



Introduction to Phylogenetic Comparative Methods

Analytical Paleobiology Workshop 2024 | 10.08.2024

Emma Dunne
(emma.dunne@fau.de)

Learning objectives

After today's session, you should be able to:

- Understand the broad application of phylogenetic comparative methods (PCMs) to research questions in evolutionary biology and paleobiology
- Confidently implement PCM analyses (i.e. phylogenetic signal detection and evolutionary model fitting) in R using bespoke packages
- Appreciate the evolutionary relationship between frog eye size and ecology



Evolution

Evolution is happening all around us

- We can now even describe the evolutionary process in exquisite detail
- e.g. frequency of gene changes in White Sands lizards ([Rosenblum et al. 2009](#))

Macroevolution involves studying patterns on the tree of life *above* species level

- Across the whole tree of life



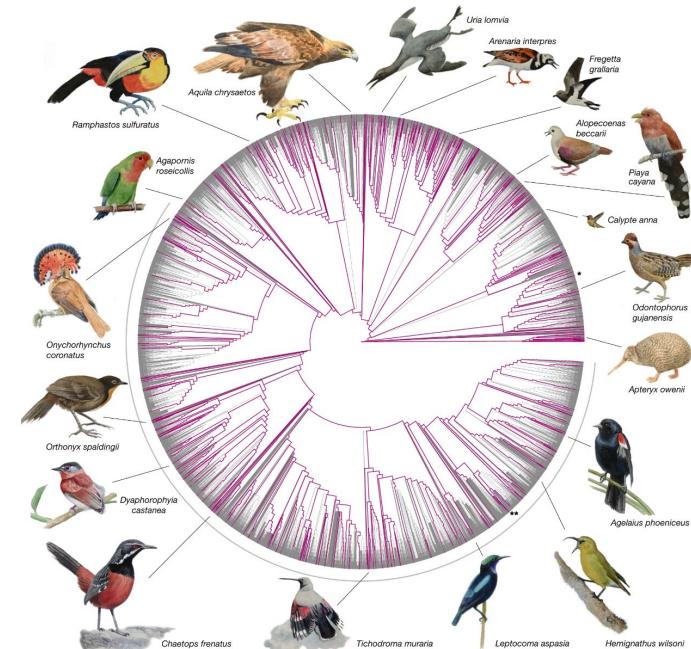
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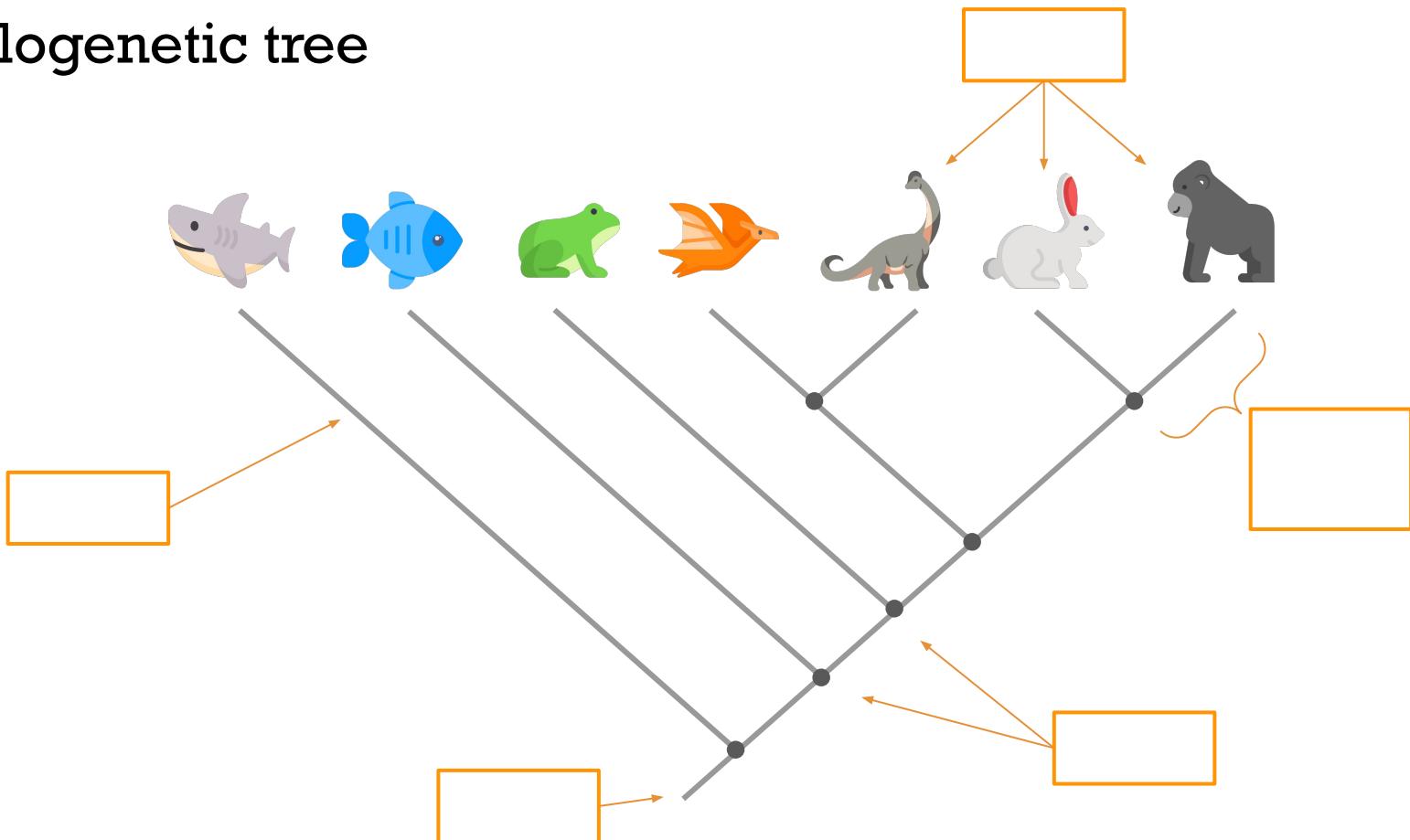
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Phylogenetic Comparative Methods (PCMs)

