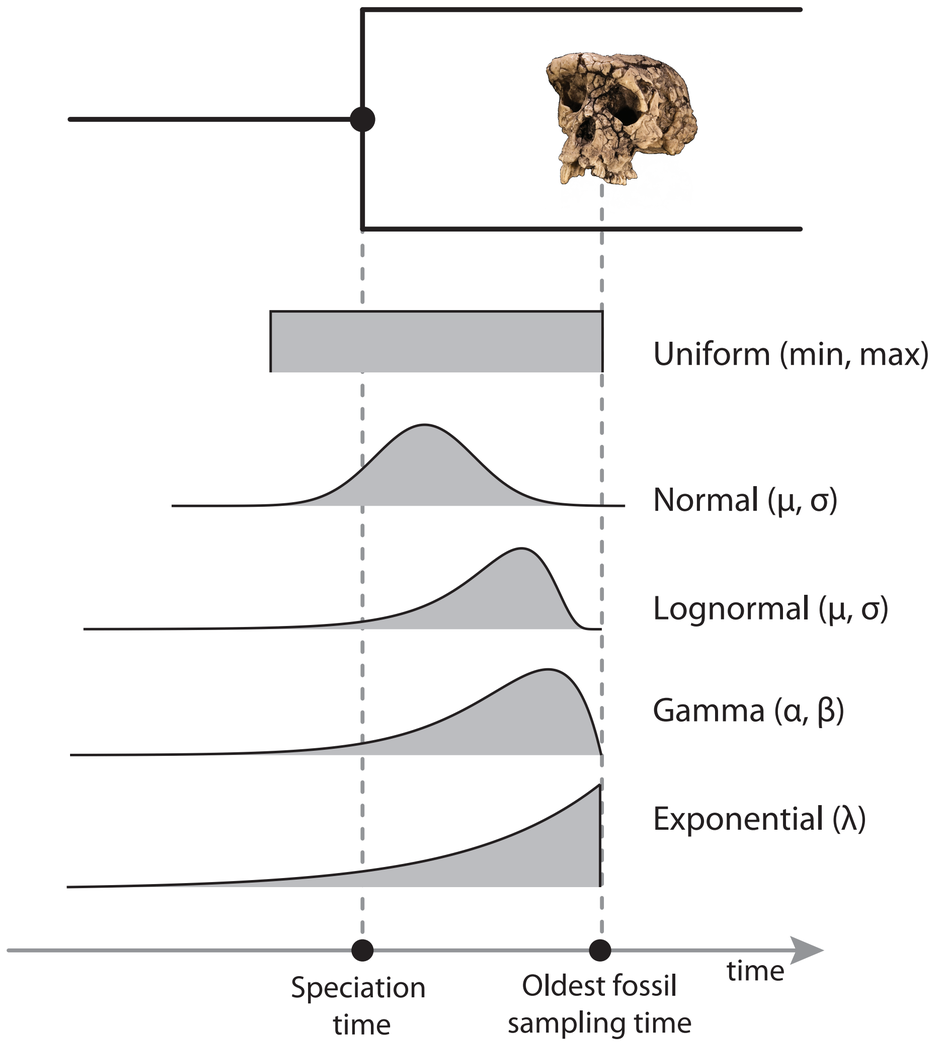
Prior

Prior

Likelihood

1.

Minimum and maximum constraints



Hard minimum bounds are based on first appearances

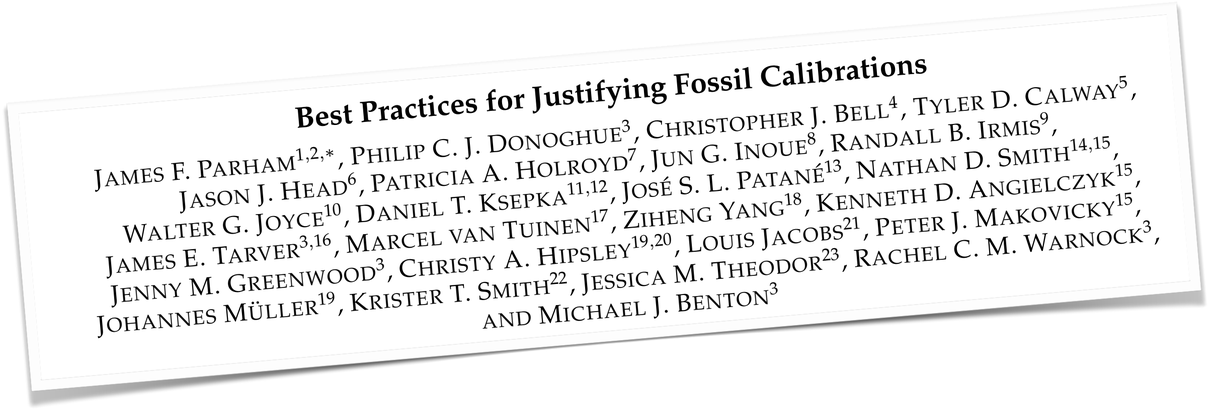
Soft maximum bounds are based on more tenuous evidence — typically the 97.5% limit of the calibration density

The upper bounds often influence the results

2.

Adapted from *Heath* (2012) *Sys Bio*

Maximum constraints



Best Practices for Justifying Fossil Calibrations

JAMES F. PARHAM[1,2,*], PHILIP C. J. DONOGHUE[3], CHRISTOPHER J. BELL[4], TYLER D. CALWAY[5], JASON J. HEAD[6], PATRICIA A. HOLROYD[7], JUN G. INOUE[8], RANDALL B. IRMIS[9], WALTER G. JOYCE[10], DANIEL T. KSEPKA[11,12], JOSÉ S. L. PATANÉ[13], NATHAN D. SMITH[14,15], JAMES E. TARVER[3,16], MARCEL VAN TUINEN[17], ZIHENG YANG[18], KENNETH D. ANGIELCZYK[15], JENNY M. GREENWOOD[3], CHRISTY A. HIPSLEY[19,20], LOUIS JACOBS[21], PETER J. MAKOVICKY[15], JOHANNES MÜLLER[19], KRISTER T. SMITH[22], JESSICA M. THEODOR[23], RACHEL C. M. WARNOCK[3], AND MICHAEL J. BENTON[3]

Goal - to make calibration choices transparent and explicit

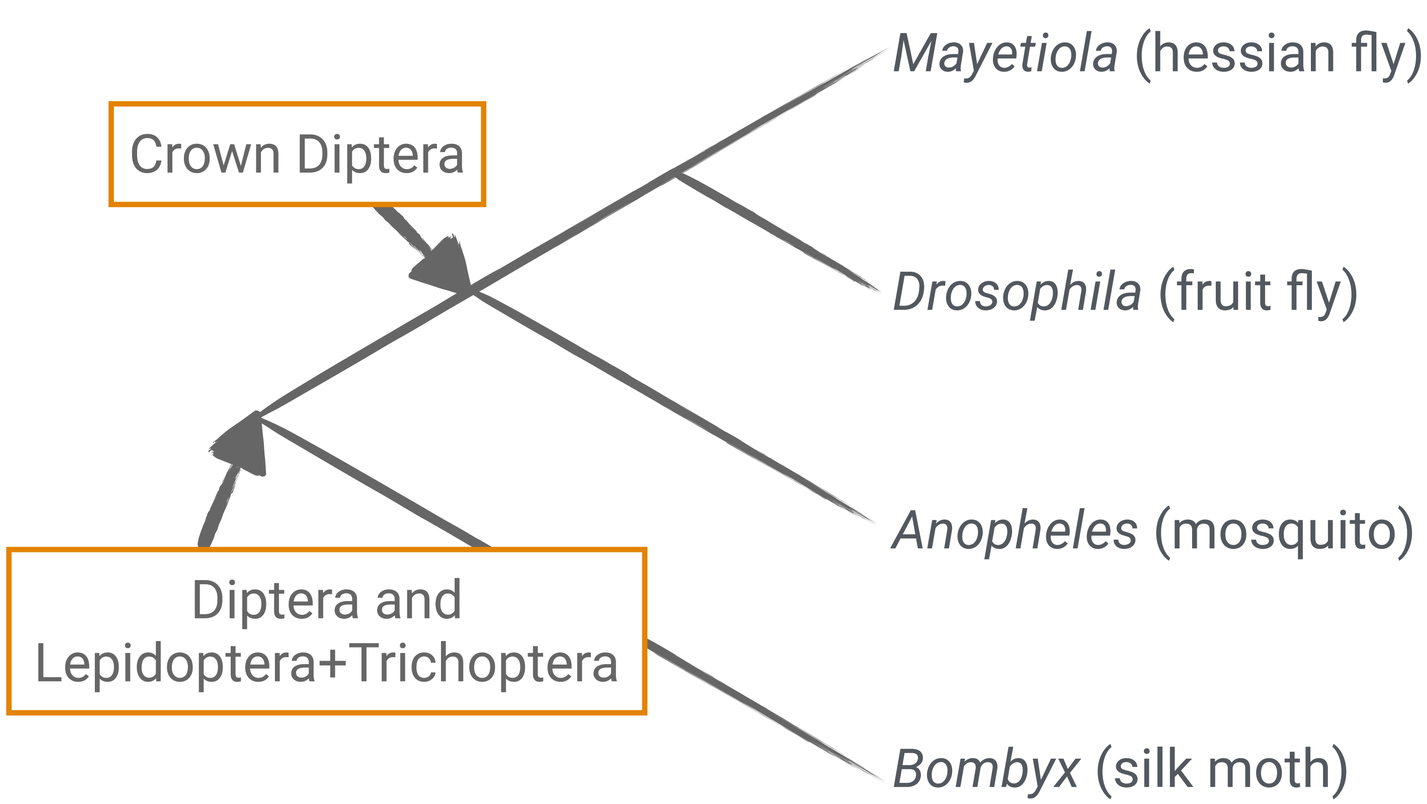
"The [soft] maximum constraint is established as older than all the oldest possible records, extending back to encompass a time when the ecologic, biogeographic, geologic, and taphonomic ***conditions for the existence of the lineage are met, but no records are known****."*

2.

Parham et al. (2011) *Sys Bio*

Min & max constraints

Example from insects



Minimum (all nodes)

- 238.5 Ma
- Triassic Grès-a-Voltzia Frm, France
- Earliest (non-controversial) evidence for all 4 lineages

Maximum (all nodes)

- 295.4 Ma
- Boskovice Furrow, Moravia, Czechia
- Huge diversity of insects described from here - no members of even total group Diptera from here or younger deposits

2.

Warnock et al. (2011)

The user “specified priors” don’t always match the “effective priors” used during analysis



We can run our analysis “under the prior” (we ignore the sequence data) to see how the software actually constructs the prior density
— accounts for the interaction between nodes

3.

See *Warnock et al.* (2011, 2015); *Budd and Mann* (2024)

The model doesn’t describe the process that generated the fossil sampling times, meaning the model is **statistically incoherent**

The calibration priors are difficult to specify objectively and can have a massive impact on the divergence times. They can also interact with each other and / or the birth-death process prior in unintuitive ways

Some references on issues with specified vs effective priors
Yang and Rannala (2006)
Heled and Drummond (2012)
Warnock et al. (2012, 2015)

3.



Point of View

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Advance Access Publication September 11, 2023

Two Notorious Nodes: A Critical Examination of Relaxed Molecular Clock Age Estimates of the Bilaterian Animals and Placental Mammals

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[2]Department of Statistics, School of Mathematics, University of Leeds, Leeds LS2 9JT, UK

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Associate Editor: Jeremy Beaulieu

Abstract.—The popularity of relaxed clock Bayesian inference of clade origin timings has generated several recent publications with focal results considerably older than the fossils of the clades in question. Here, we critically examine two such clades: the animals (with a focus on the bilaterians) and the mammals (with a focus on the placentals). Each example displays a set of characteristic pathologies which, although much commented on, are rarely corrected for. We conclude that in neither case does the molecular clock analysis provide any evidence for an origin of the clade deeper than what is suggested by the fossil record. In addition, both these clades have other features (including, in the case of the placental mammals, proximity to a large mass extinction) that allow us to generate precise expectations of the timings of their origins. Thus, in these instances, the fossil record can provide a powerful test of molecular clock methodology, and why it goes astray, and we have every reason to think these problems are general. [Cambrian explosion; mammalian evolution; molecular clocks.]

The apparent clash between molecular clock estimates of the time of origins of clades versus what the fossil record might be thought to say has been a significant source of anxiety in the last two decades (e.g. dos Reis and Yang 2013; Bromham et al. 2018; Bromham 2019; Klopfstein 2021). Nevertheless, the fossil record clearly shows a significant structure that would be difficult to reconcile with such *general* unreliability (Benton et al. 2000, 2009). In addition, our ability to map rapid post-extinction radiations (Budd and Jensen 2003) such as at least ordinal-level placental mammals strongly suggests that, in some cases, the fossil record must be giving us a more or less accurate picture of temporal evolution.

Molecular clock estimates, which have sometimes been argued to have essentially taken over from the fossil record as the ultimate measures of evolutionary time (Warnock et al. 2012), conversely, often give much larger gaps between first appearances of clades and the fossil record. To give some recent examples of the estimated gaps between the first recognized fossil of a clade and the 95% credible interval of molecular clock estimates: beetles (55–134 myr older than the oldest fossil (Cai et al. 2022)); sand dollar and sea biscuit echinoids (40–65 myr (Mongiardino Koch et al. 2022)); cheilostome bryozoans (132–238 myr (Barbá-Montoya et al. 2022)); angiosperms (23–121 myr (dos Reis et al. 2018)); and bilaterians (50–143 myr (dos Reis et al. 2015)). Thus, one ends up in the curious situation where the fossil record is taken seriously in providing a prior for the ages of nodes, but in retrospect is discovered to be wildly unreliable. The possible reasons for these sorts of large gaps have been much discussed, but here we wish to focus on how calibration ranges are converted to priors, and the influence that those priors then have on the outcome. Whilst these issues have been the subject of considerable discussion in the literature (Warnock et al. 2015; Barba-Montoya et al. 2017), we do not believe that these discussions have been followed through to their logical conclusion, which, as we argue here, is that relaxed clocks do not provide good evidence for large gaps between clade origins and their fossil record. As a focal point for our investigation, we take two rather notorious nodes: the origin of the animals (Álvarez-Carretero et al. 2022); both of which have generated considerable controversy. We have chosen these two studies, first because they are of widespread interest in their own right, and indeed are widely taken (as we shall argue below, incorrectly) to show that the fossil record of the early parts of these radiations is unreliable; and secondly, because of the broader implications that can be drawn from them; that is, we believe the problems we discuss are inherent in relaxed clock analyses in general.

In the following, we use the following terminology: *calibration density*: the user-defined distribution of plausible ages of a tree node based on (in these cases) the fossil record; *effective prior*: the prior probability distribution that is constructed from the calibration densities by enforcement of known topological constraints. We note that while calibration densities are defined independently for each node, the effective priors of all the nodes are interdependent to some degree since they must obey the topological ordering of the tree.

