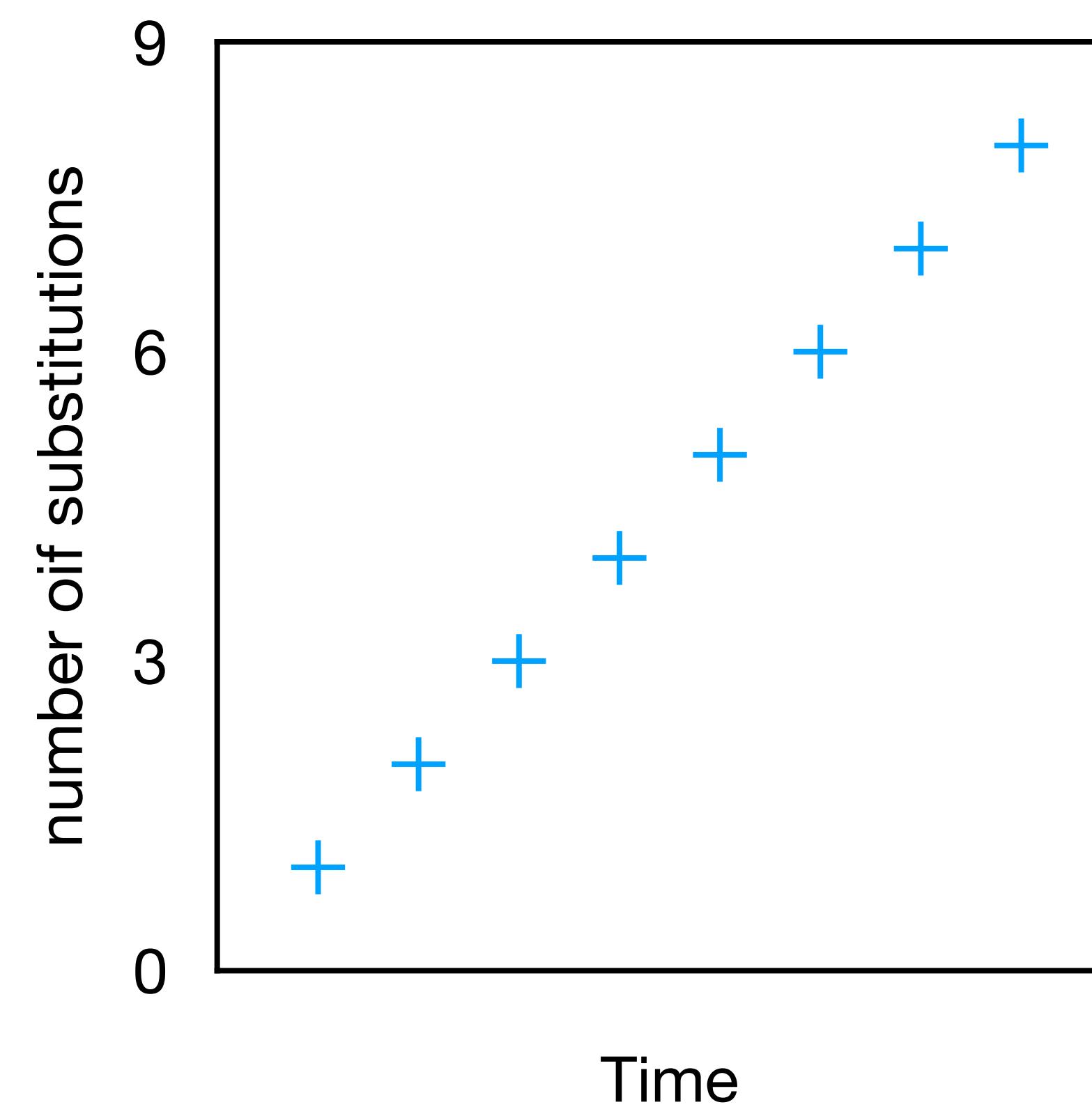