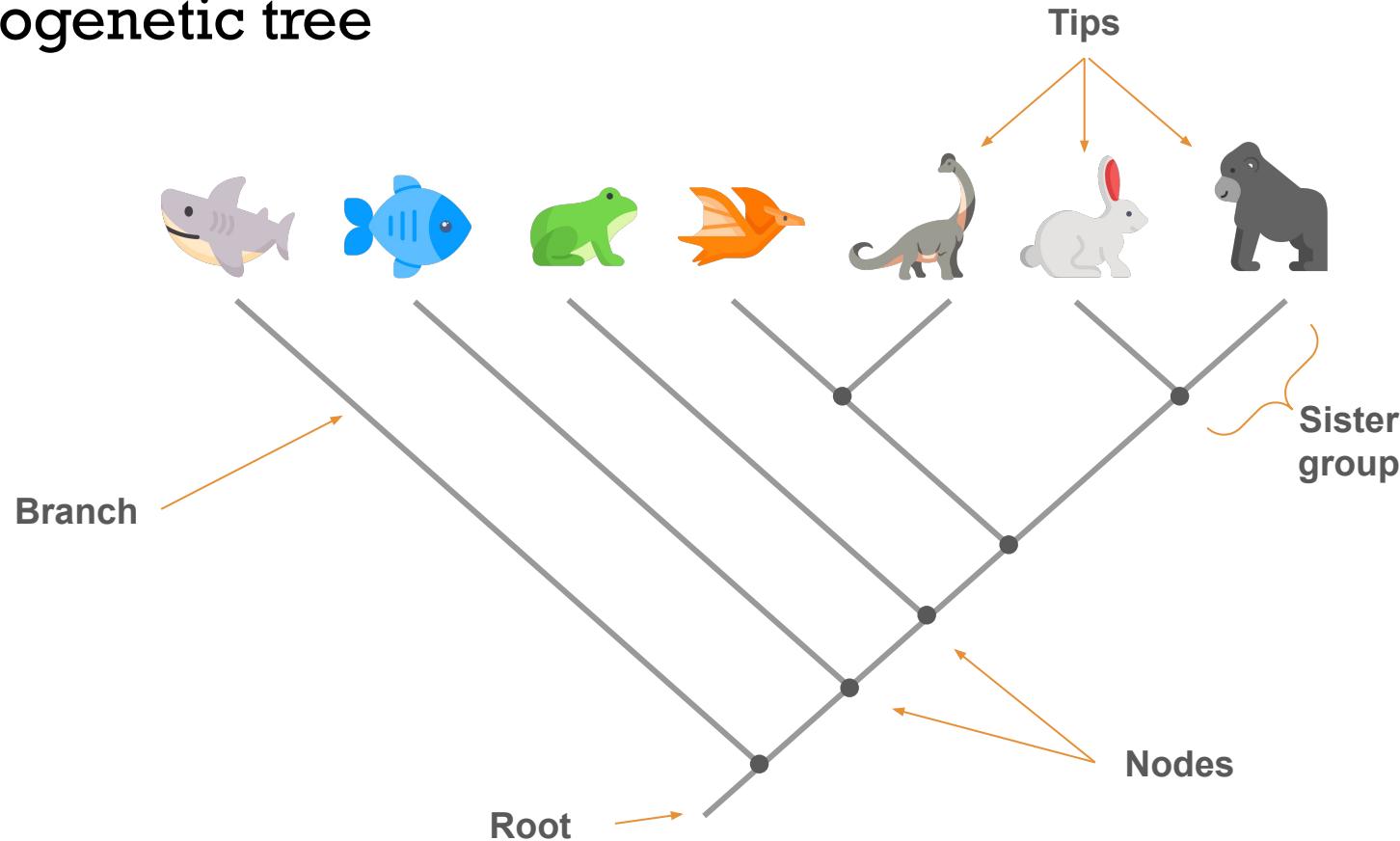
- Modified statistical tests that take into account non-independence in data that come from different species
- PCMs are applied to regression and other standard tests, and they can be used to estimate rates of evolution and to reconstruct ancestral trait states on a phylogeny
- PCMs use a **phylogenetic tree**, combined with **trait data** for the taxa on the tree, **to learn something about evolution**
(Pennell & Harmon, 2013)



Phylogenetic tree

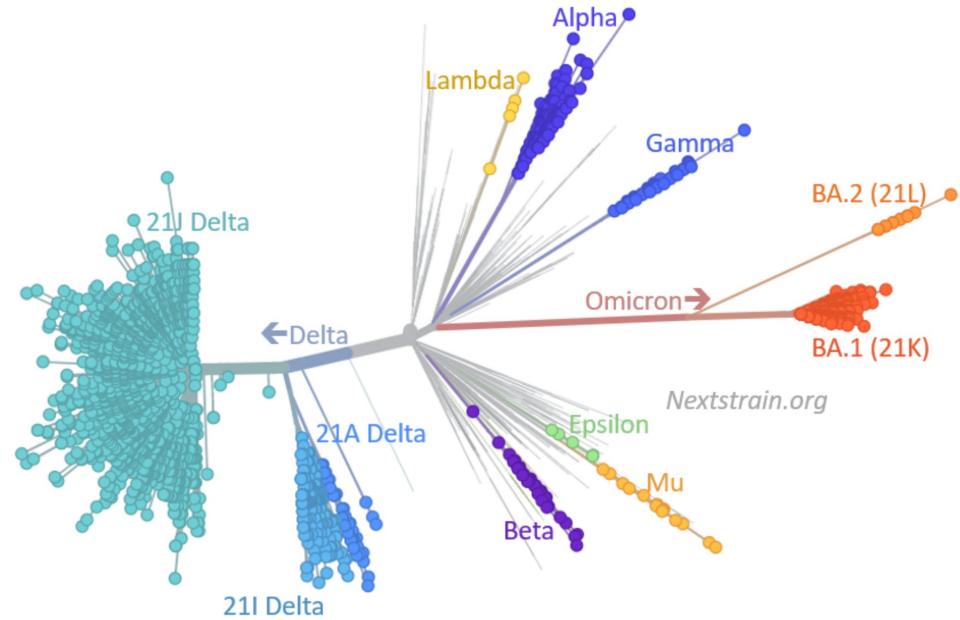


Phylogenetic tree



Phylogenetic Comparative Methods (PCMs)