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3. *Budd and Mann (2024)*



Point of View

Syst. Biol. 73(1):223–234, 2024

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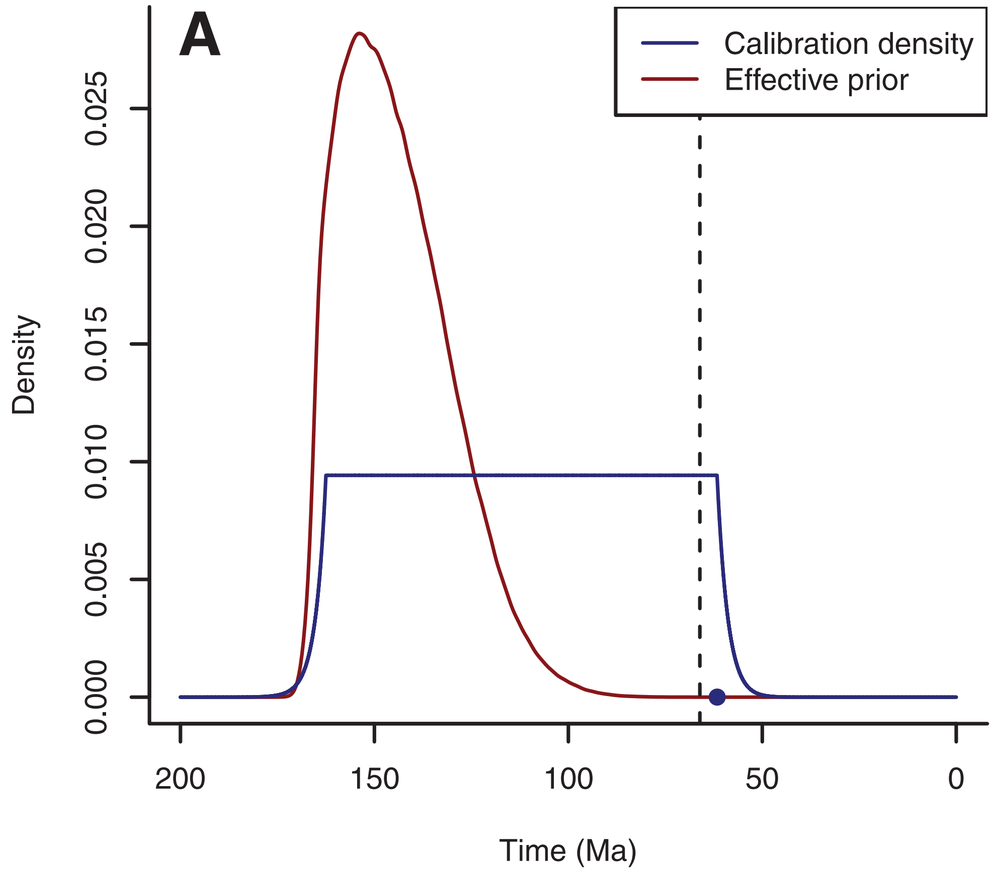
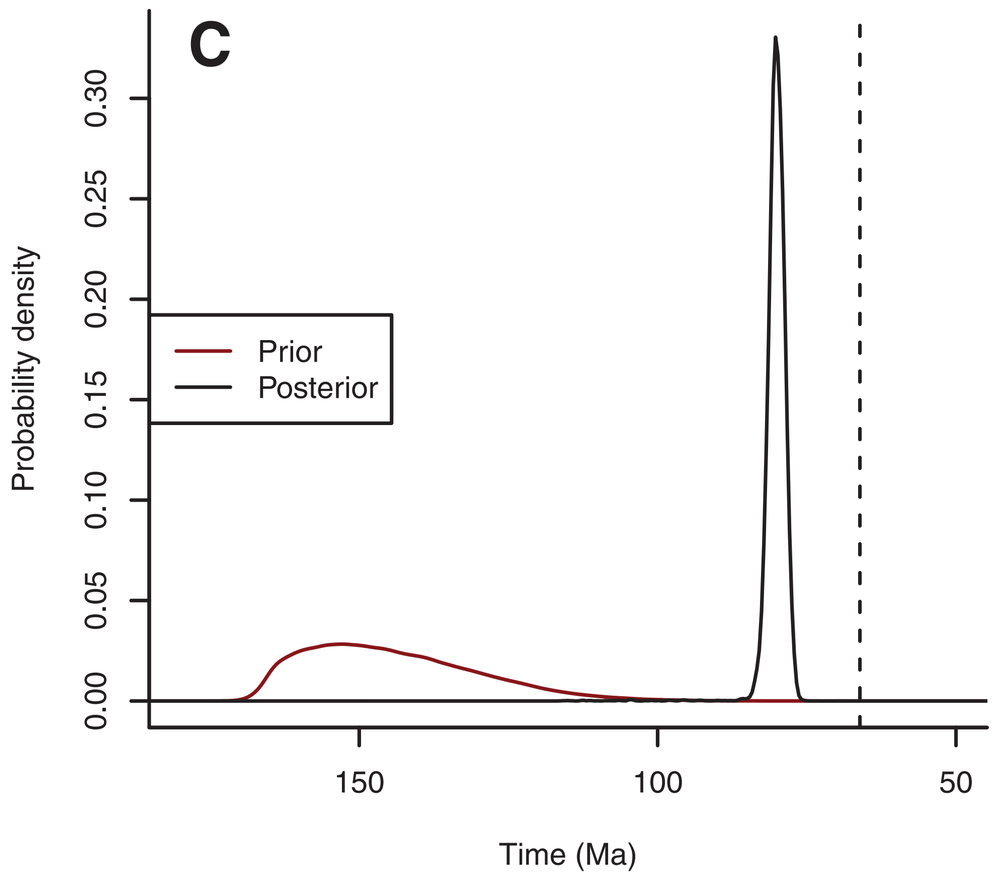
- angiosperms (23–121 myr)
- bilaterians (50–143 myr)

“Thus, one ends up in the curious situation where the fossil record is taken seriously in providing a prior for the ages of nodes, but in retrospect is discovered to be wildly unreliable.”

3. *Budd and Mann (2024)*

Placental mammals



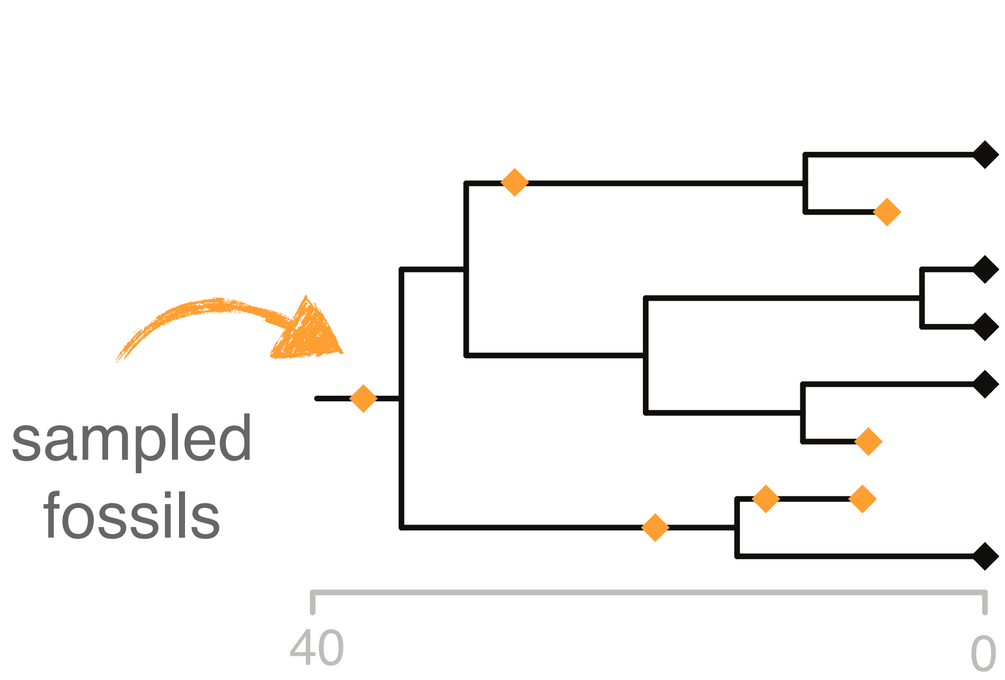


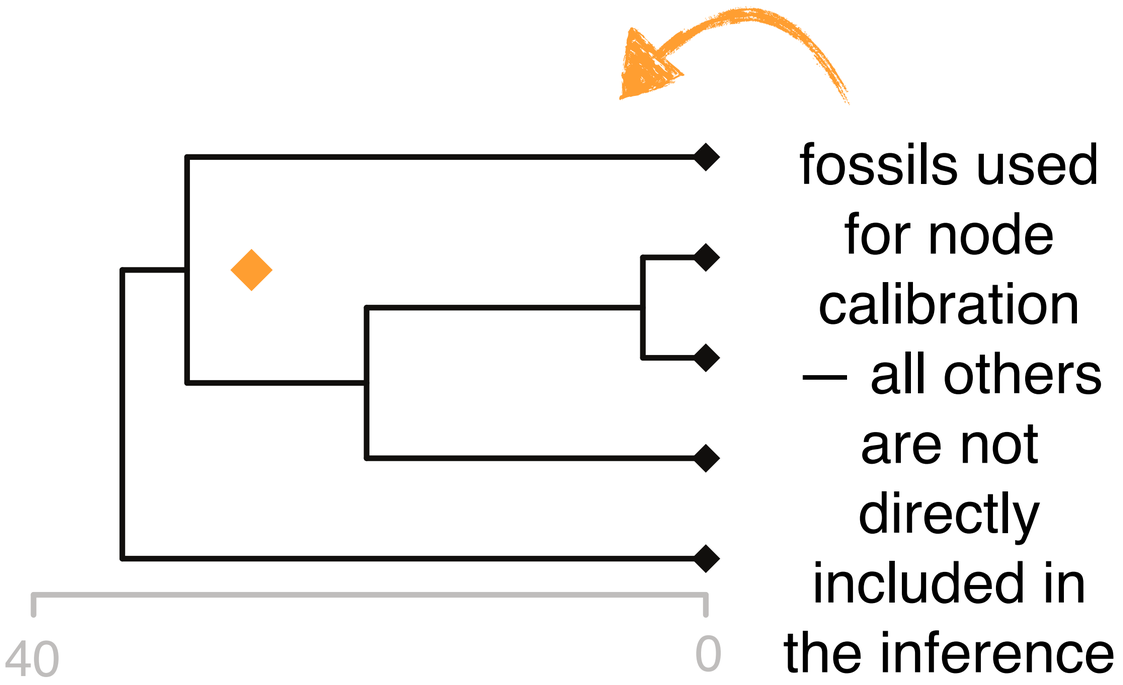
3. *Budd and Mann (2024)*

Node dating: potential issues

There are many!

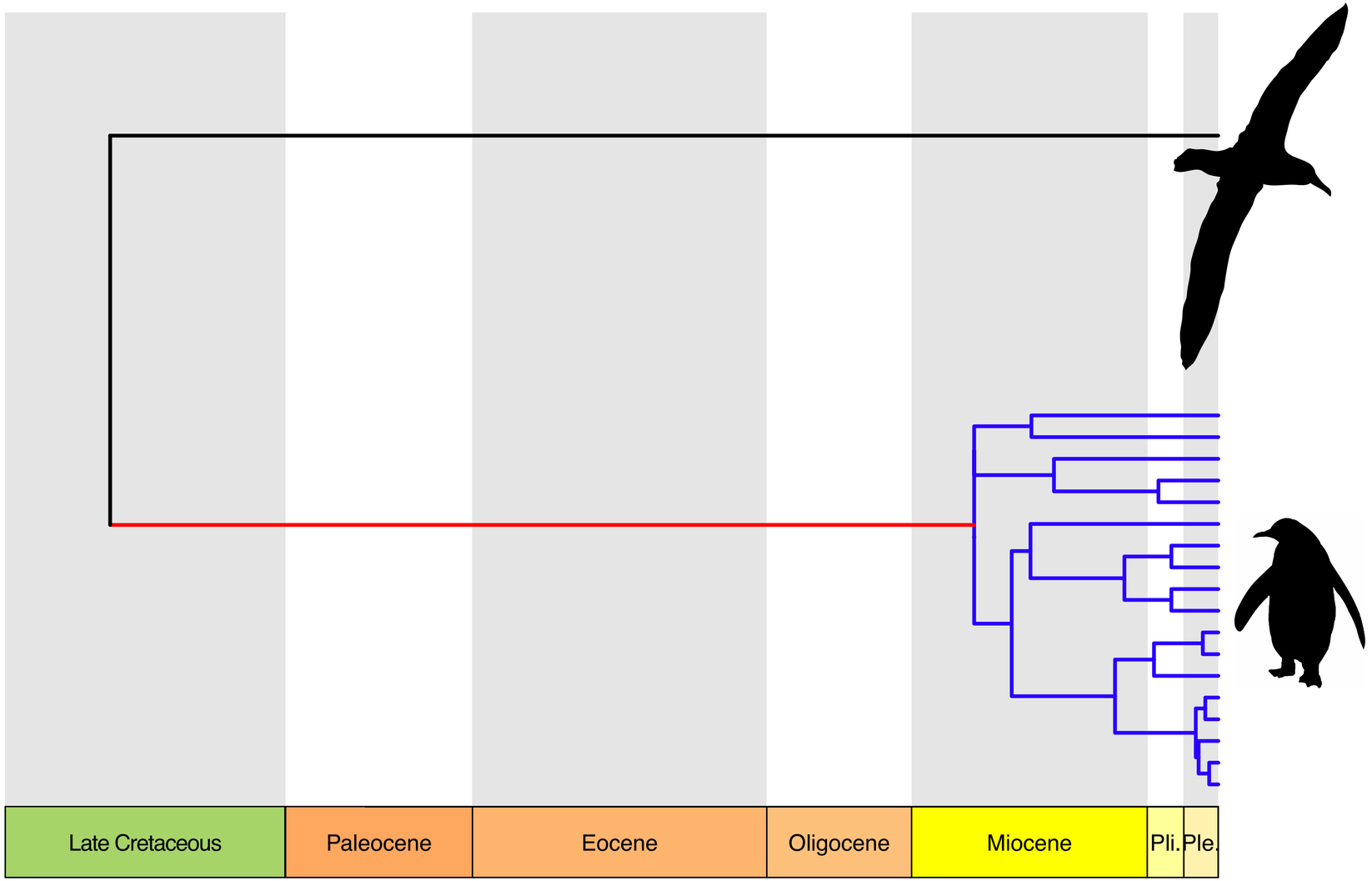
A lot of information is excluded, since typically we assign one fossil per calibration node





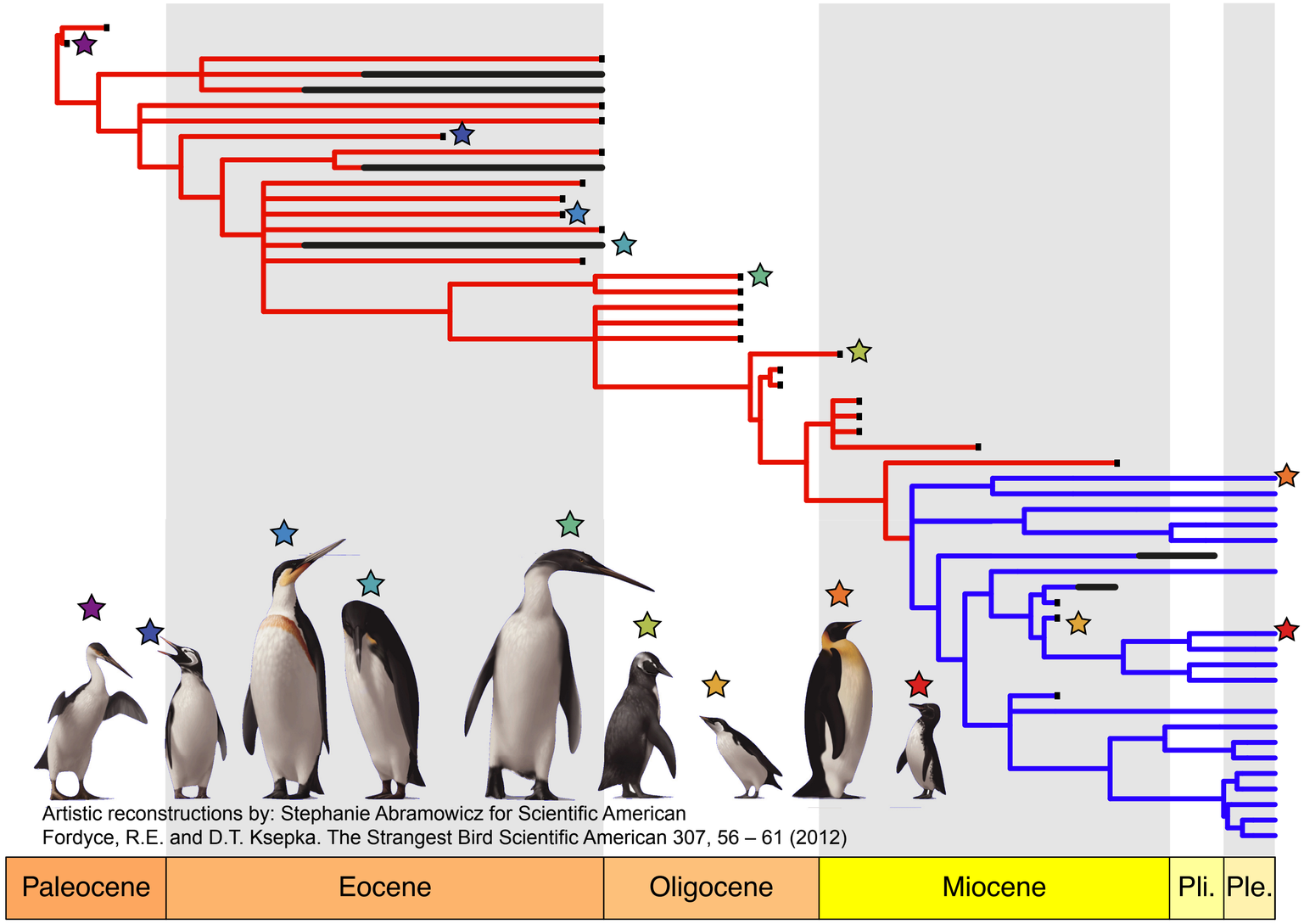
4.

