Modelos generativos

Ejemplo: Total evidence dating

Hay un area de la filogenética que no hemos abordado durante todo el semestre...

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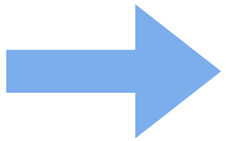
Inferencia de relaciones filogenéticas

- Estimación de árboles filogenéticos a partir de datos morfológicos y/o moleculares
- Estimación de tiempos de divergencia.

Nuestro paradigma hasta ahorita ha sido:

Paso 1

Obtengo una filogenia calibrada en tiempo absoluto



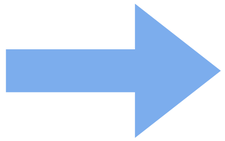
Paso 2

Uso esta filogenia para entender una pregunta evolutiva

Nuestro paradigma hasta ahorita ha sido:

Paso 1

Obtengo una filogenia calibrada en tiempo absoluto

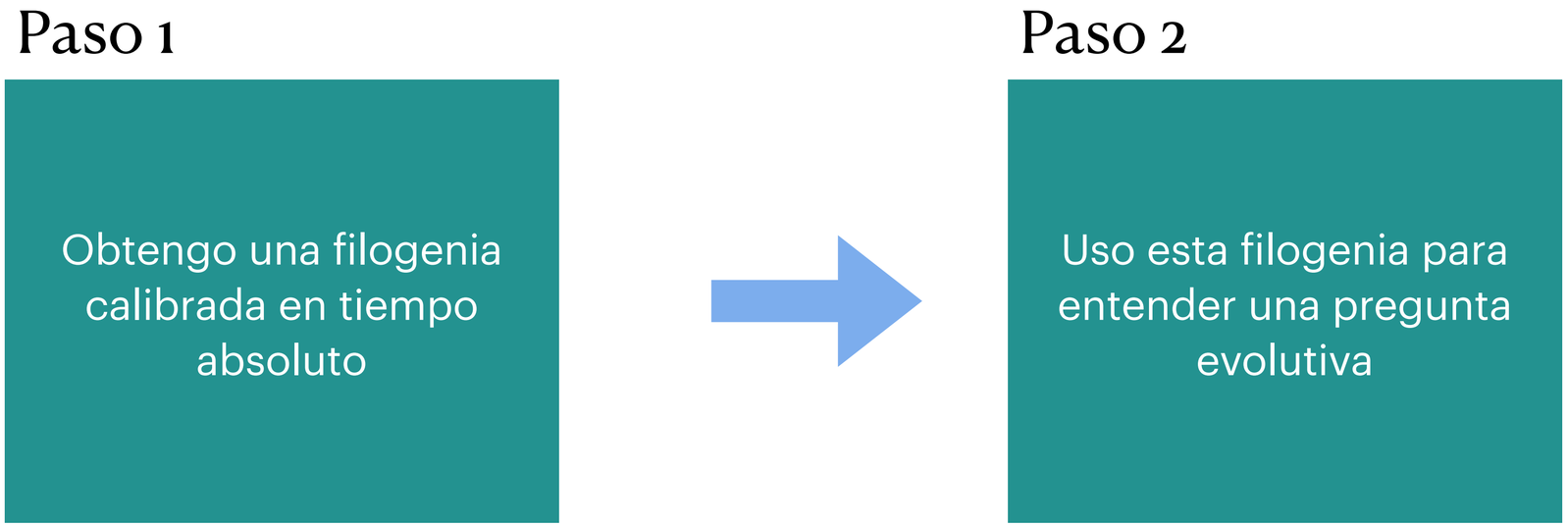


Paso 2

Uso esta filogenia para entender una pregunta evolutiva

En ocasiones integramos algo de la incertidumbre en el paso 1 en nuestros análisis del paso 2.

Nuestro paradigma hasta ahorita ha sido:



En ocasiones integramos algo de la incertidumbre en el paso 1 en nuestros análisis del paso 2.

¿Se te ocurren algunas limitantes de este enfoque?

Los linajes y todos sus atributos evolucionan de manera conjunta.

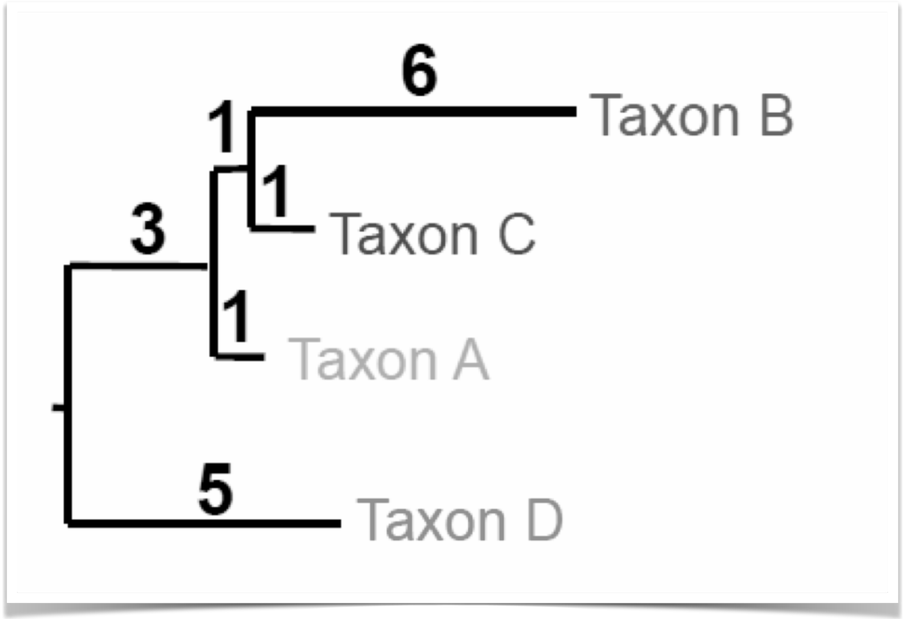
¿Qué son los modelos generativos?

Son modelos evolutivos **bayesianos** en los que se considera que las filogenias y sus caracteres asociados son el **resultado de un mismo proceso**. El modelo genera tanto la filogenia como los parámetros de interés.

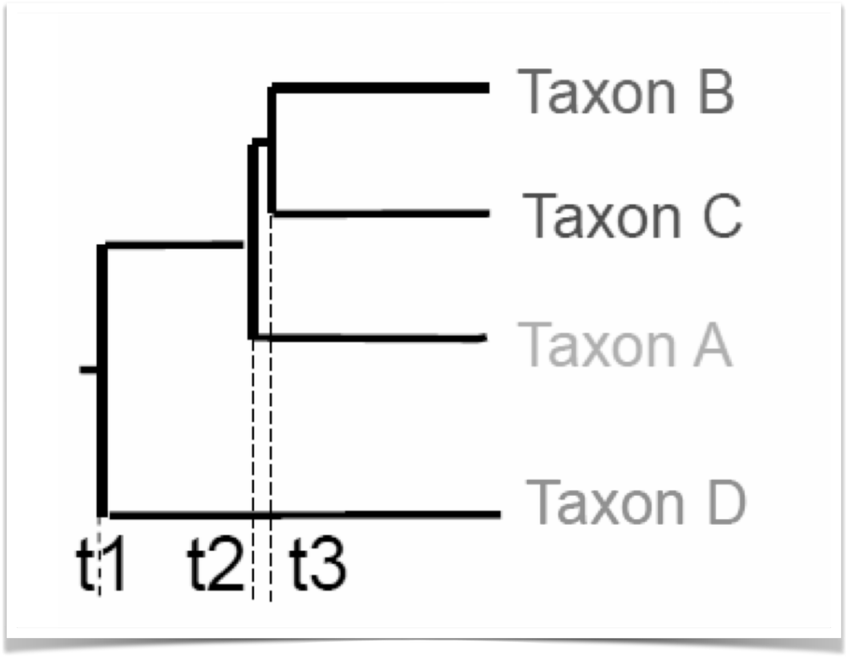
El uso de estos modelos comúnmente involucra inferencia conjunta de relaciones filogenéticas y otros procesos evolutivos.

1) Total evidence dating

Estimating divergence times

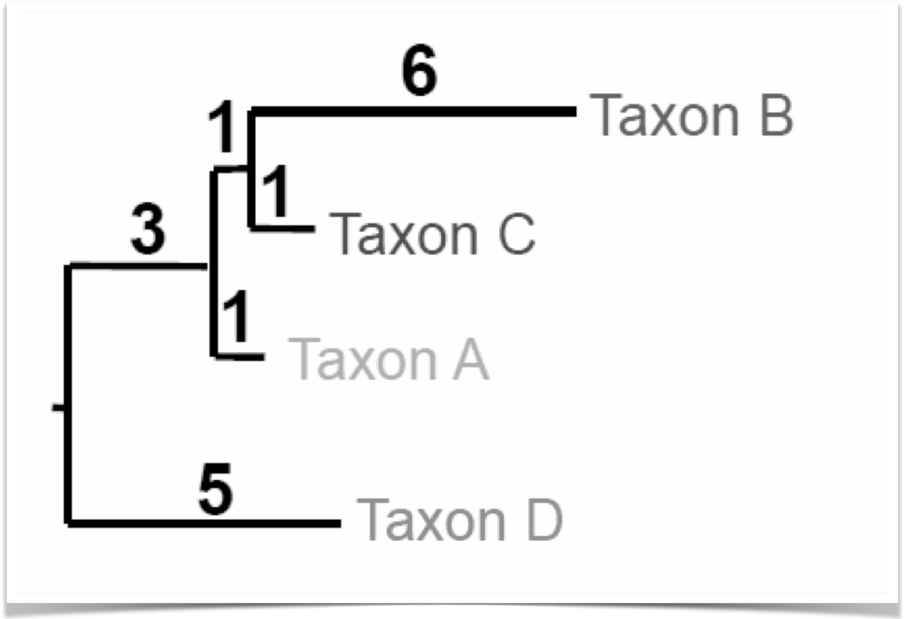


# of expected substitutions per unit of time

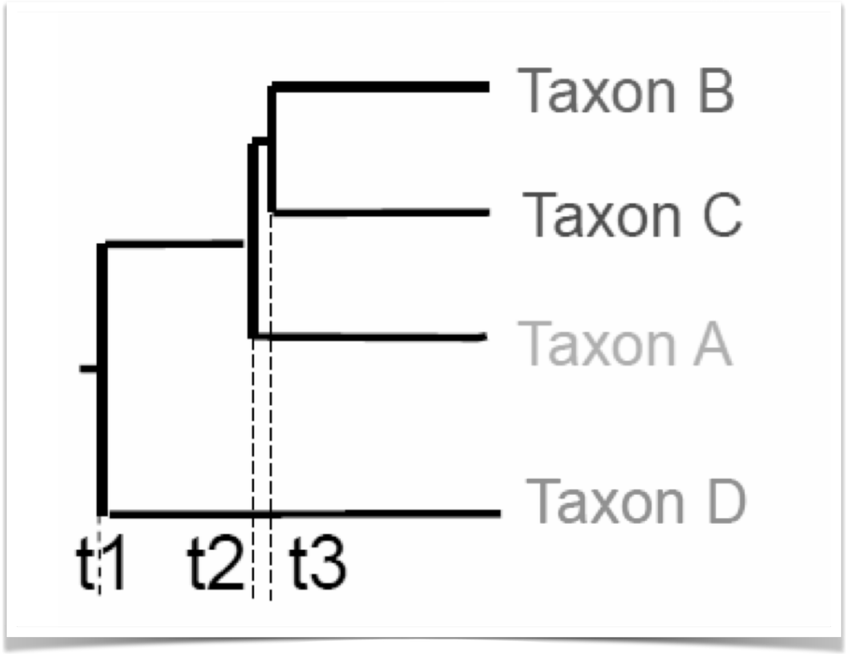


Units of time

Estimating divergence times



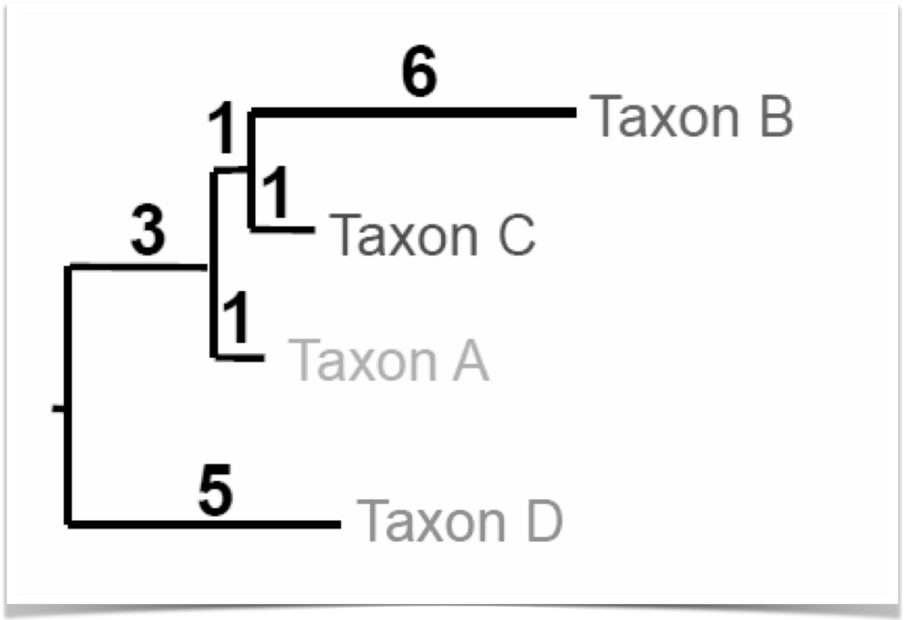
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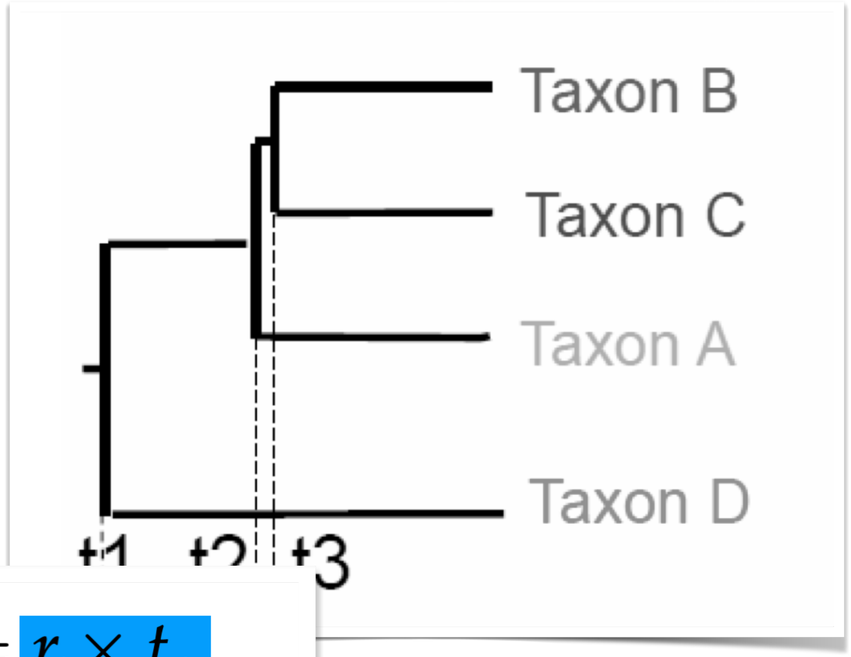
Units of time

$$v = r \times t$$

Estimating divergence times



# of expected substitutions per unit of time



Units of time

$$v = r \times t$$

$$v = r_1 \times t_1$$
$$v = r_2 \times t_2$$
$$v = r_3 \times t_3$$
$$v = r_4 \times t_4$$
$$\vdots$$

The temporal data comes from fossils:

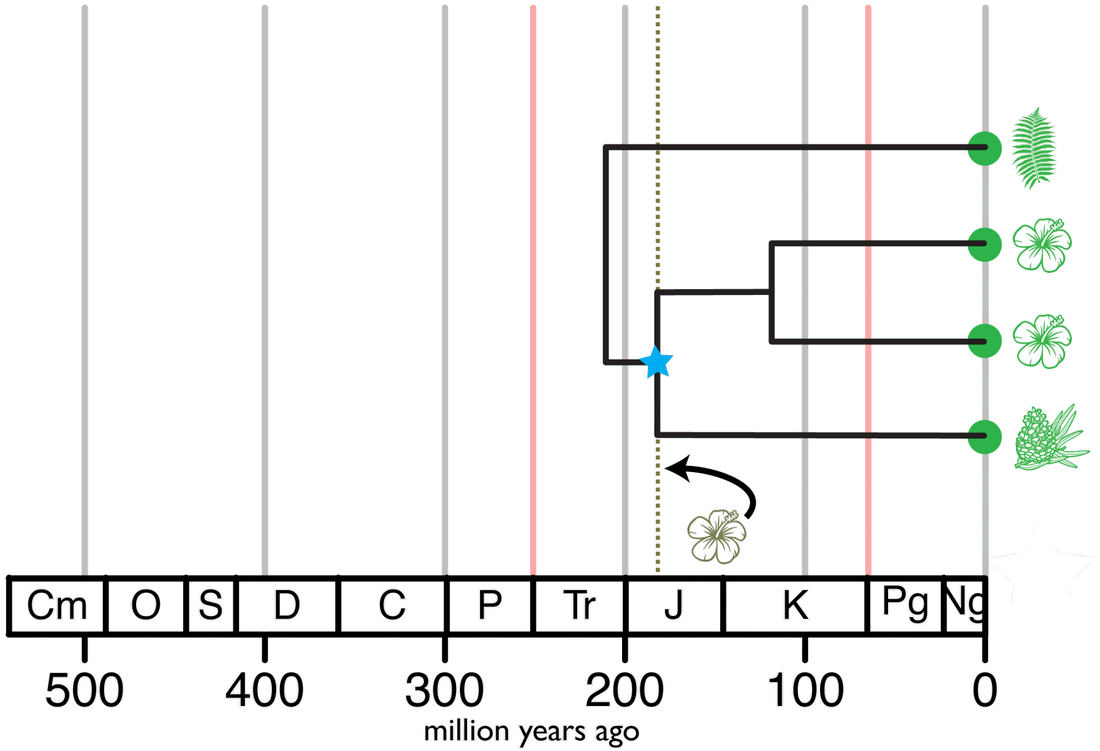




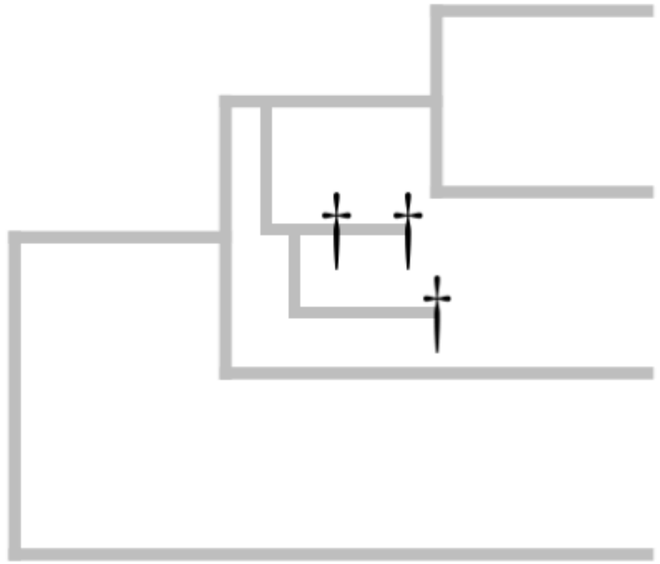




Two different approaches to divergence time estimation:



Node dating

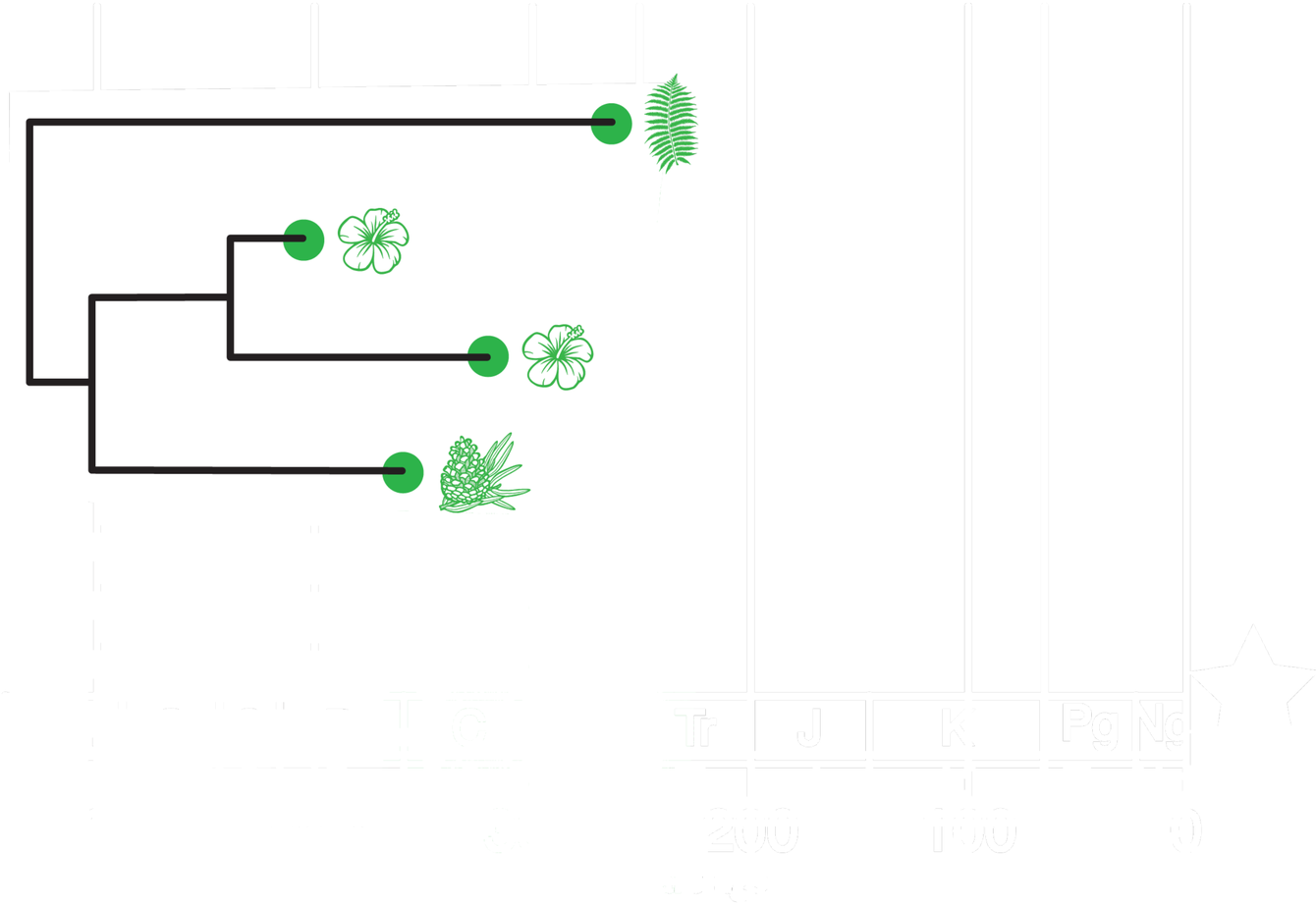


Tip dating

(Bayesian total evidence dating)

Node dating

We have a phylogeny with branch lengths in units of **expected number of substitutions per site.**

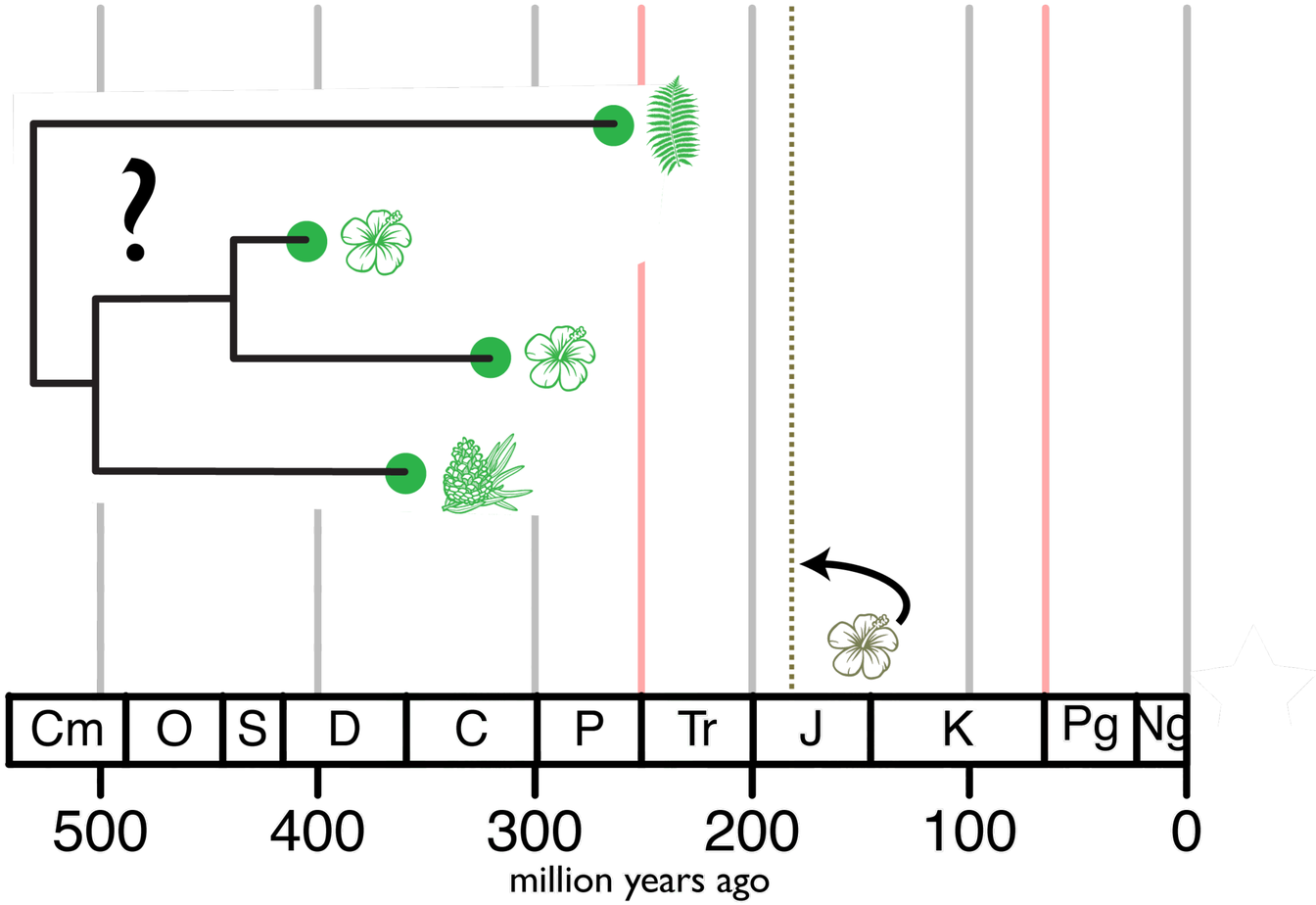


Slides modified from Carl Rothfels'

Node dating

We have a group of terminals with branch lengths in units of expected number of substitutions per site.

We have **one fossil available**.



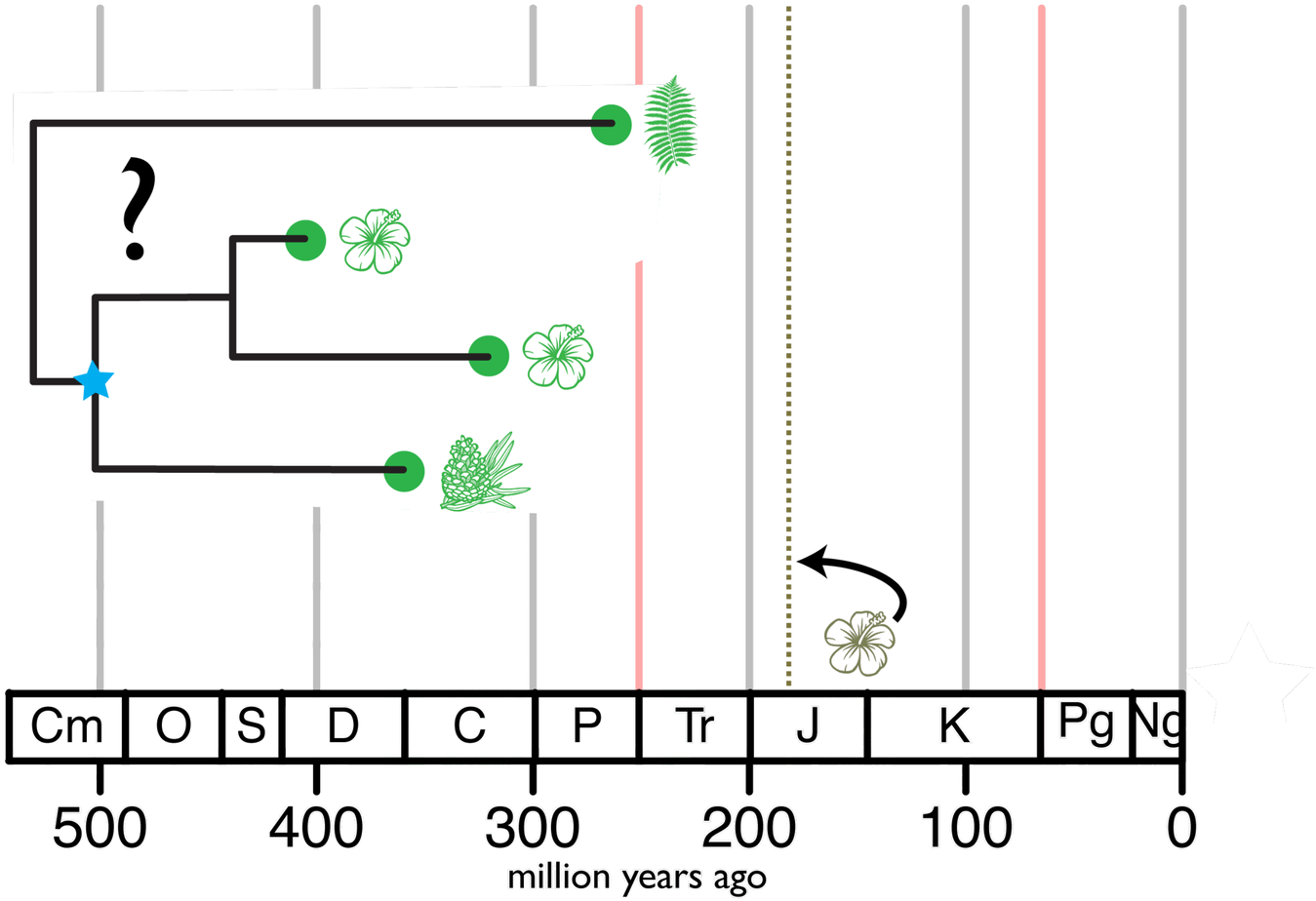
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Node dating

We have a group of terminals with branch lengths in units of expected number of substitutions per site

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If we know what group the fossil belongs to, then we know that the stem age of that group has to be at least as old as the fossil…



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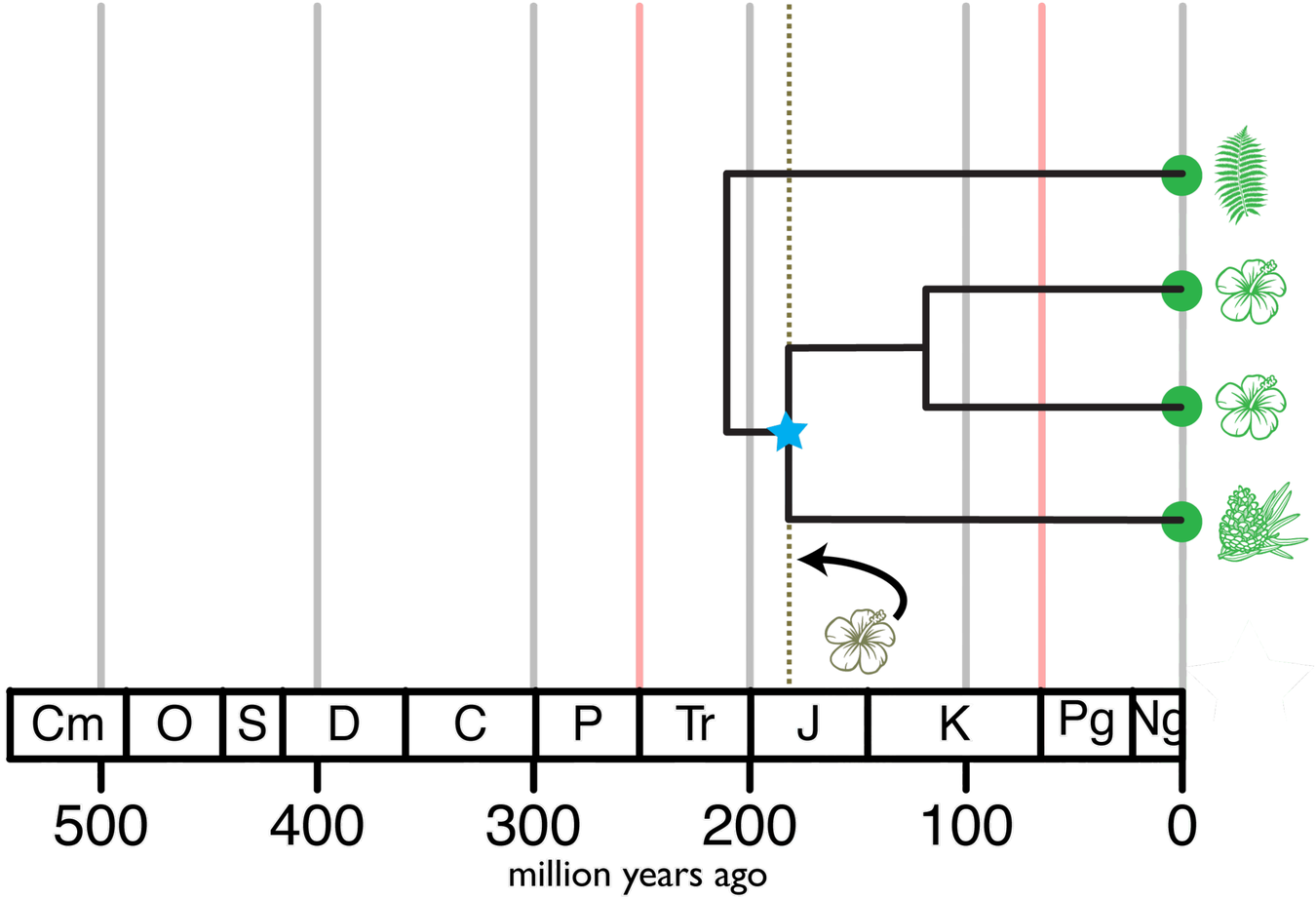
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…this gives us an **absolute time**, and our clock and tree models can give us the **relative times**.