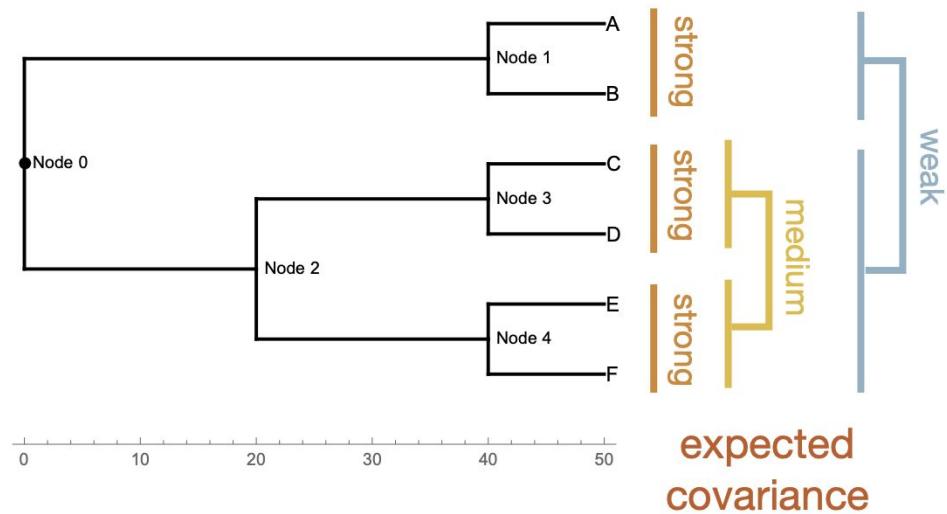
- **Scientific applications** in evolutionary biology, paleobiology, ecology and even linguistics (evolution of languages)
- **Societal applications** (e.g. modelling of SARS-CoV-2 [Covid] evolution)
- Easy to implement in R with various packages (e.g. ape, geiger, and phytools)



Source

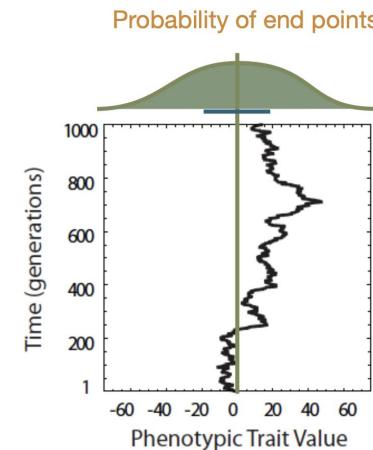
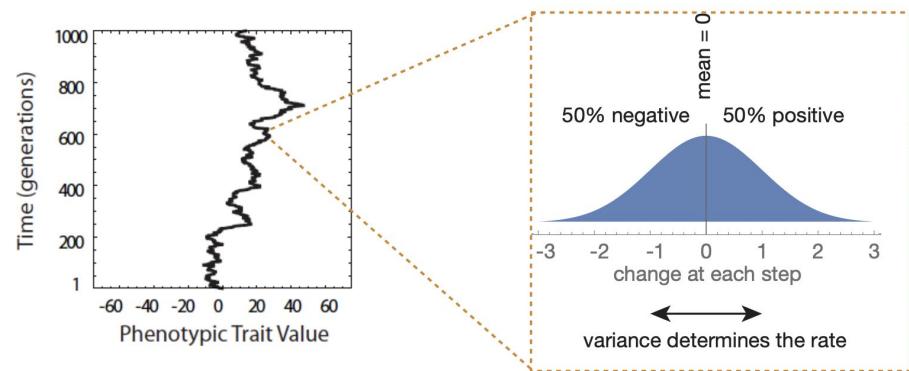
How do PCMs work?

- PCMs estimate how much **covariance** a trait should have between taxa (and between traits) is expected from the phylogenetic topology
- The expected phylogenetic covariance is removed, leaving the residual between-trait covariance
- Statistical tests are carried out on the residual component



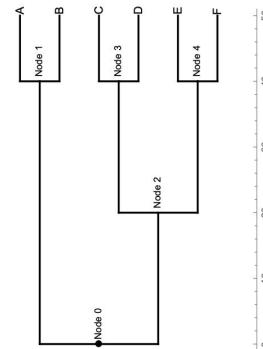
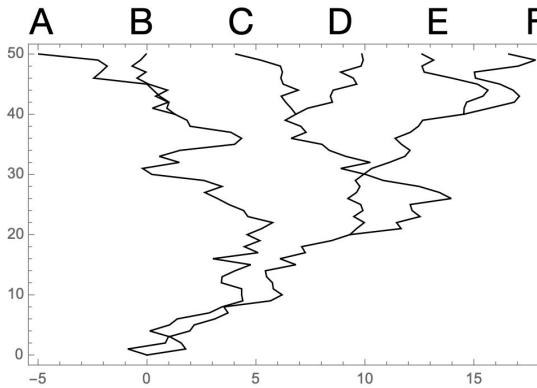
How do PCMs work?

- How do we know the expected covariance? - depends on how the traits evolve
- **Brownian motion** (purely random evolution) is usually used for PCMs
 - change at each step has an equal chance of moving in positive or negative direction
- Evolution is change in the mean trait value from generation to generation
 - Probability of endpoints is a normal distribution



How do PCMs work?

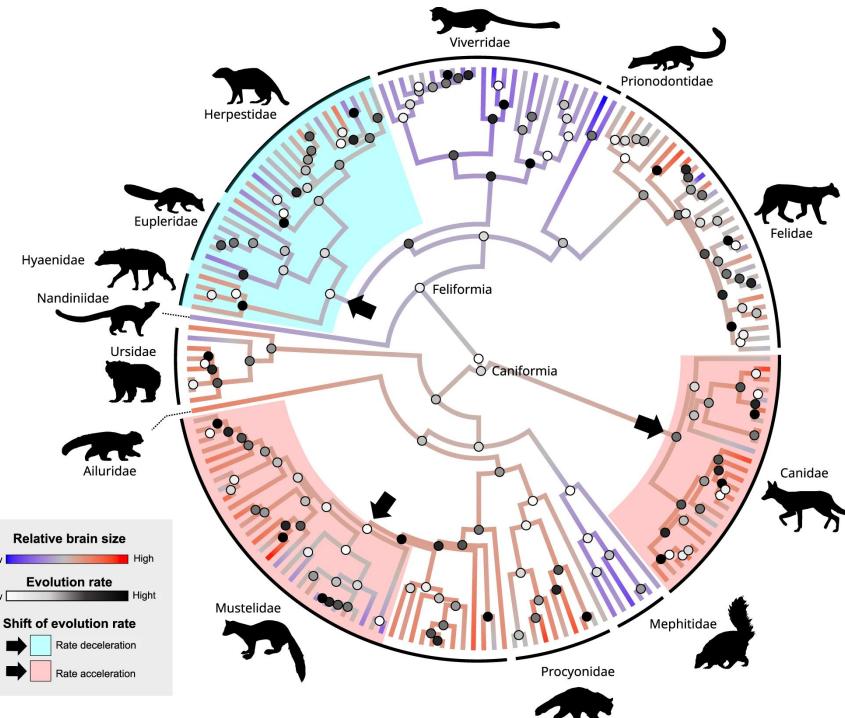
- Expected covariance among tips is proportional to shared branch lengths
- Because variance increases linearly with time, covariance between tips is linear with respect to shared branch time
- The phylogenetic covariance matrix ("C") has diagonal equal to total branch length between tip and base and off diagonals equal to length of shared branches.