Example: living penguins



Nearest living relative is the group containing falcons - separated by ~60 Ma

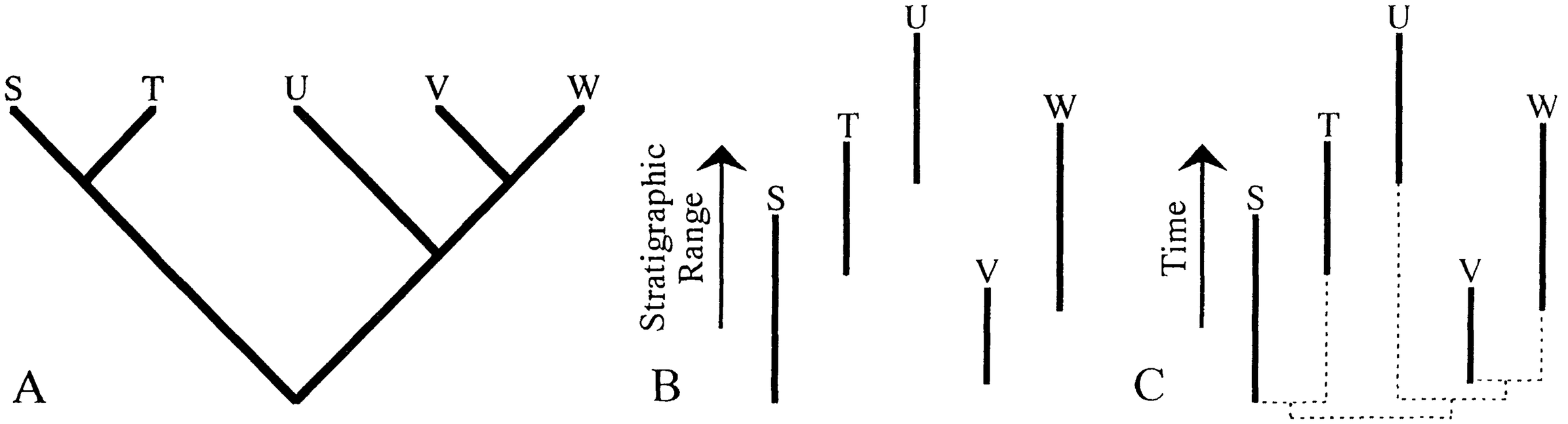
Example: living penguins



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

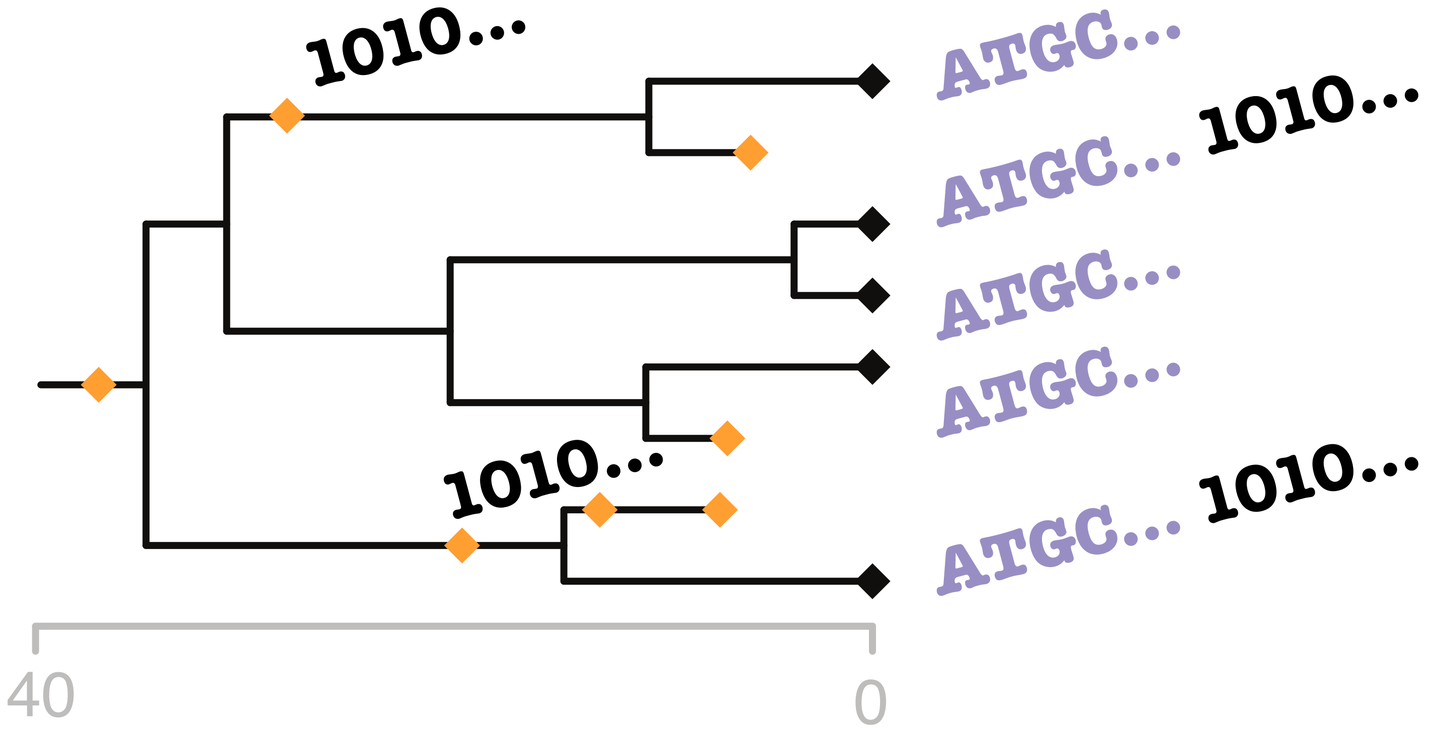
But penguins have a rich fossil record!

Total-evidence dating



Stratigraphic tests of cladistic hypotheses
Wagner (1995) *Paleobiology*
See also *Bapst* (2013)

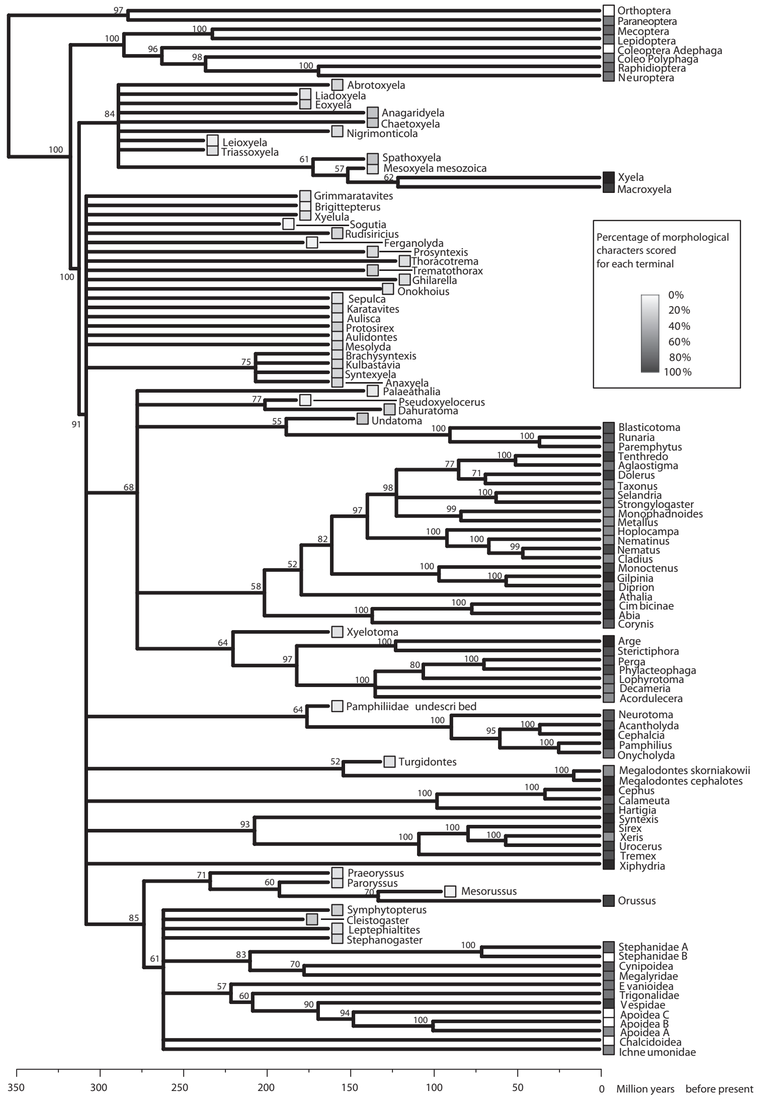
Tip-dating or “total-evidence” dating



We have DNA for living species. We have morphology for living *and* fossil species

Fossils can be positioned on the basis of morphology → accounts for uncertainty in fossil placement

The uniform tree prior





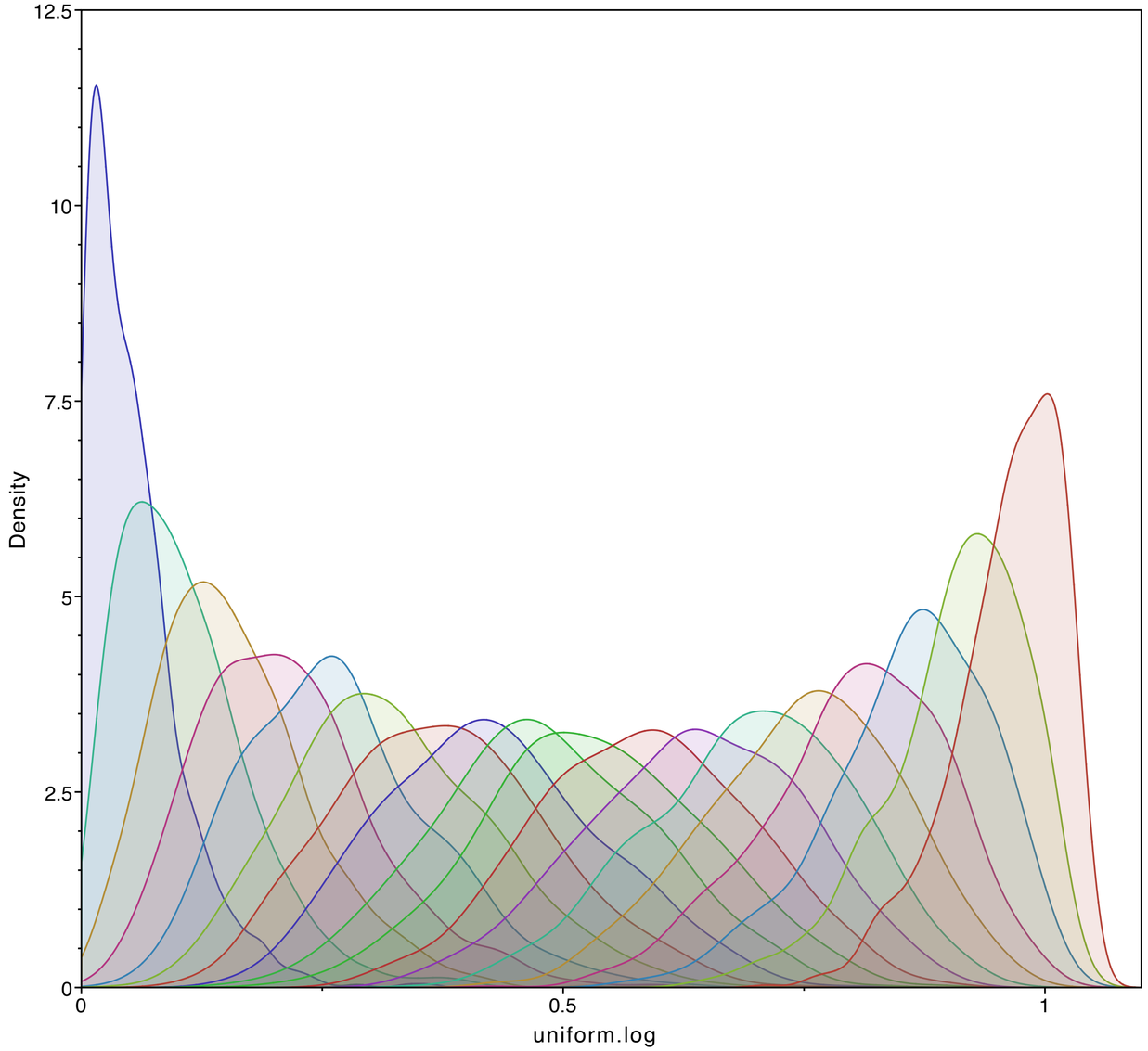


Dated tree of Hymenoptera

The uniform tree prior assumes all trees and branch lengths are equally likely within the bounds of the fossil ages (+ a max upper bound)

It does not explicitly account for the fossil sampling process

Ronquist et al. (2012)



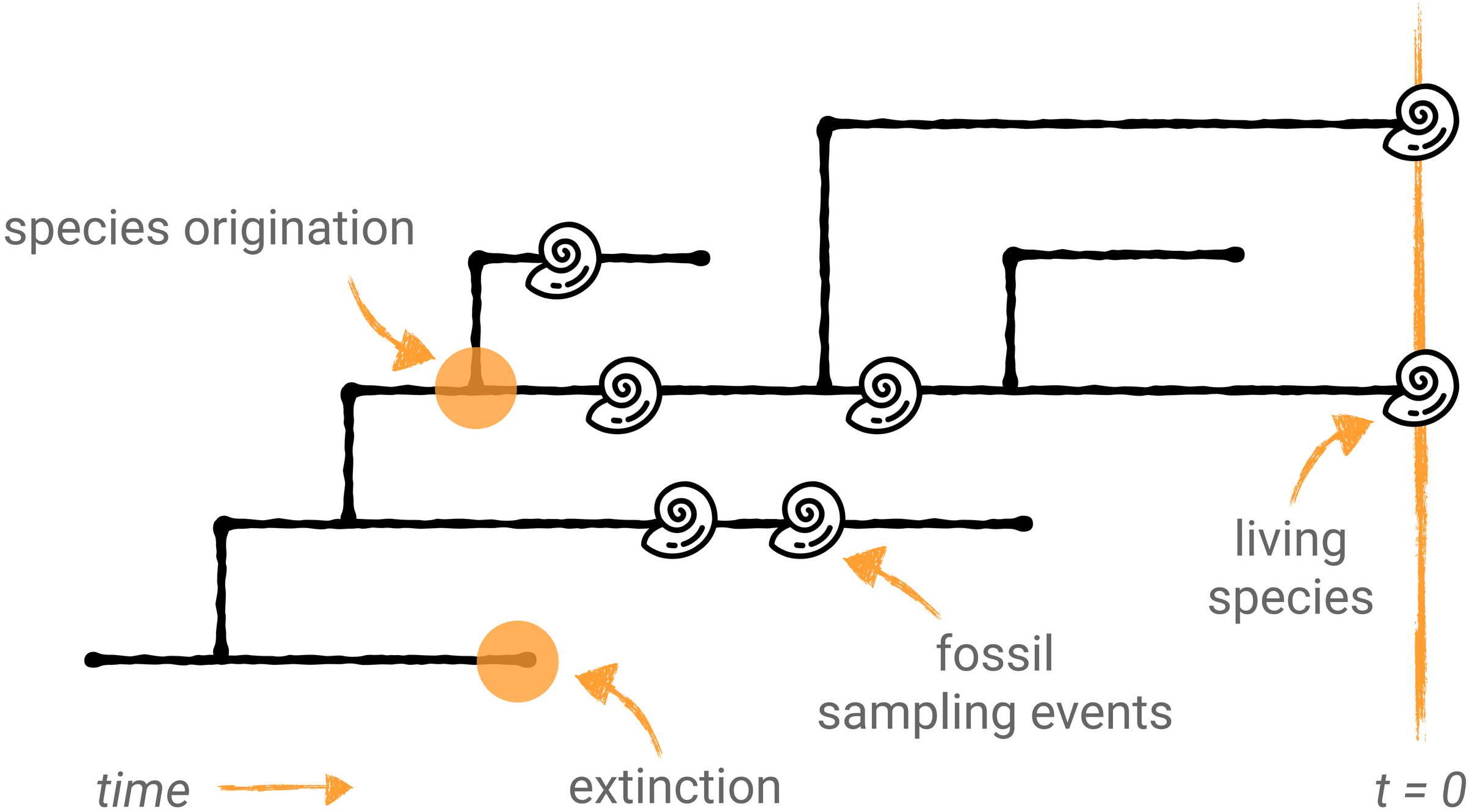
A uniform tree prior implies time till the next split is independent of how many lineages there are present

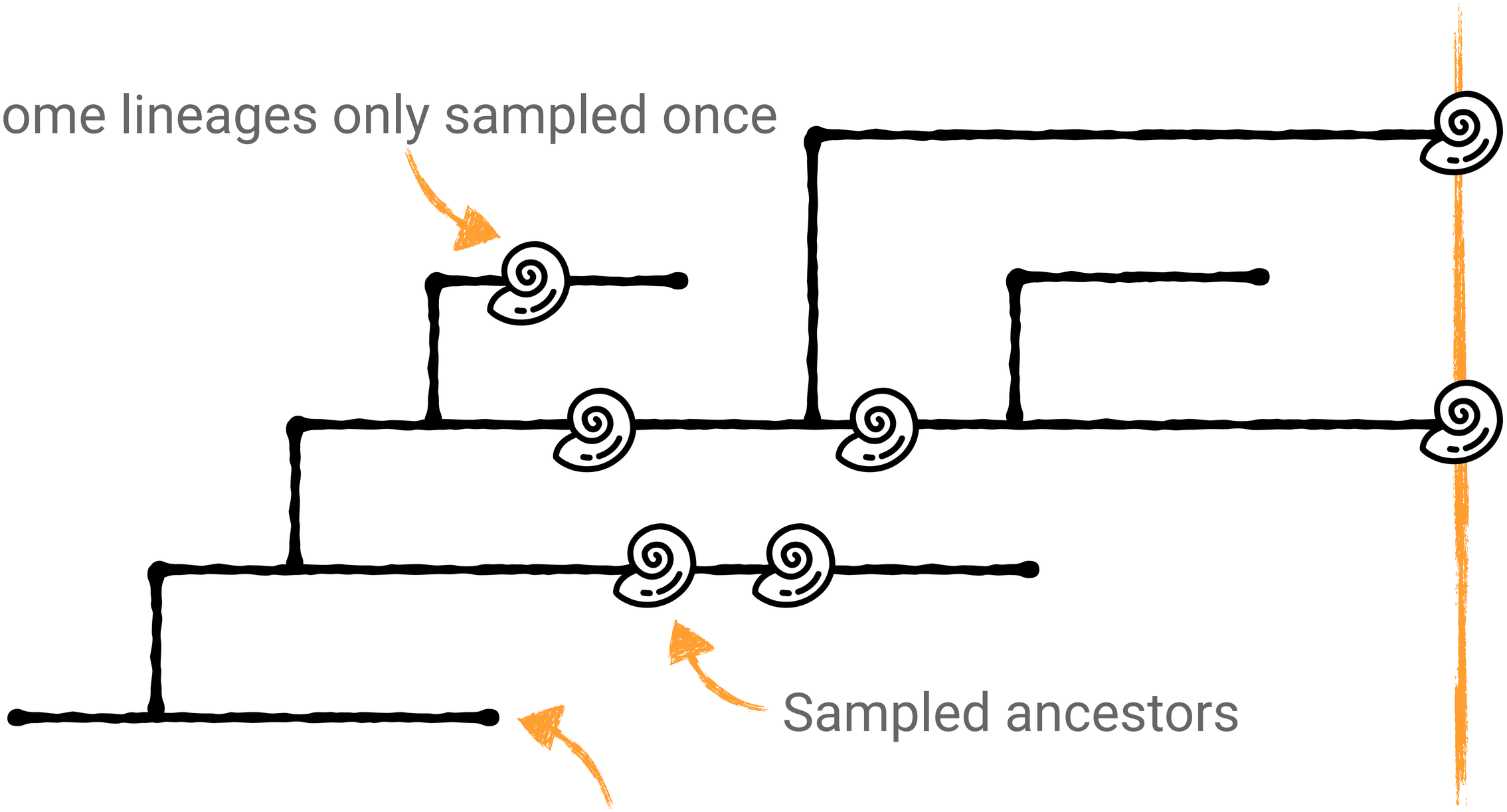
This is in contrast to birth-death processes, where more lineages mean a higher chance of observing a split in one of these lineages