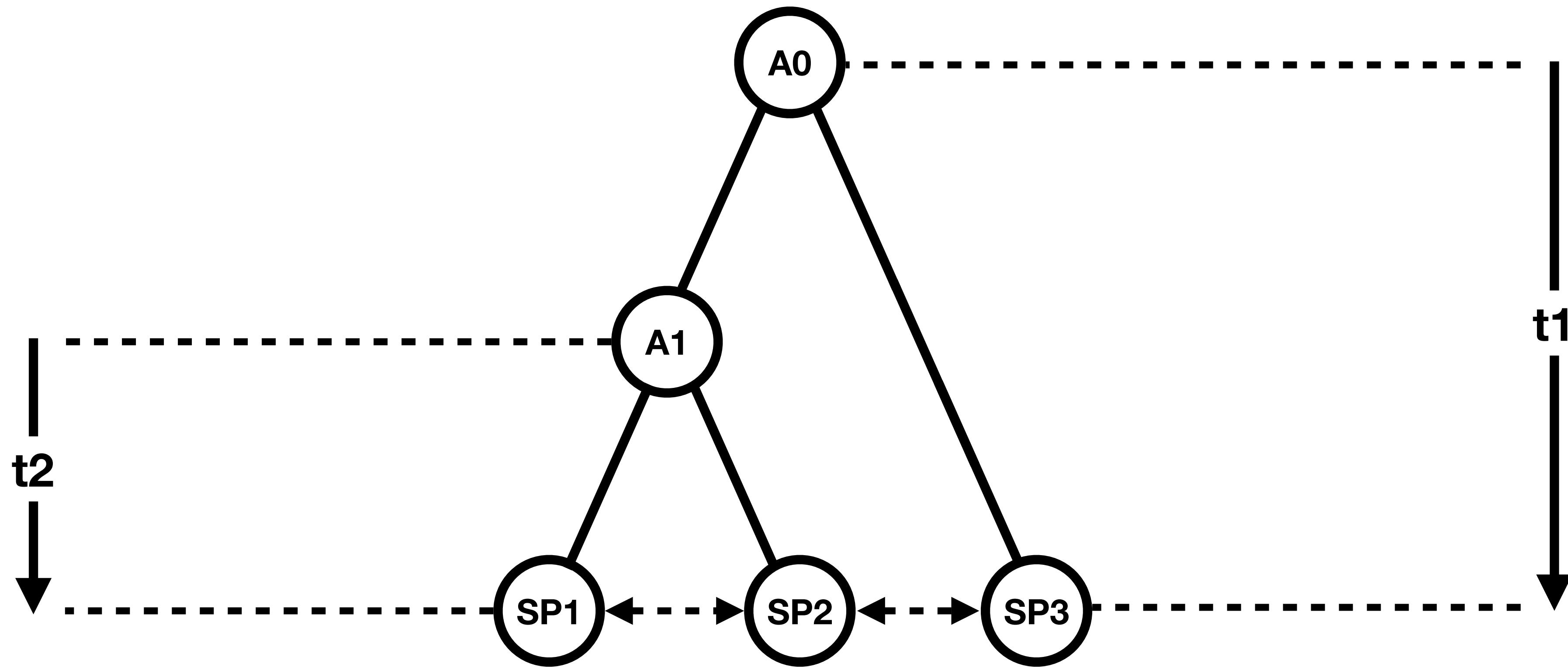