$$\left(\begin{array}{ccccccc} \text{Var} & \text{Y} & \text{A} & \text{B} & \text{C} & \text{D} & \text{E} & \text{F} \\ \text{A} & 50 & 40 & 0 & 0 & 0 & 0 & 0 \\ \text{B} & 40 & 50 & 0 & 0 & 0 & 0 & 0 \\ \text{C} & 0 & 0 & 50 & 40 & 20 & 20 & 20 \\ \text{D} & 0 & 0 & 40 & 50 & 20 & 20 & 20 \\ \text{E} & 0 & 0 & 20 & 20 & 50 & 40 & 40 \\ \text{F} & 0 & 0 & 20 & 20 & 40 & 50 & 50 \end{array} \right)$$


Phylogenetic Comparative Methods (PCMs)

Example Qs for mammal evolution:

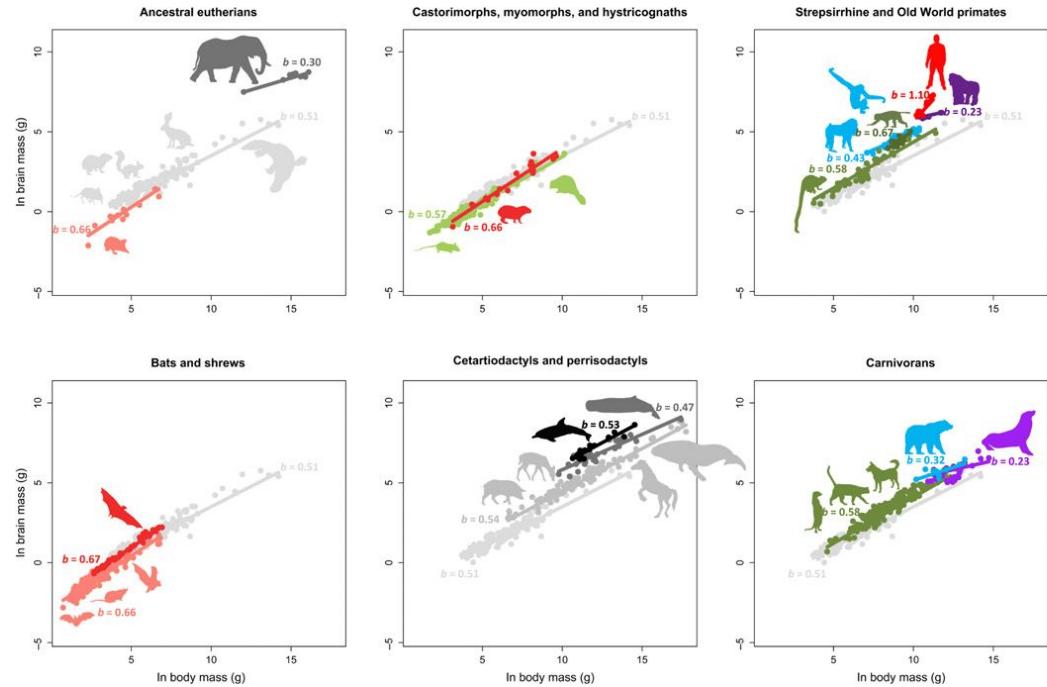
- How does brain mass vary in relation to body size in mammals?
- Do carnivores have larger home ranges than herbivores?
- When did endothermy evolve in the mammalian lineage?
- When did fur evolve in mammals?
- What impact did the K/Pg mass extinction have on mammalian body size?



Phylogenetic Comparative Methods (PCMs)

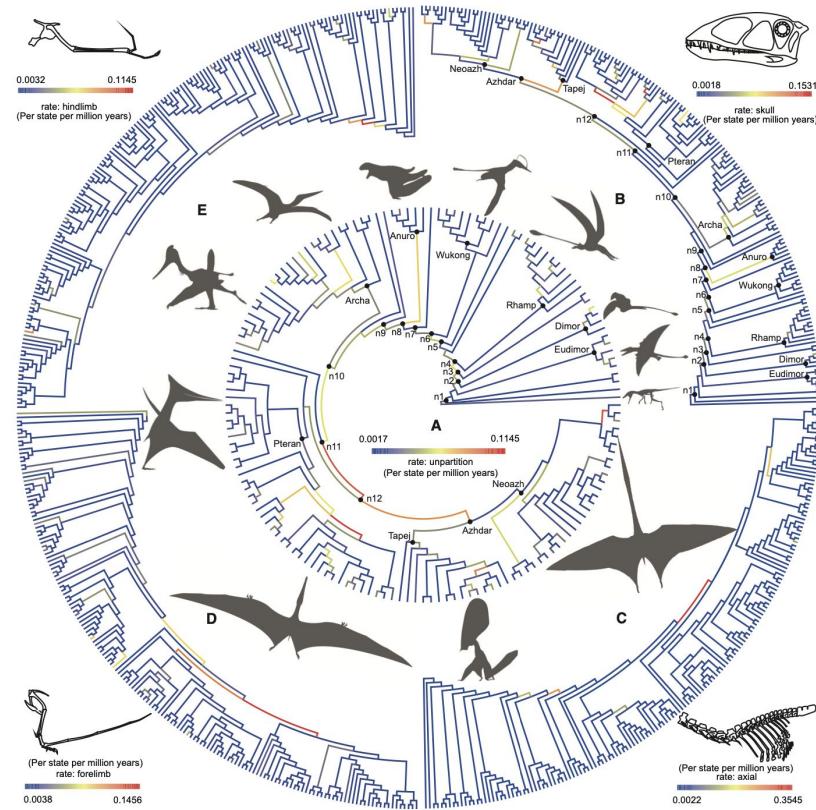
Examples of PCMs:

- Test for phylogenetic signal
- Phylogenetic MANOVA
- Phylogenetic generalised least squares (PGLS)
- Phylogenetic Principal Components Analysis (pPCA)
- Evolutionary model fitting analysis
- Ancestral state reconstruction



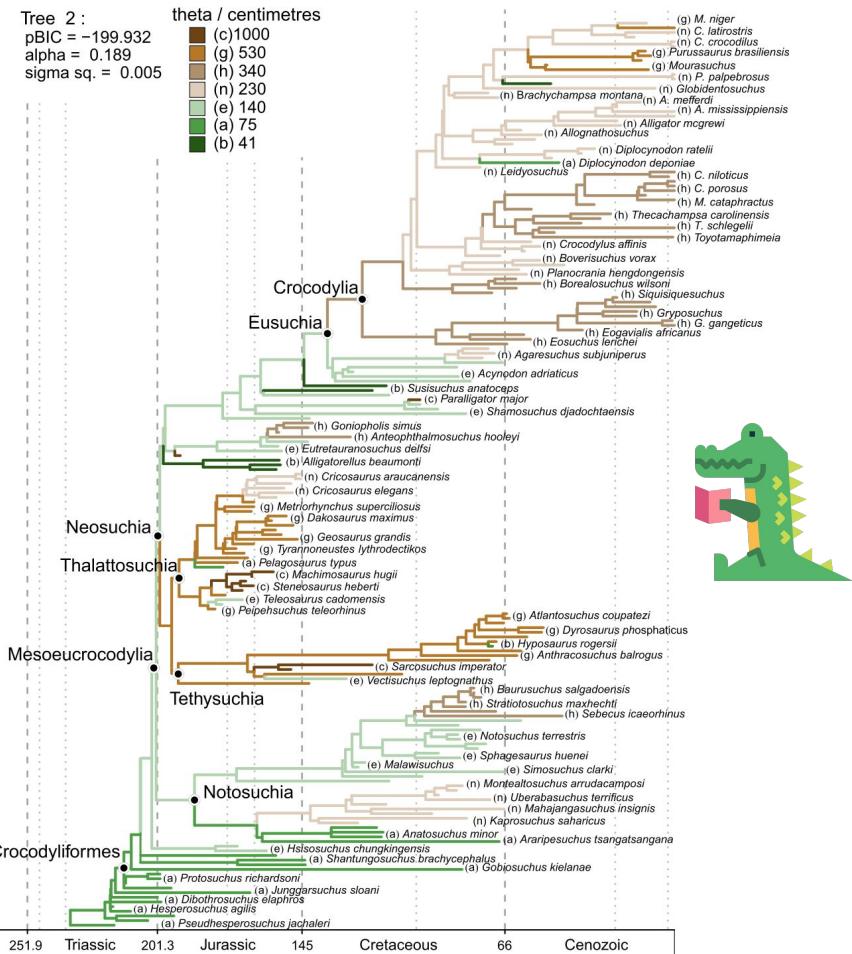
PCMs in palaeontology

- **Pterosaur** diversification and evolution across the Mesozoic
- Evolutionary rate of morphological features (e.g. limb length)
- Early Triassic–Early Cretaceous = increasing net diversification rates and disparity + morphological rates
- Early Cretaceous–extinction = mostly negative net diversification rates, decreasing disparity, + relatively low morphological rates



PCMs in palaeontology

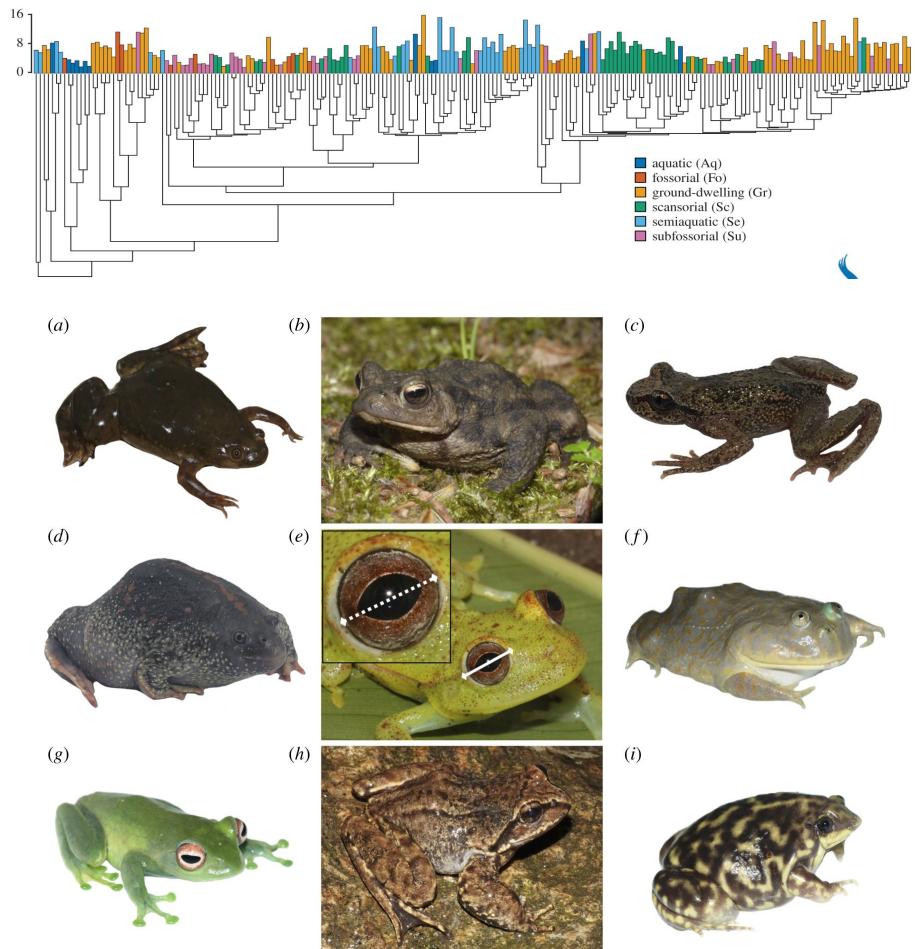
- **Crocodylomorph** body size evolution from Triassic to present day
- Extinct crocodylomorphs = wider range of phenotypes
- Peak in body size disparity during Late Jurassic - essentially continual decline since then
- Evolution of more aquatic lifestyle (especially marine) correlates with increases in average body size (with exceptions!)