[Uniform tree priors - why not use them?](#)
Remco Bouckaert

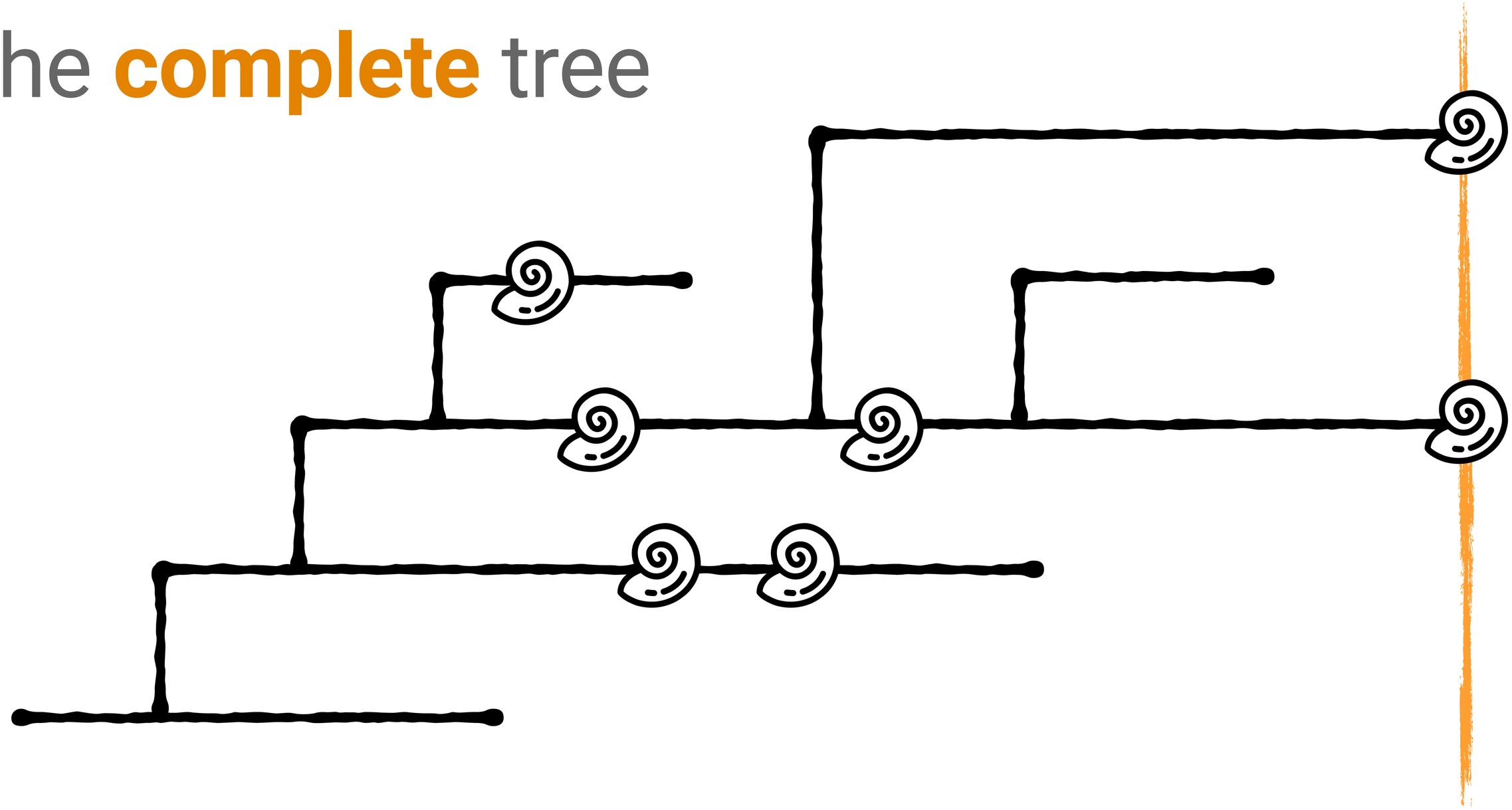
What does a generating prior for the fossil record look like?

The fossilised birth-death process


species origination
living species
fossil sampling events
extinction
time
t = 0


Some lineages only sampled once
Sampled ancestors
Some lineages go completely unsampled
t = 0

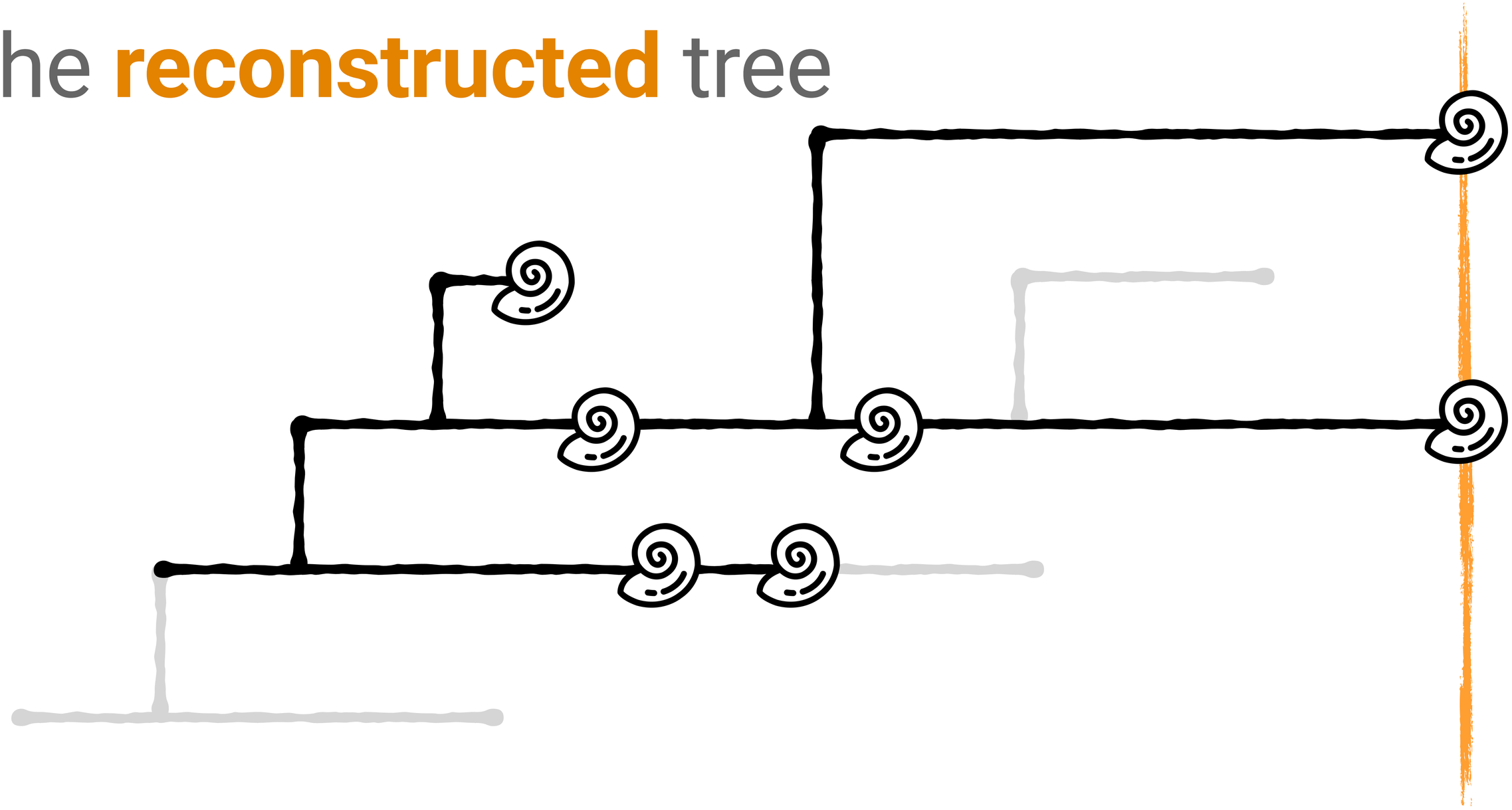
The **complete** tree



time →

t = 0

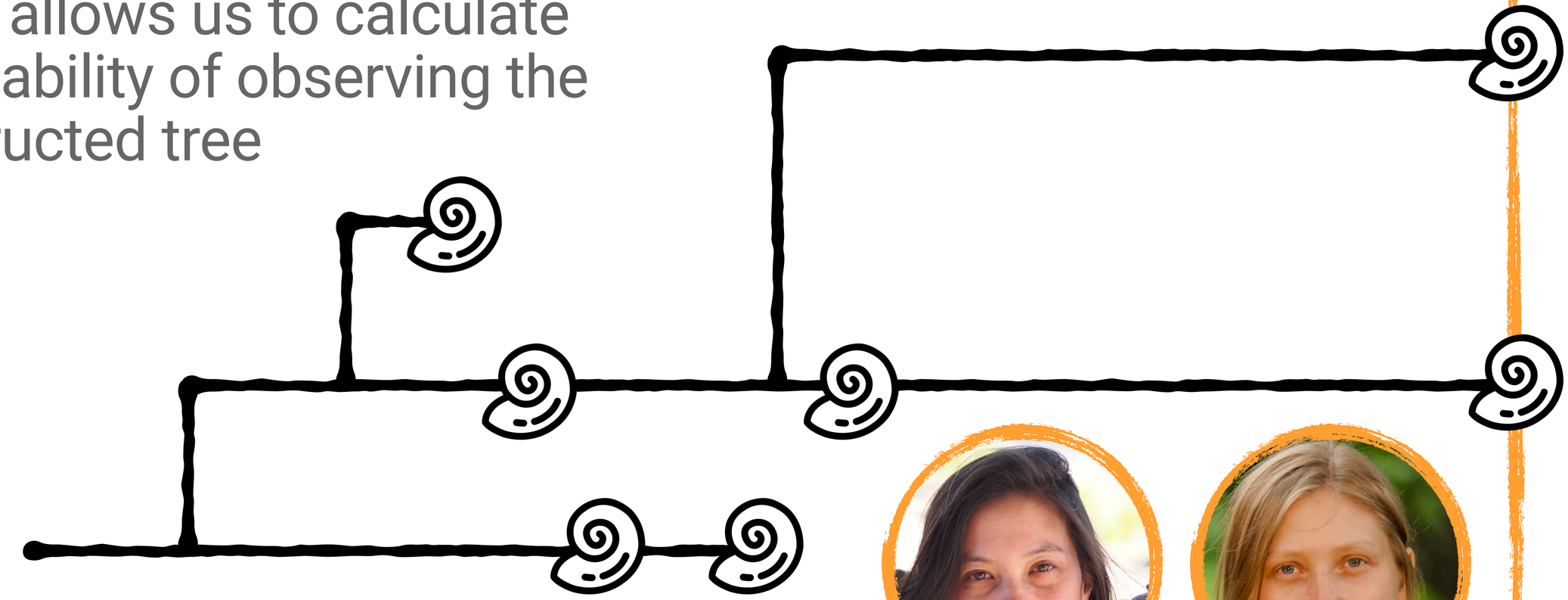
The **reconstructed** tree



time →

t = 0

The **fossilised birth-death (FBD) process** allows us to calculate the probability of observing the reconstructed tree

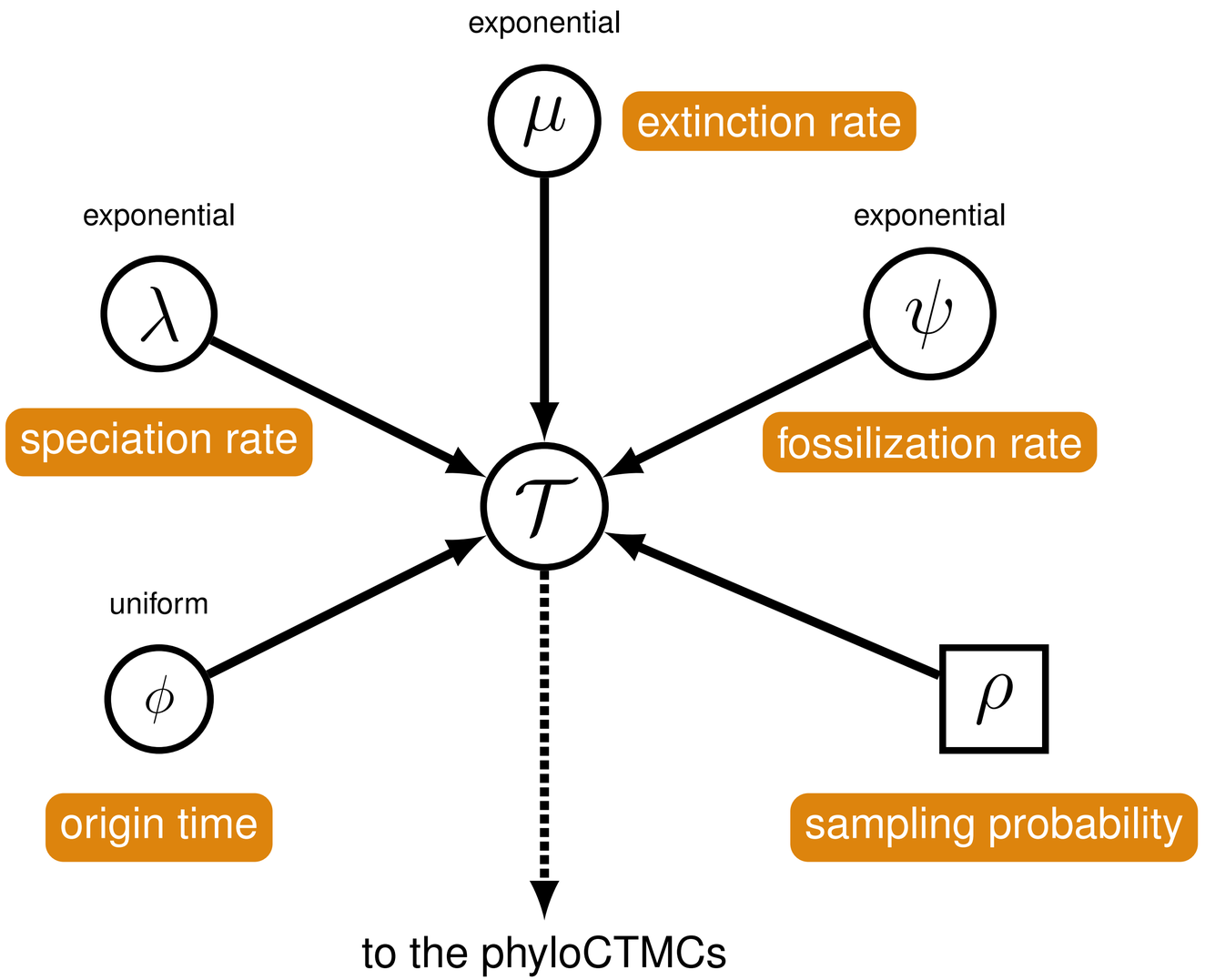


$$P(\mathbb{T}|\lambda,\mu,\psi,\rho)$$



Sampling-through-time in birth-death trees. Stadler. (2010)
First implemented: Heath et al. (2014) and *Gavryushkina et al.* (2014)

FBD model parameters



Speciation, extinction, and fossil sampling are instantaneous rates

Extant species sampling is a probability at $t = 0$

The origin parameter is the start of the process, i.e., before the first branching event

Adapted from *Barido-Sottani et al.* (2020)

Parameterisation of the process

We can put priors on different combinations of parameters

Parameter	**Transformation**
Net diversification	$d = \lambda - \mu$
Turnover	$v = \mu/\lambda$
Sampling proportion	$s = \psi/(\mu + \psi)$
Speciation	$\lambda = d/(1 - v)$
Extinction	$\mu = (vd)(1 - v)$
Sampling	$\psi = (s/(1 - s))((vd)/(1 - v))$

Why the FBD model so cool?

