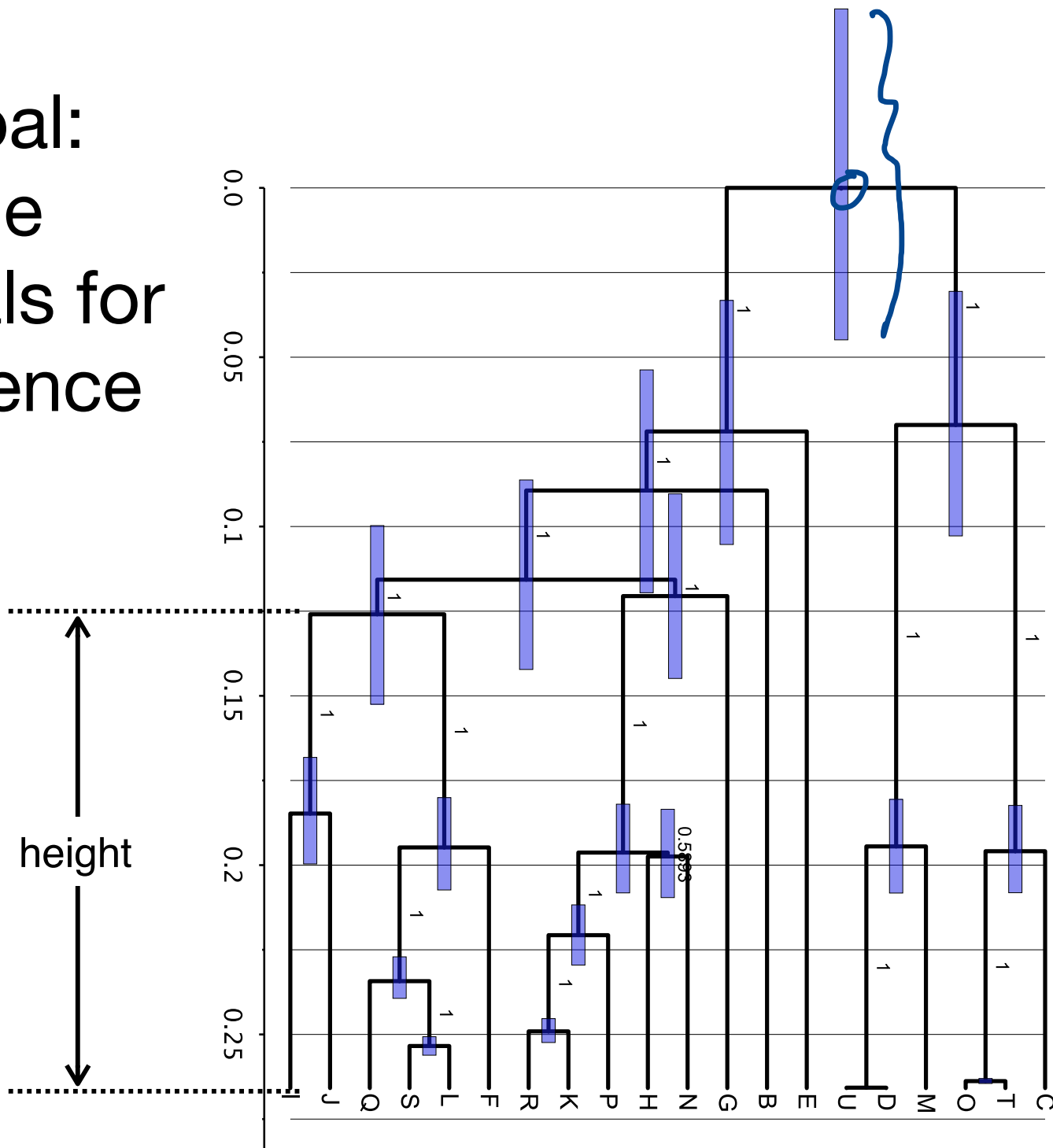
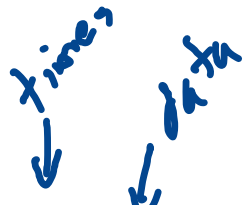


The goal:
credible
intervals for
divergence
times



Posterior density for times \mathbf{t} given data \mathbf{y}


$$p(\mathbf{t}|\mathbf{y}) = \int p(\mathbf{t}, \mathbf{r}|\mathbf{y}) d\mathbf{r}$$

Bold symbols denote vector quantities.
That is, \mathbf{t} represents a vector of ancestral node times.

Marginalize over rates \mathbf{r} : we are only interested in the distribution of times.

You must have known that Bayes' rule was coming sooner or later...

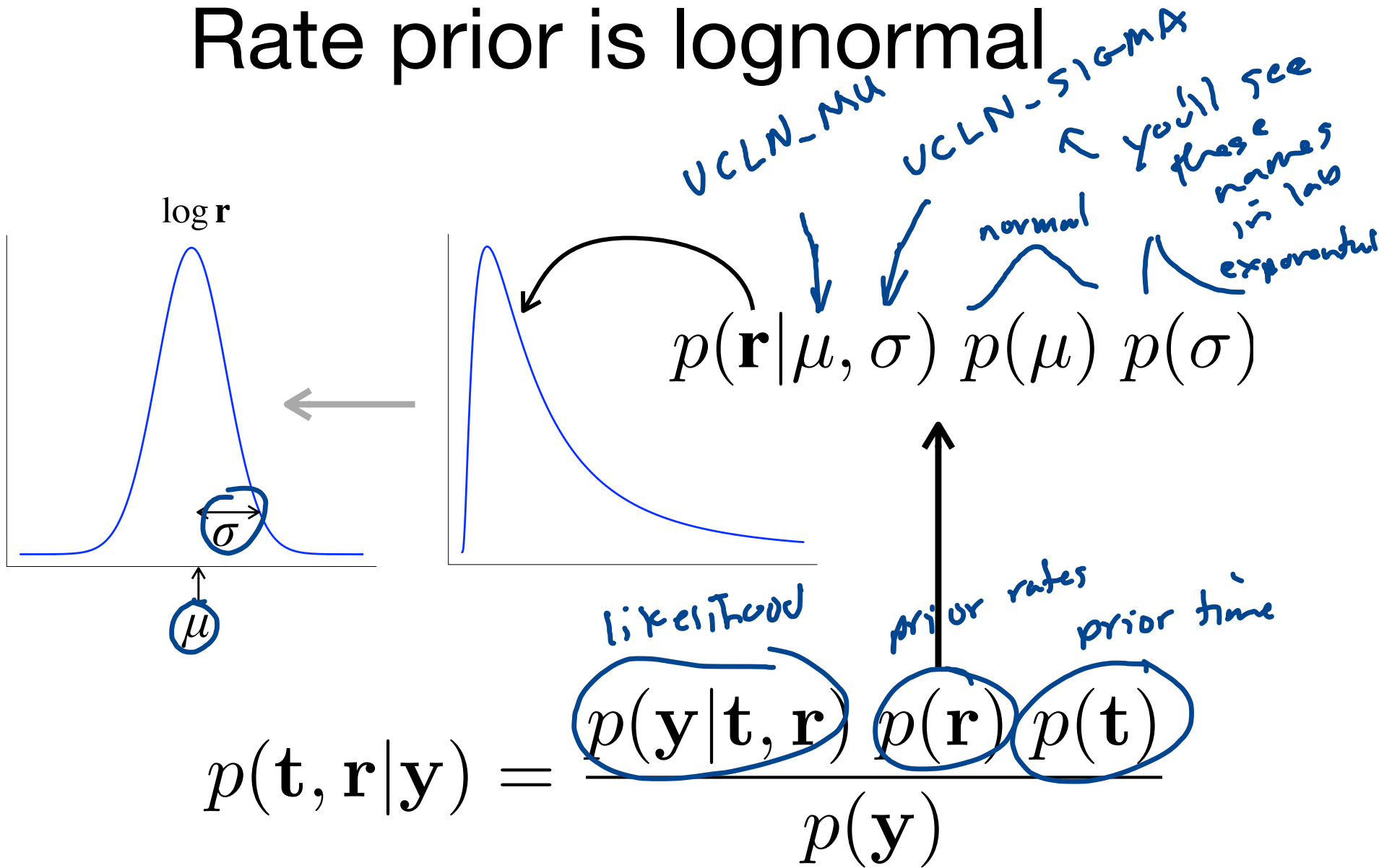
$$p(\mathbf{t}|\mathbf{y}) = \int p(\mathbf{t}, \mathbf{r}|\mathbf{y}) d\mathbf{r}$$

