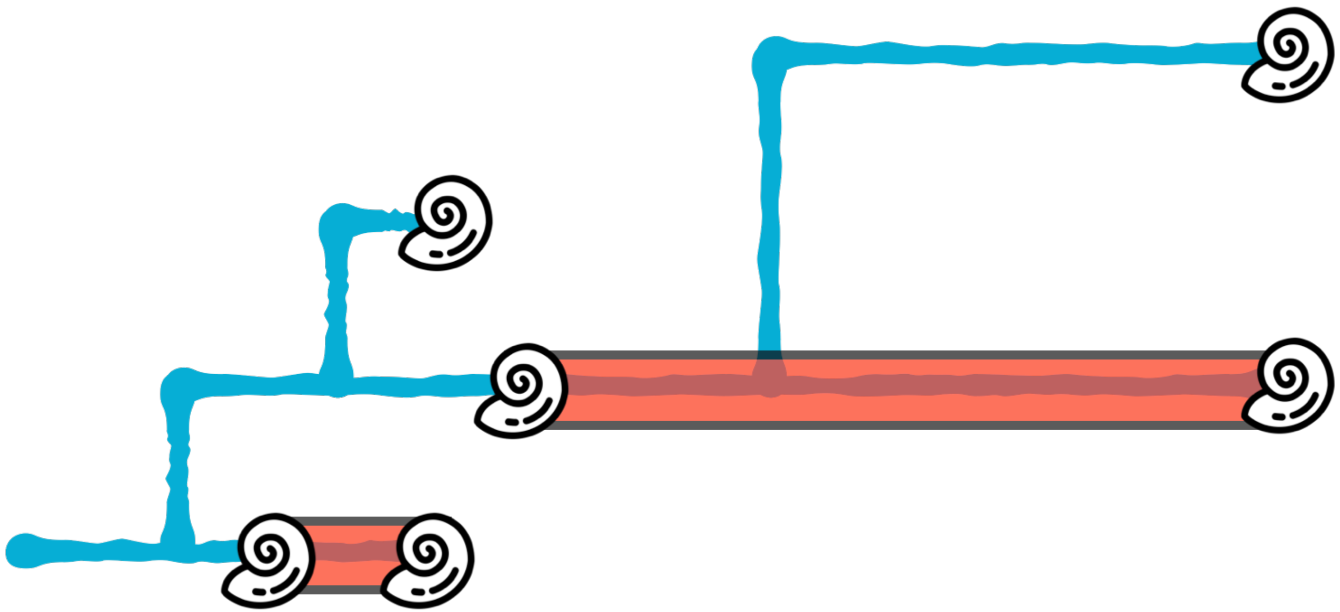
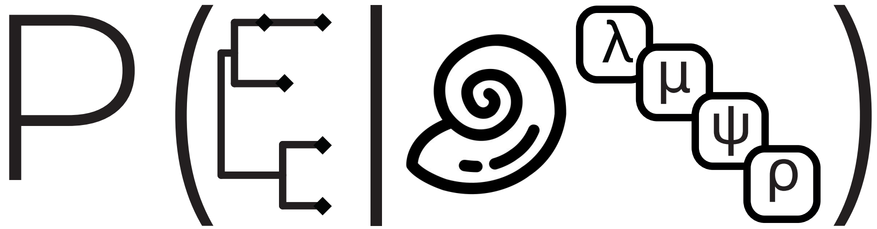




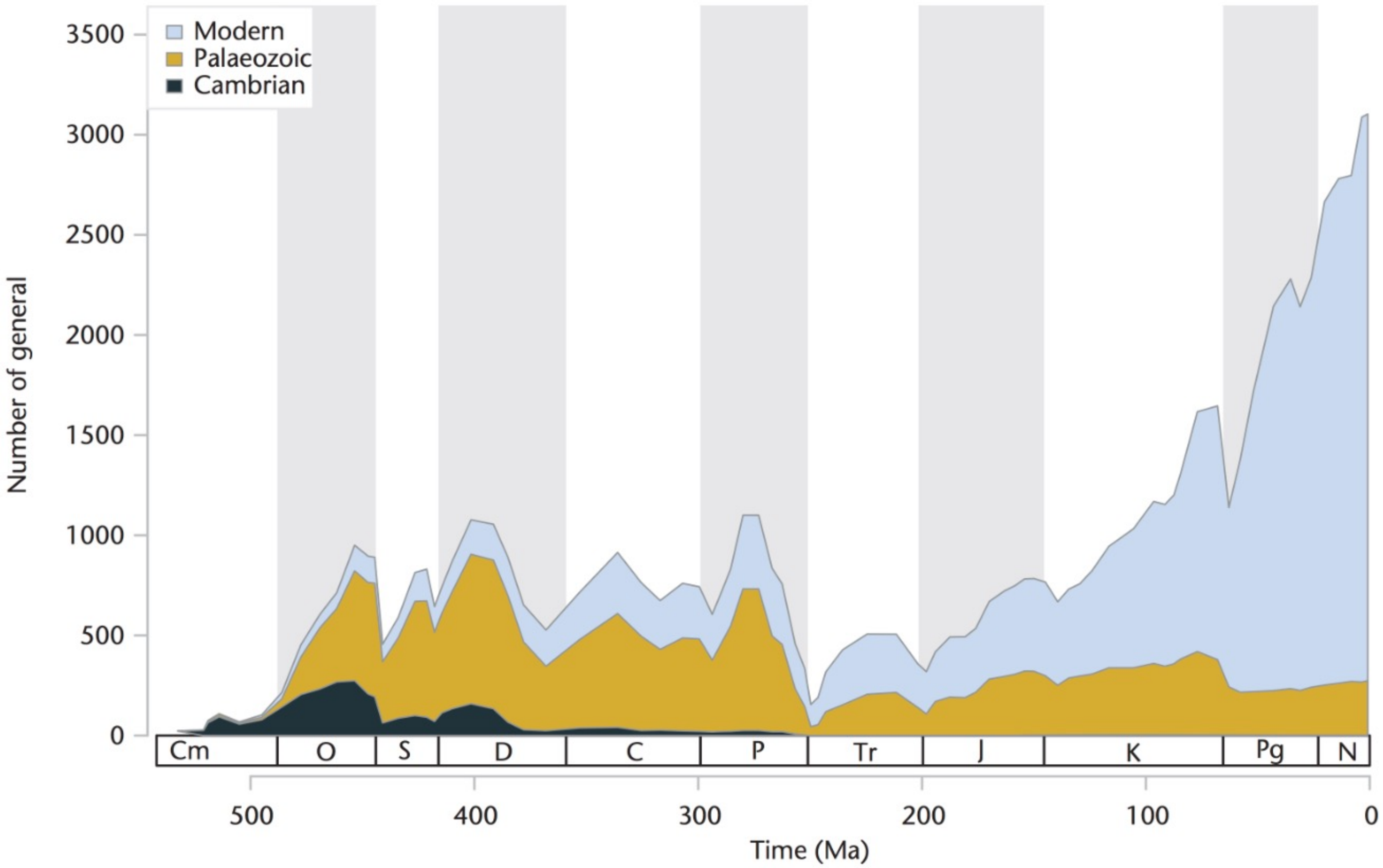
The Fossilized Birth-Death Process:

Application in Palaeontology

Laura Mulvey

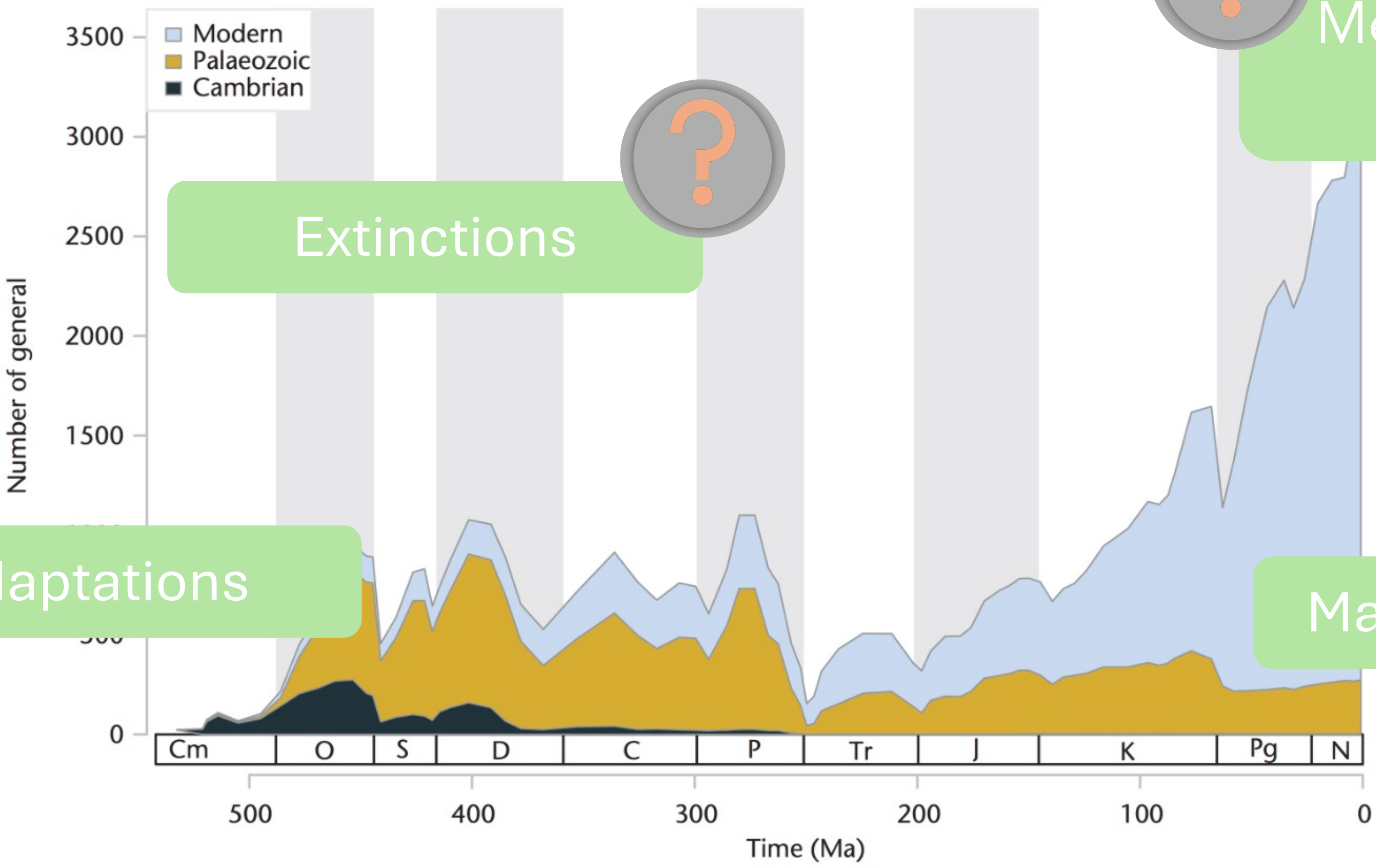
(slides adapted from Rachel Warnock)

Evolutionary processes in the fossil record



Simpson et al 2010

Evolutionary processes in the fossil record



?

Mechanisms of evolution

?

Extinctions

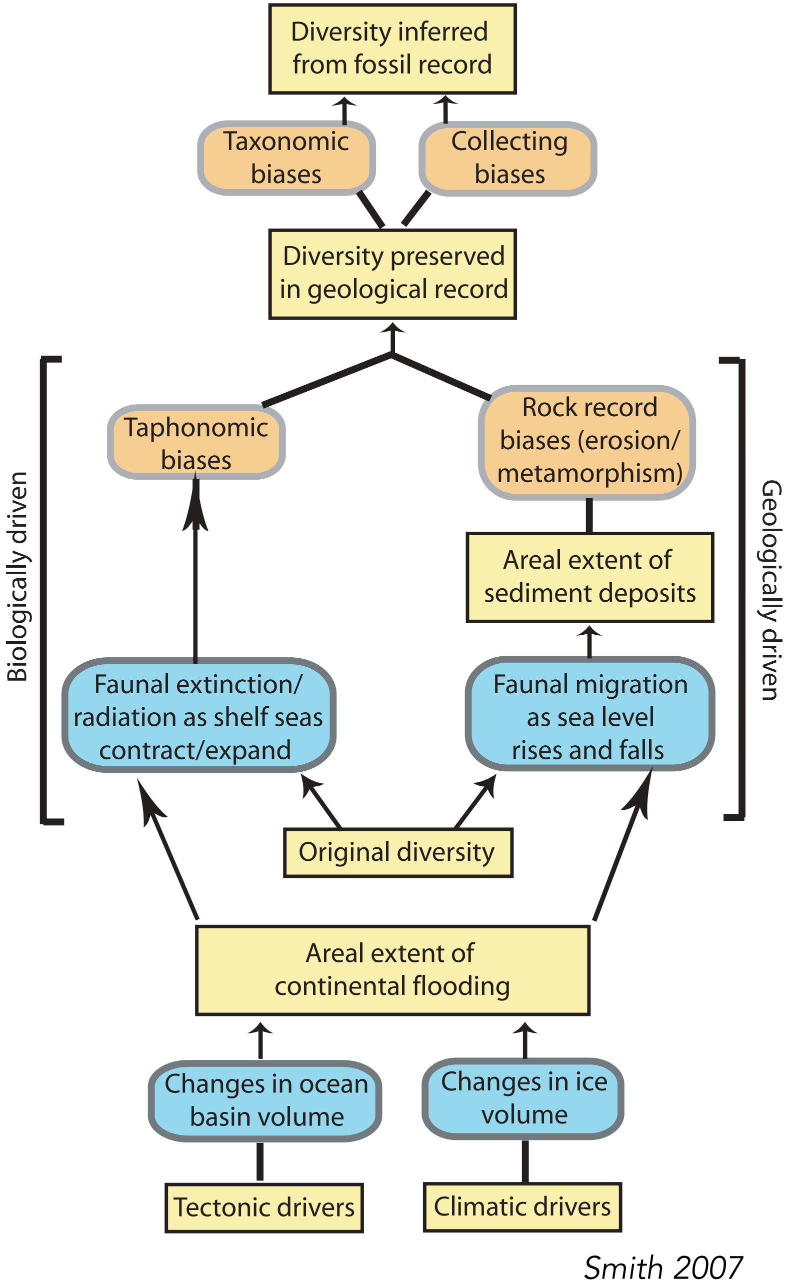
?

Adaptations

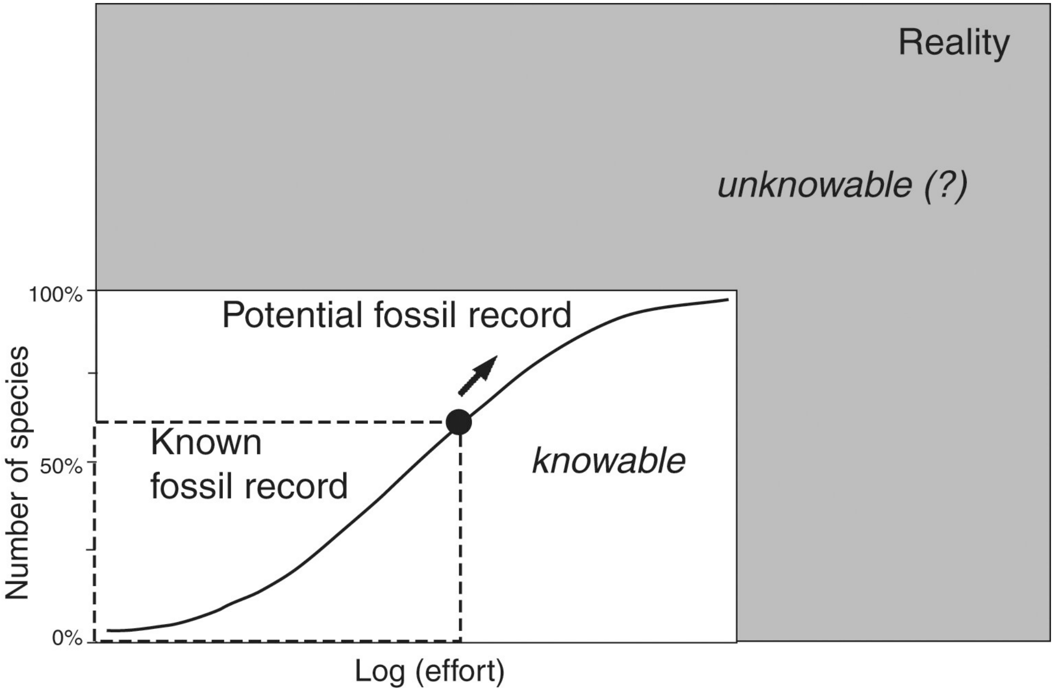
?

Major transitions

Simpson et al 2010



Smith 2007

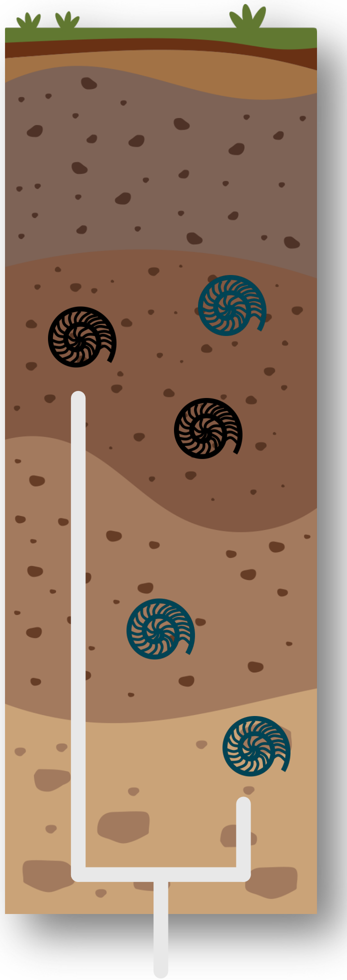


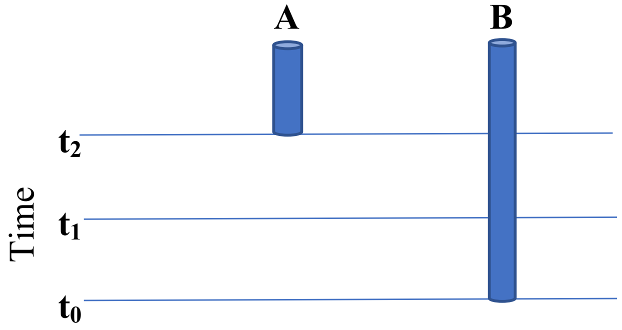
Benton et al 2011

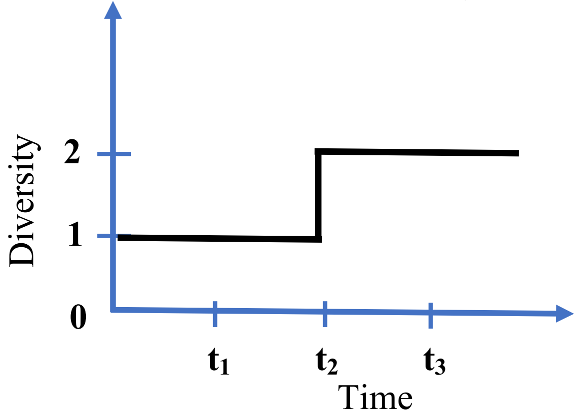
There are a number of **analytical approaches** available for disentangling the true biological signal from signals produced by the geology/sampling

How is phylogenetics useful in palaeontology?