Eye size evolution in frogs

- Compared to other vertebrates, frogs (anurans) have relatively large eyes for their body size
- Eye size was significantly correlated with habitat
 - burrowing and aquatic species have smaller eyes
 - most frogs = nocturnal
- Vision is of high importance

Thomas et al. (2020)



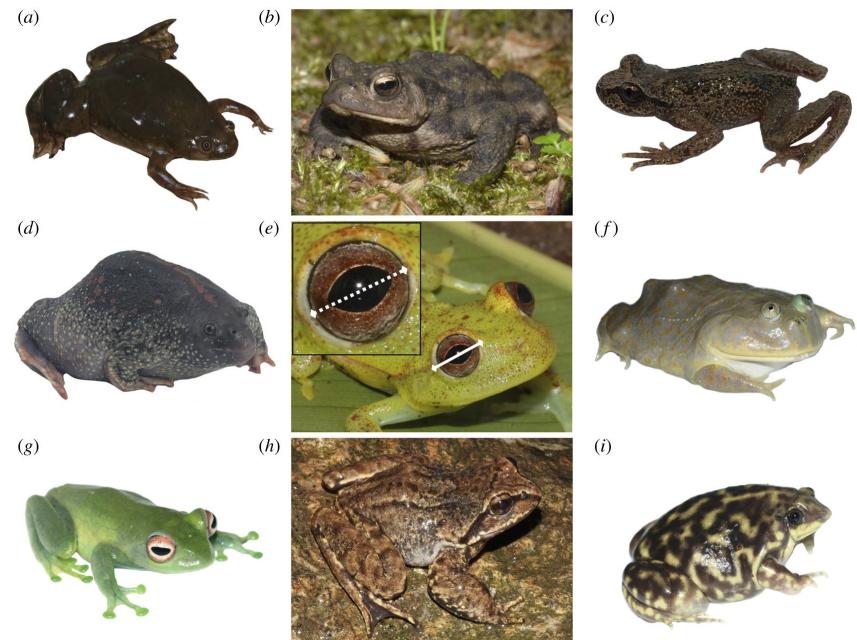
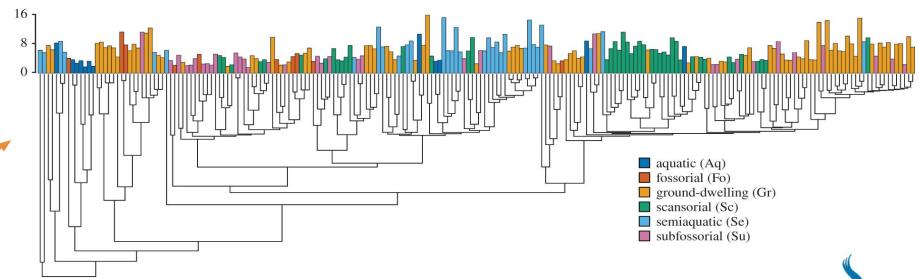
R exercise

Part 1: Data organisation + visualisation



Eye size evolution in frogs

- For our exercise, we're going to borrow [Thomas et al.](#)'s tree and trait data and apply some PCMs of our own!
- Before we begin our analyses, we need to clean our data using the code in:
 - “00_frog_cleaning.R”



Why is data cleaning so important?

Eye size evolution in frogs

Examining the tree you have just created, what do you think:

1. Does eye size in frogs have a phylogenetic signal?
2. How does eye size evolve across the frog phylogeny?
(e.g. is it random?)



What is our hypothesis for the evolution of frog eye size?



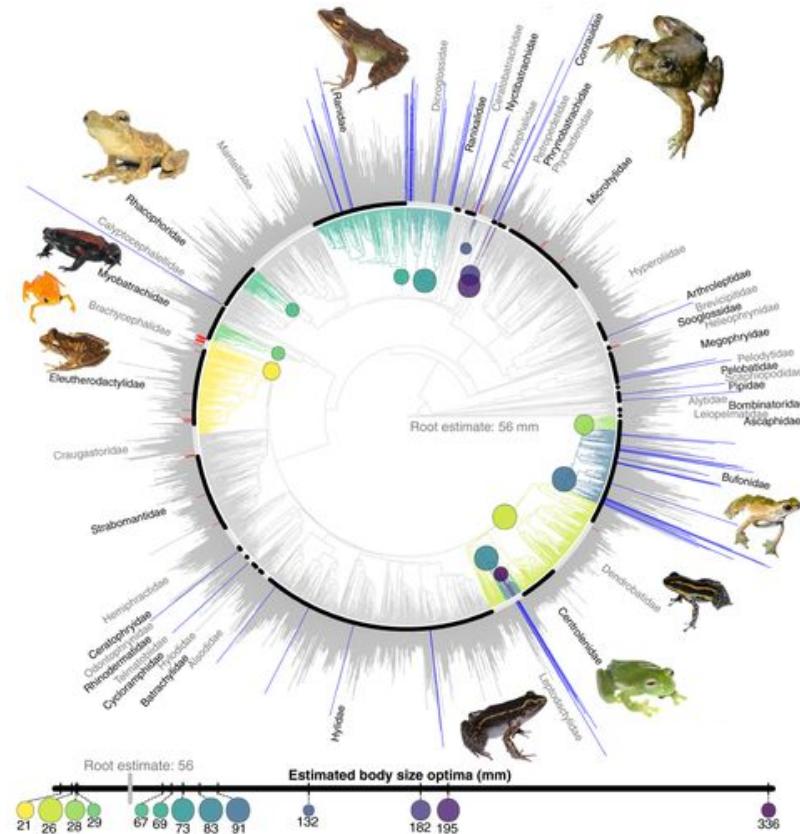
R exercise

Part 2: Phylogenetic signal



Phylogenetic signal

- Phylogenetic signal describes the tendency for closely related organisms to be more similar to one another than chance
- There are different ways to measure phylogenetic signal e.g.:
 - Pagel's λ (lambda)
 - Blomberg's K