posterior

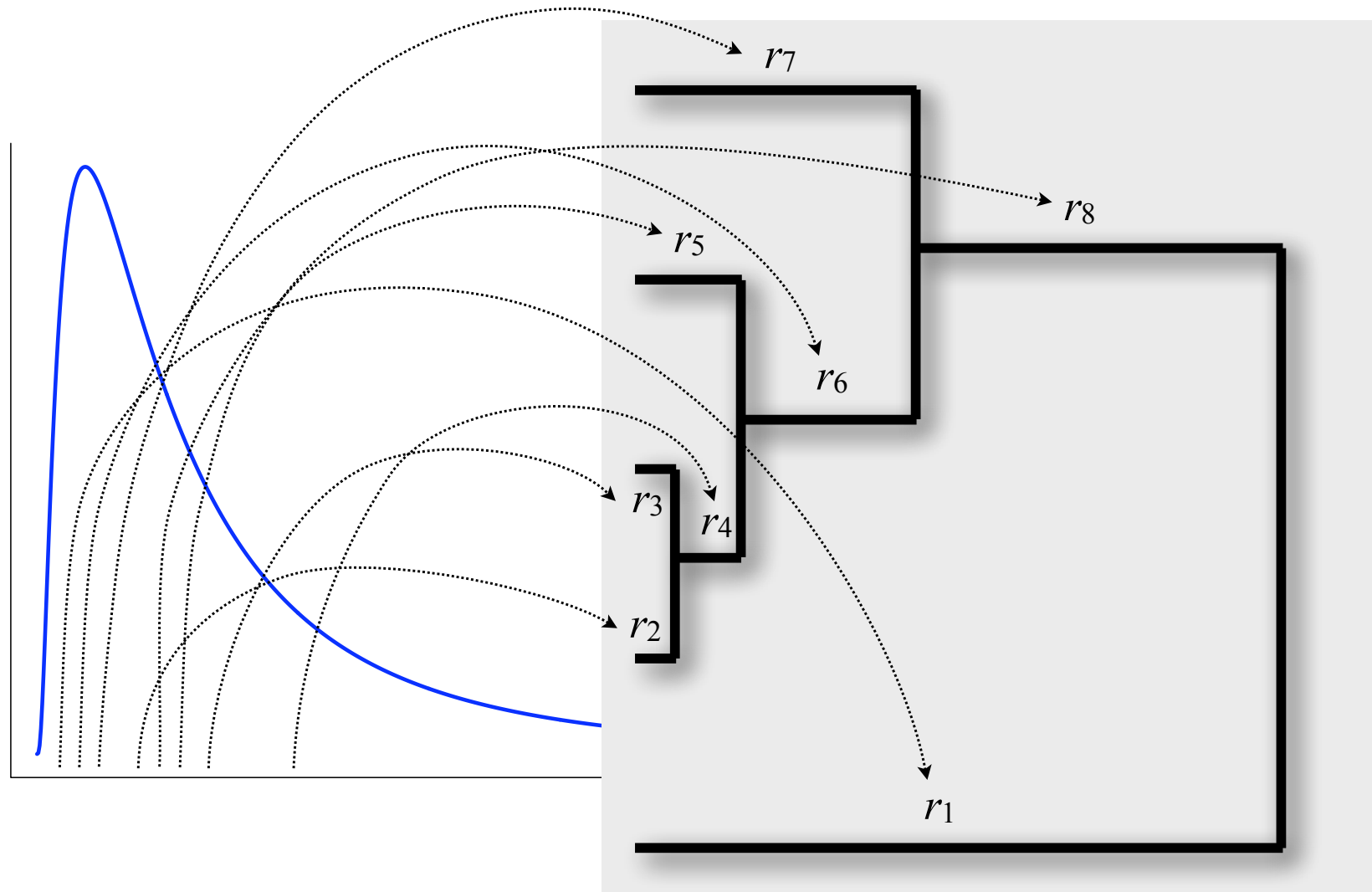
↓

likelihood	← prior →
$p(\mathbf{y} \mathbf{t}, \mathbf{r})$	$p(\mathbf{r}) p(\mathbf{t})$
$p(\mathbf{y})$	
marginal likelihood	

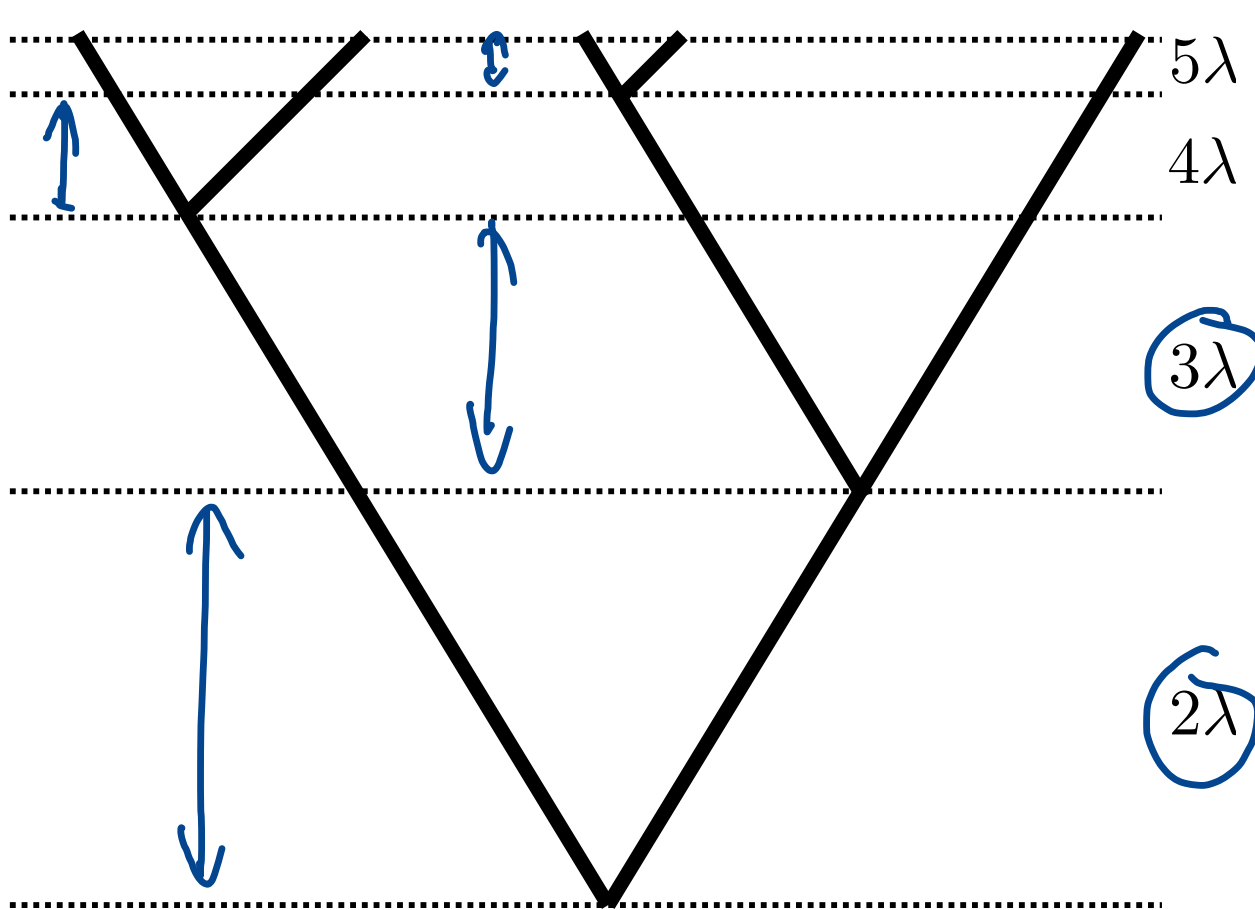
Rate prior is lognormal



Rates are **conditionally independent** - any correlation between rates is due only to the fact that they all share the same lognormal prior distribution.



Time prior provided by birth-death model



Yule model (pure birth):
 exponential sojourn
 times between
 speciation events

*extinction rate
 zero*

$p(\mathbf{t}|\lambda)$ $p(\lambda)$

$$\frac{p(\mathbf{y}|\mathbf{t}, \mathbf{r}) p(\mathbf{r}|\mu, \sigma) p(\mu) p(\sigma) p(\mathbf{t})}{p(\mathbf{y})}$$

Full uncorrelated lognormal relaxed clock model

$$p(\mathbf{t}, \mathbf{r}, \mu, \sigma, \lambda | \mathbf{y})$$

$$= \frac{p(\mathbf{y} | \mathbf{t}, \mathbf{r}) p(\mathbf{r} | \mu, \sigma) p(\mu) p(\sigma) p(\mathbf{t} | \lambda) p(\lambda)}{p(\mathbf{y})}$$

This uses the JC69 model (the likelihood involves only branch lengths).

