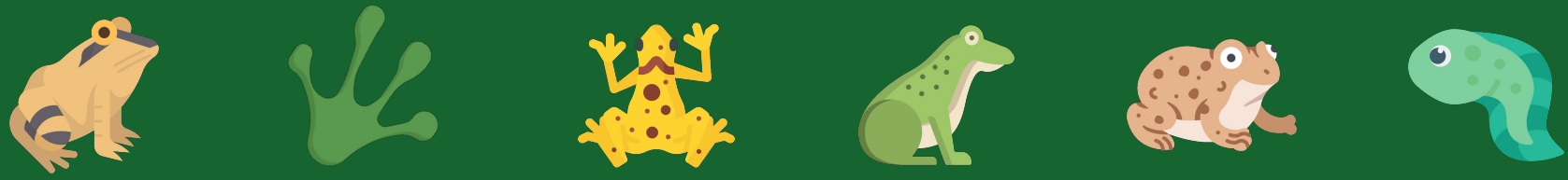

Introduction to Phylogenetic Comparative Methods

04.06.2024

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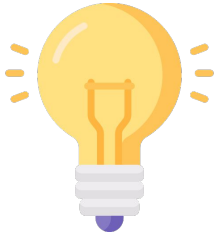
Learning objectives

After today's class, 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)

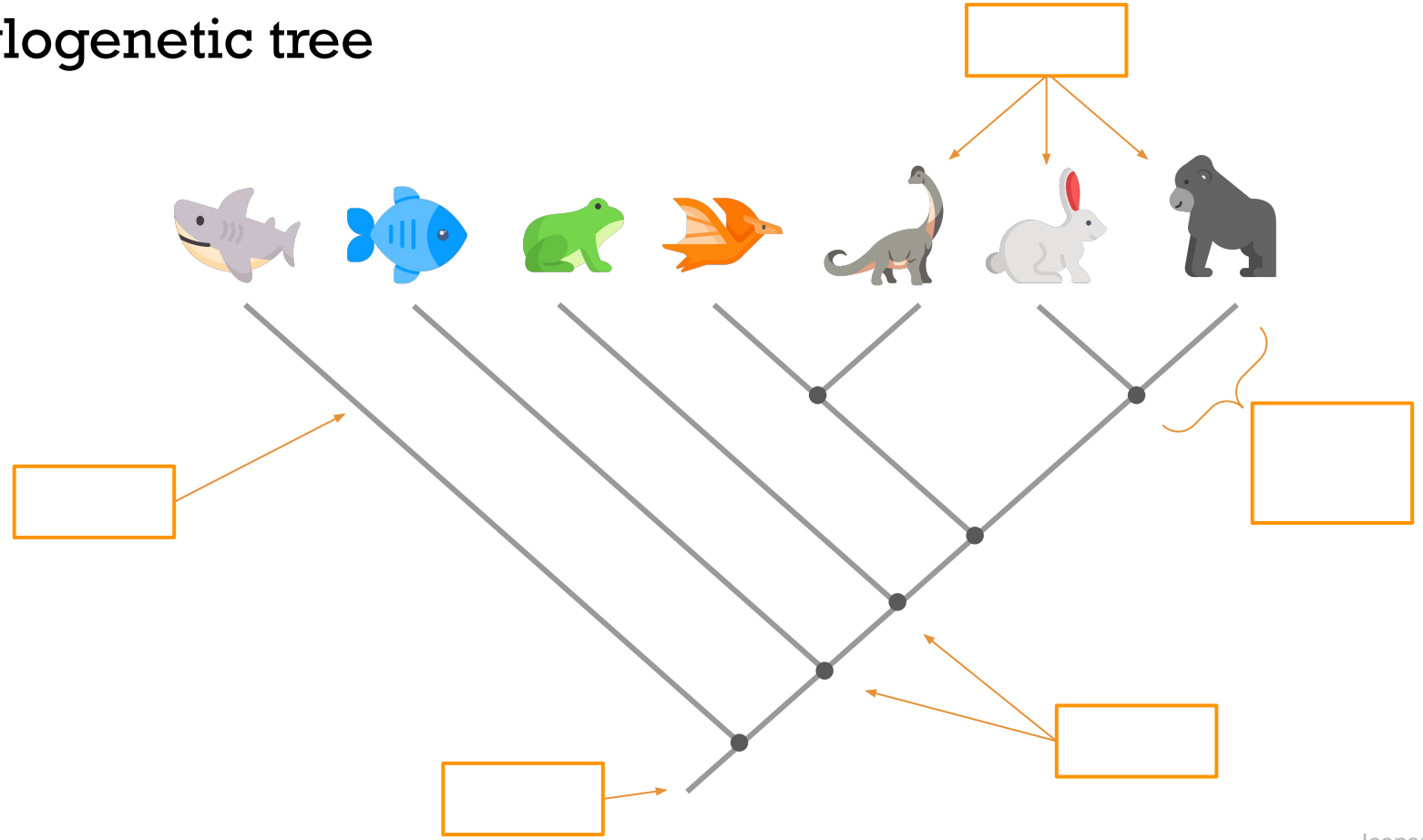
Macroevolution involves studying patterns on the tree of life *above* species level

- Across the whole tree of life

Phylogenetic Comparative Methods (PCMs)

