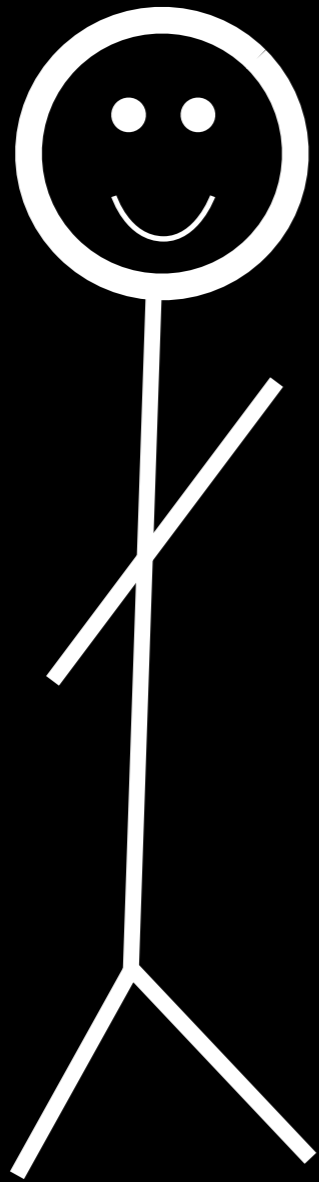
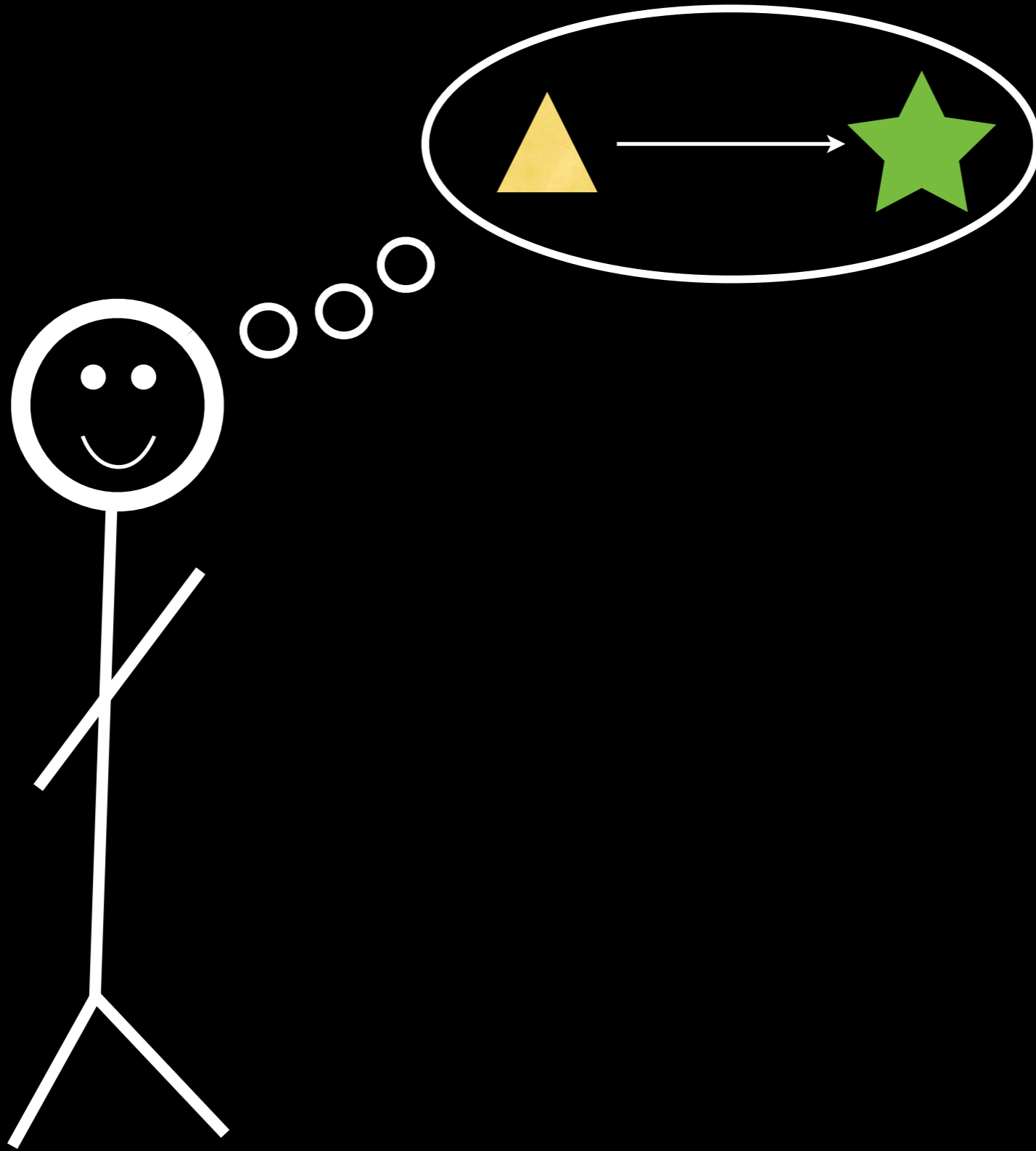