Gaps in the fossil record

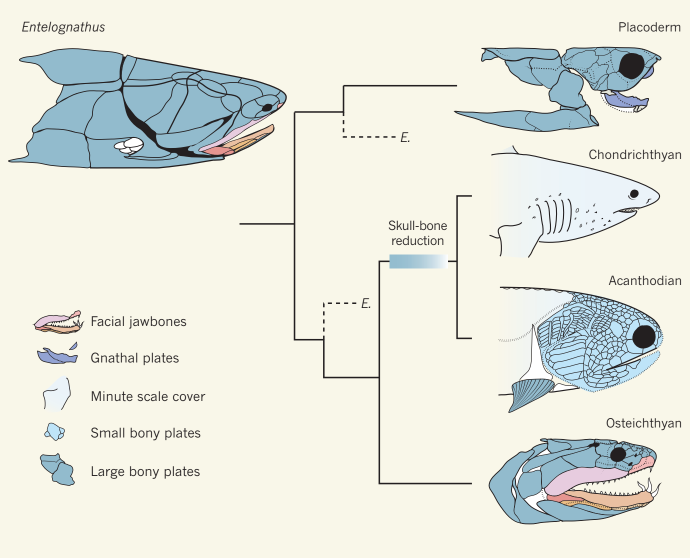



Uncorrected Fossil Data Lineages


Uncorrected Diversity Curve

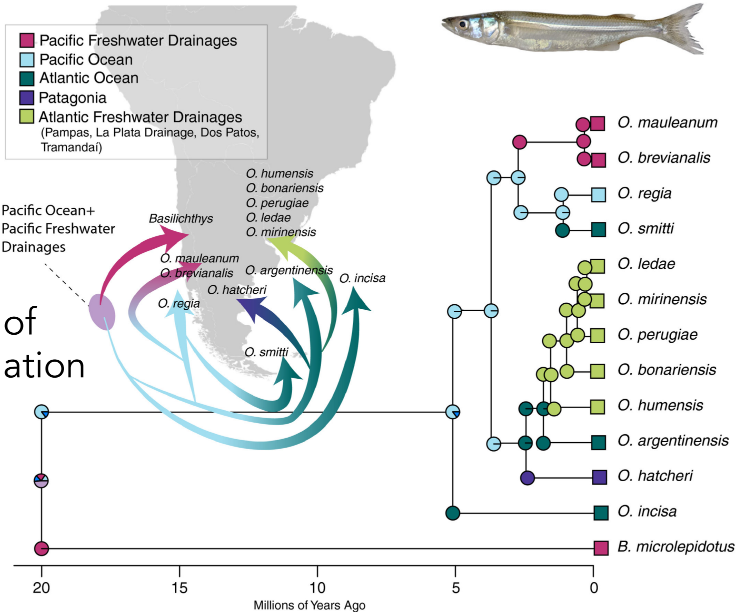
Bokulich 2017

Trait evolution



Friedman et al 2013

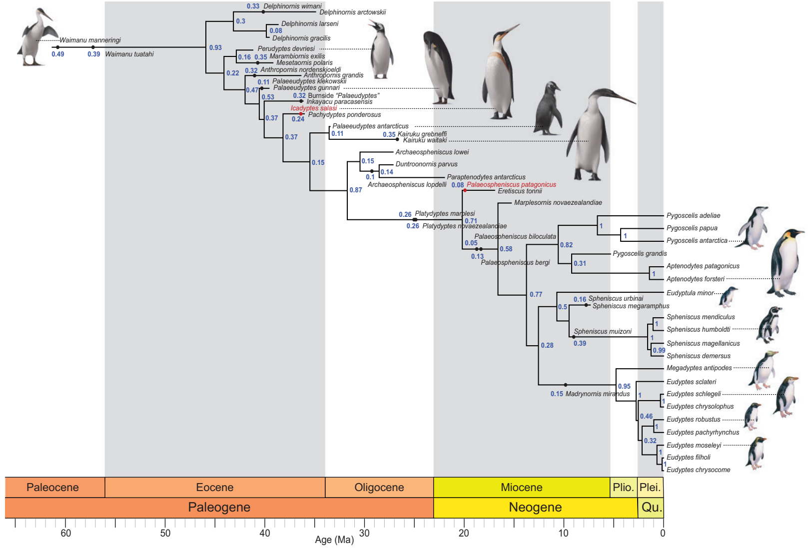
Biogeography movements



Point of origination

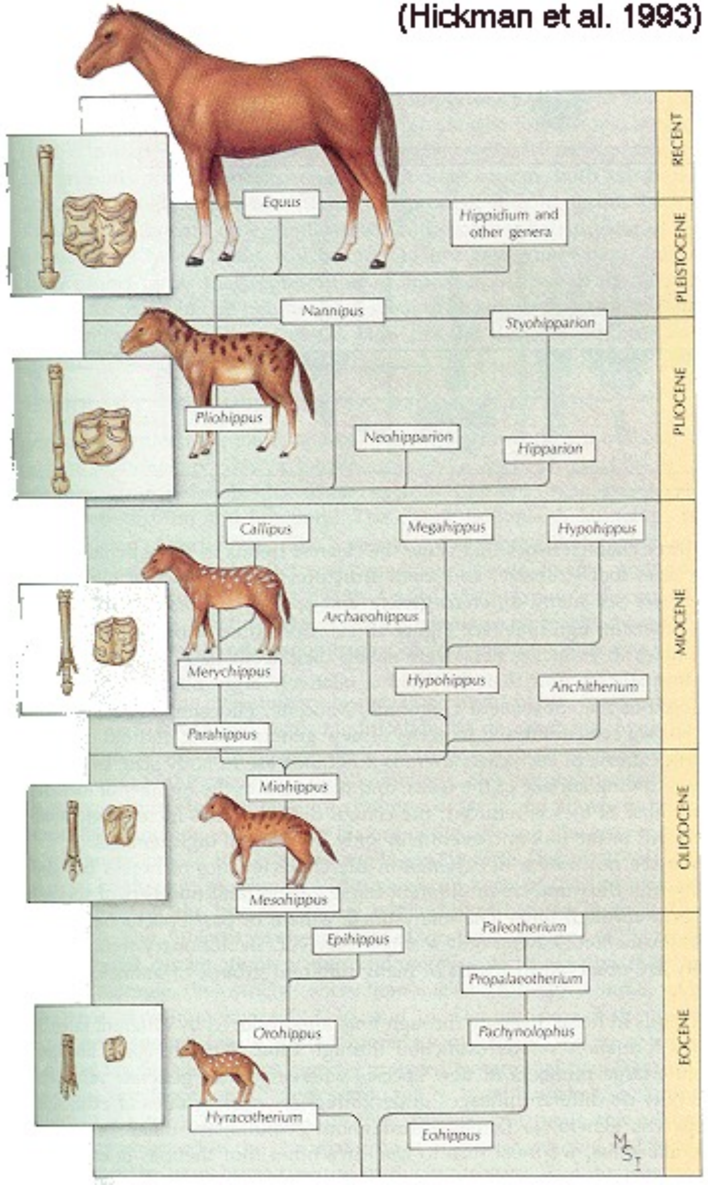
Hughes et al 2020

Relationships of extinct and extant taxa



Gavryushkina et al 2017

The fossil record provides direct evidence of past events and the time at which they occurred



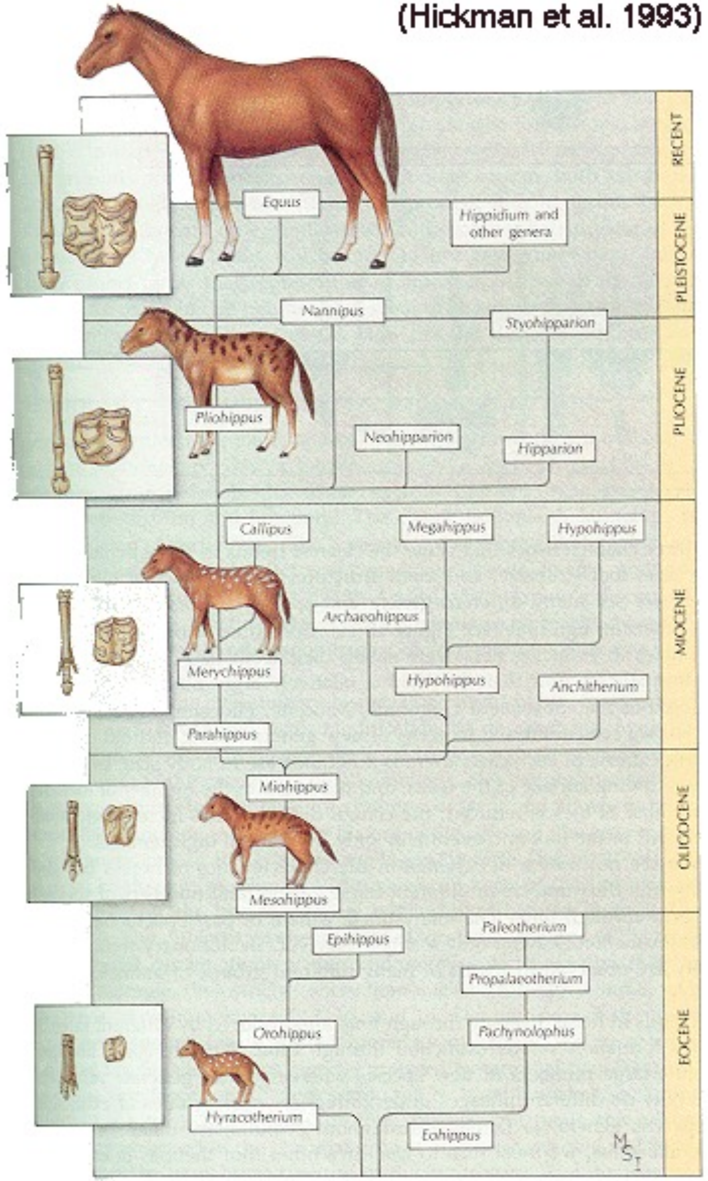
(Hickman et al. 1993)

Morphology

The fossil record provides direct evidence of past events and the time at which they occurred

Fossil calibrations

(Hickman et al. 1993)



The data

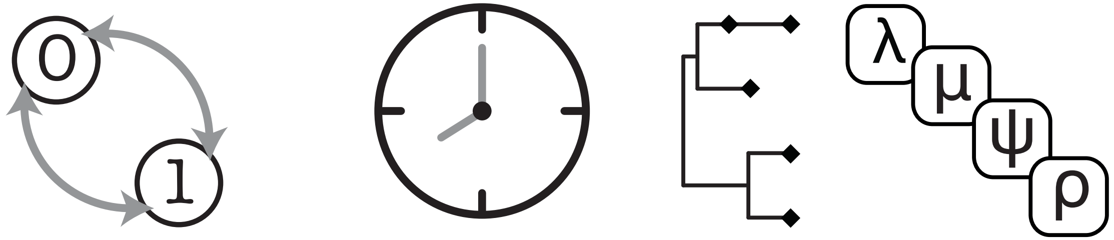
AND/OR

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

Phylogenetic characters

Fossil ages

Tripartite model components



Substitution model

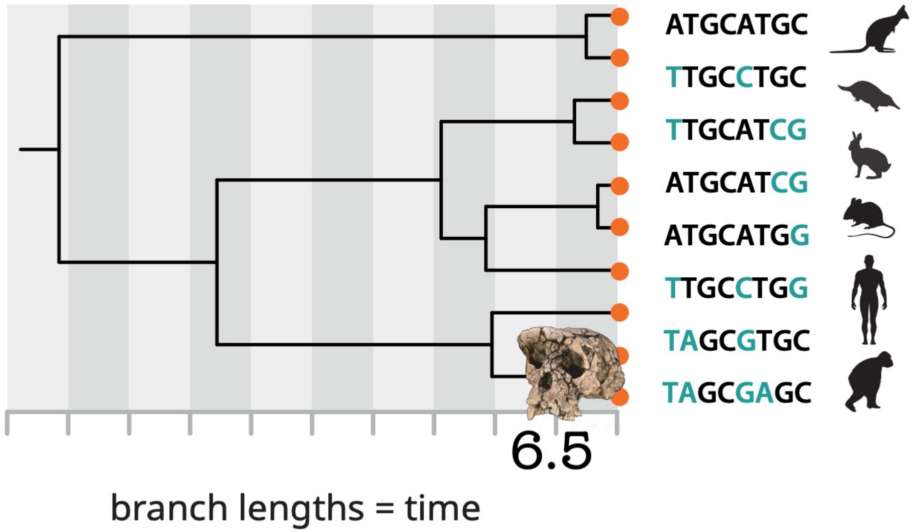
Clock model

Tree and tree model

Warnock & Wright. 2020

Molecular (or morphological) characters are not independently informative about time

Goal: to disentangle evolutionary rate and time



The data

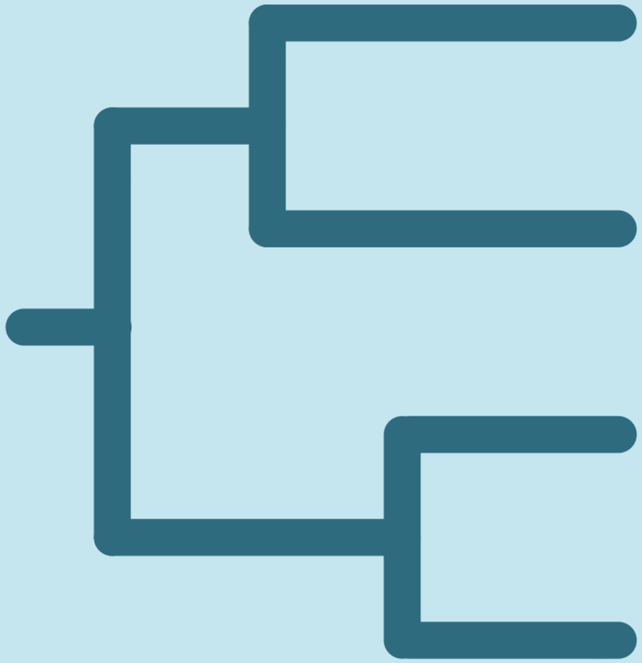
AND/OR

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

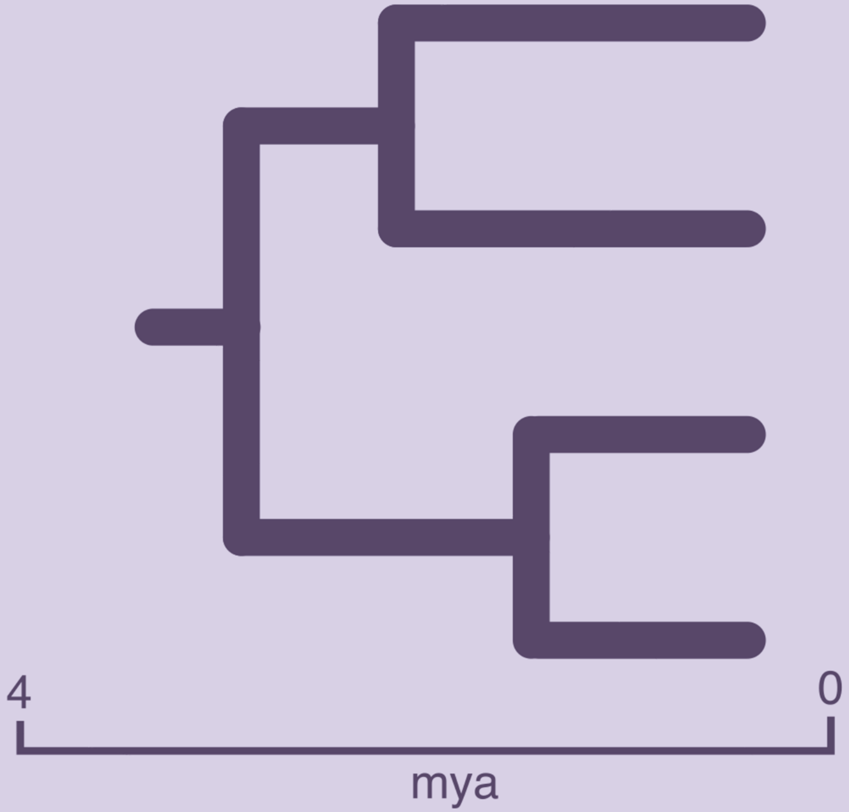
Phylogenetic characters

Fossil ages

Temporal evidence of divergence for one species pair let's us calibrate the average rate of molecular evolution

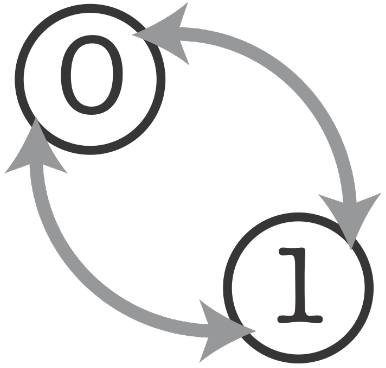


branch lengths in genetic distance



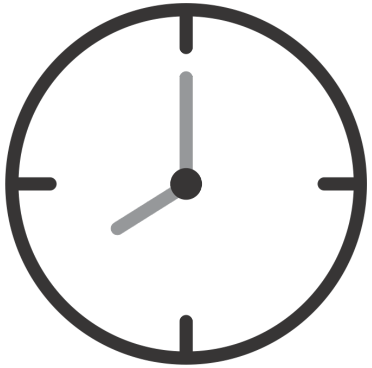
branch lengths in time

substitution model

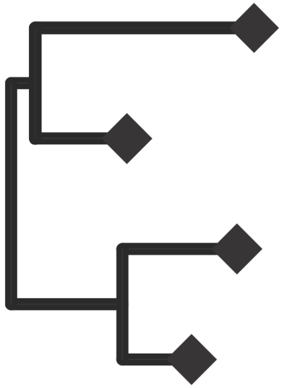


This will be covered tomorrow!