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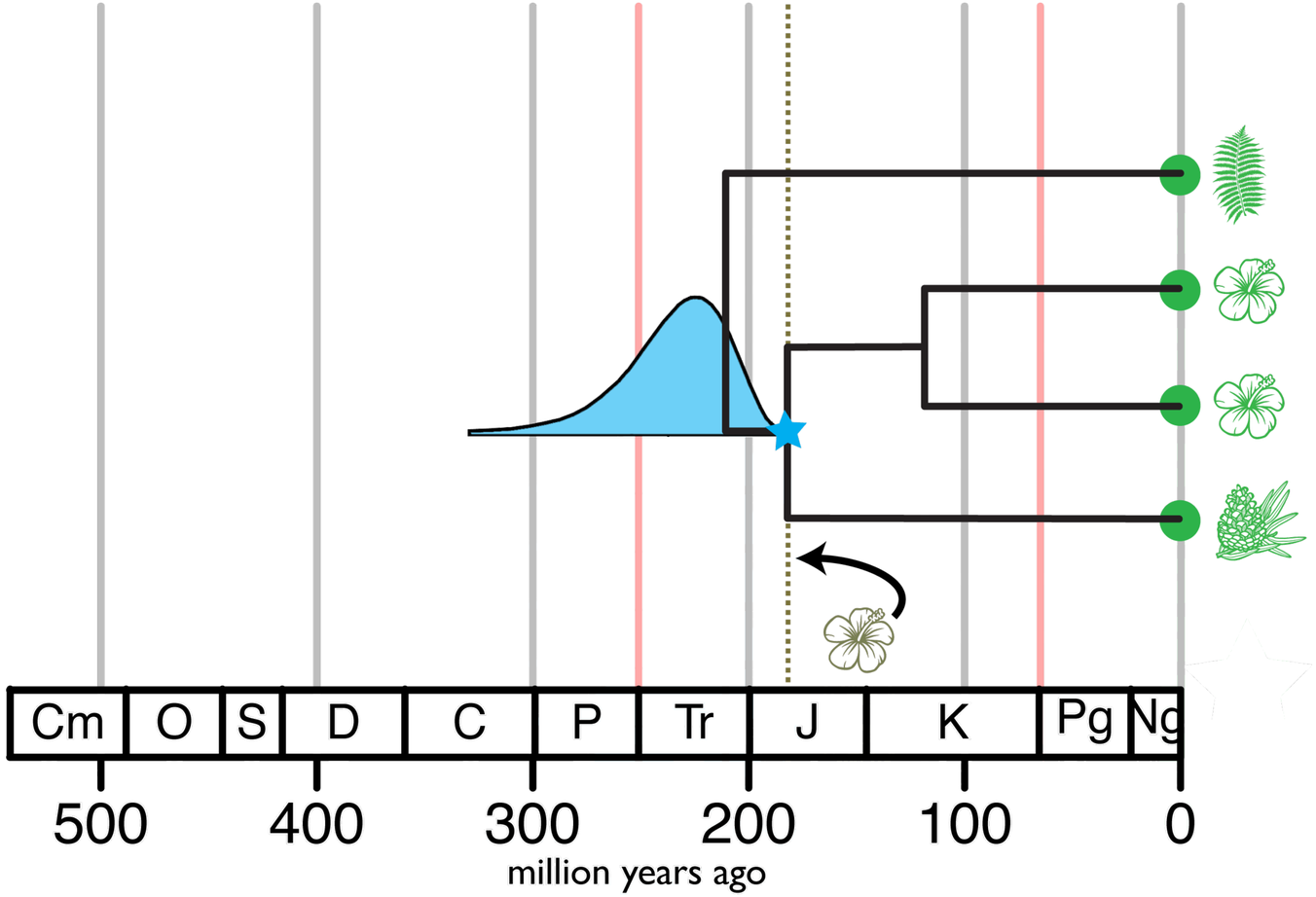
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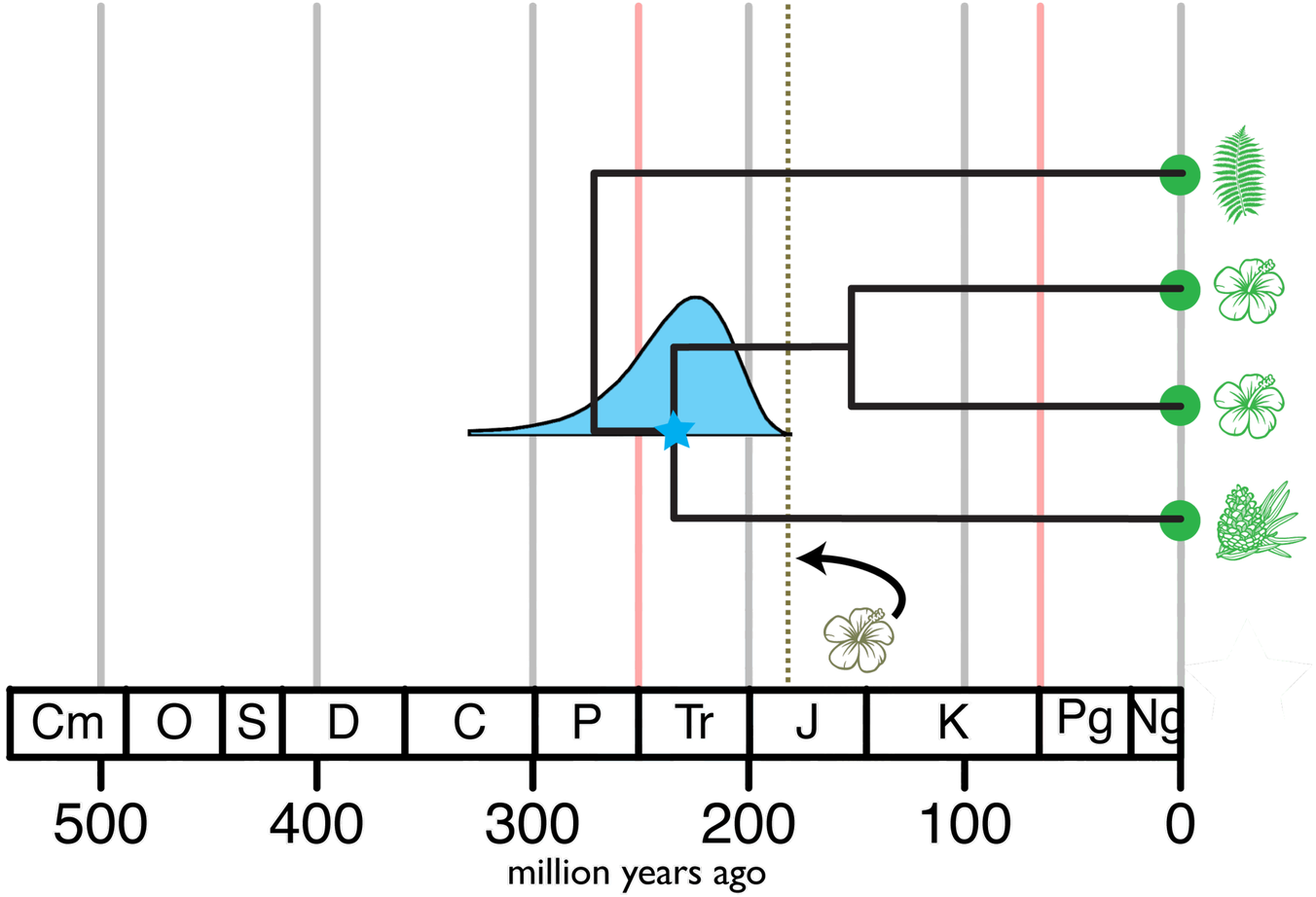
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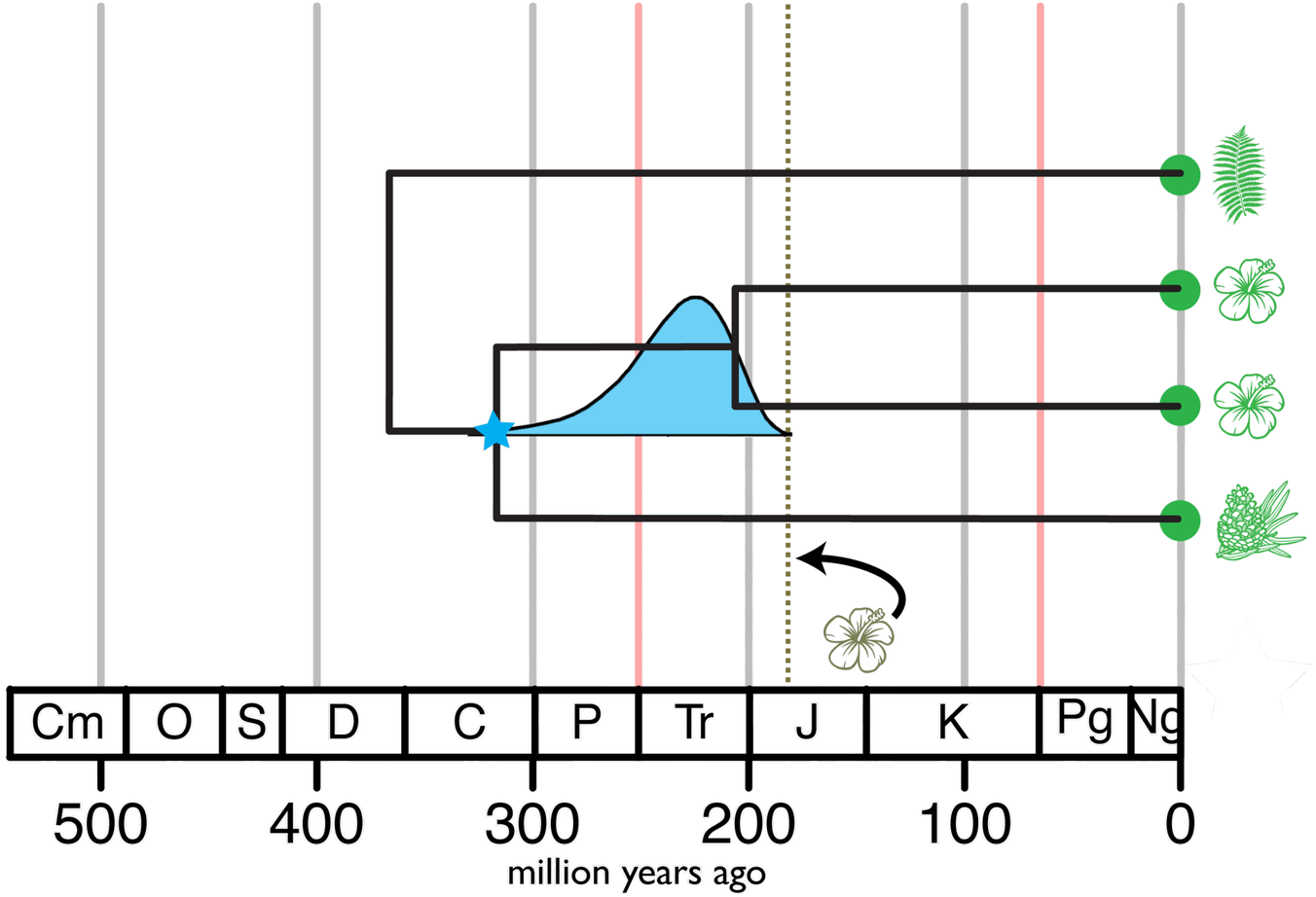
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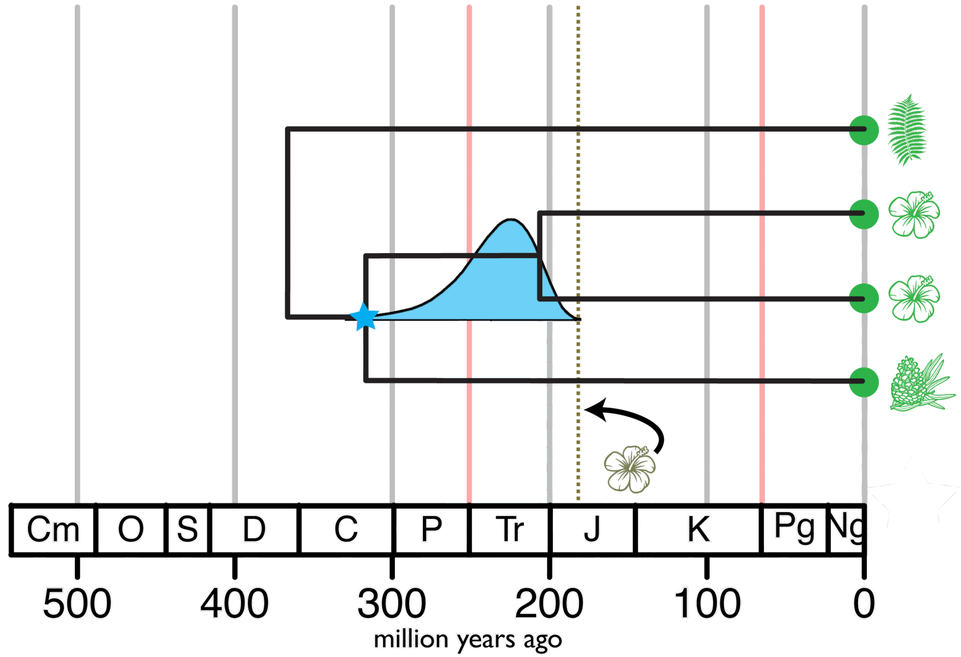


Slides modified from Carl Rothfels'

Node dating

This node-dating approach has a series of drawbacks:

1. Each fossil has to be **unequivocally assigned** to a particular node in the tree.
2. Only the **oldest fossi**l is relevant.
3. The relationship between the fossil and the node (**the type of calibration distribution** to use) is determined by the investigator, often based on implicit assumptions of morphological evolution and of the fossilization process



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Total Evidence Dating (One type of tip dating)

Total-evidence dating conveniently resolves these problems.

Slides modified from Carl Rothfels'

Total Evidence Dating

Total-evidence dating conveniently resolves these problems.

Where does the fossil go?

How old is the node?

Slides modified from Carl Rothfels'

Total Evidence Dating

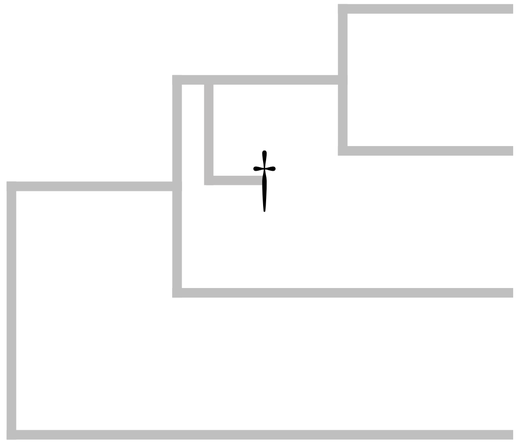
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Where does the fossil go?

Position inferred from the data!

How old is the node?

Branch lengths inferred from the data!



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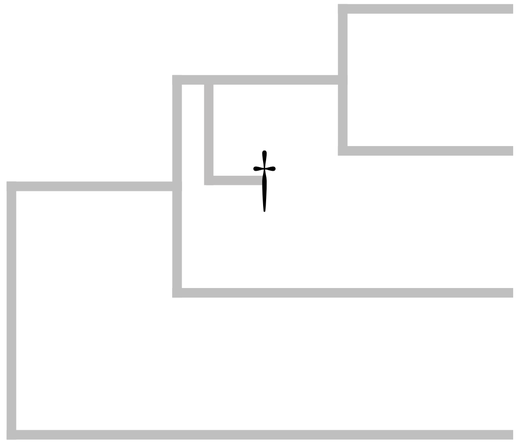
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What if there are multiple fossils?

Slides modified from Carl Rothfels'

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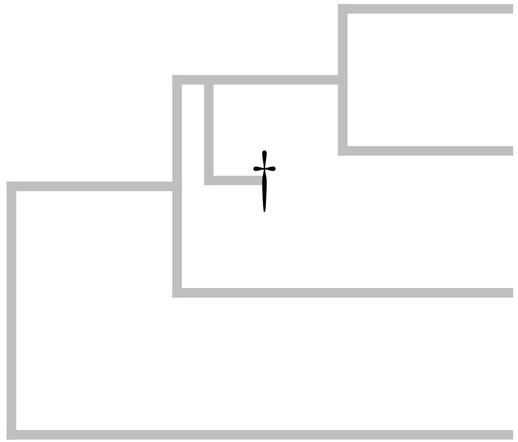
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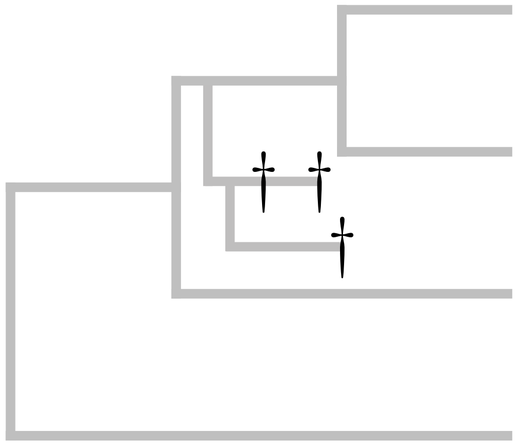
How old is the node?

Branch lengths inferred from the data!



What if there are multiple fossils?

No problem!—More information for the model



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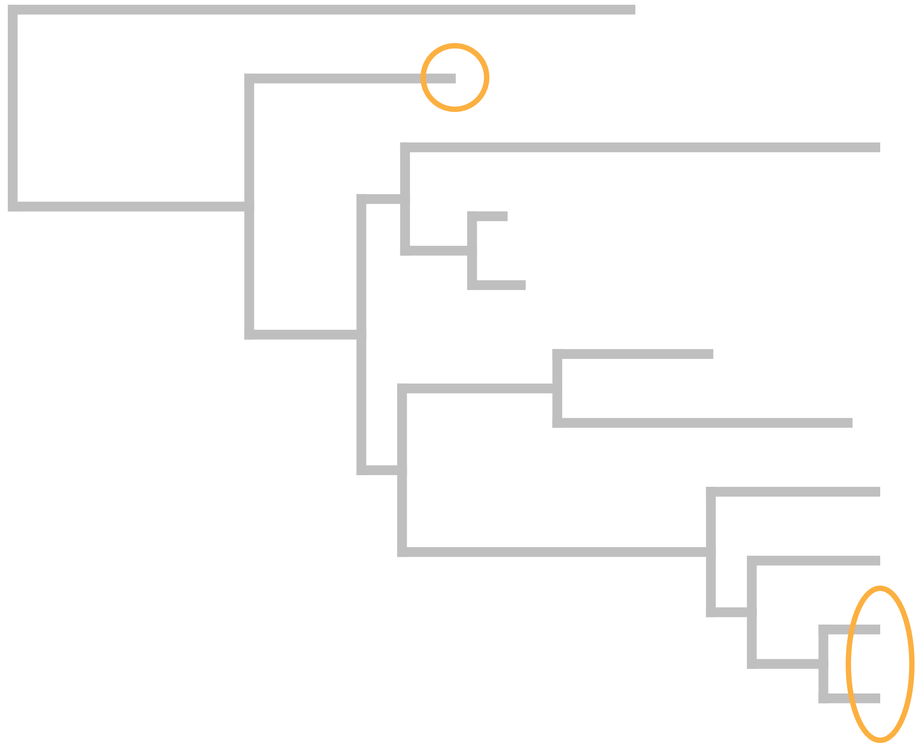
Additionally, fossil ages contain topological information. Ignoring this can be misleading.



Slides modified from Carl Rothfels'

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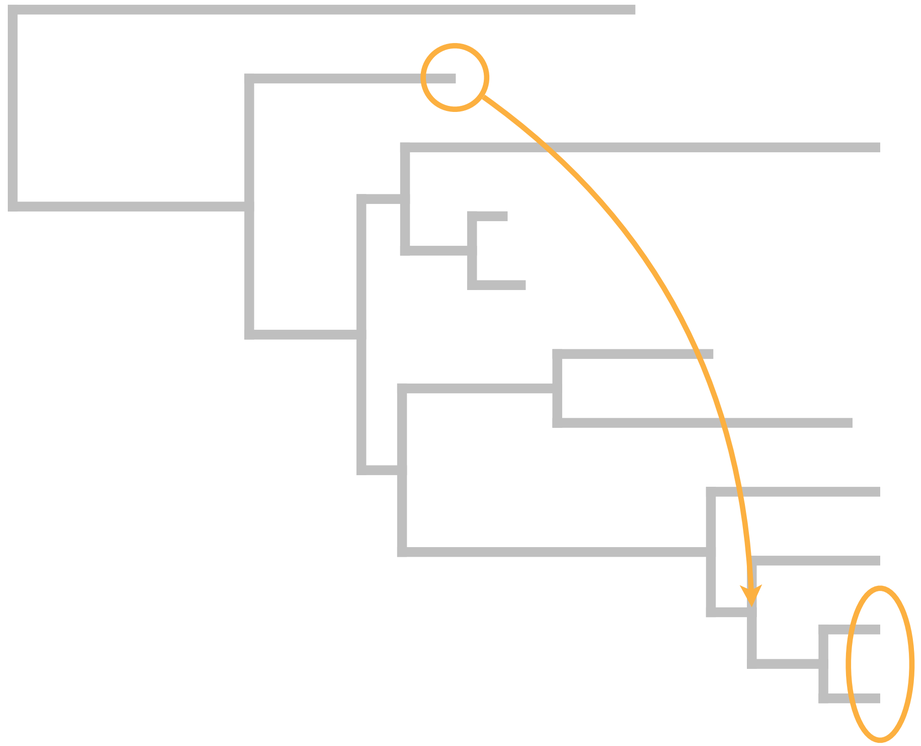
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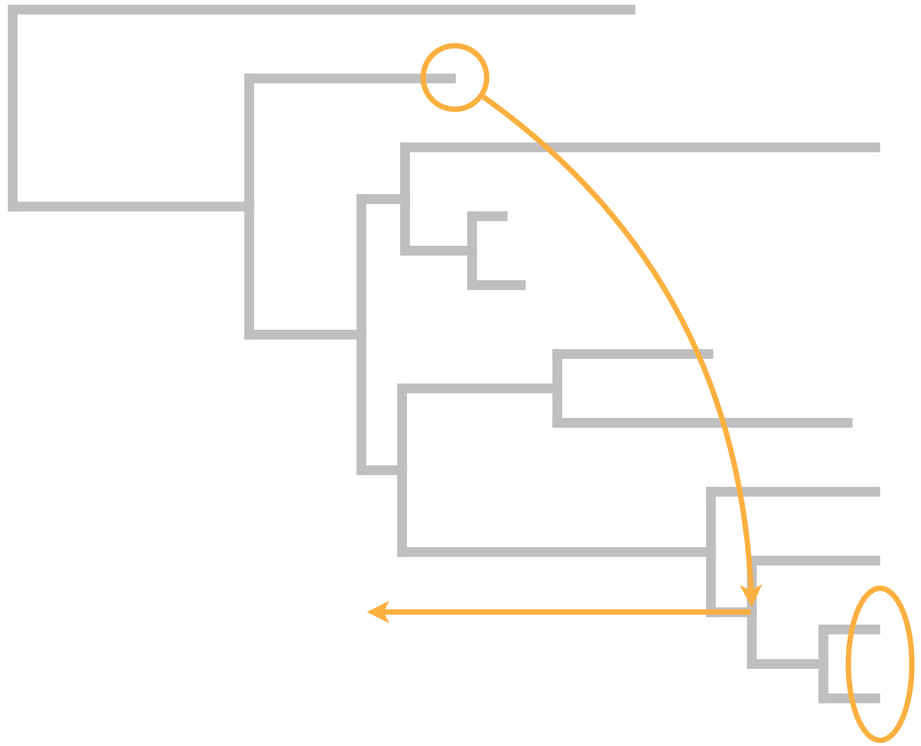
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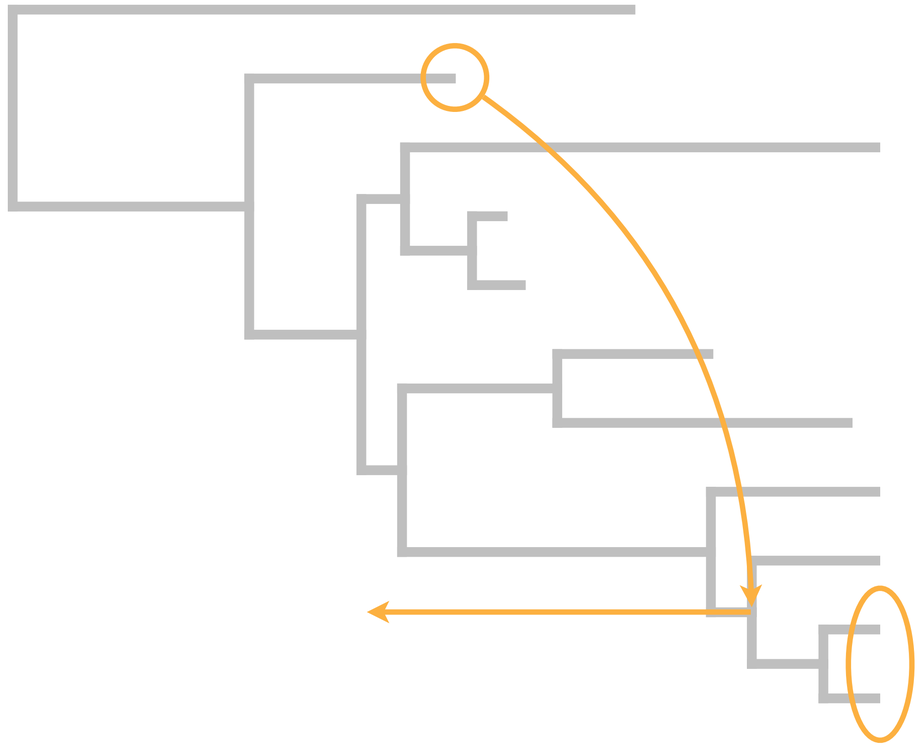
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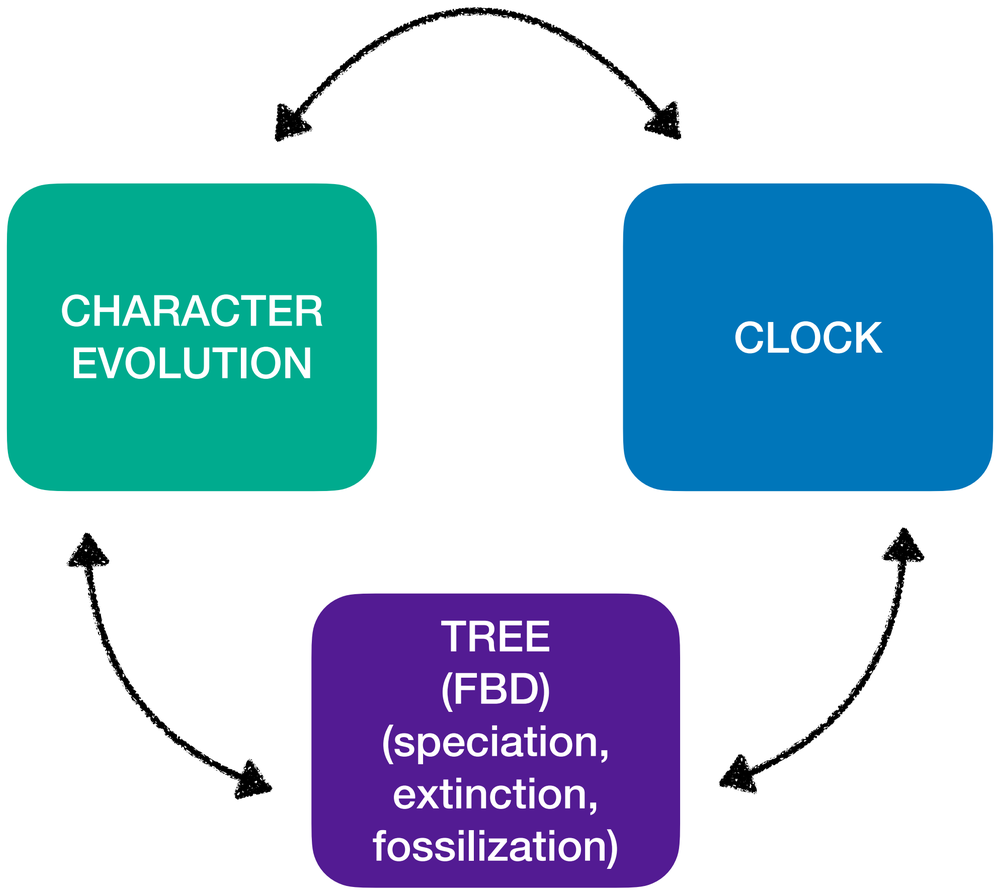
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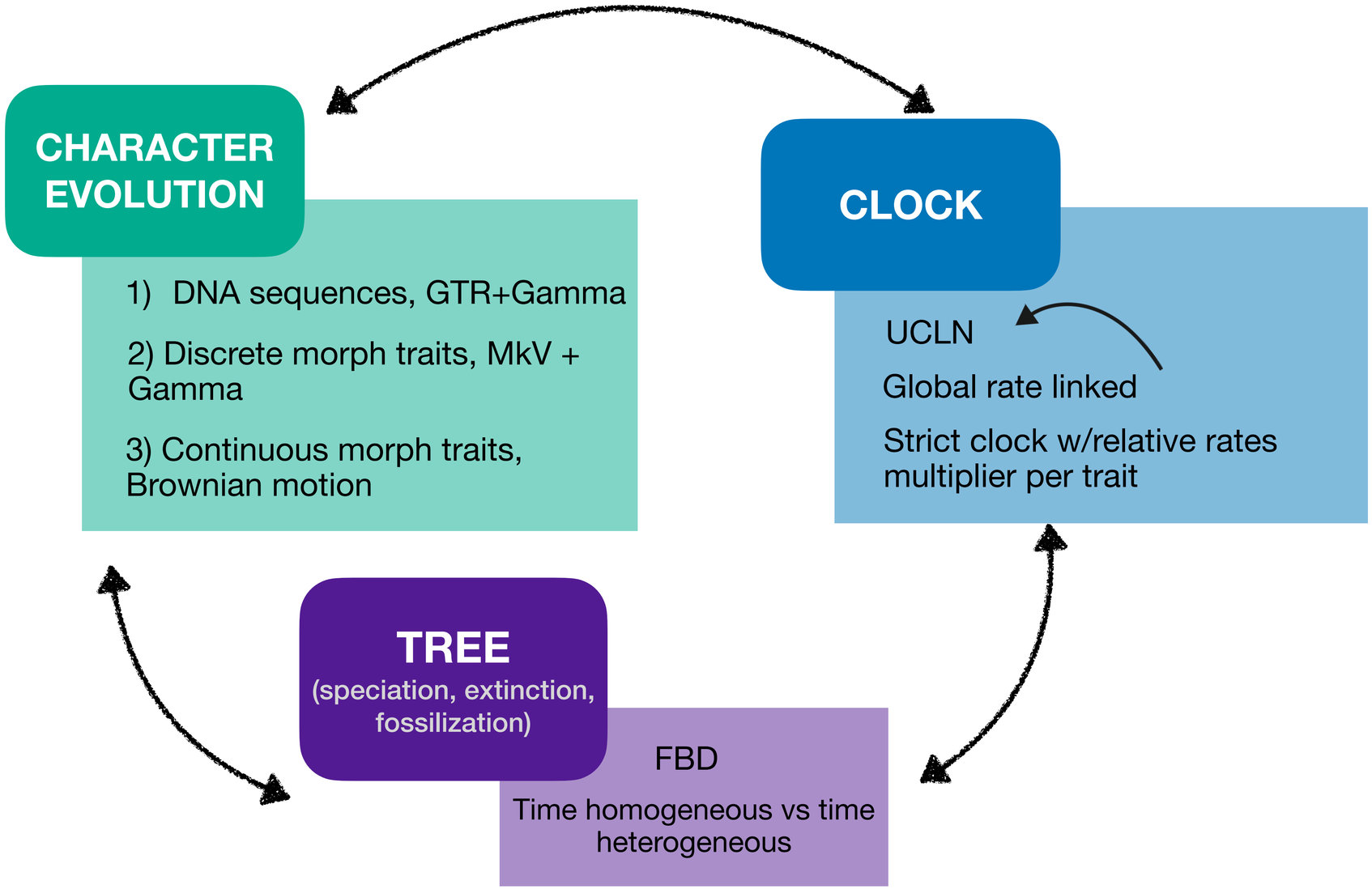