divergence time
analyses

The molecular clock hypothesis suggests that **genetic changes** tend to accumulate at a relatively **constant rate** over long periods 🕒

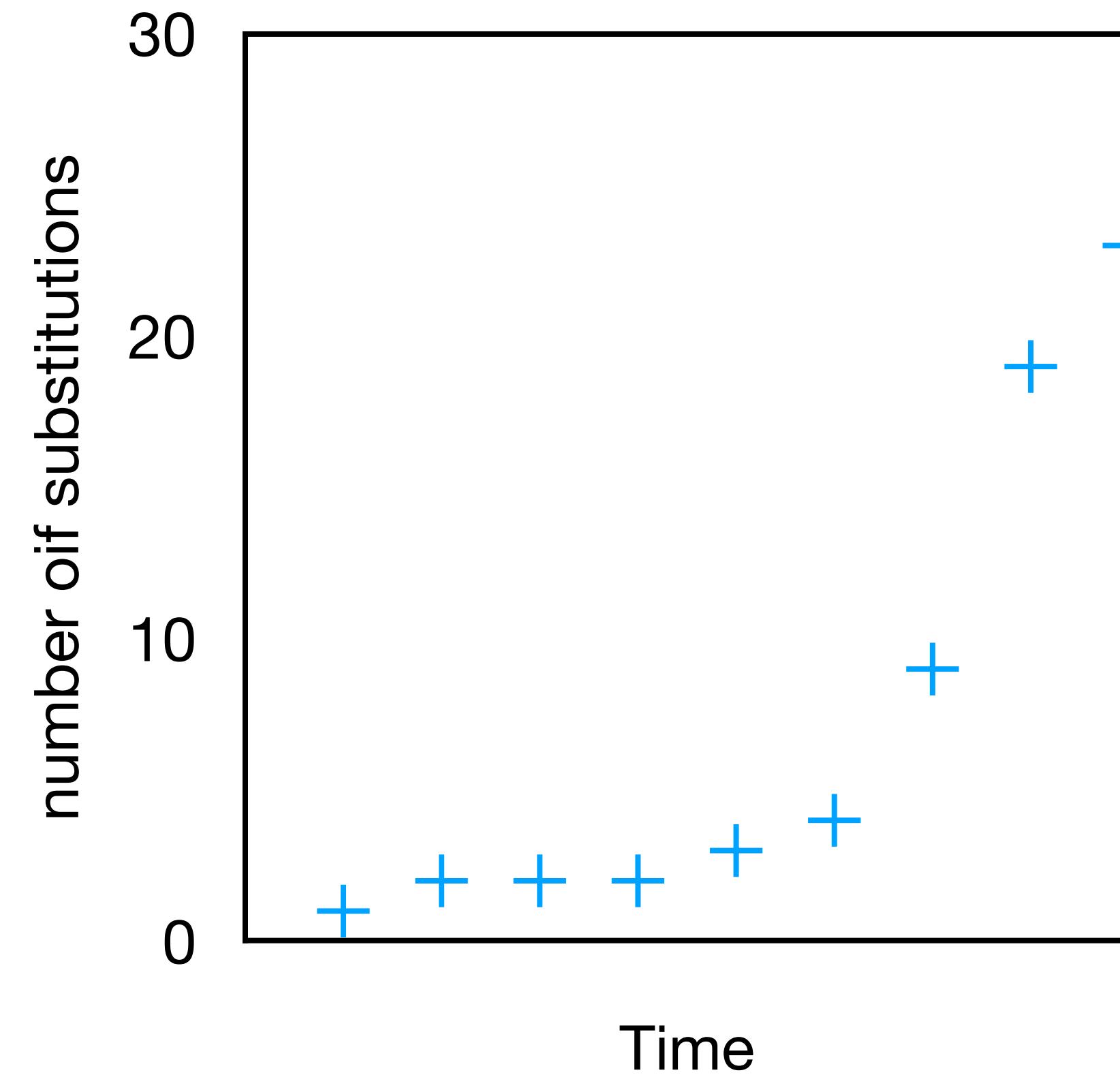


That would make estimating divergence times between species a breeze 😊



$$\text{Divergence Time } (\text{sp}_1 - \text{sp}_3) = \frac{\text{Molecular Distance } (\text{sp}_1 - \text{sp}_3)}{2}$$

... however, **the molecular clock assumption is often violated** ...



... here, the plot suggest a non-linear pattern, suggesting accelerated rates at some point of the evolutionary history of a lineage ...