clock model

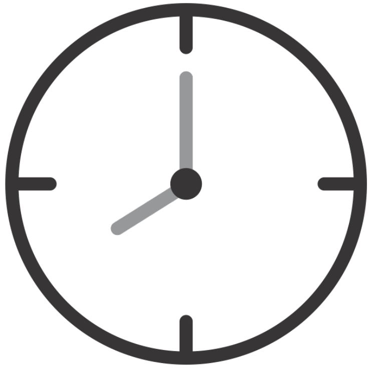


tree model



*A model refers to a set of assumptions the describe the evolutionary processes and mechanisms that produced our data

clock model

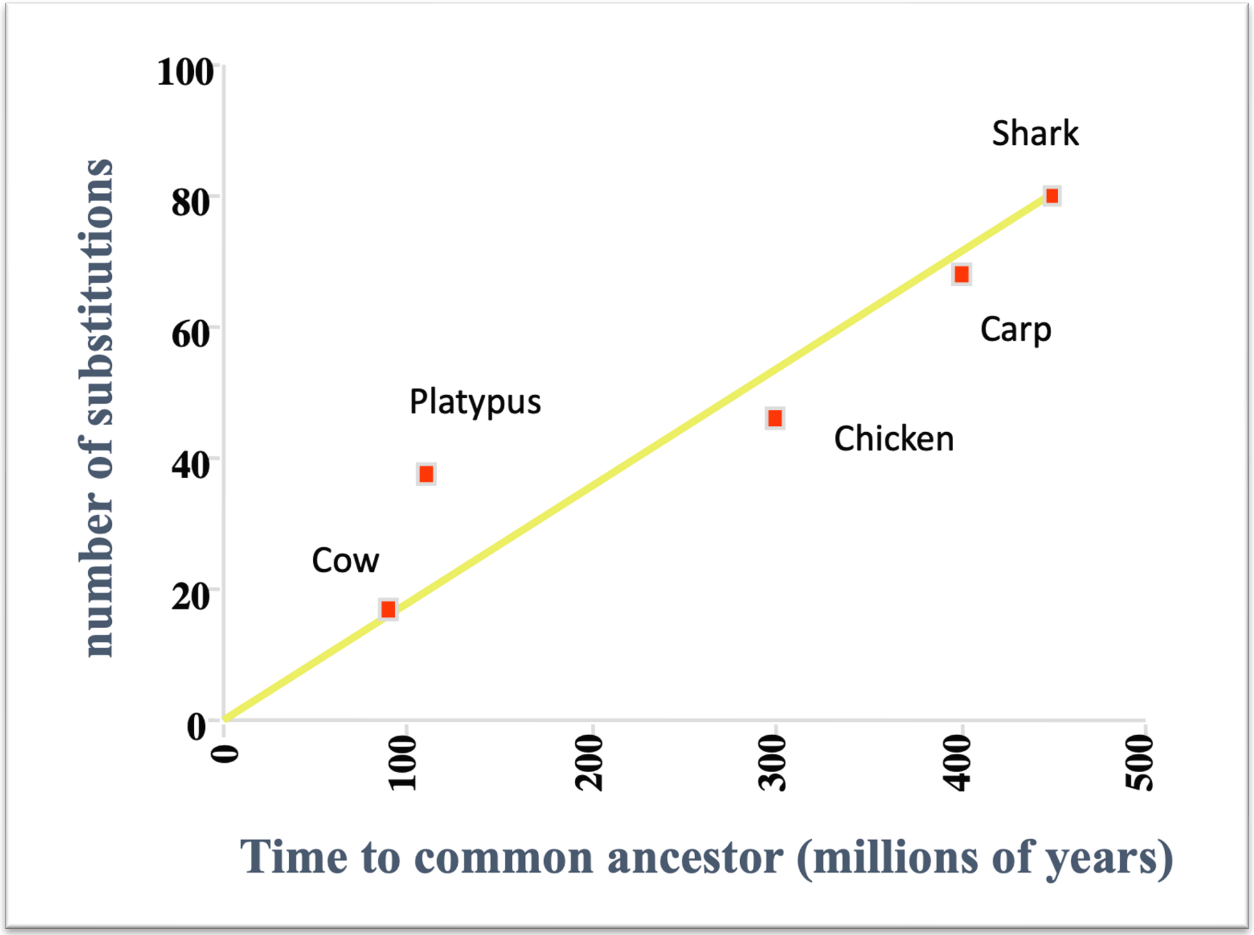


*A model refers to a set of assumptions the describe the evolutionary processes and mechanisms that produced our data

Clock model

The idea of a molecular clock was initially suggested by Zuckerkandl and Pauling in 1962 and 1965

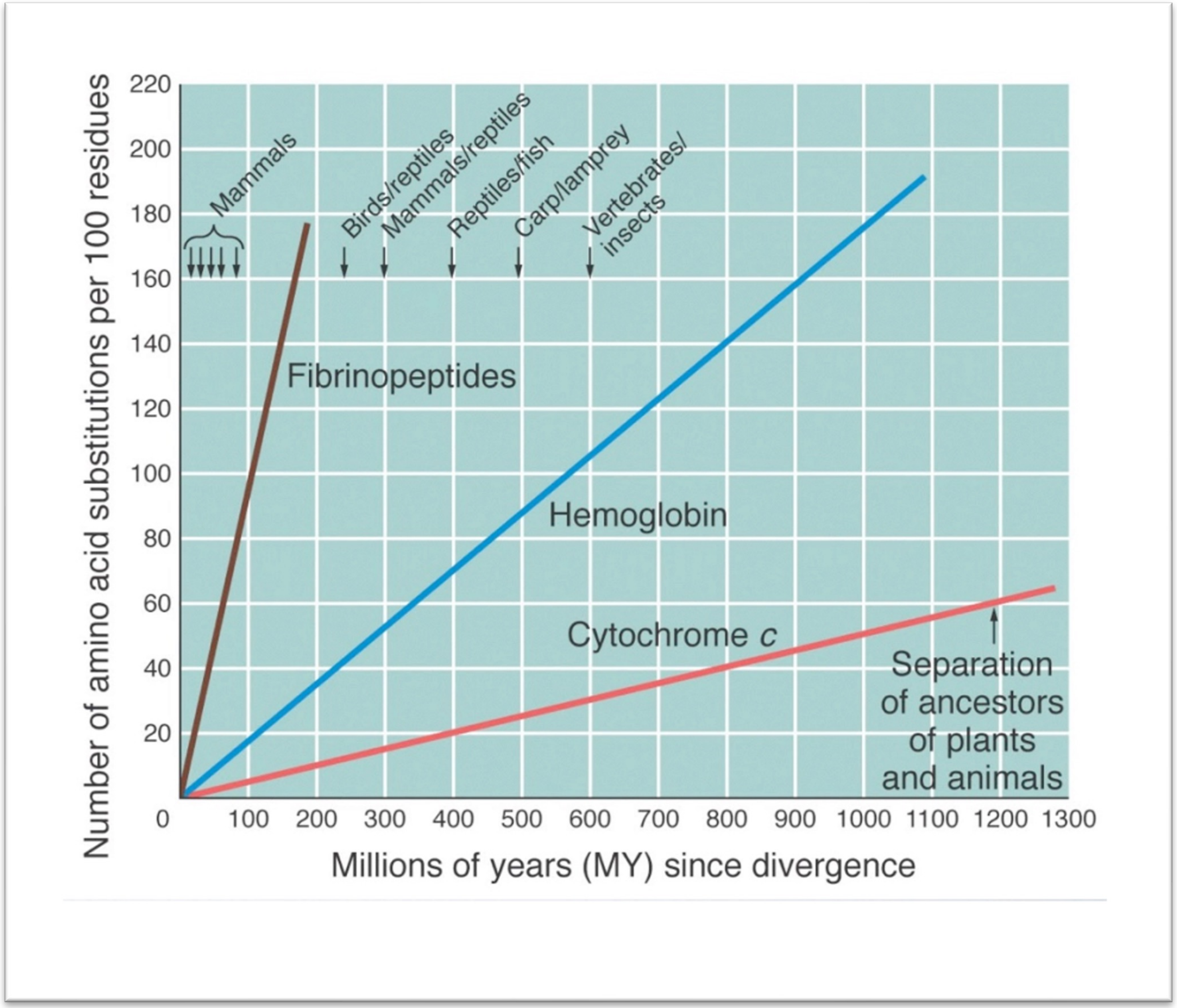
They noted that rates of amino acid replacements in animal haemoglobins were roughly proportional to time - as judged against the fossil record