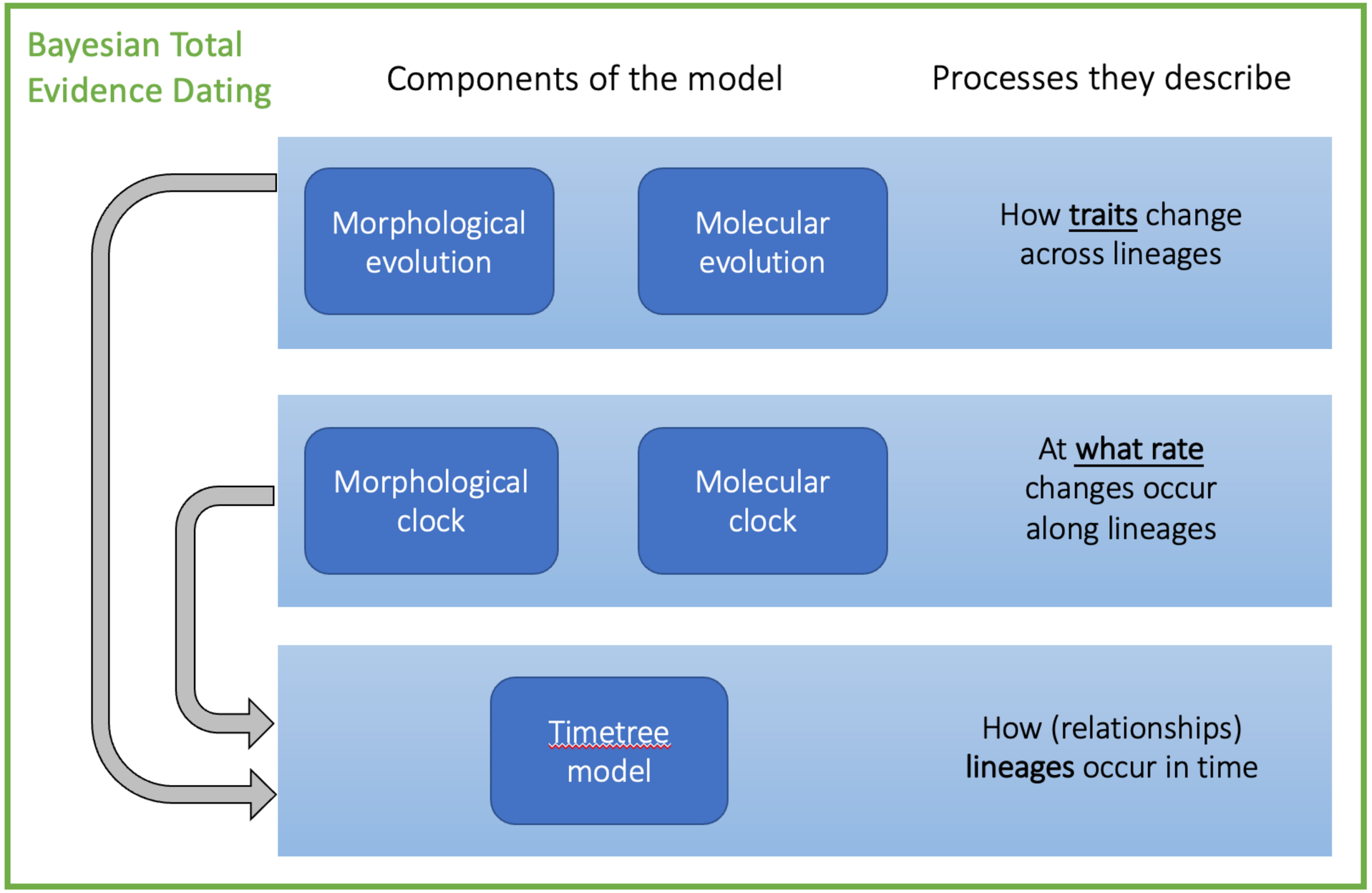
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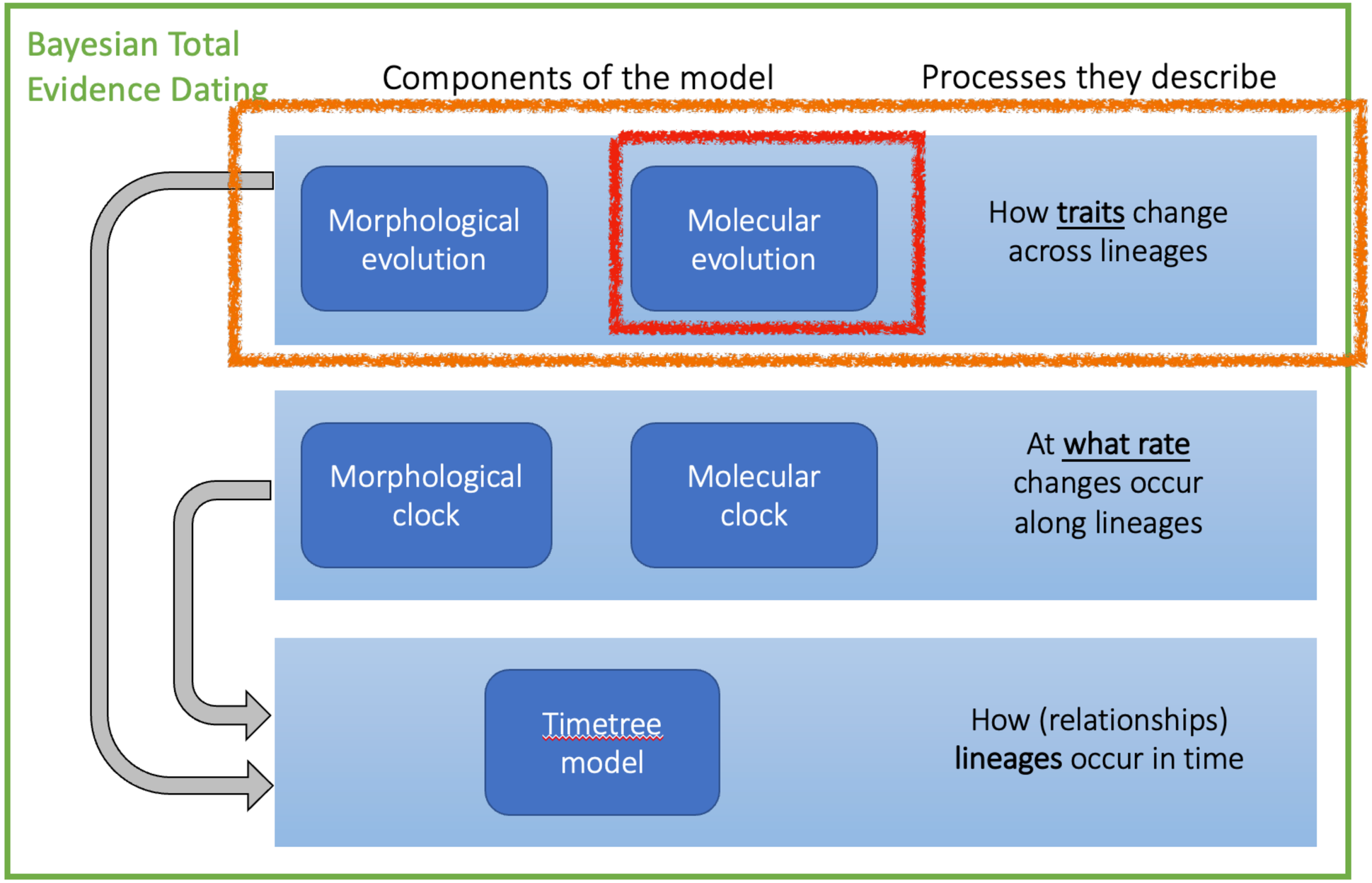
The Bayesian TED approach



The Bayesian TED approach




Bayesian Total Evidence Dating
Components of the model
Processes they describe
Morphological evolution
Molecular evolution
How traits change across lineages
Morphological clock
Molecular clock
At what rate changes occur along lineages
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How (relationships) lineages occur in time


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The trait evolution model: Molecular evolution

Describes how nucleotides evolve

GTR + G

Rate matrix Q

$$Q = \begin{pmatrix} - & q_{AC} & q_{AG} & q_{AT} \\ q_{CA} & - & q_{CG} & q_{CT} \\ q_{GA} & q_{GC} & - & q_{GT} \\ q_{TA} & q_{TC} & q_{TG} & - \end{pmatrix}$$

Describes the transition rates among nucleotides

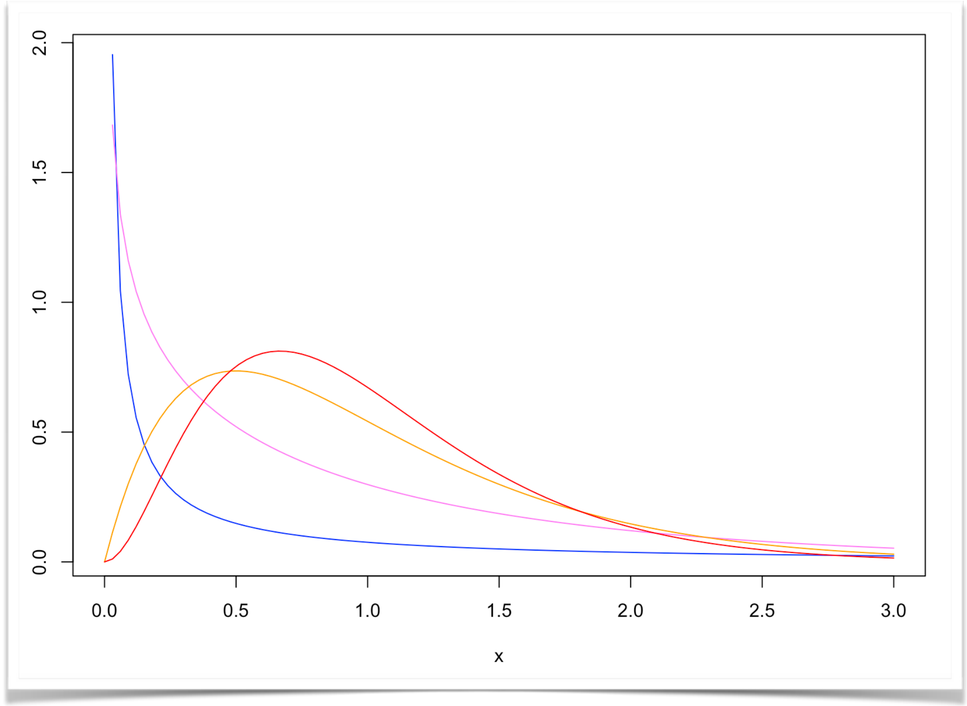
Gamma

The trait evolution model: Molecular evolution

Describes how nucleotides evolve

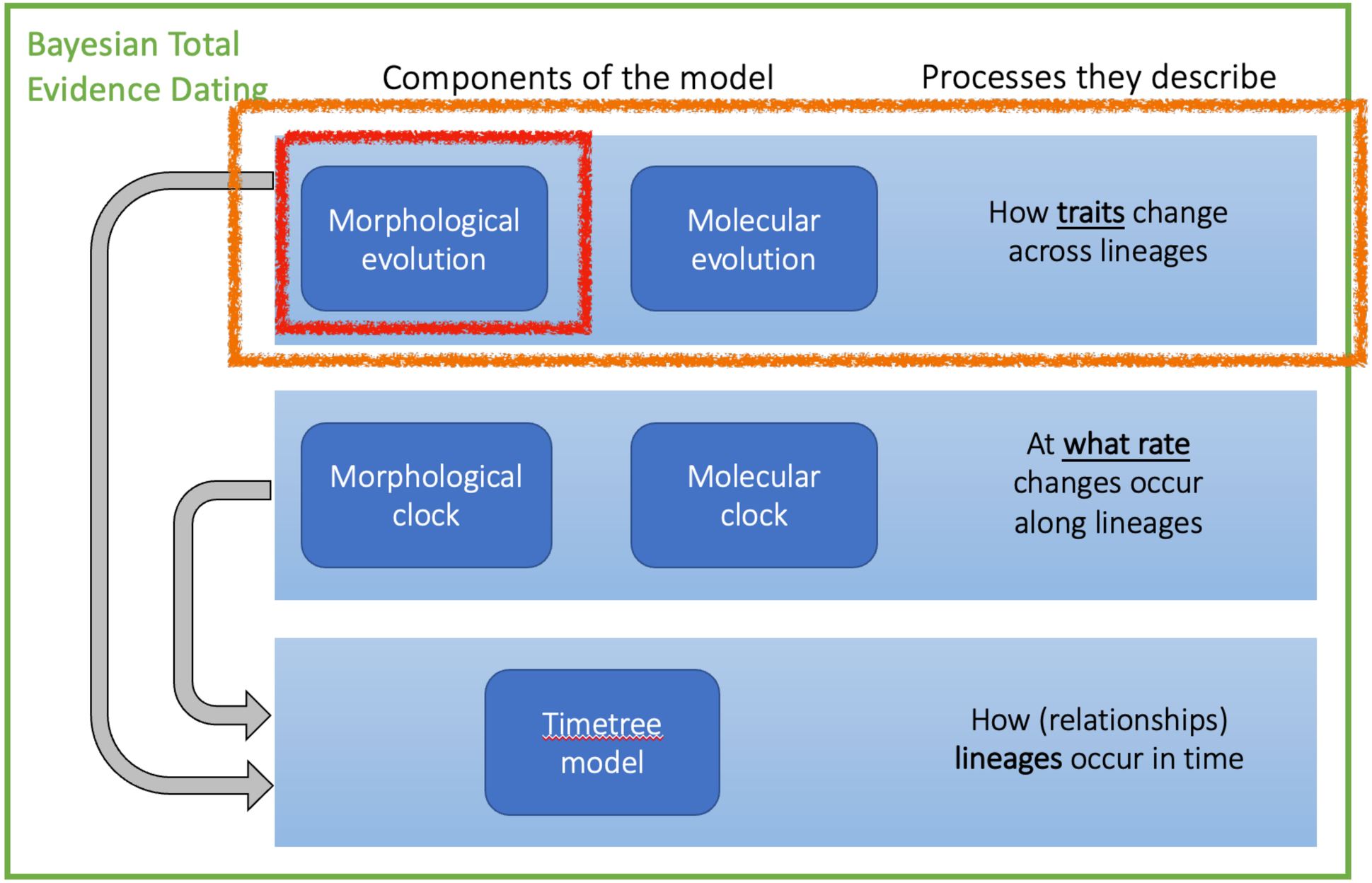
GTR + G

Rate matrix
Q



Gamma

Describes the variation in the rates among sites of the same alignment

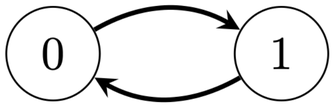

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The trait evolution model: Morphological evolution

Describes how morphological traits evolve

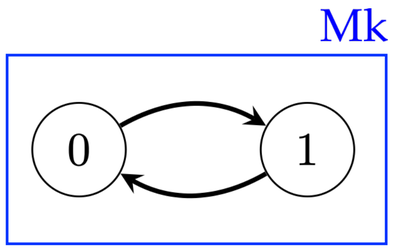
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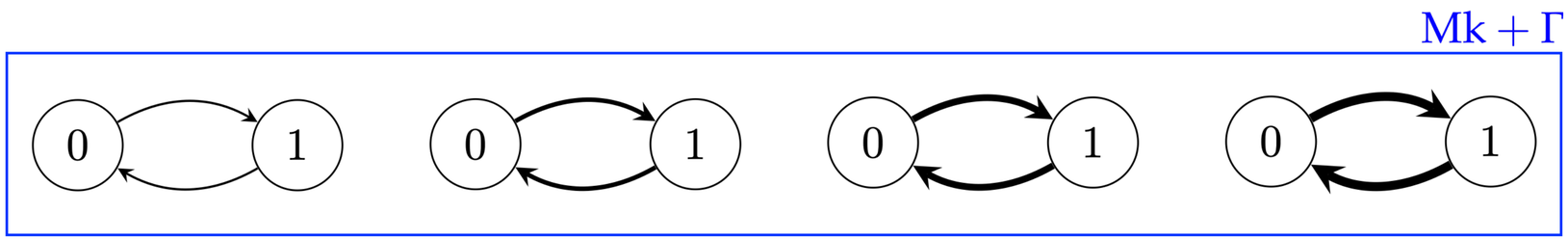
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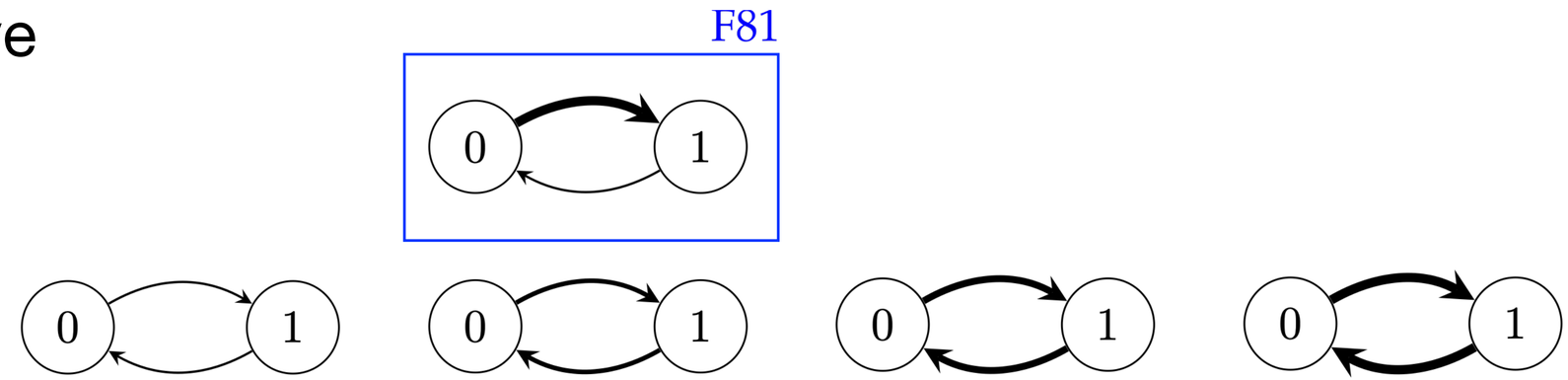
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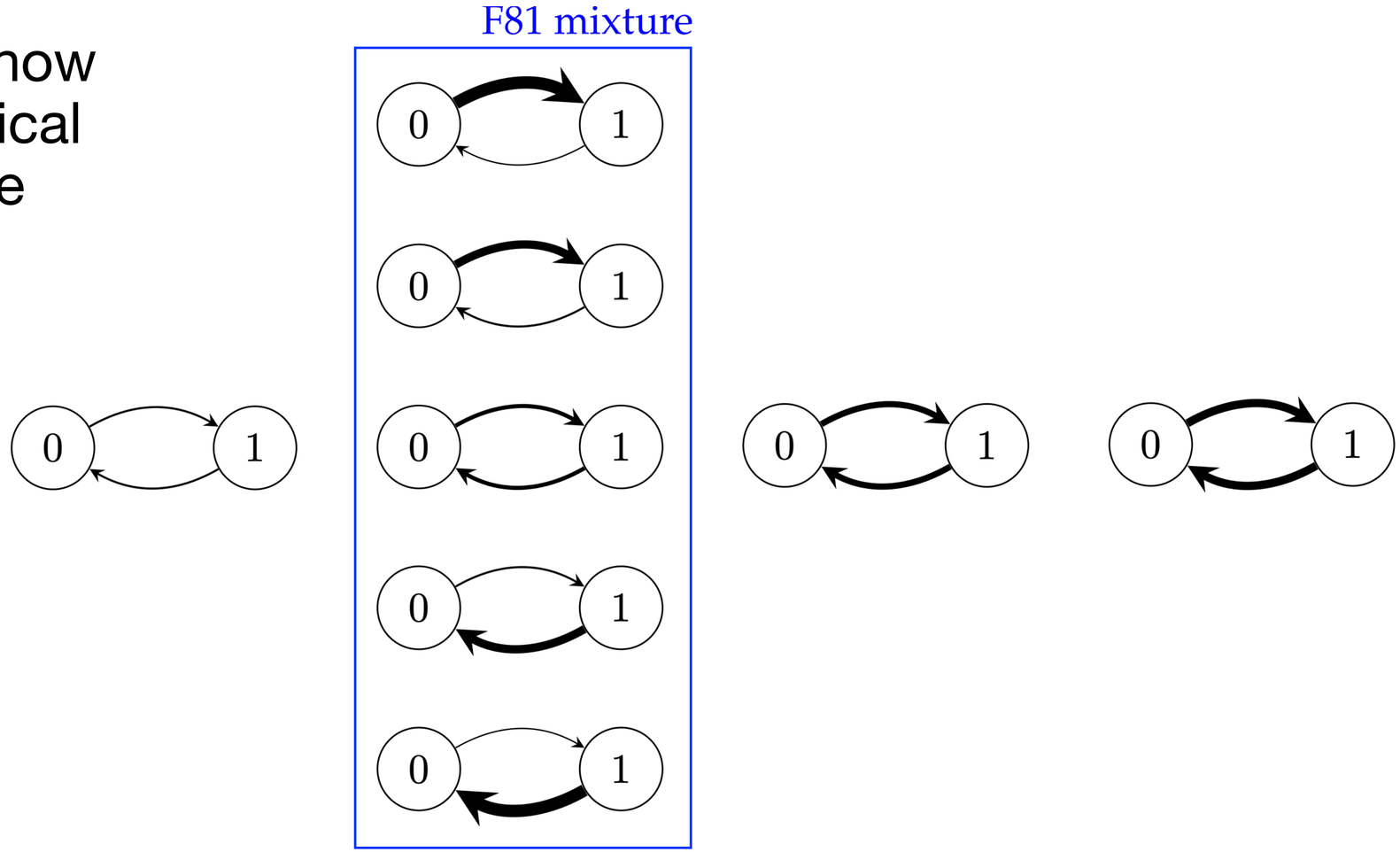
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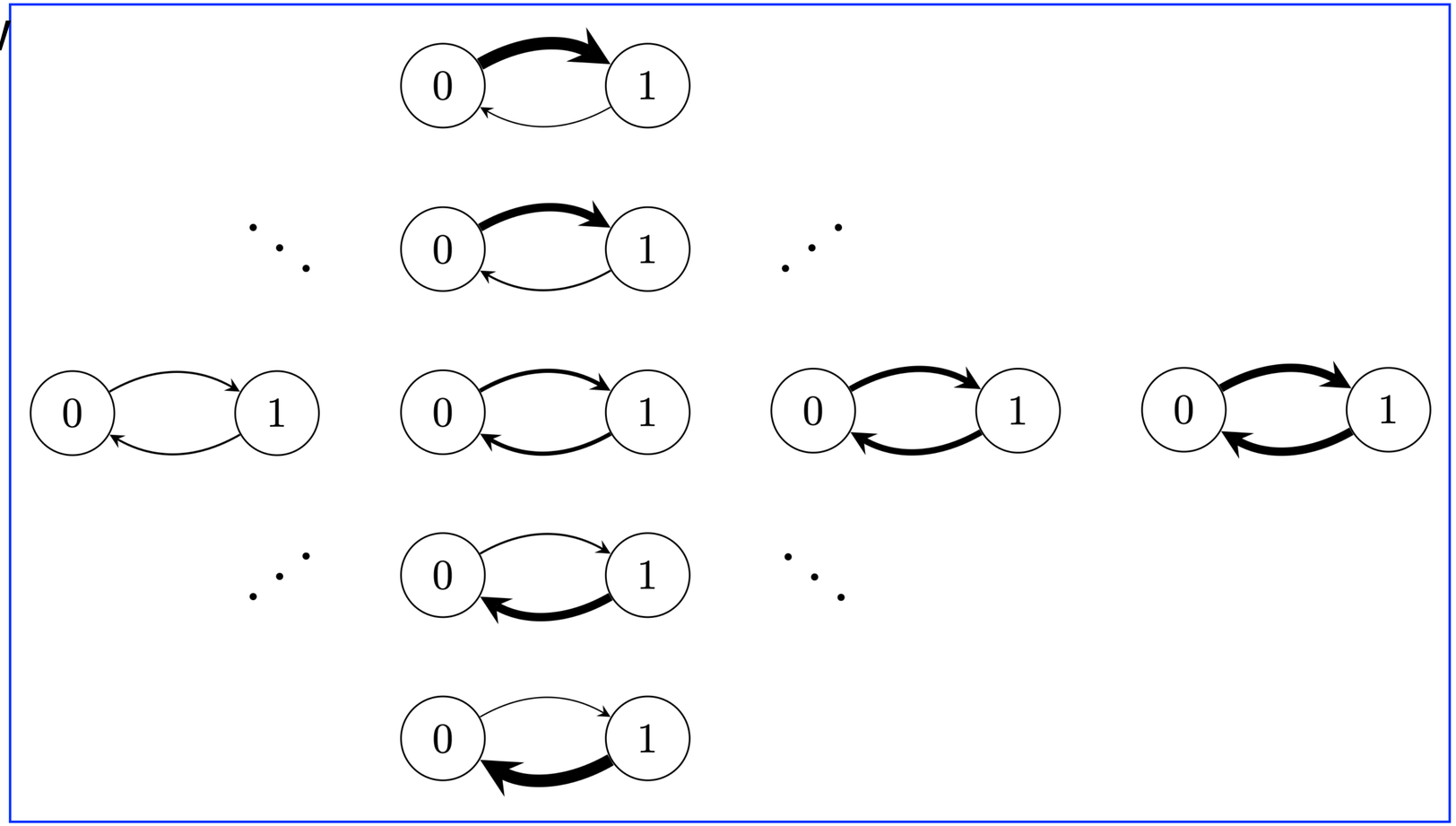
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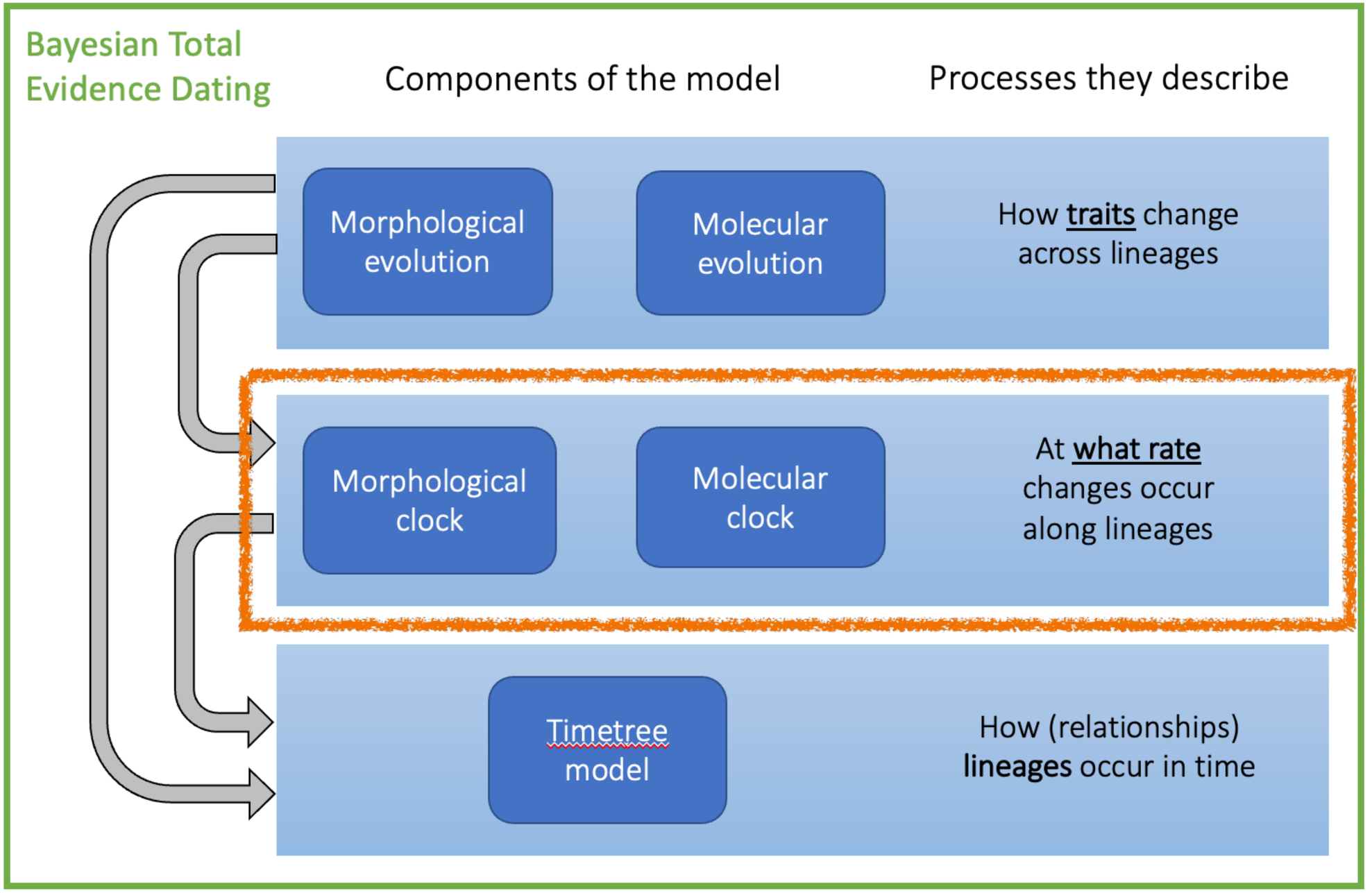


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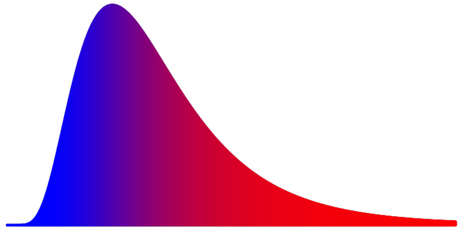
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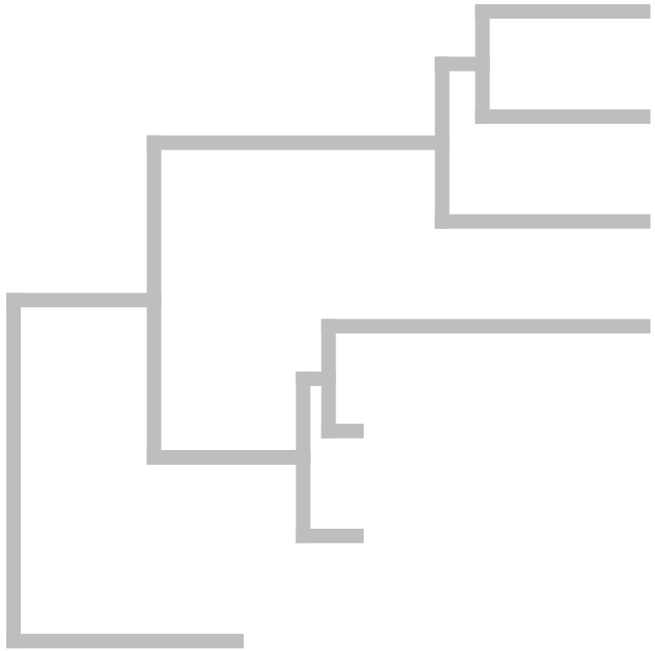
F81 mixture + Γ



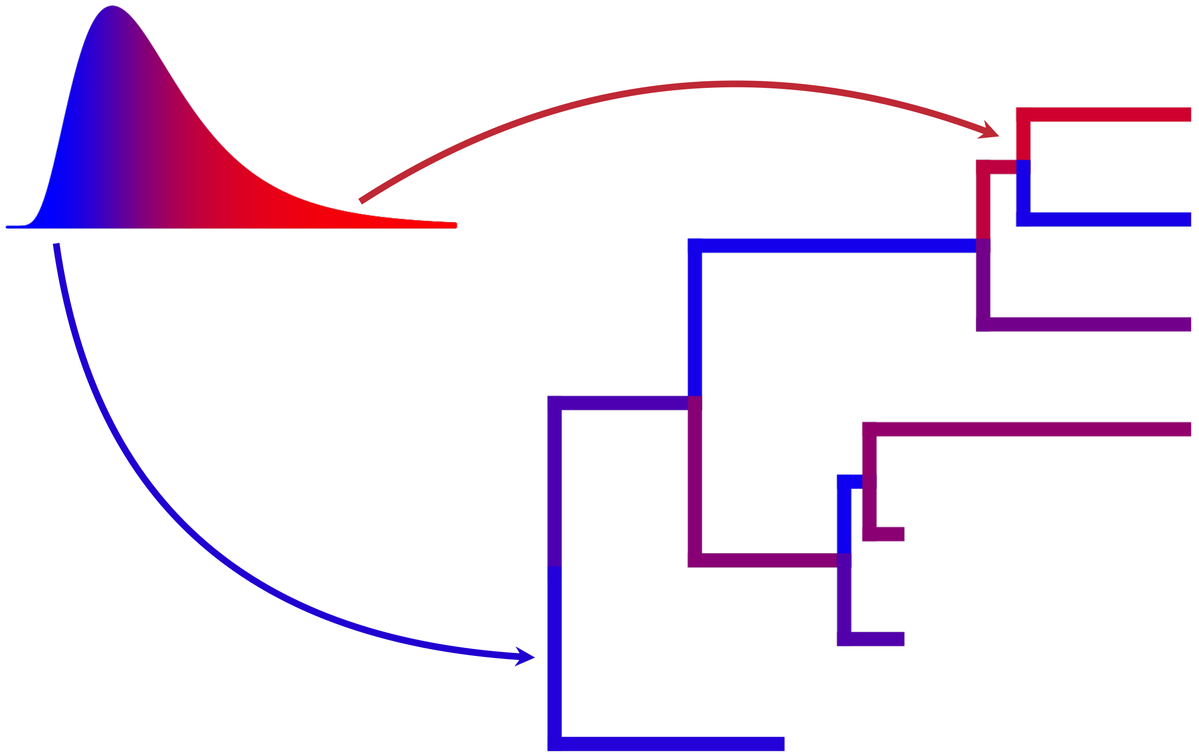

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The relaxed clock model:

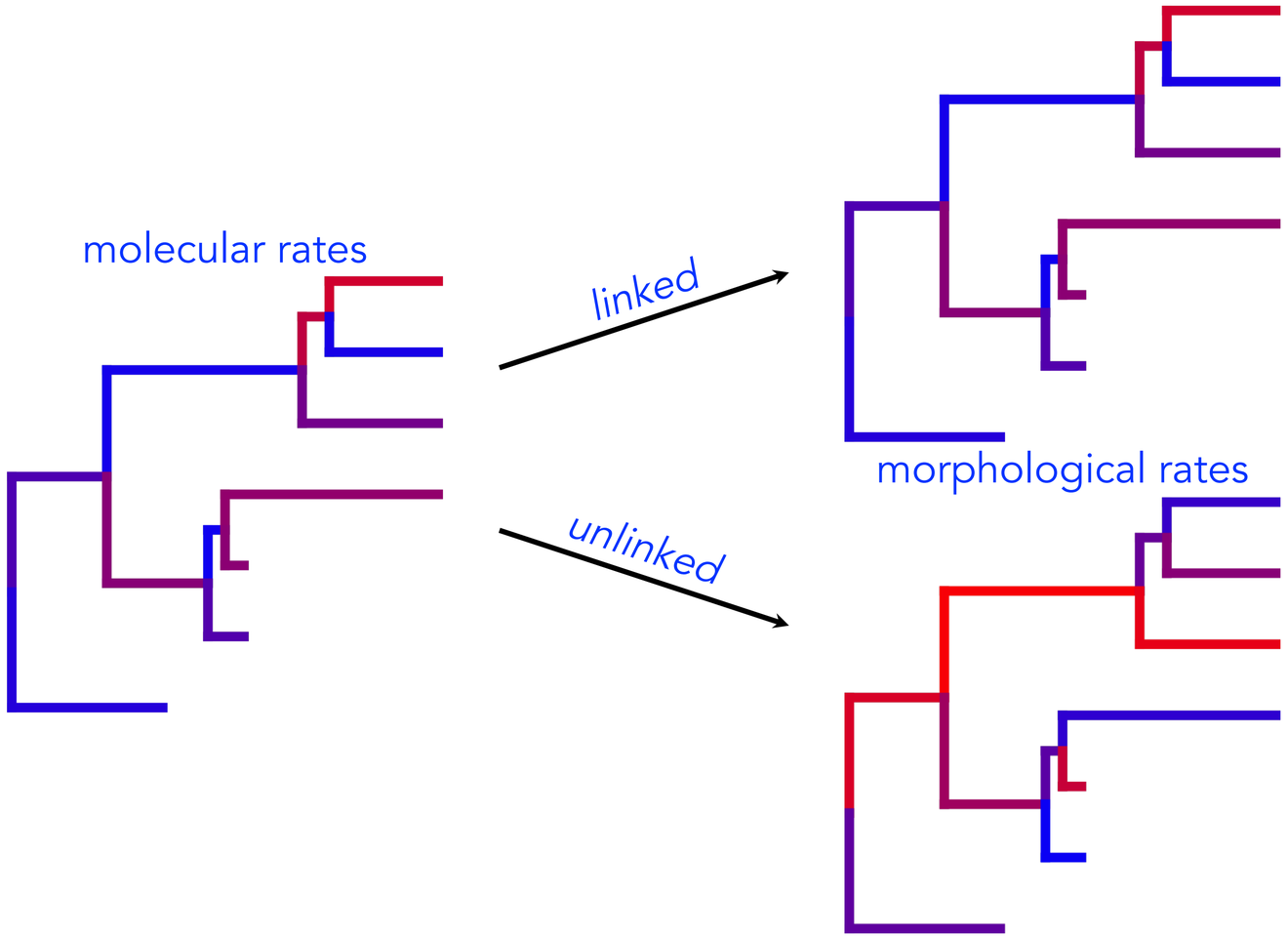


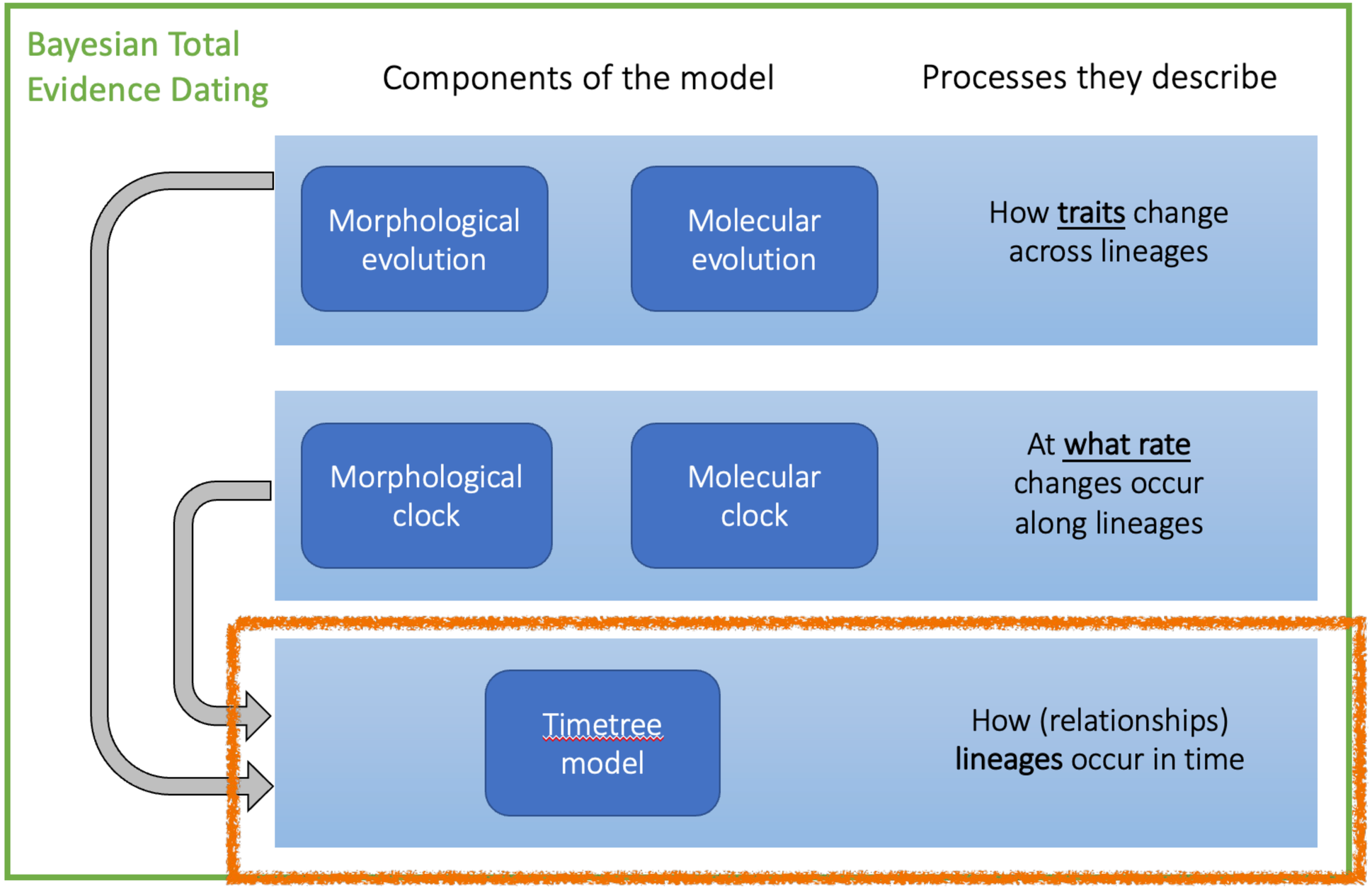


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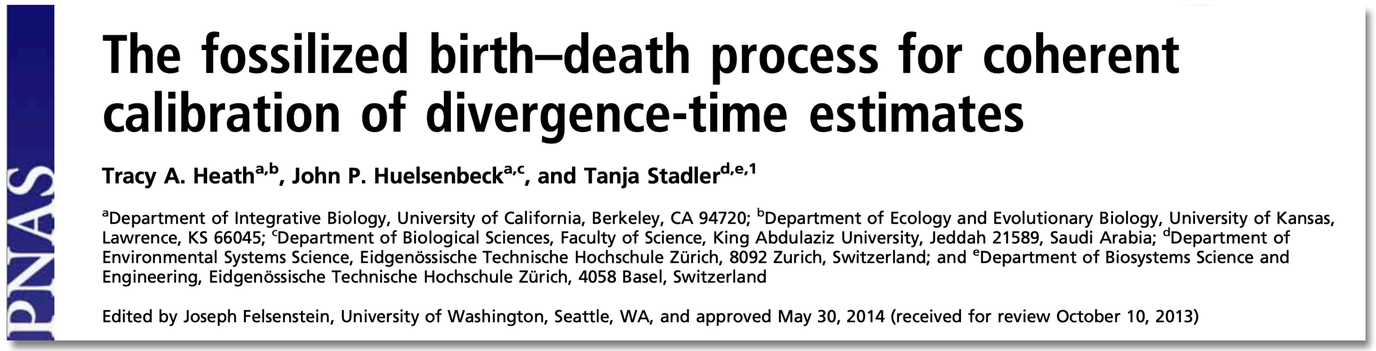


The relaxed clock model:




Bayesian Total Evidence Dating
Components of the model
Processes they describe
Morphological evolution
Molecular evolution
How traits change across lineages
Morphological clock
Molecular clock
At what rate changes occur along lineages
Timetree model
How (relationships) lineages occur in time

The tree model: Fossilized Birth Death (FBD)



PNAS

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]

[a]Department of Integrative Biology, University of California, Berkeley, CA 94720; [b]Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045; [c]Department of Biological Sciences, Faculty of Science, King Abdulaziz University, Jeddah 21589, Saudi Arabia; [d]Department of Environmental Systems Science, Eidgenössische Technische Hochschule Zürich, 8092 Zurich, Switzerland; and [e]Department of Biosystems Science and Engineering, Eidgenössische Technische Hochschule Zürich, 4058 Basel, Switzerland

Edited by Joseph Felsenstein, University of Washington, Seattle, WA, and approved May 30, 2014 (received for review October 10, 2013)

Used to model the evolution of a **tree with extinct and extant taxa.**

Birth-death models are attractive because they have **biologically interpretable parameters**.

- λ **(speciation rate)**: the rate at which a lineage produces new lineages
- μ **(extinction rate):** the rate at which a lineage goes extinct
- ψ **(fossilization rate):** the rate at which a lineage produces fossils (recovered, described, etc…)
- ρ **(sampling fraction):** the fraction of extant diversity that is included in the phylogeny

The tree model: Fossilized Birth Death (FBD)

Parameters of the model:

- λ (speciation rate)
- μ (extinction rate)
- ψ (fossilization rate)
- ρ (sampling fraction)



The tree model: Fossilized Birth Death (FBD)

Parameters of the model:

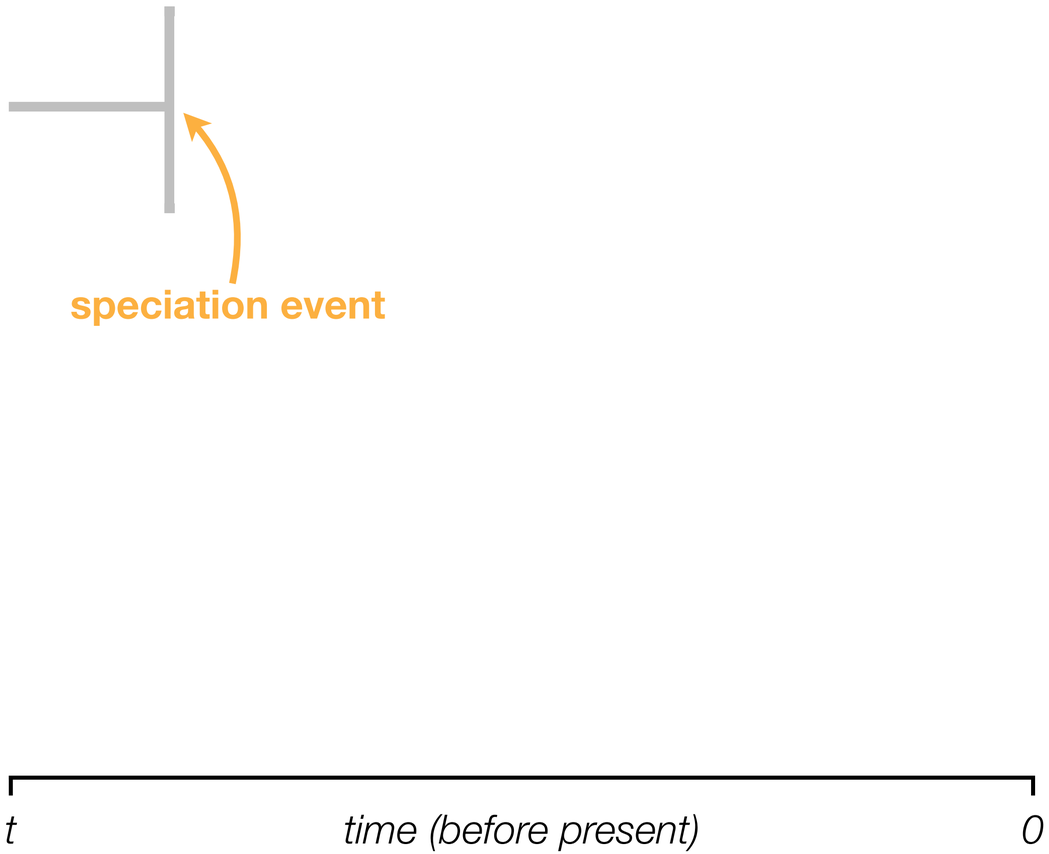
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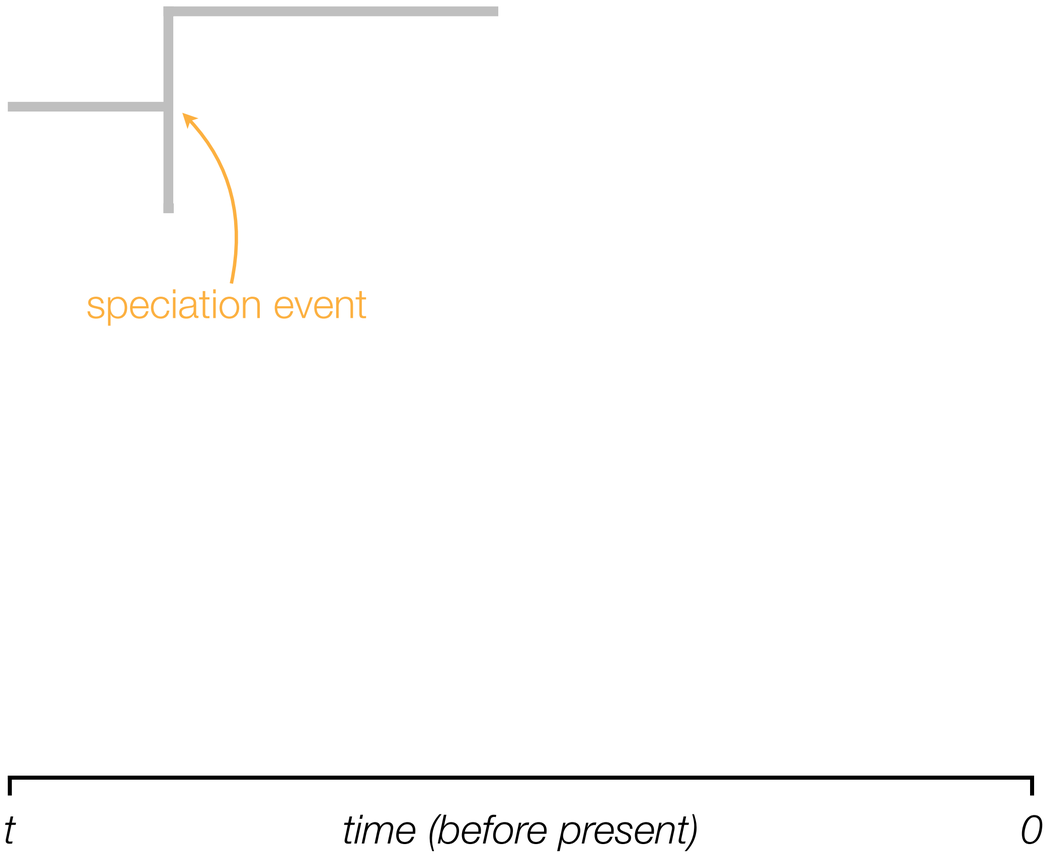
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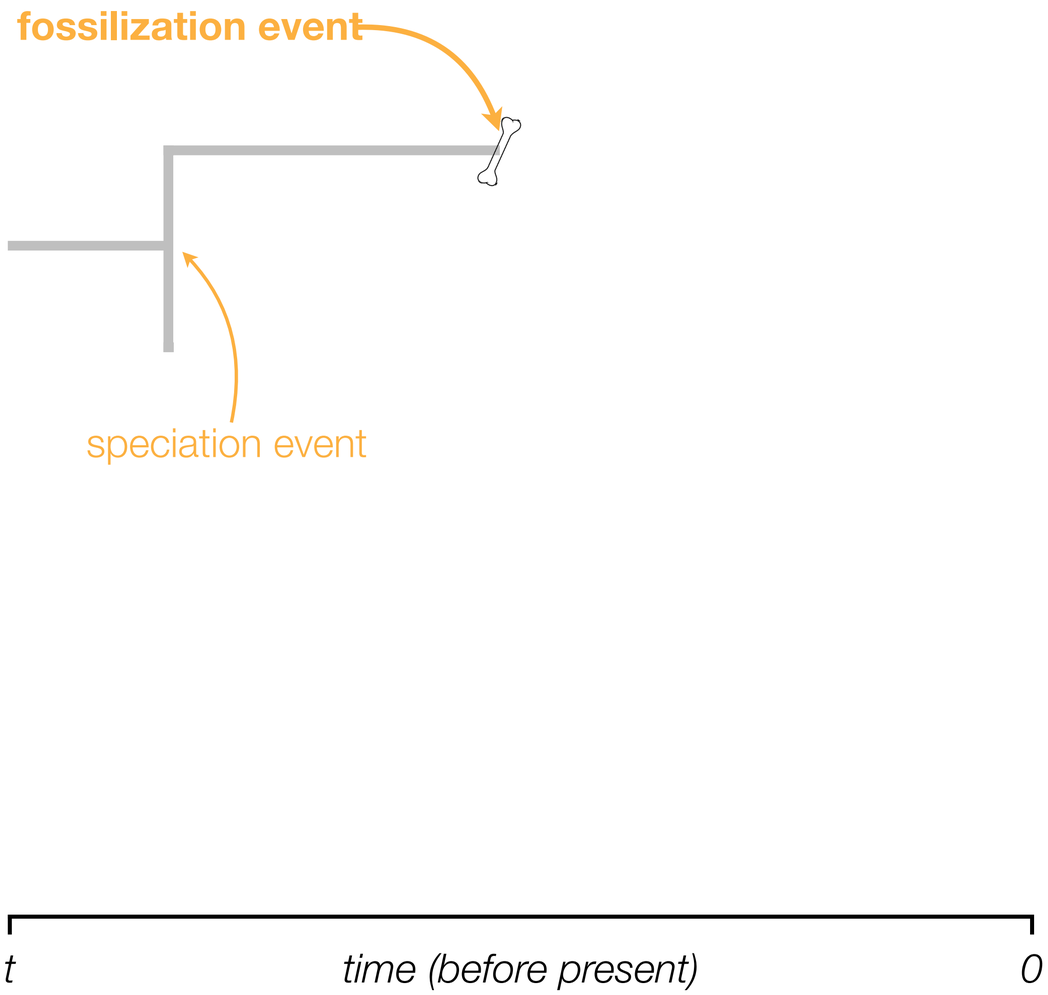
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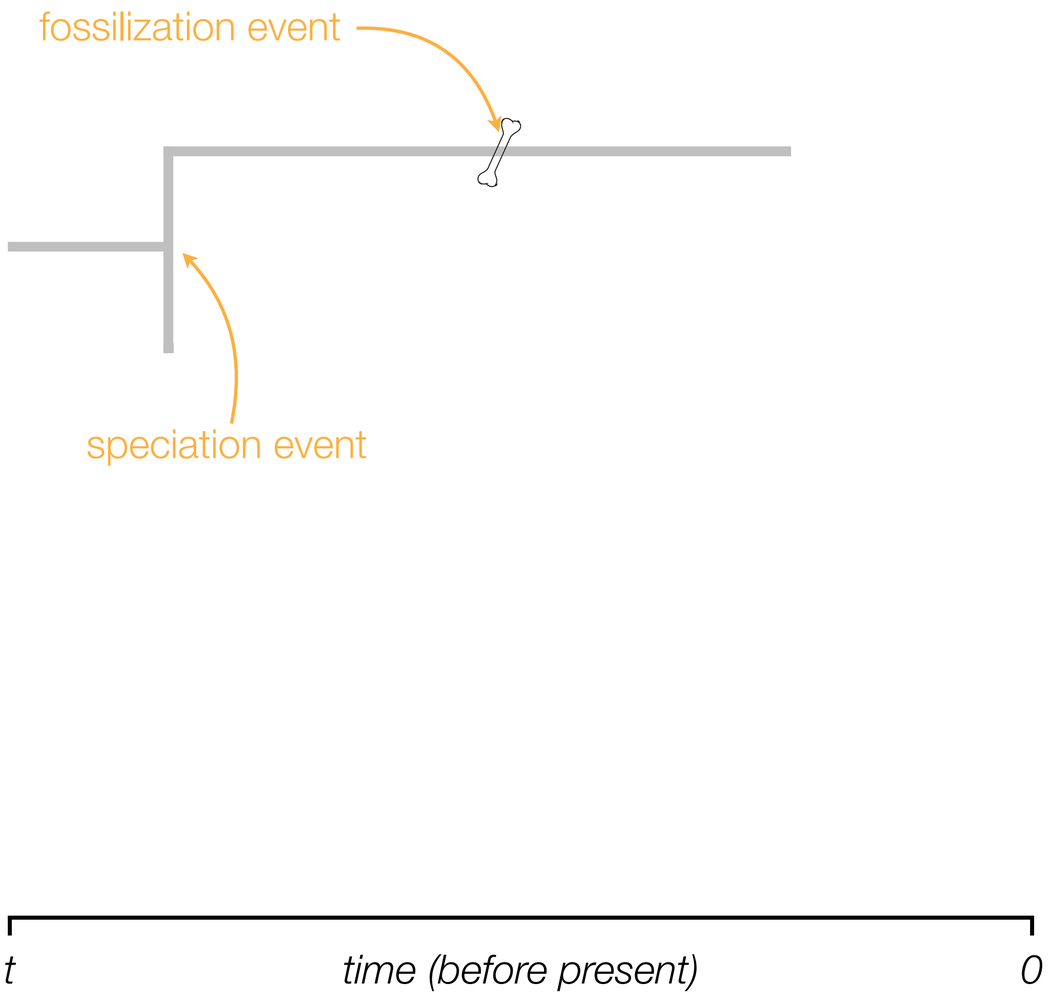
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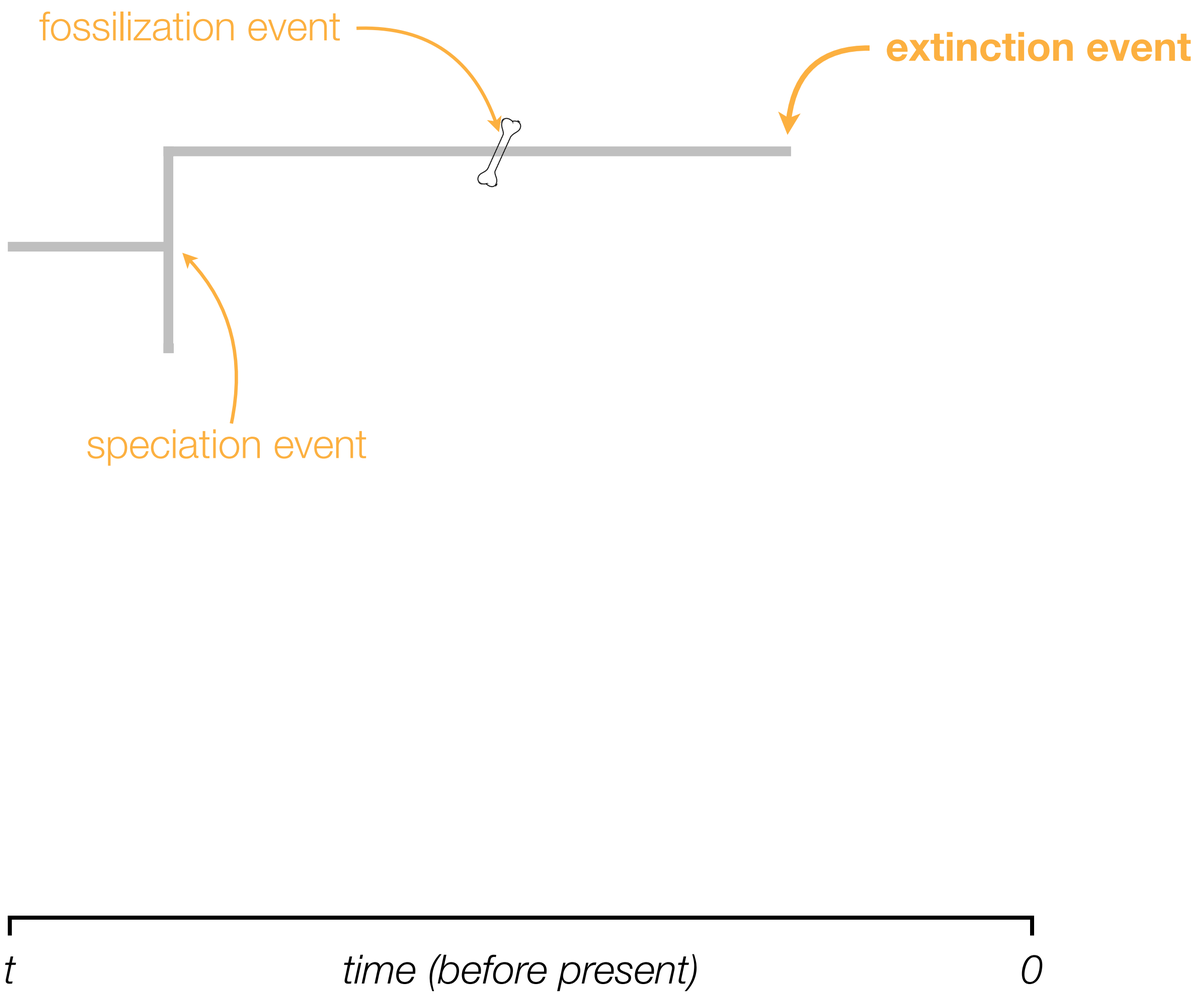
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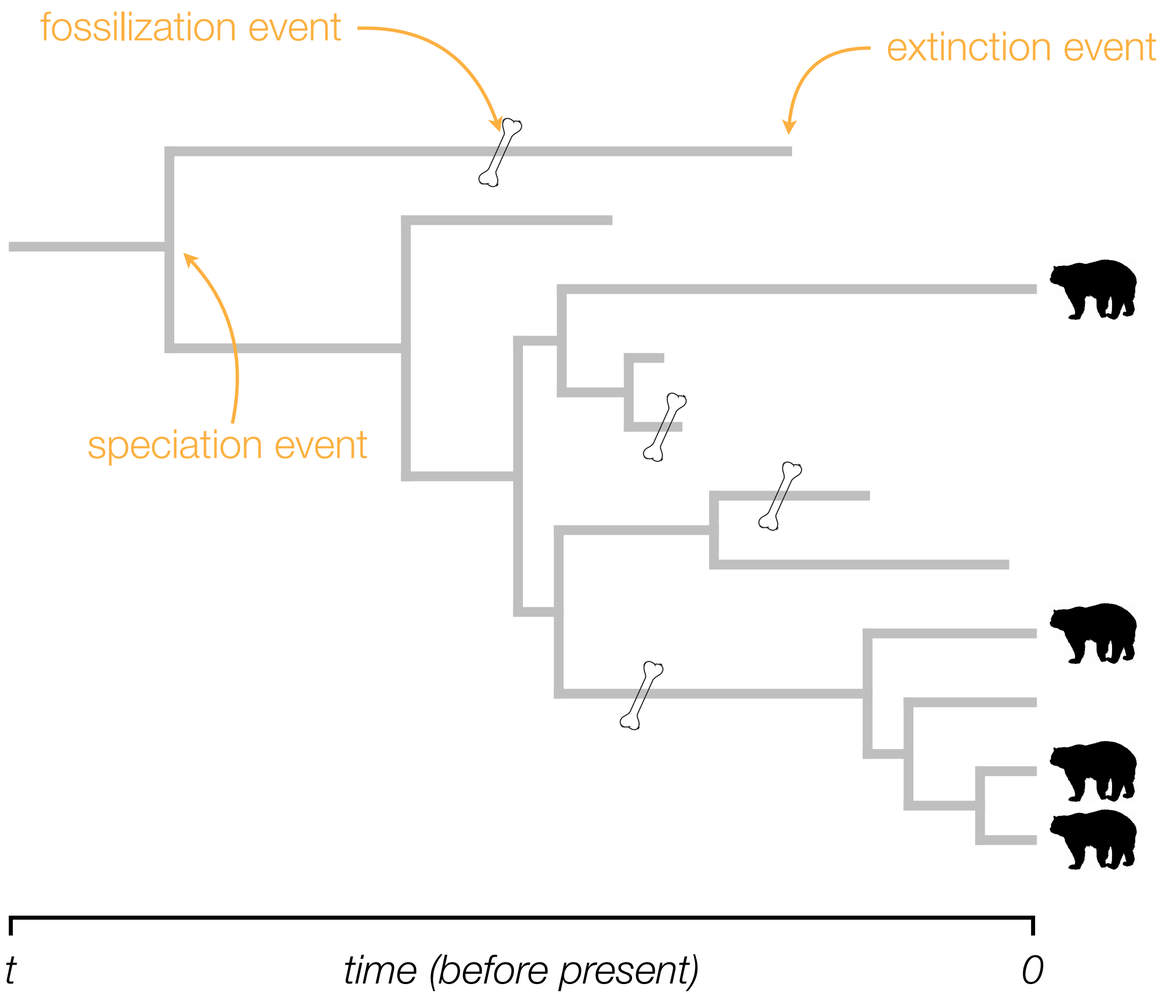
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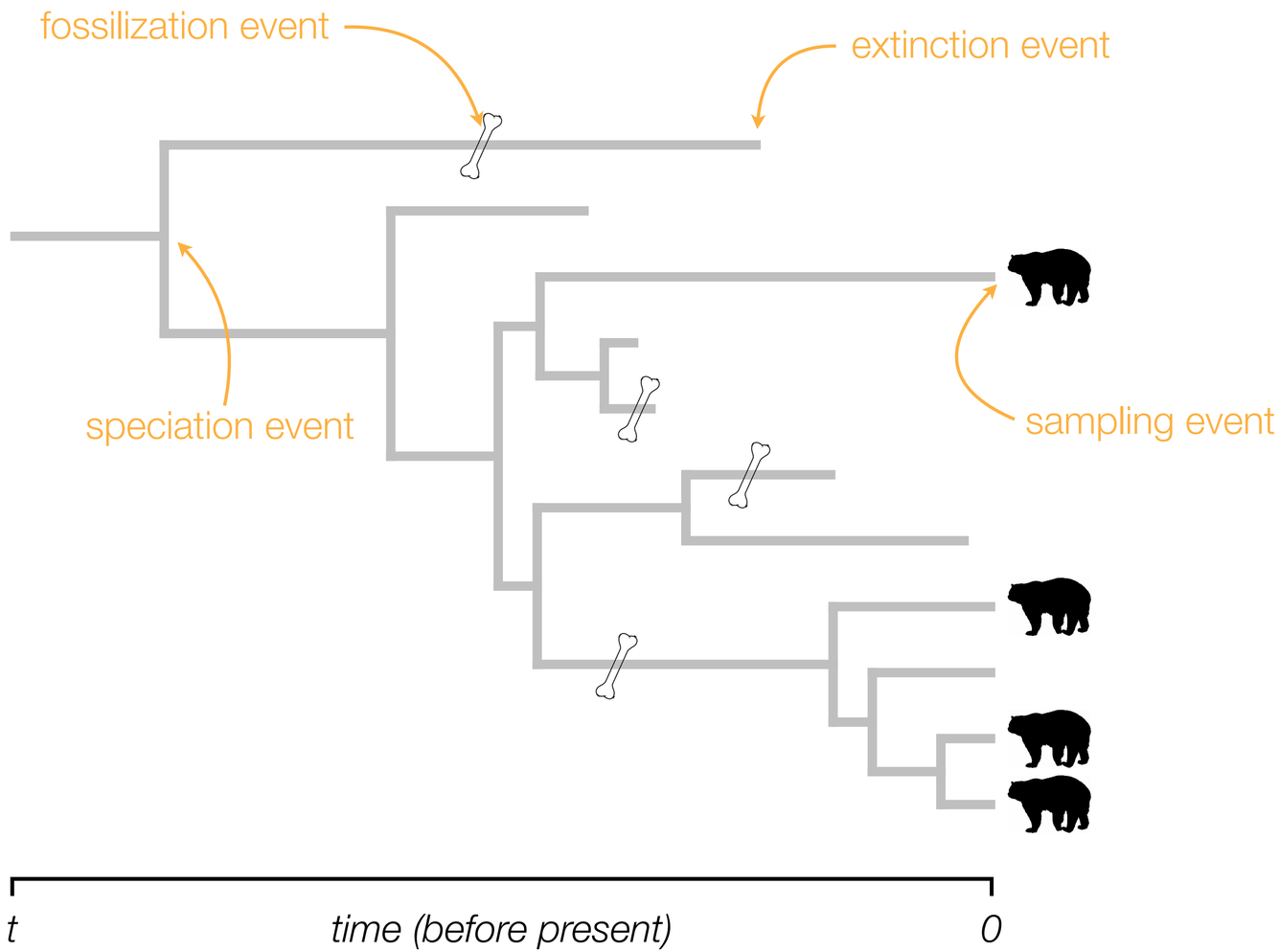
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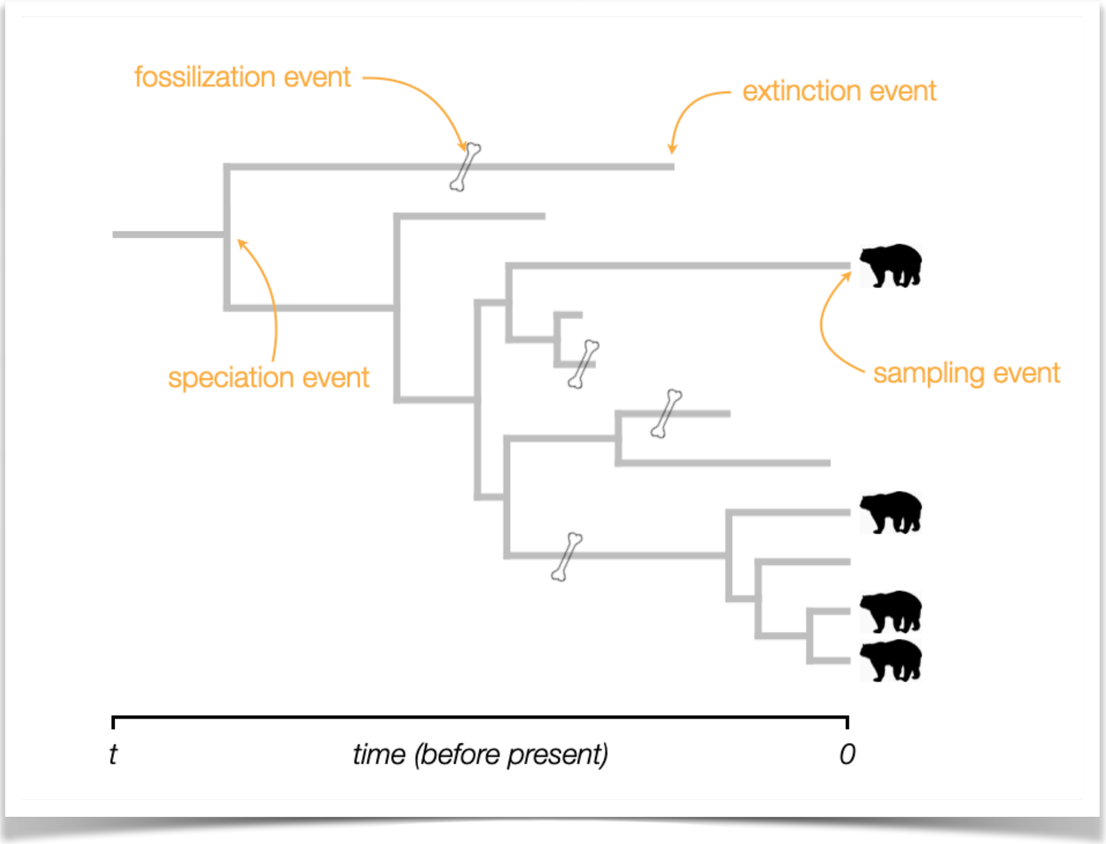
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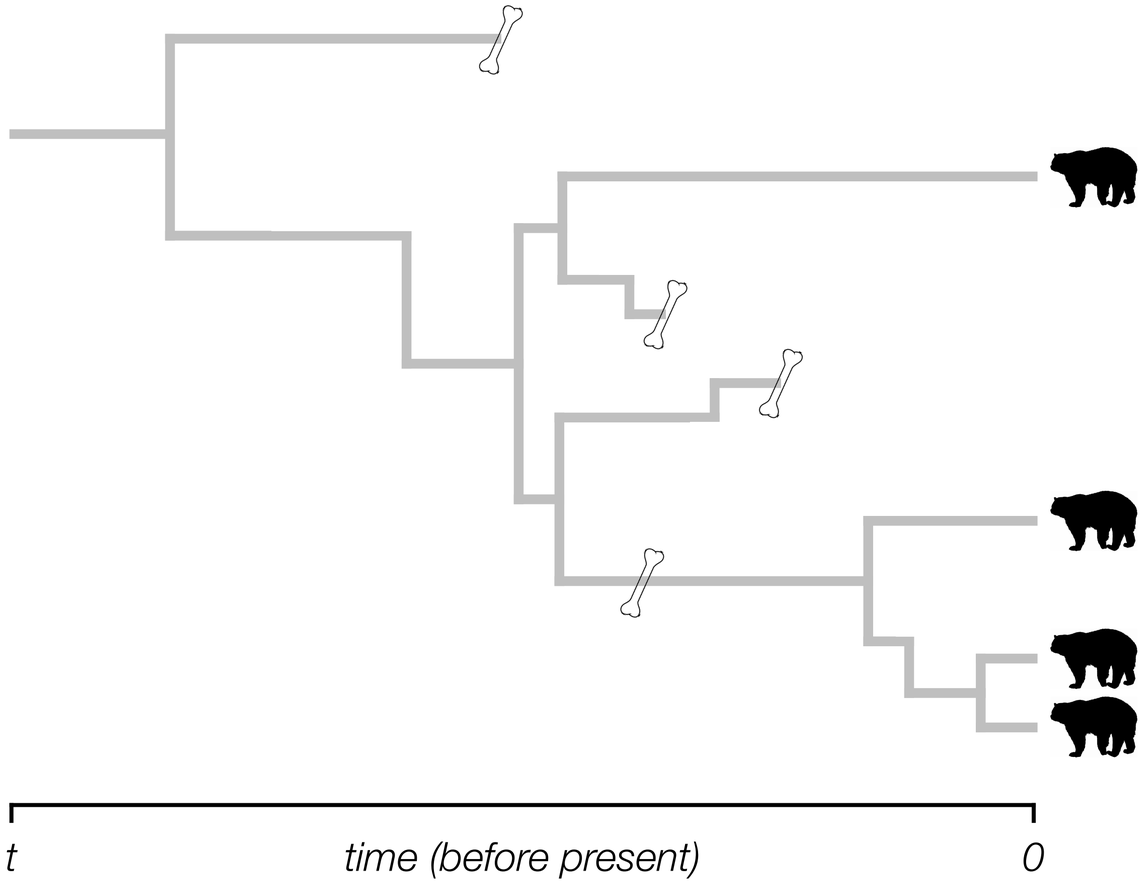
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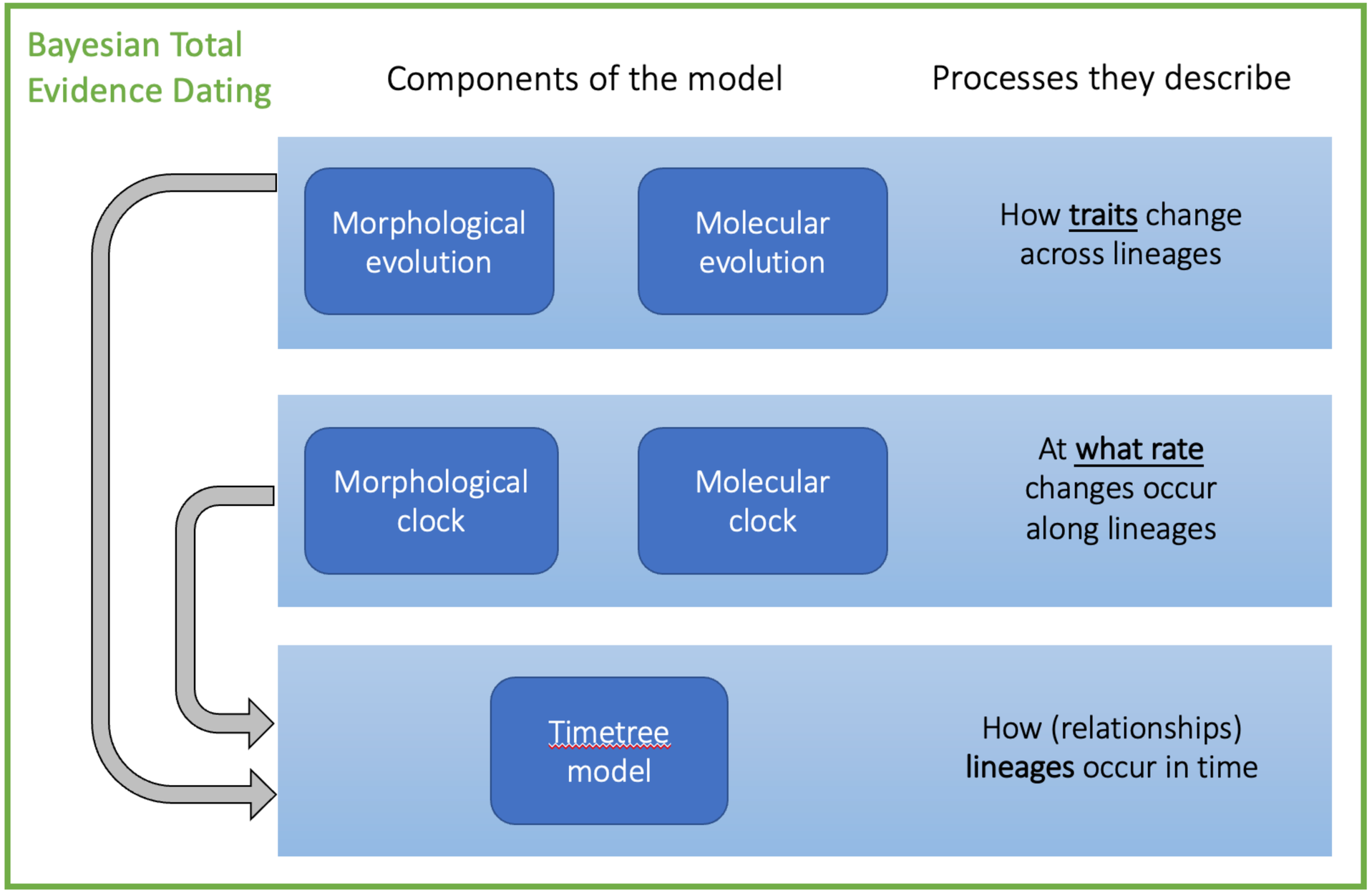
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The tree model: Fossilized Birth Death (FBD)