 **Strict Molecular Clock**

assumes **constant rate of evolution** across all lineages
often **unrealistic** for large or heterogeneous datasets
can produce **biased age estimates** when rate variation exists

From the **relaxation** of the strict molecular clock **assumption** we get ...

 **Local Molecular Clock**

different **substitution rates** apply to different **monophyletic groups** within a tree
Each **local clock group** evolves at its own constant rate

 **Relaxed Molecular Clock**

allows **rate variation among lineages**
2 main types:

- **Uncorrelated clocks:** rates vary independently (e.g., lognormal or exponential priors)
- **Correlated clocks:** rates in neighboring branches are related



Autocorrelated Relaxed Clock

- Substitution rates change gradually along the tree
- Daughter branches tend to inherit their parent's rate
- Models evolutionary “clock drift” (e.g., lognormal distribution)



Uncorrelated (General) Relaxed Clock

- Substitution rates are drawn independently for each branch
- No assumption of rate similarity between parent and daughter
- Common distributions: lognormal, exponential, gamma

Least Squares Dating

- fits divergence times to branch lengths by minimizing squared differences
- Uses a **strict or relaxed clock**, depending on rate smoothing
- Requires a **fixed topology and branch lengths**, **extremely fast and** ideal for large datasets
- Less sensitive to model violations, but lacks full probabilistic framework
- Tools: IQ-TREE

Penalized Likelihood Methods

- **Semi-parametric** approach balancing fit and rate smoothness
- Allows **rate heterogeneity** while discouraging sudden shifts
- Requires a **fixed topology and branch lengths**
- Computationally efficient for **large-scale phylogenies**
- Tools: r8s, treePL

Bayesian Approach

- Fully **probabilistic framework**: models uncertainty in topology, rates, and dates
- Can implement the **Fossilized Birth-Death (FBD) model**:
 - Models speciation, extinction, and **fossil sampling**
 - Allows fossils as **tips**, not just node calibrations
- Avoids arbitrary calibration bounds by integrating fossil distributions
- **Total-evidence dating** combines morphological + molecular data
- Tools: BEAST, RevBayes, MrBayes

Tip Dating

- Dates are assigned directly to the **tips** of the tree
- Uses **dated samples** (e.g. ancient DNA or fossils as terminals)
- Integrates fossil information as part of the phylogenetic inference
- Allows estimation of divergence times **without node calibrations**
- More sensitive to **tip age accuracy and fossil placement**
- Often used in **total-evidence dating** approaches

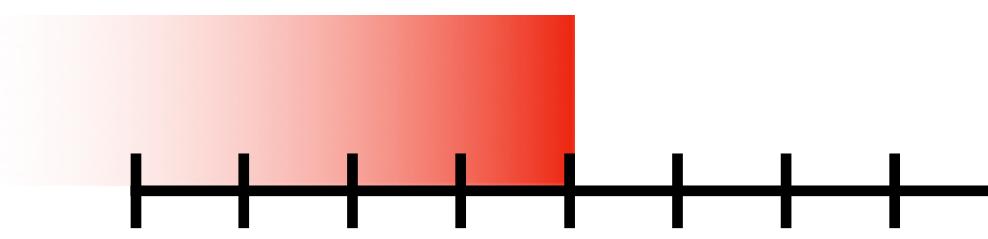
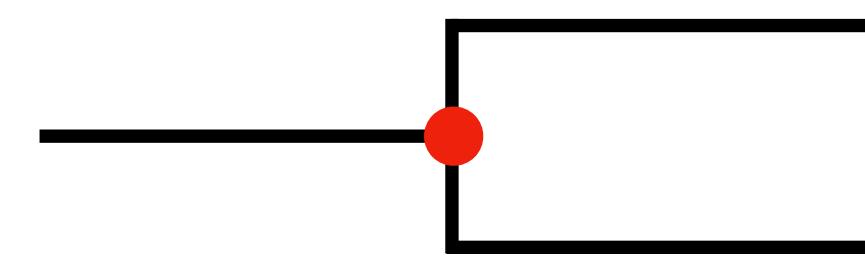
Node Dating