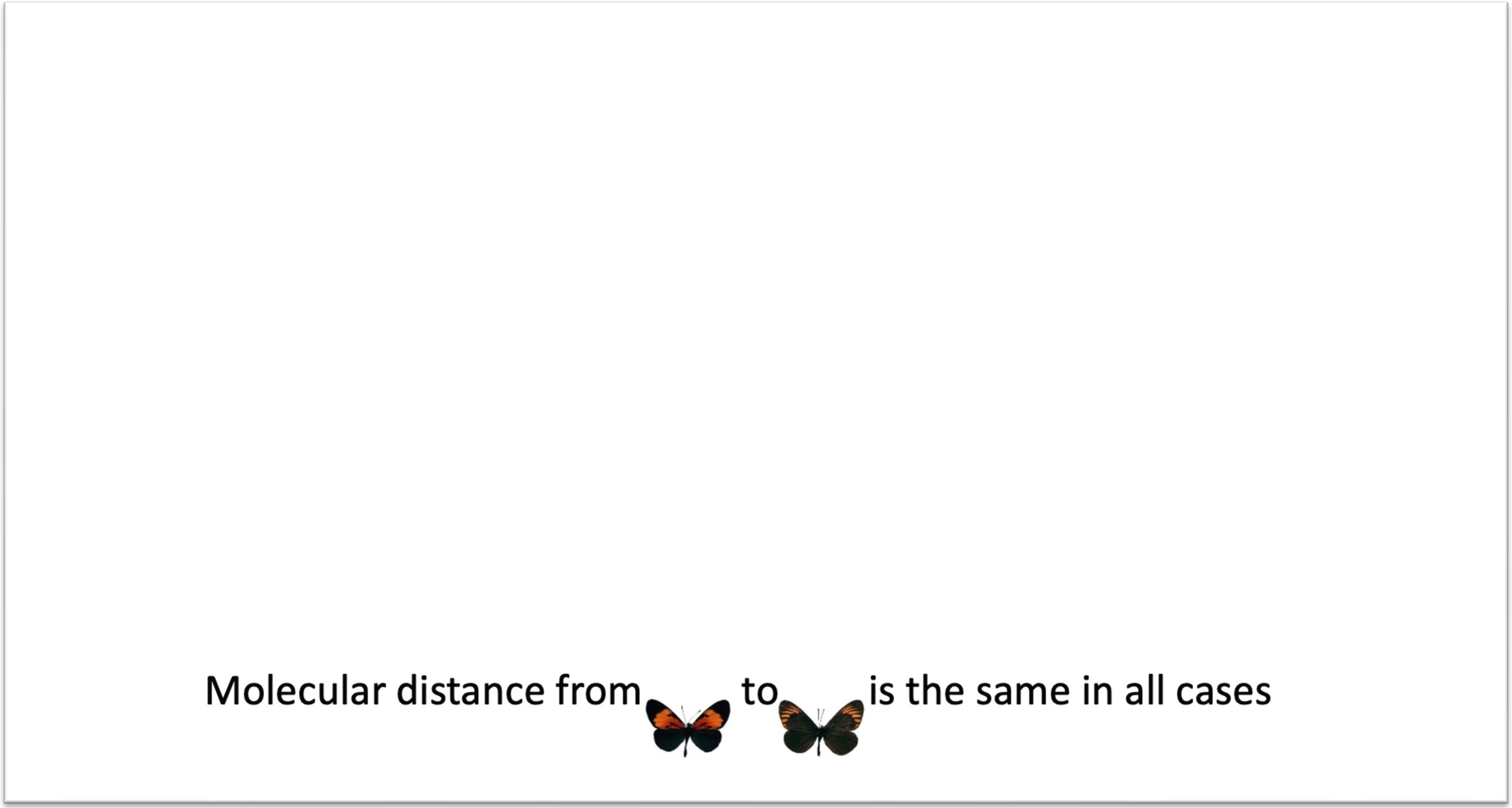
Clock model

The molecular clock is not constant

Rates vary across:
- taxa
- time
- genes
- sites within the same gene



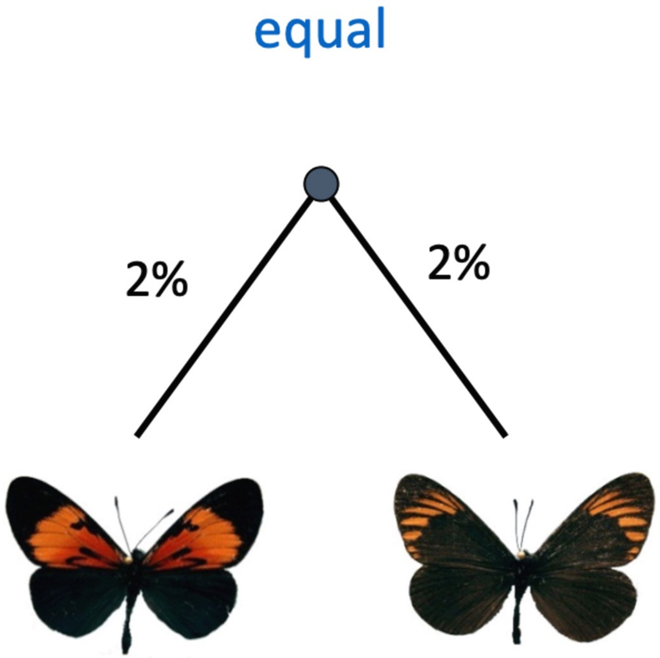
Clock model



Molecular distance from to is the same in all cases

Slides by Sergi Tarasov

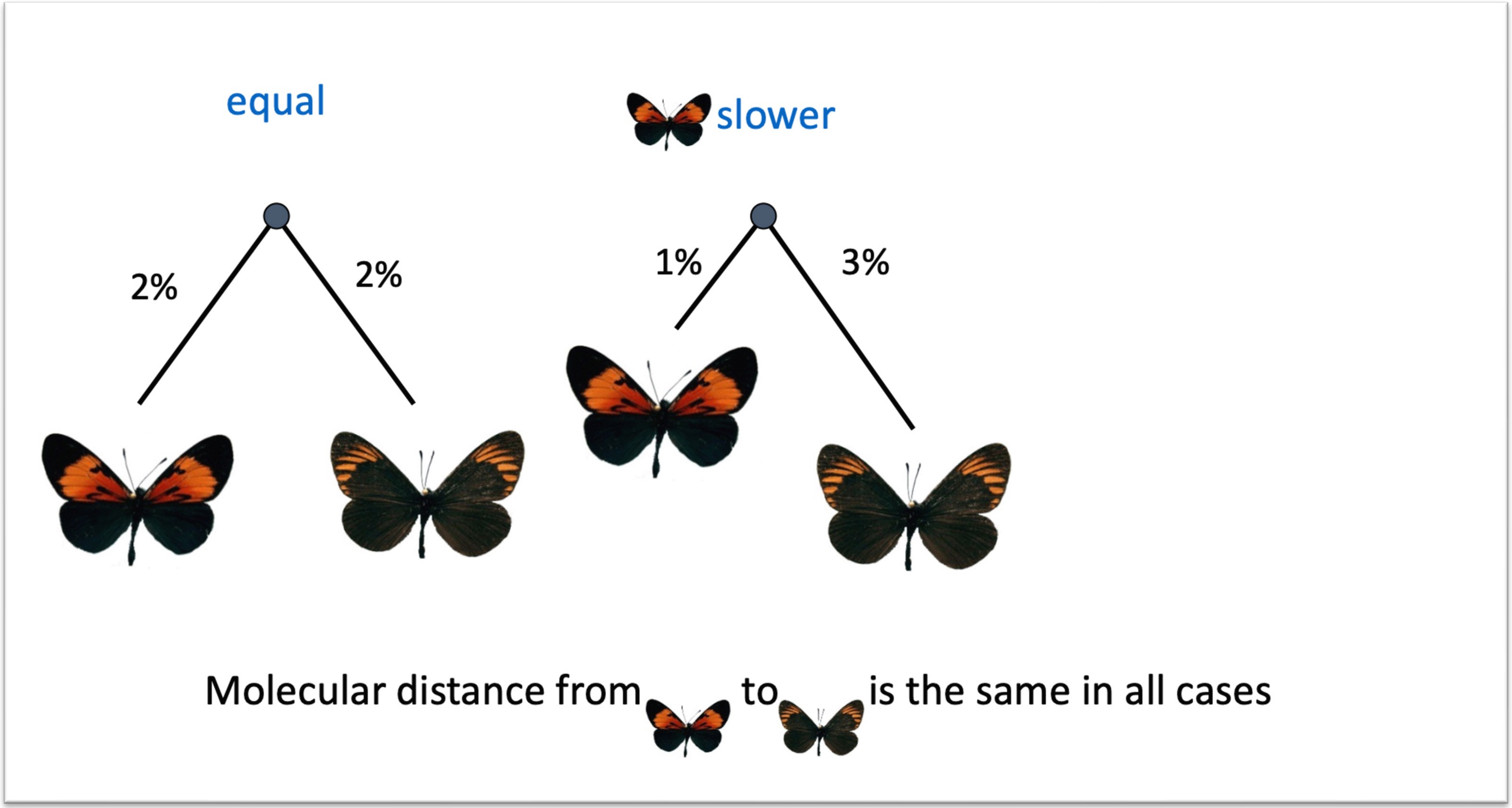
Clock model



Molecular distance from  to  is the same in all cases

Slides by Sergi Tarasov

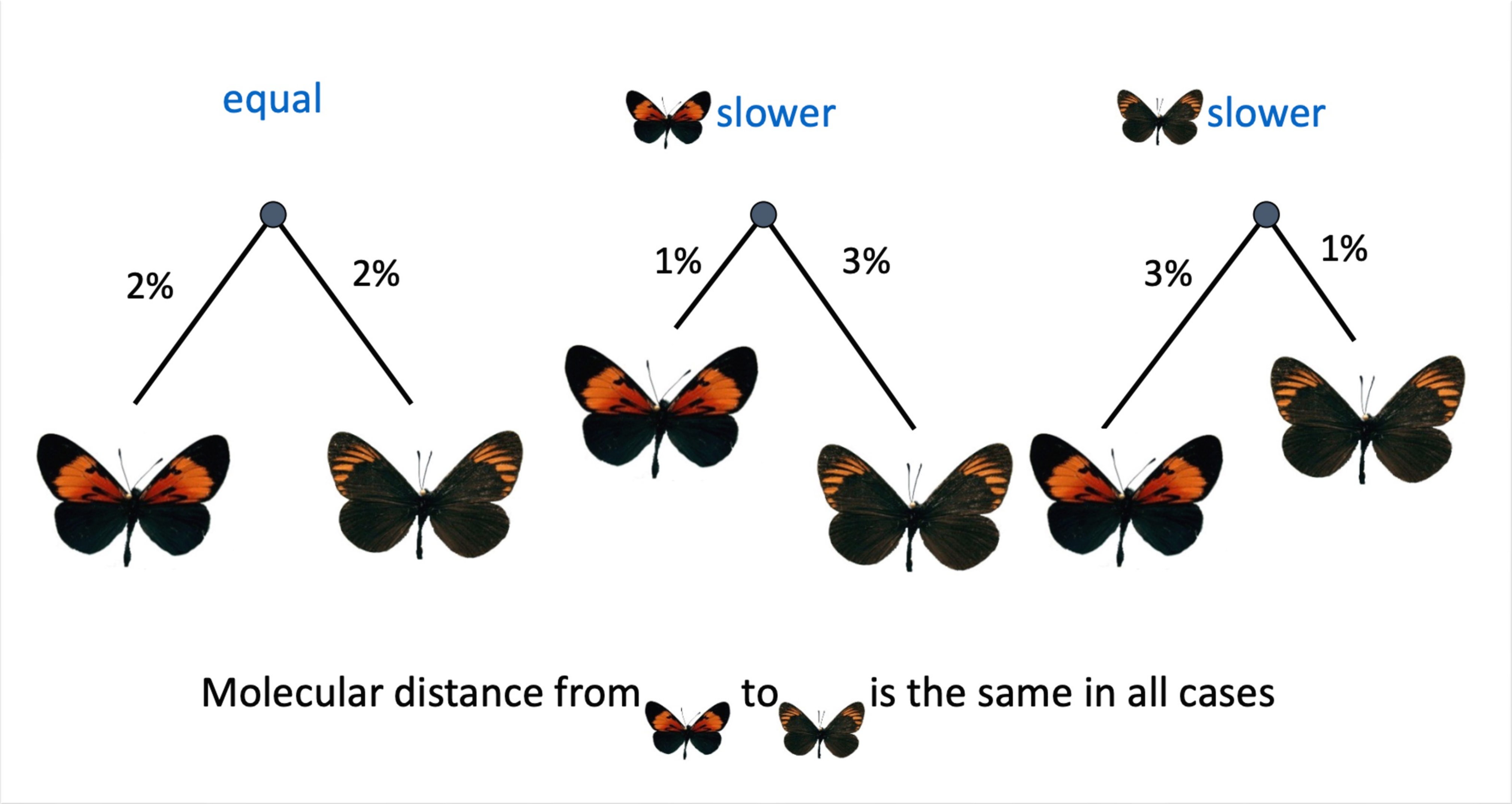
Clock model



Molecular distance from to is the same in all cases

Slides by Sergi Tarasov

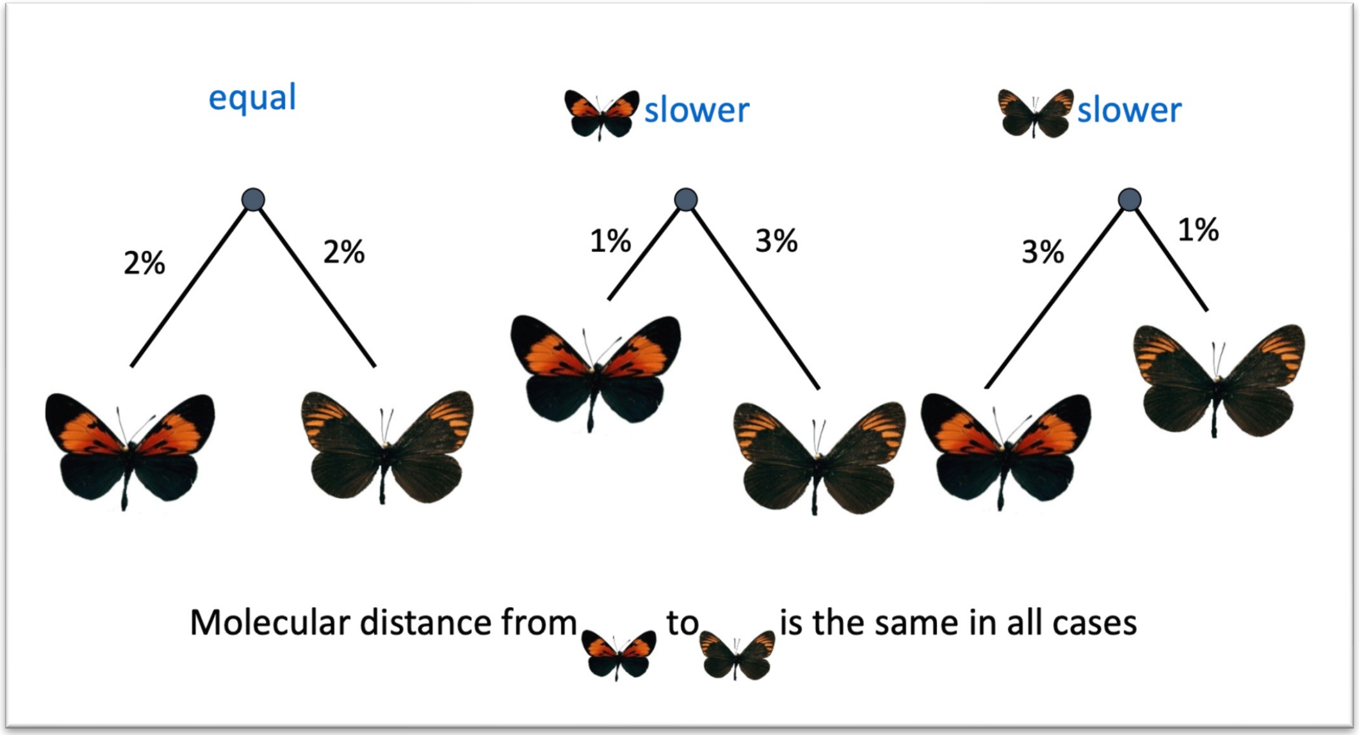
Clock model



Molecular distance from to is the same in all cases

Slides by Sergi Tarasov

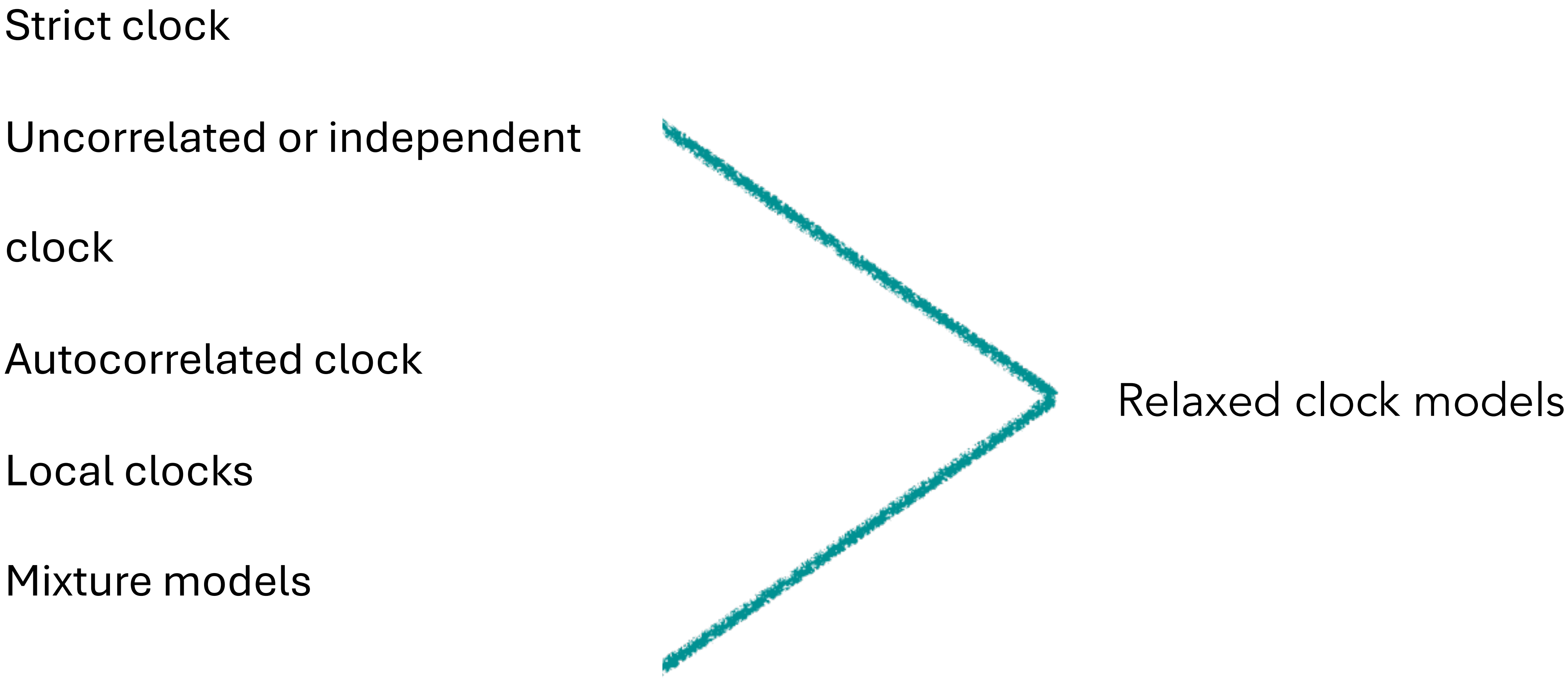
Clock model



Strict clock: one rate for all branches

Relaxed clock: different rates across branches

Clock model



Strict clock

Uncorrelated or independent clock

Autocorrelated clock

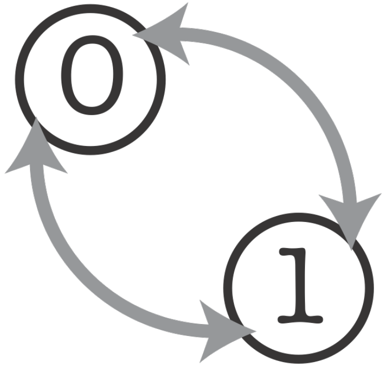
Local clocks

Mixture models

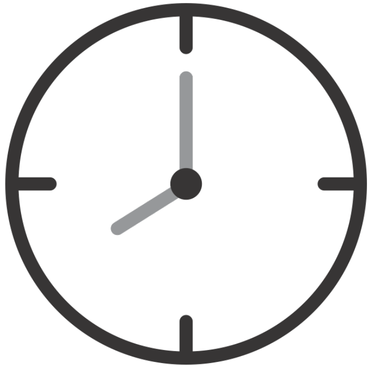
Relaxed clock models

Warnock & Wright. 2020
Heath, Moore 2014

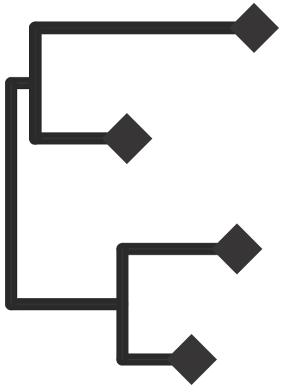
substitution model



clock model

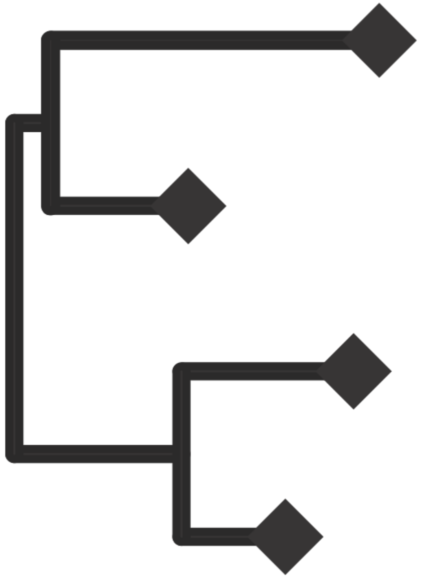


tree model



*A model refers to a set of assumptions the describe the evolutionary processes and mechanisms that produced our data

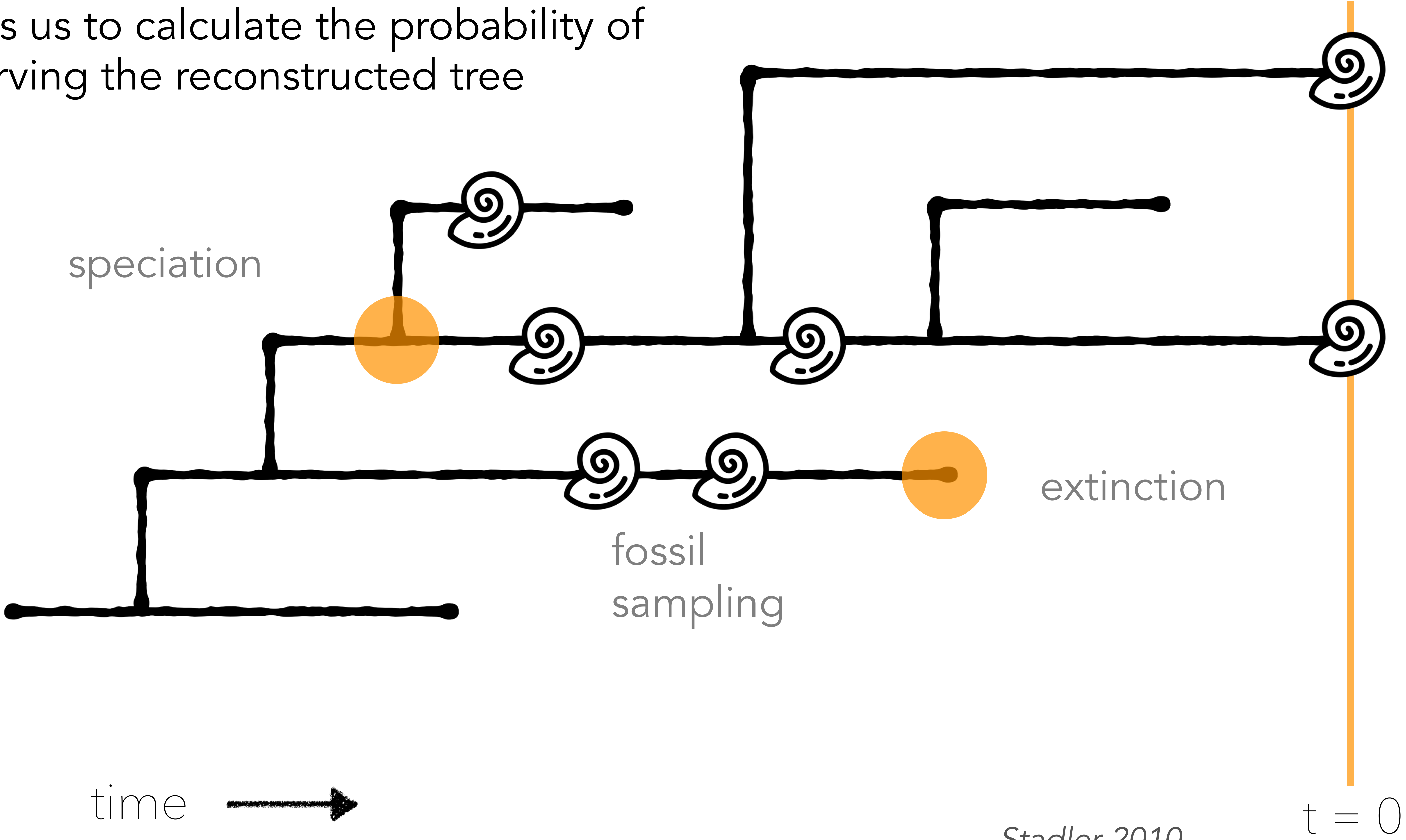
tree model



fossilised birth-death (FBD) process

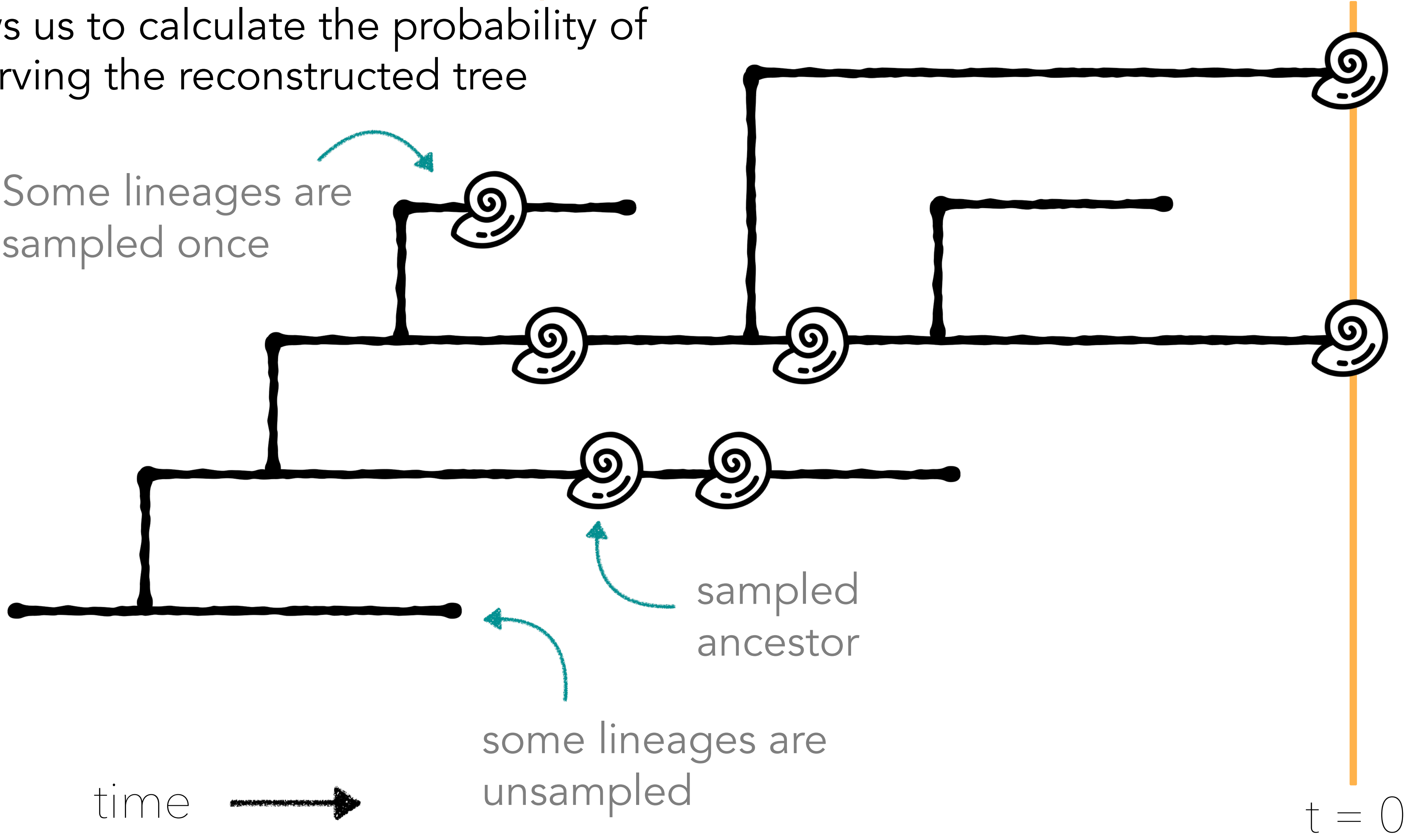
The tree model in phylogenetics is the probabilistic description of how lineages diversify and split over time.