Bayesian Total Evidence Dating
Components of the model
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Molecular evolution
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How (relationships) lineages occur in time

Implementing the analysis

The cost of implementing a TED analysis

- Requires multiple types of data
- Very time consuming
  - Computationally intensive
  - Iterative process
- Making a lot of informed decisions
  - Technical skills
  - Iterative process

The data

148 taxa

14 fossils

134 extant

Molecular data

10 markers

Nuclear: ITS, LFY, waxy.

Plastid: matK, ndhF, Ndhf-rpl32, psbA, rbcL, trnLF, trnSG

Morphological data

17 categorical and 8 continuous traits

1 compression
2 hilum_position
3 embryo
4 cavity
5 testal_walls
6 wings
7 elaiosomes
8 base_invaginated
9 angled
10 lobe_sinus
11 widest_veins
12 secondary_veins
13 secondary_veins_fork
14 fruit_type
15 calyx_inflated
16 venation_pattern
17 calyx_teeth

1 seed_length,
2 seed_ratio,
3 fruiting_calyx_LT,
4 fruiting_calyx_ratio,
5 calyx_lobe_LT,
6 calyx_LT_lobe_ratio,
7 fruiting_pedicel,
8 fruit_ratio

2) Ejemplo con Solanaceae

Annals of Botany **00**: 1–16, 2026
https://doi.org/10.1093/aob/mcag011, available online at www.academic.oup.com/aob

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ORIGINAL ARTICLE

Late Cretaceous origins for major nightshade lineages from total-evidence timetree analysis

Ixchel S. González-Ramírez[1,2,*‡], **Rocío Deanna**[3,*†‡] **and Stacey D. Smith**[3]

[1]*University and Jepson Herbaria and Department of Integrative Biology, University of California, Berkeley, CA 94720, USA,* [2]*Missouri Botanical Garden, 4344 Shaw Blvd, St. Louis, MO 63110, USA and* [3]*Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA*
[†]*Present address: Botany and Mycology Unit, Finnish Museum of Natural History, University of Helsinki, 00100 Helsinki, Finland.*



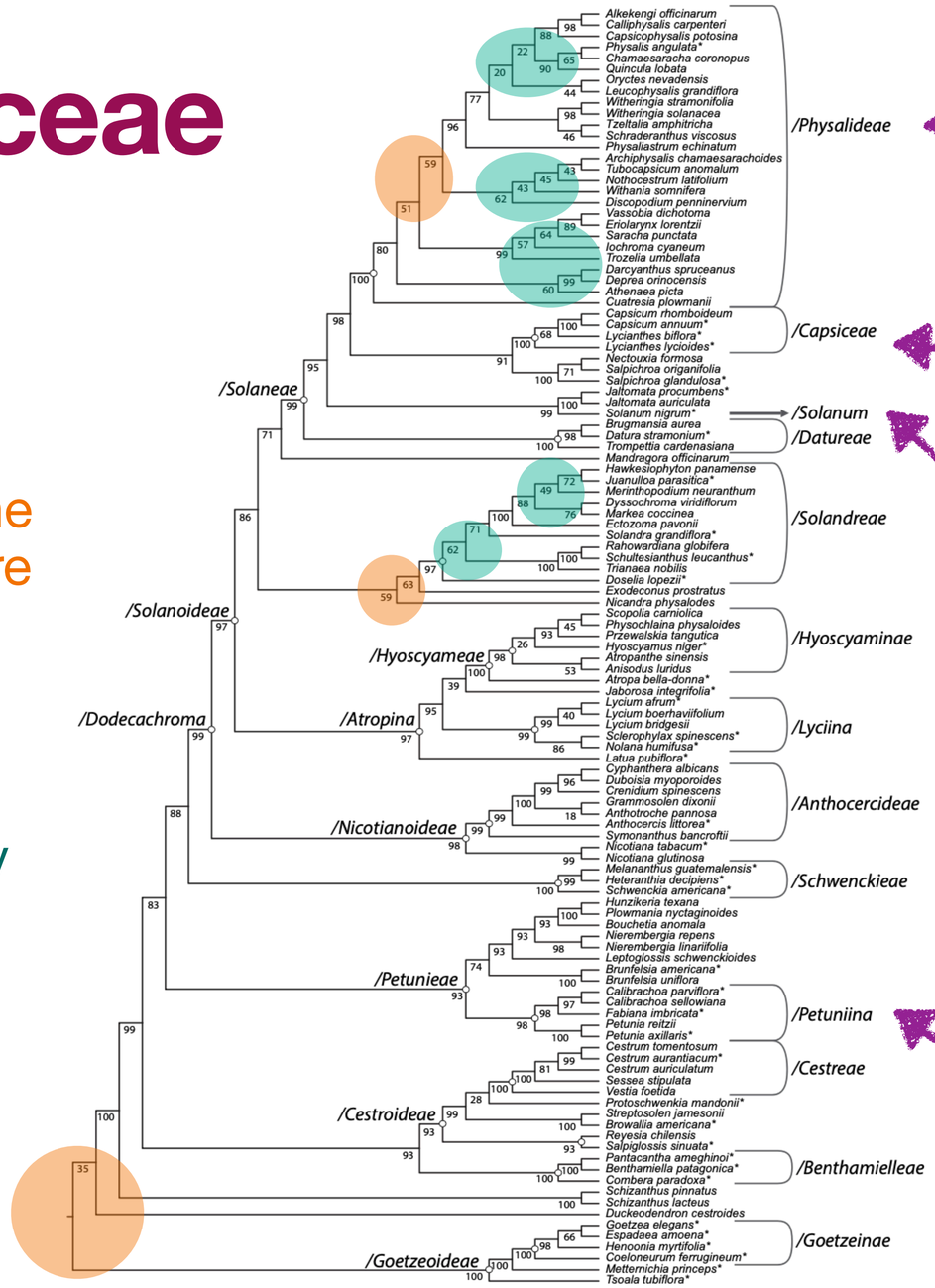
Rocío Deanna
University of Helsinki



Stacey Smith
University of Colorado

Solanaceae

- 2850 spp
- Cosmopolitan
- Some backbone relationships are contentious
- As well as relationships within the berry clade









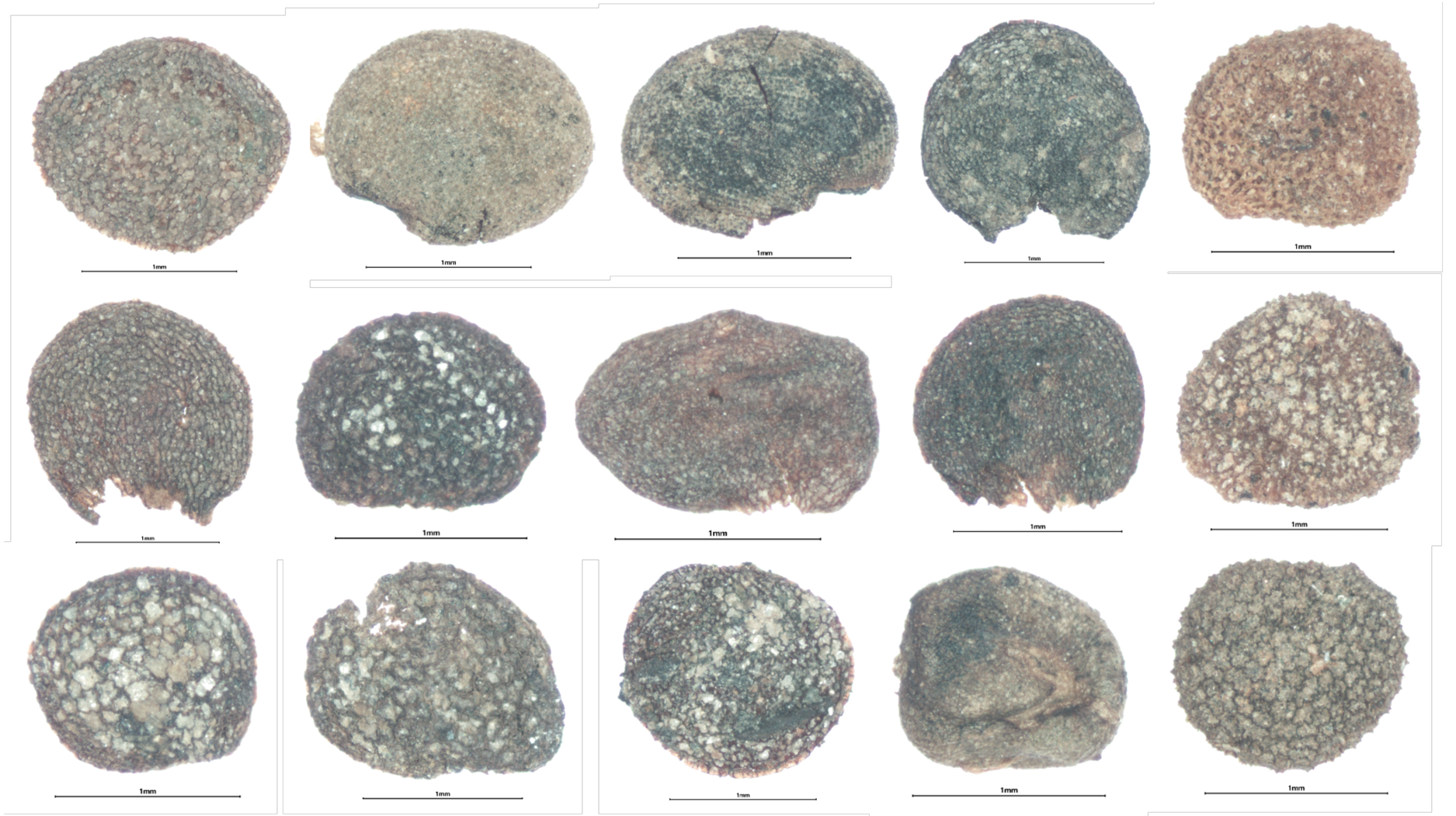




(Deanna et al., under review)

Fossil seeds

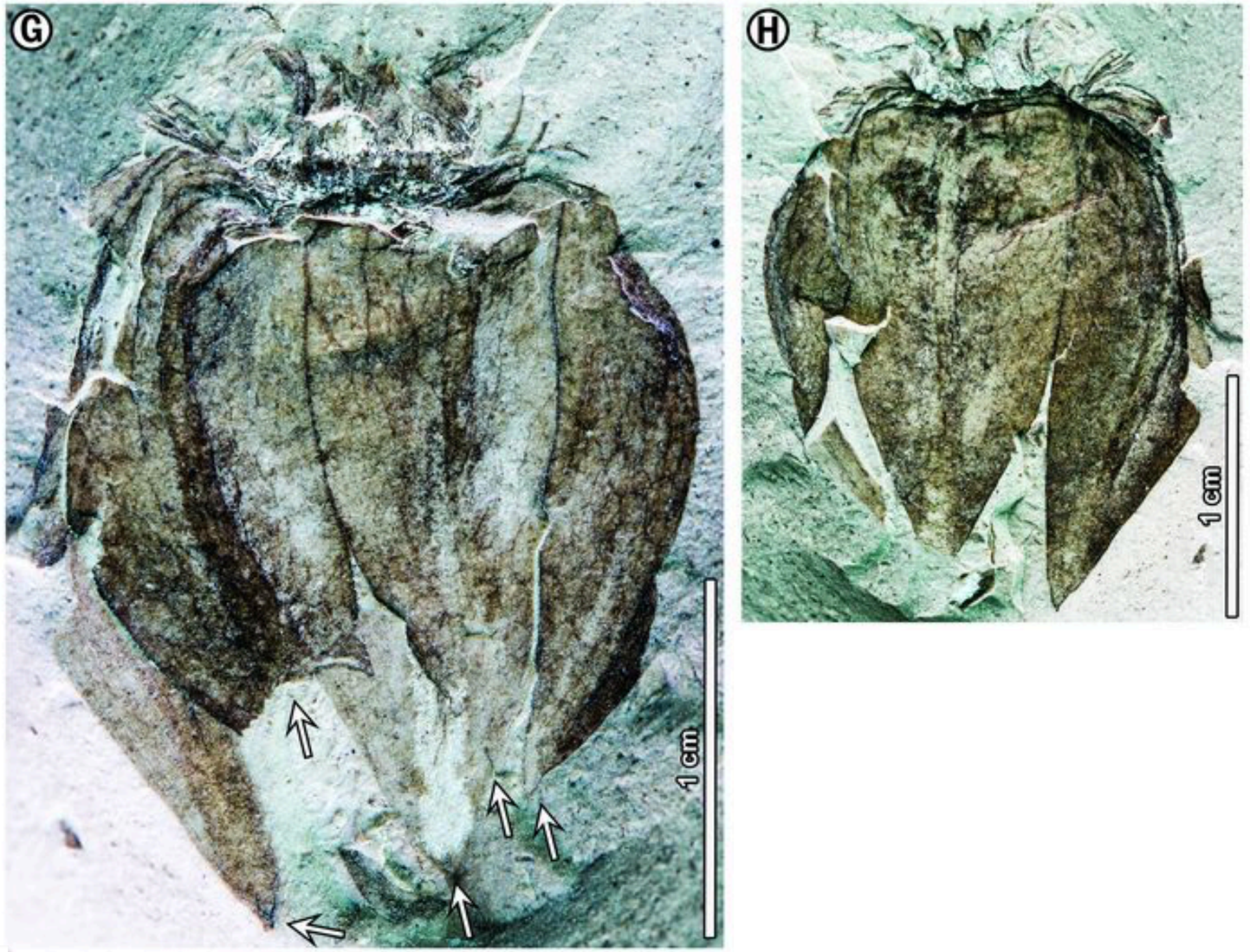
- 110 fossil seeds
- Geographically widespread



Dorofeev 1951, 1955, 1957, 1966

Eocene berries

Fruits with inflated five-angled calyces.



Physalis infinemundi

52.2 MYA

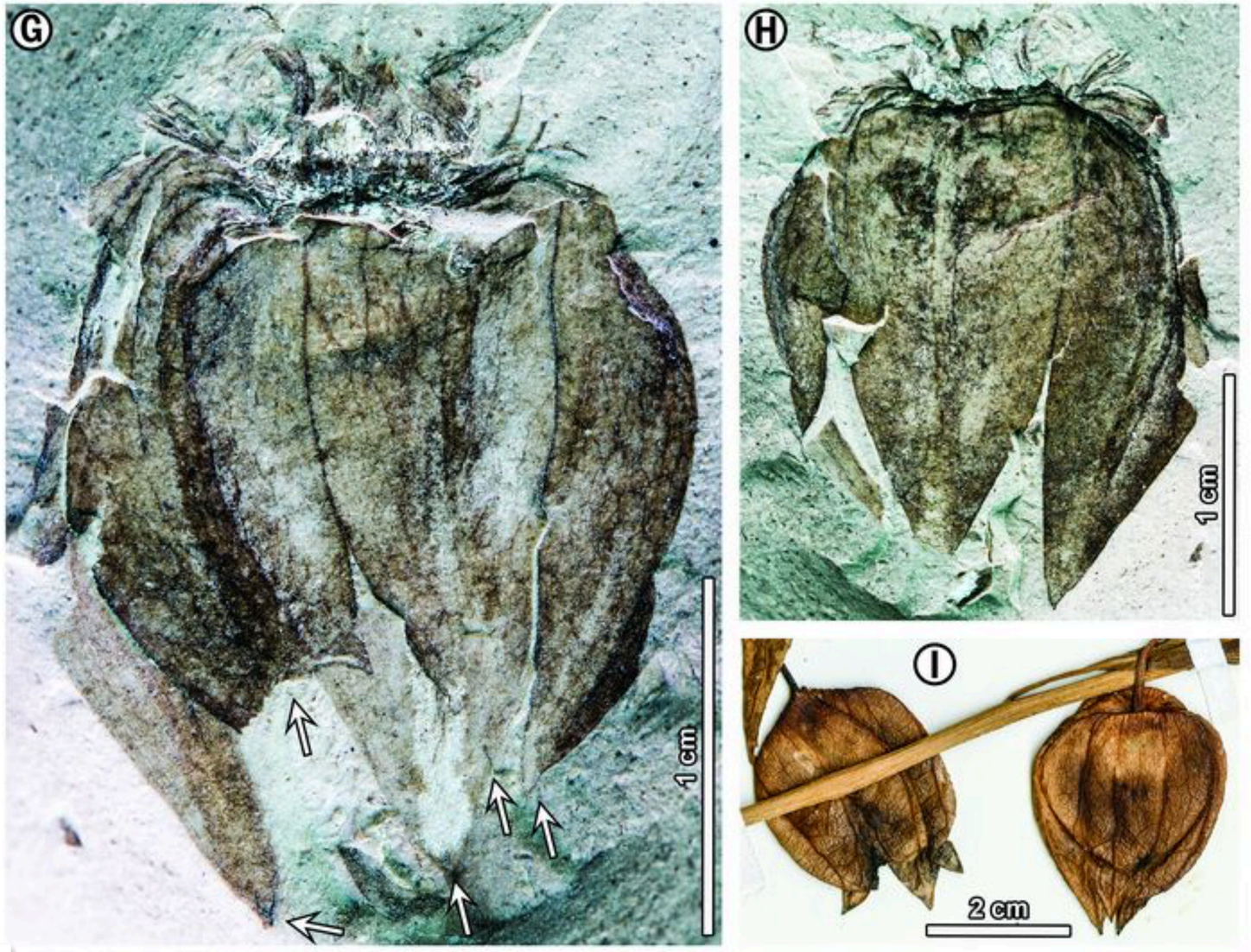
(Wilf et al. 2017)

Eocene lantern fruits from Gondwanan Patagonia and the early origins of Solanaceae

PETER WILF, MÓNICA R. CARVALHO, [...] , AND N. RUBÉN CÚNEO +1 authors Authors Info & Affiliations

Eocene berries

Fruits with inflated five-angled calyces.



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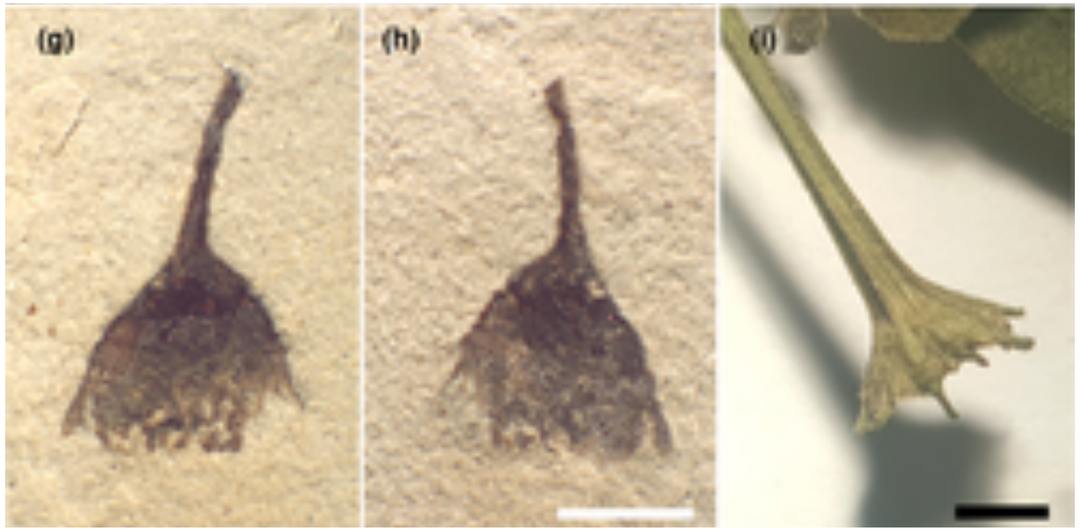
PETER WILF, MÓNICA R. CARVALHO, [...], AND N. RUBÉN CÚNEO +1 authors Authors Info & Affiliations

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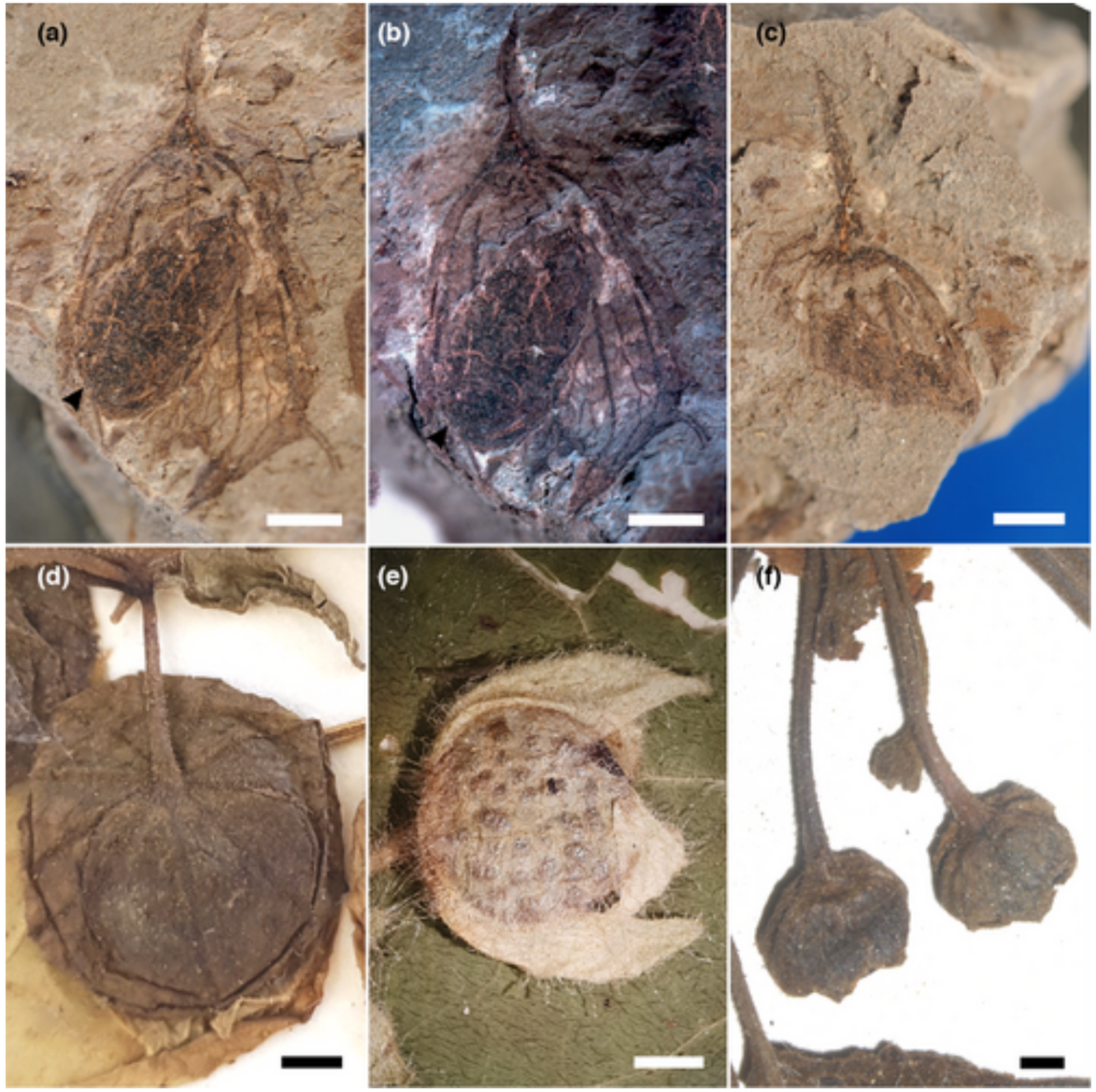


Lycianthoides calycina (Deanna et al. 2023)

49.5–51.5Ma

Fossil berries reveal global radiation of the nightshade family by the early Cenozoic

Rocío Deanna ✉, Camila Martínez, Steven Manchester, Peter Wilf, Abel Campos, Sandra Knapp, Franco E. Chiarini, Gloria E. Barboza **... See all authors** ›



Eophysaloides inflata

(Deanna et al. 2023)

Goal

Infer divergence time estimates for Solanaceae using a Bayesian total evidence dating approach

1. Timing of Solanaceae evolution

2. Placement of the fossils

Data

148 taxa

14 fossils

134 extant

Molecular data

10 markers

Nuclear: ITS, LFY, waxy.