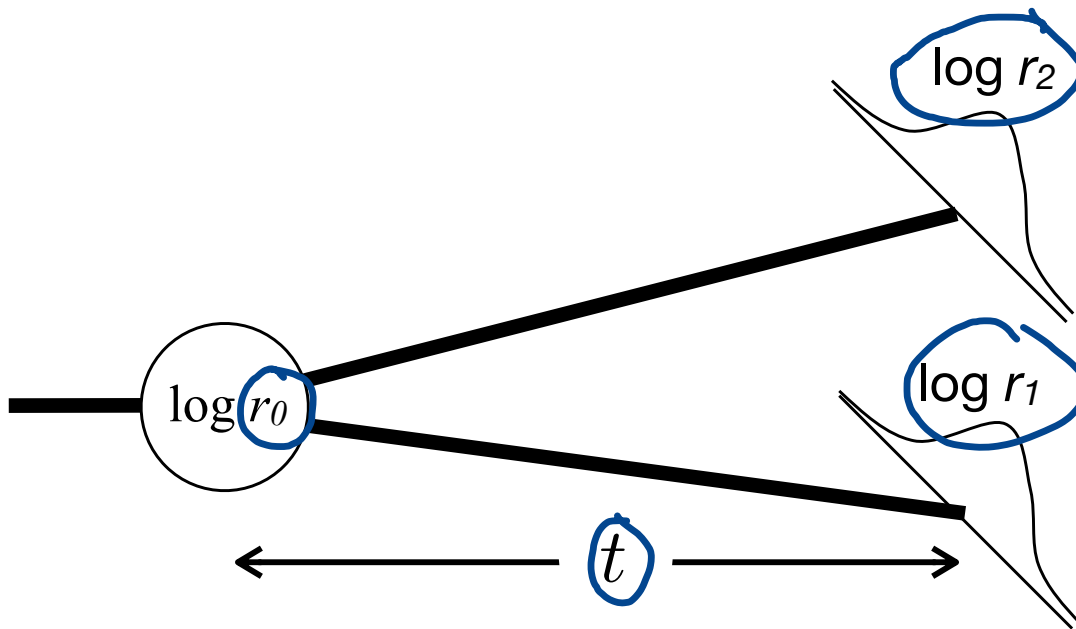
Is this a hierarchical model?

Bayesian correlated relaxed clock model

Thorne et al. (1998); Kishino et al. (2001)

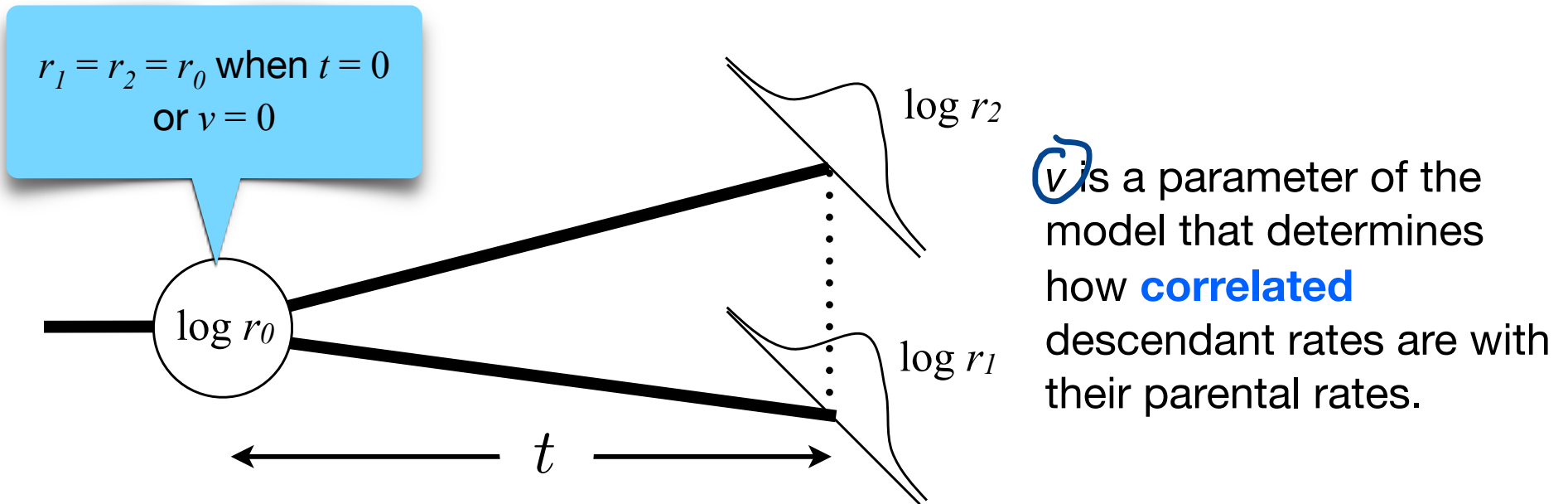
Thorne/Kishino model

Each node in the tree has its own rate.



Both $\log r_1$ and $\log r_2$ are normally distributed with:
mean = $\log r_0$
variance = vt

Thorne/Kishino model



$v = 0$ corresponds to a strict molecular clock

large values of v mean less constrained rates (and correspondingly less certainty about divergence times)

Correlated Rates

Almost all rates in this tree are predicted well by the rate of their parent, so a correlated rates or local clock model would work well.