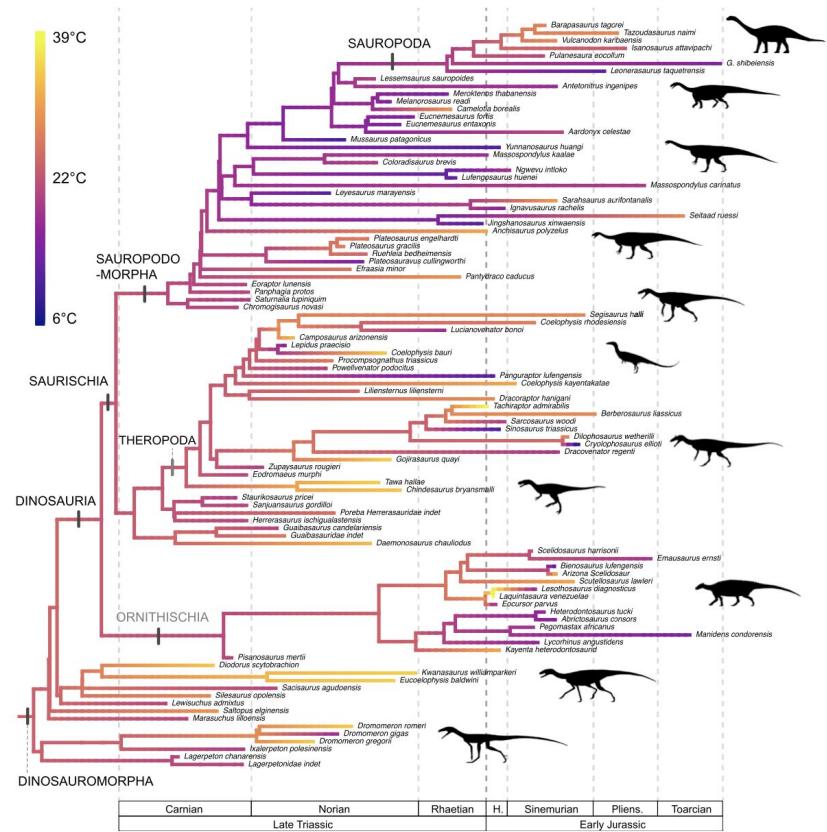
R exercise

Part 3: Model-fitting analyses



Evolutionary model-fitting analyses

- Evolutionary model-fitting analyses characterise the **evolutionary mode** of a trait across a phylogeny
 - Usually **test a hypothesis**
 - We'll fit two commonly used evolutionary models to the data:
 - the Brownian motion (BM) model
 - the single peak Ornstein-Uhlenbeck (OU) model

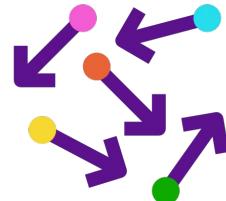
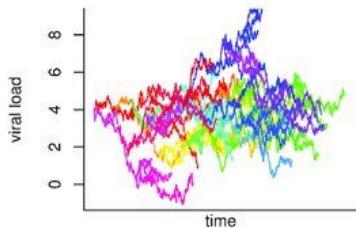


Brownian motion (BM)

Ornstein-Uhlenbeck (OU)

Brownian motion (BM)

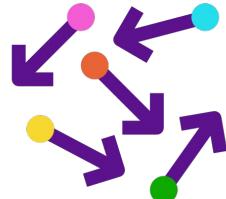
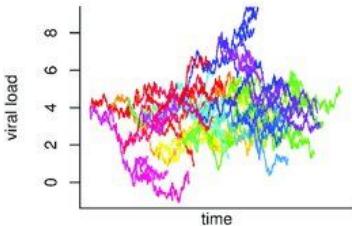
- BM model is a so-called “random walk” model where traits change gradually through time
- Null model of evolution
- The model is ‘simple’, with just two parameters



Ornstein-Uhlenbeck (OU)

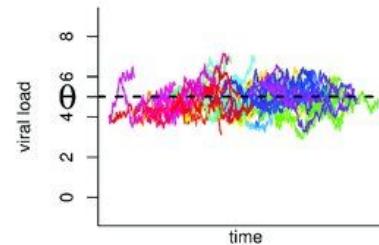
Brownian motion (BM)

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Ornstein-Uhlenbeck (OU)

- The OU model is a random walk where trait values are pulled back towards some “optimal” value
- The attraction strength is proportional to the "rubber-band" parameter α
- (α close to 0 = random)



R exercise

Interpretations & discussion



Interpretations

- Closely related frogs have eye sizes more similar to each other than chance
- The Ornstein-Uhlenbeck (OU) model was the preferred model (based on AIC)
- This suggests that frog eye size evolution is constrained around an 'optimum'



Ornate Horned Toad



Cameroon
forest tree
frog

Interpretations

- Closely related frogs have eye sizes more similar to each other than chance
- The Ornstein-Uhlenbeck (OU) model was the preferred model (based on AIC)
- This suggests that frog eye size evolution is constrained around an 'optimum'
- **What do you think is constraining frog eye size?**
- **Can frog eyes grow infinitely bigger? Why/why not?**

Hint: Think back to Thomas *et al.* (2020)!