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



Stadler 2010

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



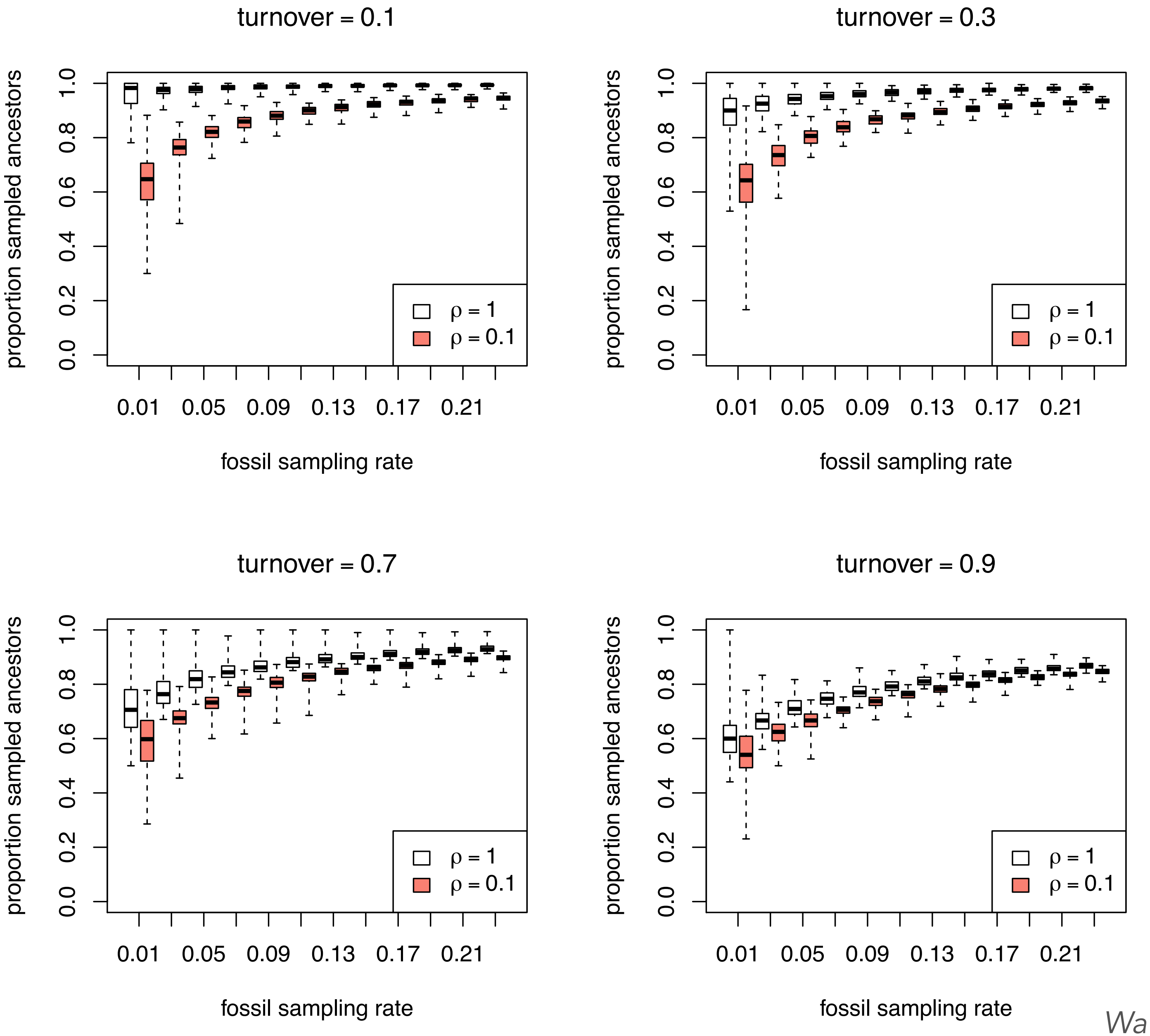
Some lineages are sampled once

sampled ancestor

some lineages are unsampled

The inclusion of sampled ancestors in an inference is very important

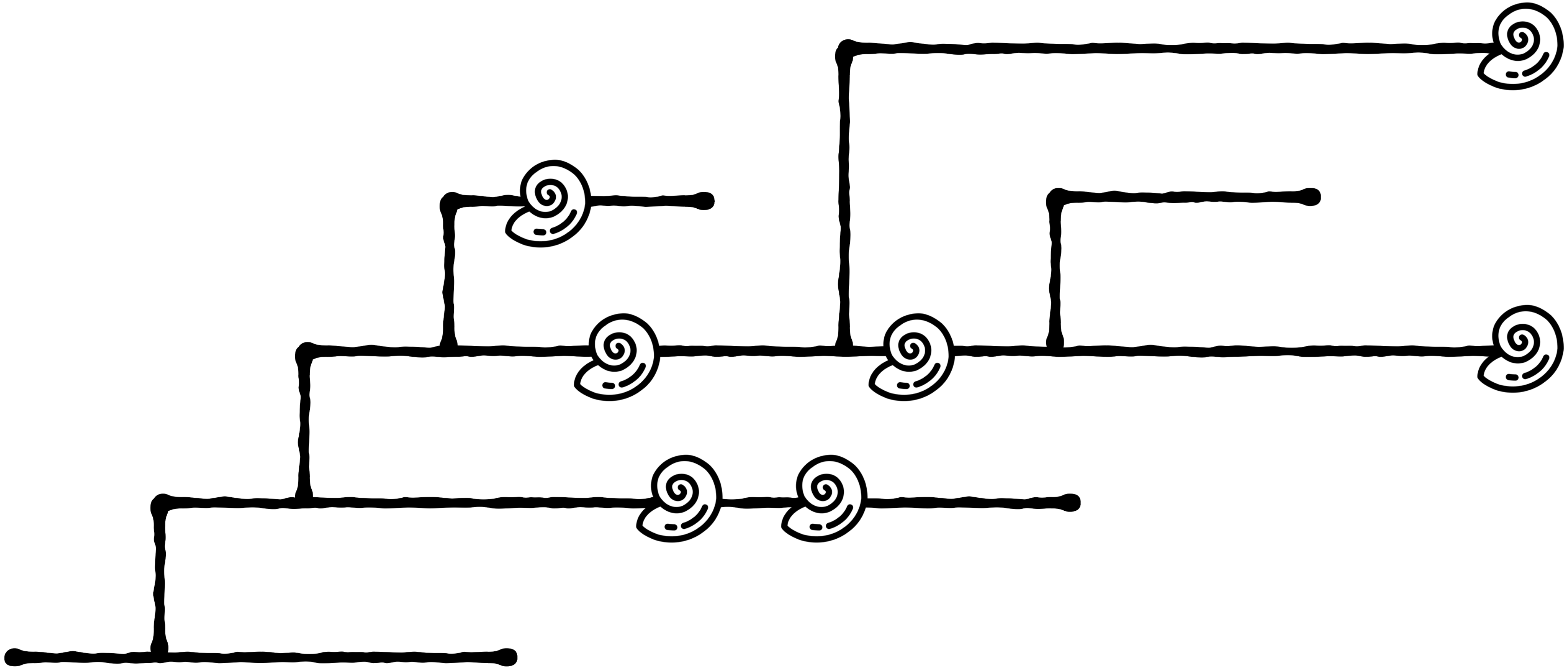
More realistic modelling of the evolutionary process



Higher turnover lower extinction

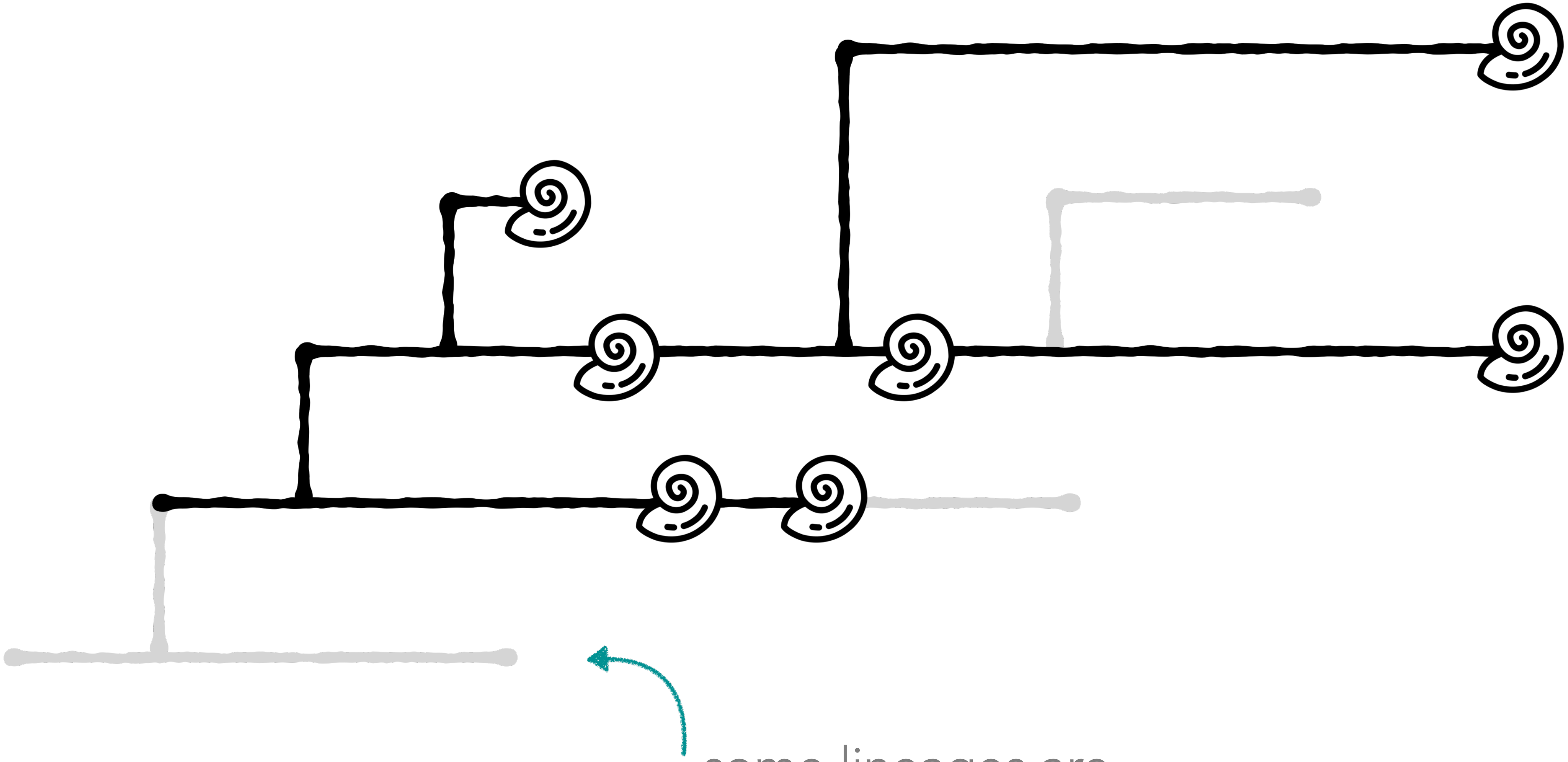
Walker & Heath 2020

Fossil sampling



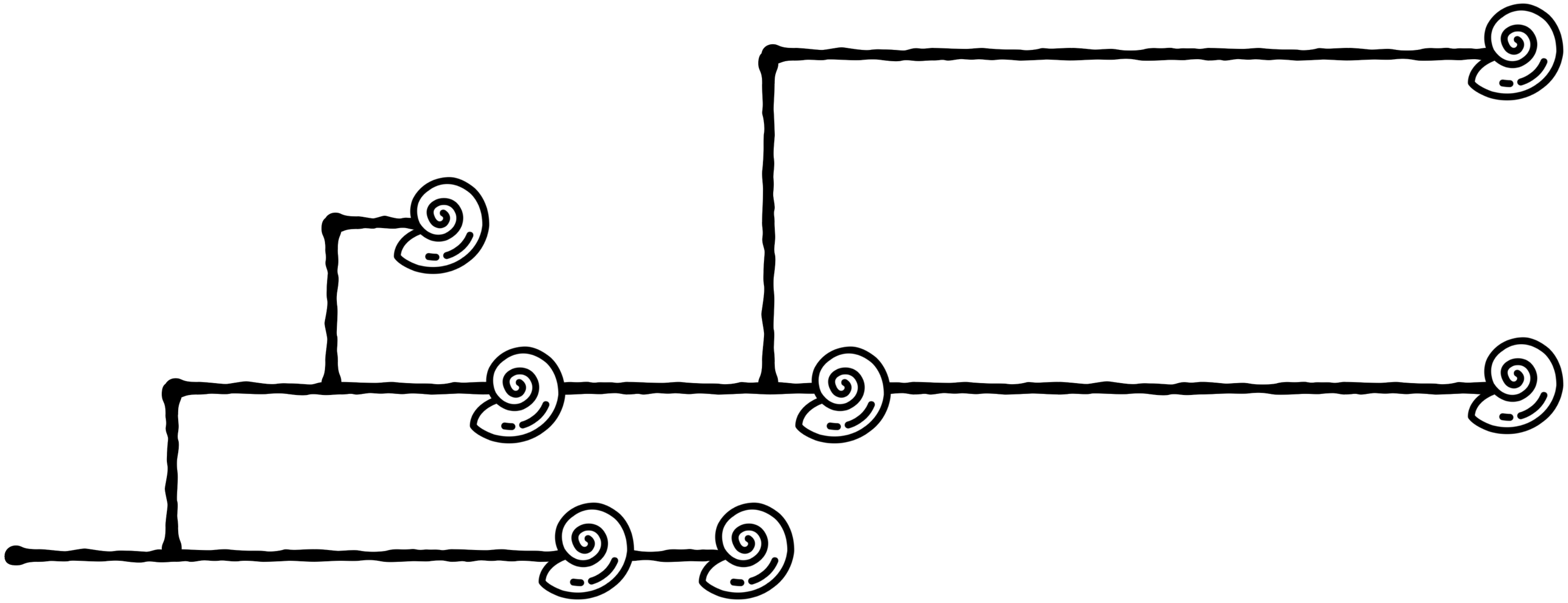
True tree

Fossil sampling



some lineages are
unsampled

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



Stadler 2010
Gavryushkina et al. (2014)