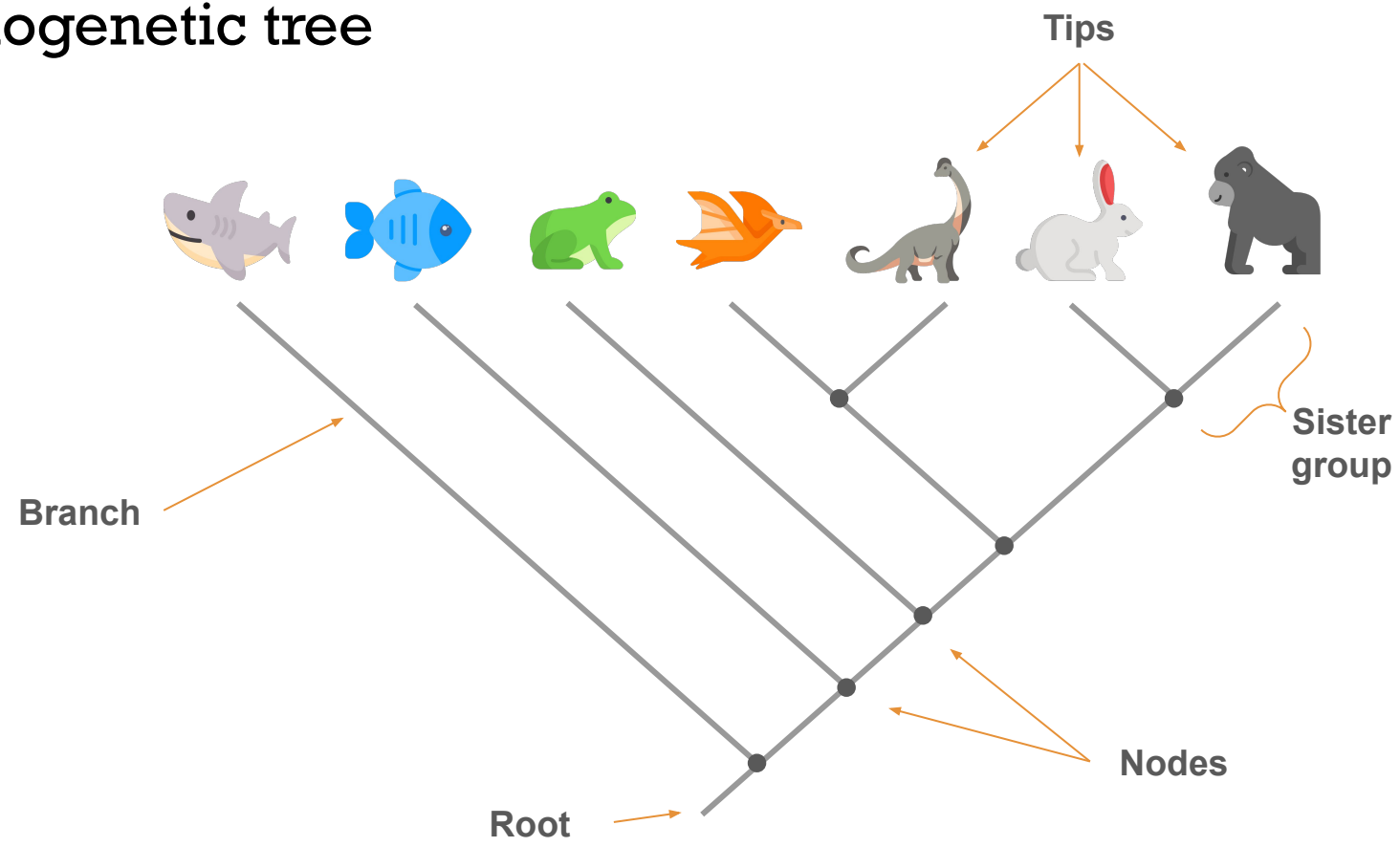
- Modified statistical tests that take into account non-independence in data that come from different species
- PCMs are applied to regression and other standard tests, and they can be used to estimate rates of evolution and to reconstruct ancestral trait states on a phylogeny
- PCMs use a **phylogenetic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

Phylogenetic tree



Icons: Flaticon.com

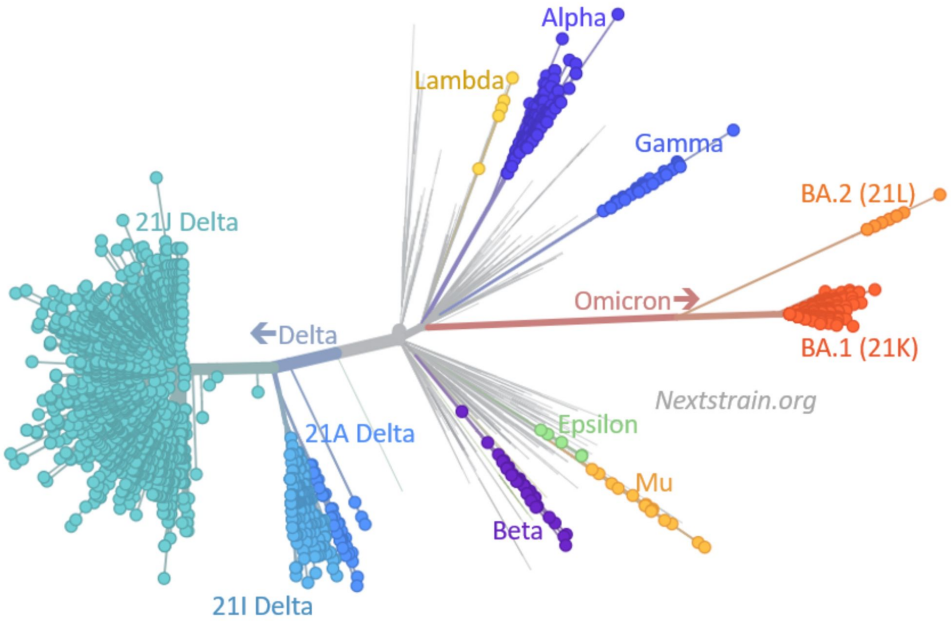
Phylogenetic tree



Icons: Flaticon.com

Phylogenetic Comparative Methods (PCMs)