Plastid: matK, ndhF, Ndhf-rpl32, psbA, rbcL, trnLF, trnSG

Morphological data

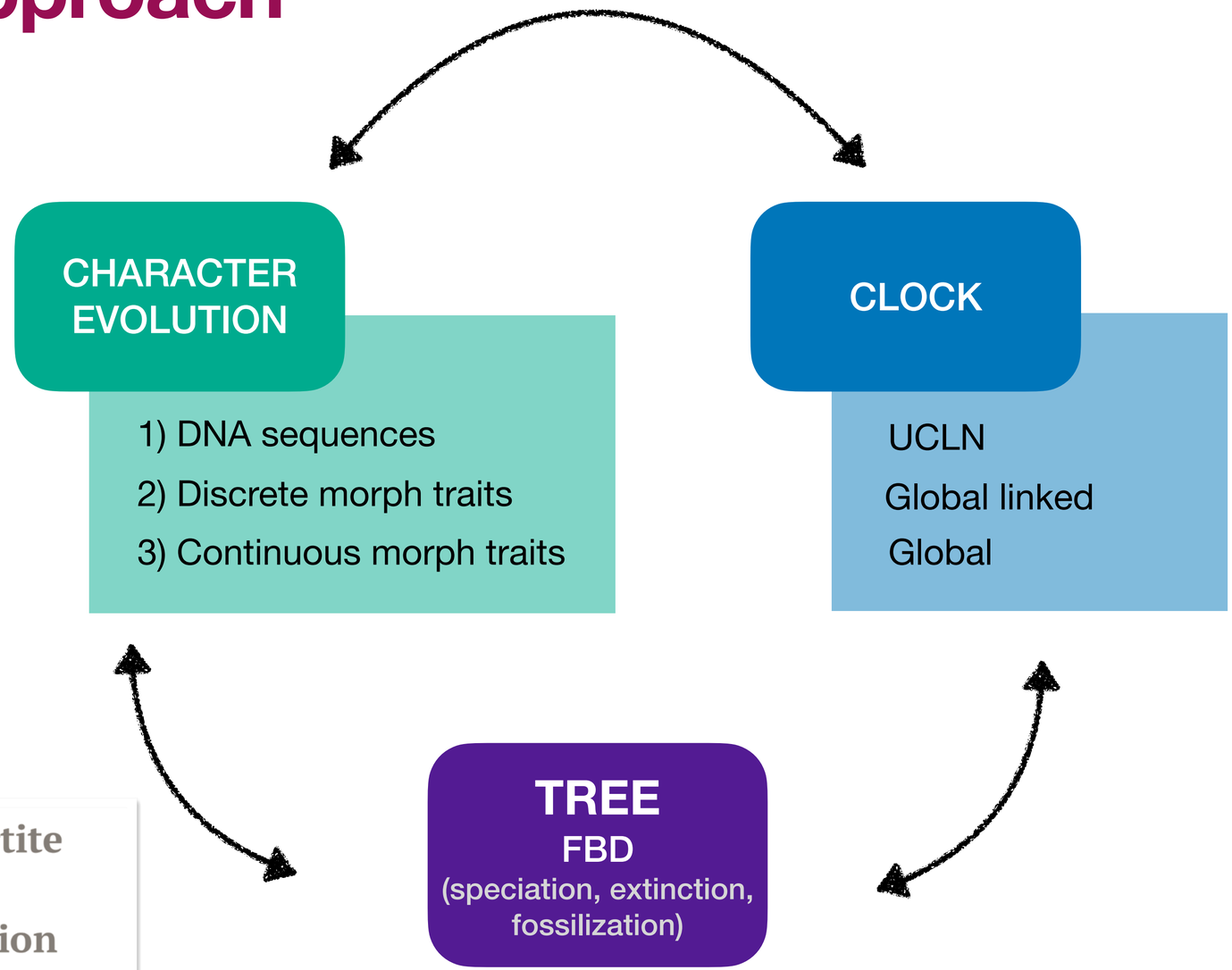
17 categorical and 8 continuous traits

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9 angled
10 lobe_sinus
11 widest_veins
12 secondary_veins
13 secondary_veins_fork
14 fruit_type
15 calyx_inflated
16 venation_pattern
17 calyx_teeth

1 seed_length,
2 seed_ratio,
3 fruiting_calyx_LT,
4 fruiting_calyx_ratio,
5 calyx_lobe_LT,
6 calyx_LT_lobe_ratio,
7 fruiting_pedicel,
8 fruit_ratio

The Bayesian TED approach

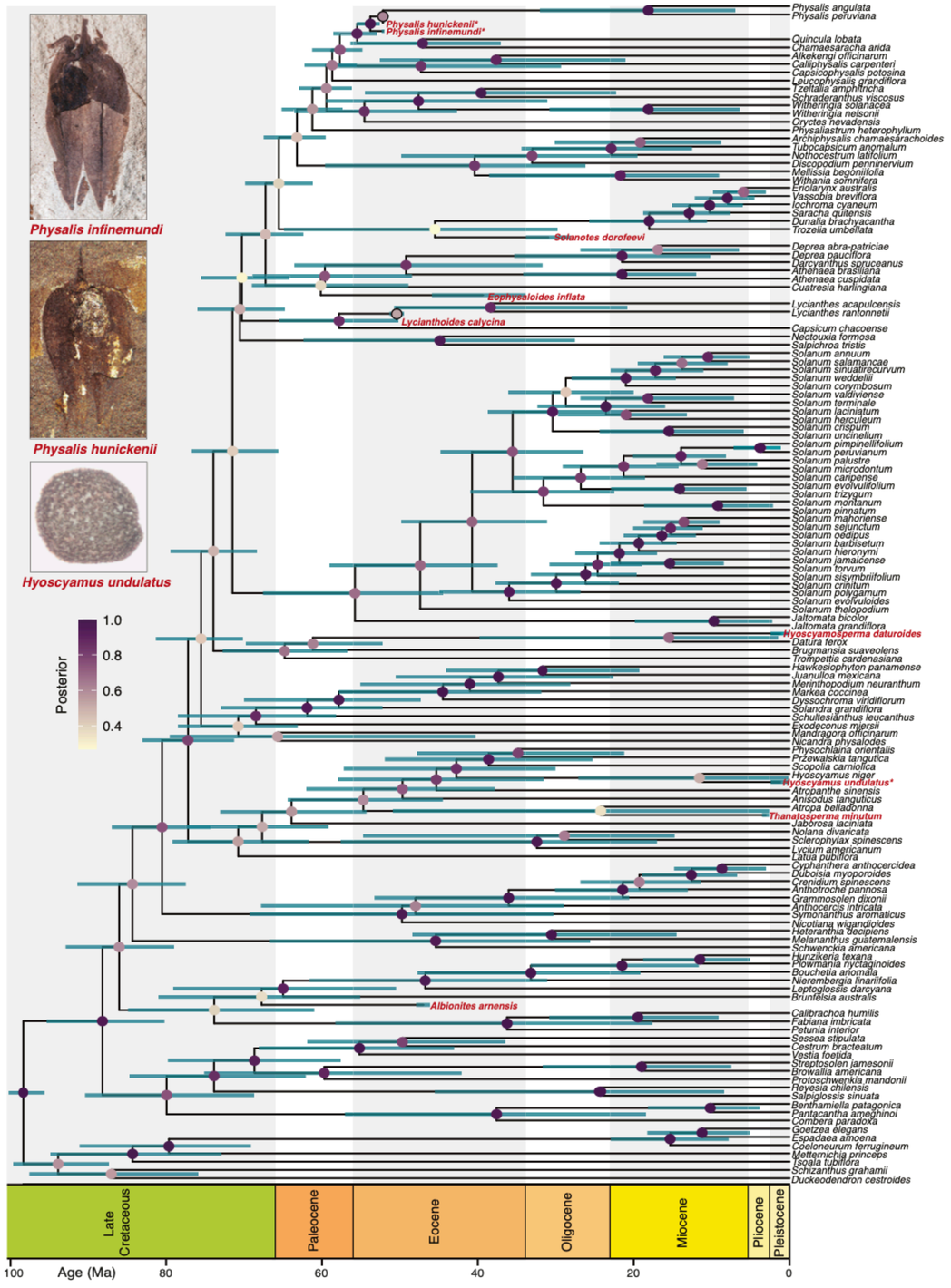
- Simultaneously infers topology and divergence times.
- Averages over topological uncertainty.
- Allows the use of multiple fossils.



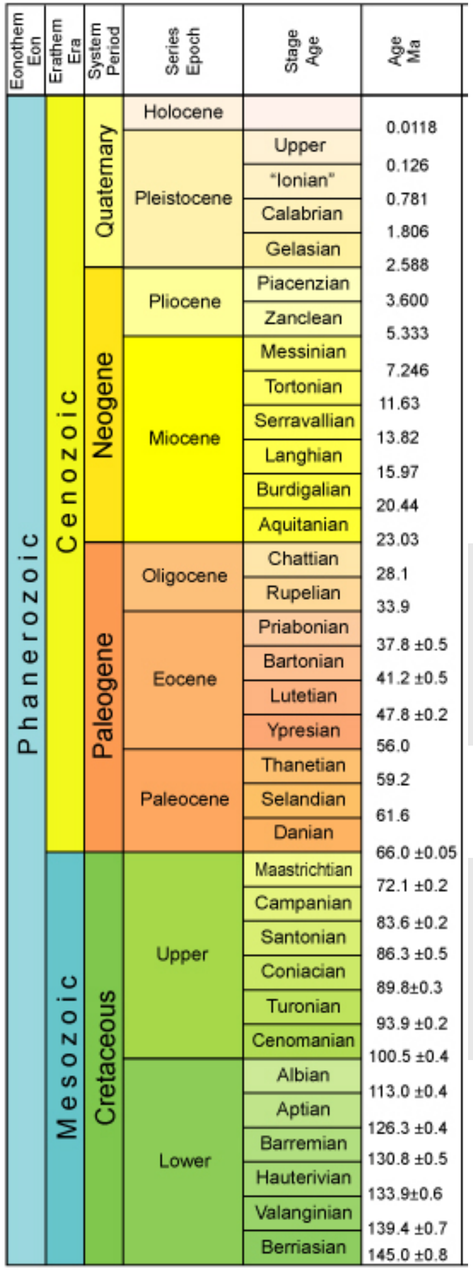
Understanding the Tripartite Approach to Bayesian Divergence Time Estimation

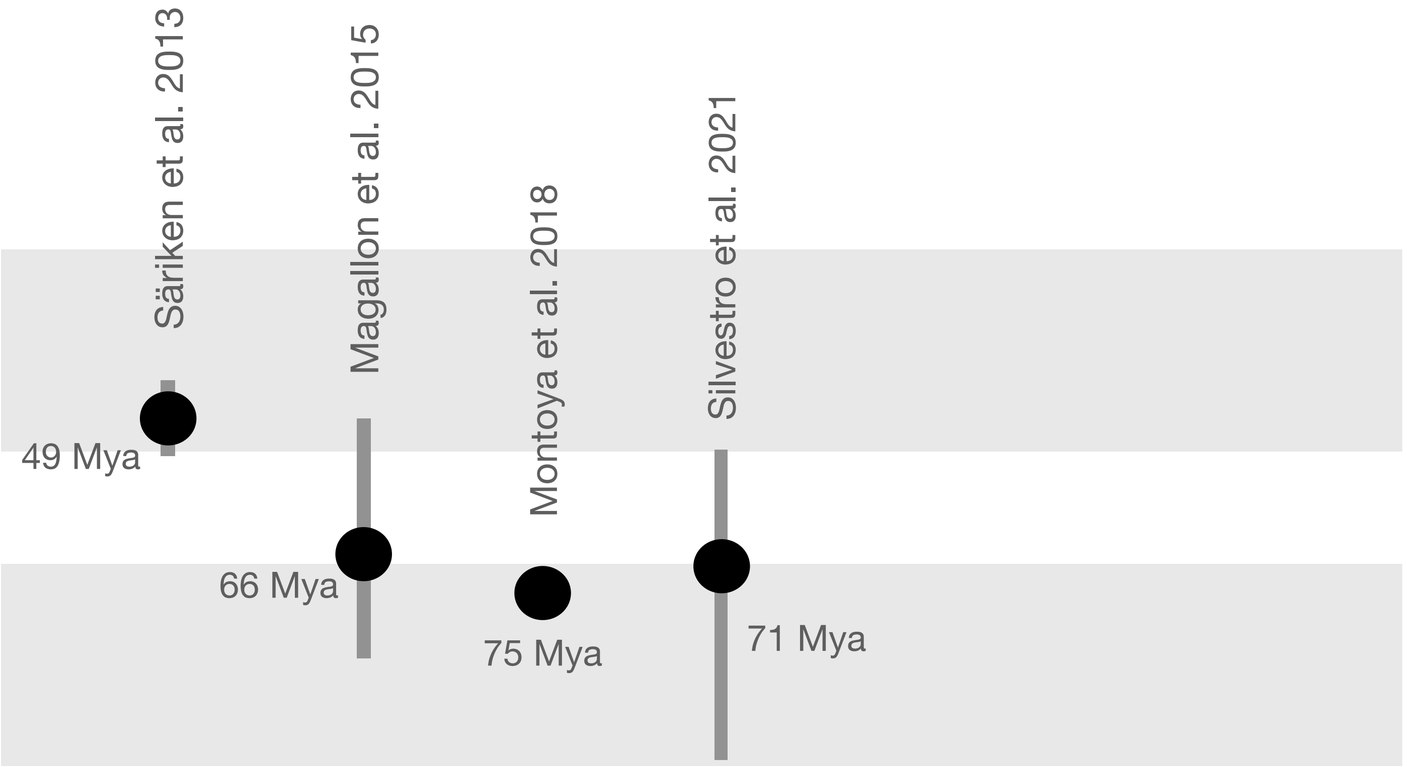
Rachel C. M. Warnock
Friedrich-Alexander Universität Erlangen-Nürnberg
April M. Wright
Southeastern Louisiana University

Results


Physalis infinemundi
Physalis hunickenii
Hyoscyamus undulatus
Posterior
1.0
0.8
0.6
0.4
Physalis hunickenii*
Physalis infinemundi*
Solanotes doroteevi
Eophysaloides inflata
Lycianthoides calycina
Albionites arnensis
Hyoscyamus undulatus*
Thanatosperma minutum
Hyoscyamosperma daturoides
Late Cretaceous
Paleocene
Eocene
Oligocene
Miocene
Pliocene
Pleistocene
100
80
60
40
20
0
Age (Ma)

How old are Solanaceae?

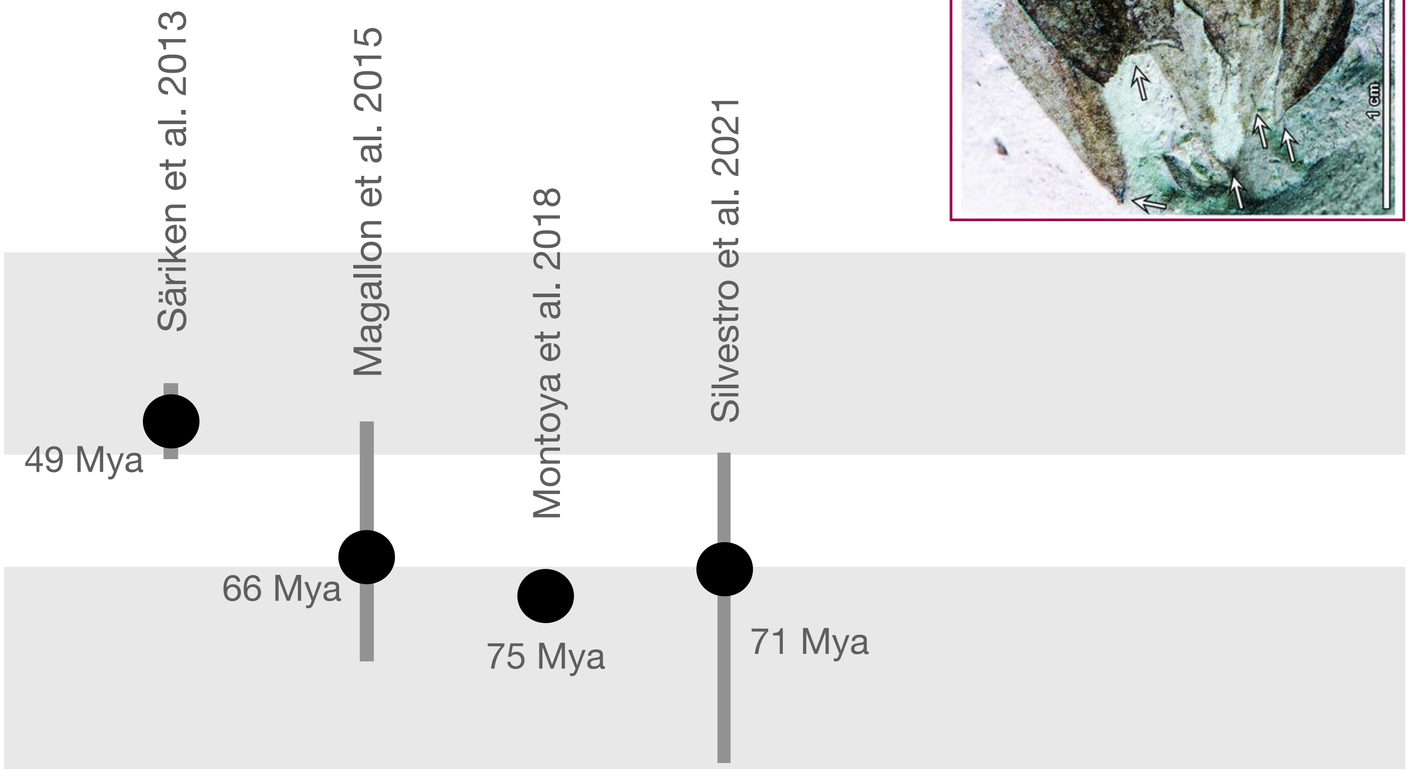




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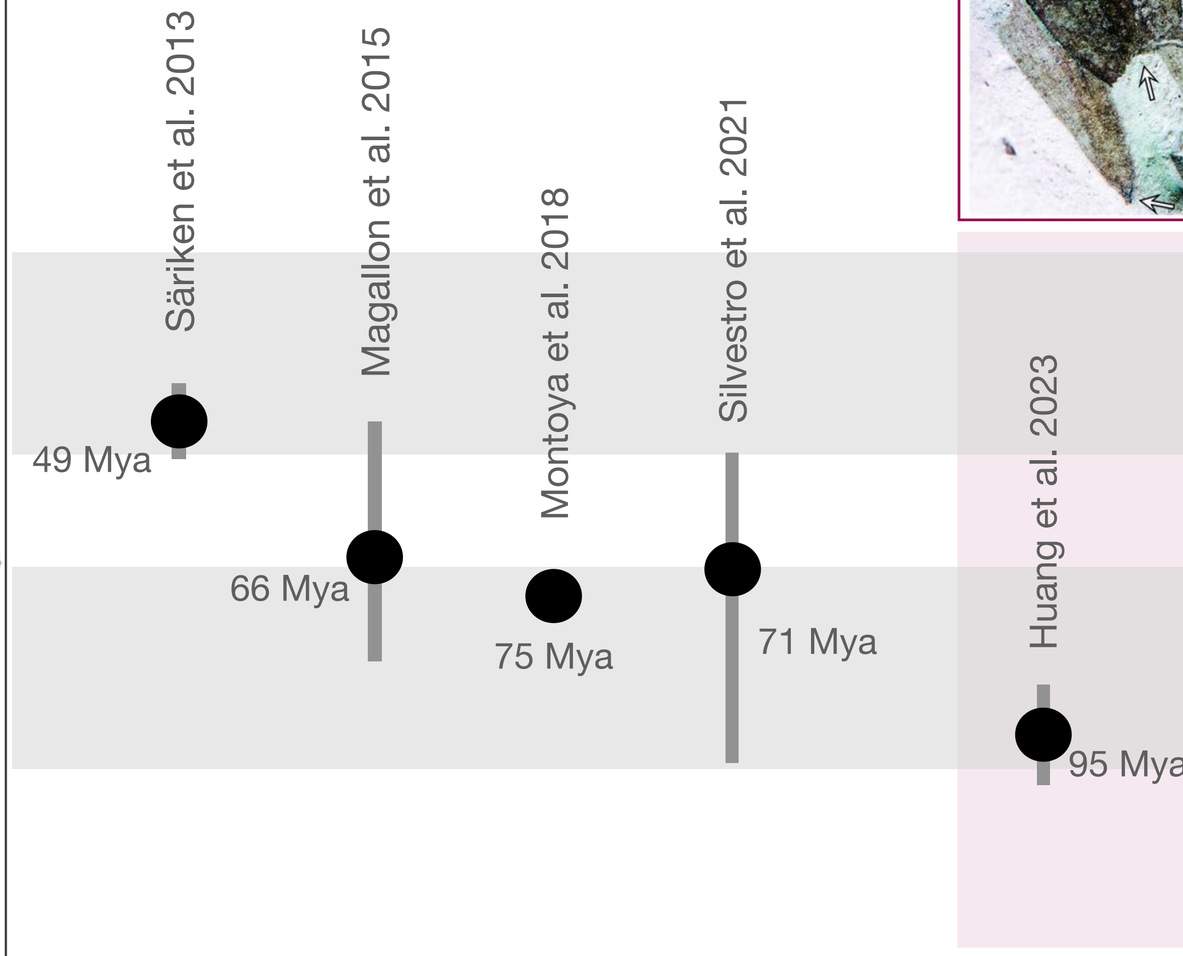
Eonothem Eon	Erathem Era	System Period	Series Epoch	Stage Age	Age Ma
Phanerozoic	Cenozoic	Quaternary	Holocene		0.0118
			Pleistocene	Upper	0.126
				"Ionian"	0.781
				Calabrian	1.806
				Gelasian	2.588
		Neogene	Pliocene	Piacenzian	3.600
				Zanclean	5.333
			Miocene	Messinian	7.246
				Tortonian	11.63
				Serravallian	13.82
				Langhian	15.97
				Burdigalian	20.44
				Aquitanian	23.03
		Paleogene	Oligocene	Chattian	28.1
				Rupelian	33.9
			Eocene	Priabonian	37.8 ±0.5
				Bartonian	41.2 ±0.5
				Lutetian	47.8 ±0.2
				Ypresian	56.0
			Paleocene	Thanetian	59.2
				Selandian	61.6
				Danian	66.0 ±0.05
	Mesozoic	Cretaceous	Upper	Maastrichtian	72.1 ±0.2
				Campanian	83.6 ±0.2
				Santonian	86.3 ±0.5
				Coniacian	89.8±0.3
				Turonian	93.9 ±0.2
				Cenomanian	100.5 ±0.4
			Lower	Albian	113.0 ±0.4
				Aptian	126.3 ±0.4
				Barremian	130.8 ±0.5
				Hauterivian	133.9±0.6
				Valanginian	139.4 ±0.7
				Berriasian	145.0 ±0.8





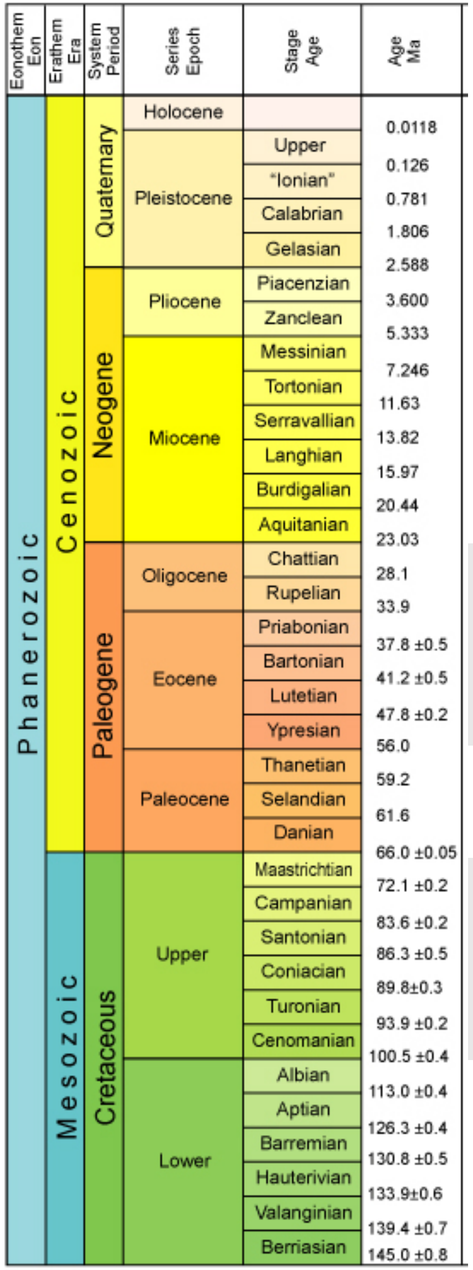
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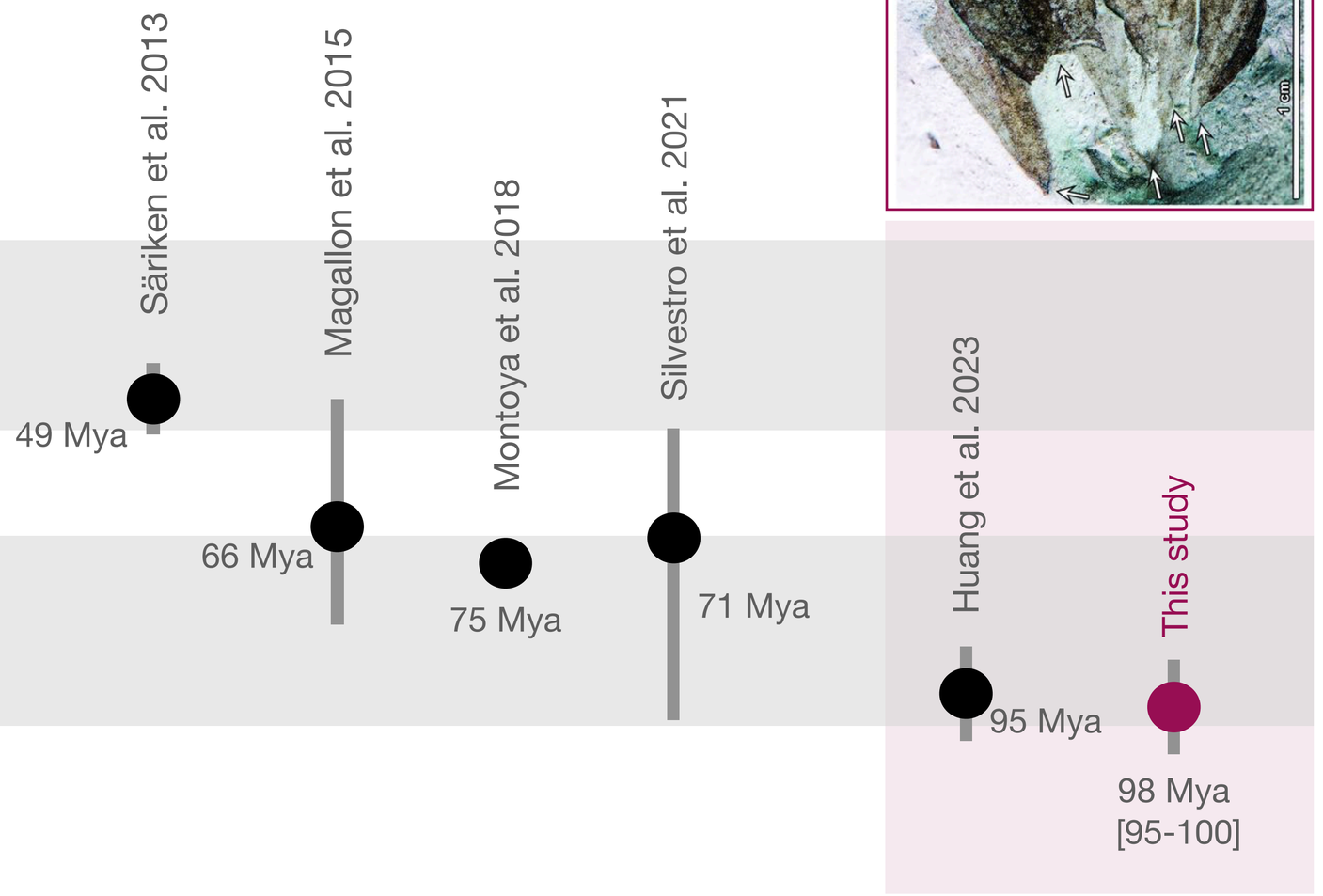
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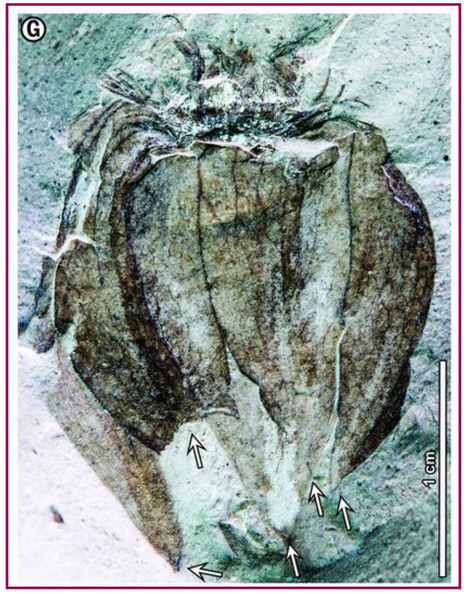




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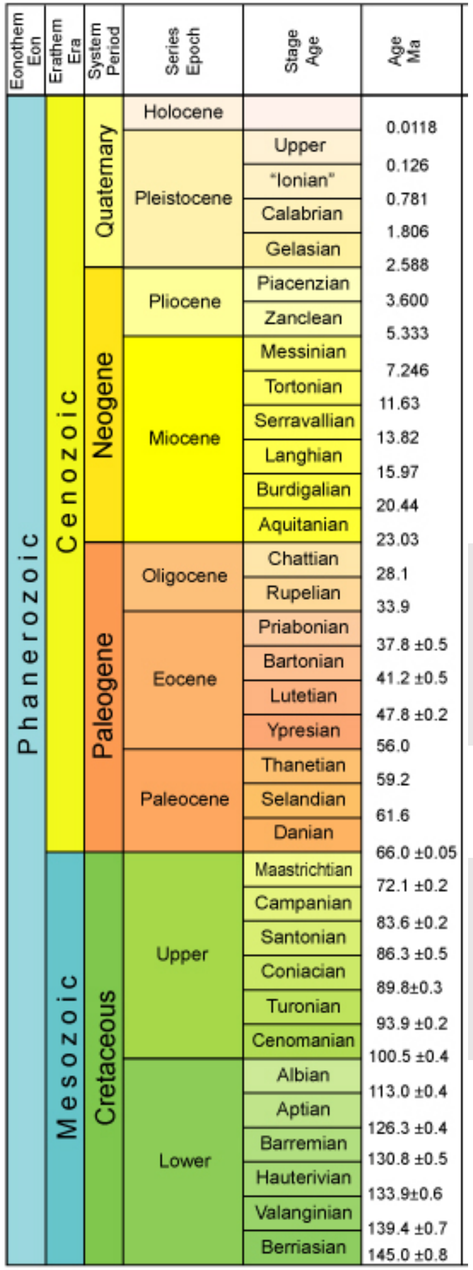


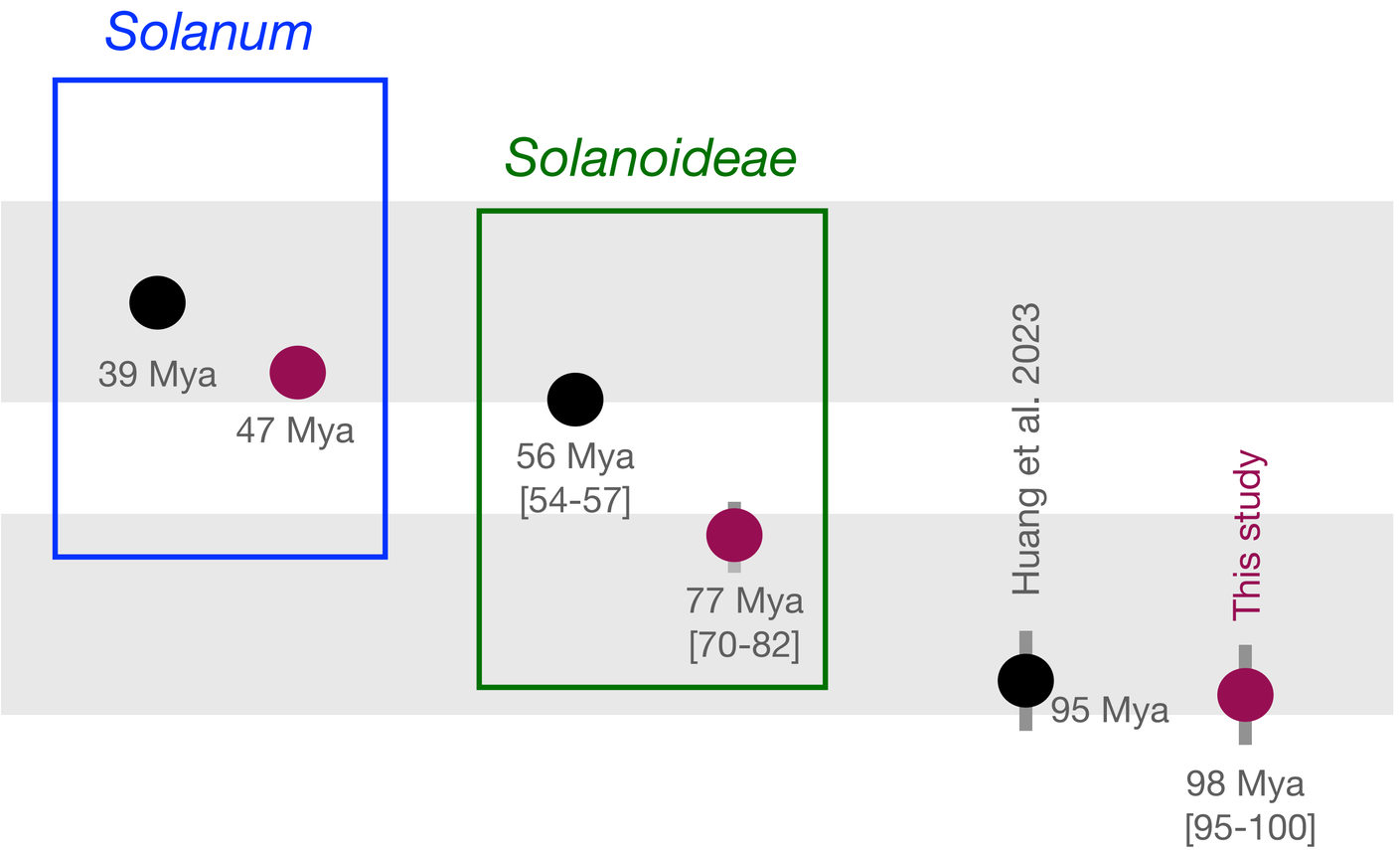




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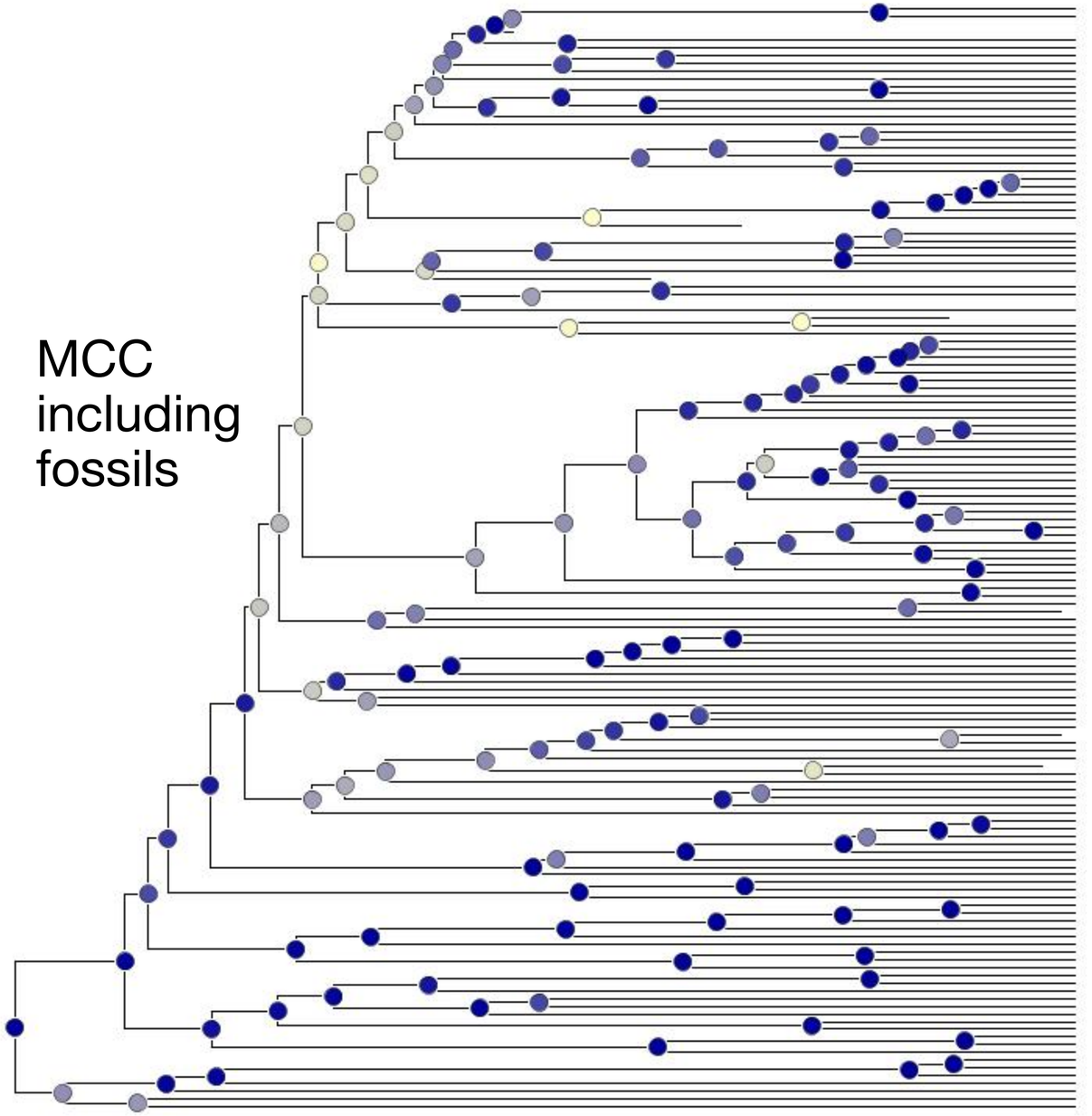
- Implications for internal nodes?