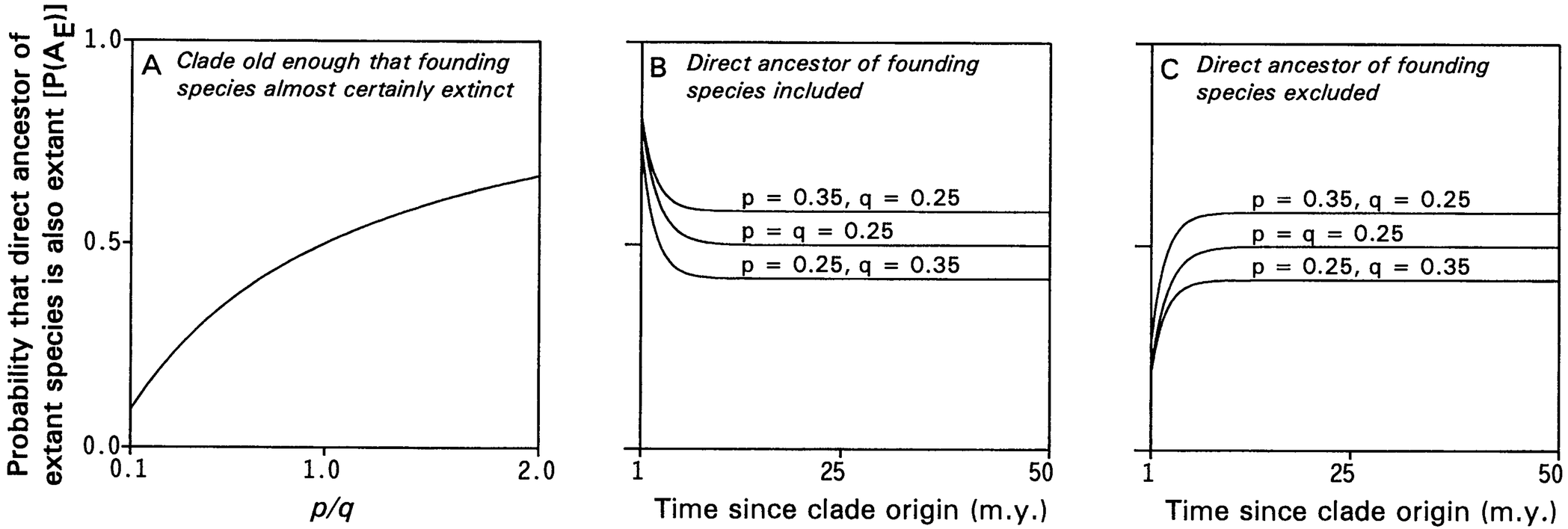
There are many statistical advantages to having a generative model:

- greater accuracy
- better reflection of uncertainty
- increased flexibility

We can include fossils directly in the tree + much more fossil data

We can combine data in ways that weren’t previously possible and even link the model parameters to abiotic processes

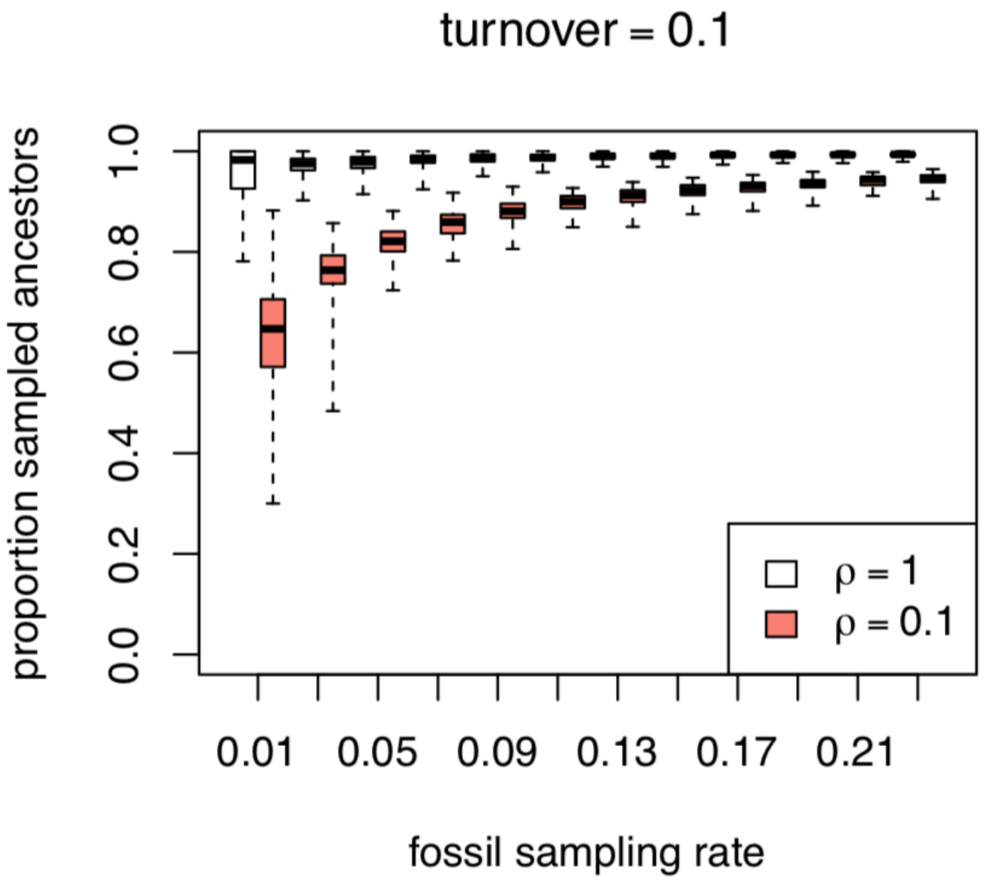
Sampled ancestors

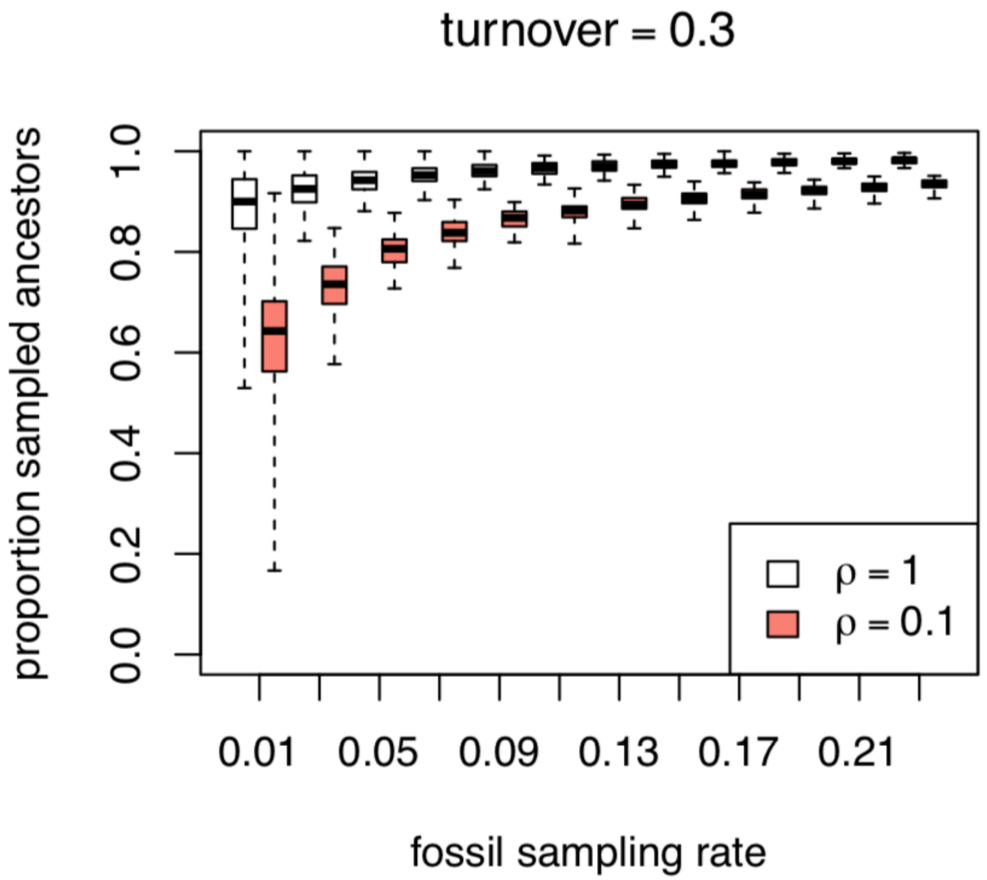


On the probability of ancestors in the fossil record
Foote (1996) *Paleobiology*

Sampled ancestors

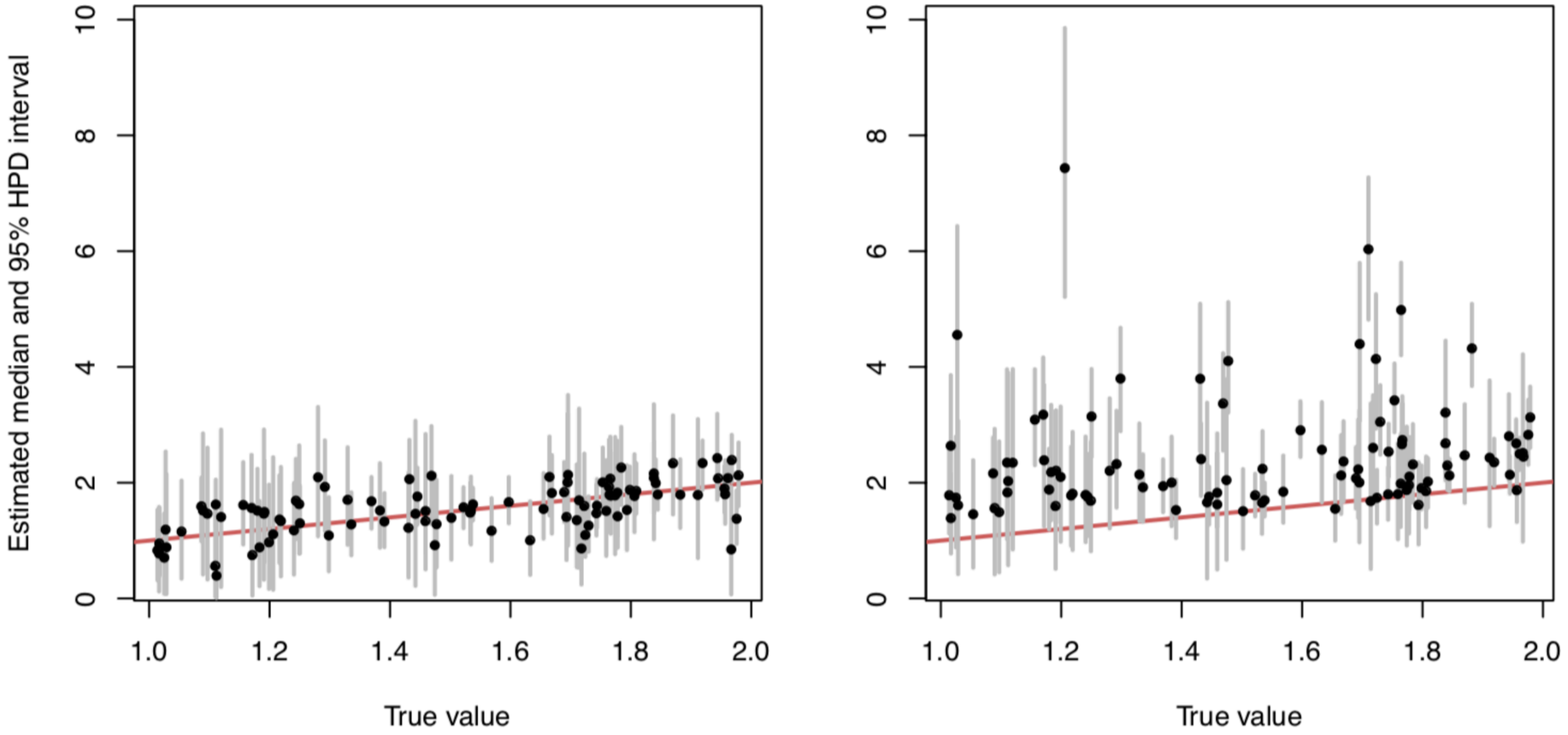
The proportion increases with higher turnover (birth - death) or higher sampling





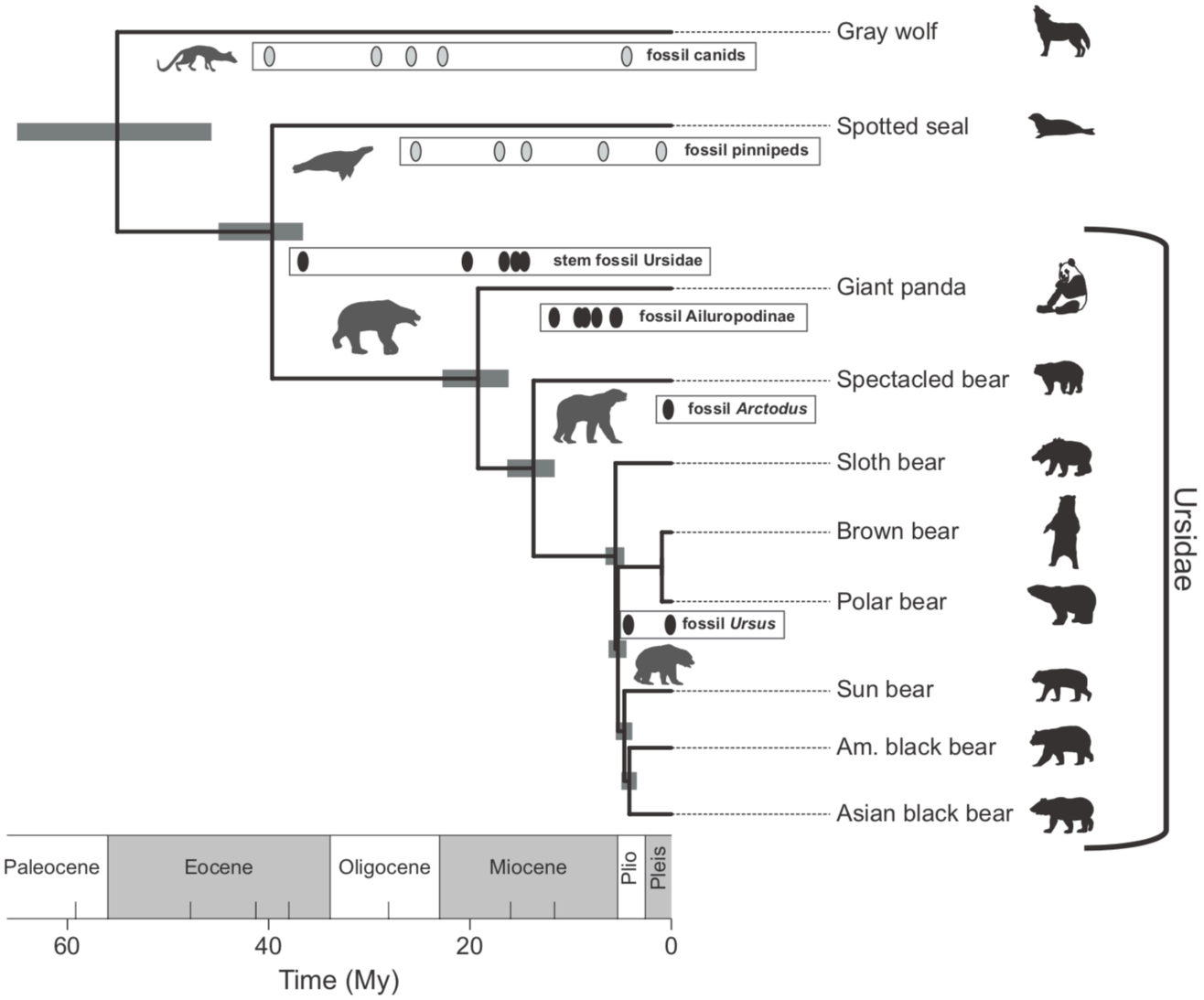
Sampled ancestors

Ignoring sampled ancestors can lead to inaccurate parameter estimates



Gavryushkina et al. (2014) *PLoS Comp Bio*

Time calibrated tree of living and fossil bears



First application of the FBD model

Fossils are incorporated via constraints, not character data. Their precise placement can not be inferred, but this uncertainty will be reflected in the posterior

Heath et al. (2014)

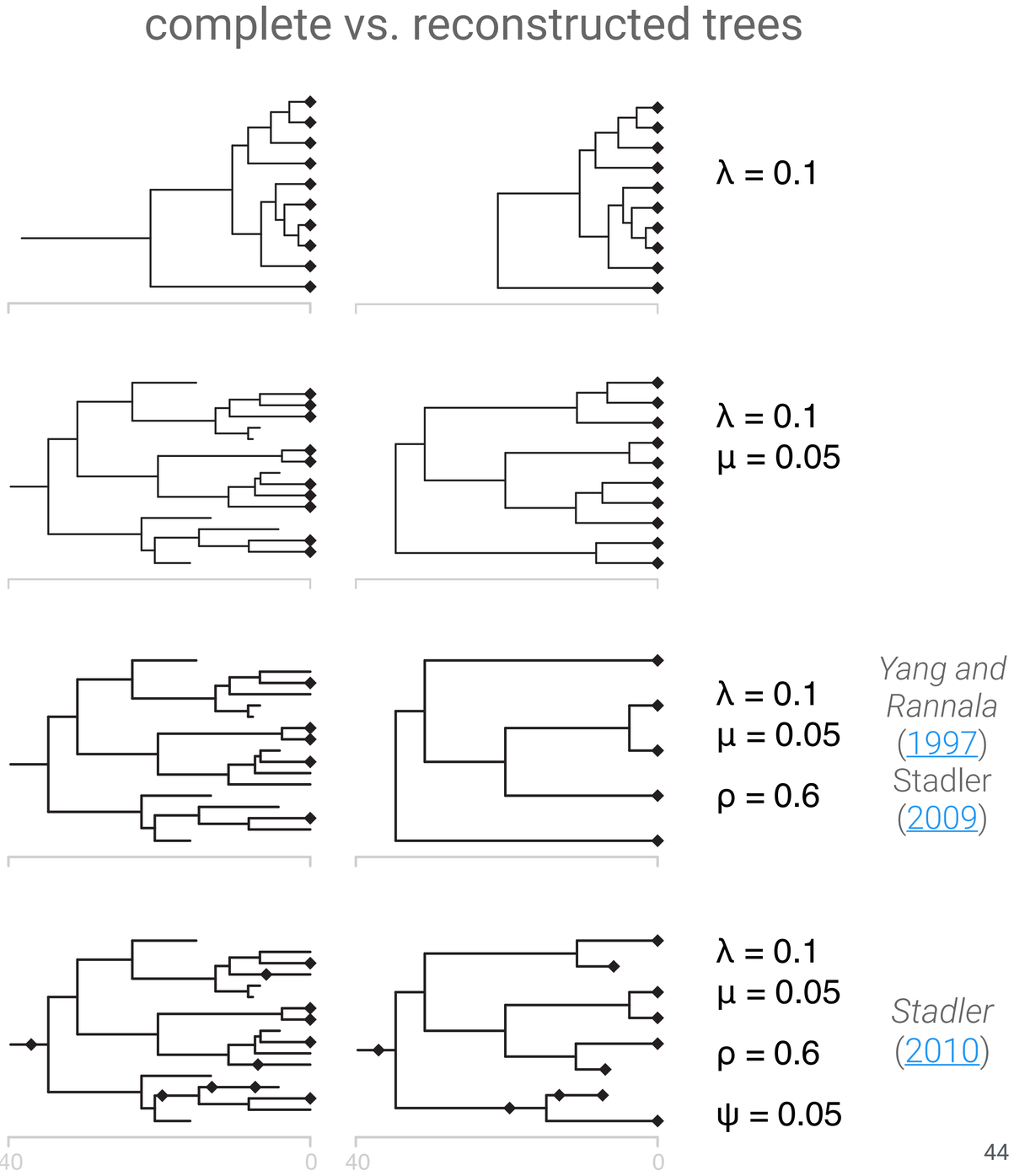
Exercise

Relationship to (some) other birth-death process models

These models are special cases of the FBD process, with fossil sampling (ψ) = zero