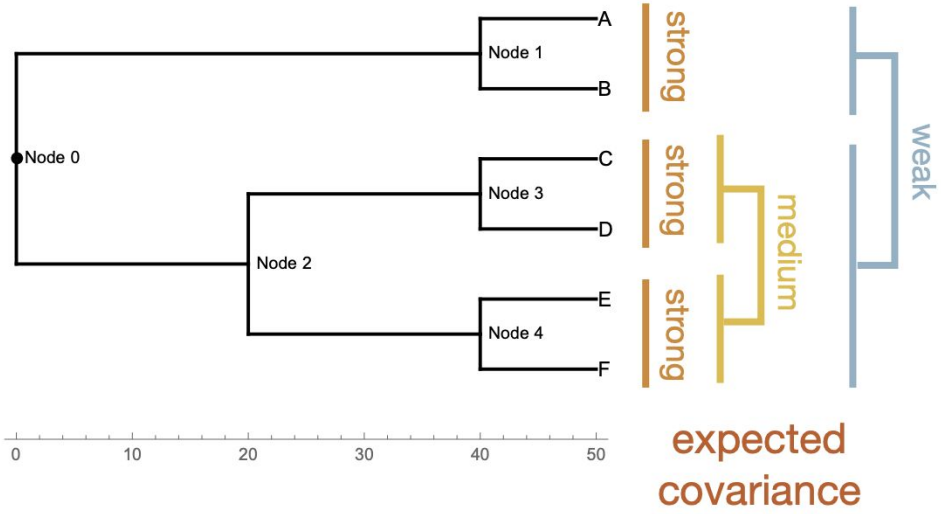
- **Scientific applications** in evolutionary biology, paleobiology, ecology and even linguistics (evolution of languages)
- **Societal applications** (e.g. modelling of SARS-CoV-2 [Covid] evolution)
- Easy to implement in R with various packages (e.g. `ape`, `geiger`, and `phytools`)



Source

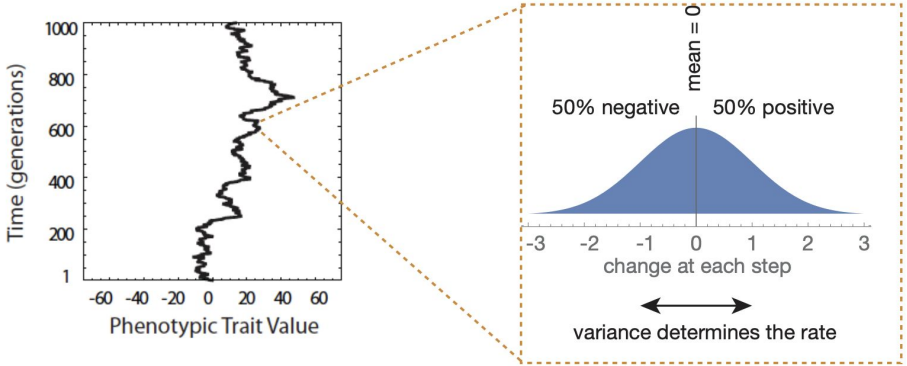
How do PCMs work?

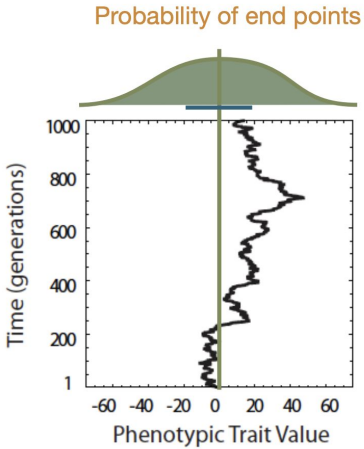
- PCMs estimate how much covariance a trait should have between taxa (and between traits) is expected from the phylogenetic topology
- The expected phylogenetic covariance is removed, leaving the residual between-trait covariance
- Statistical tests are carried out on the residual component



How do PCMs work?

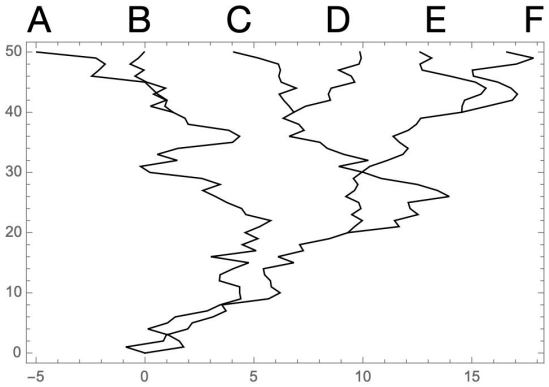
- How do we know the expected covariance? - depends on how the traits evolve
- **Brownian motion** (purely random evolution) is usually used for PCMs
  - change at each step has an equal chance of moving in positive or negative direction
- Evolution is change in the mean trait value from generation to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

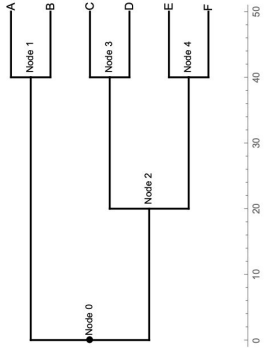




How do PCMs work?

- 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.