Ornate Horned Toad



Cameroon
forest tree
frog

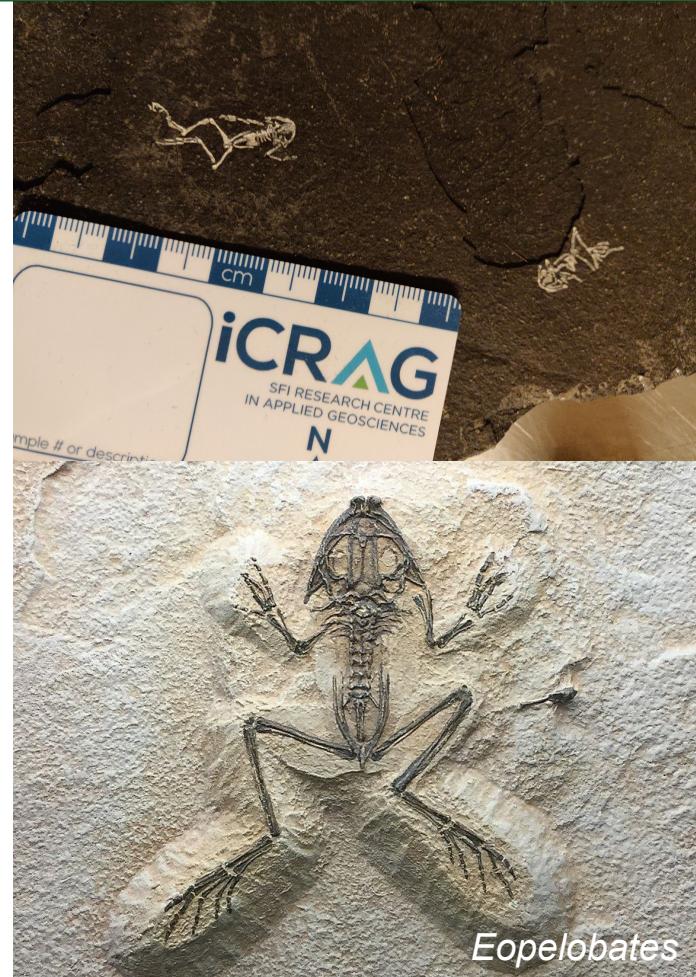
What are the advantages of adding fossils to phylogenetic comparative analyses?



Adding fossils!

Advantages of adding fossils:

- Additional species information
 - traits, ecology (niches), biogeography
- Deeper temporal insights
- Assist with calibrating divergence times



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Challenges & considerations

- Gaps and biases in the fossil record
- Trait measurements

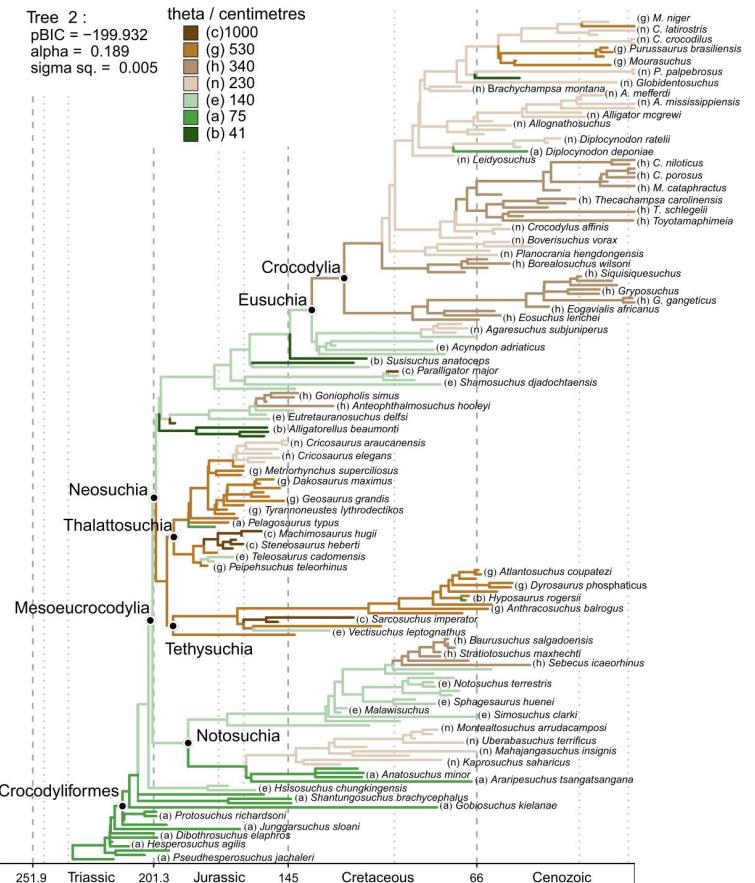


Eopelobates

PCMs in palaeo

Returning to Godoy et al. (2019)...

- Using PCMs to test hypotheses
- Ornstein-Uhlenbeck model preferred = macroevolutionary dynamics of crocodylomorph body size are better described within the concept of an adaptive landscape
- No support for trend towards larger sizes among lineages (i.e., Cope's rule)
- No support for strong correlations of body size with climate



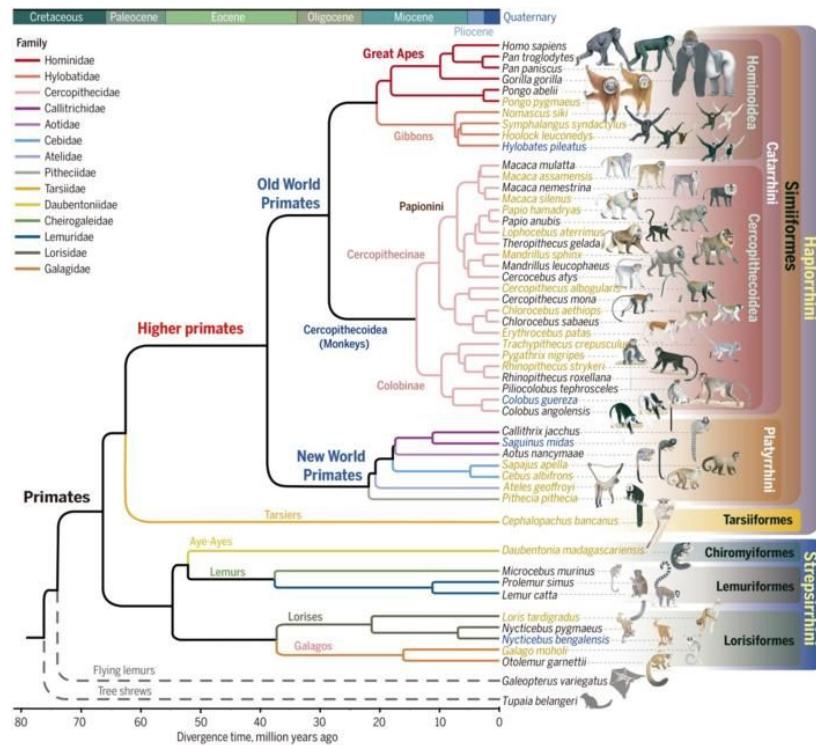
Godoy et al. (2019)

Independent exercise



Independent exercise

- In the data folder there is another tree ([primate-tree.nex](#)) and trait dataset ([primate-data.csv](#)) for investigating the evolution of primate life-history variables
- These data come from the [PanTHERIA database](#) and [10kTrees](#)
- Take the code from the frog exercise to examine body mass and/or gestation length evolution in primates



Source

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