We can also use *ρ* at *t > 0* to model serial sampling

For epidemiology: *Stadler et al.* (2012)
See also: *Stadler and Yang* (2013)
Review: *MacPherson et al.* (2022)



Fossils can be incorporated via **taxonomy** or **character data** (total-evidence)

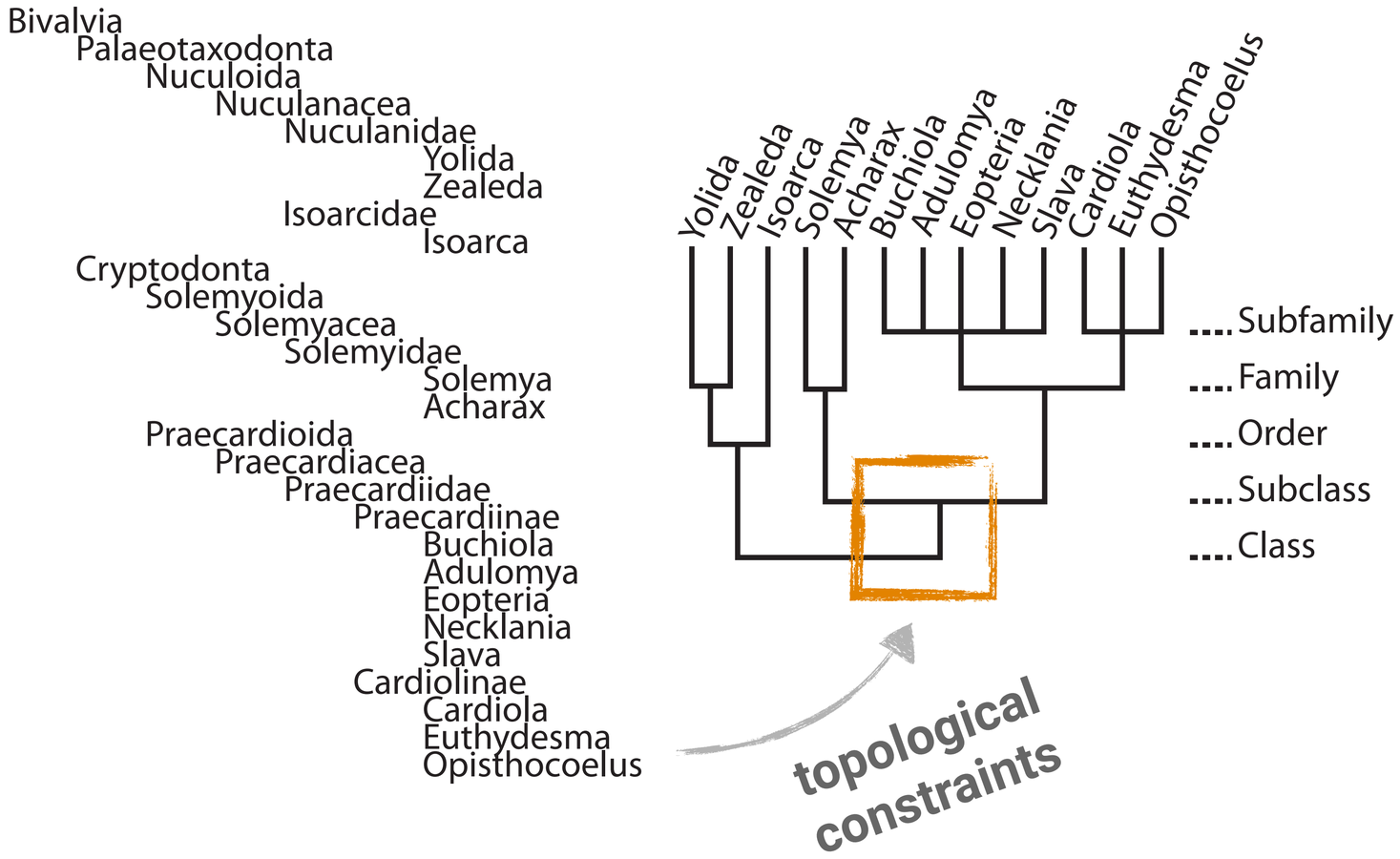
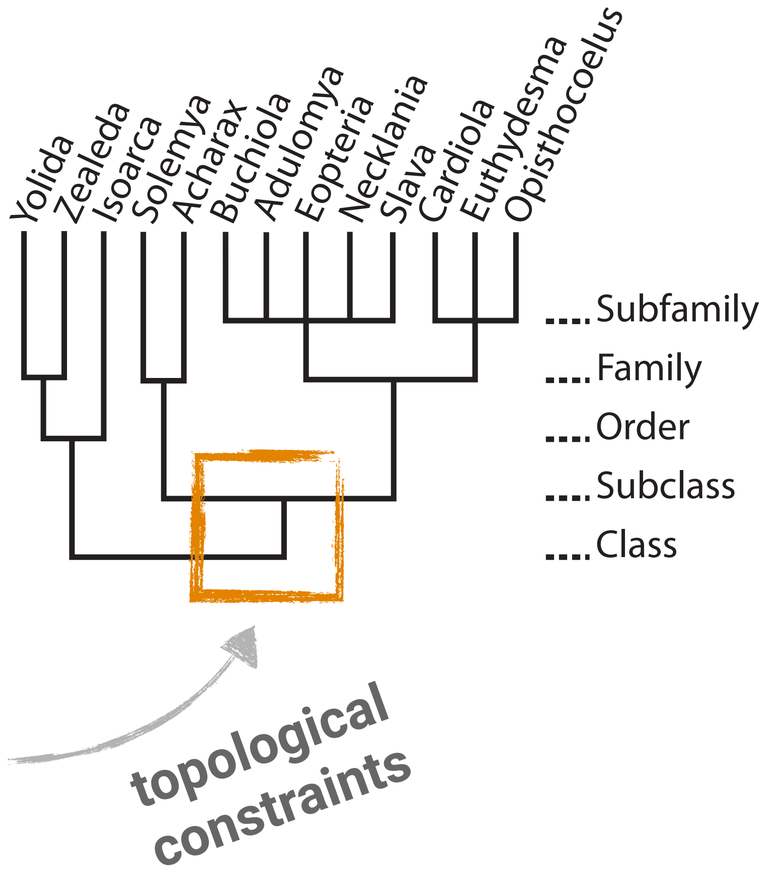


Image source *Soul & Friedman* (2015)

Fossils can be incorporated via **taxonomy** or **character data** (total-evidence)





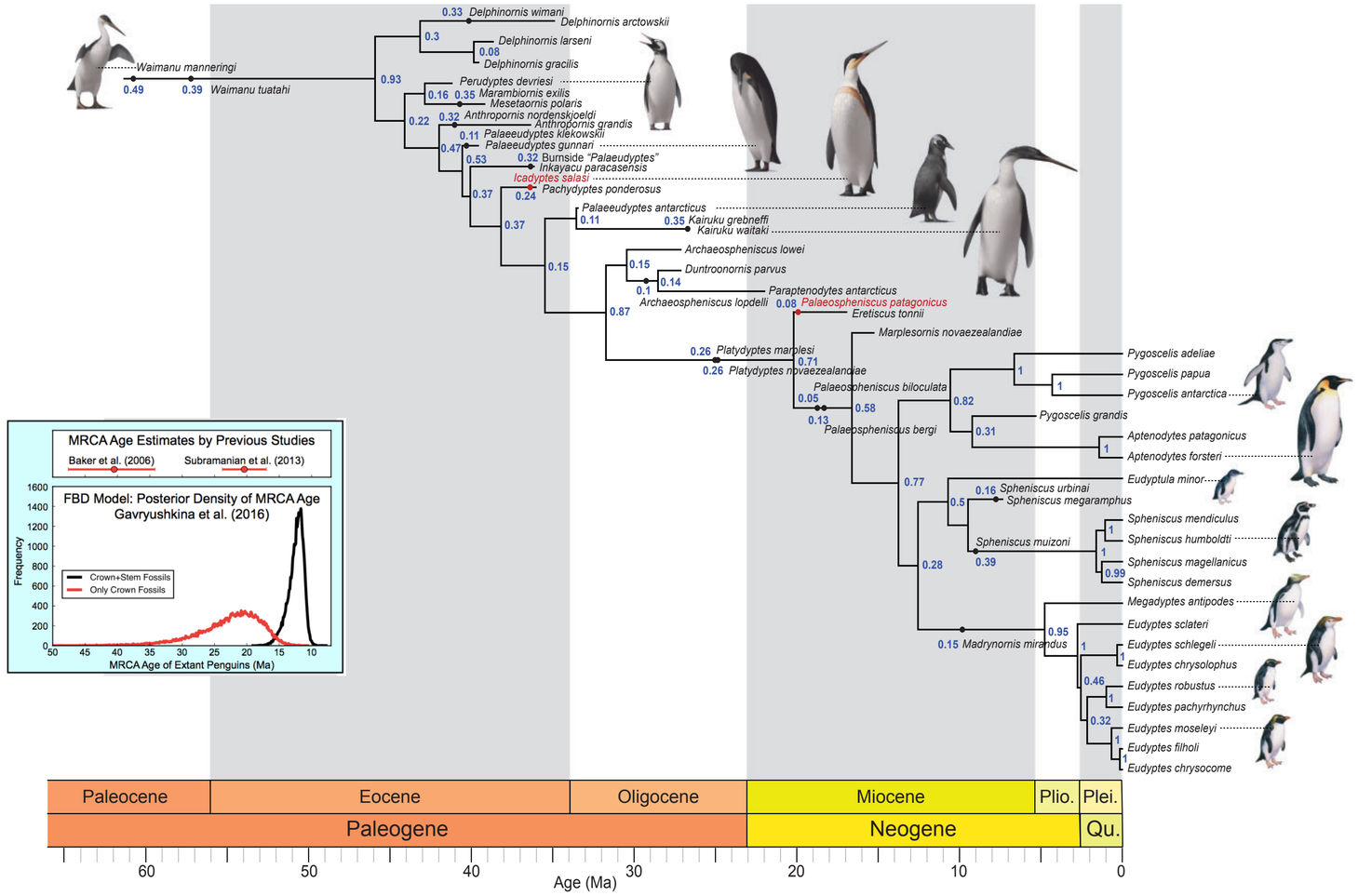
AND/ OR

ATAT...
TCAC...
????...

1001...
1101...
0100...

Image source *Soul & Friedman* (2015)

Time calibrated tree of living and fossil penguins

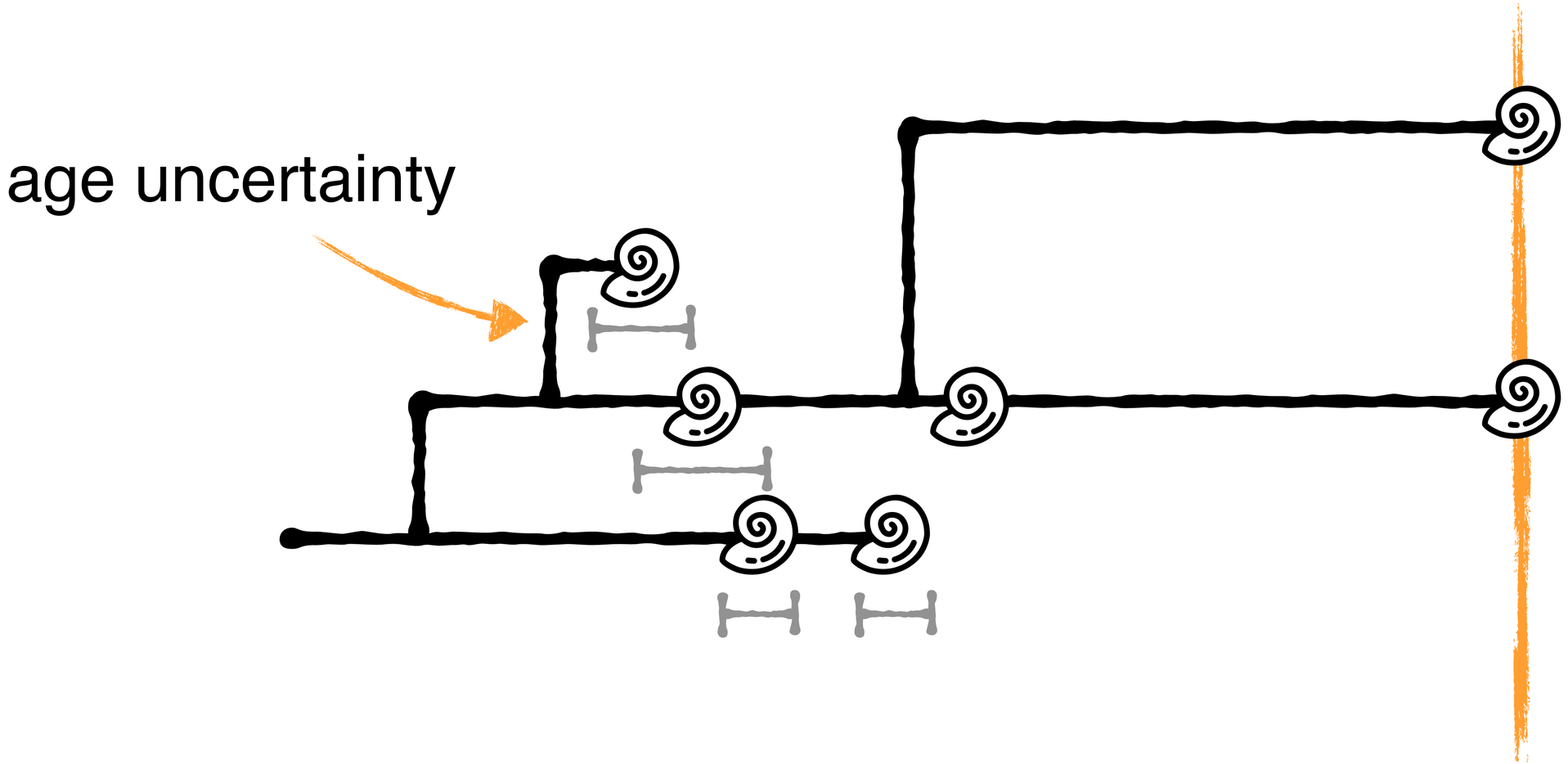


First application of total evidence dating using the FBD model

Fossils are incorporated using character data

Gavryushkina et al. (2016)

Sample age uncertainty



Ignoring stratigraphic age uncertainty leads to erroneous estimates of species divergence times and topology

Barido-Sottani et al. (2018, 2020)

Fossils as data

Phylogeny with branch lengths in units of time

Clock model

Morphological character model

FBD model parameters

Fossil age information

011001
010001
001011
101100
Morphological characters

Posterior distribution

$$P(\Psi, \rho, \gamma, \psi, \mathbf{M} \mid \mathbf{D}) =$$

Likelihood **FBD** **Prior Probabilities**

$$\frac{P(\mathbf{D} \mid \Psi, \mathbf{M})\, P(\mathbf{D} \mid \rho, \gamma, \psi)\, P(\Psi \mid \rho, \gamma, \psi)\, P(\rho, \gamma, \psi)\, P(\mathbf{M})}{P(\mathbf{D})}$$

Marginal Likelihood



Diversification models conflate likelihood and prior, and cannot be compared using conventional model-comparison tools