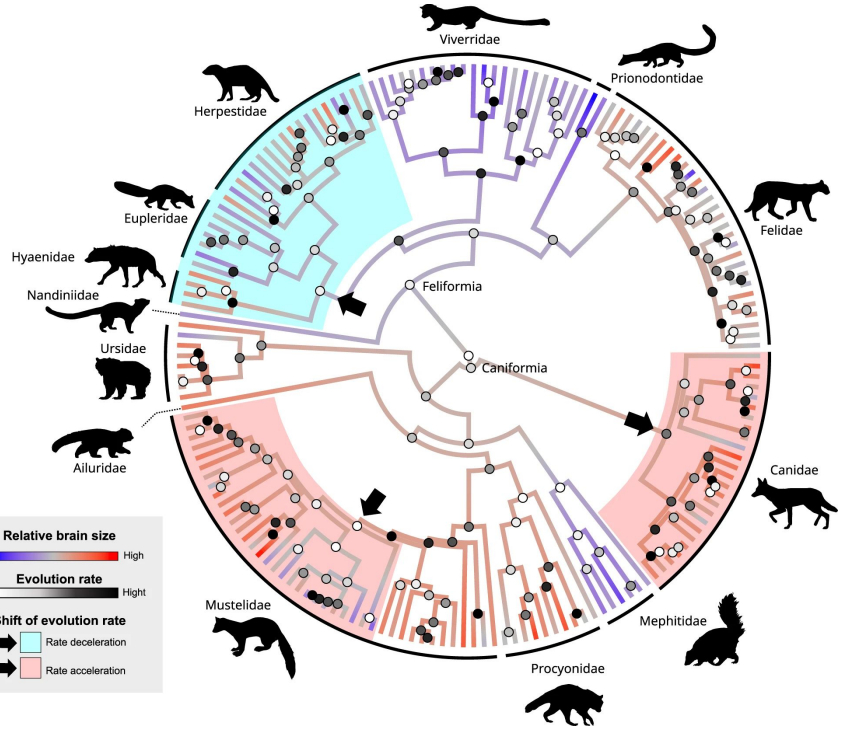


Var Y	A	B	C	D	E	F
A	50	40	0	0	0	0
B	40	50	0	0	0	0
C	0	0	50	40	20	20
D	0	0	40	50	20	20
E	0	0	20	20	50	40
F	0	0	20	20	40	50

Phylogenetic Comparative Methods (PCMs)

Questions

- 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?

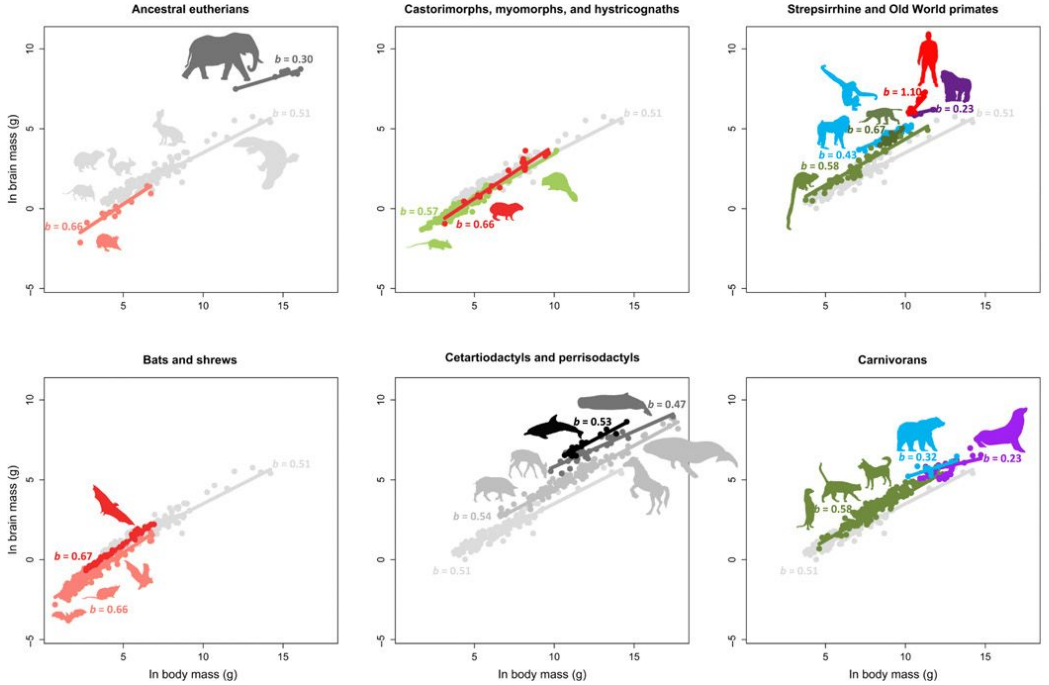


Michaud *et al.* (2022)

Phylogenetic Comparative Methods (PCMs)

Examples of PCMs:

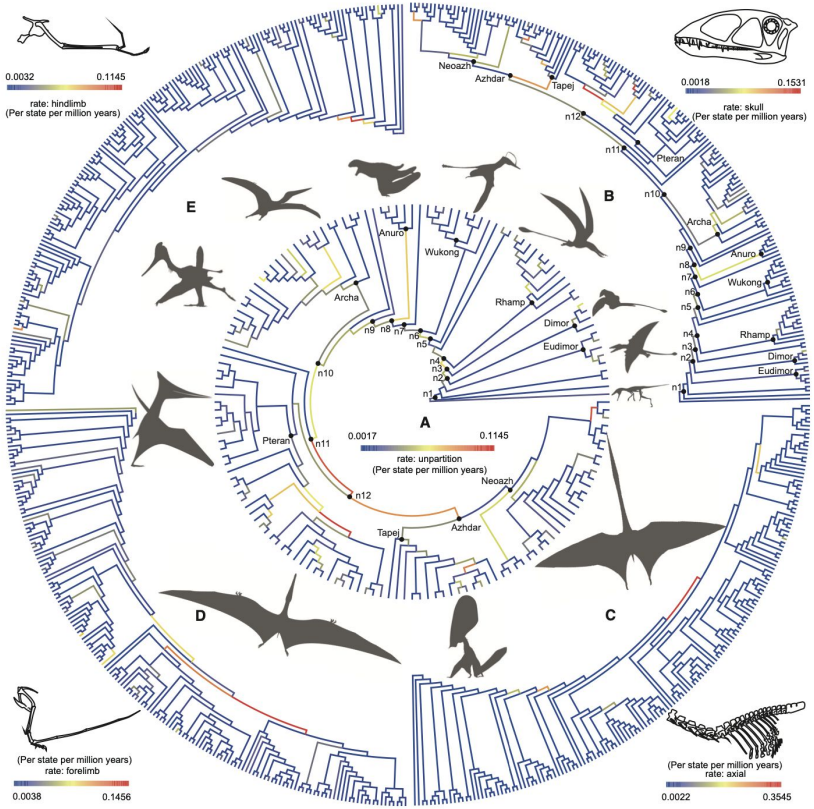
- Test for phylogenetic signal
- Phylogenetic MANOVA
- Phylogenetic generalised least squares (PGLS)
- Phylogenetic Principal Components Analysis (pPCA)
- Evolutionary model fitting analysis
- Ancestral state reconstruction



Michaud *et al.* (2022)

PCMs in palaeontology

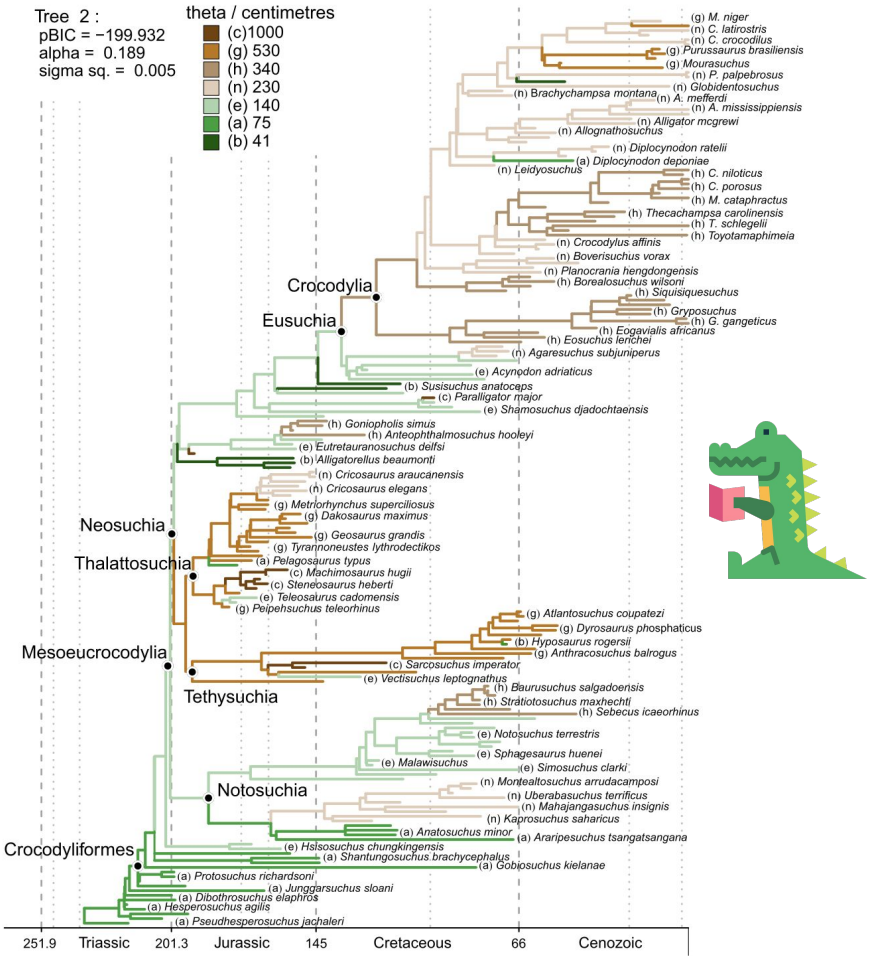
- **Pterosaur** diversification and evolution across the Mesozoic
- Evolutionary rate of morphological features (e.g. limb length)
- Early Triassic–Early Cretaceous = increasing net diversification rates and disparity + morphological rates
- Early Cretaceous–extinction = mostly negative net diversification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



Yu *et al.* (2023)

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!)