- Dates are assigned to **internal nodes** of a phylogeny
- Relies on **fossil calibrations** placed at ancestral nodes
- Fossils provide **minimum age constraints**
- Assumes correct placement of fossils and accurate tree topology
- Common in analyses using **only extant taxa**

fossils

...

usually give only the minimum age



MAXIMUM
(SOFT)

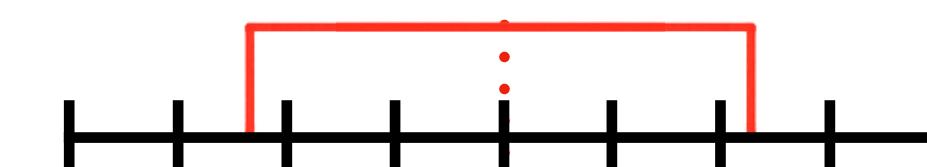
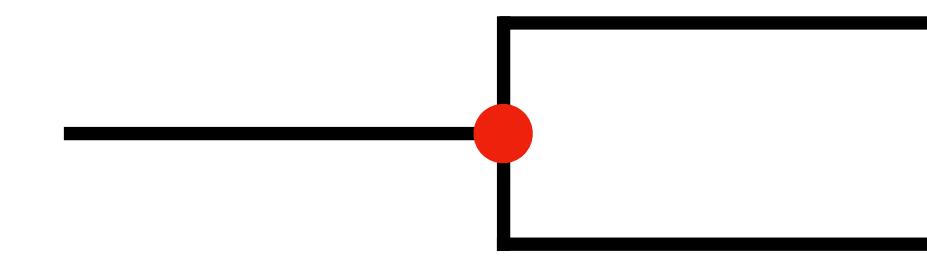


MINIMUM
(HARD)

More common fossil prior shapes

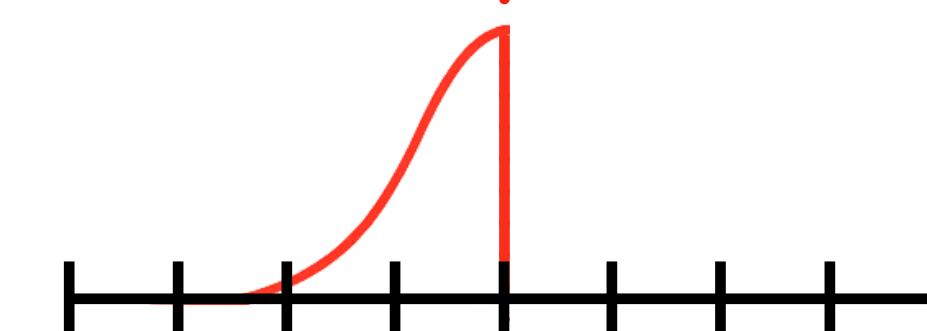
Uniform

- equal probability between minimum and maximum ages
- dimple and non-informative, often unrealistic
- use only when maximum bound is well-justified



Lognormal

- probability concentrated just above the minimum
- heavy tail toward older ages
- divergence likely predicated the fossil, but not arbitrarily far back