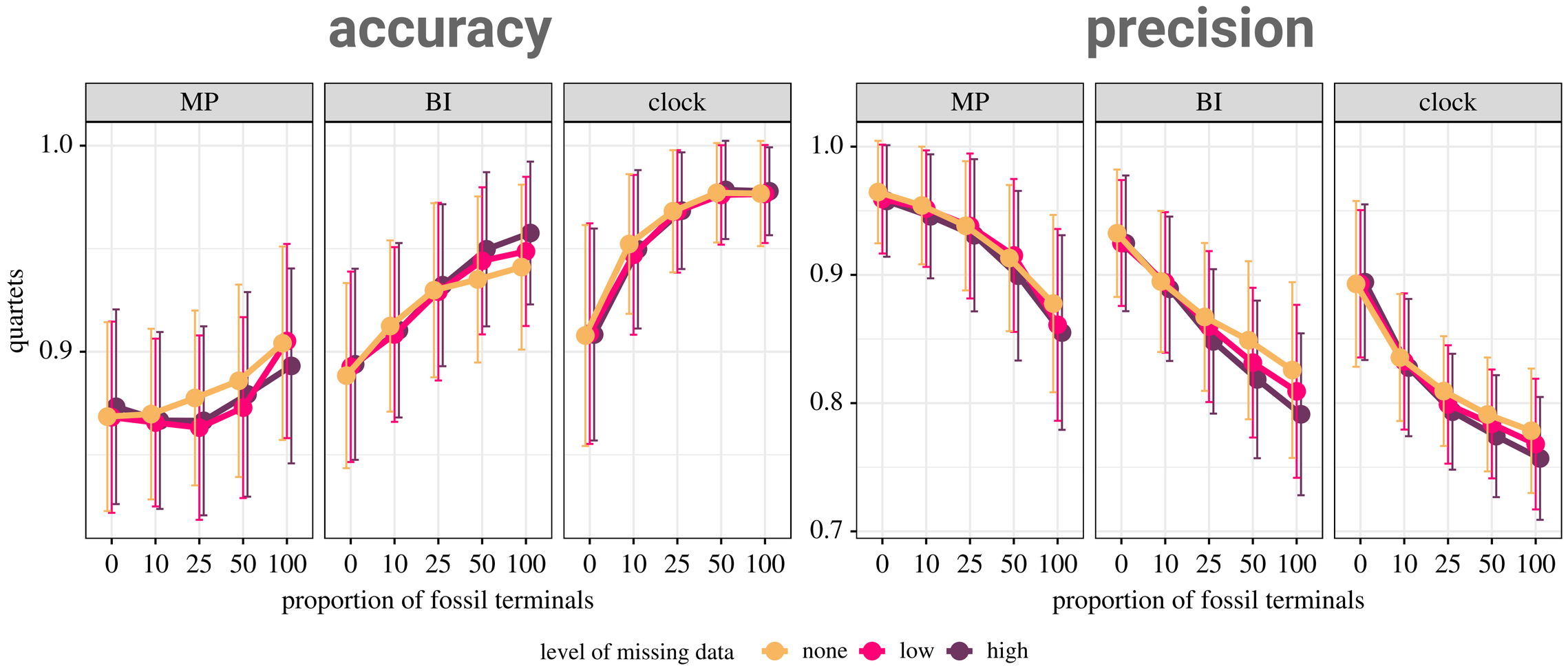
May & Rothfels (2023) *Sys Bio*

Image *Mulvey et al.* (2025) *Paleobiology*

Other lessons learned from simulations

- The topology of extant taxa is largely unaffected by how fossils are incorporated
- Fossils and age information help inform topology
- Divergence times are much more sensitive to **errors in fossil placement** and model misspecification
- Total-evidence dating is more robust to model misspecification

Ignoring stratigraphic age uncertainty leads to erroneous estimates of species divergence times and topology
Barido-Sottani et al. (2019, 2020) *Proc Royal Soc B; Frontiers in Ecology and Evolution.*
Barido-Sottani et al. (2023) *Putting the F in FBD analyses: tree constraints or morphological data? Palaeontology*

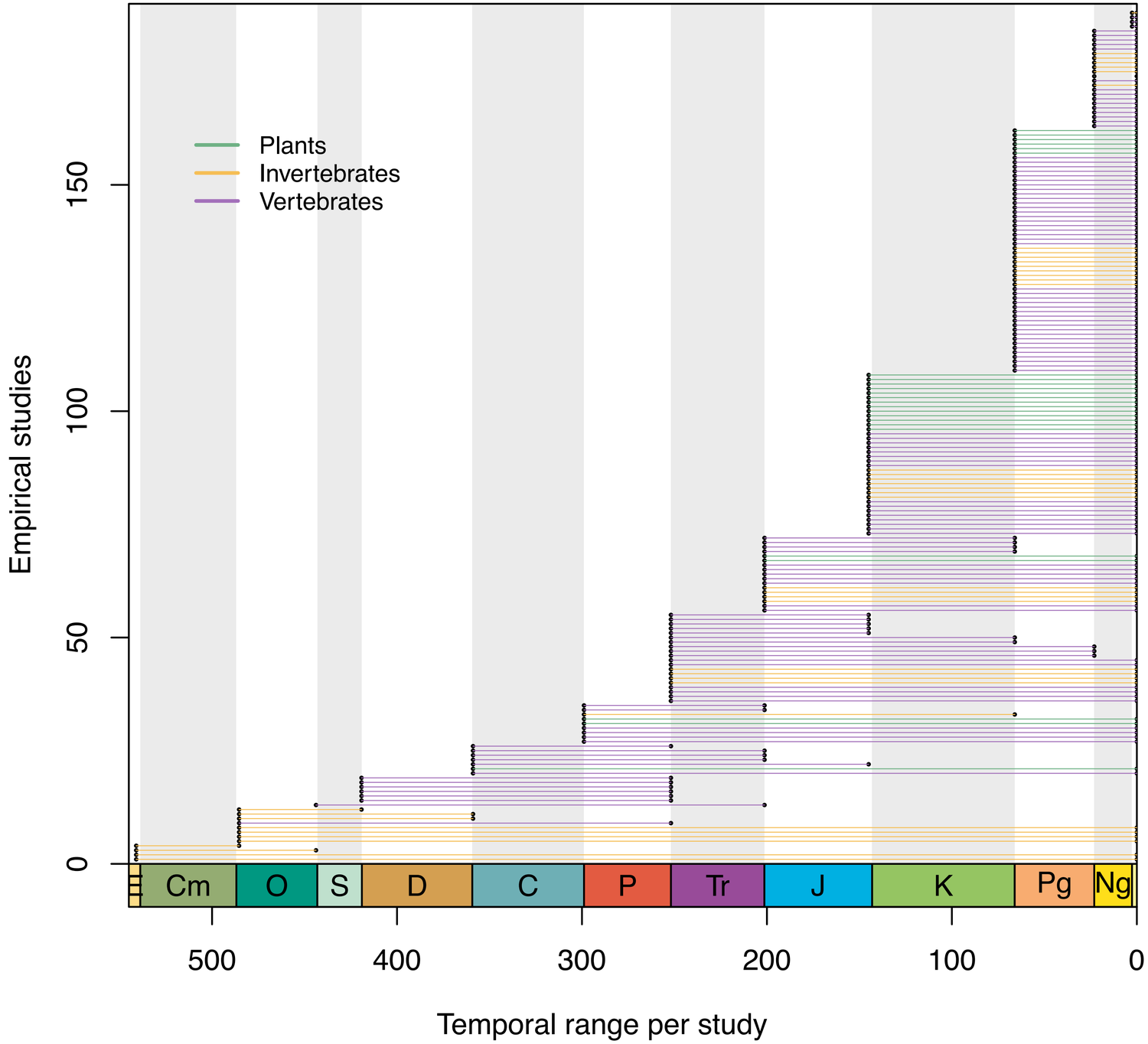


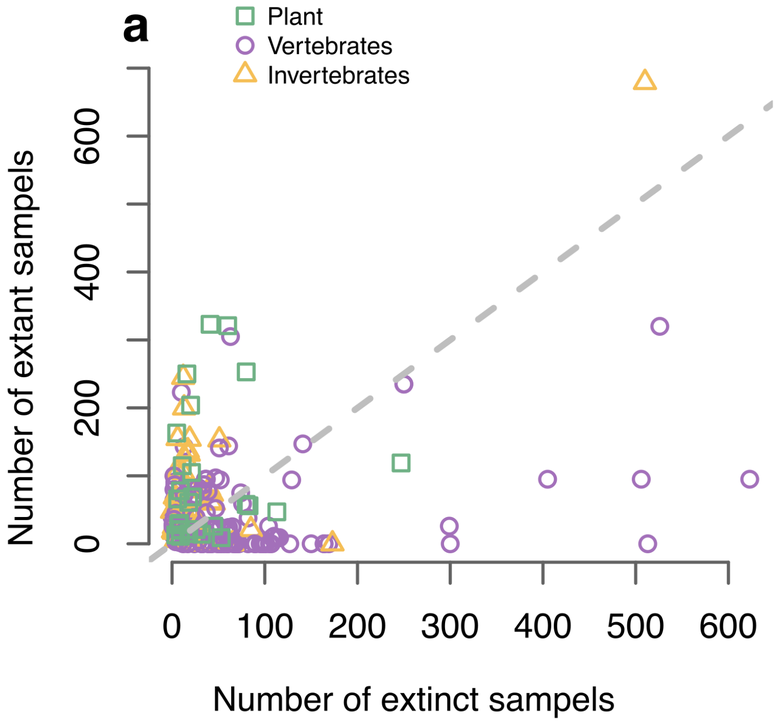
Fossils improve phylogenetic analyses of morphological characters
Koch, Garwood, Parry (2020) *Proc B*

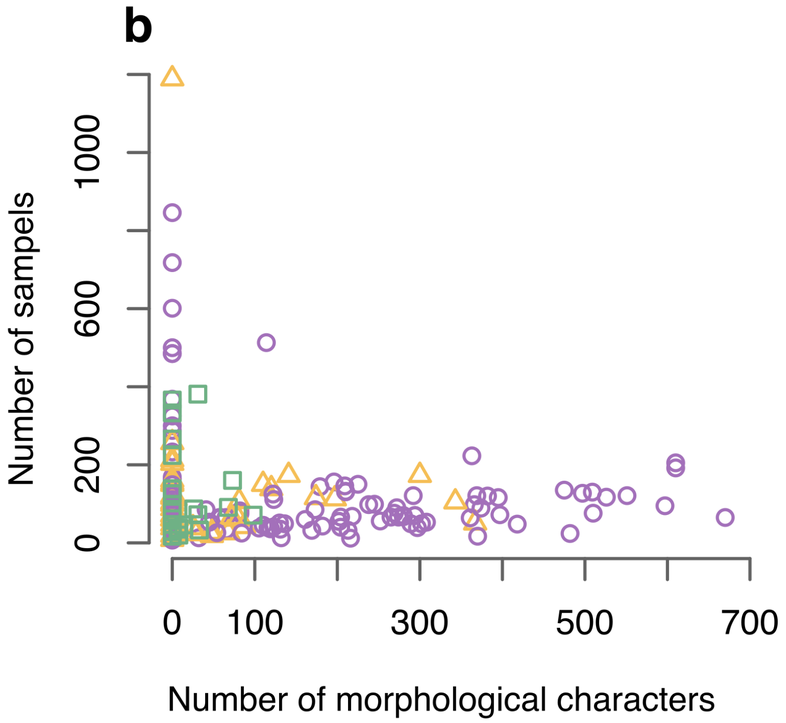
Literature survey: FBD use to date

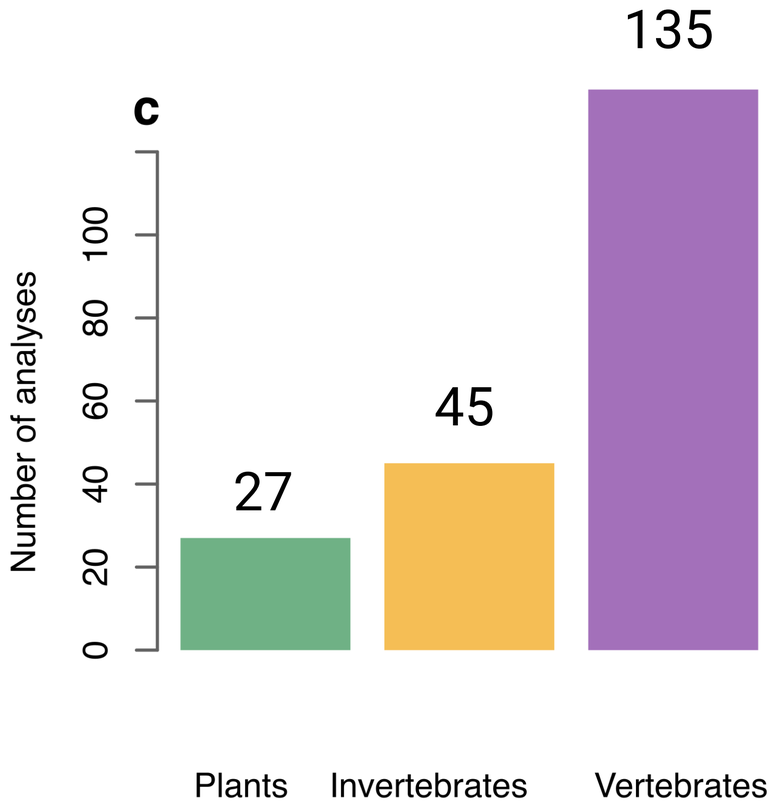
- 176 studies, with 208 empirical analyses, applying the FBD process (since February 2024)
- Used across a huge range of time intervals, data sets (mean extant samples = 74, mean extinct samples = 60)
- 109 studies used BEAST2, 93 used MrBayes, 10 used RevBayes

Mulvey et al. (2025) *Paleobiology*


Plants
Invertebrates
Vertebrates
Empirical studies
0
50
100
150
Cm
O
S
D
C
P
Tr
J
K
Pg
Ng
500
400
300
200
100
0
Temporal range per study

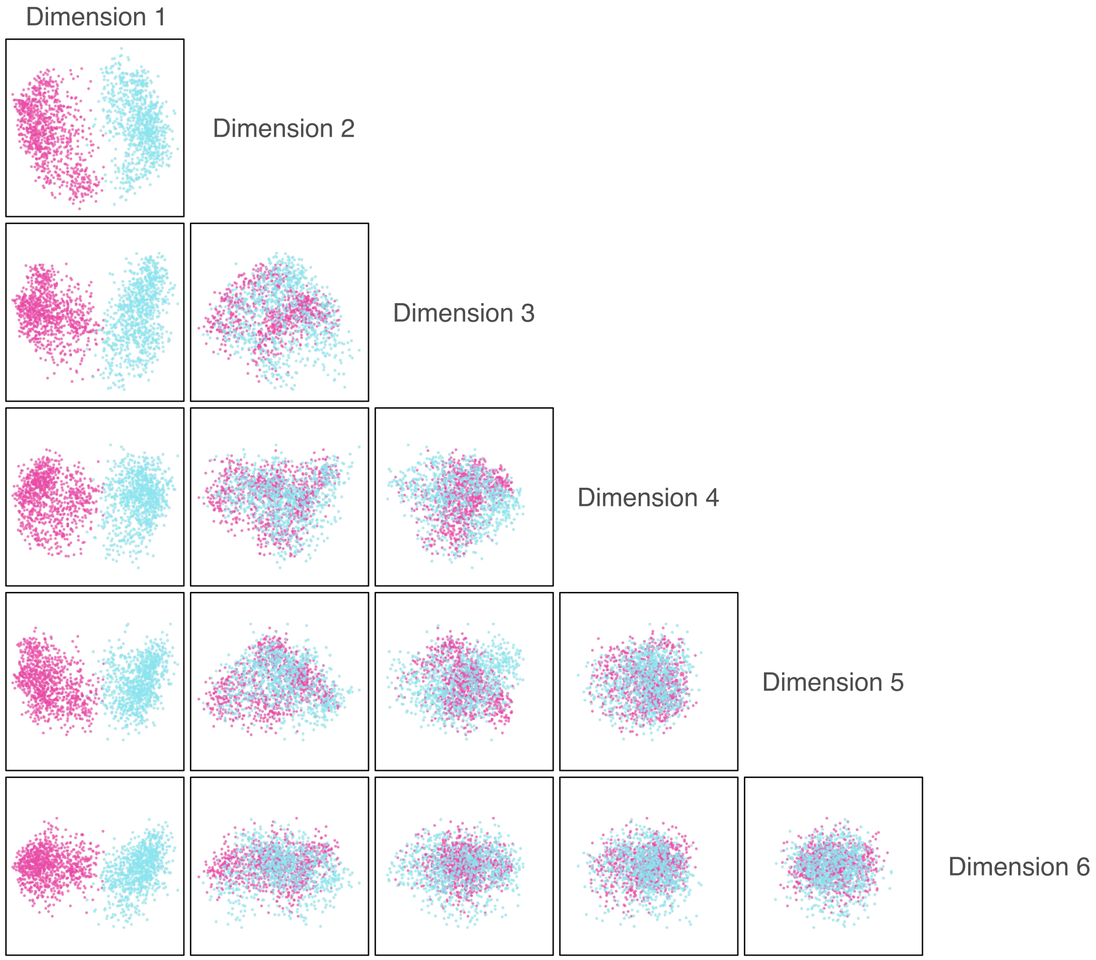

a
Plant
Vertebrates
Invertebrates
Number of extant sampels
0
200
400
600
0
100
200
300
400
500
600
Number of extinct sampels


b
Number of sampels
0
200
600
1000
0
100
300
500
700
Number of morphological characters


c
Number of analyses
0
20
40
60
80
100
27
45
135
Plants
Invertebrates
Vertebrates

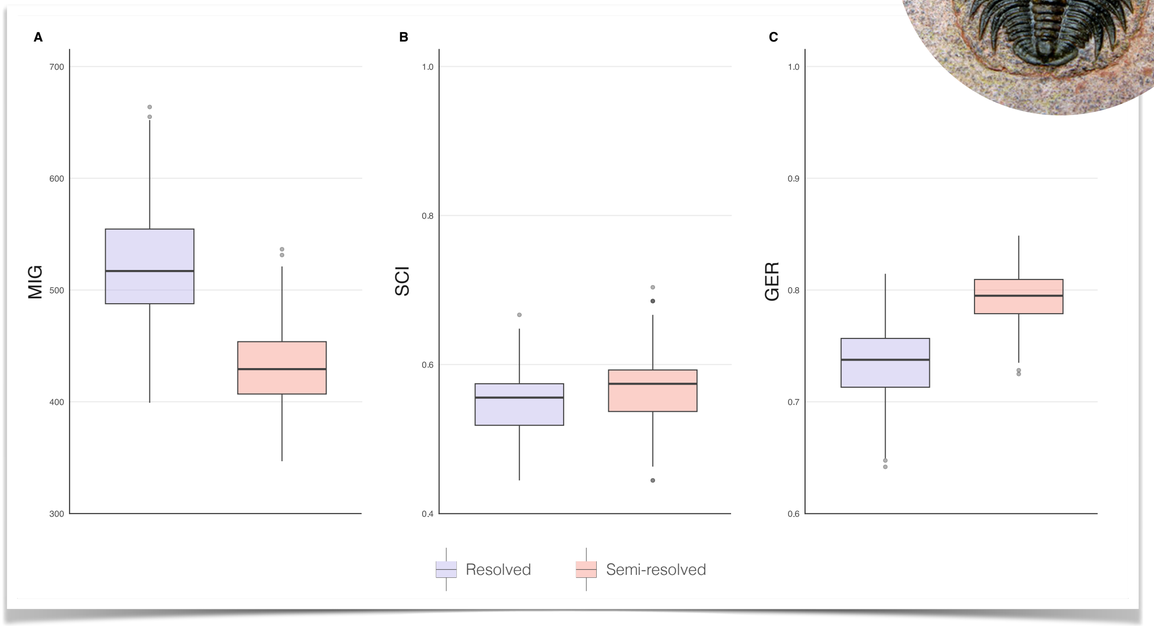
Analysis type	Phylogenetic data			No. of analyses
	Molecular	Morphology	Morphology†	
Total evidence	✓	✓	✓	53
Extant only	✓			78
Morphology		✓	✓	26
Extinct only			✓	35
No phylogenetic data				16