# New frontiers for the comparative analysis of adaptive radiation

Luke J. Harmon  
University of Idaho









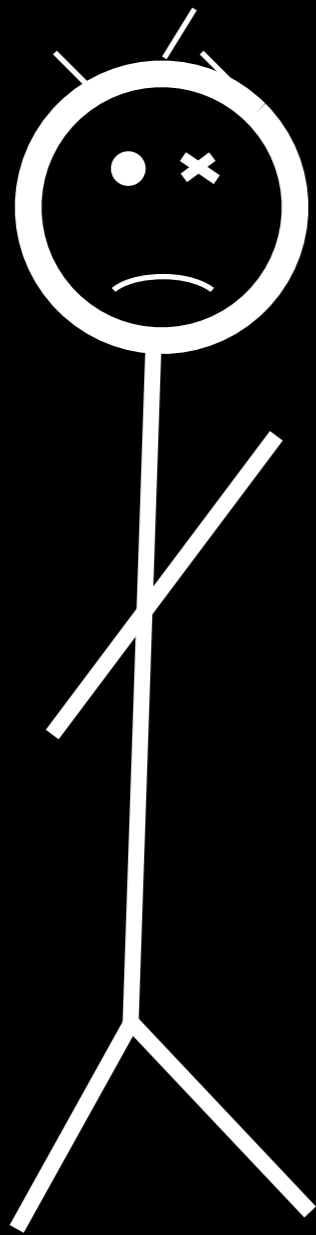




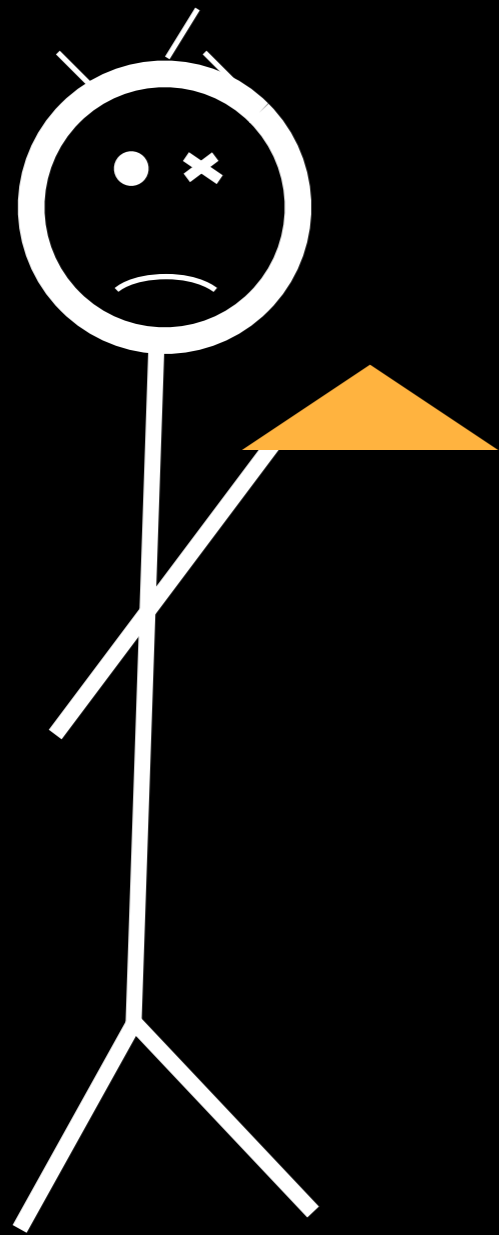


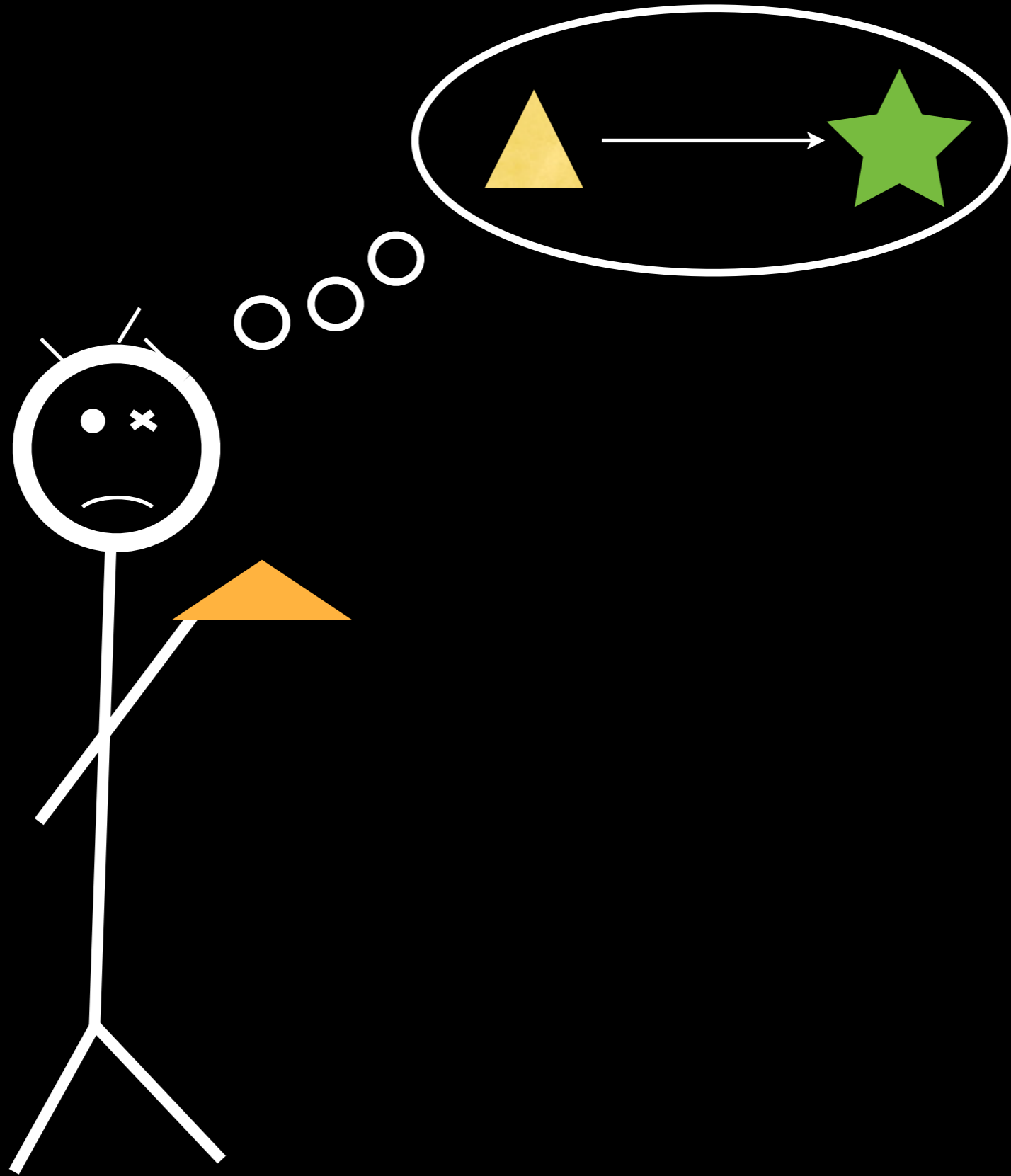




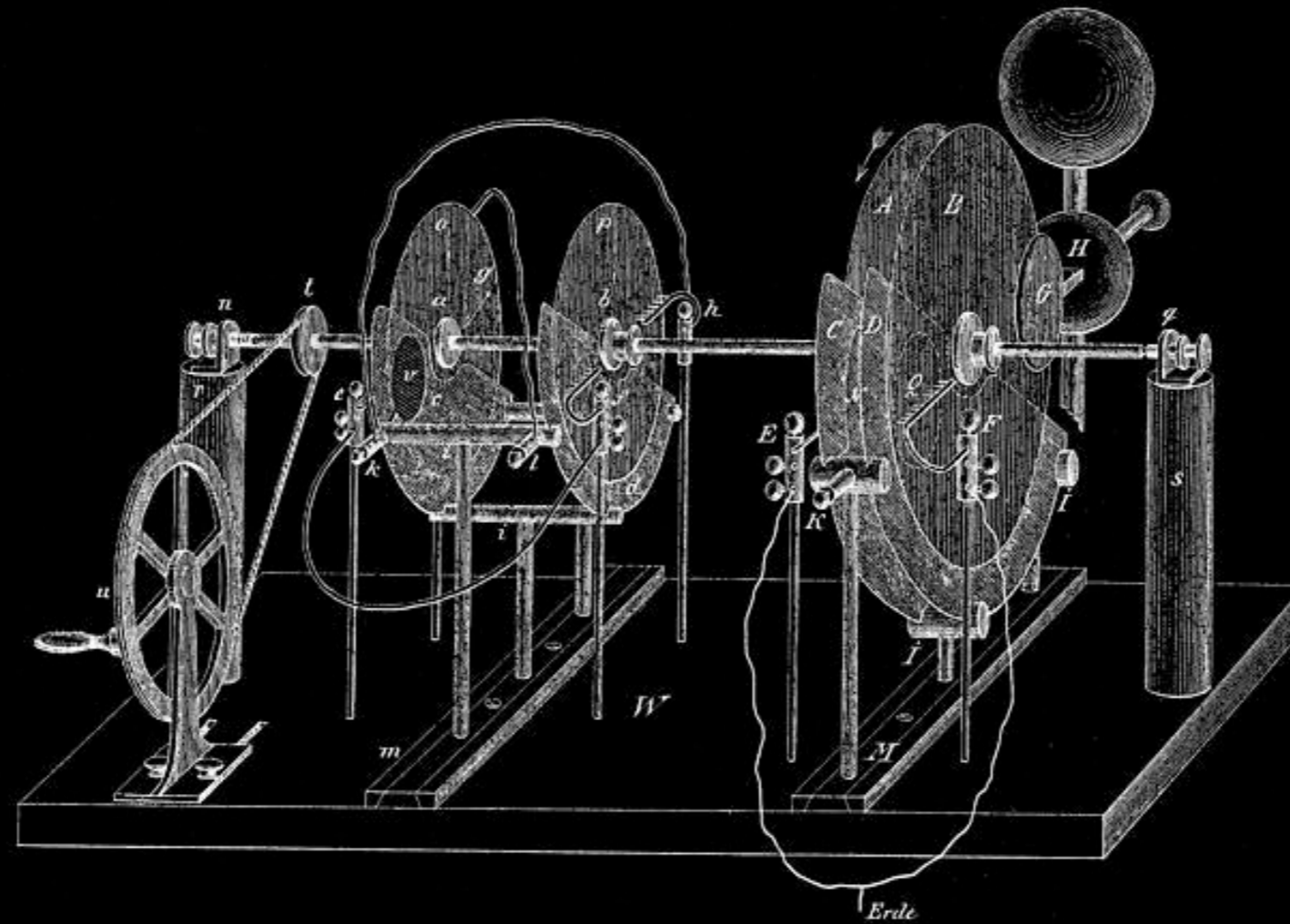






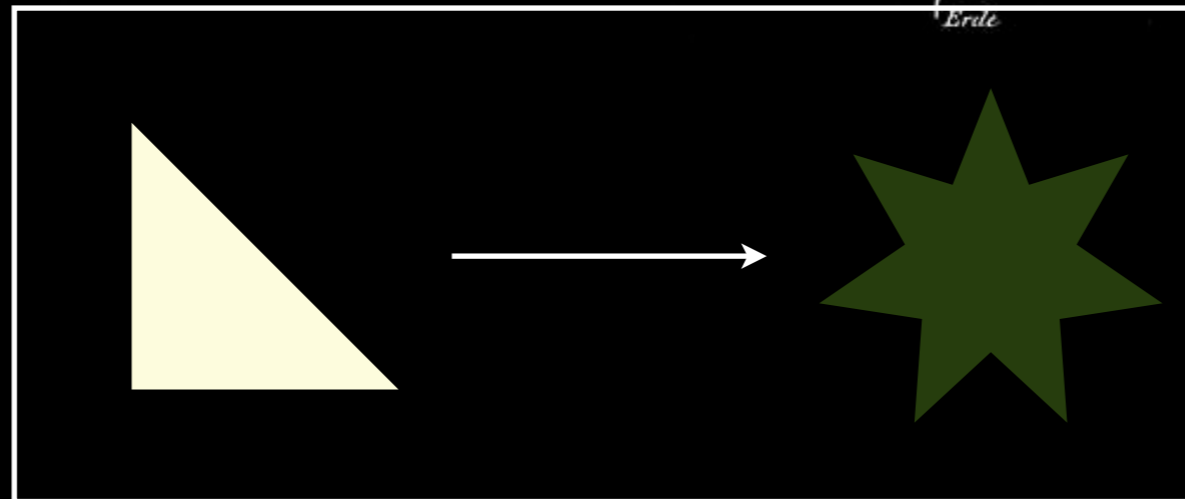
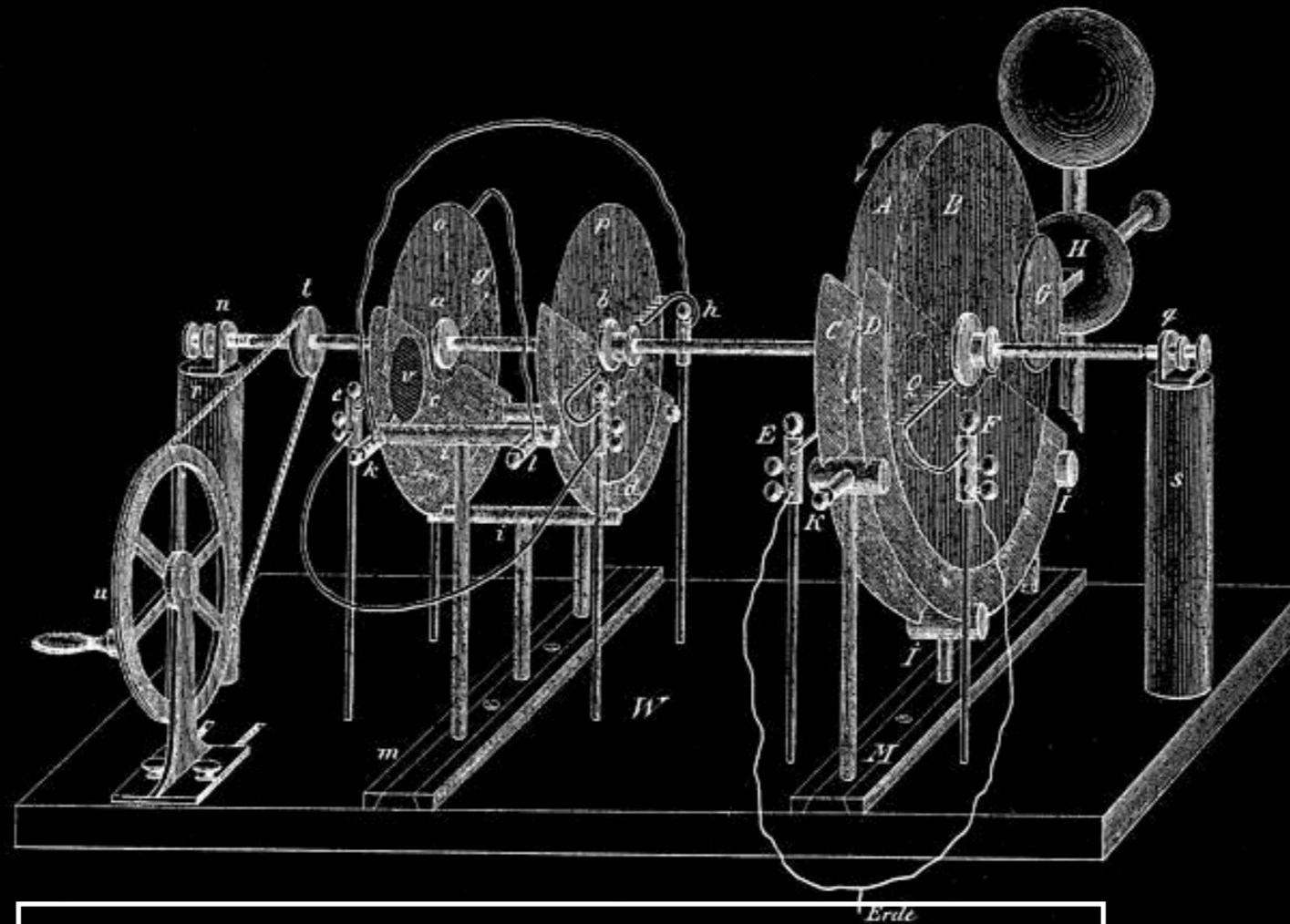


# Statistical comparative methods machine

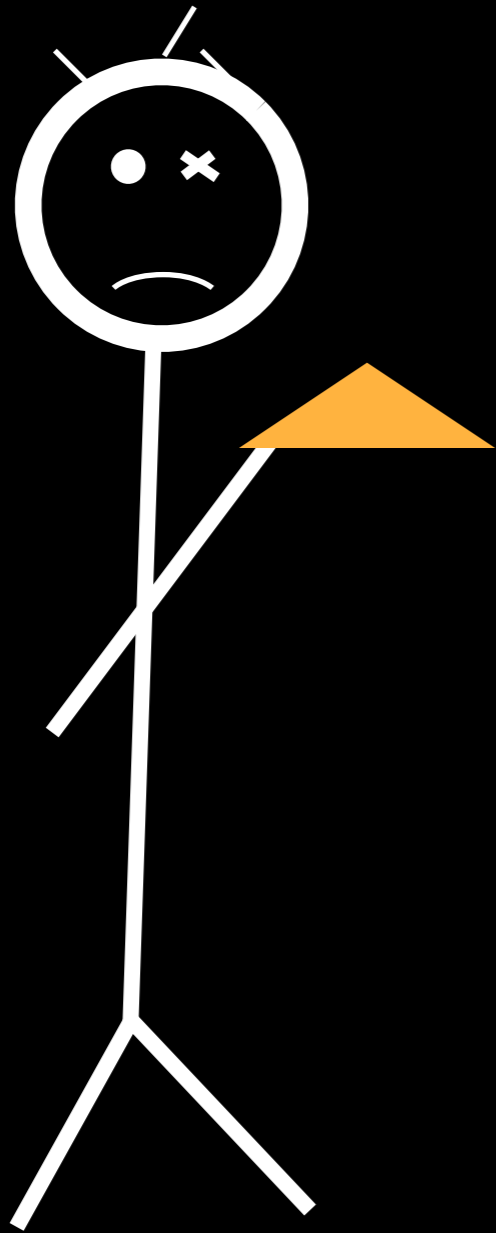




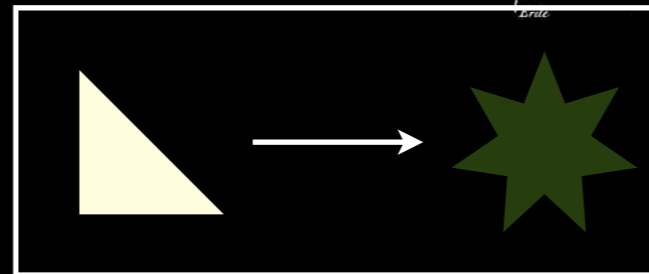
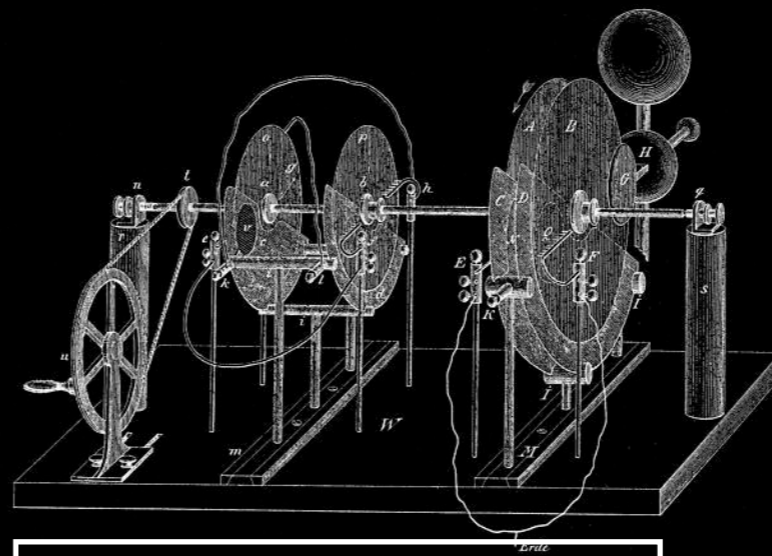
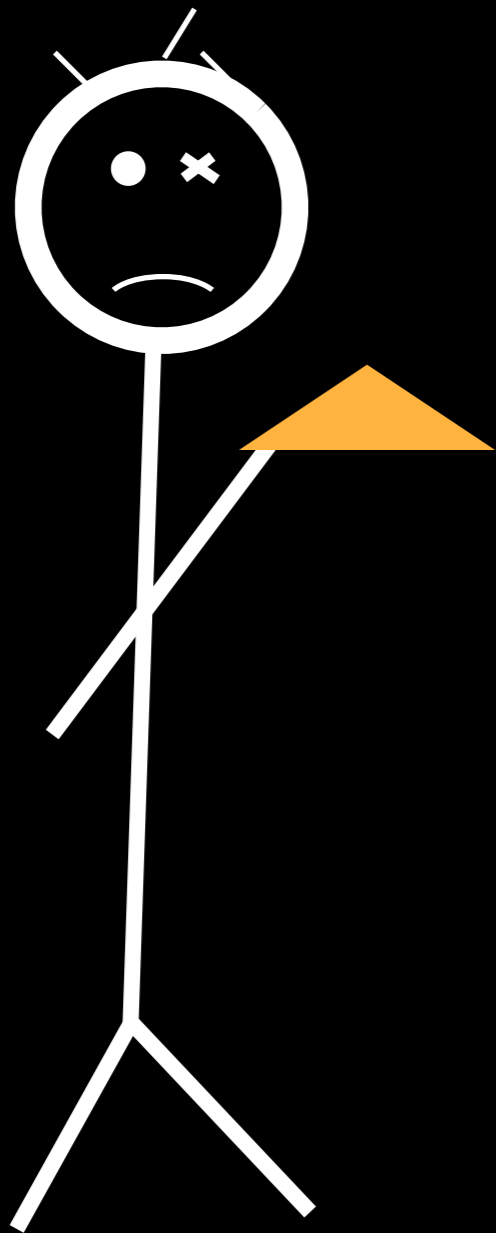
# Statistical comparative methods machine



# How comparative methods work:

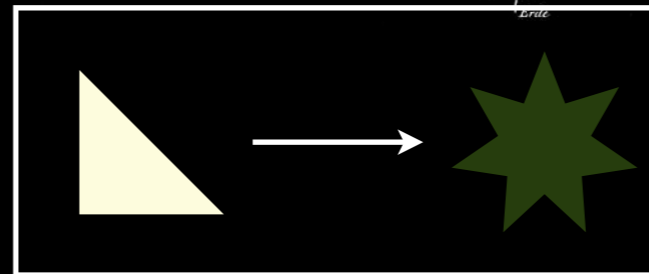
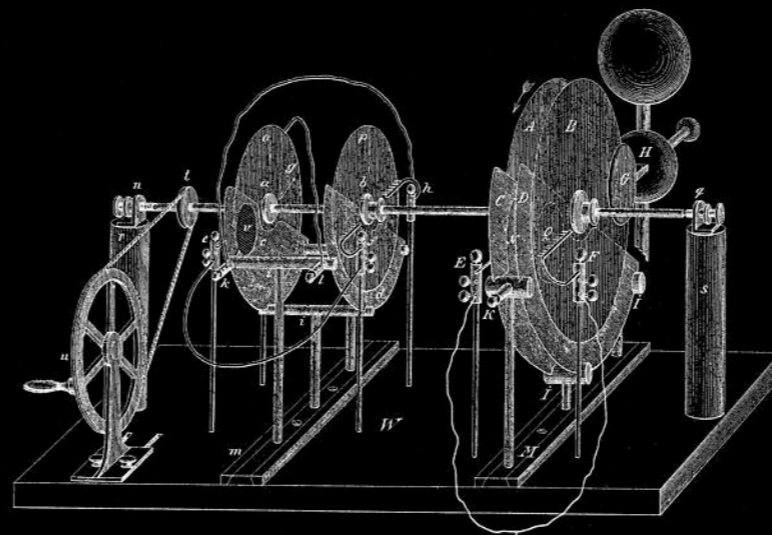
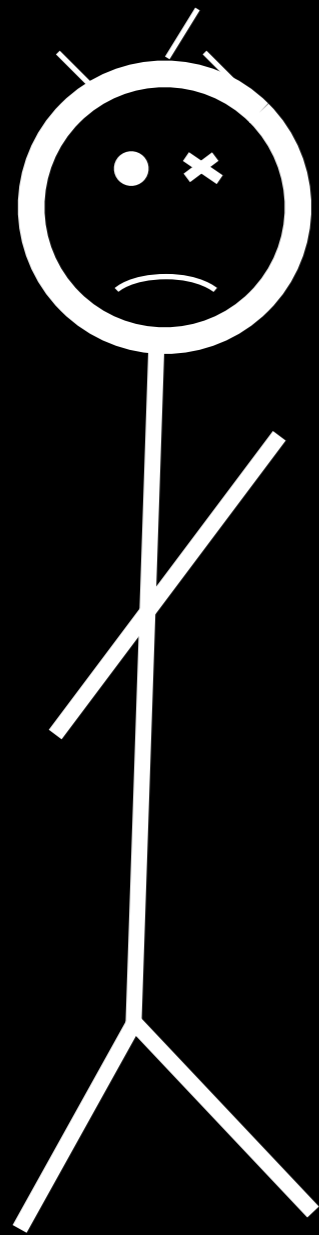


# How comparative methods work:

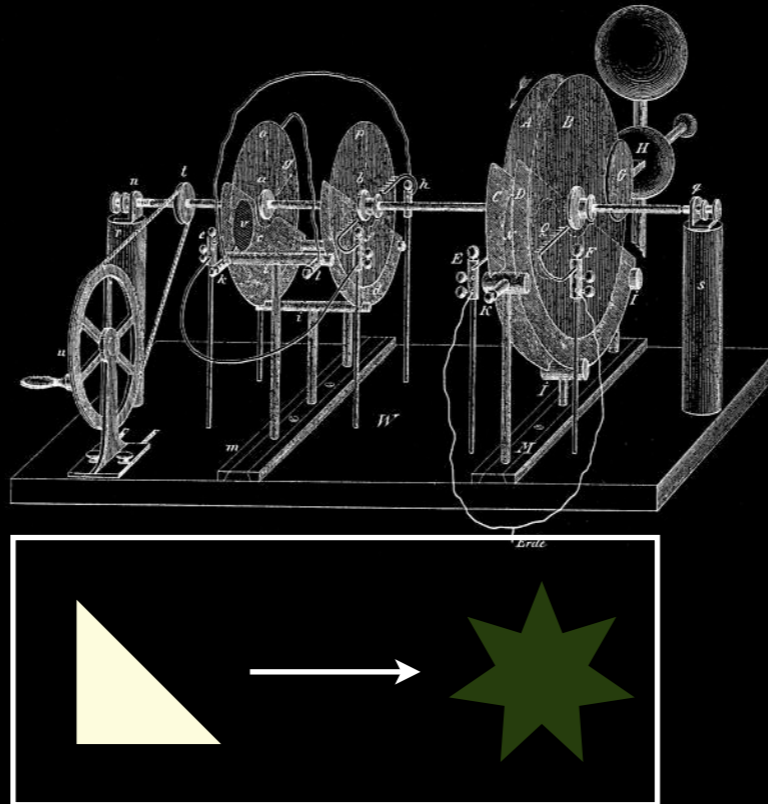
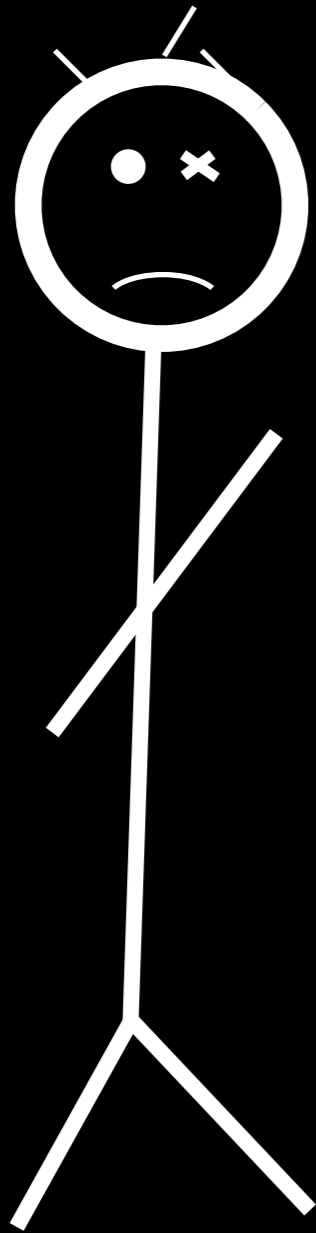