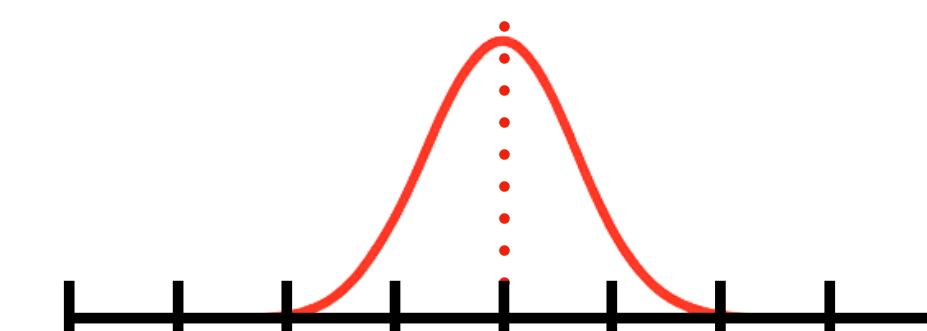
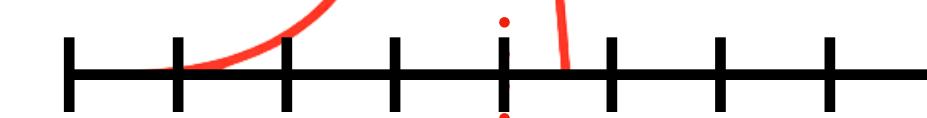
Exponential

- Peaks at the minimum bound, then declines rapidly
- Suitable when fossil is likely close to the actual divergence
- Simple and interpretable with one parameter (mean)



Normal

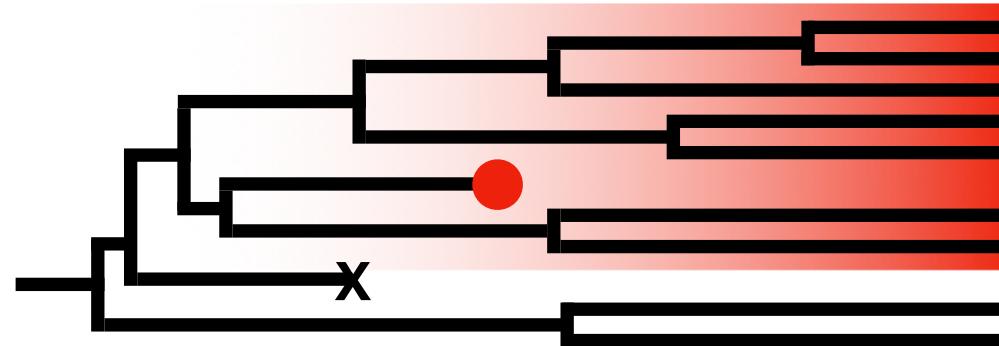
- Bell-shaped, centered at a hypothesized mean
- Requires strong justification for both center and spread
- Less common for fossils, more for geological calibrations



fossils placement: Crown versus Stem

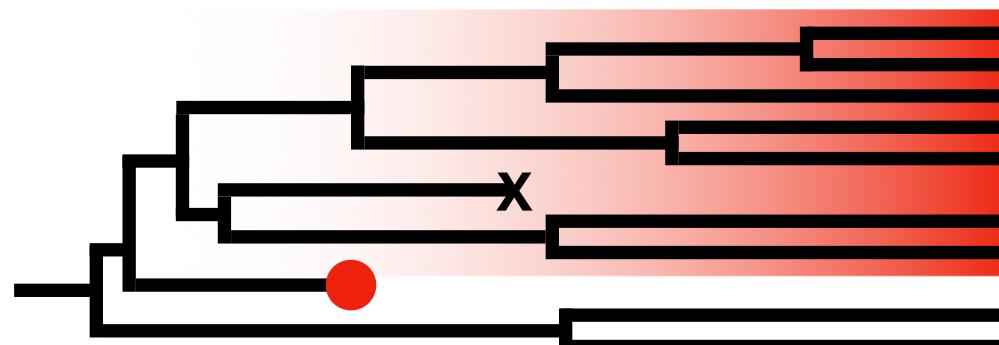
Crown Group

- includes the last common ancestor of all living members of a clade and all of its descendants.
- fossils placed here are within the clade, sharing all its defining synapomorphies.
- Exp: a fossil assigned to crown birds must postdate the divergence from non-avian dinosaurs.



Stem Group

- includes extinct lineages closer to a crown group than to any other, but outside the crown itself.
- stem fossils help bracket the minimum age of the crown group.
- Example: feathered theropod fossils - e.g. a velociraptor - are stem birds.



FINISH