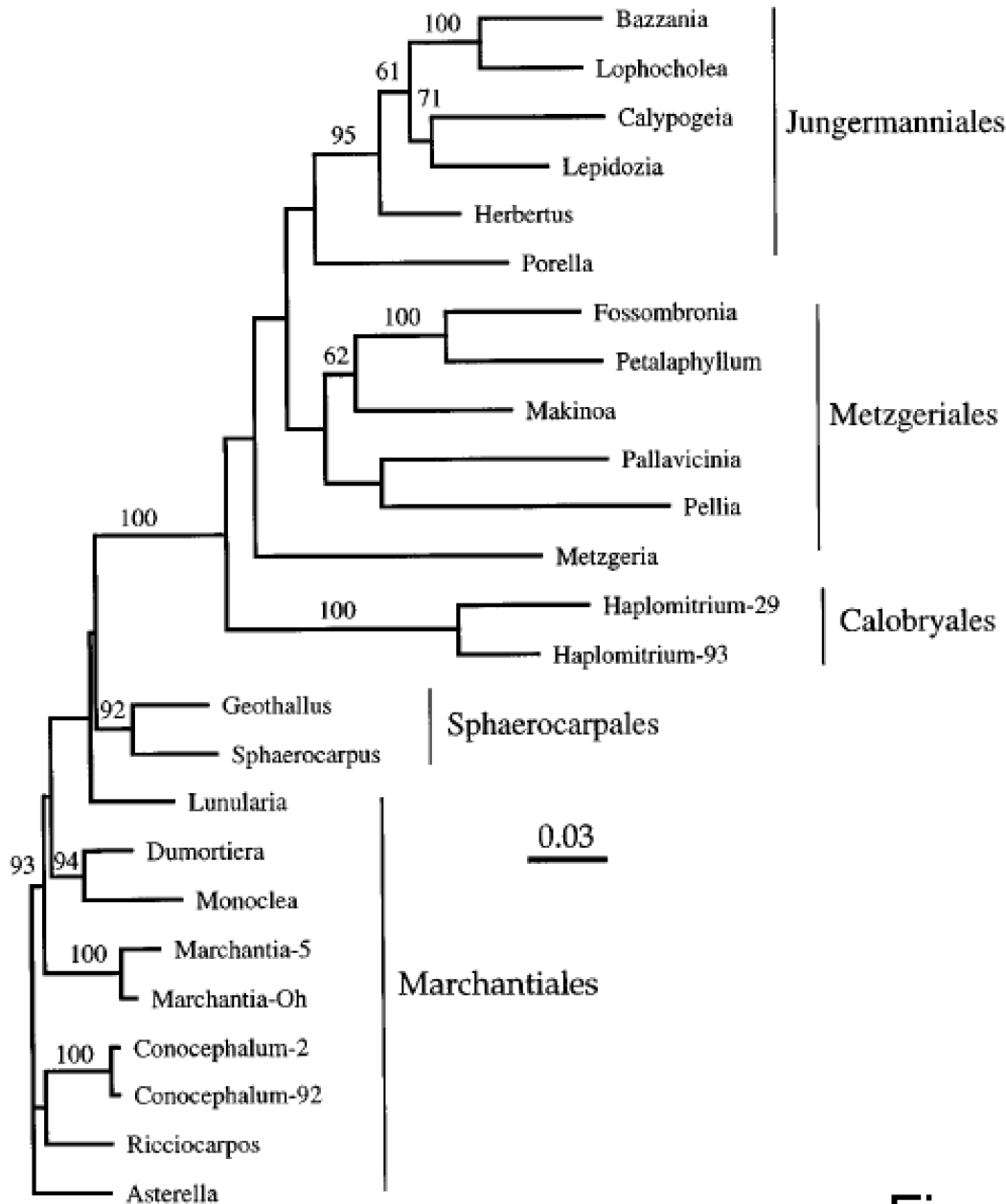
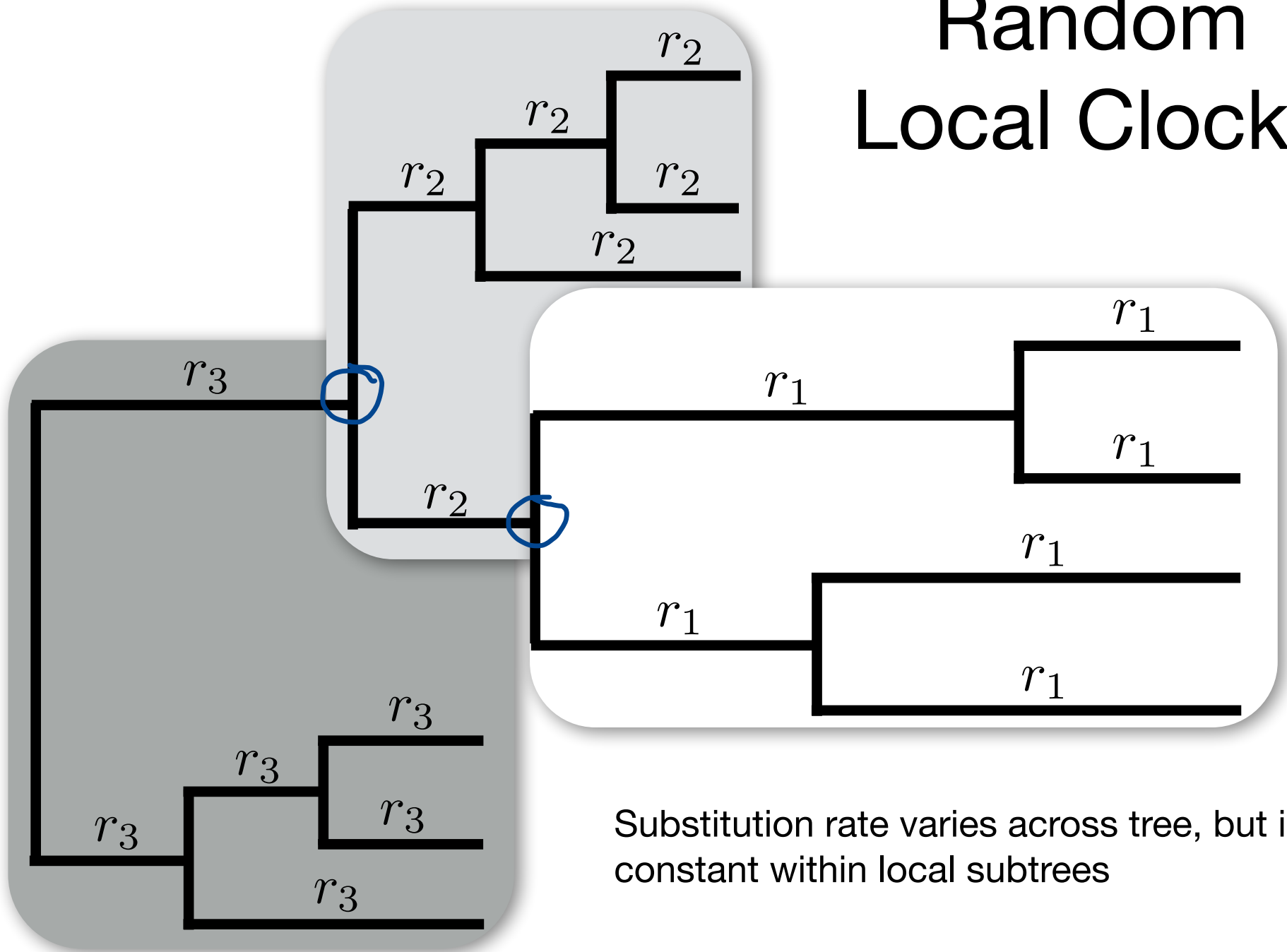


Fig. 5 in Lewis et al. (1997)

Bayesian random local clocks model

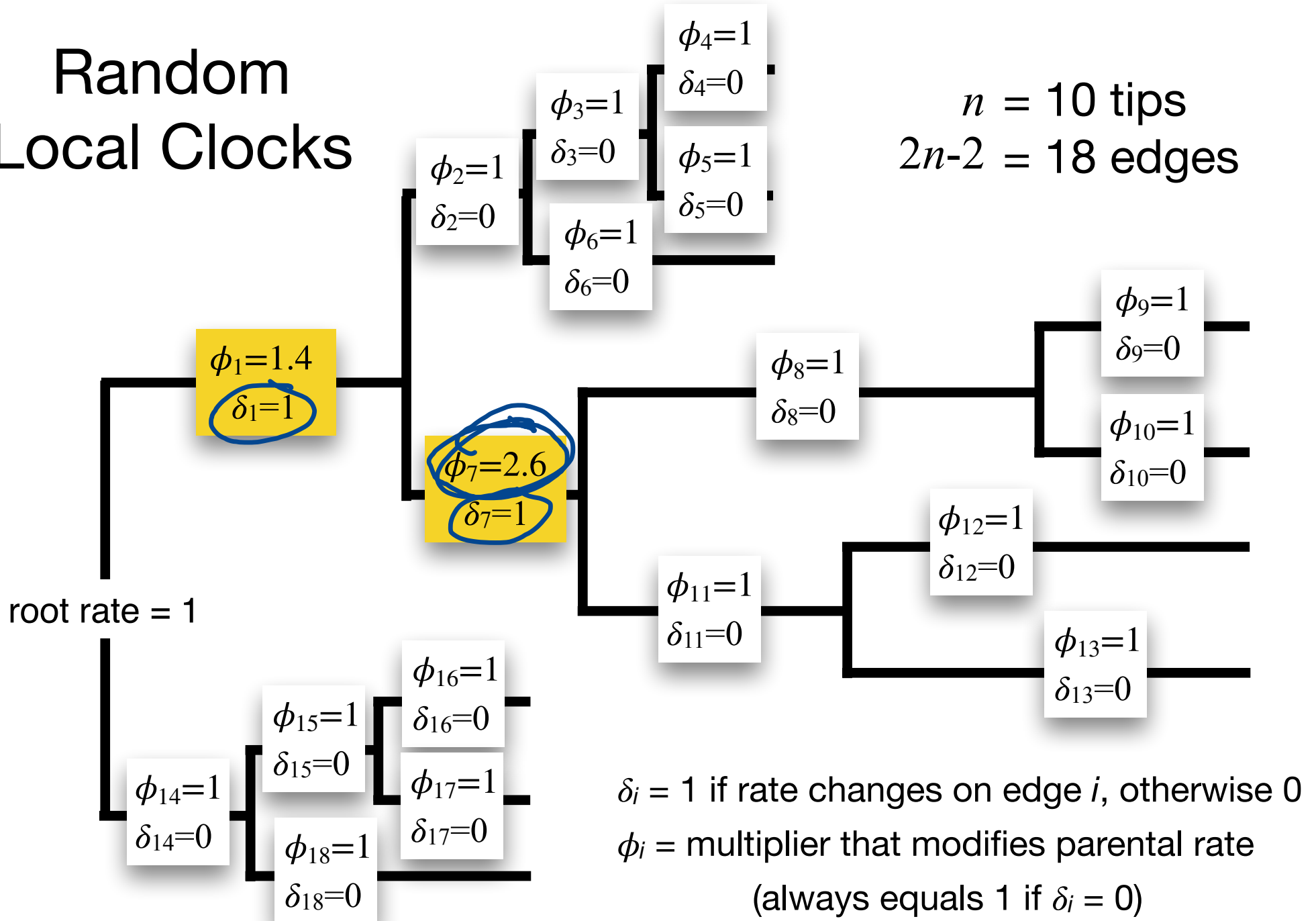
Drummond and Suchard (2010)