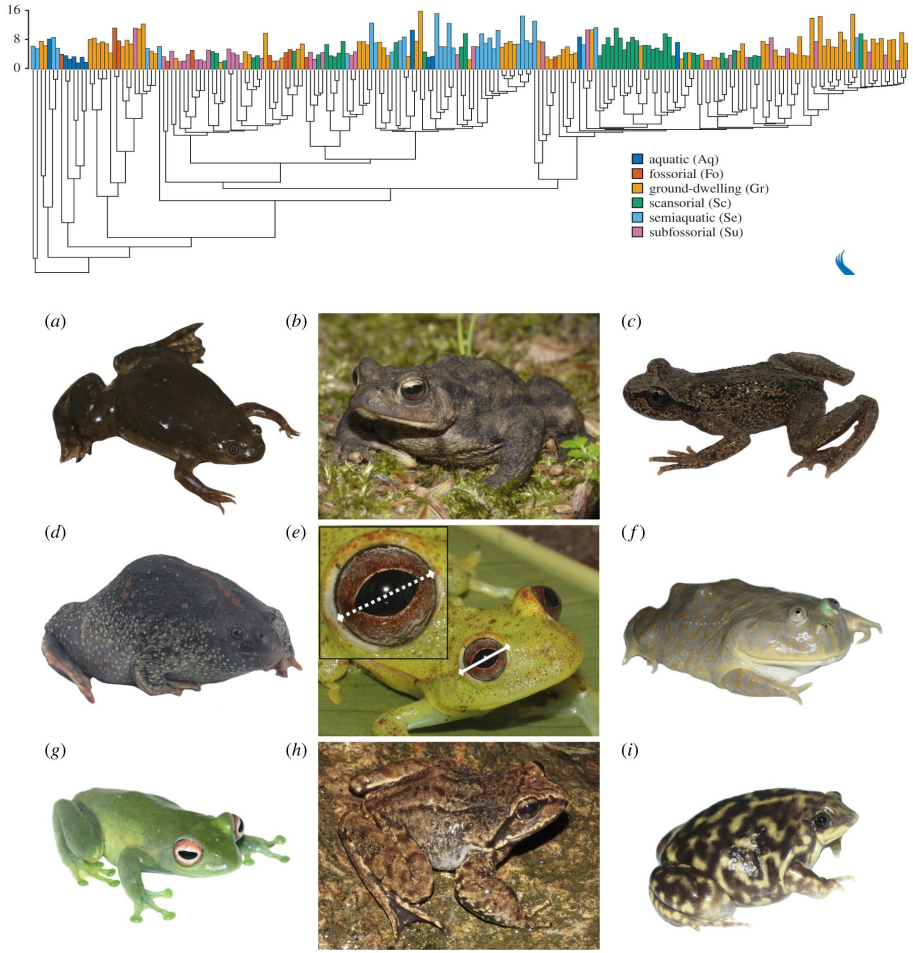


Godoy et al. (2019)

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

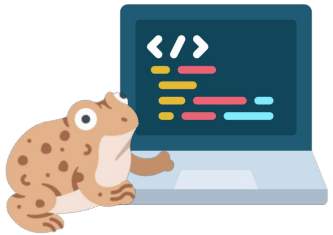
Thomas *et al.* (2020)



R exercise

Part 1: Data organisation + visualisation

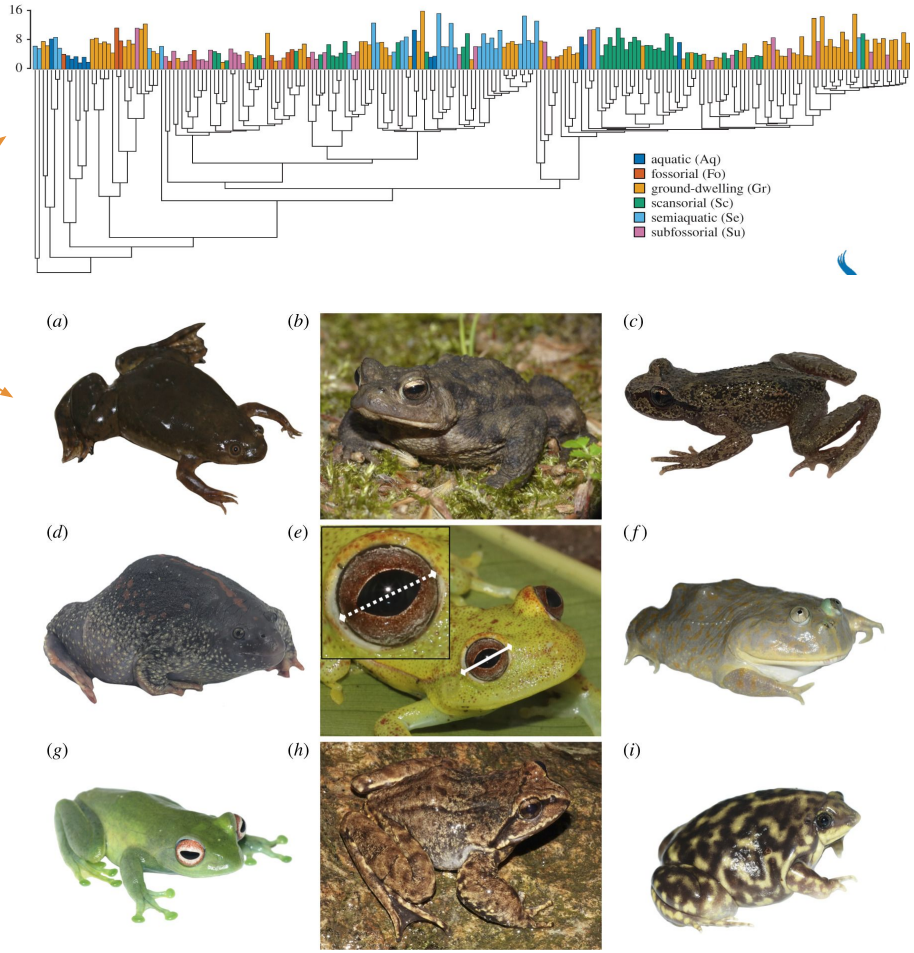
`01_frogs_PCMs.R`



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:

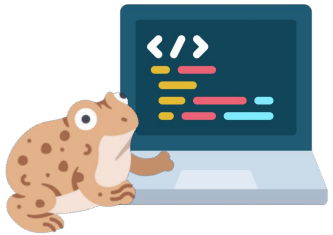
1. Does eye size in frogs have a phylogenetic signal?

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?