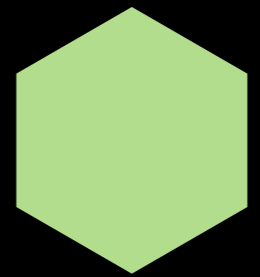
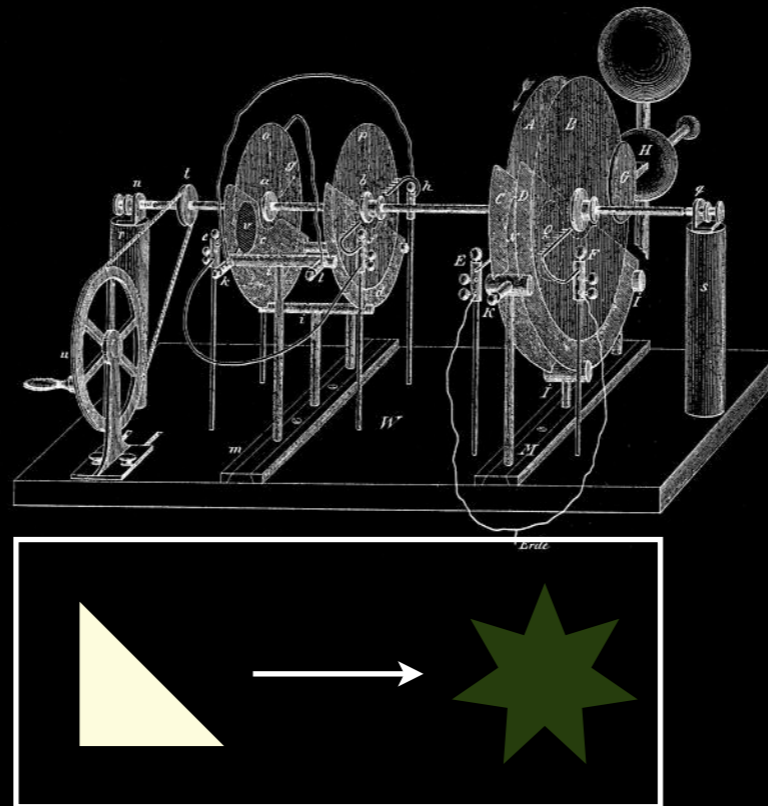
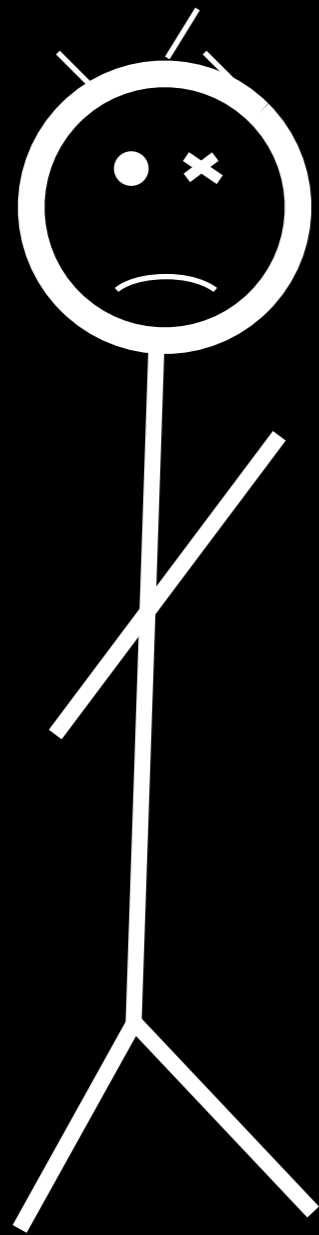
# How comparative methods work:



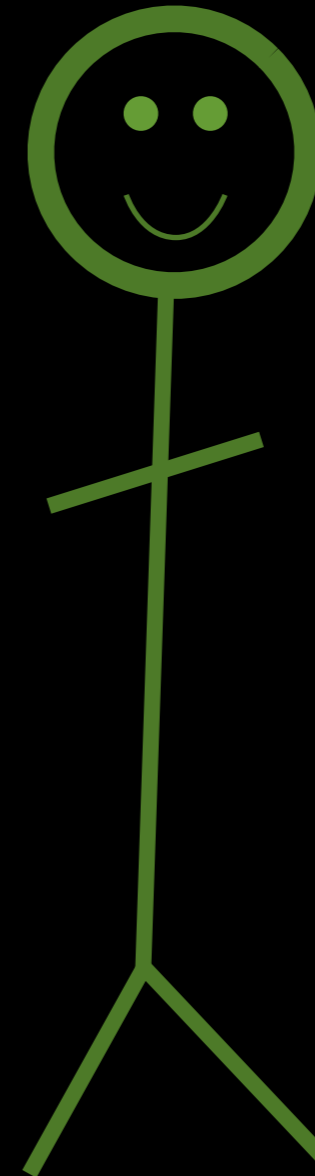
# How comparative methods work:



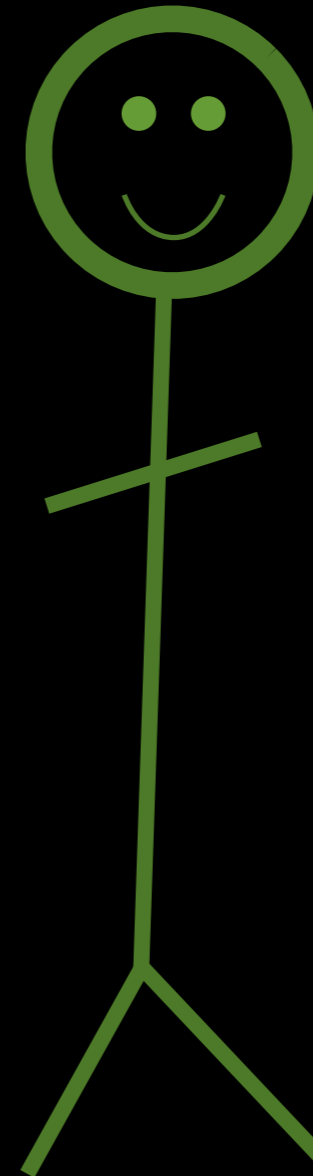
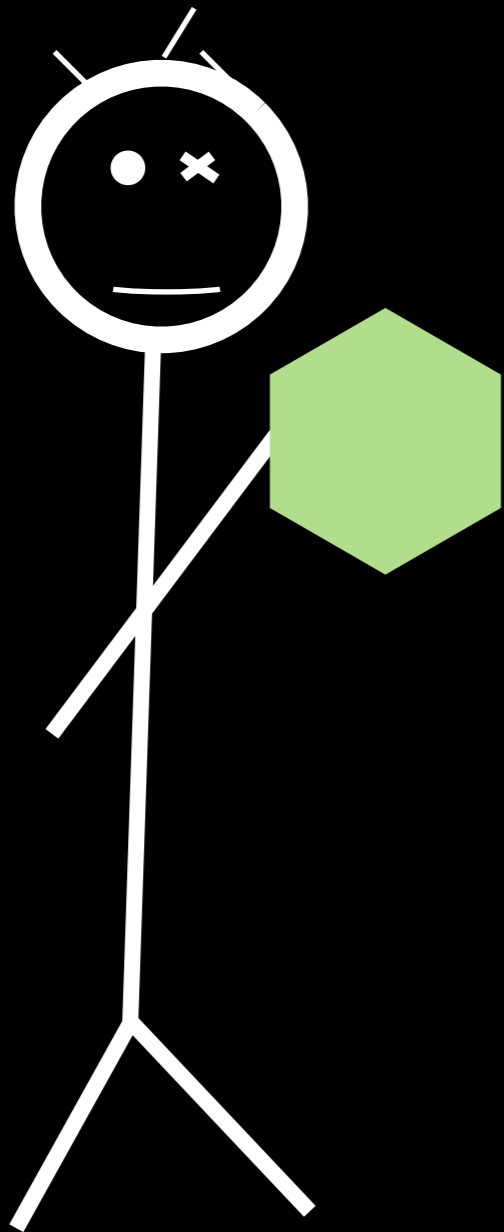
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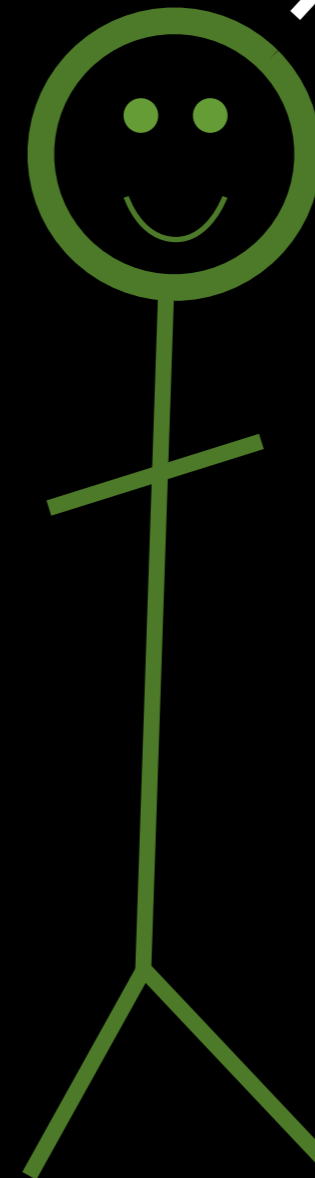
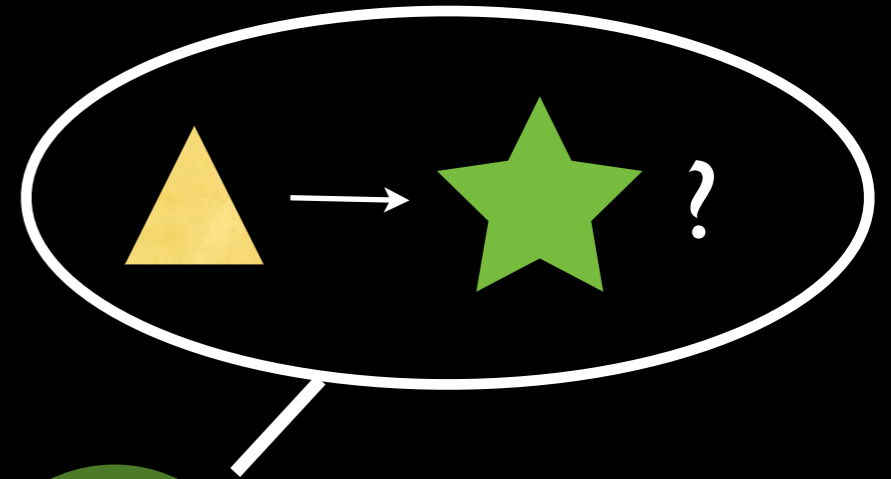
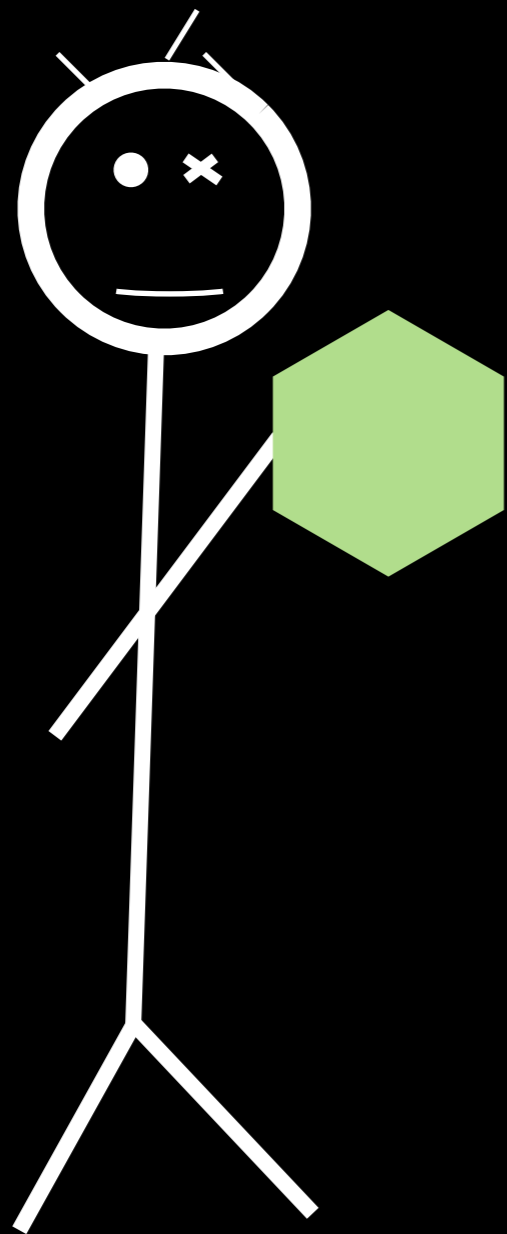