Phylogeny with branch lengths in units of time

Clock model

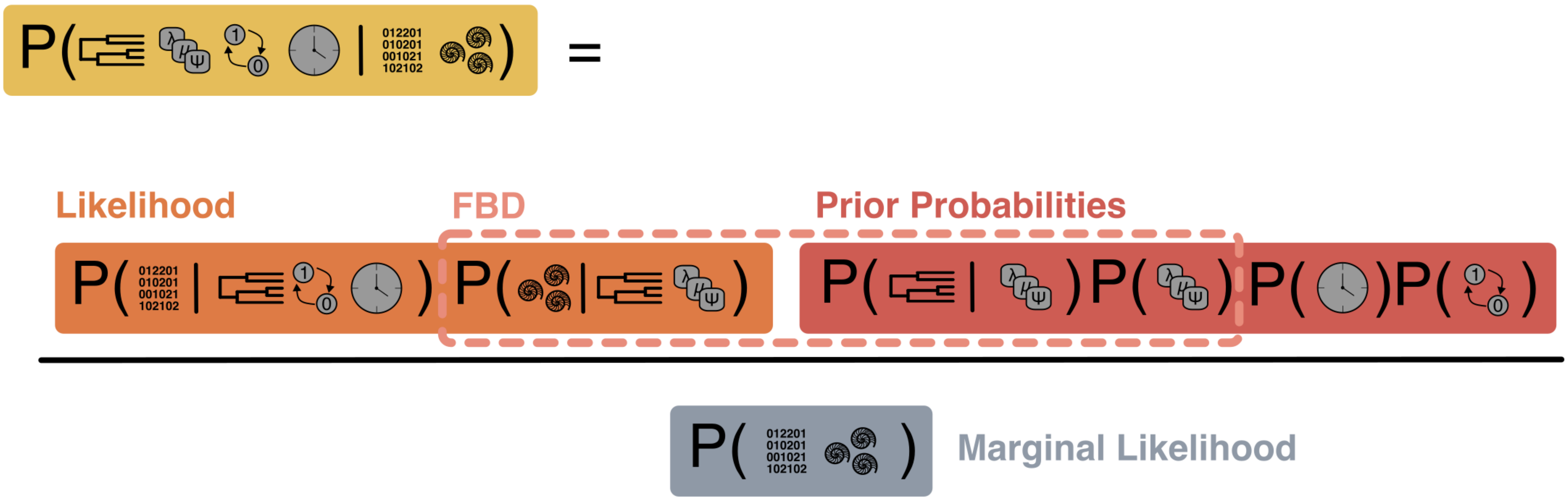
Morphological character model

FBD model parameters

Fossil age information

011001
010001
001011
101100
Morphological characters

Posterior distribution



Likelihood

FBD

Prior Probabilities

Marginal Likelihood

Mulvey et al. 2025

5 key model parameters

Speciation rate - λ

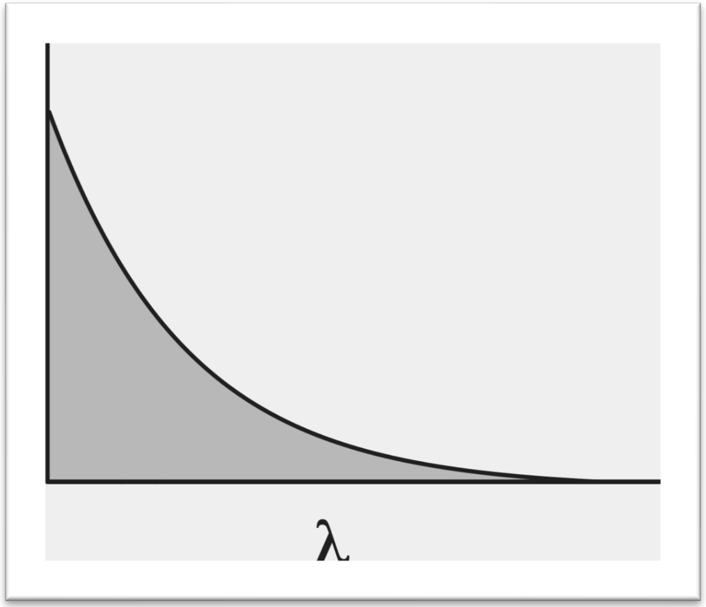
Extinction rate - μ

Fossil sampling rate – ψ

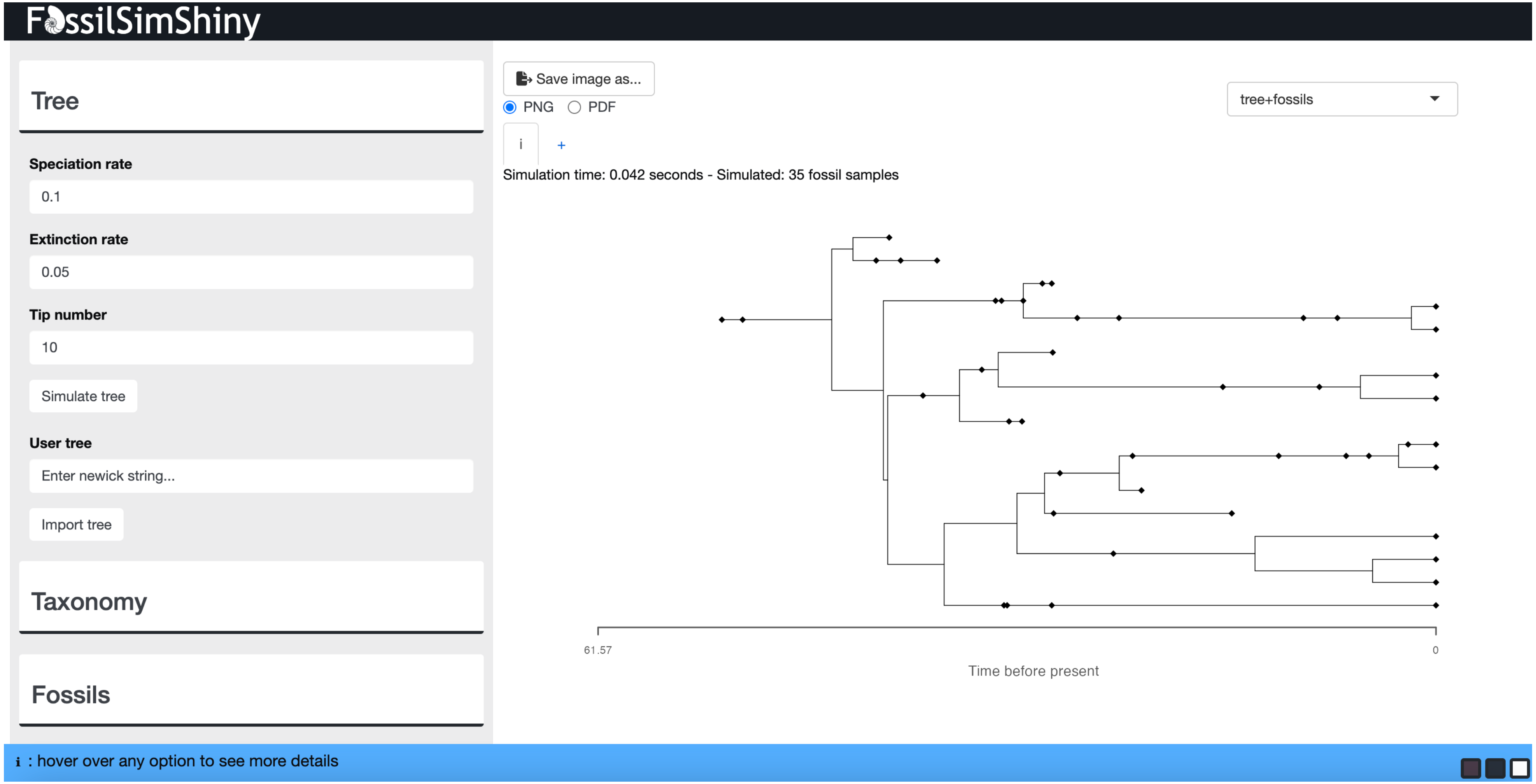
Origin time - t_{origin}

Extant sampling probability – ρ

Estimated during inference from a prior distirbution



Often fixed as this is the parameter we have the most information about



Speciation rate: 0.1

Extinction rate: 0.05

Tip number: 10

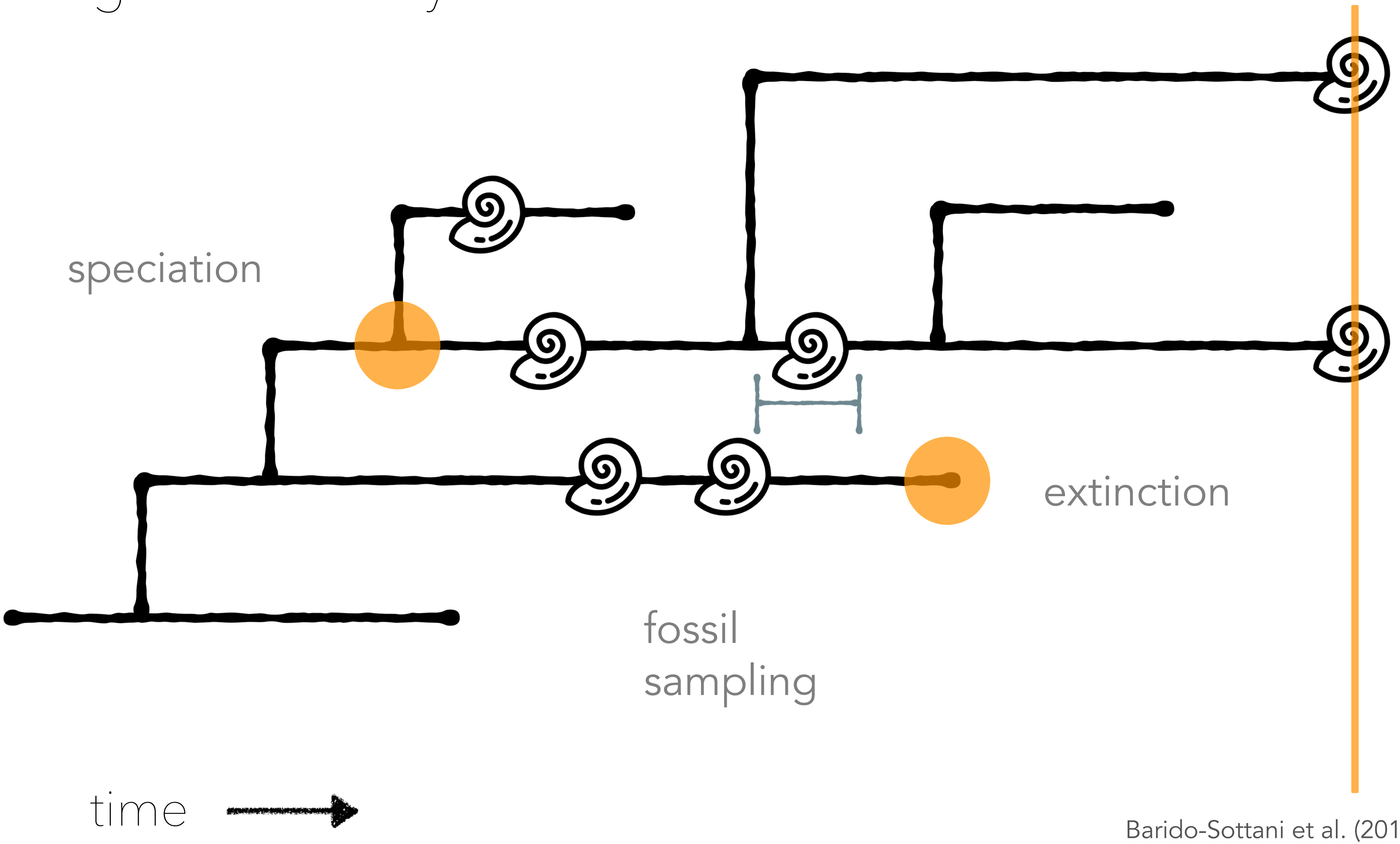
User tree: Enter newick string...

Simulation time: 0.042 seconds - Simulated: 35 fossil samples

i : hover over any option to see more details

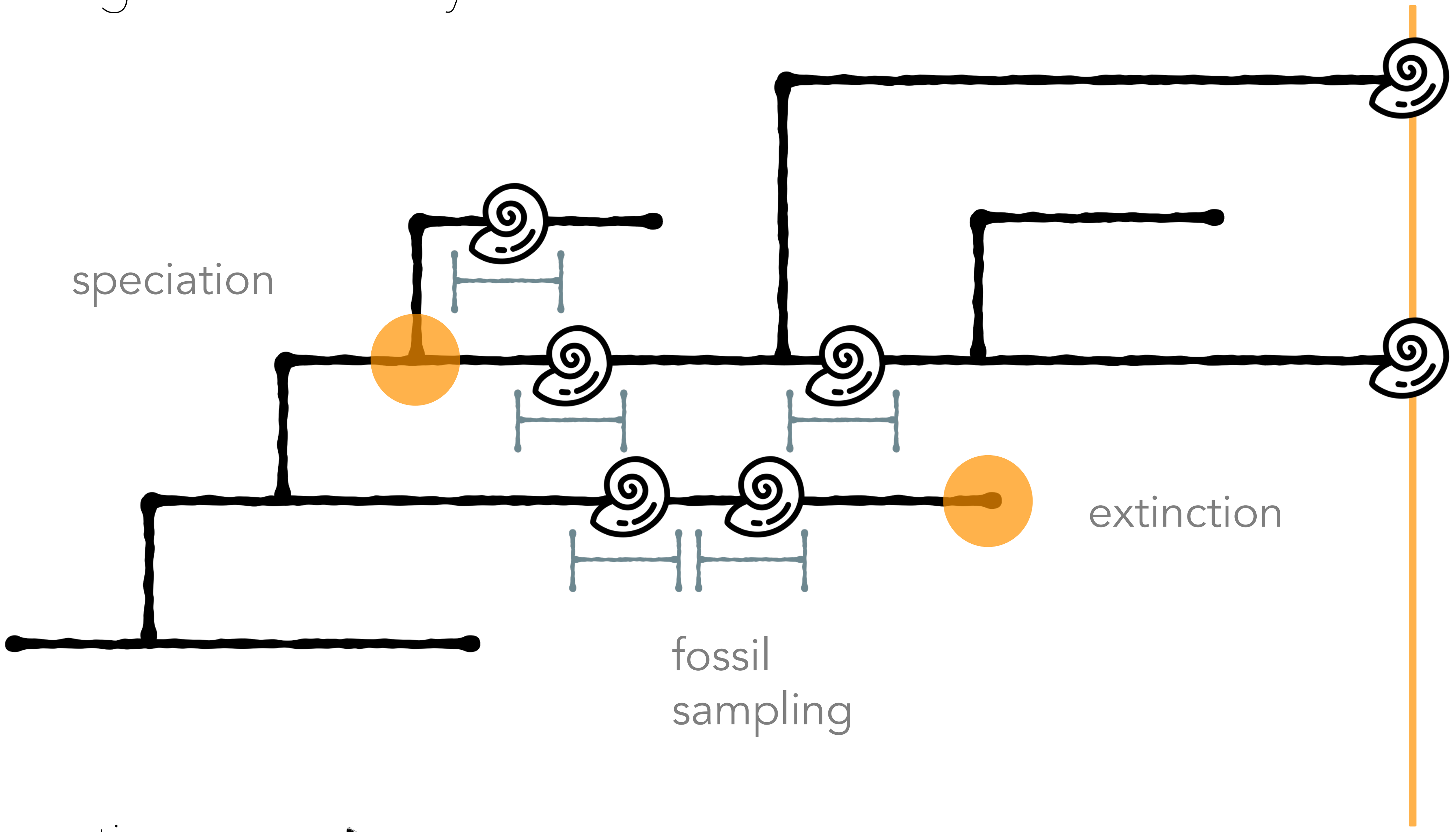
https://github.com/fossilsim/FossilSimShiny

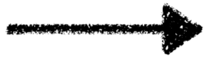
Fossil age uncertainty



Barido-Sottani et al. (2018, 2020, 2023),
Warnock 2018

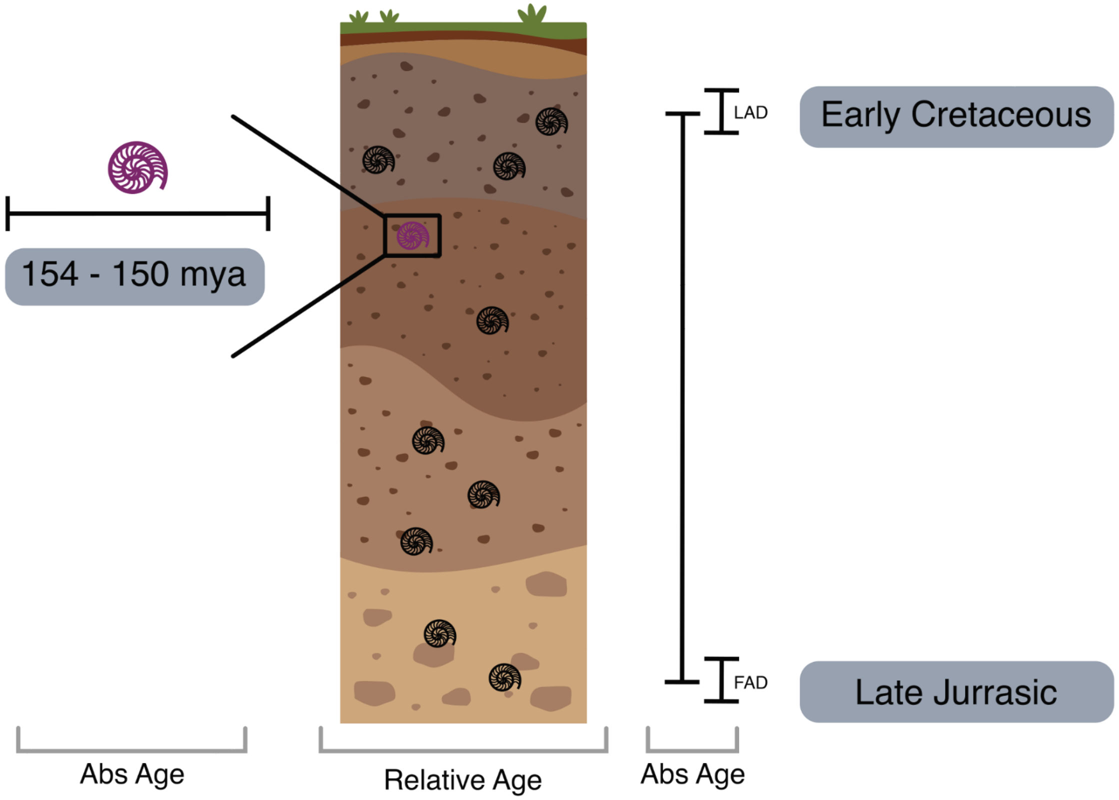
Fossil age uncertainty





Barido-Sottani et al. (2018, 2020, 2023),
Warnock 2018

Fossil Ages



Occurrence

Stratigraphic Range

154 - 150 mya

LAD

Early Cretaceous

FAD

Late Jurrasic

Abs Age

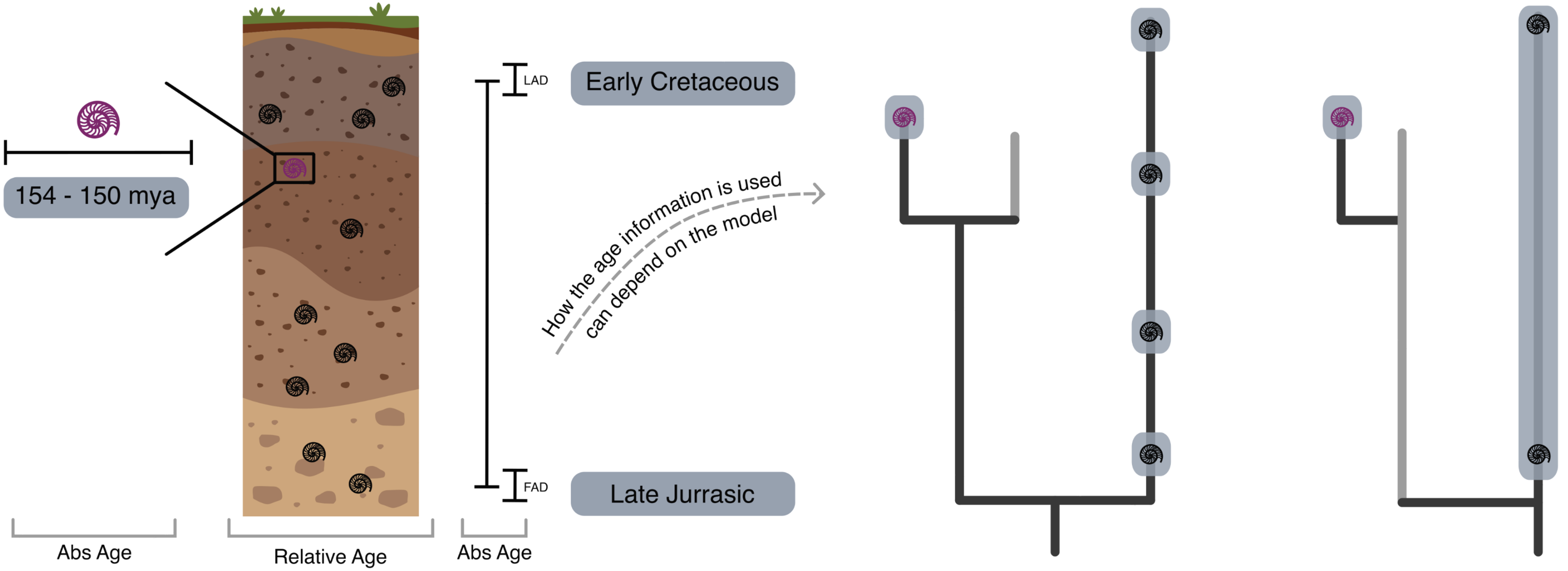
Relative Age

Abs Age

Fossil Ages

FBD Specimen

FBD Range



Occurrence

Stratigraphic Range

Fossil age uncertainty

In the field

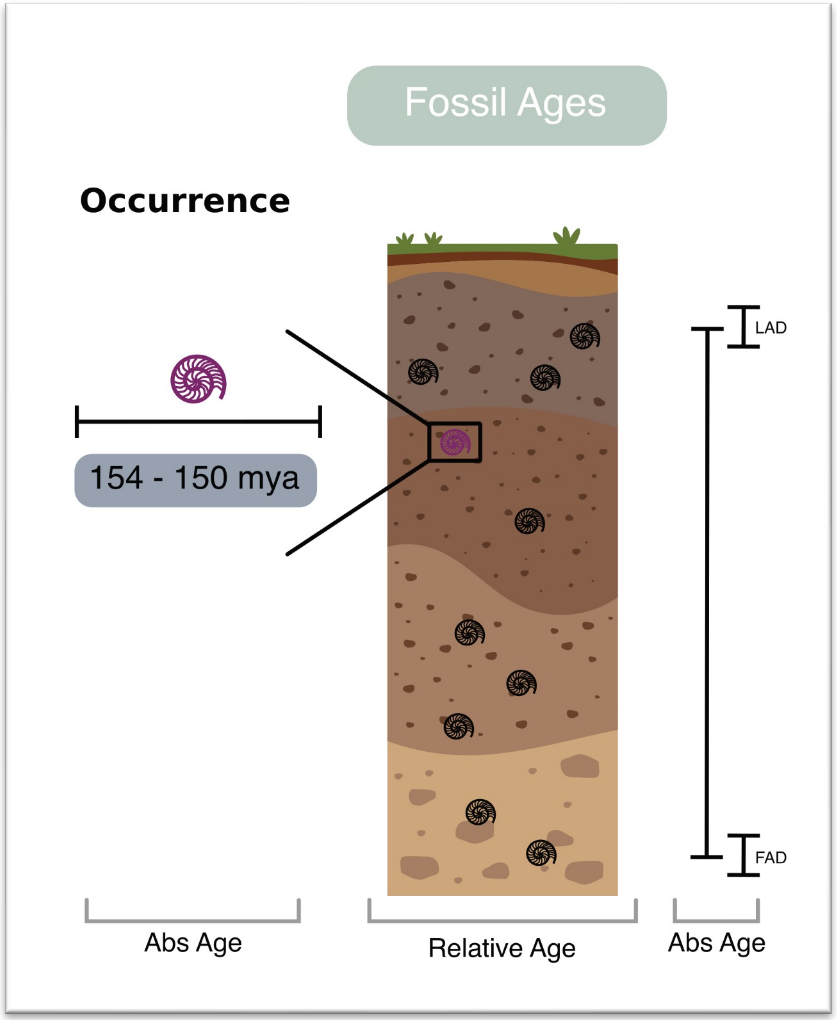
It may be possible to directly date the bed in which a fossil was found, for example, using isotopic analysis of an **ash layer**, but this is uncommon.