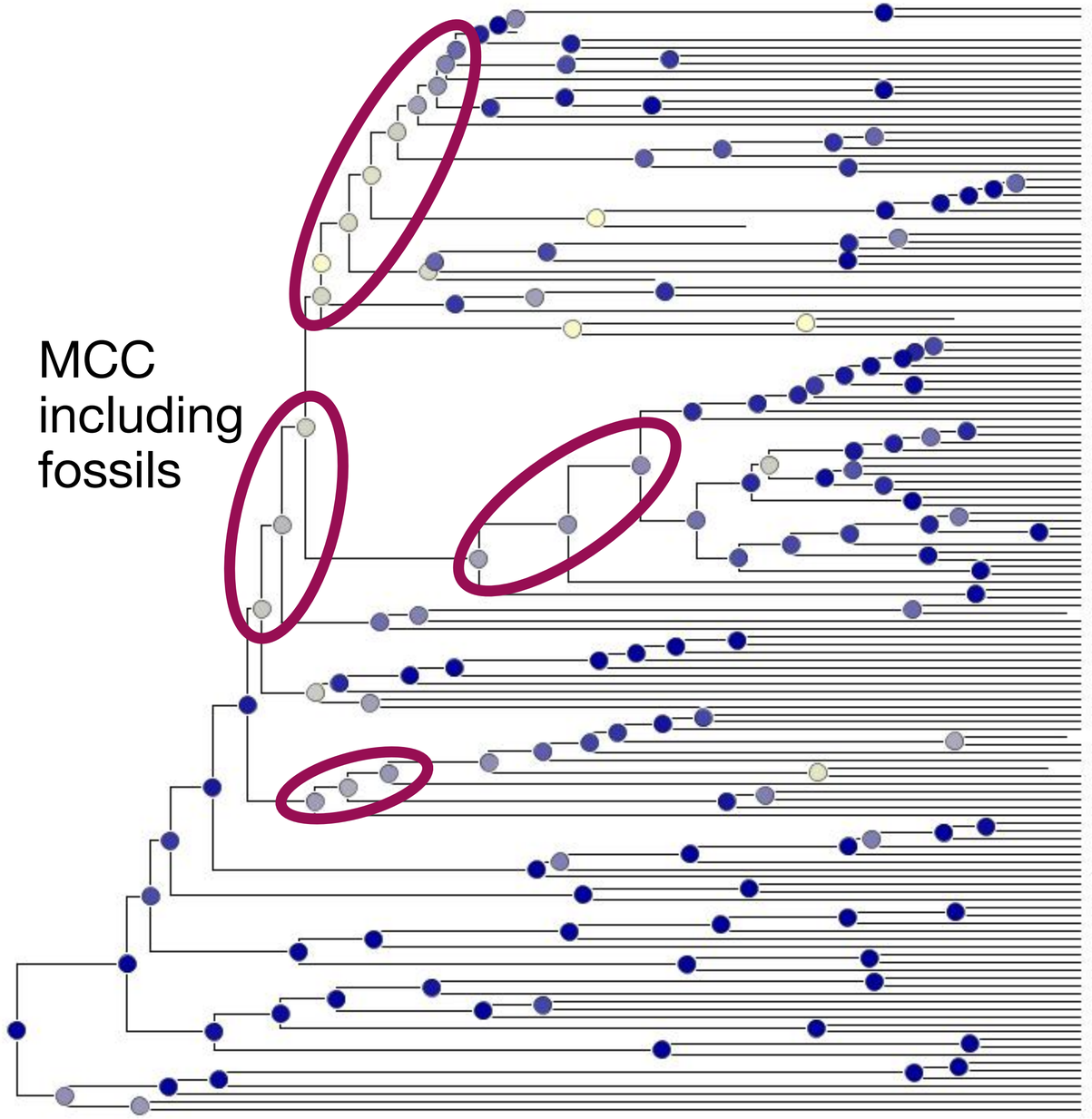


How certain are we about phylogenetic relationships?

How certain are we about phylogenetic relationships?

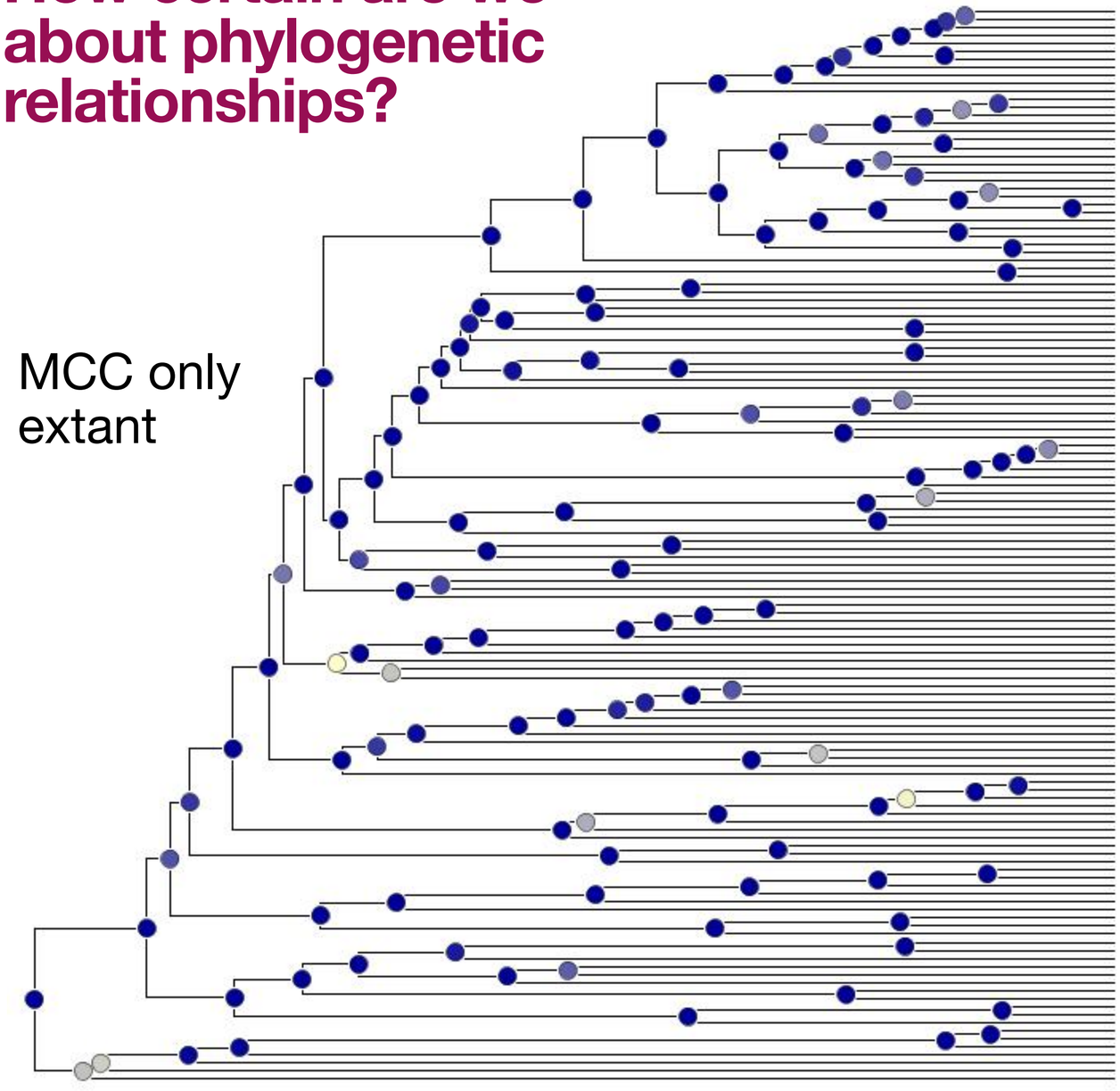


How certain are we about phylogenetic relationships?

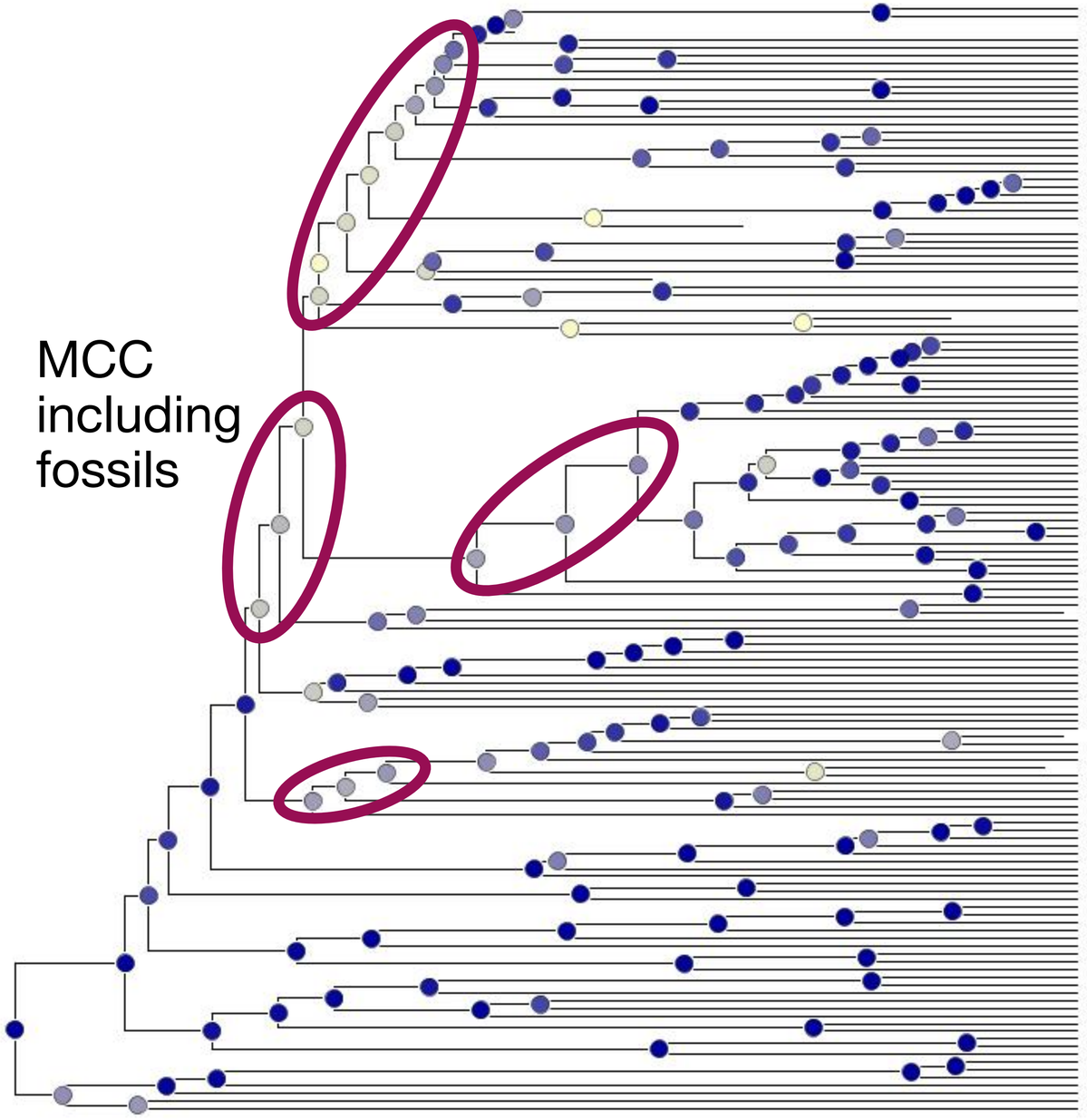


How certain are we about phylogenetic relationships?

MCC only extant



MCC including fossils



Fossils

Take the full sample of trees from the posterior

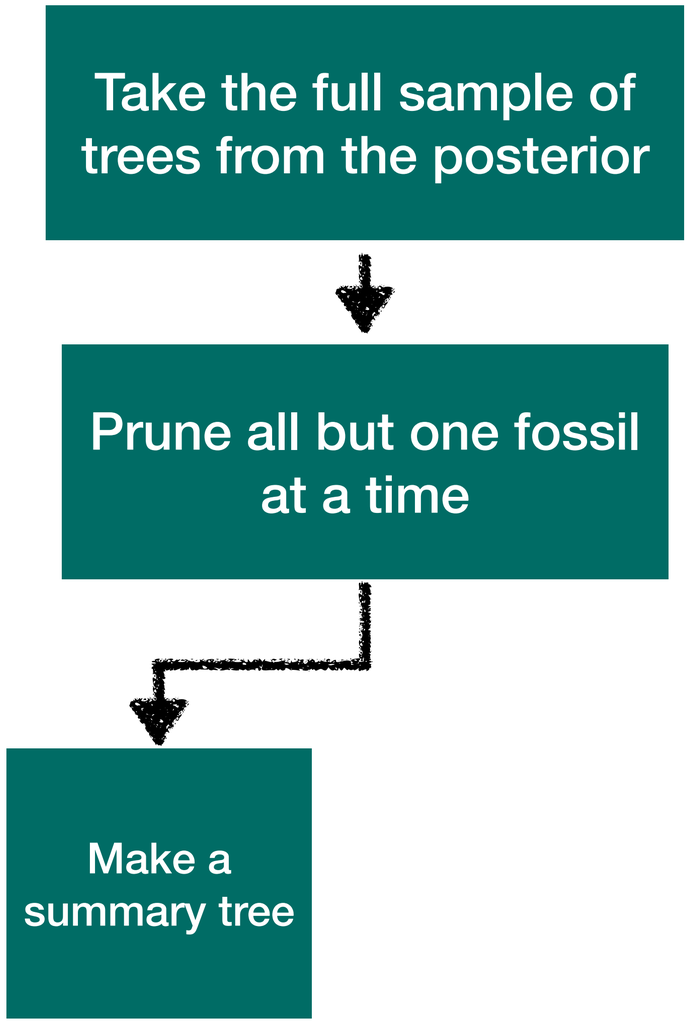
Fossils

Take the full sample of trees from the posterior

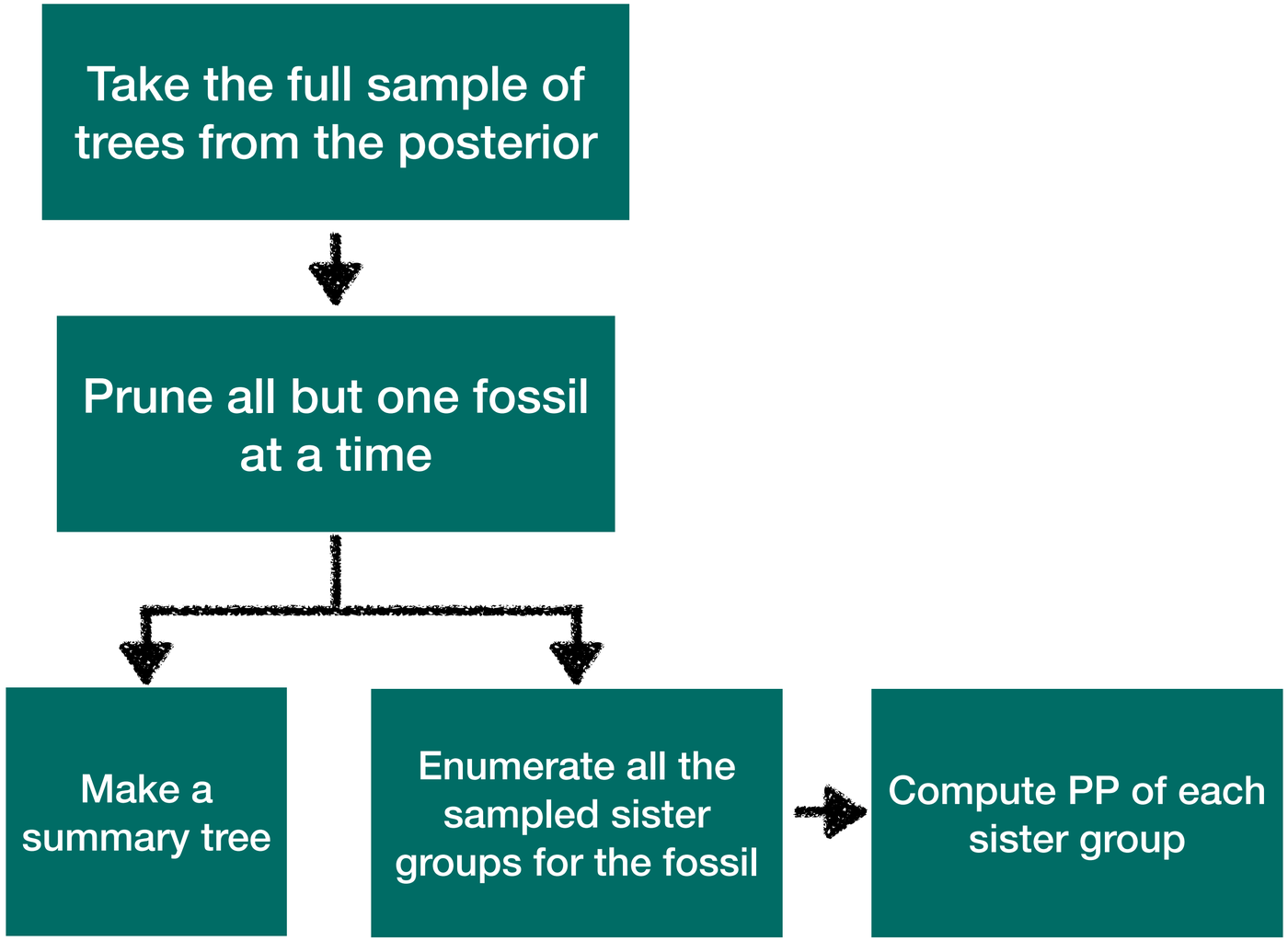


Prune all but one fossil at a time

Fossils


Take the full sample of trees from the posterior
Prune all but one fossil at a time
Make a summary tree

Fossils


Take the full sample of trees from the posterior
Prune all but one fossil at a time
Make a summary tree
Enumerate all the sampled sister groups for the fossil
Compute PP of each sister group

Fossils

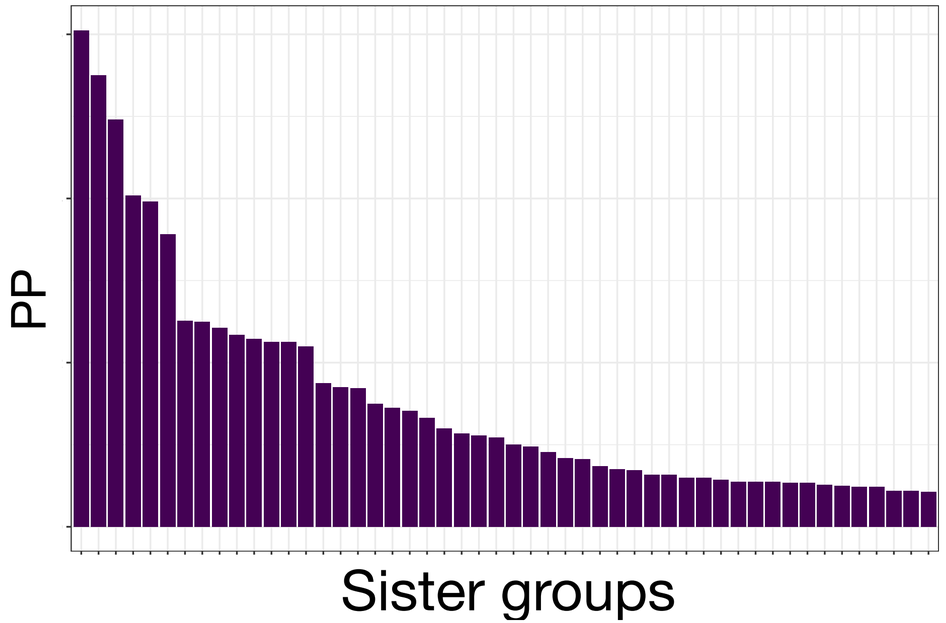
Take the full sample of trees from the posterior

Prune all but one fossil at a time

Make a summary tree

Enumerate all the sampled sister groups for the fossil

Compute PP of each sister group



Fossils

Take the full sample of trees from the posterior

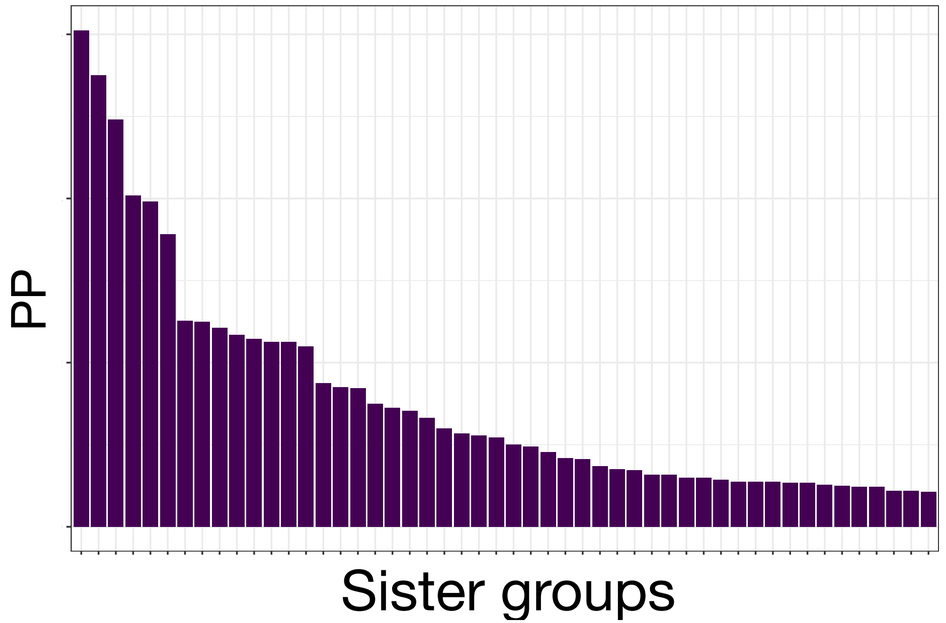
Prune all but one fossil at a time

Make a summary tree

Enumerate all the sampled sister groups for the fossil

Compute PP of each sister group

Fossil placement uncertainty



Fossils

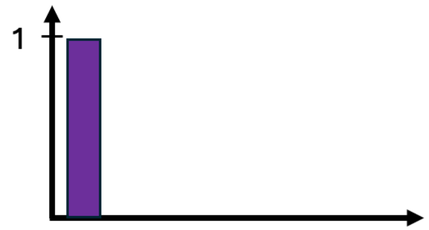
Take the full sample of trees from the posterior

Prune all but one fossil at a time

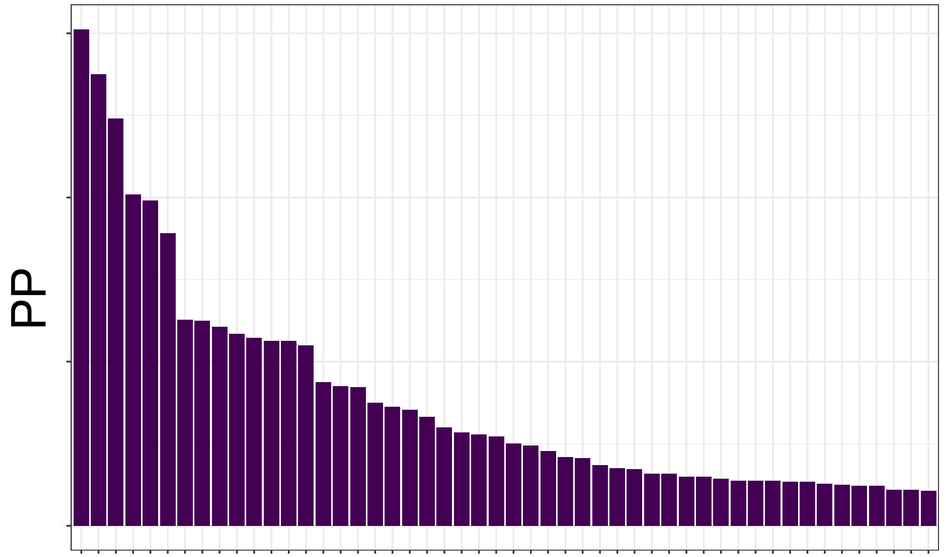
Make a summary tree

Enumerate all the sampled sister groups for the fossil

Compute PP of each sister group



Fossil placement uncertainty



Fossils

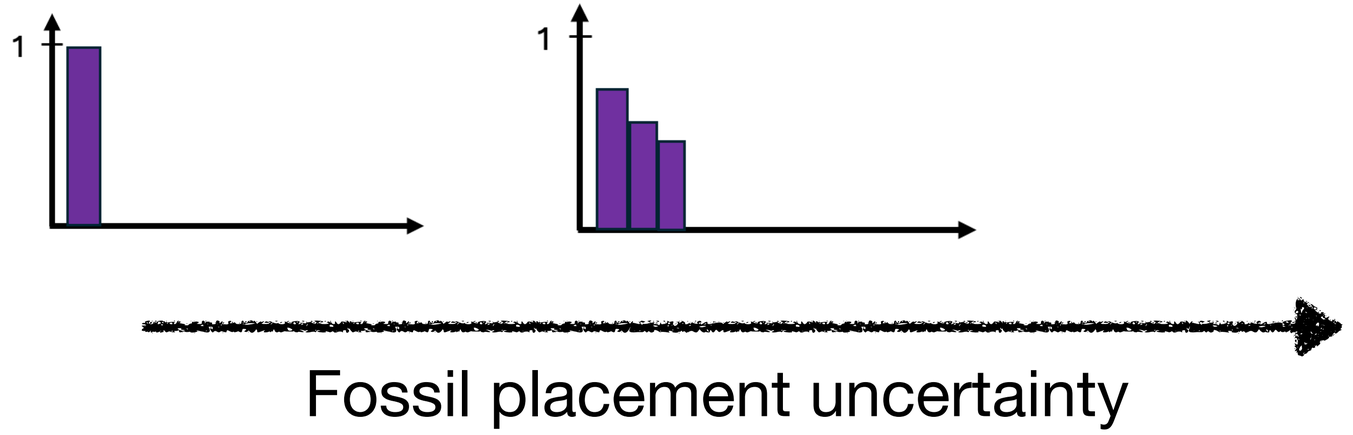
Take the full sample of trees from the posterior

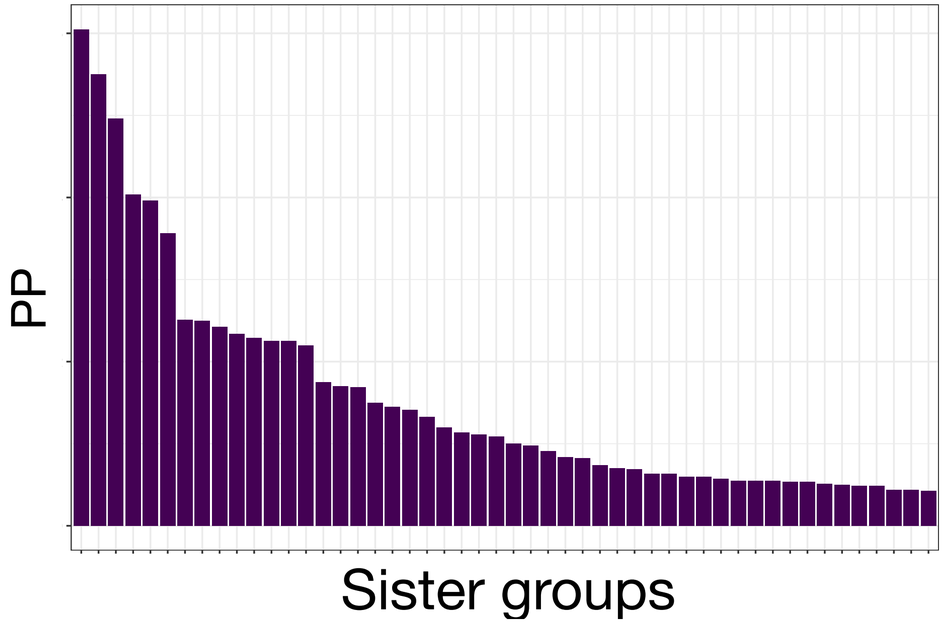
Prune all but one fossil at a time

Make a summary tree

Enumerate all the sampled sister groups for the fossil

Compute PP of each sister group





Fossils

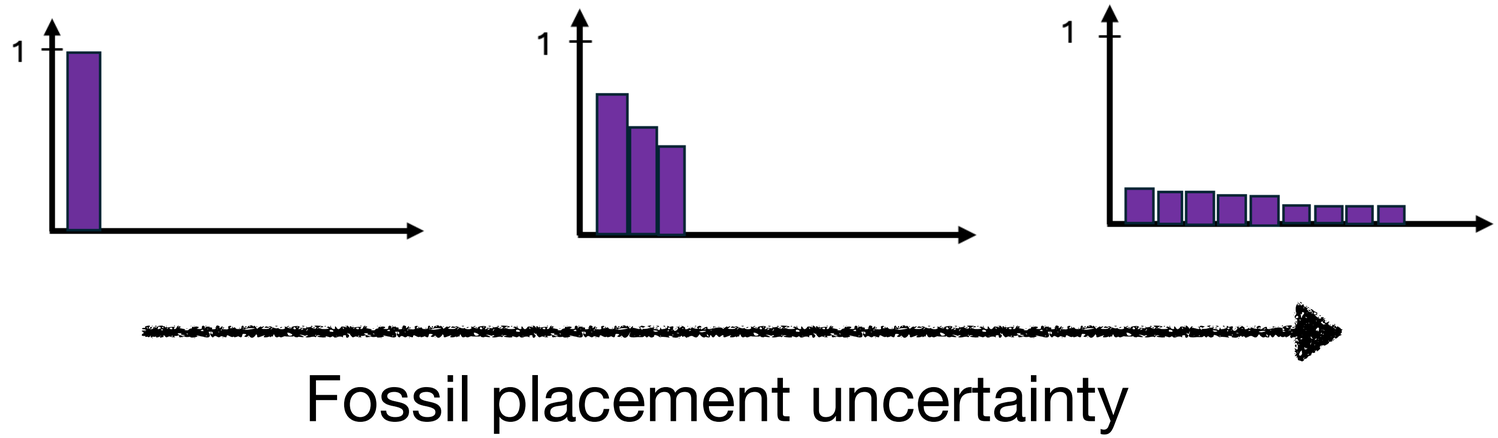
Take the full sample of trees from the posterior

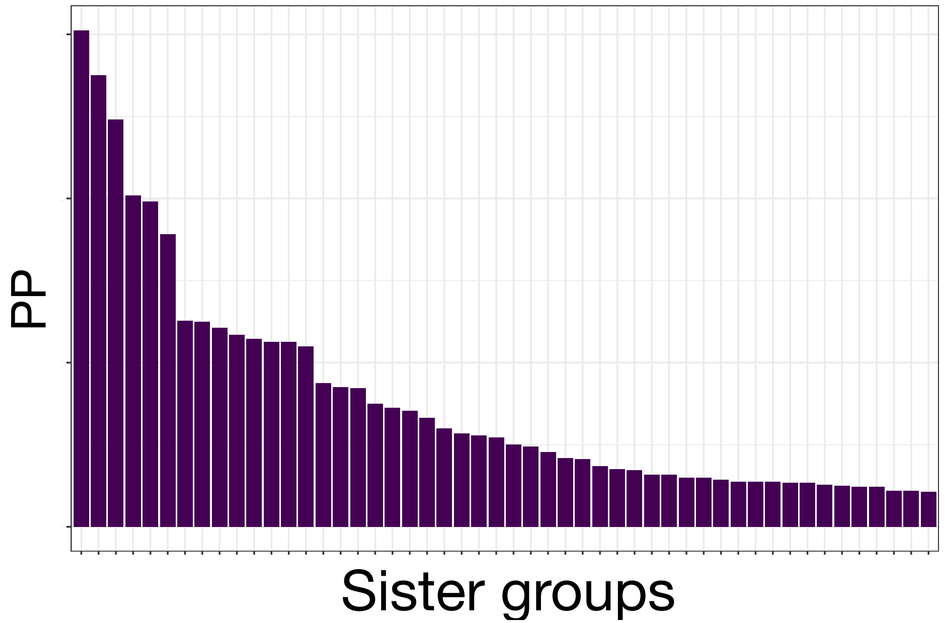
Prune all but one fossil at a time

Make a summary tree

Enumerate all the sampled sister groups for the fossil

Compute PP of each sister group





Fossils



Solanum miocenicus (seed)



Solanum foveolatum (seed)