Random Local Clocks



Substitution rate varies across tree, but is constant within local subtrees

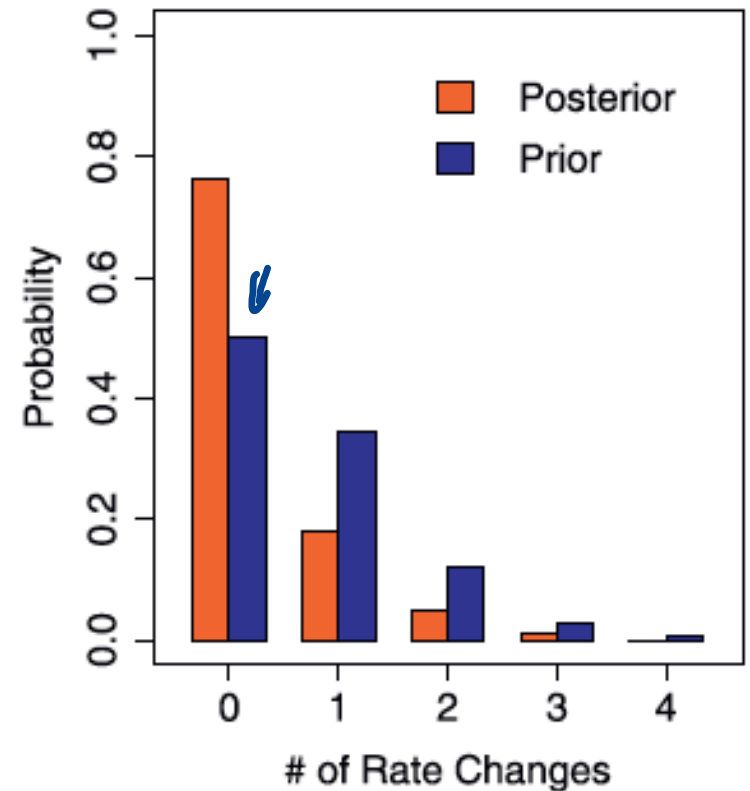
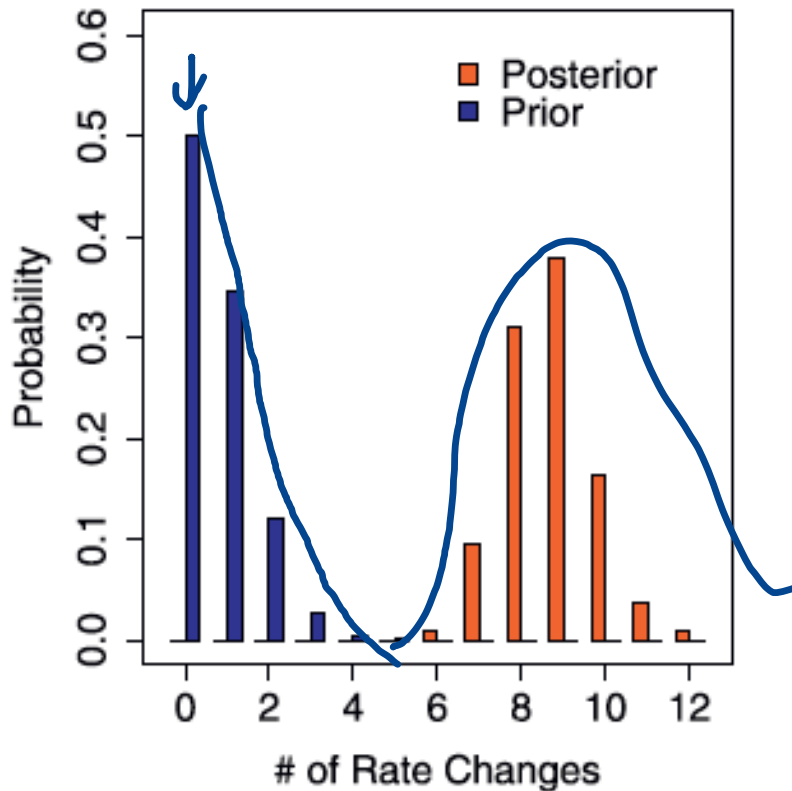
Random Local Clocks



Random Local Clocks

Definitely not a strict clock

May be a strict clock



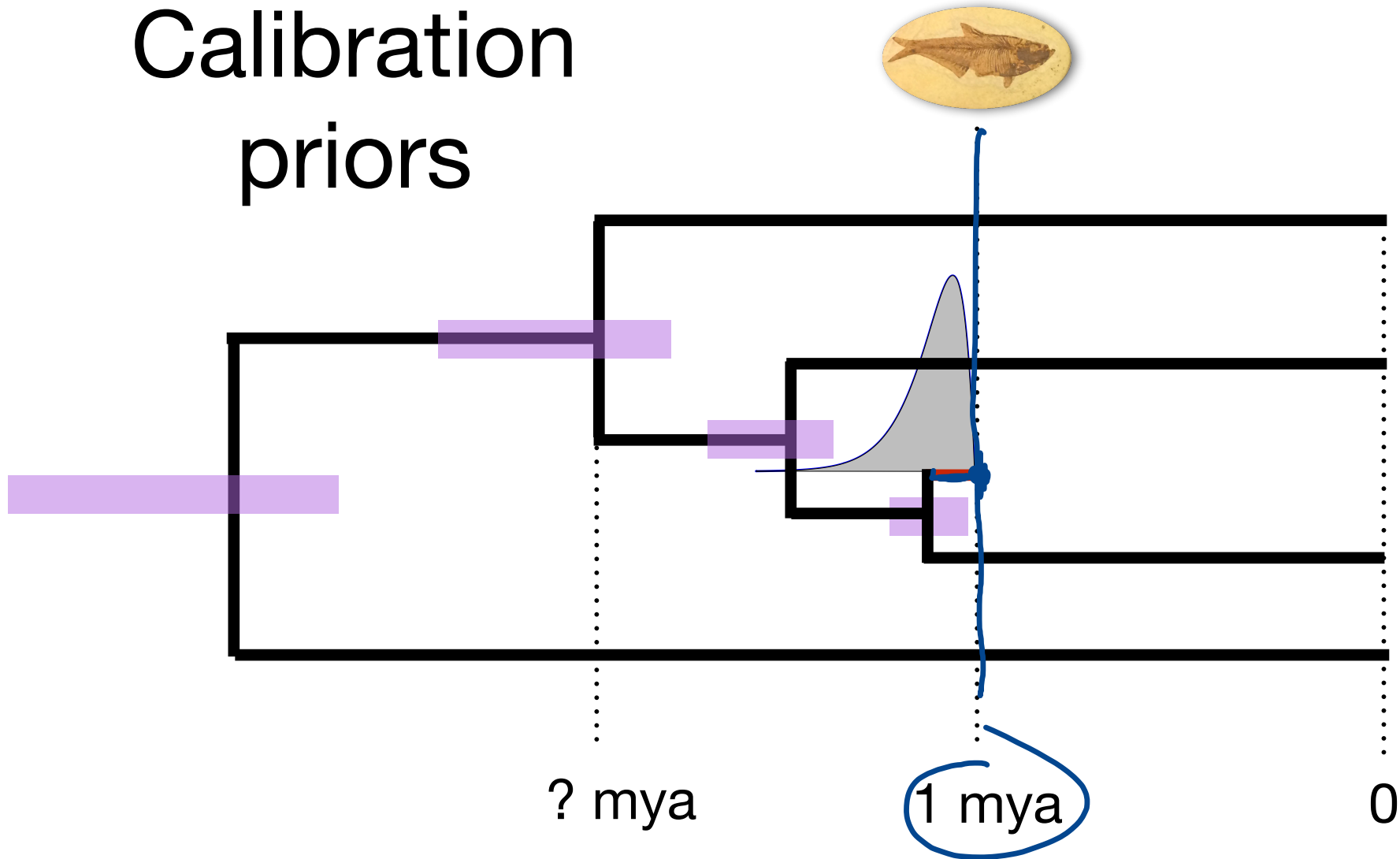
(a) 3 nuclear genes from 42 mammals

(b) mtDNA from 7 primates

Fig. 2 from Drummond and Suchard (2010)