Biostratigraphic correlation can be used. This method relies on identifying **index fossils.**

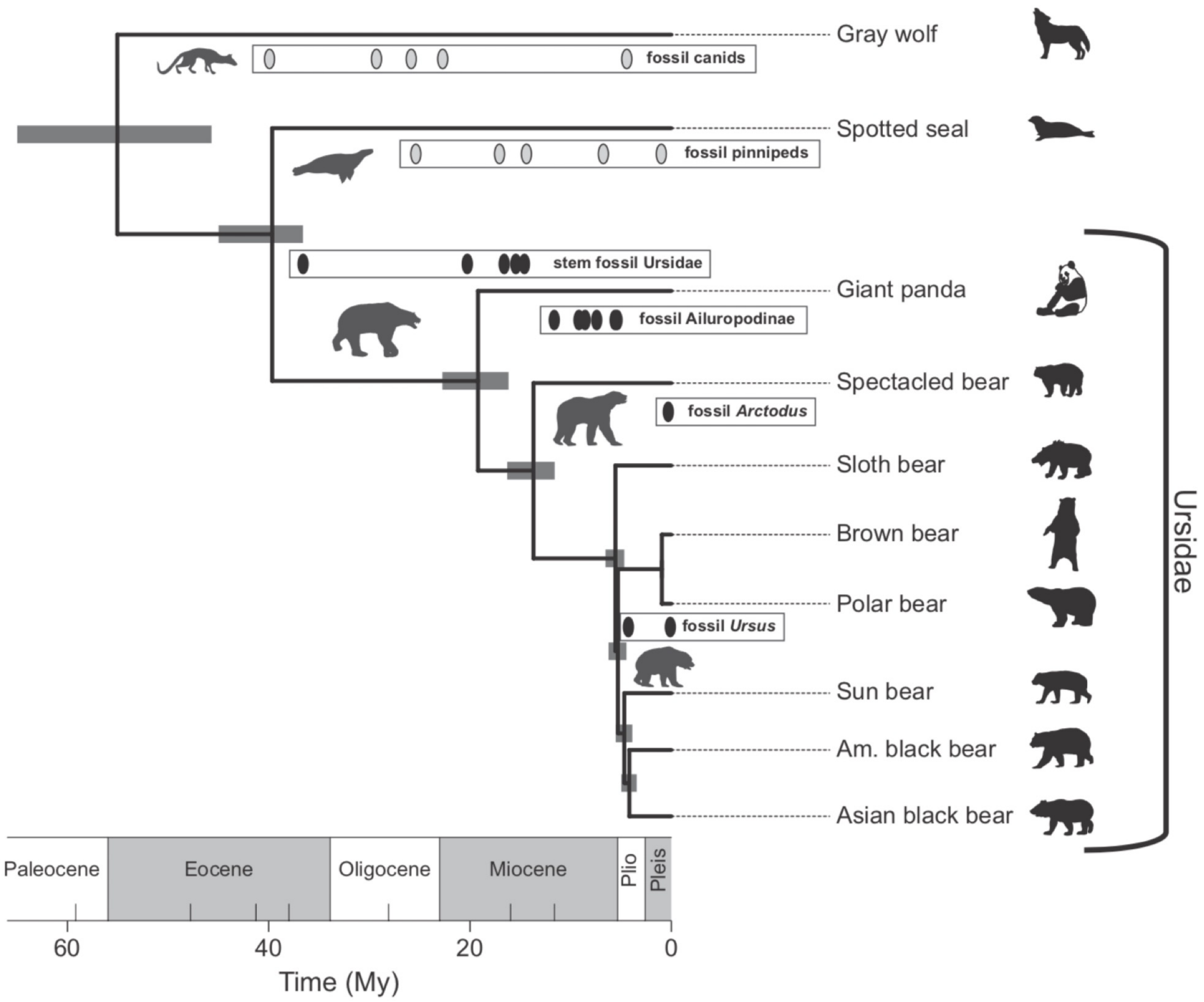
From the literature

Descriptions of fossils, particularly type specimens, usually include the stratigraphic context in which the fossil was found.

PBDB



Time calibrated tree of living and fossil bears

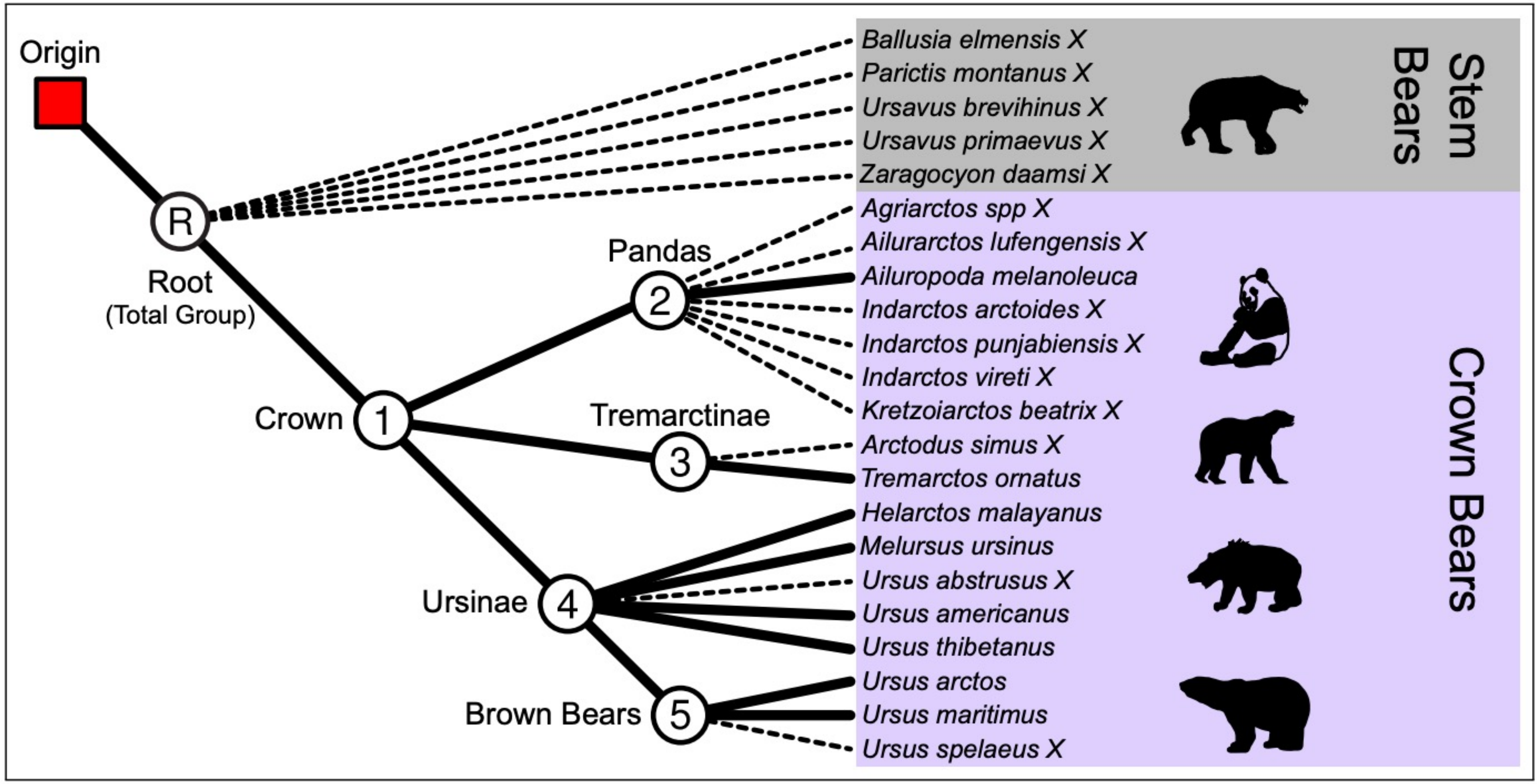


First application of the FBD model

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

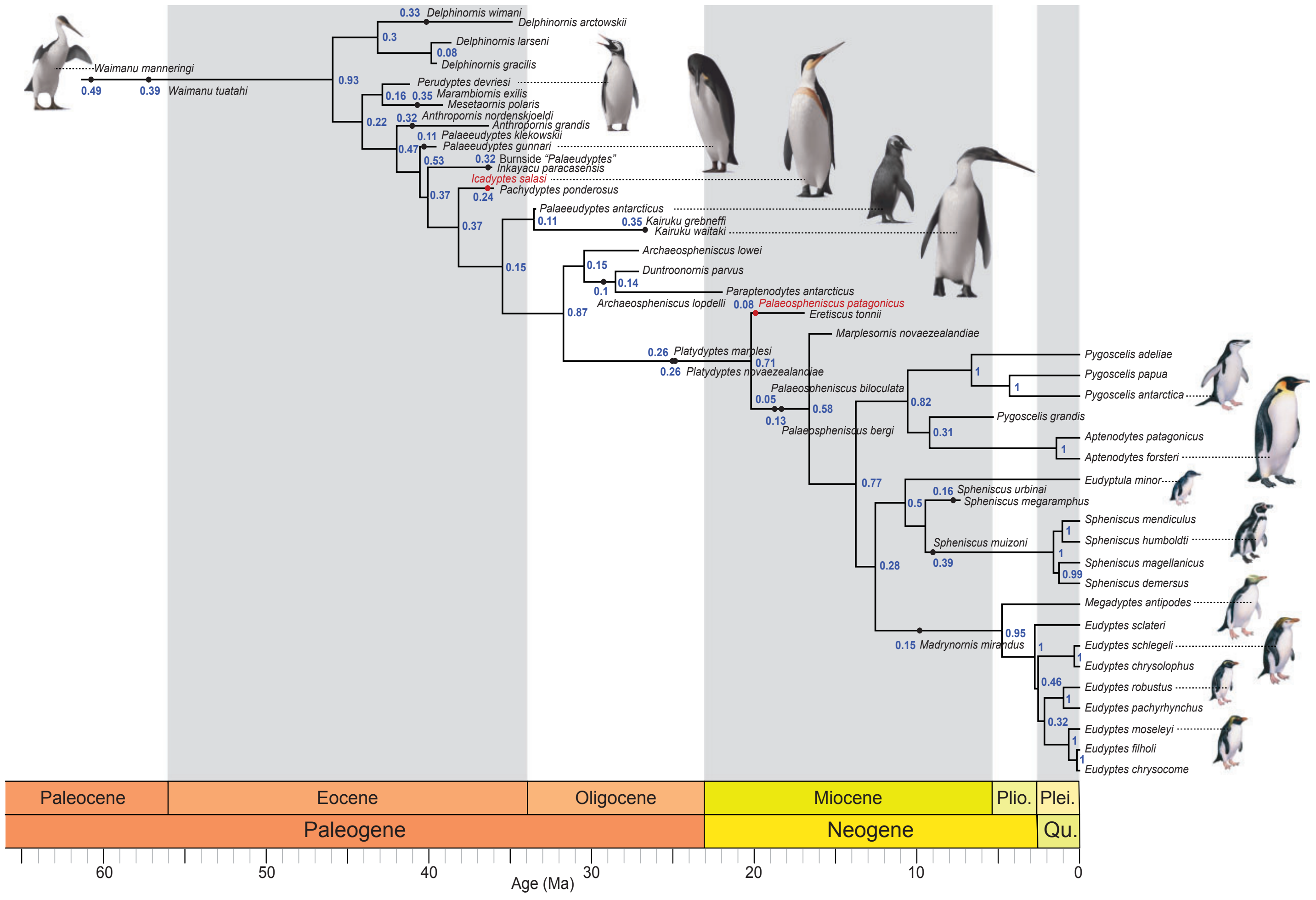
Heath et al 2014

Fossil taxa used during the inference:



Heath et al 2014

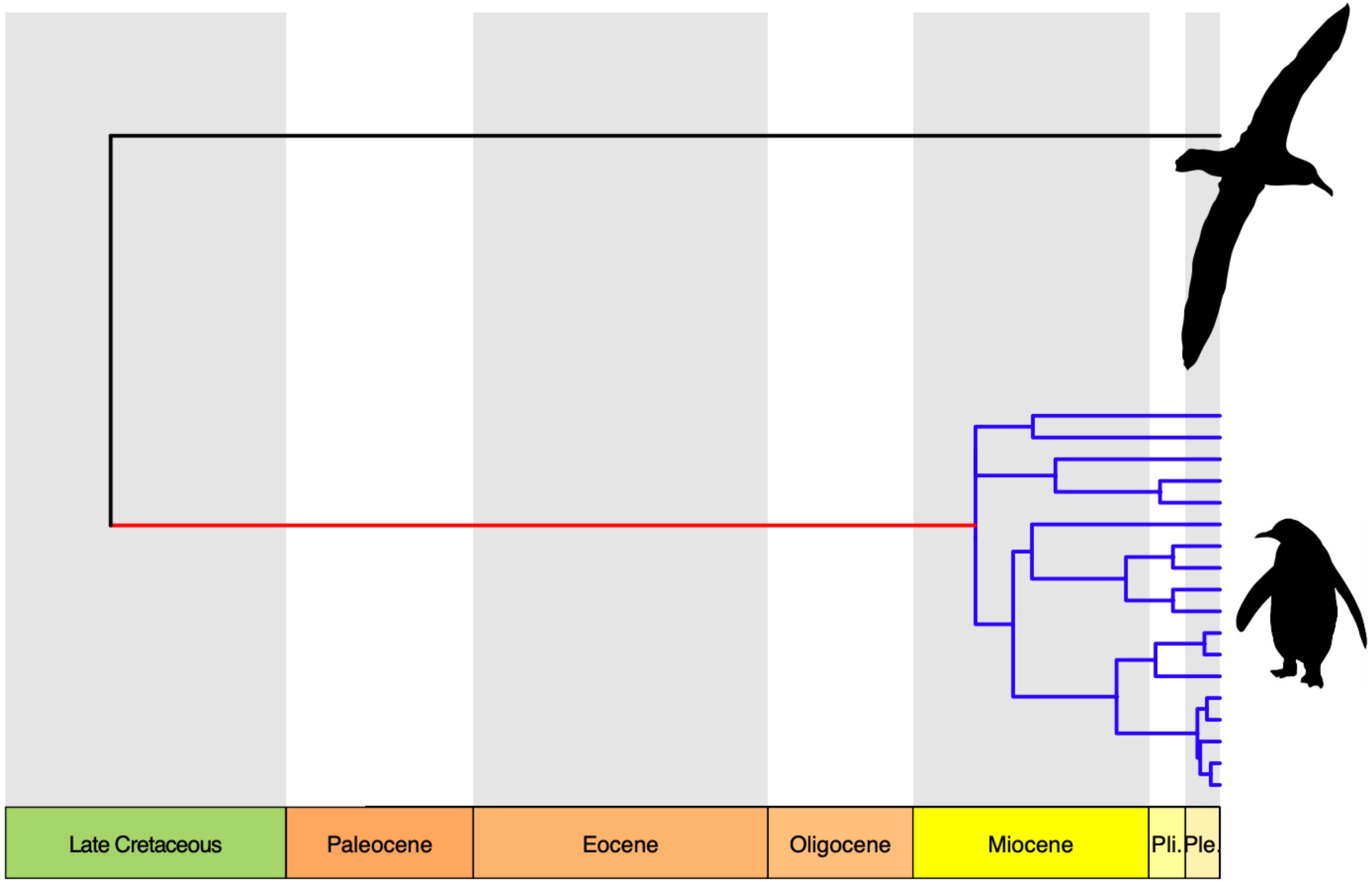
Time calibrated tree of living and fossil penguins



First application of total evidence dating using the FBD model

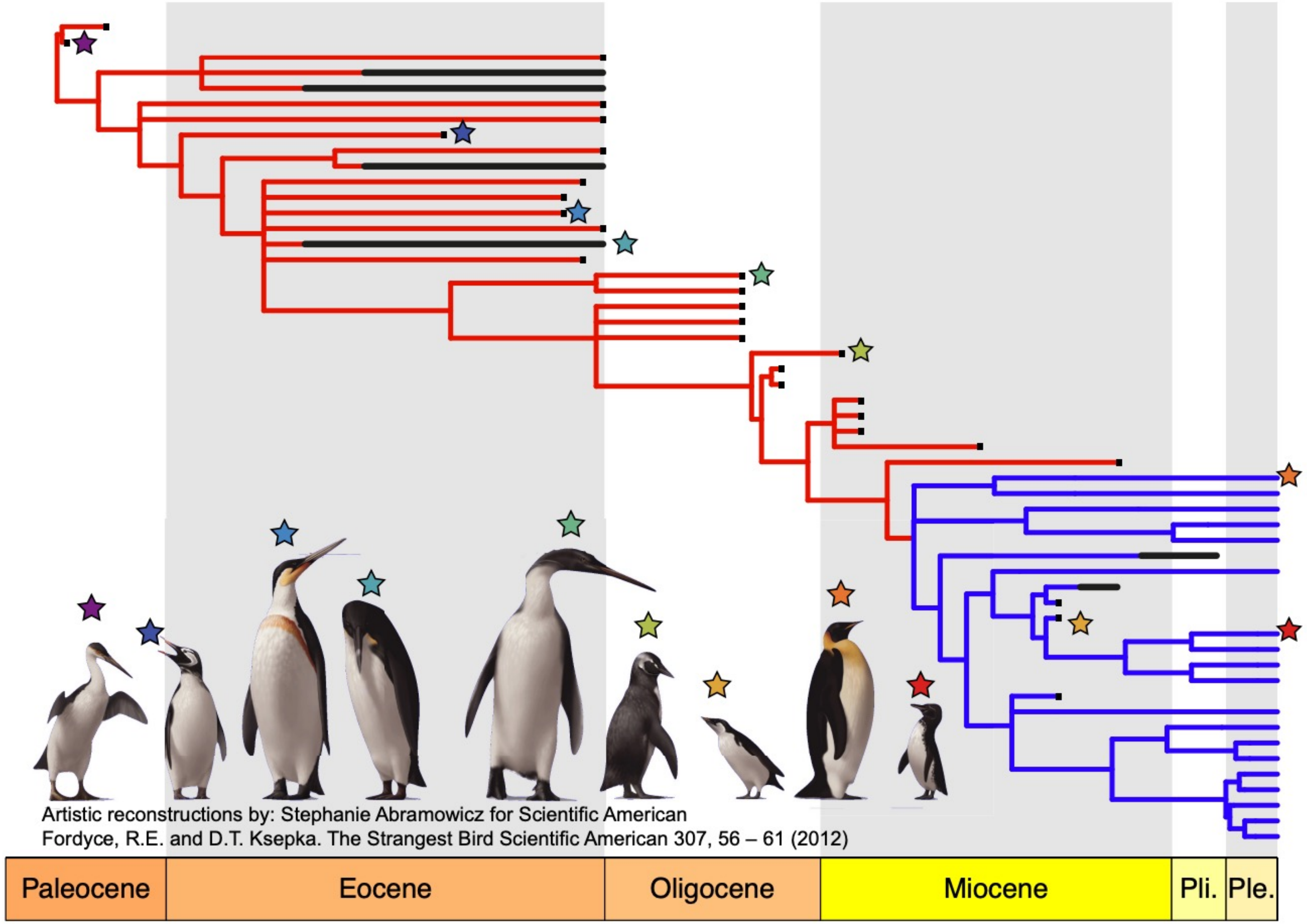
Fossils are incorporated using character data