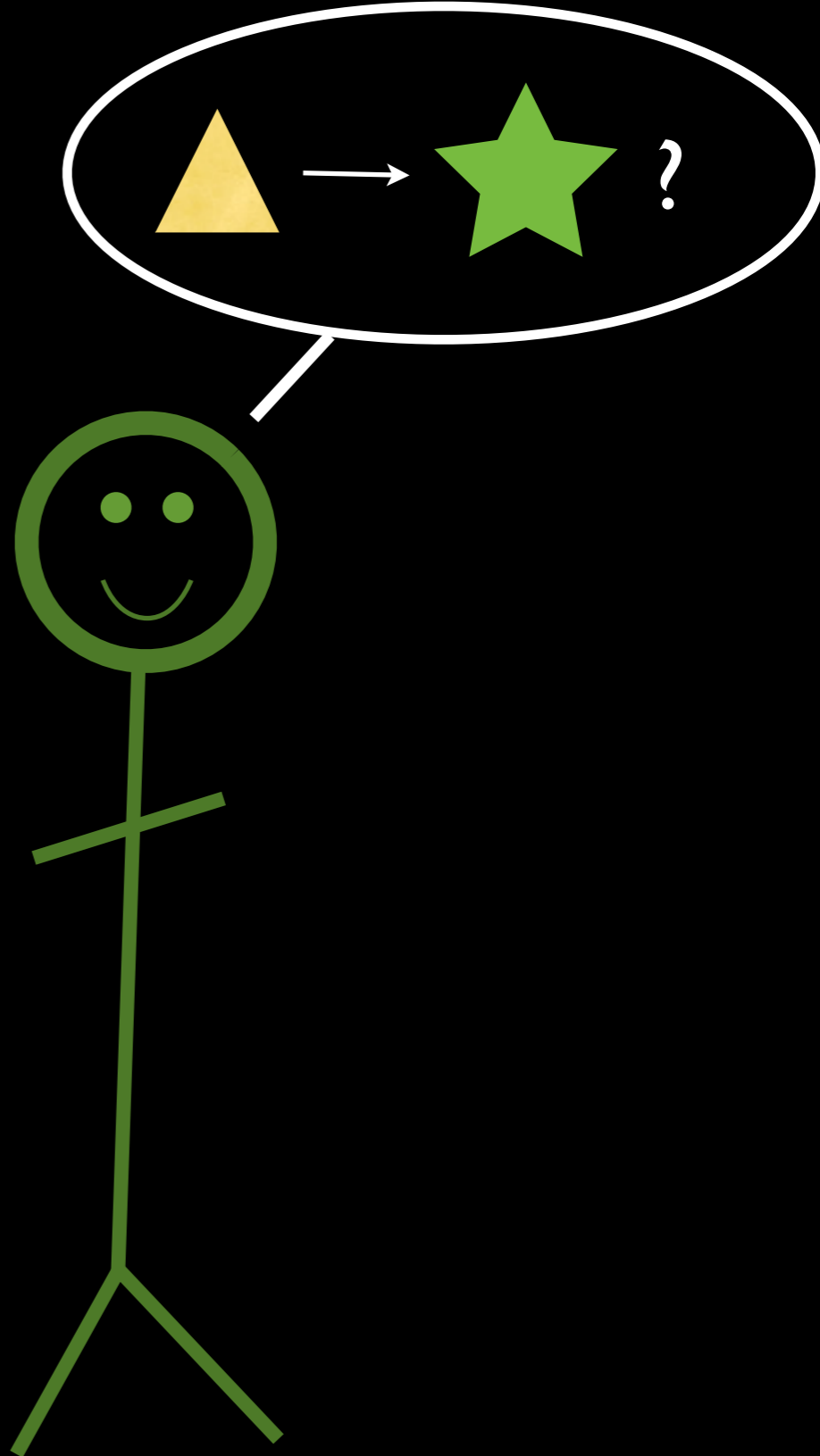
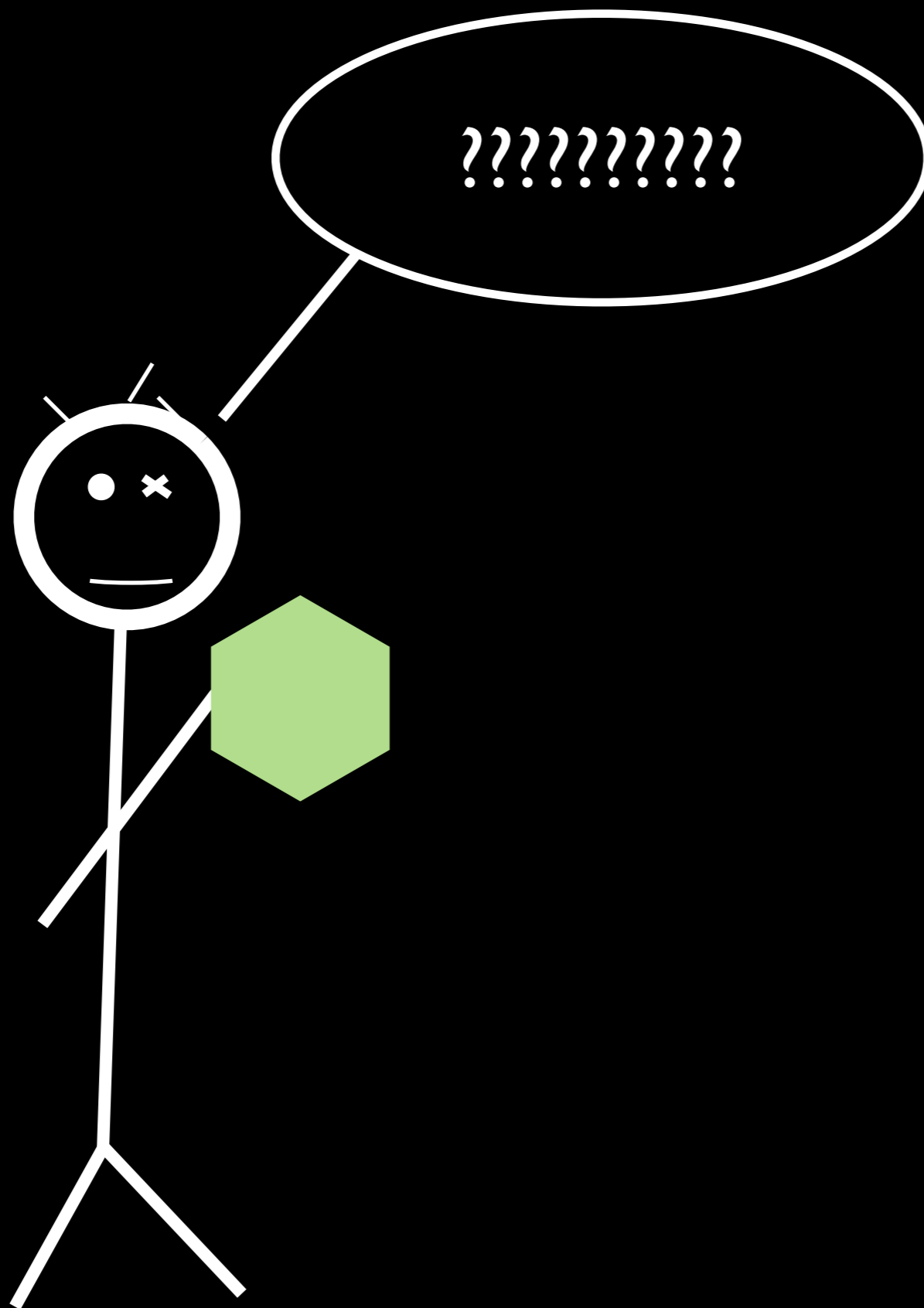
Dr. So-and-so



Dr. So-and-so



Dr. So-and-so



Dr. So-and-so

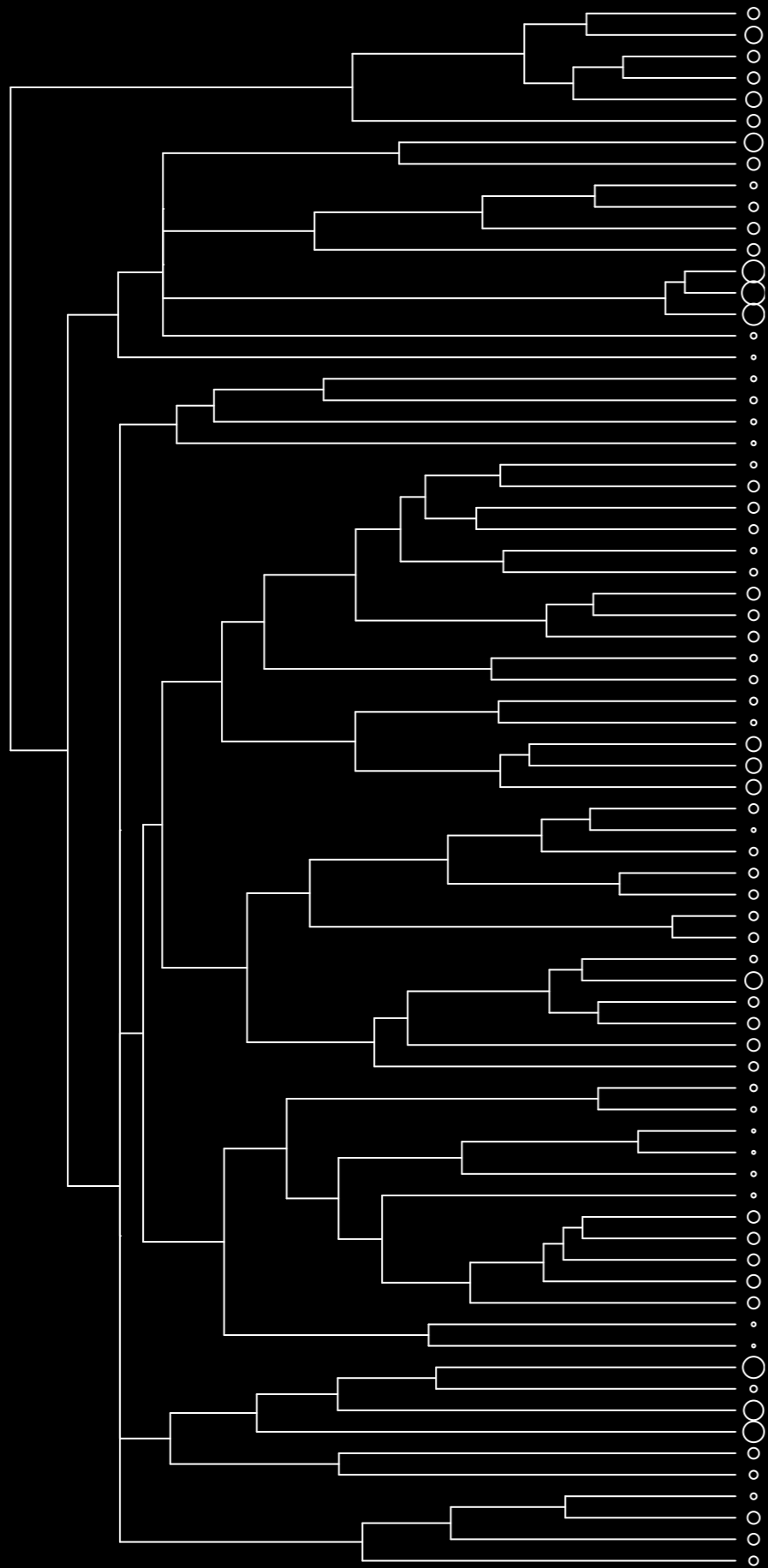




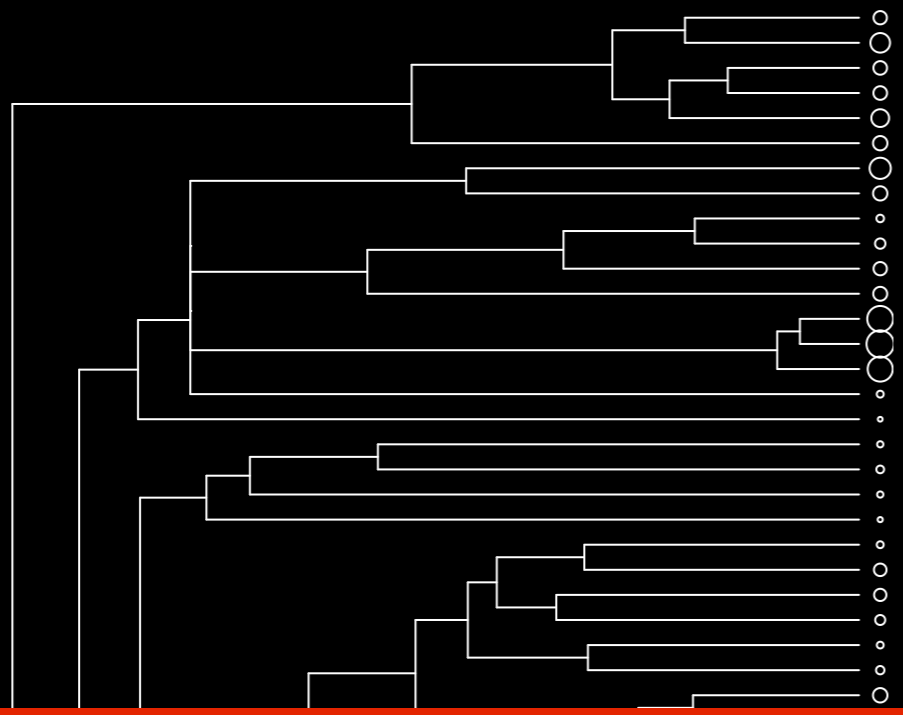
# Goal:

- Create methods that analyze the data that people **actually have** to estimate things that they **really want to know**

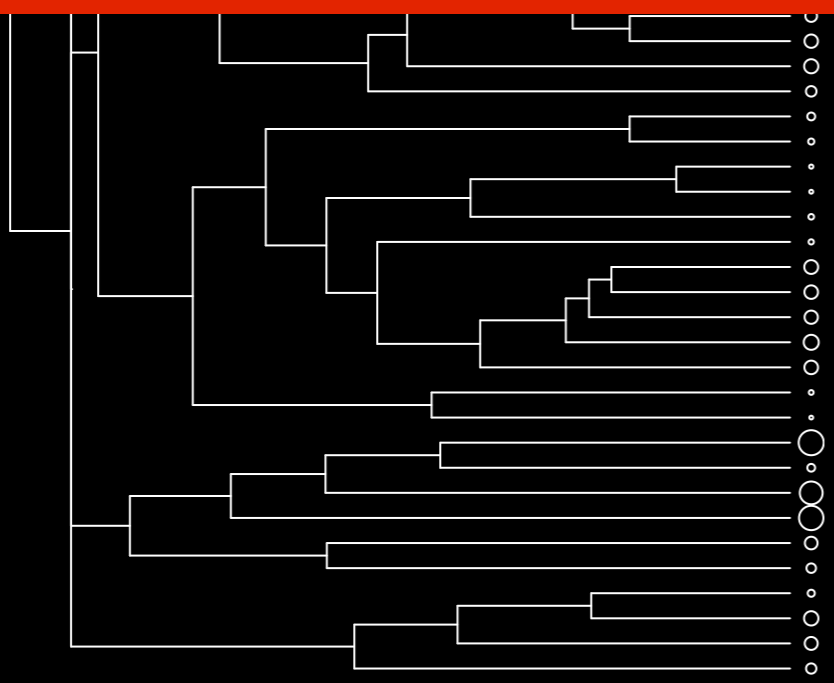
What data do people actually have?