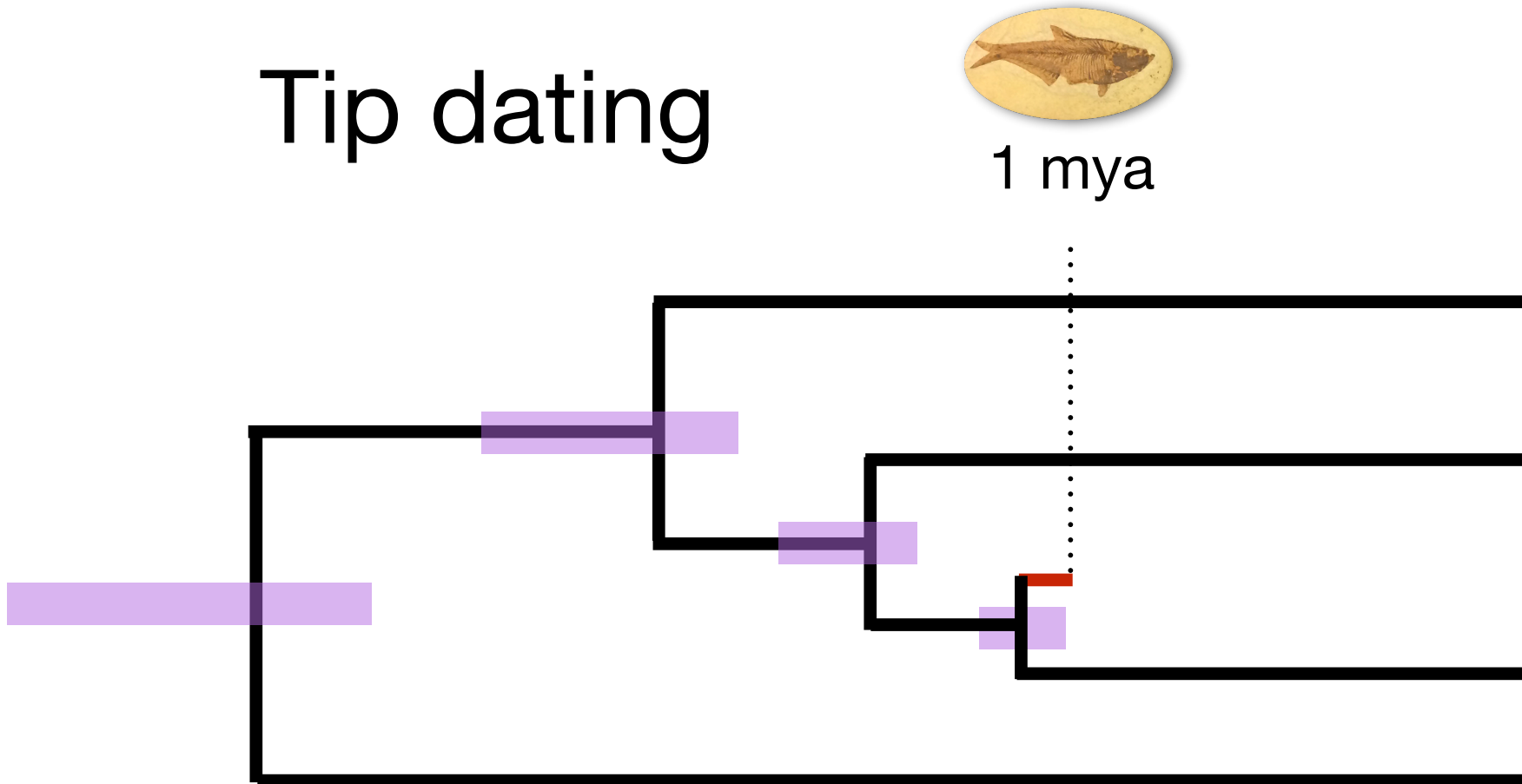
Calibrating the clock

Calibration priors



Calibration priors provide a plausible time frame for when the fossil branch joins the main tree

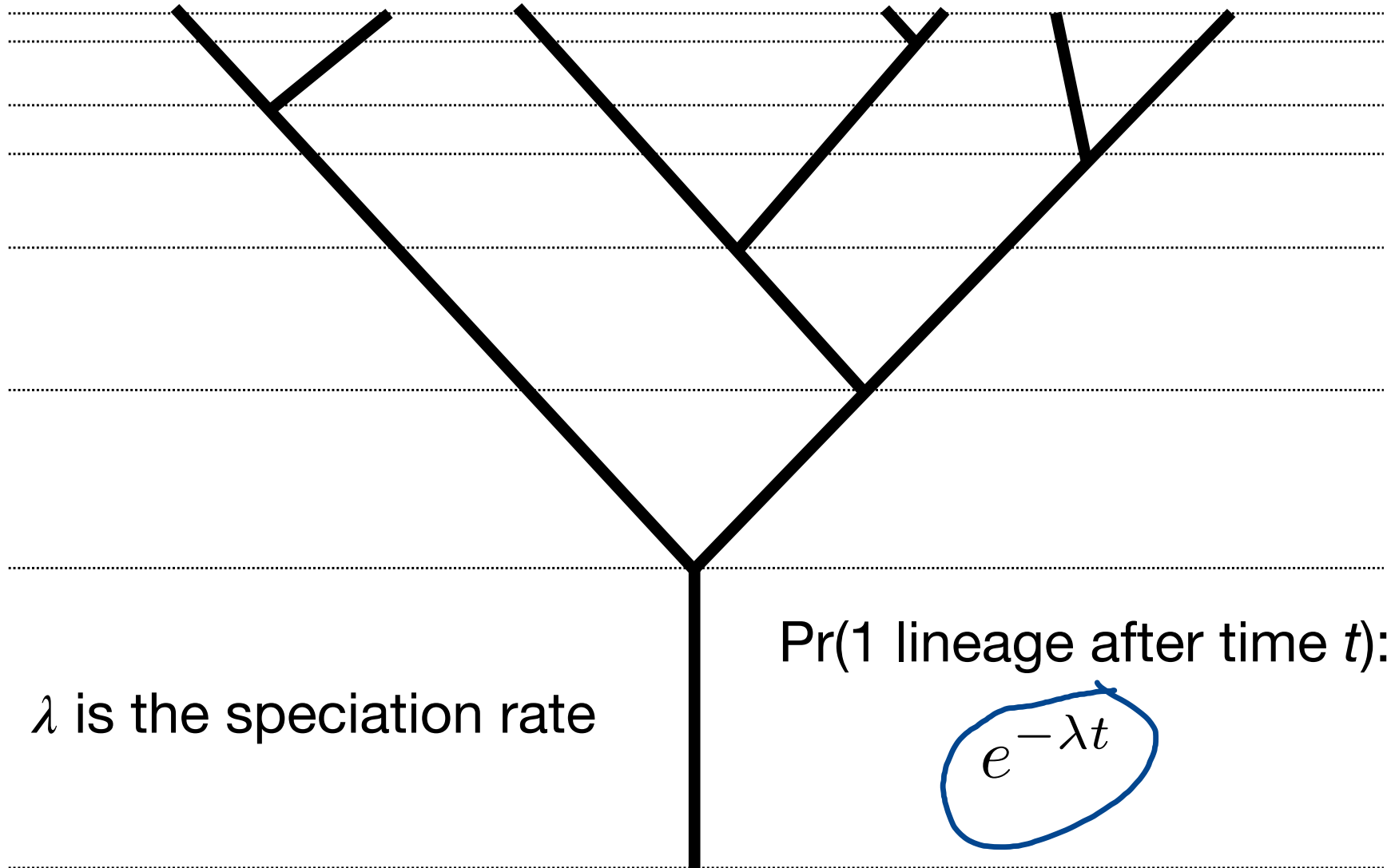
Tip dating



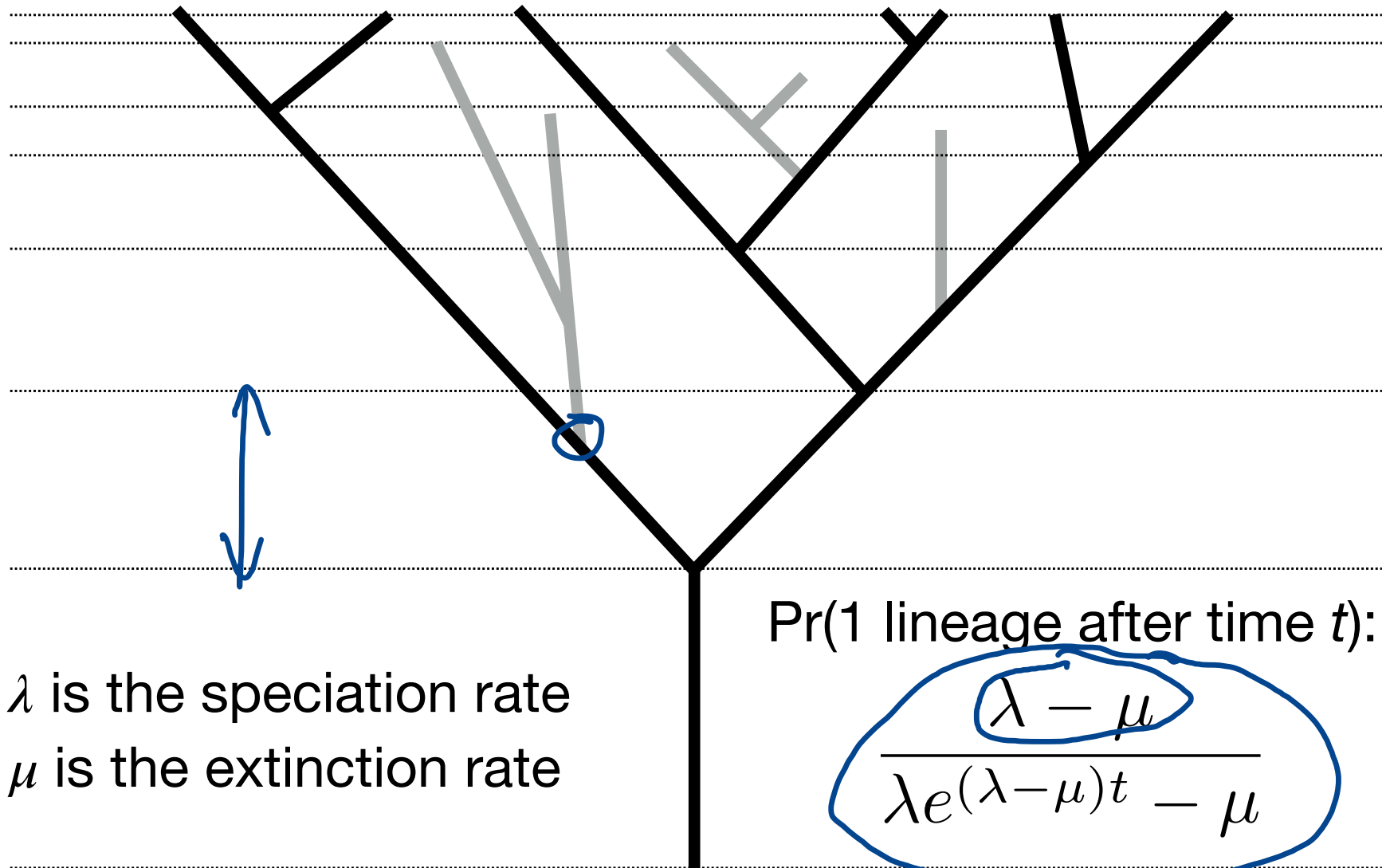
Tip dating uses morphology to place the fossils in the tree. The morphological data thus determines the length of the edge leading to the fossil.