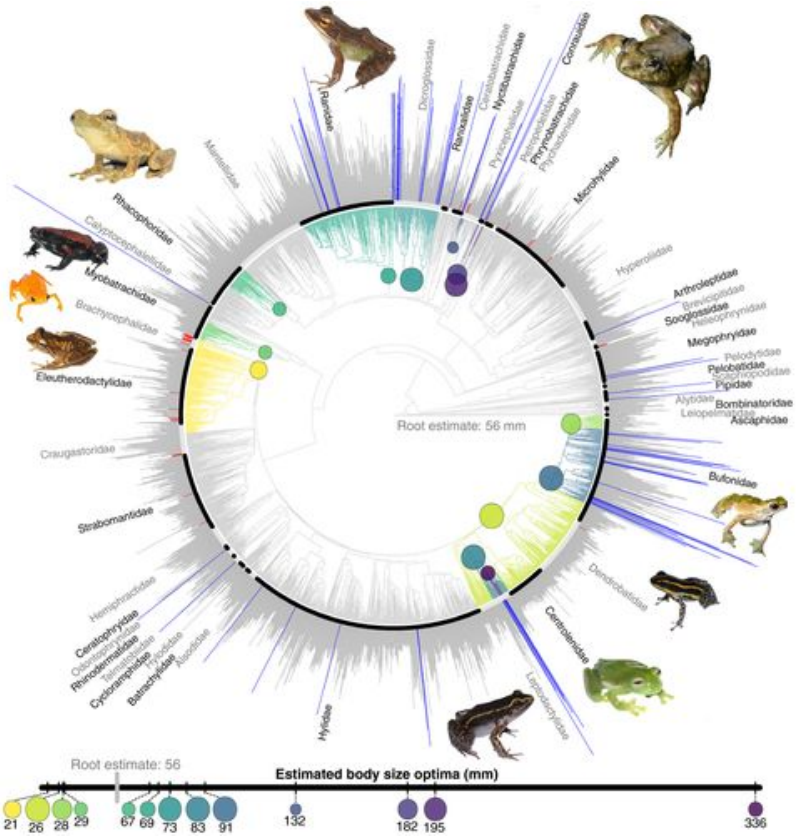
R exercise

Part 2: Phylogenetic signal



Phylogenetic signal

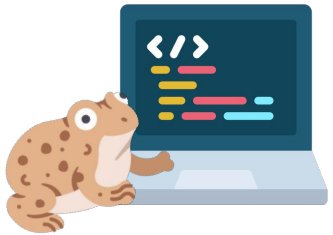
- Phylogenetic signal describes the tendency for closely related organisms to be more similar to one another than chance
- There are different ways to measure phylogenetic signal e.g.:
  - Pagel's λ (lambda)
  - Blomberg's *K*



Womack & Bell (2020)

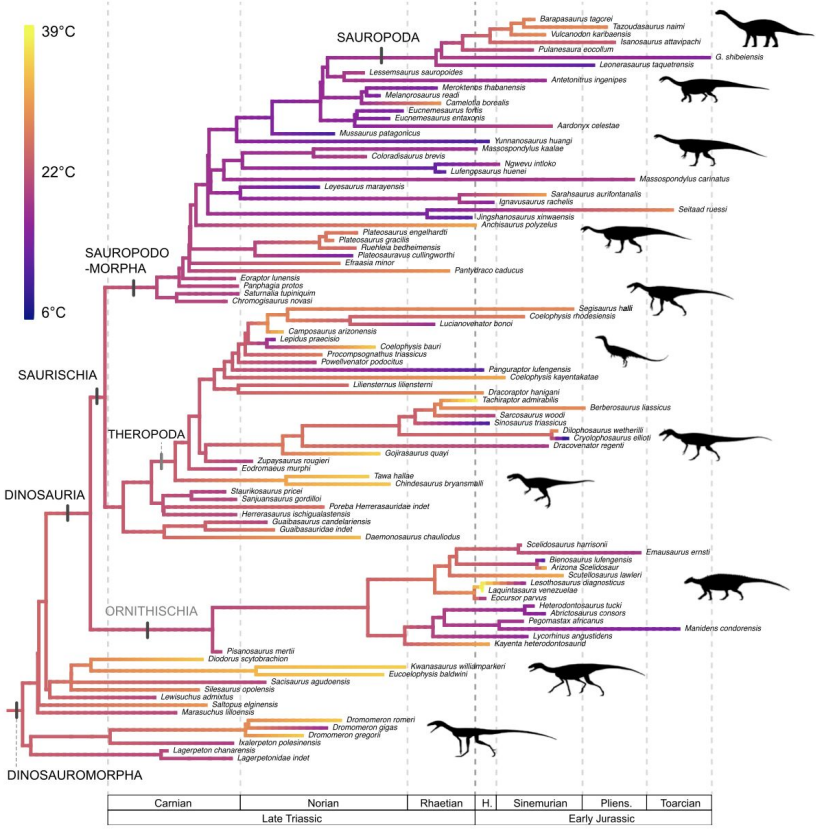
R exercise

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



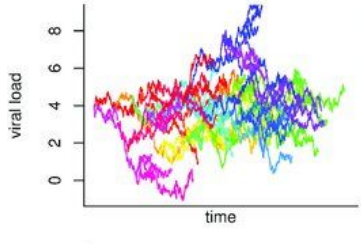
Dunne *et al.* (2023)

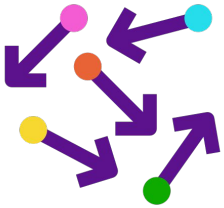
Brownian motion (BM)

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)

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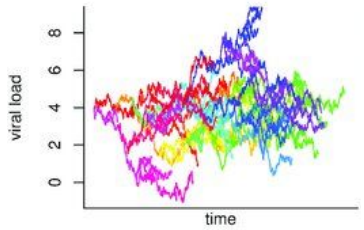
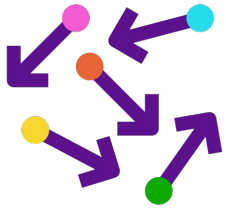
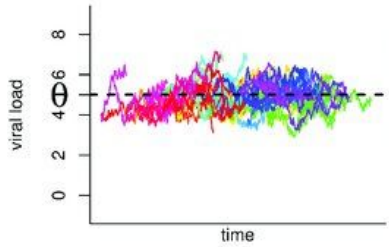




Ornstein-Uhlenbeck (OU)

- 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’

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

Adding fossils!