Including samples with no character data improves inference



Trees occupy different regions of tree space

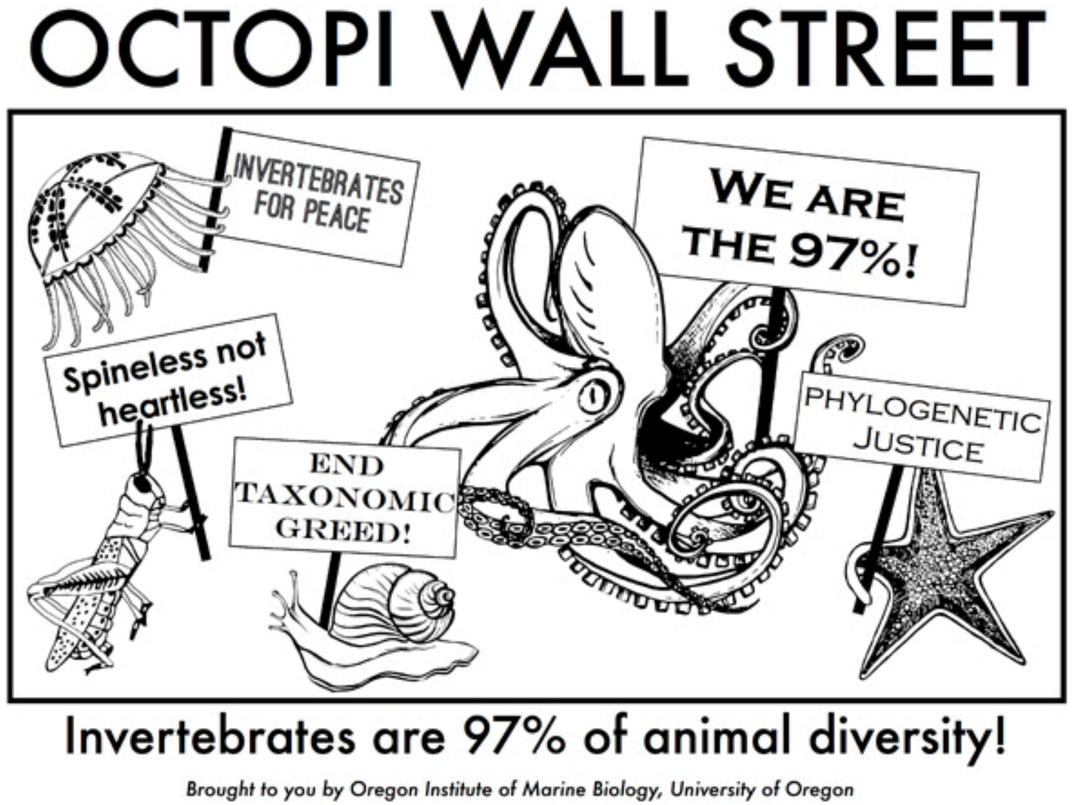




And show worse / better correspondence with the fossil record

Nikolic et al. (2025)

FBD analyses
need taxonomists!



*“It is, it must be admitted, a **humbling** task to infer ancient events, and the results in many cases are tenuous at best. Given the obvious limitations of working with extant species and few, if any, fossils, **it is necessary to integrate all of the available sources of evidence** if we hope to produce assuring answers.”*

Landis et al. (2023) *Systematic Biology*
Joint phylogenetic estimation of geographic movements and biome shifts

More details in extra slides

Short break



Exercise

Further reading

- From fossils to phylogenies: exploring the integration of paleontological data into Bayesian phylogenetic inference *Mulvey et al*. (2025)
- Integrating fossil observations into phylogenetics using the fossilized birth-death model. *Wright et al.* (2022)
- Unifying birth-death models in epidemiology and macroevolution. *MacPherson et al.* (2022)

Extra slides

Joint phylogenetic estimation of geographic movements and biome shifts

Landis et al. (2023) *Systematic Biology*









Global diversity of *Viburnum*

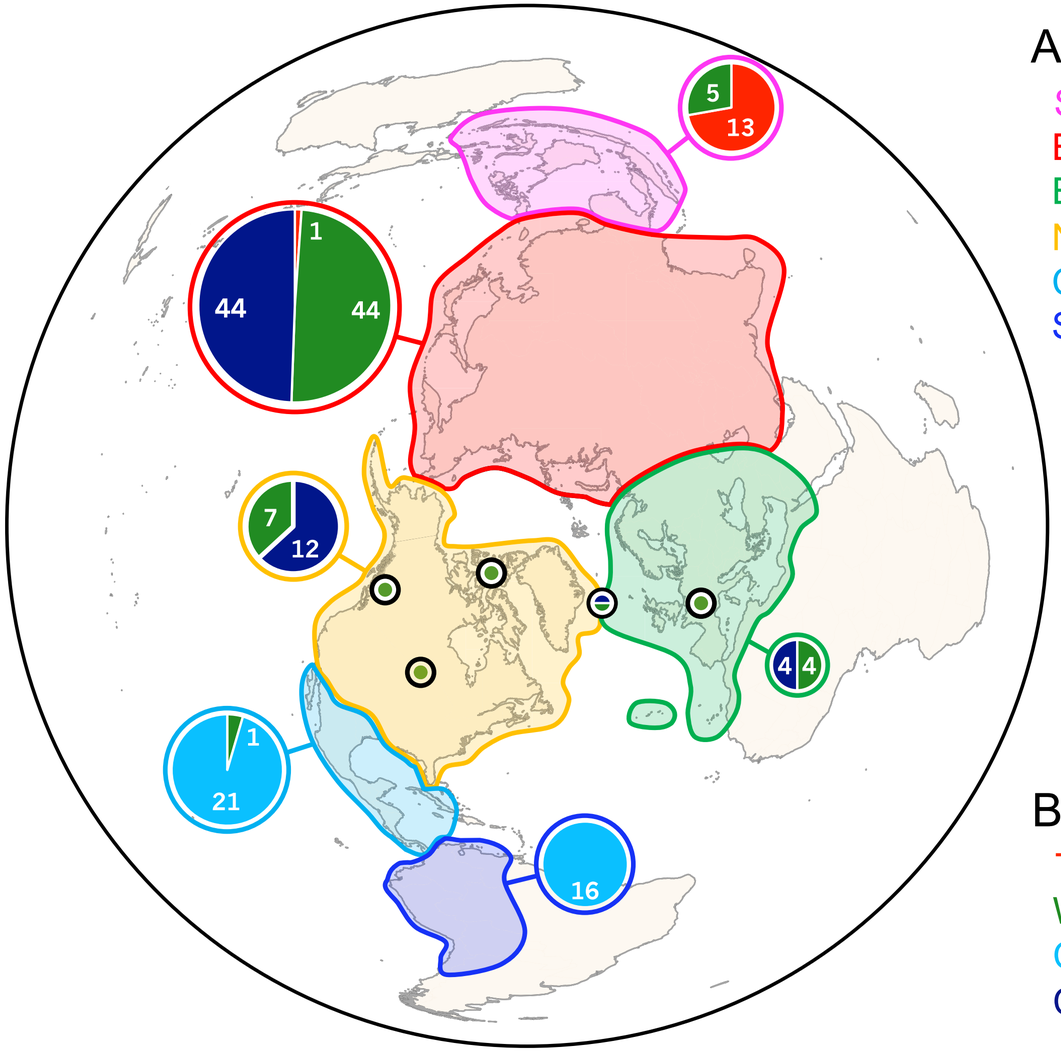
Data

163 extant species (127 with DNA)

5 fossils (with taxonomic constraints)

6 geographic areas

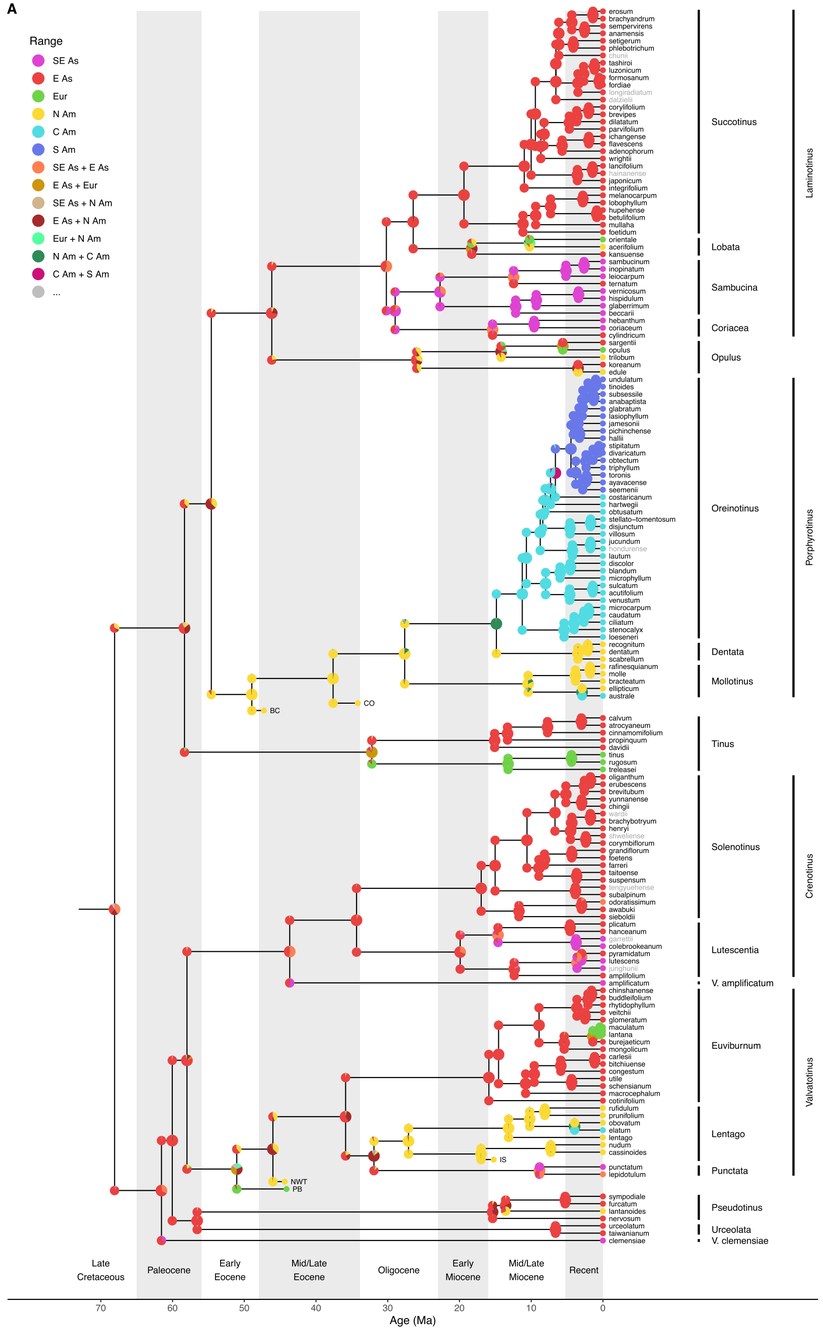
4 biomes

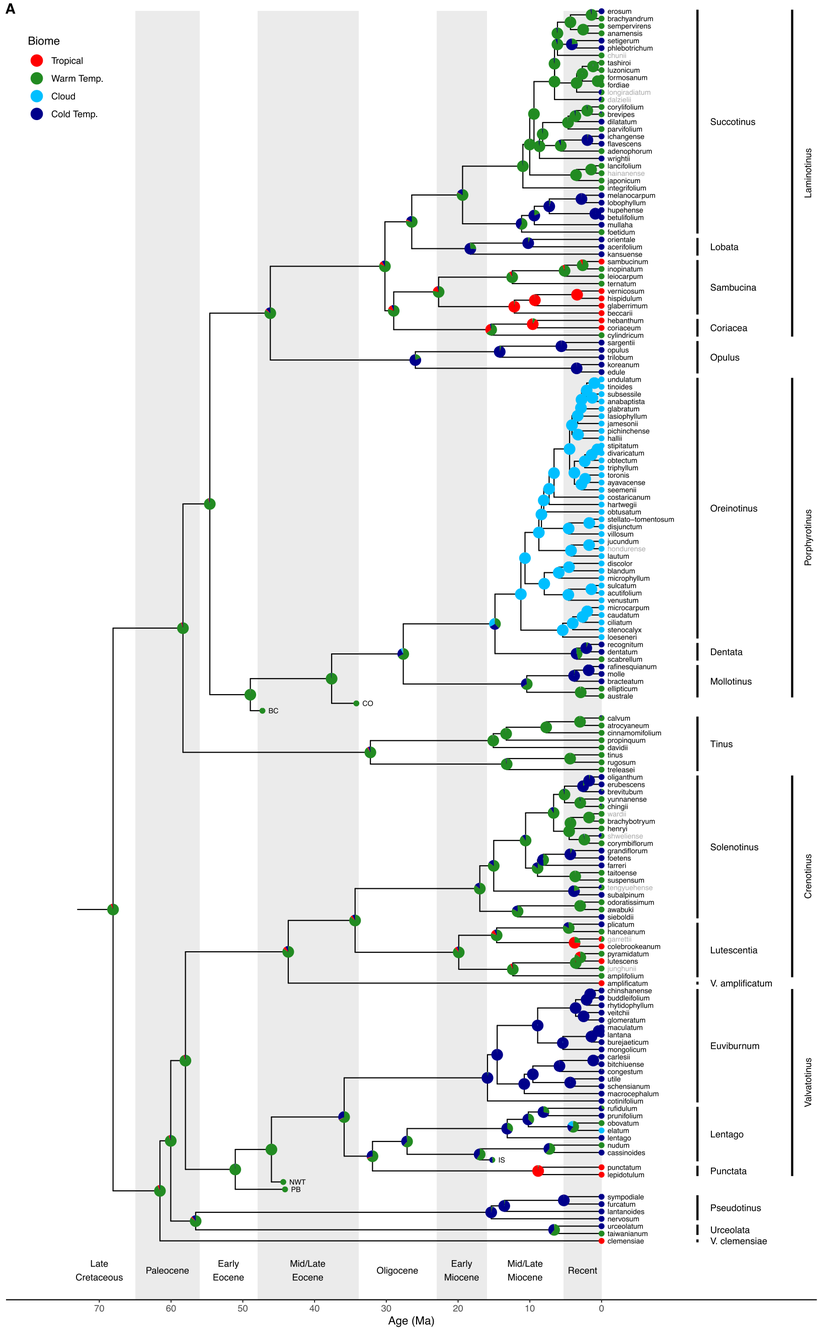


- Can we integrate **geographic range** and **biome data** into analysis using the FBD model?
- What can we learn about the **diversification history** of the *Viburnum*?

Analysis

1. Estimate the extant topology using maximum likelihood
2. Joint inference divergence times, biogeographic and biome history (normally we *first* infer a dated tree, and *then* separately infer biogeographic history)
3. Ancestral state reconstruction
4. + various sensitivity analyses


A
Range
SE As
E As
Eur
N Am
C Am
S Am
SE As + E As
E As + Eur
SE As + N Am
E As + N Am
Eur + N Am
N Am + C Am
C Am + S Am
...
Laminotinus
Succotinus
Lobata
Sambucina
Coriacea
Opulus
Porphyrotinus
Oreinotinus
Dentata
Mollotinus
Crenotinus
Tinus
Solenotinus
Lutescentia
V. amplificatum
Valvatotinus
Euviburnum
Lentago
Punctata
Pseudotinus
Urceolata
V. clemensiae
BC
CO
NWT
PB
IS
Late Cretaceous
Paleocene
Early Eocene
Mid/Late Eocene
Oligocene
Early Miocene
Mid/Late Miocene
Recent
70
60
50
40
30
20
10
0
Age (Ma)


A
Biome
Tropical
Warm Temp.
Cloud
Cold Temp.
Laminotinus
Succotinus
Lobata
Sambucina
Coriacea
Opulus
Porphyrotinus
Oreinotinus
Dentata
Mollotinus
Crenotinus
Tinus
Solenotinus
Lutescentia
V. amplificatum
Valvatotinus
Euviburnum
Lentago
Punctata
Pseudotinus
Urceolata
V. clemensiae
BC
CO
NWT
PB
IS
Late Cretaceous
Paleocene
Early Eocene
Mid/Late Eocene
Oligocene
Early Miocene
Mid/Late Miocene
Recent
70
60
50
40
30
20
10
0
Age (Ma)

Results summary

- Joint inference using the FBD and biogeographic models allows us to estimate a rich diversification history
- Major lineages of *Viburnum* likely originated in warm / temperate regions and later adapted to the cold
- Fossils can change the results