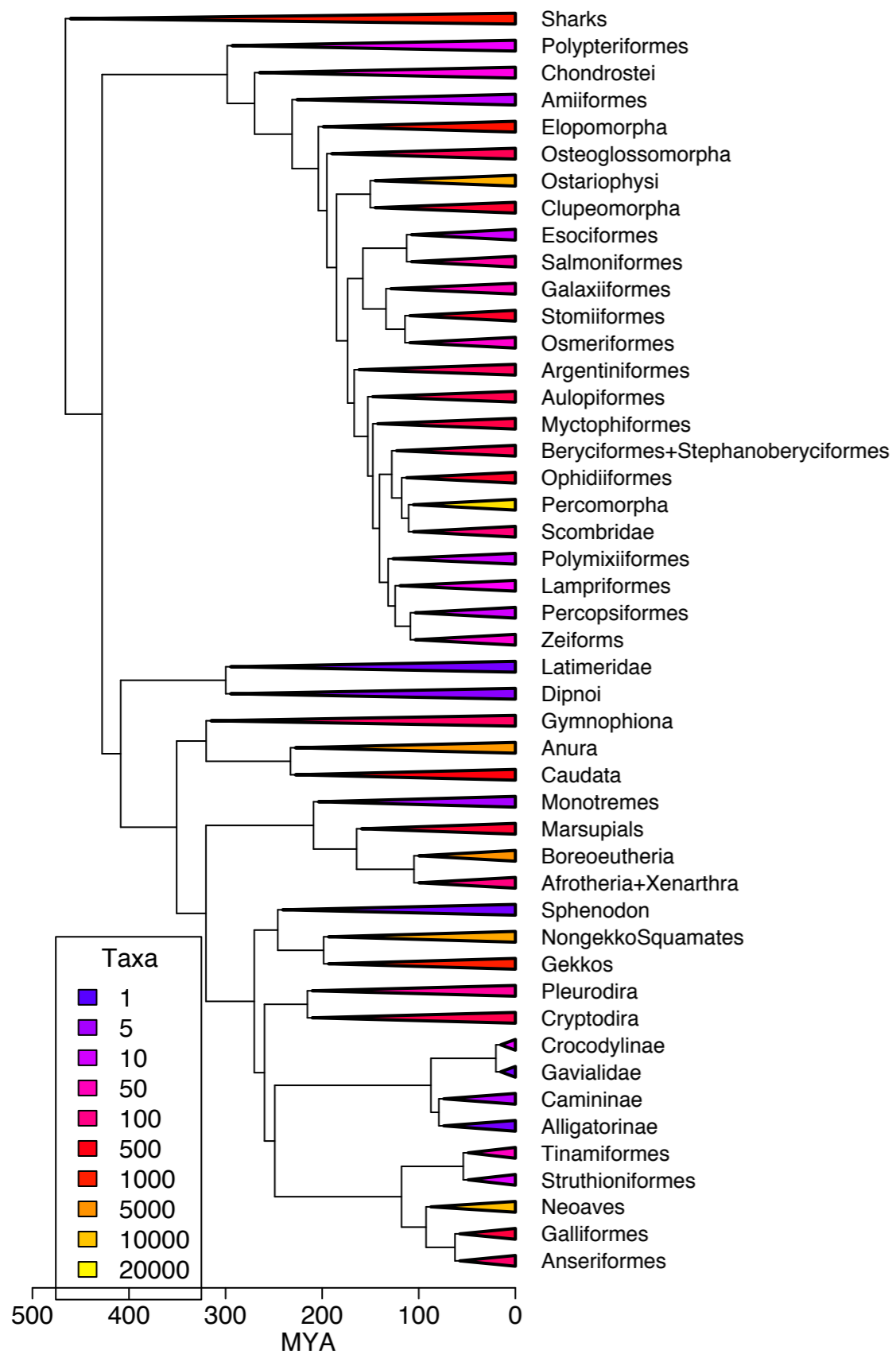




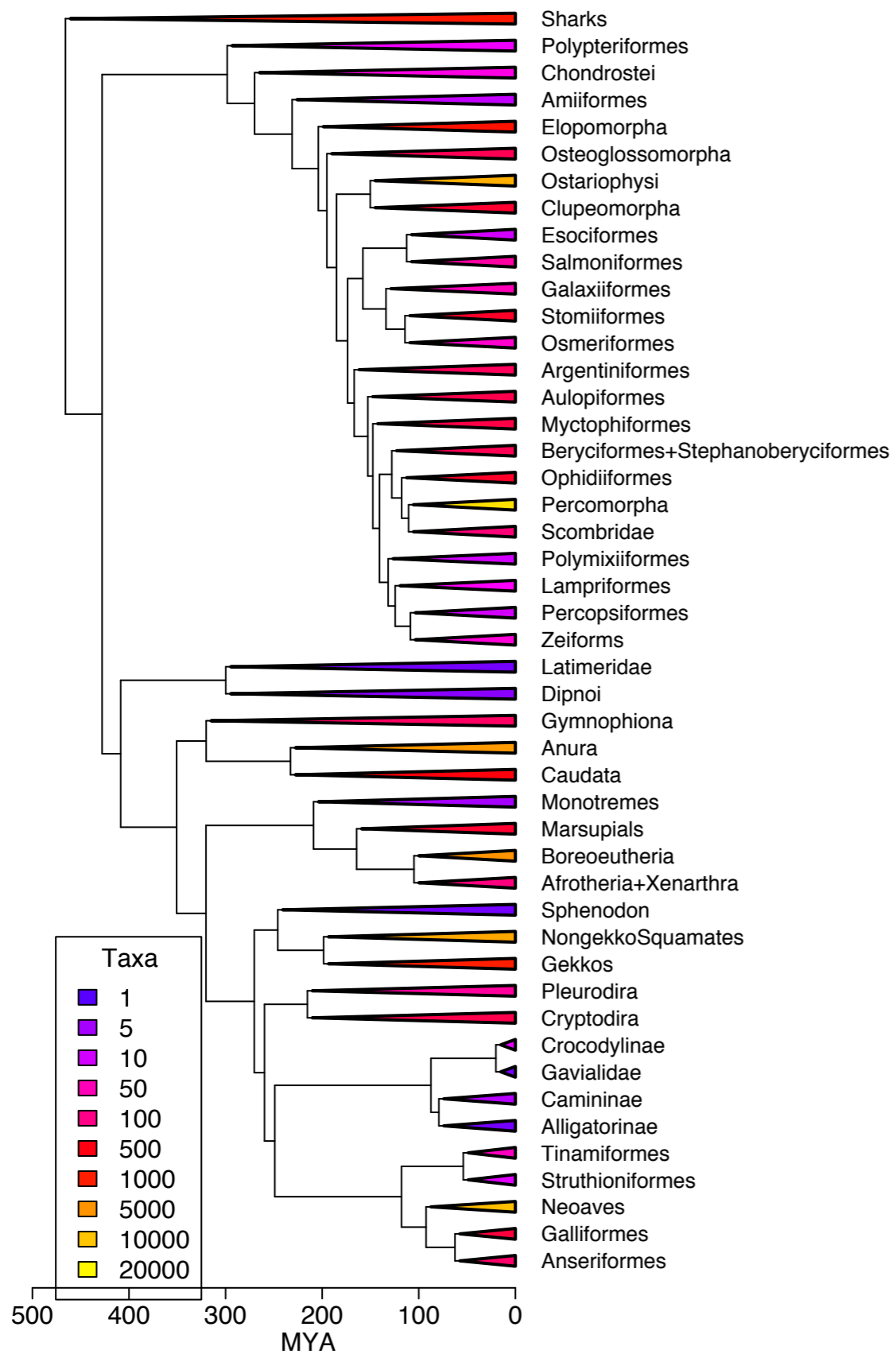


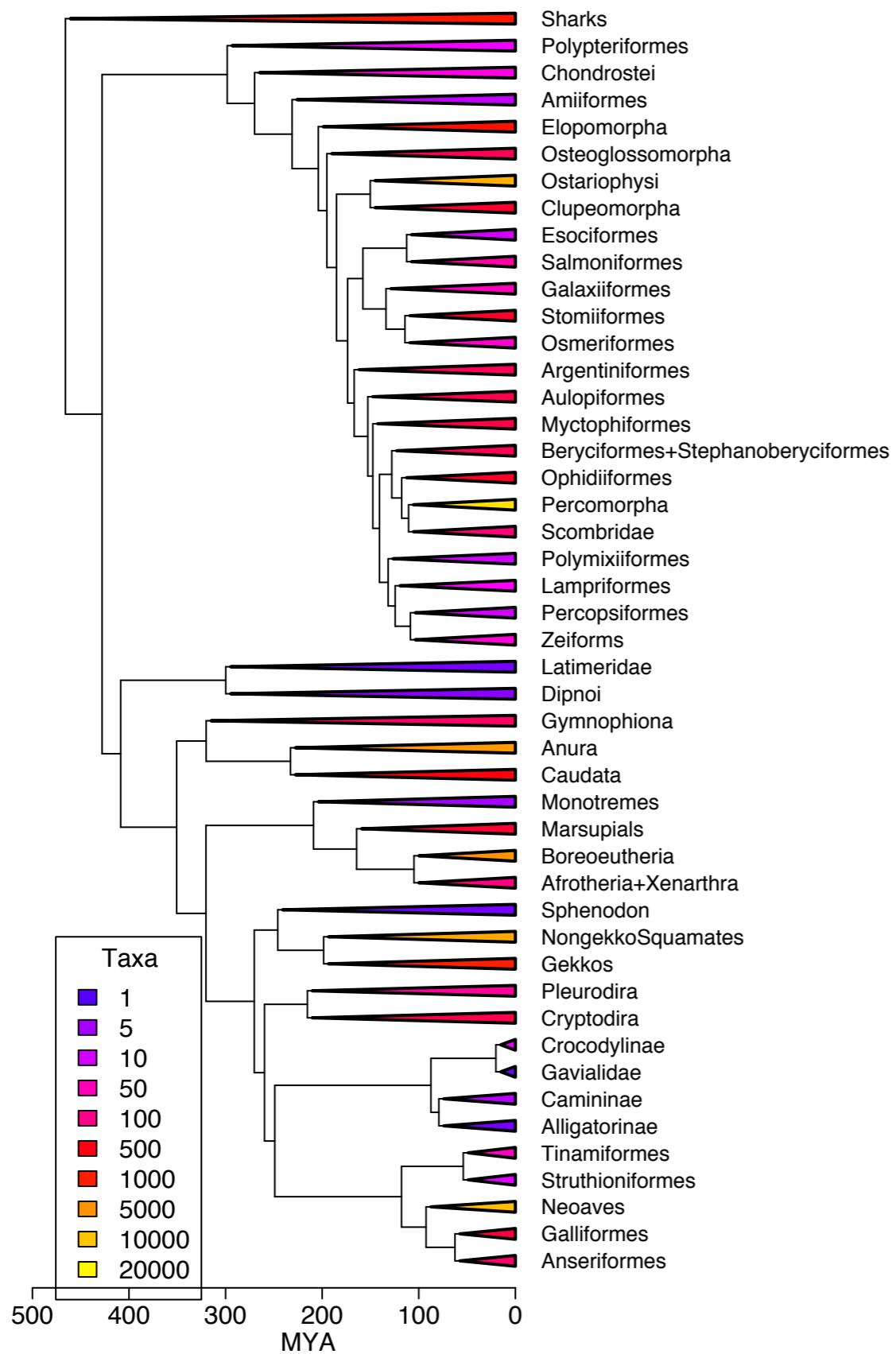
# NOT TYPICAL



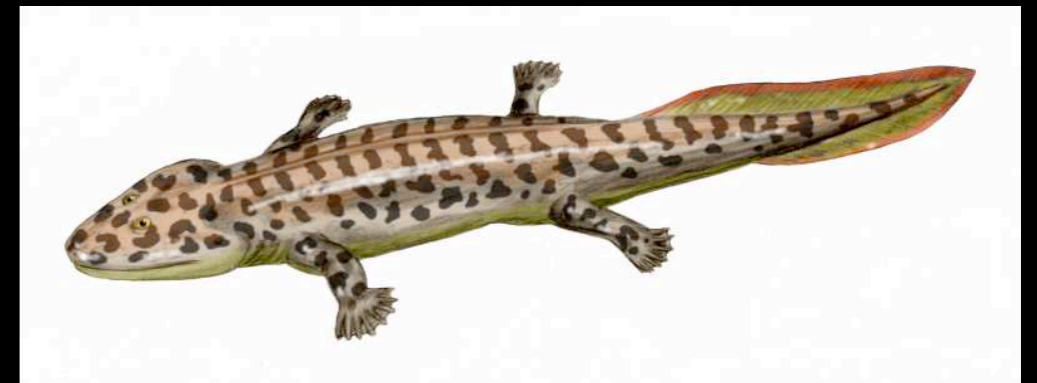
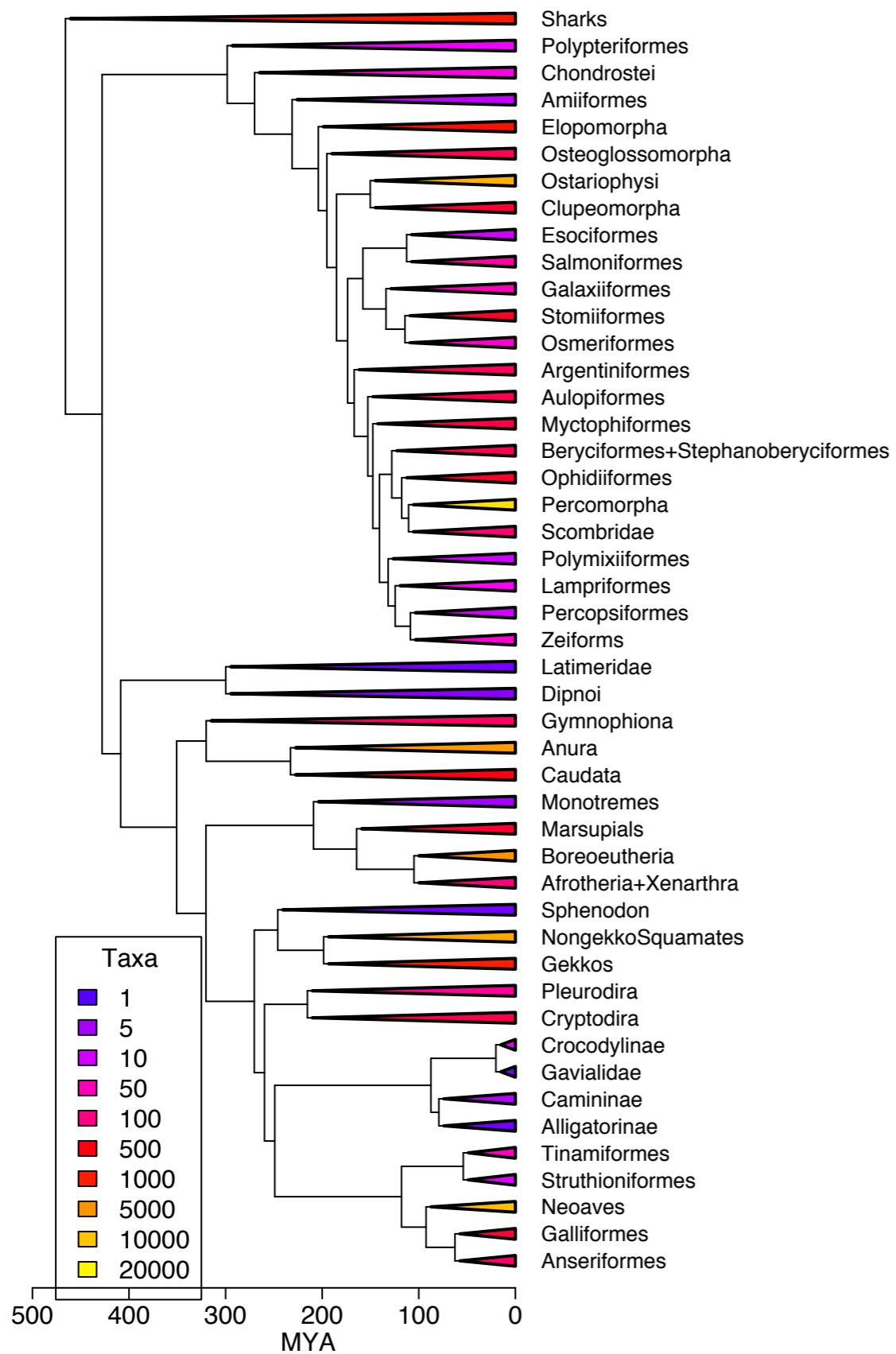


More common to have  
 incomplete trees  
 where tips represent  
 unsampled clades