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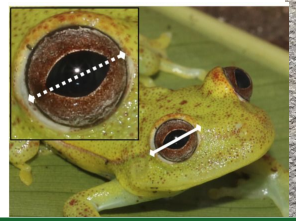
Challenges & considerations

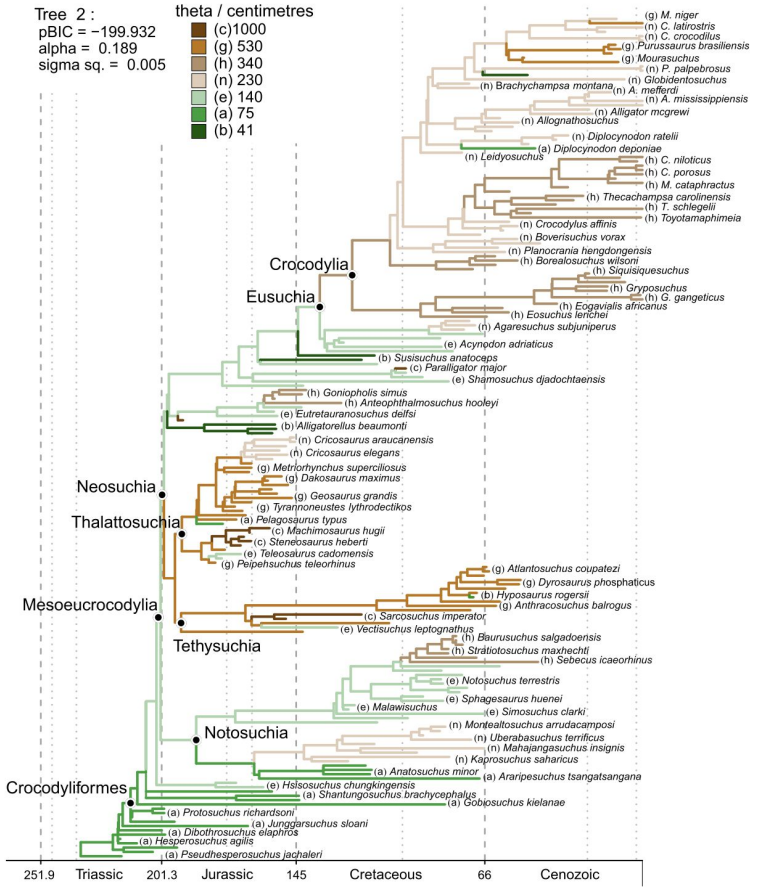
- Gaps and biases in the fossil record
- Trait measurements



PCMs in palaeo

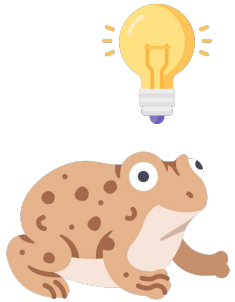
Returning to Godoy *et al.* (2019)...

- 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



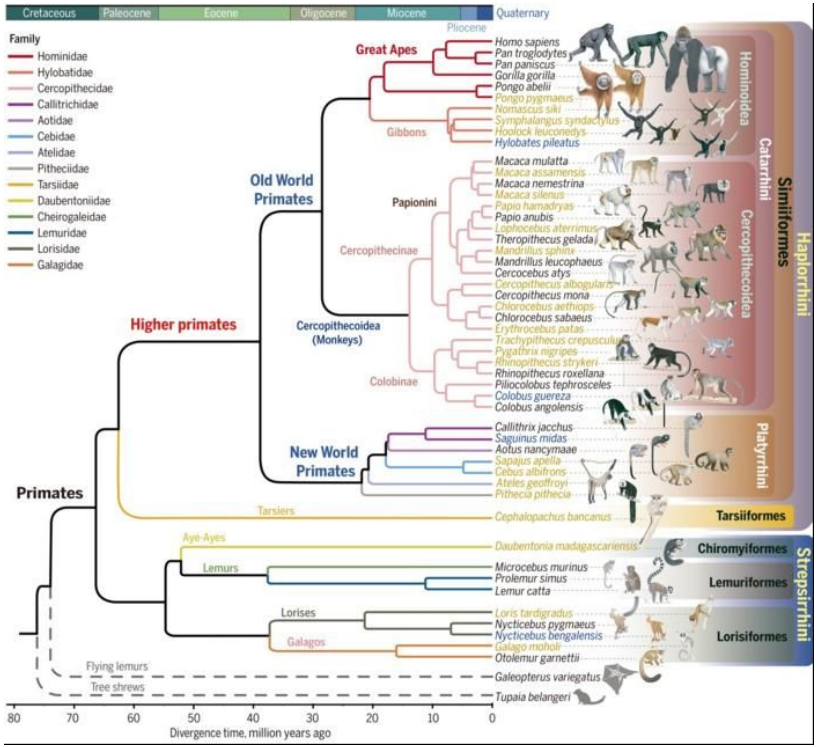
Godoy et al. (2019)

Independent exercise



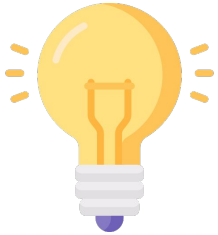
Independent exercise

- 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

Learning objectives

You should be able to:

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- 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