Ronquist et al. (2012)

Yule model: pure birth process

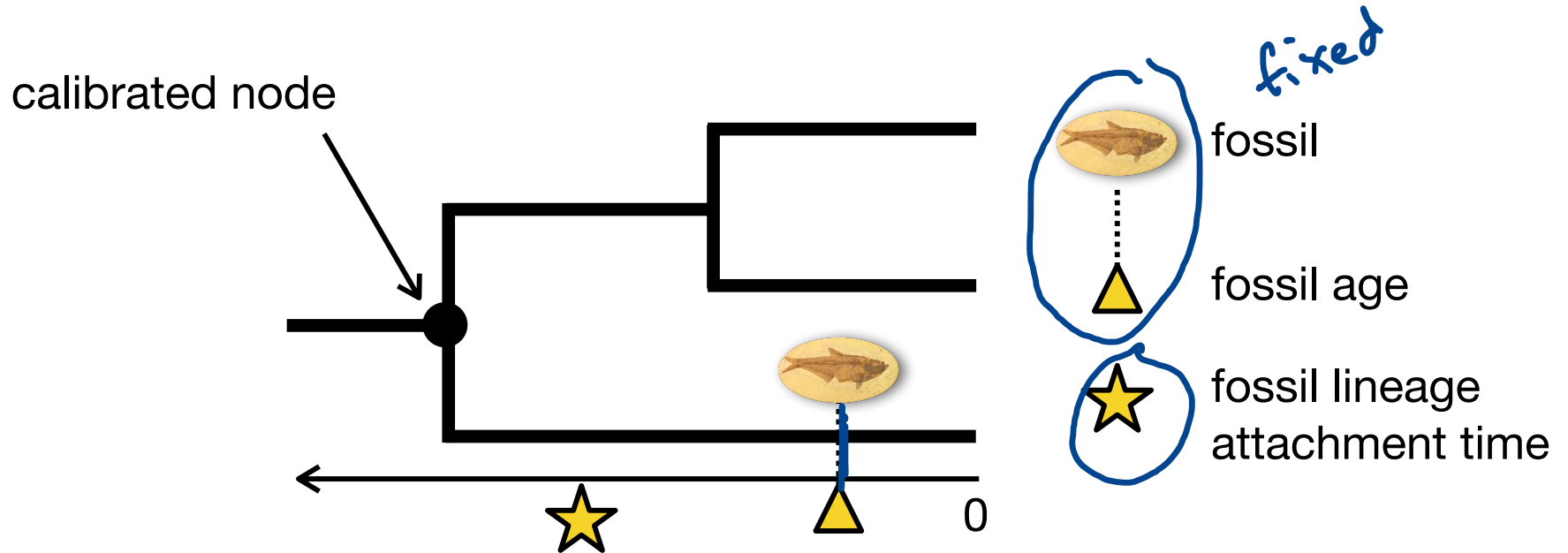


More general birth-death process



Fossilized Birth-Death Process

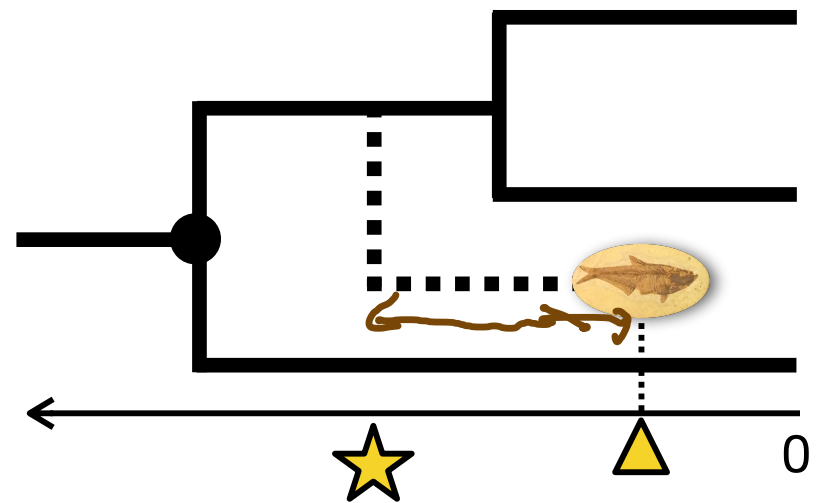
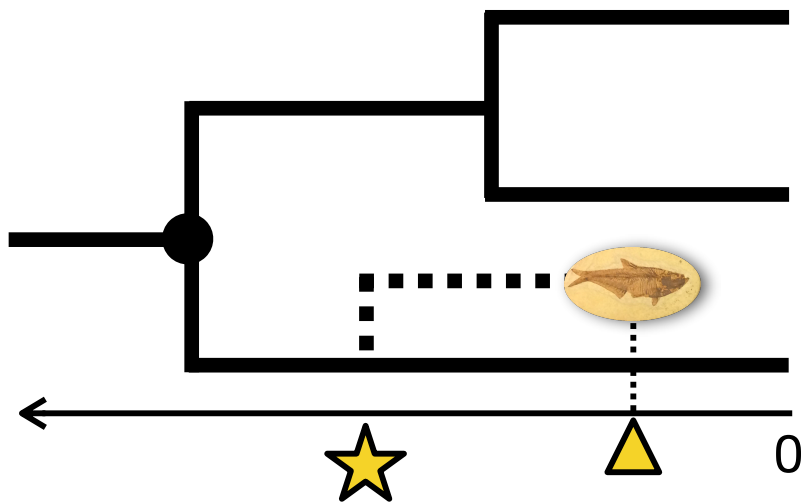
Assumes only that fossil is a descendant of the *calibrated node*



Assume for a moment that you know the age of the fossil and the time at which the fossil's lineage attached to the tree...