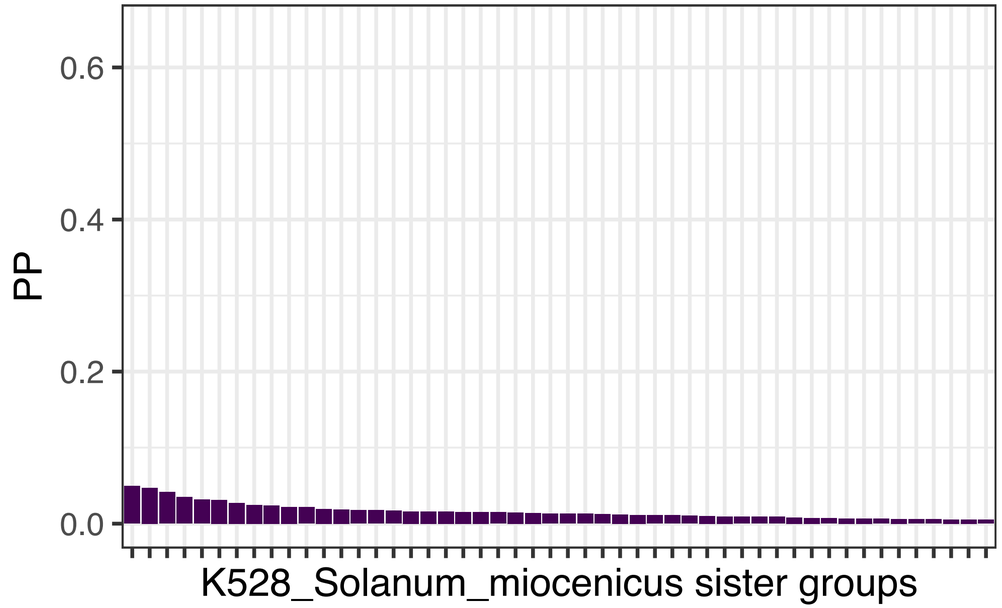
Fossils

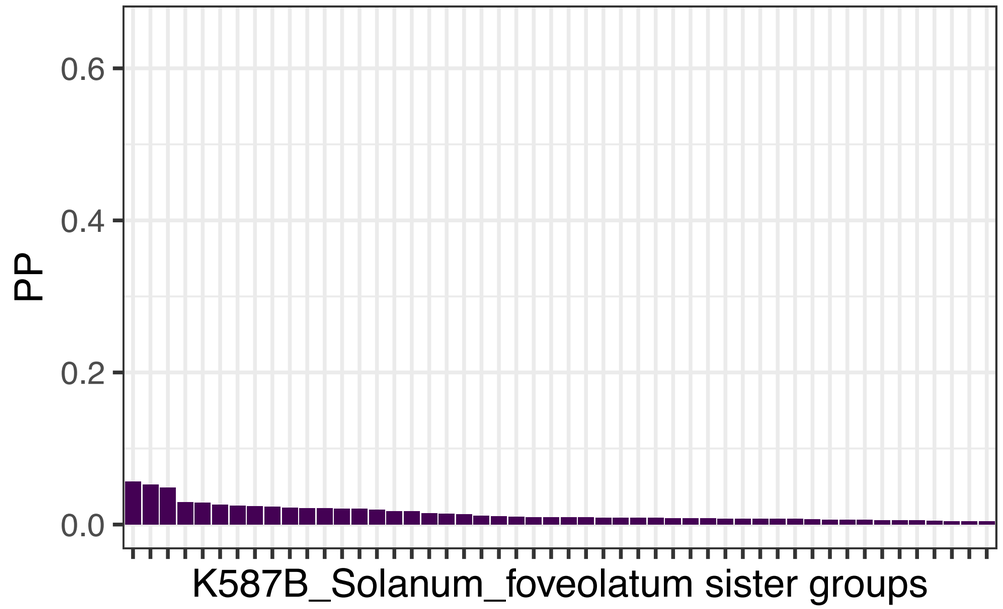


Solanum miocenicus (seed) PP = 0.05

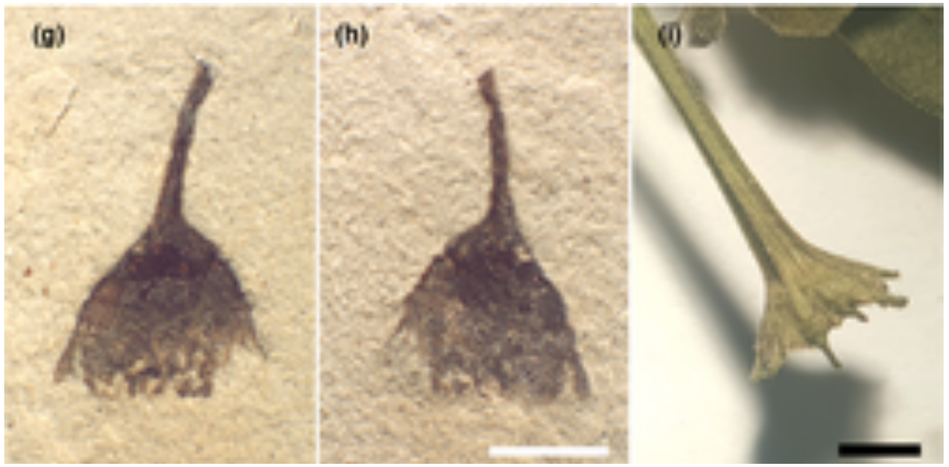


Solanum foveolatum (seed) PP = 0.05

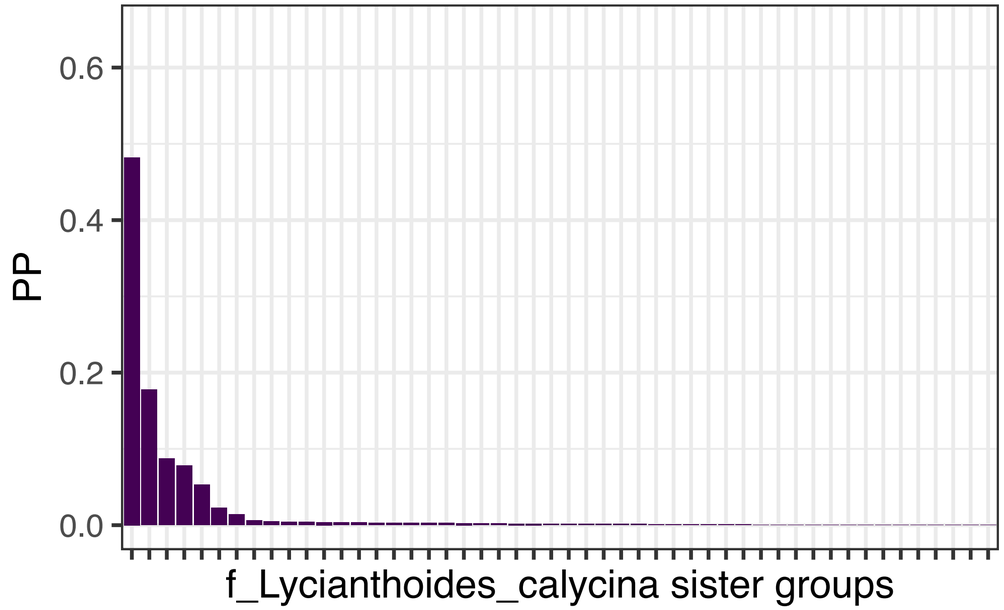




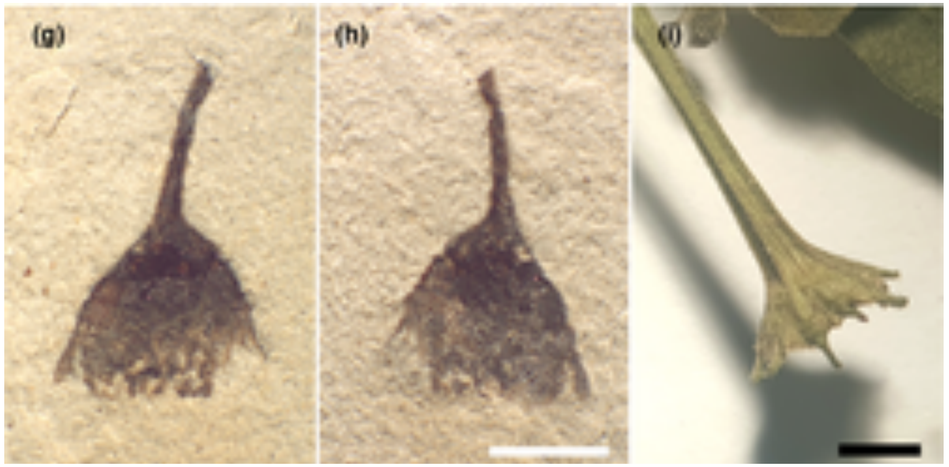
Fossils

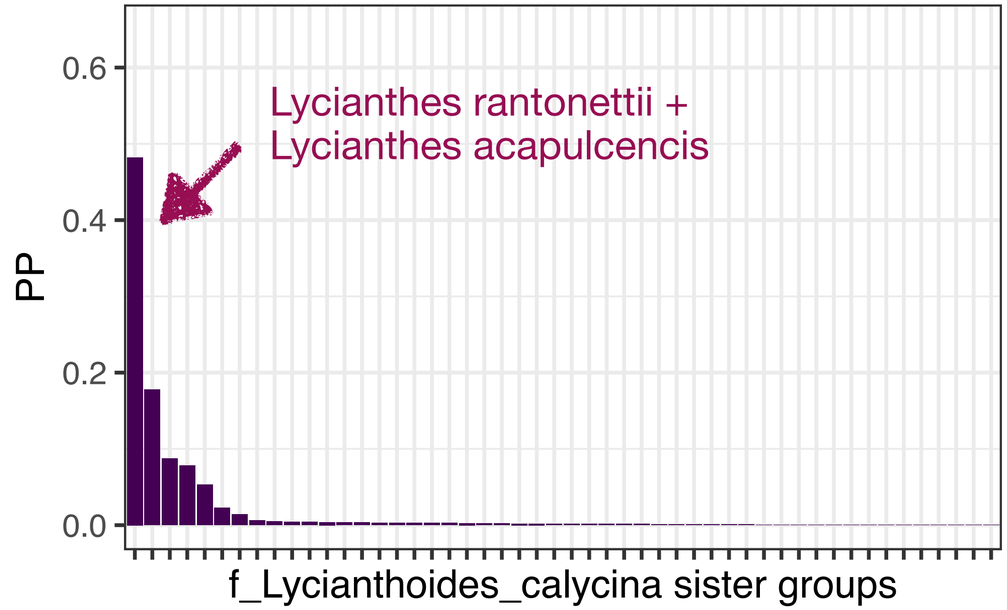


Lycianthoides calycina (fruit)



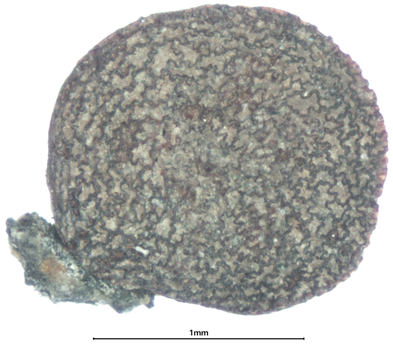
Fossils



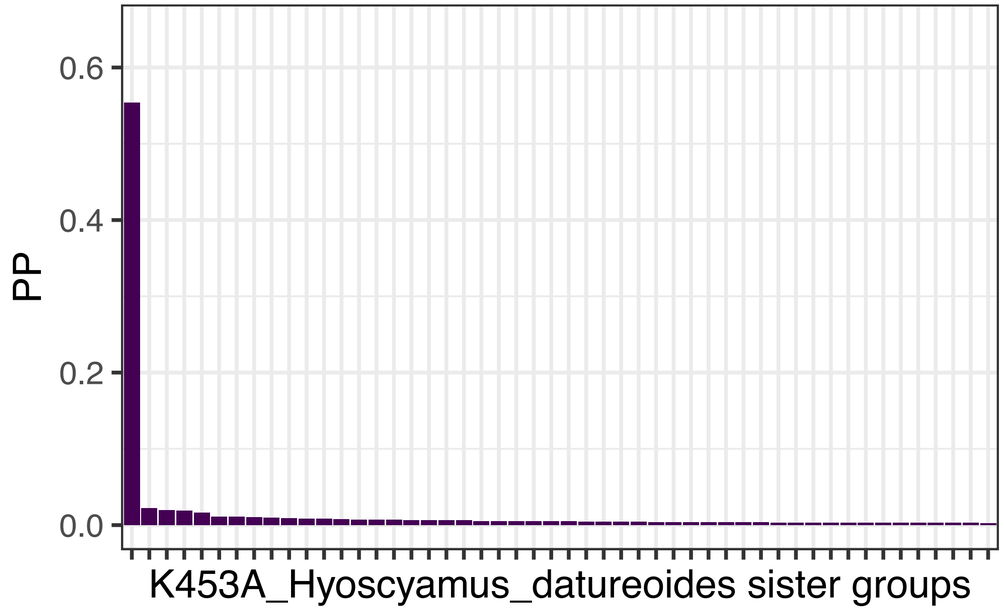


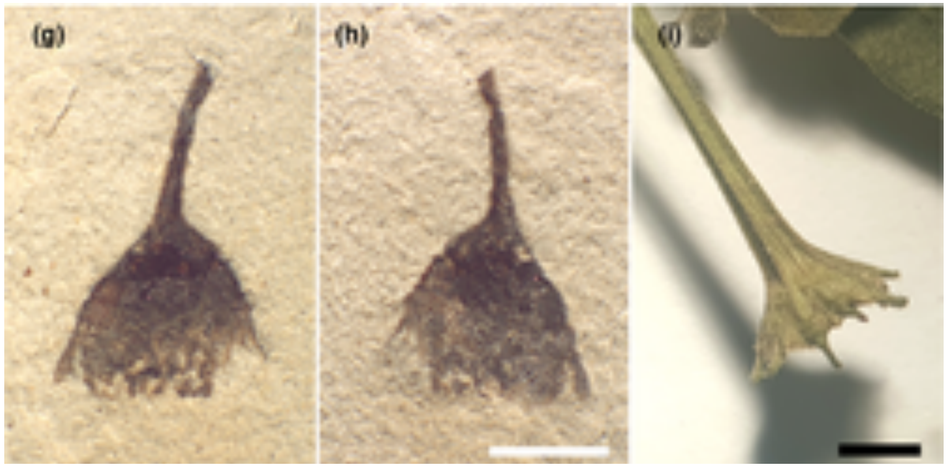
Lycianthoides calycina (fruit) PP = 0.48

Fossils

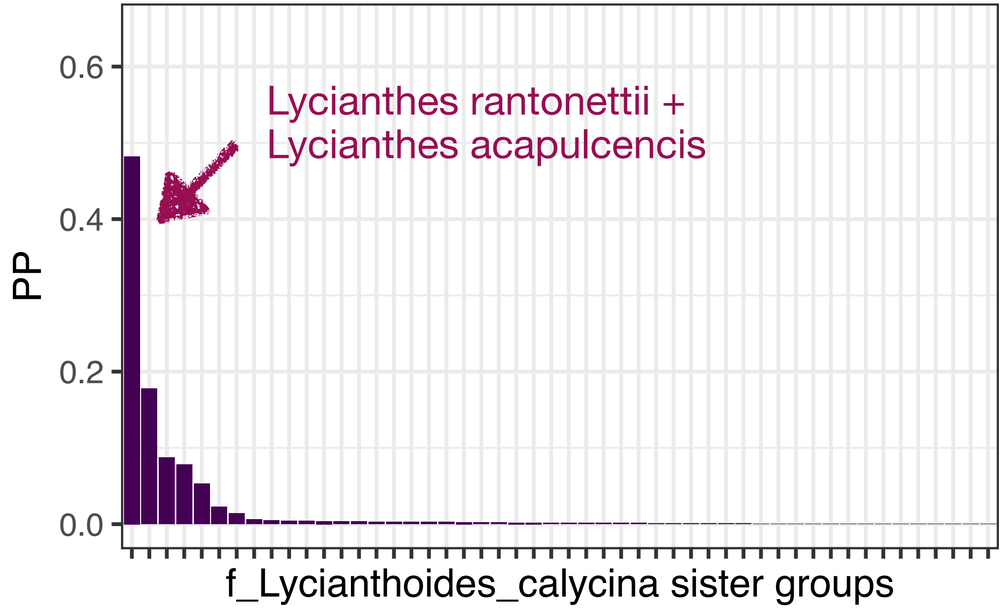


Hyoscyamus datureoides (seed) PP = 0.55

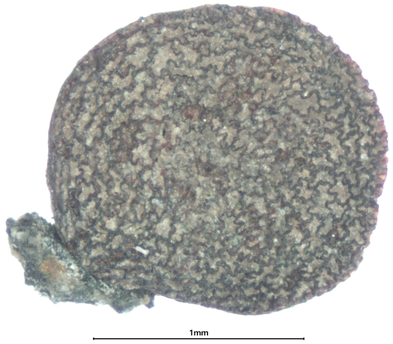




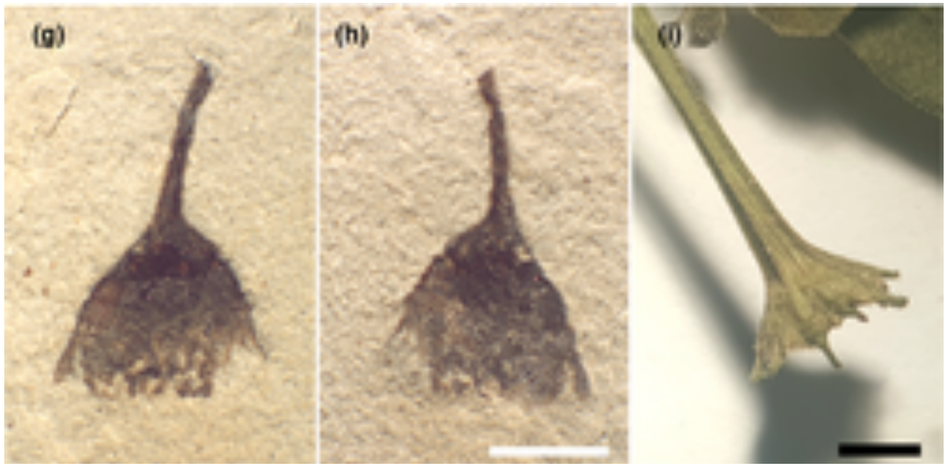
Lycianthoides calycina (fruit) PP = 0.48



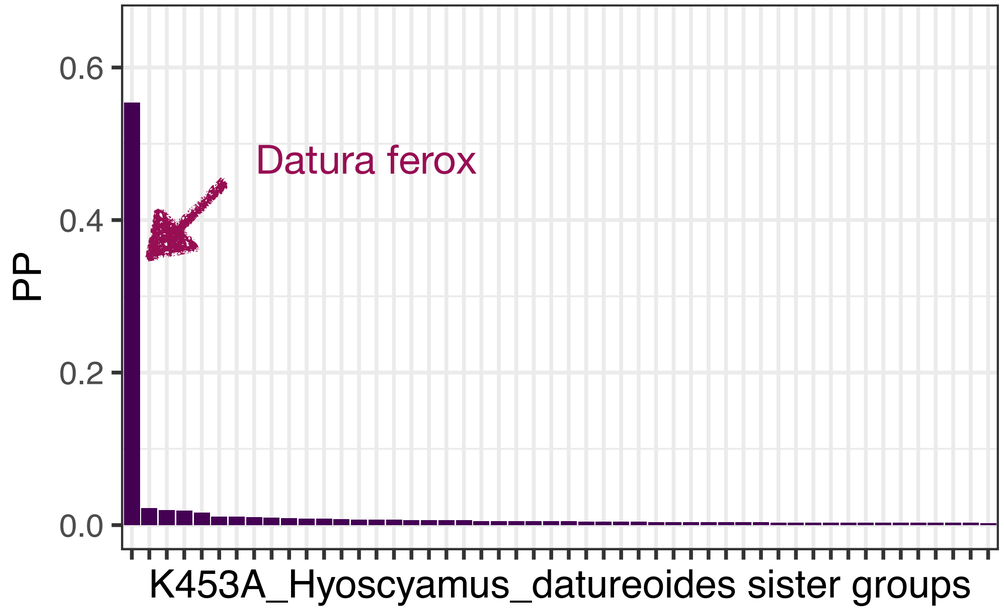
Fossils

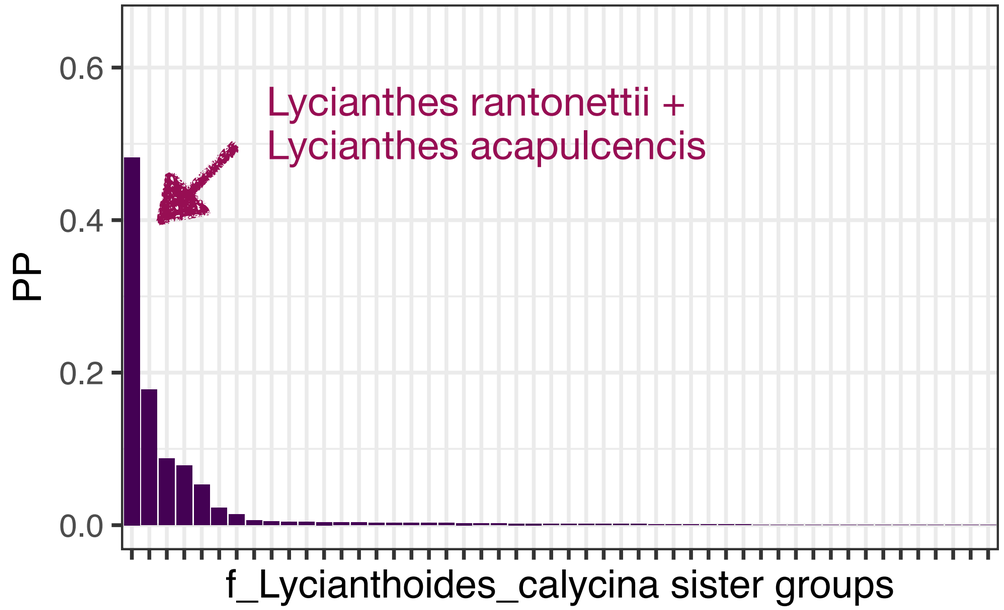


Hyoscyamus datureoides (seed) PP = 0.55



Lycianthoides calycina (fruit) PP = 0.48

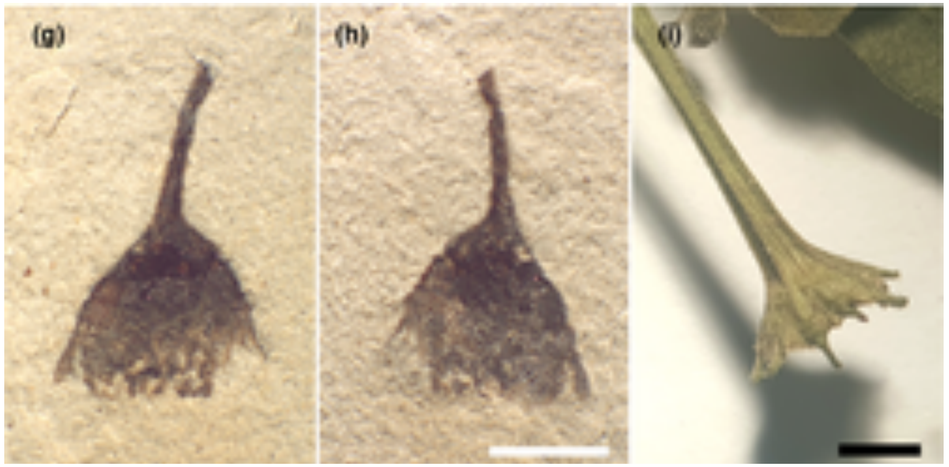




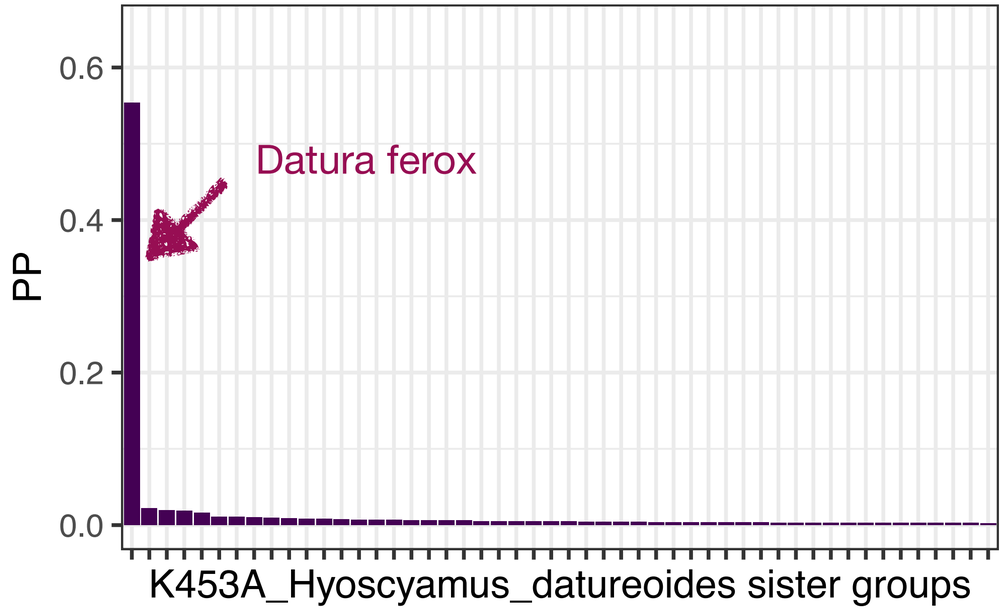
Fossils

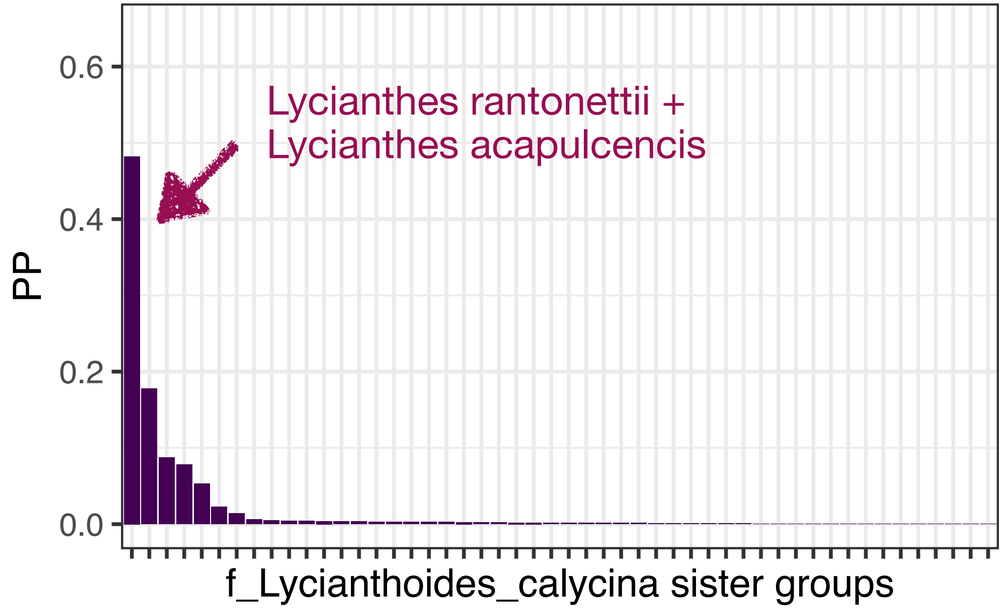


Hyoscyamus datureoides (seed) PP = 0.55



Lycianthoides calycina (fruit) PP = 0.48



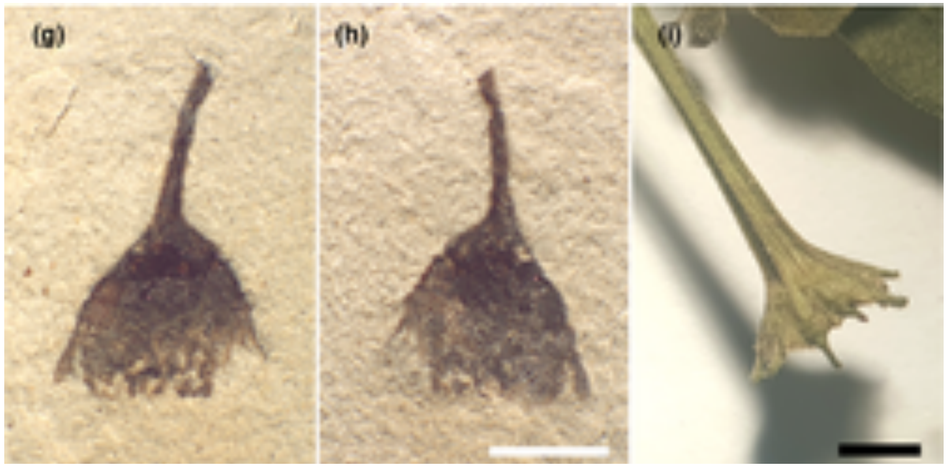


Fossils

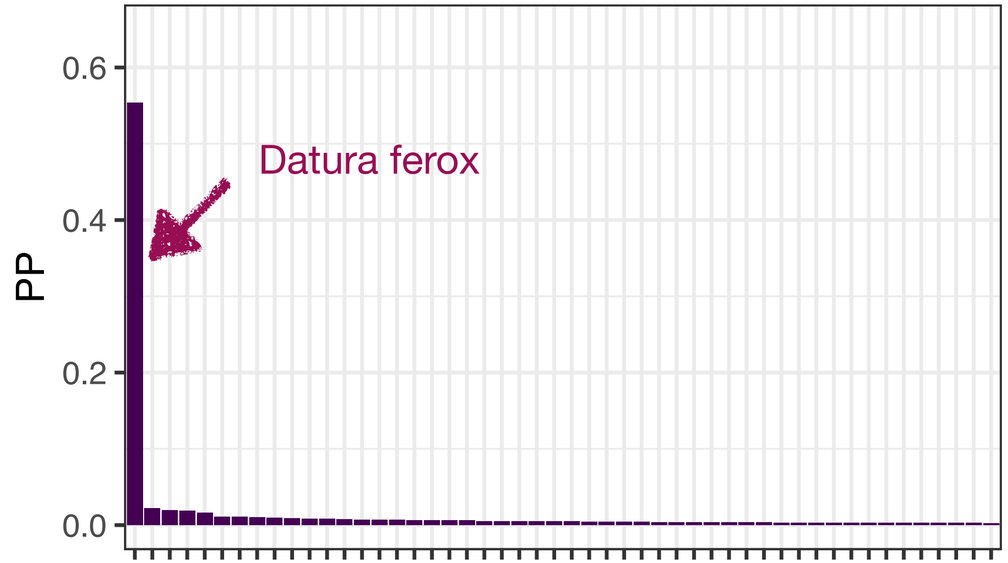


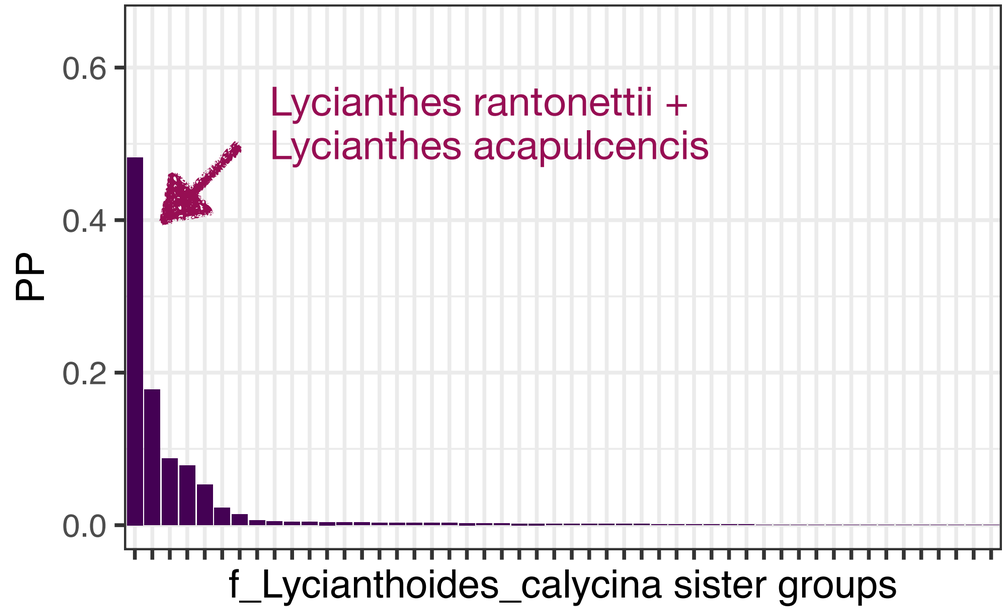


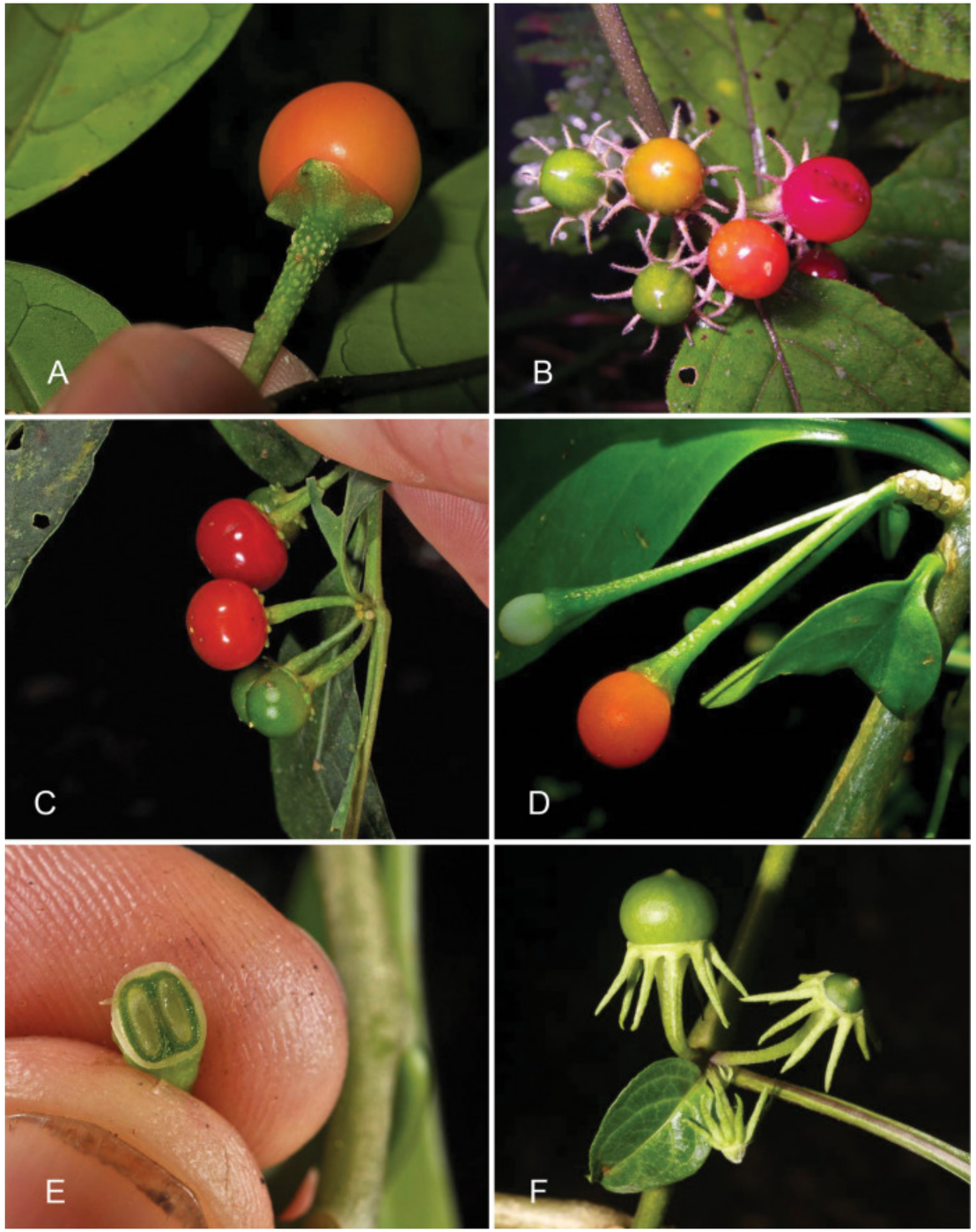
Hyoscyamus datureoides (seed) PP = 0.55



Lycianthoides calycina (fruit) PP = 0.48







Conclusions

- Morphological traits allow to confidently place some fossils, even when plugged into a complex model.
- Carefully examining the posterior helps to better understand fossil placement uncertainty.
- Fossils can inform age even when they have uncertain placement in a TED approach.

(Knapp, 2024)