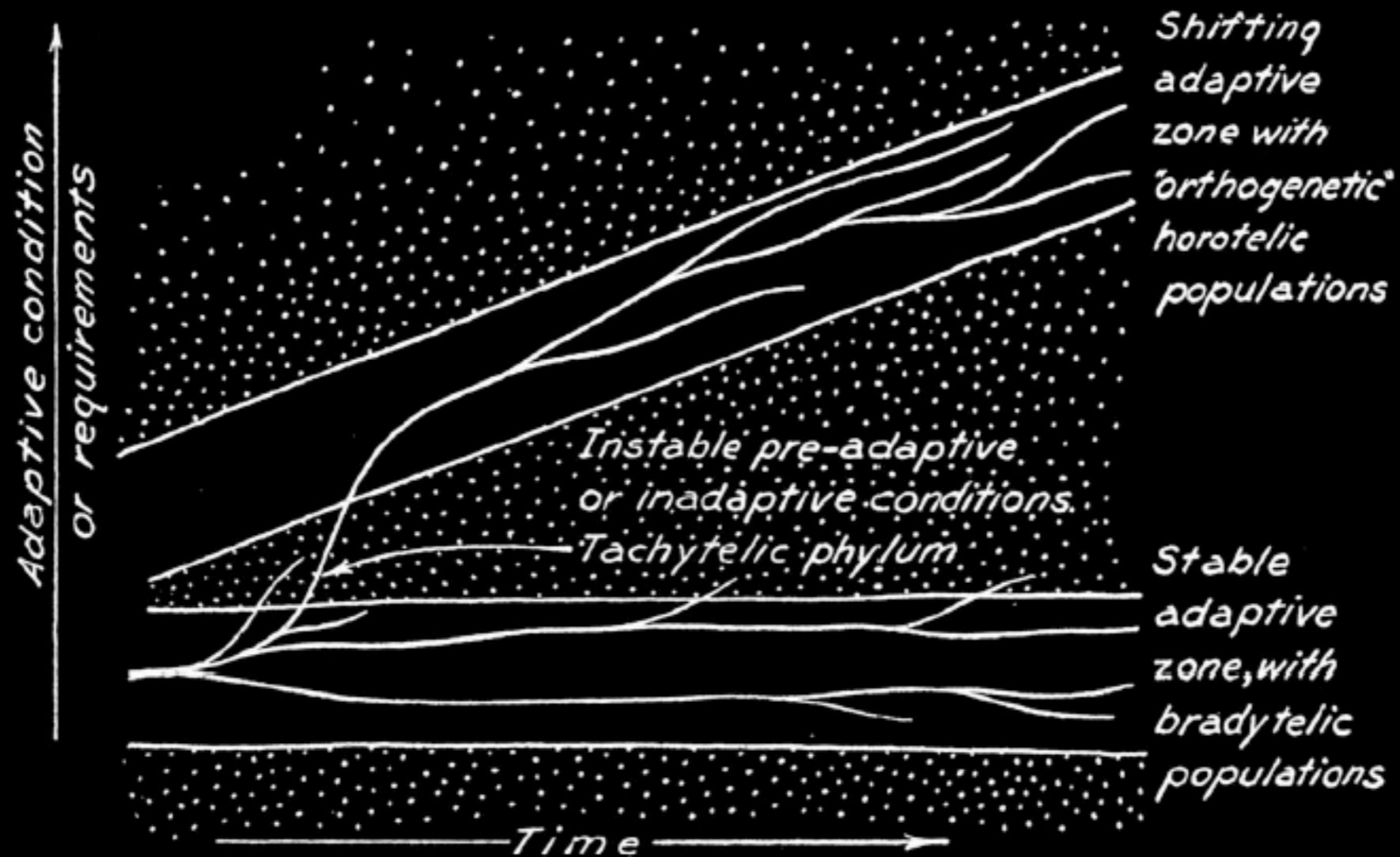






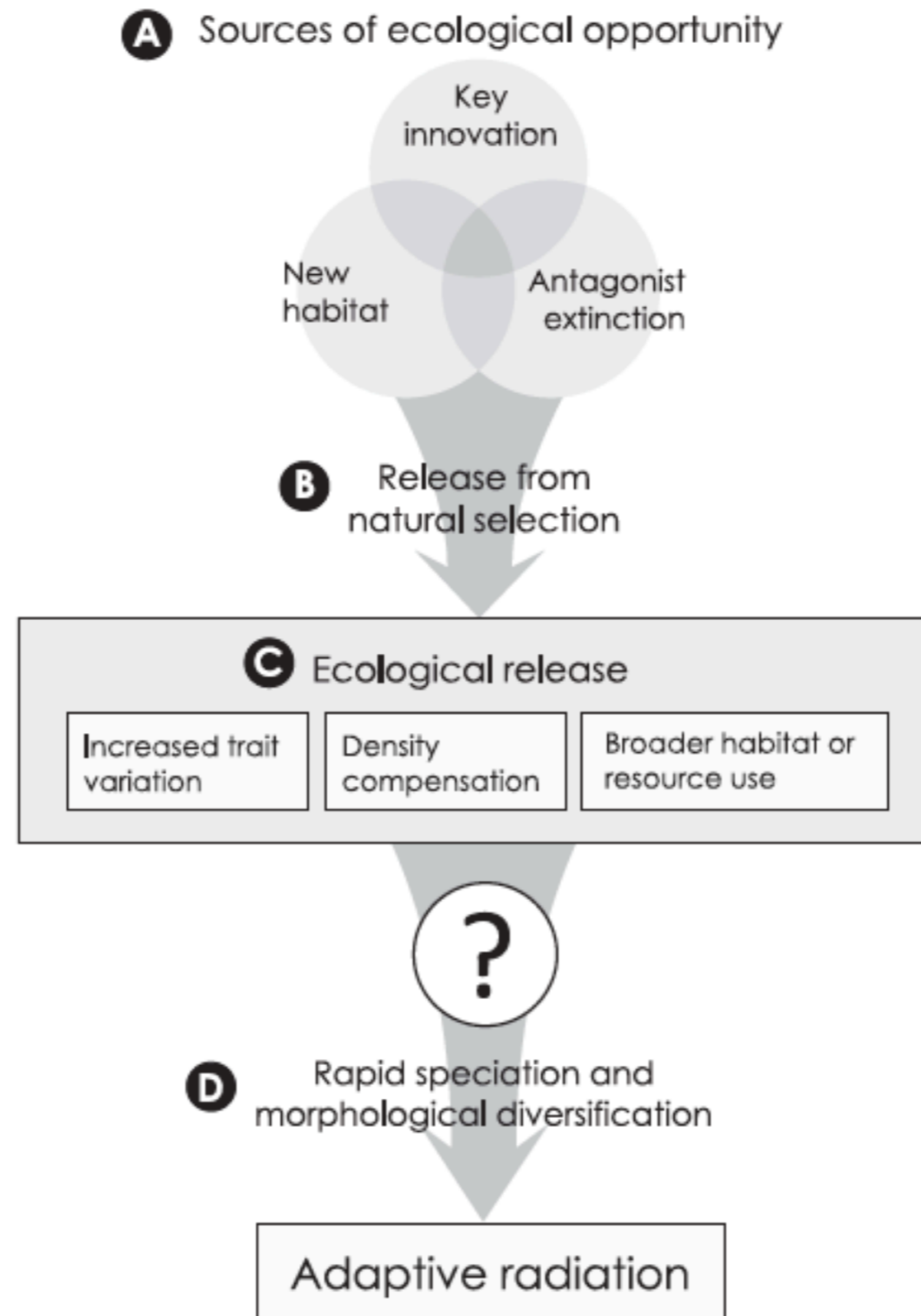
What do people really want to know?

# Adaptive Radiation



Simpson 1953

# Yoder et al. 2010

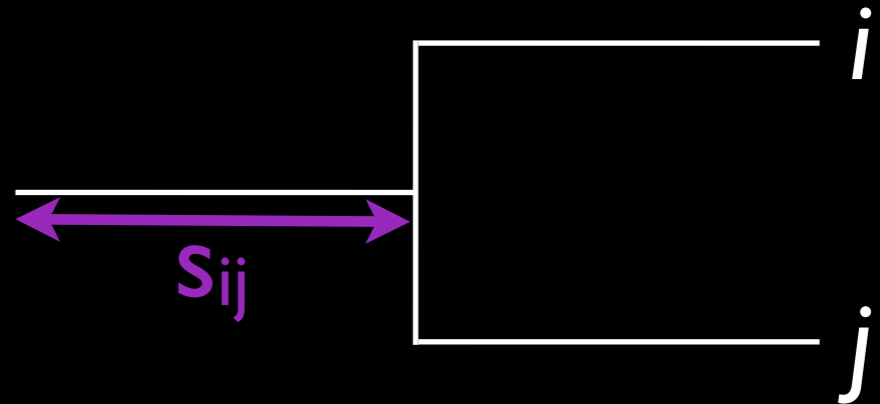


# Brownian motion

- Two parameters: starting value ( $\mu$ ) and rate ( $\sigma^2$ )

$$dX(t) = \sigma dB(t)$$

$$V_{ij} = \sigma^2 s_{ij}$$



No current comparative methods  
look very much like Simpson's vision!



# Goal:

- Create methods that analyze the data that people **actually have** to estimate things that they **really want to know**

# Three vignettes

- Fossil MEDUSA
- Reversible-jump MCMC
- MECCA

# Three vignettes

- Fossil MEDUSA
- Reversible-jump MCMC
- MECCA



Joseph Brown  
Harmon lab post-doc

# Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates

Michael E. Alfaro<sup>a,1</sup>, Francesco Santini<sup>a</sup>, Chad Brock<sup>b</sup>, Hugo Alamillo<sup>b</sup>, Alex Dornburg<sup>c</sup>, Daniel L. Rabosky<sup>d,e</sup>, Giorgio Carnevale<sup>f</sup>, and Luke J. Harmon<sup>g</sup>

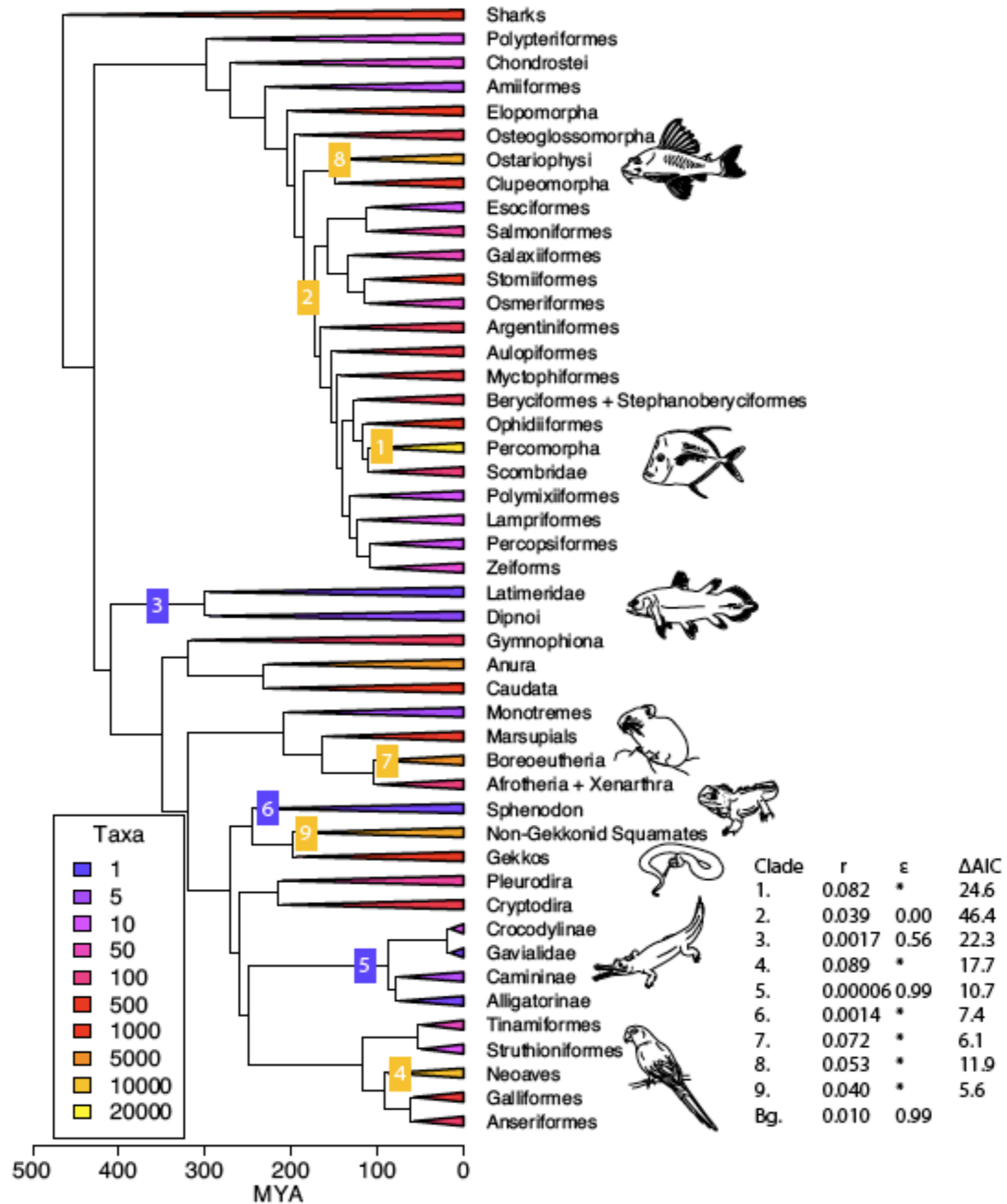
<sup>a</sup>Department of Ecology and Evolutionary Biology, University of California, Los Angeles, CA 90095; <sup>b</sup>School of Biological Sciences, Washington State University, Pullman, WA 99164; <sup>c</sup>Department of Ecology and Evolutionary Biology and <sup>d</sup>Cornell Laboratory of Ornithology, Cornell University, Ithaca, NY 14850; <sup>f</sup>Dipartimento di Scienze della Terra and Museo di Storia Naturale e del Territorio, Università di Pisa, Pisa, 56100 Italy; <sup>g</sup>Department of Biology, University of Idaho, Moscow, ID 83843; and <sup>e</sup>Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520

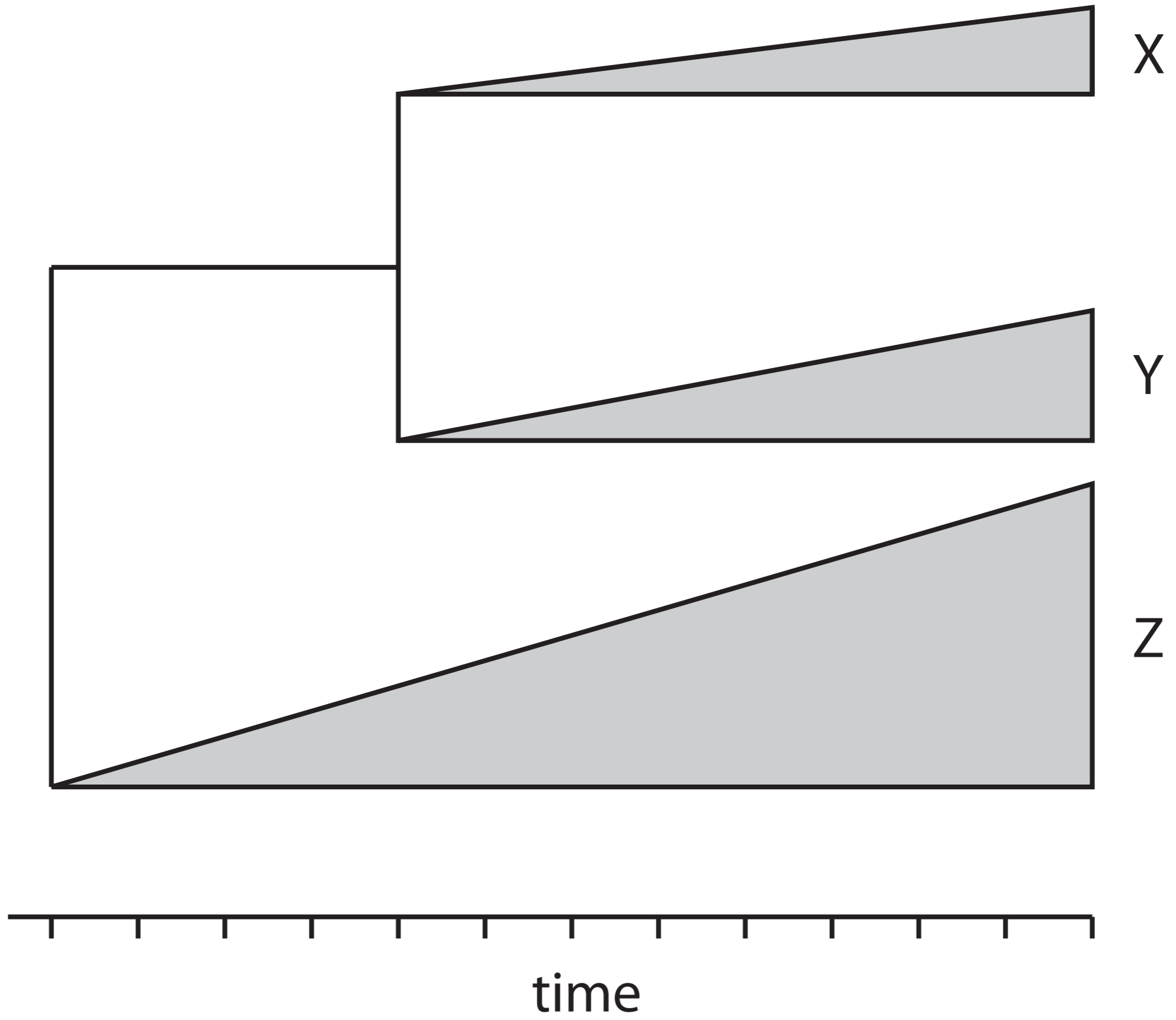
Edited by David M. Hillis, University of Texas, Austin, TX, and approved June 12, 2009 (received for review November 2, 2008)

The uneven distribution of species richness is a fundamental and unexplained pattern of vertebrate biodiversity. Although species richness in groups like mammals, birds, or teleost fishes is often attributed to accelerated cladogenesis, we lack a quantitative conceptual framework for identifying and comparing the exceptional changes of tempo in vertebrate evolutionary history. We develop MEDUSA, a stepwise approach based upon the Akaike information criterion for detecting multiple shifts in birth and death rates on an incompletely resolved phylogeny. We apply MEDUSA incompletely to a diversity tree summarizing both evolutionary relationships and species richness of 44 major clades of jawed vertebrates. We identify 9 major changes in the tempo of gnathostome diversification; the most significant of these lies at

Comparative methods like SymmeTREE (10, 11) are an exception to some degree, because they can deal with missing taxa through random resolution of tip clades. However, this approach quickly becomes impractical as the number of unsampled taxa grows.