Gavryushkina et al. (2016)



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

Gavryushkina et al. (2016)

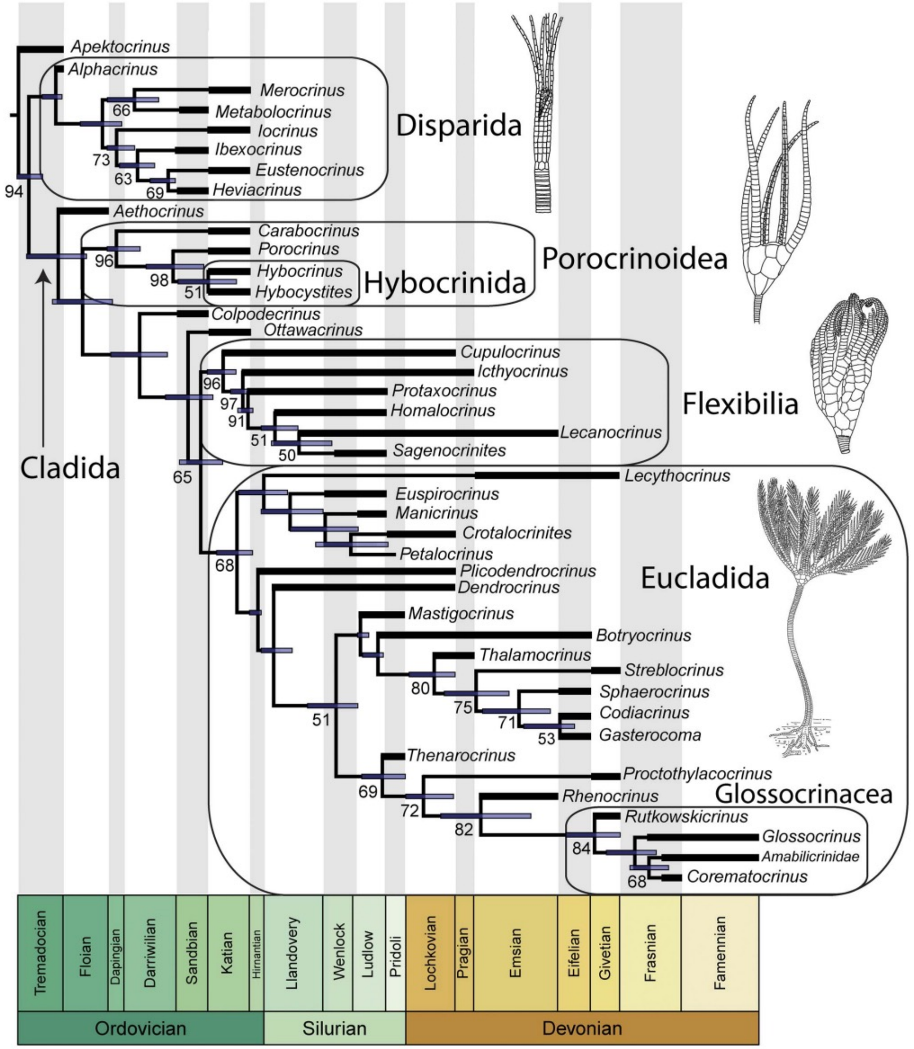

Artistic reconstructions by: Stephanie Abramowicz for Scientific American

Fordyce, R.E. and D.T. Ksepka. The Strangest Bird Scientific American 307, 56 – 61 (2012)

But penguins have a rich fossil record!

Gavryushkina et al. (2016)

Time calibrated tree of fossil echinoderms

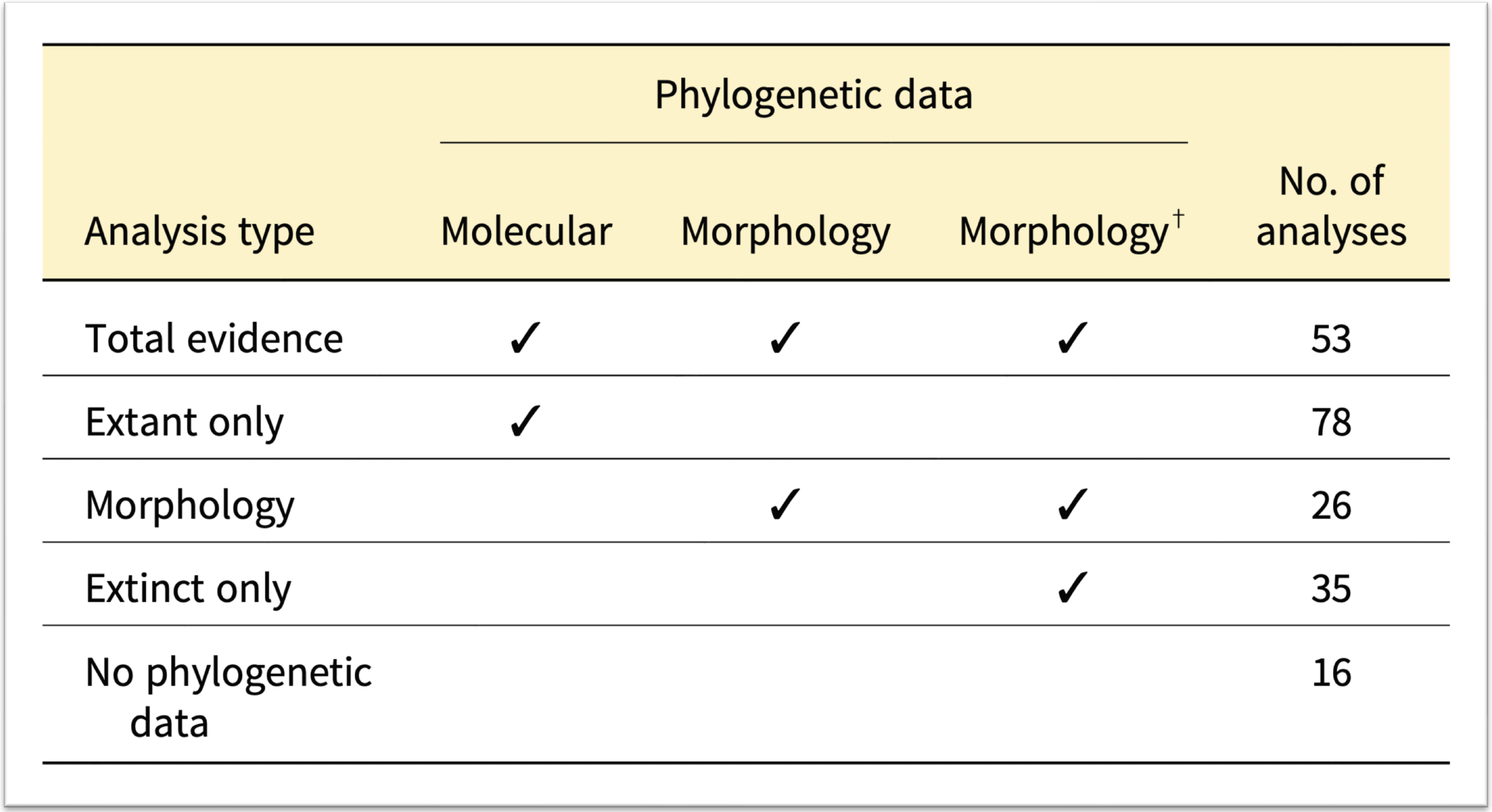


First application of the FBD model for a fully extinct clade

Extant species sampling $\rho = 0$

Estimated age uncertainty at the tips

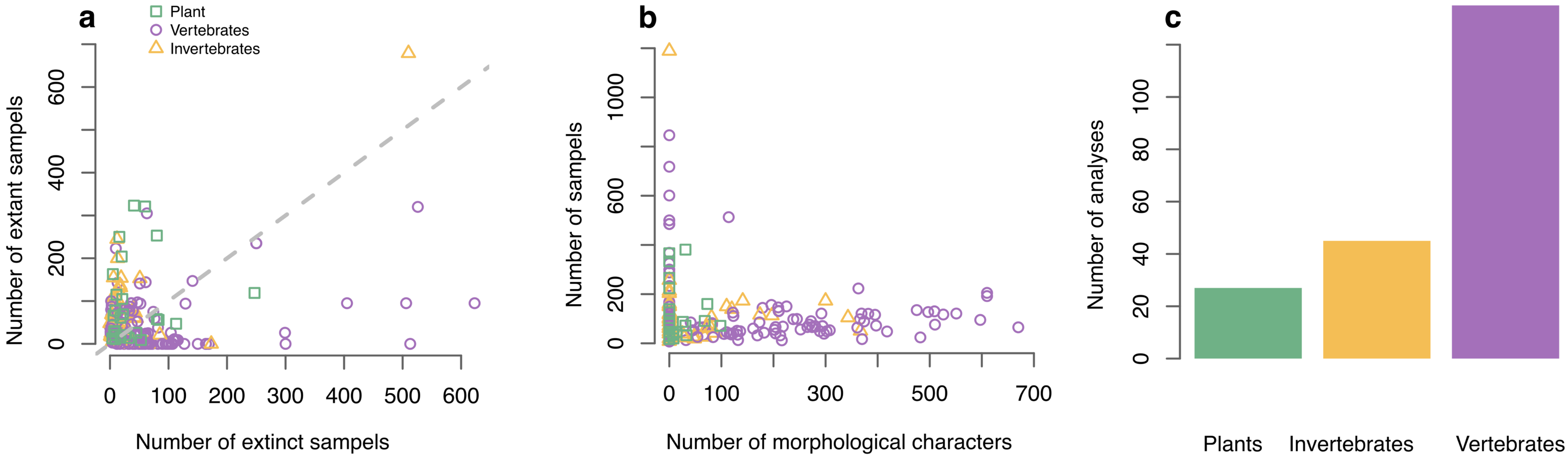
Wright 2017



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

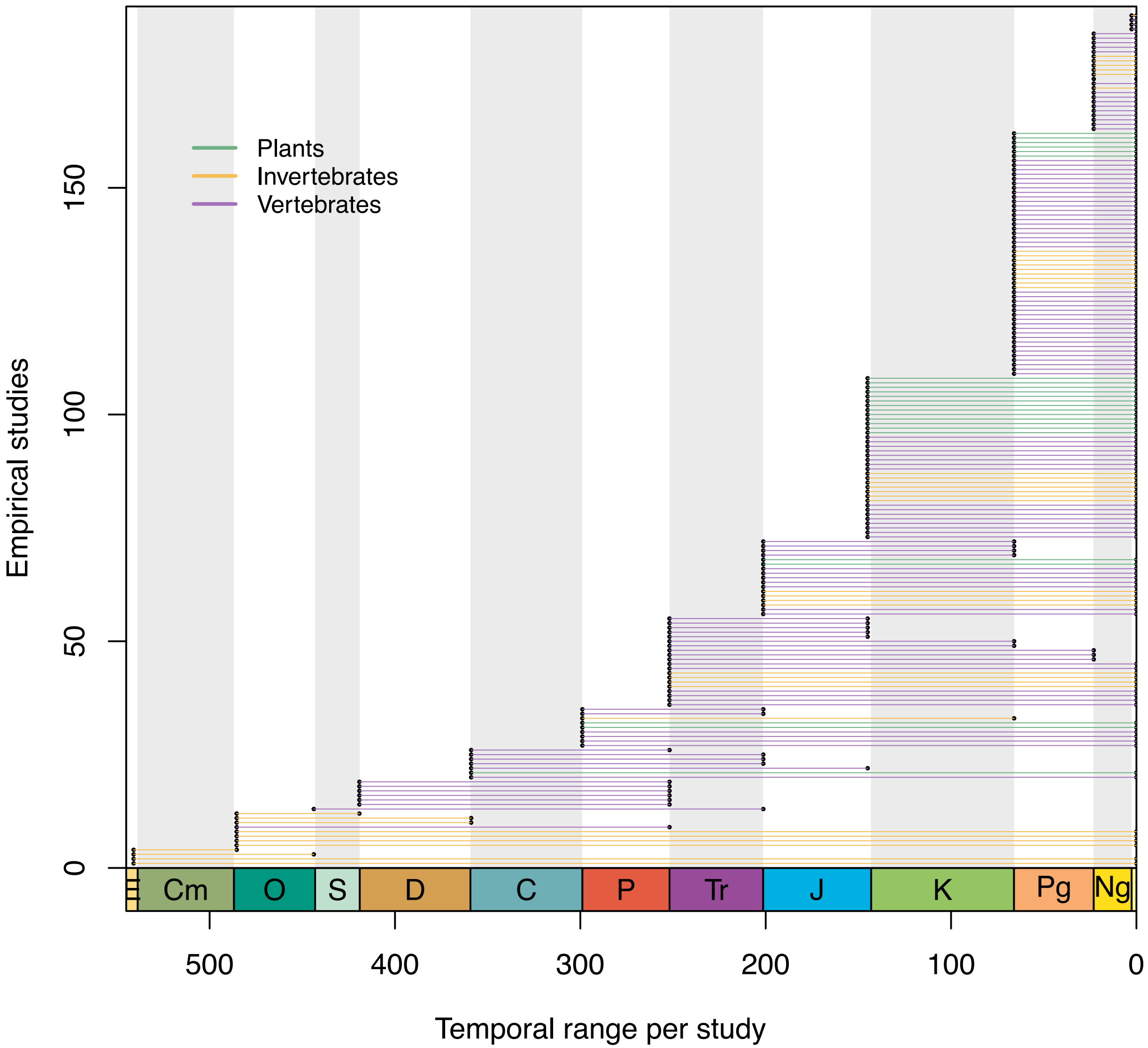
Mulvey et al. 2025

Application of the FBD model



Mulvey et al. 2025

Application of the FBD model



Mulvey et al. 2025

Application of the FBD model

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

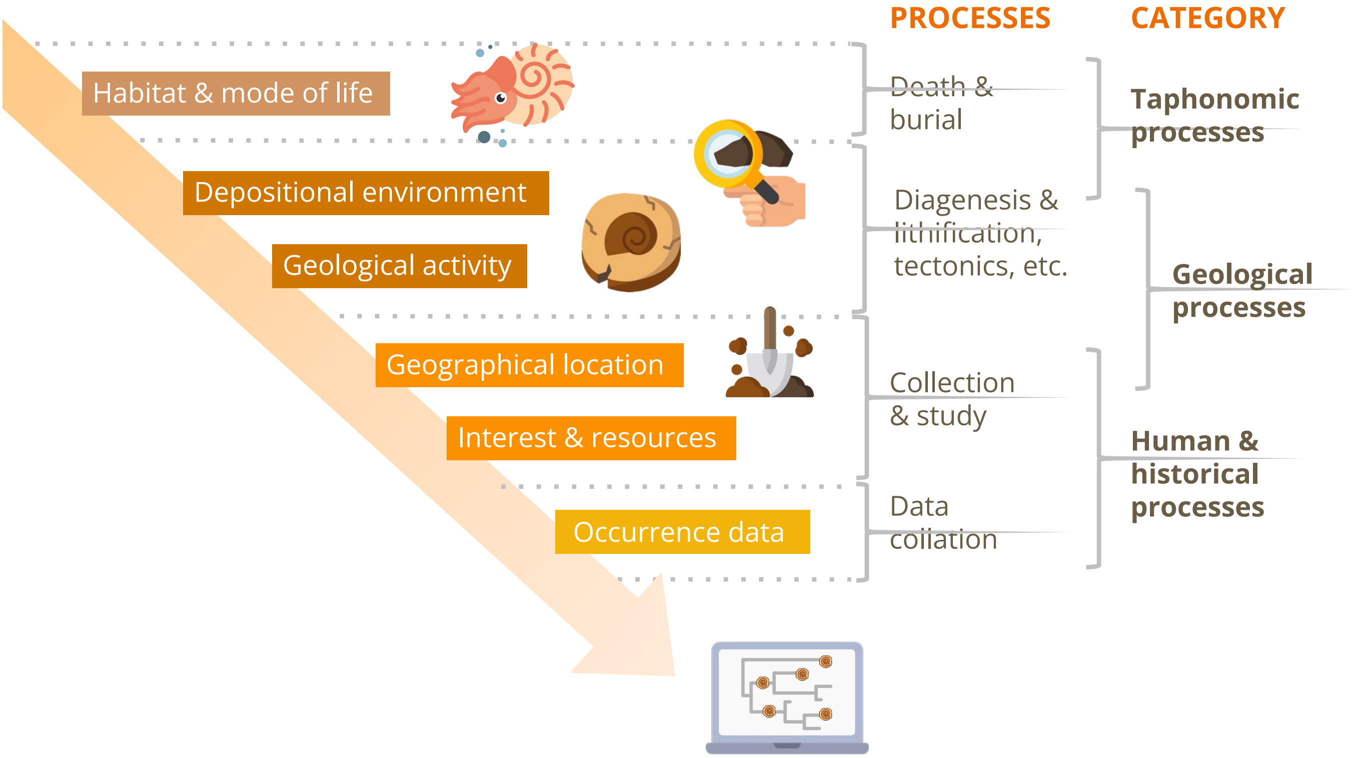
Mulvey et al. 2025

Research on the FBD model is an active field!

Simulation studies to understand the behaviour

Empirical research using different data types

Model development to better reflect reality



PROCESSES

CATEGORY

Habitat & mode of life

Depositional environment

Geological activity

Geographical location

Interest & resources

Occurrence data

Death & burial

Diagenesis & lithification, tectonics, etc.

Collection & study

Data collation

Taphonomic processes

Geological processes

Human & historical processes

Figure adapted from Emma Dunne