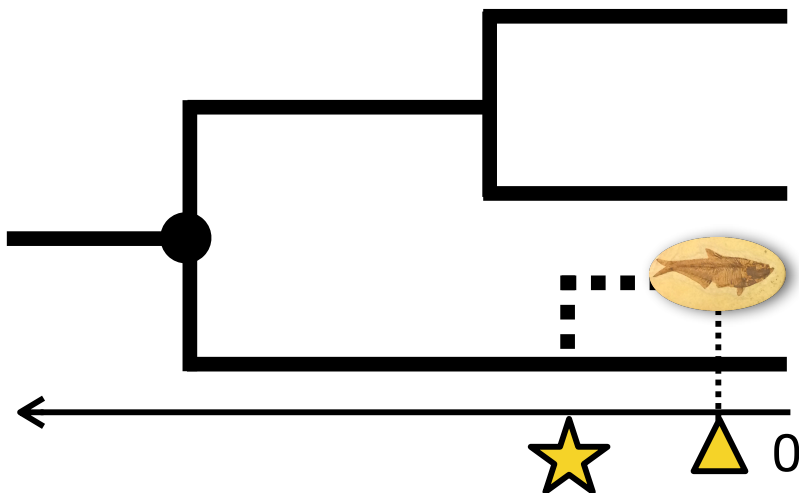
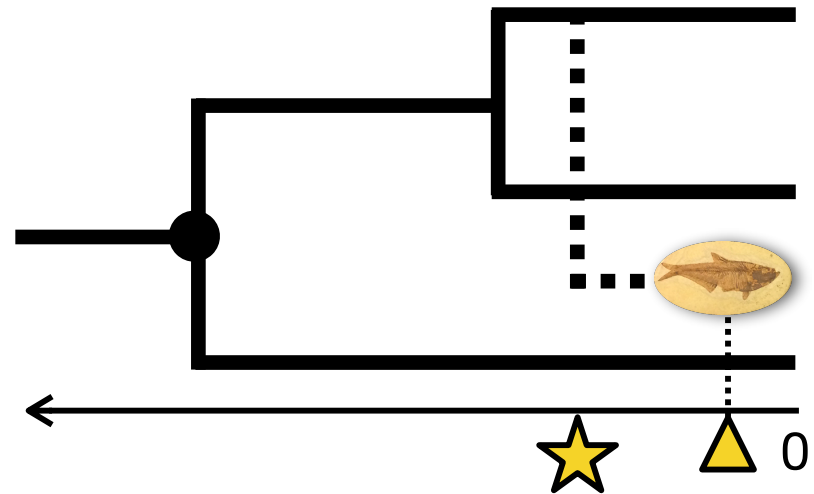
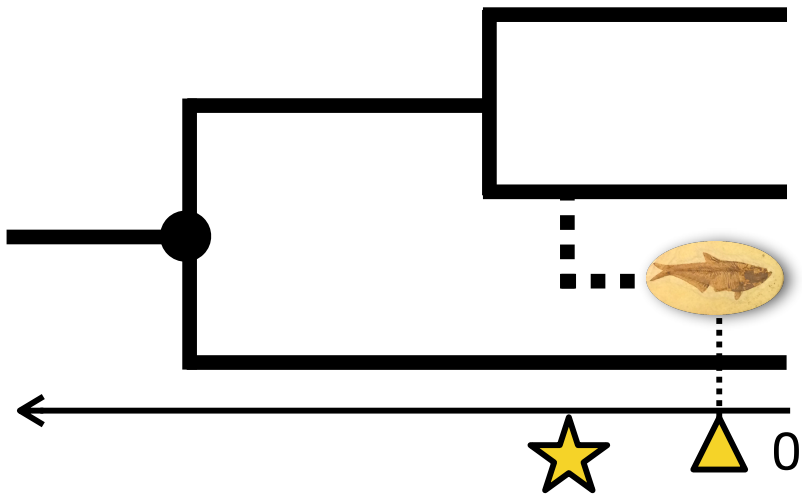
Fossilized Birth-Death Process

Given the tree, the calibrated node, the fossil age, and the attachment time, there are only **2 places** the fossil could attach to the tree



Fossilized Birth-Death Process

In this case, there are 3 possible attachment points

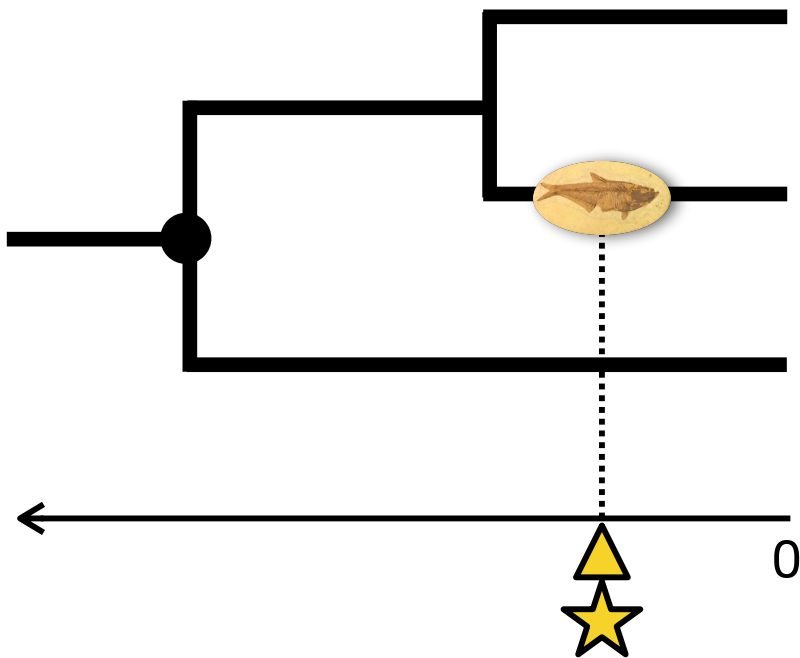


The birth-death prior model provides the probability density of each of these alternatives

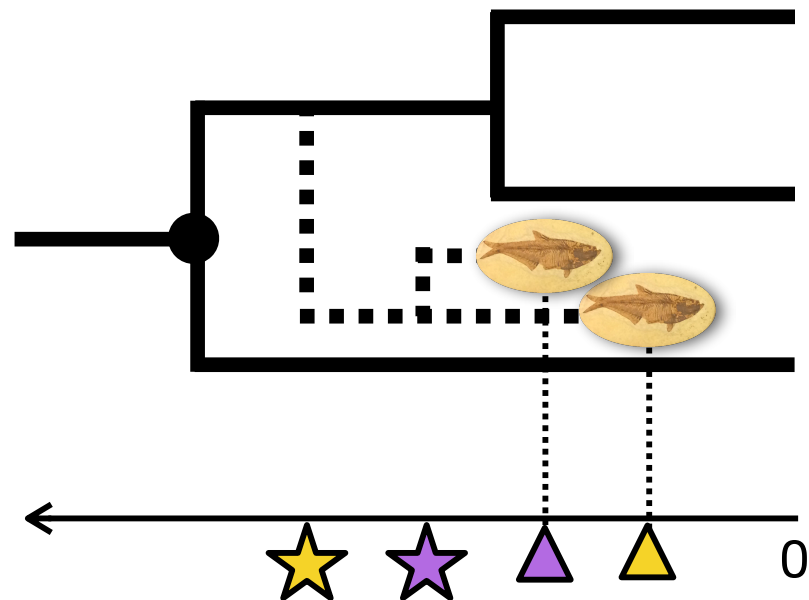
Fossilized Birth-Death Process

Direct ancestry and *ghost lineages* are also possible.

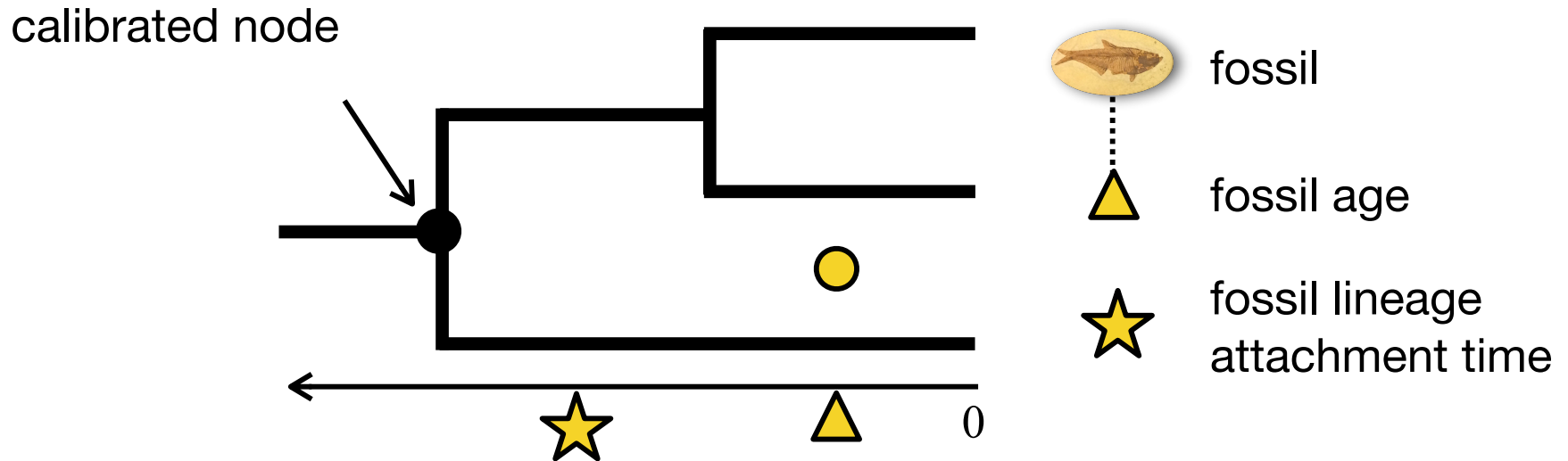
Direct ancestry means fossil is a direct ancestor of a sampled taxon (not at the end of an unsampled lineage)




Ghost lineages are fossil lineages that attach to other fossil lineages



Fossilized Birth-Death Process



MCMC is used to propose many different values of  and attachment points (conditional on attachment time) for each available fossil. This is in addition to proposed changes to edge-specific rates and divergence times.

The marginal posterior distribution of divergence times thus accounts, in principle, for all possible fossil placements consistent with the assumption that fossils descend from their calibrated nodes.