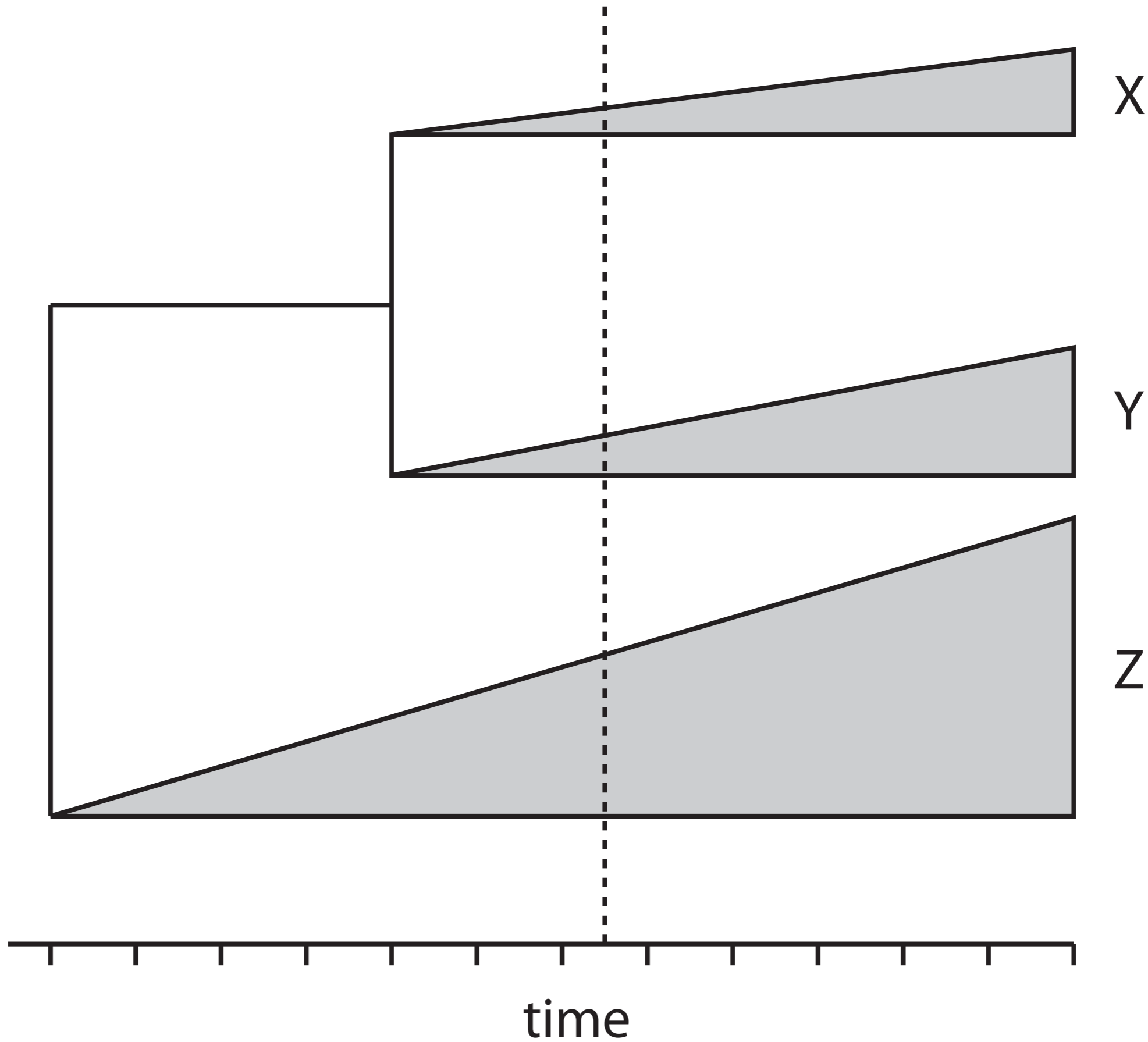
Here, we analyze a phylogenetic dataset with exemplars of 47 major vertebrate lineages using a comparative method that integrates both phylogenetic and taxonomic information to ask two general questions about the patterns of diversification across the vertebrate tree of life: (i) What is the background tempo of vertebrate diversification; and (ii) which, if any, vertebrate lineages have patterns of extant richness that are too species-rich or -poor to be outcomes of the background diversification rate?



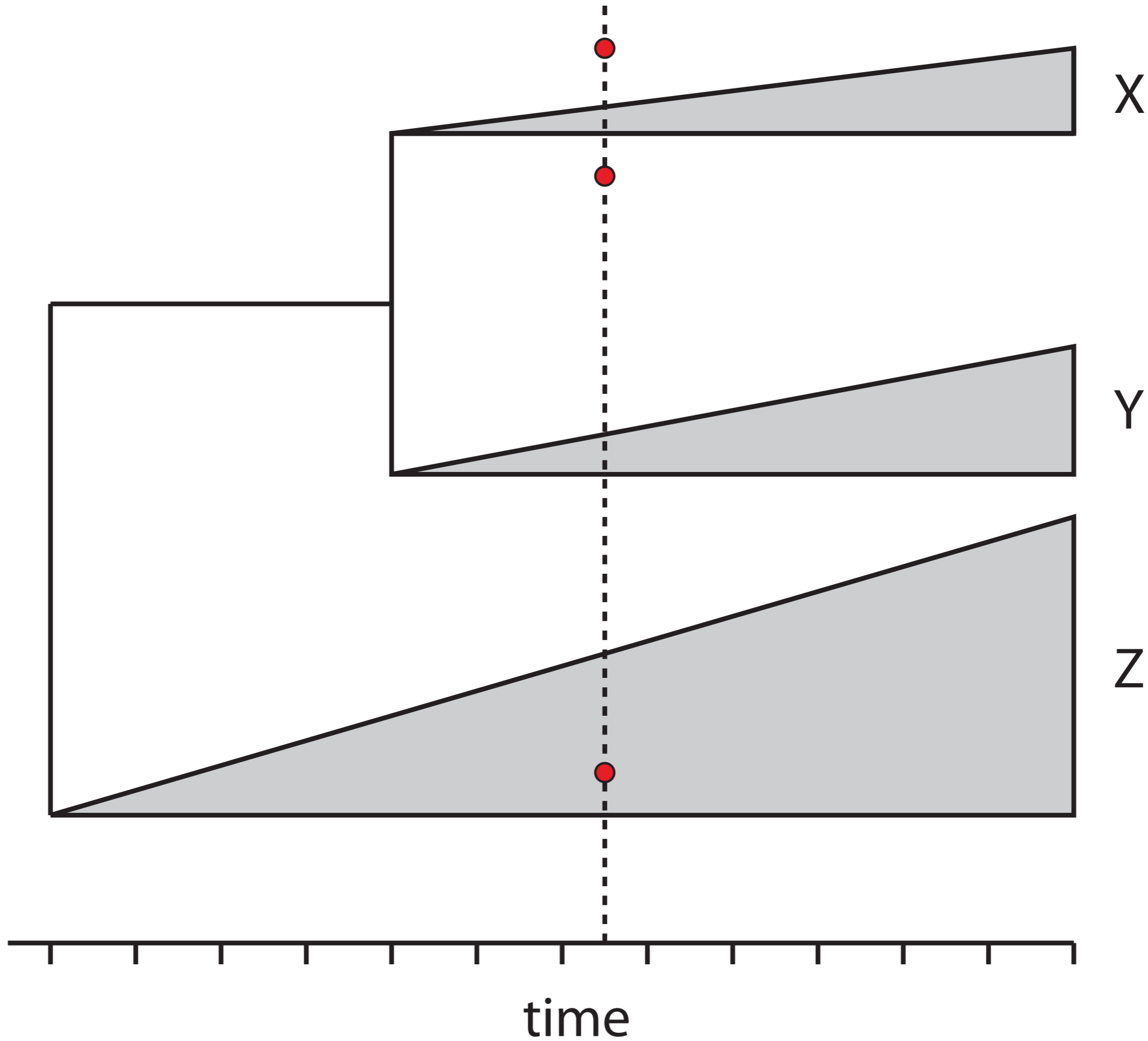




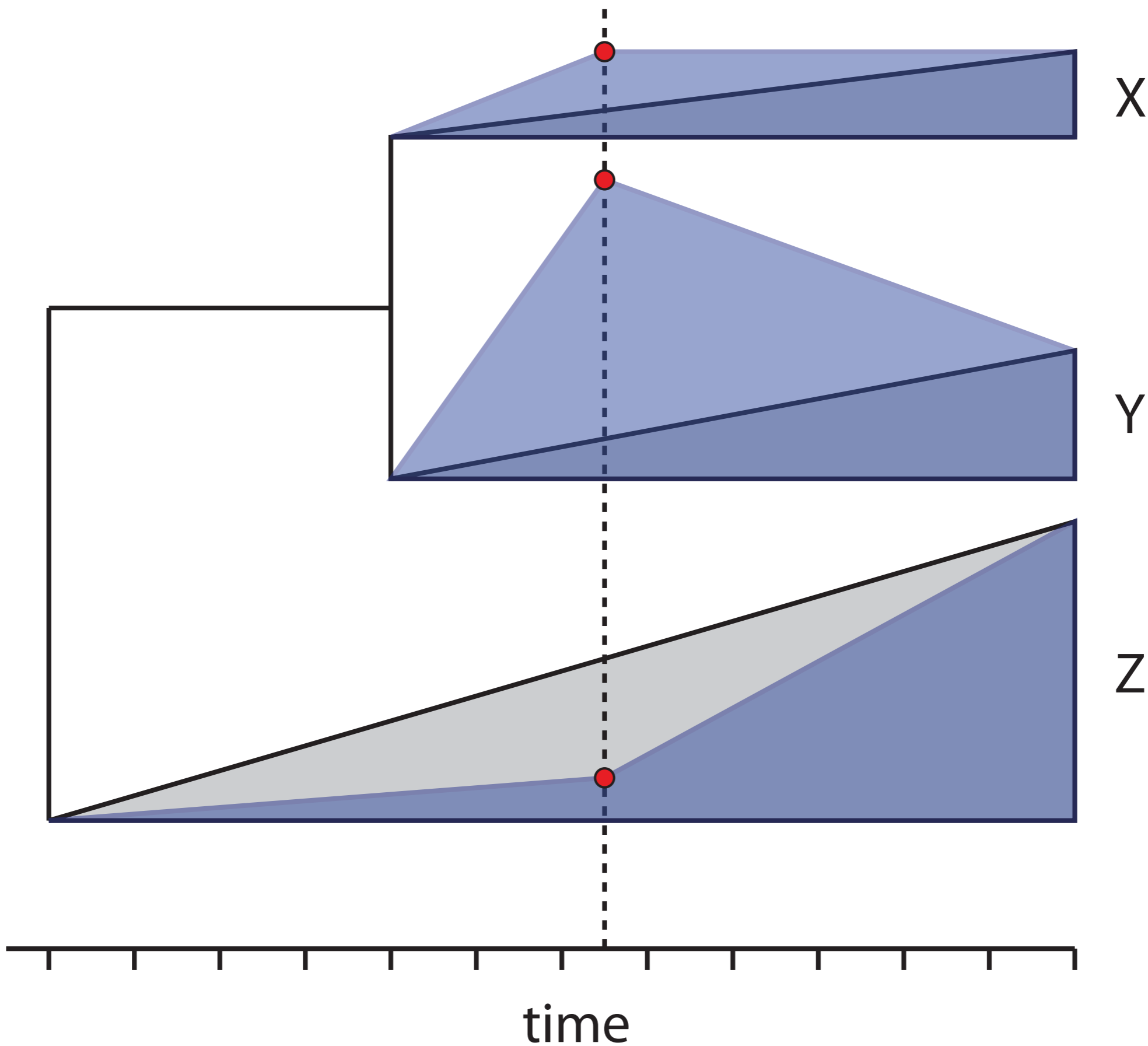
Taking a time-slice...



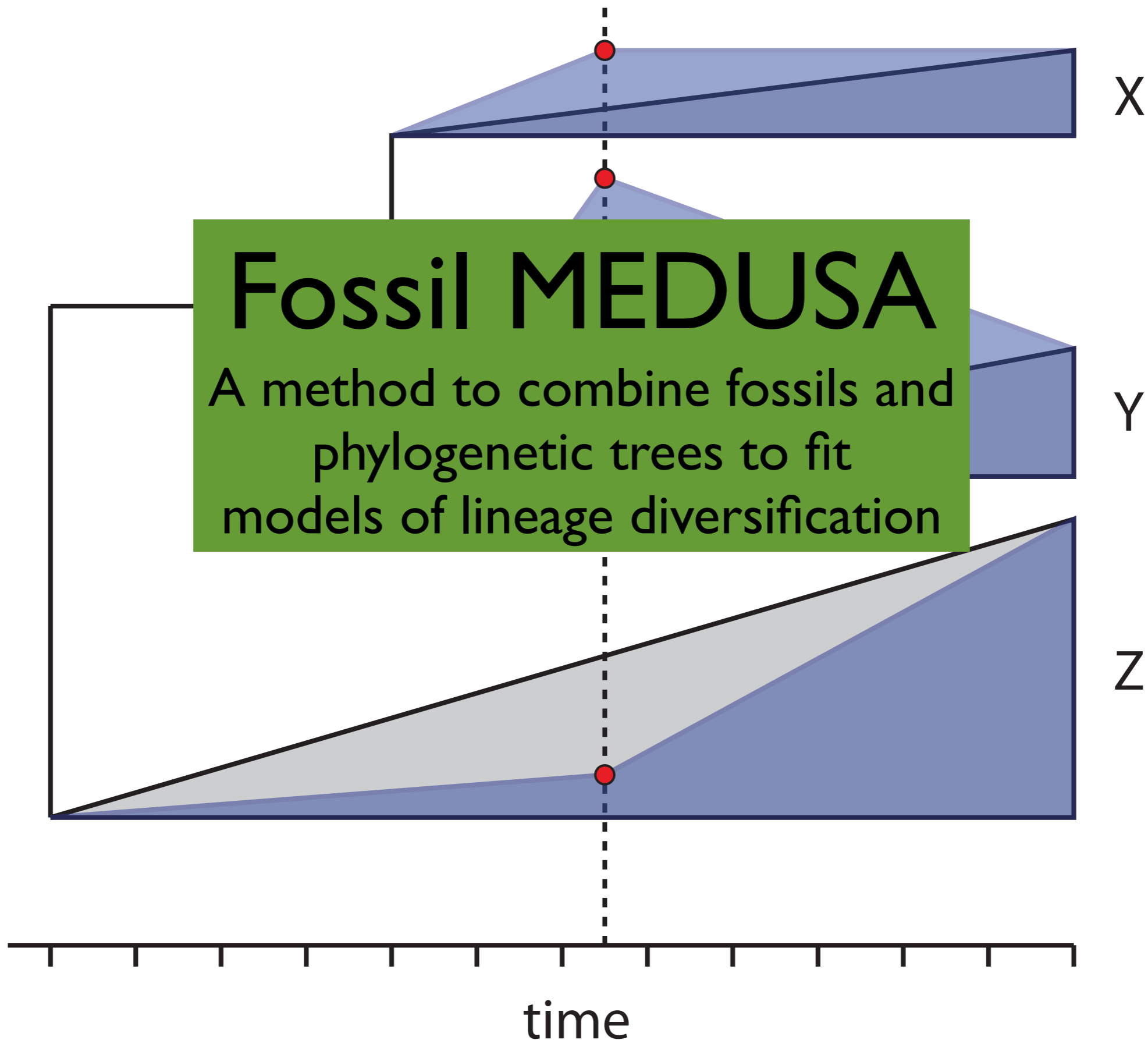
...of fossil richness...



...can reveal diversification dynamics unobservable from molecular phylogenies.



...can reveal diversification dynamics unobservable from molecular phylogenies.



# FOSSIL MEDUSA



- Fit piecewise birth-death models:
  1. Without fossil information
  2. Assuming fossil richnesses as exact
  3. Treating fossil counts as minimum richnesses

# Three vignettes

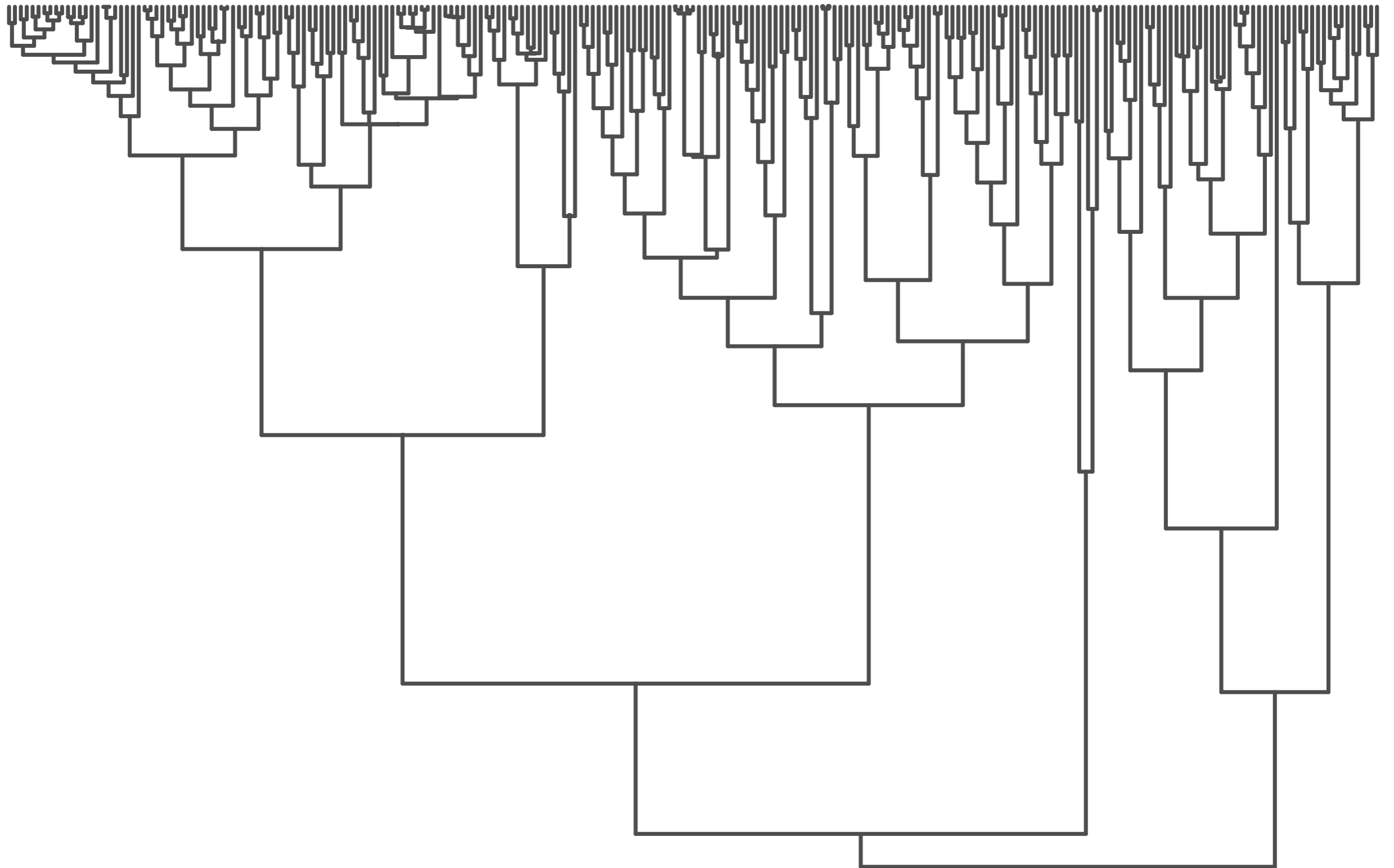
- Fossil MEDUSA
- Reversible-jump MCMC
- MECCA



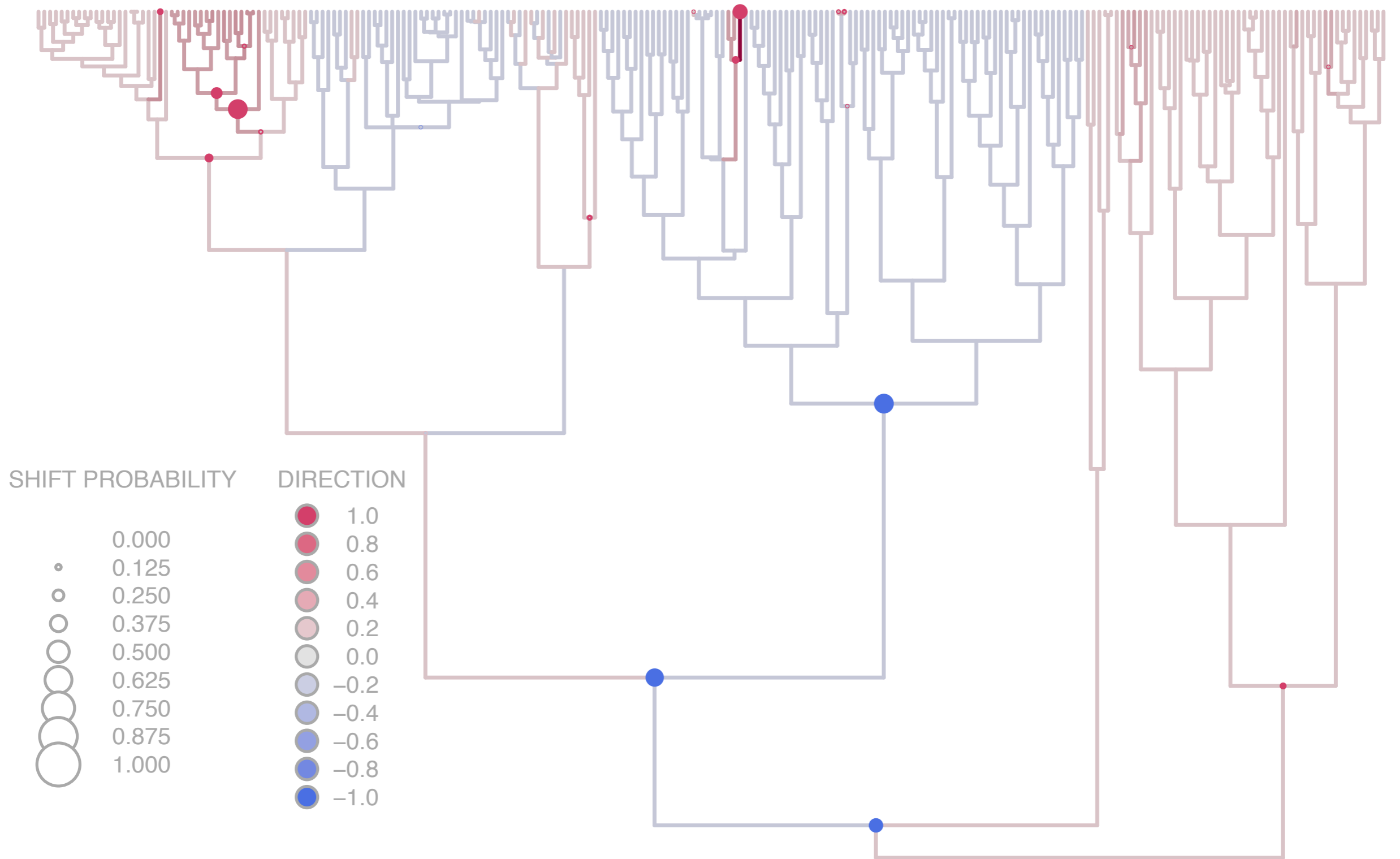
Jon Eastman  
Harmon lab post-doc



# PRIMATES



# PRIMATES



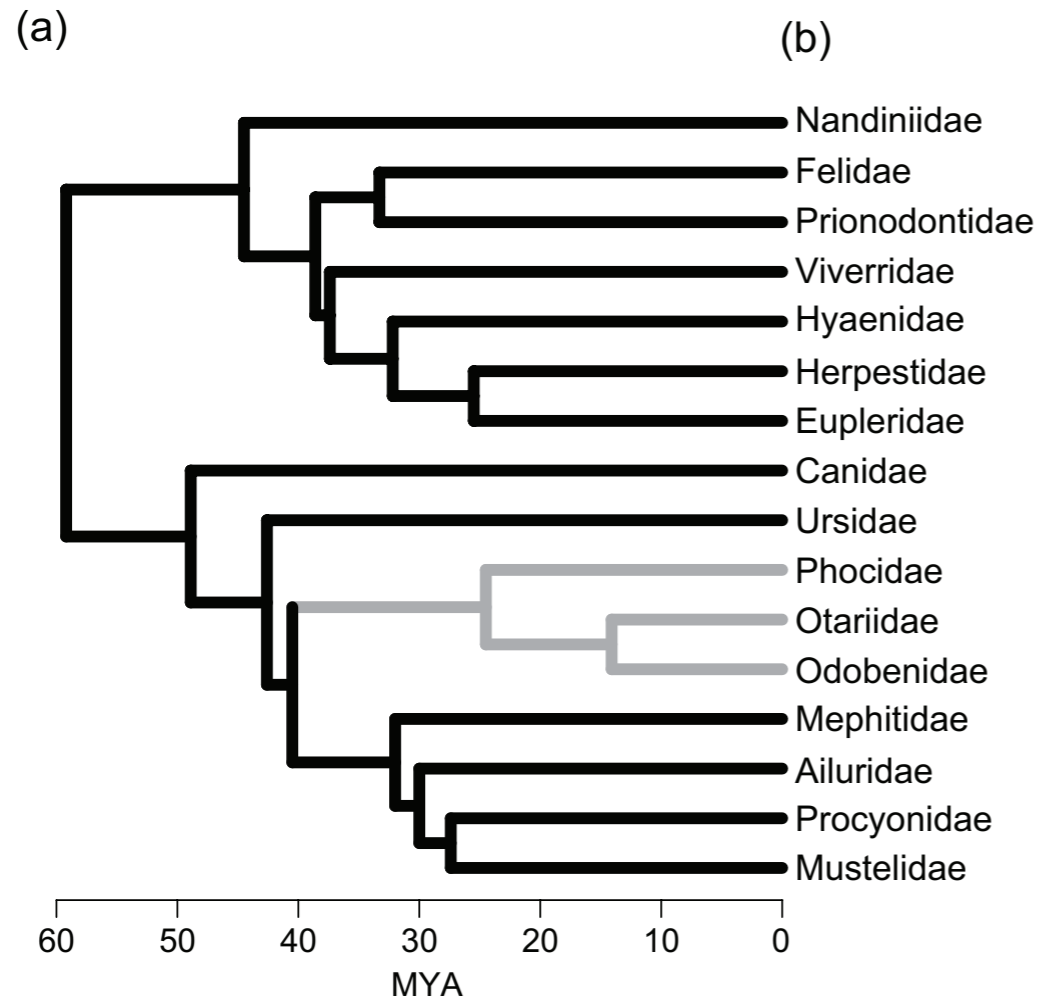




# Three vignettes

- Fossil MEDUSA
- Reversible-jump MCMC
- MECCA

# Data on body size in carnivores



Family	richness	mean log(g)	variance	sample size
Nandiniidae	1	7.68	0	1
Felidae	40	9.18	1.59	33
Prionodontidae	2	6.78	0.13	2
Viverridae	34	7.89	0.66	27
Hyaenidae	4	10.30	0.80	4
Herpestidae	33	7.18	0.48	29
Eupleridae	8	7.24	0.92	8
Canidae	35	8.58	0.68	32
Ursidae	8	11.75	0.30	8
Phocidae	19	12.24	0.75	19
Otariidae	16	11.69	0.38	14
Odobenidae	1	13.86	0	1
Mephitidae	12	7.26	0.57	10
Ailuridae	1	8.55	0	1
Procyonidae	14	7.65	0.53	13
Mustelidae	59	7.45	2.26	49

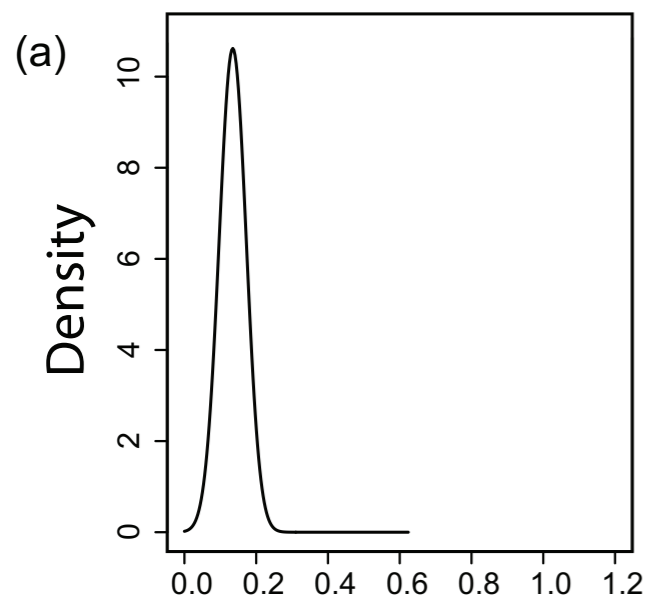


# MECCA

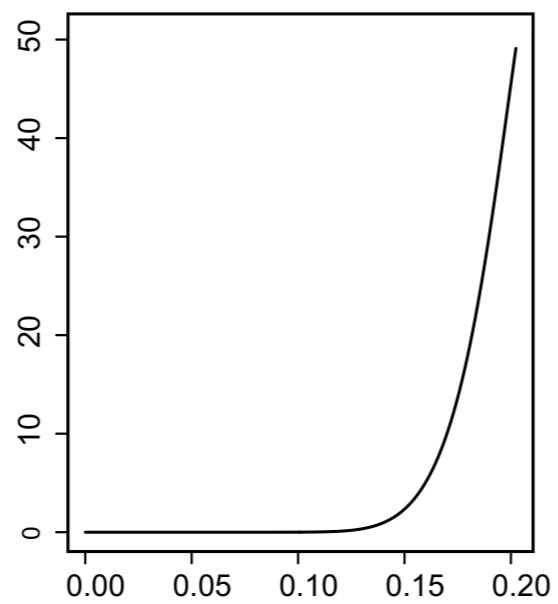
- Modeling evolution of continuous characters using ABC
- ABC = approximate Bayesian computation
- ABC is a method for calculating Bayesian posterior distributions **WITHOUT** likelihoods

# MECCA

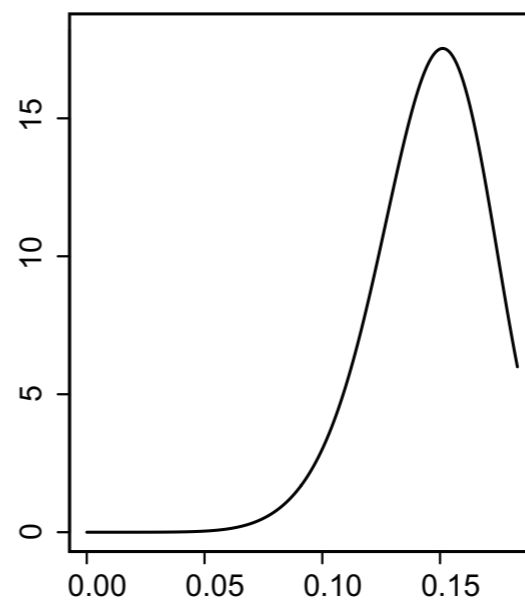
- We assume:
  - Trees grow under a birth-death model (parameters:  $\lambda$ ,  $\mu$ )
  - Traits evolve by Brownian motion (parameters:  $\sigma^2$ ,  $\theta$ )
- Use ABC to calculate posterior distribution of all four parameters given priors & the data



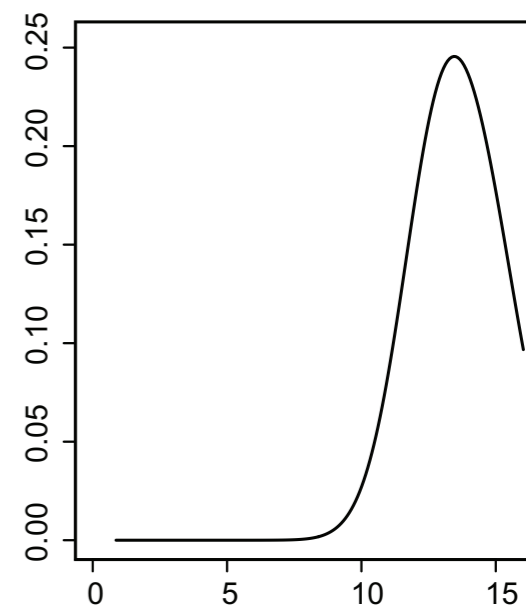
$\sigma^2$



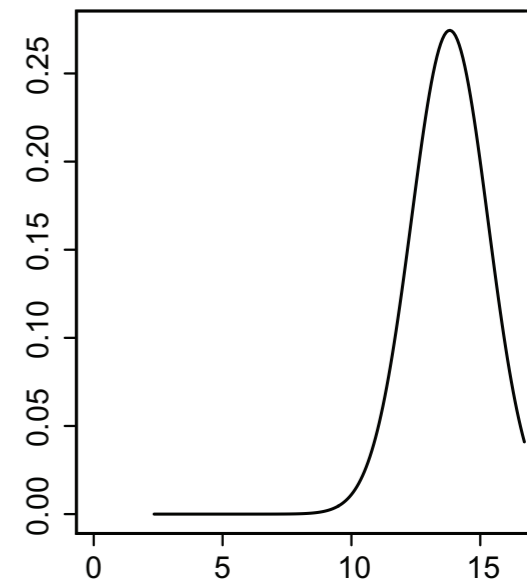
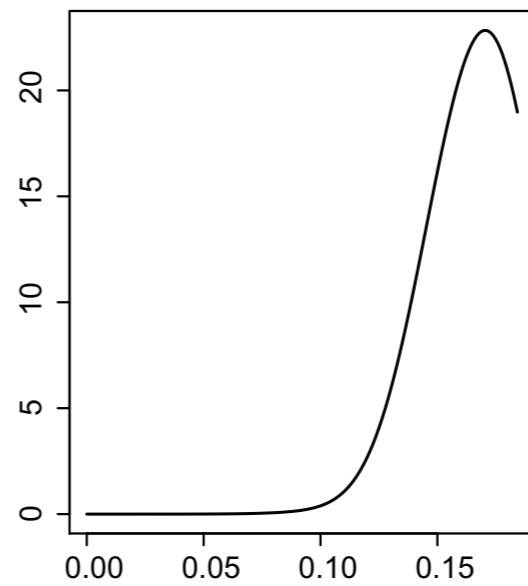
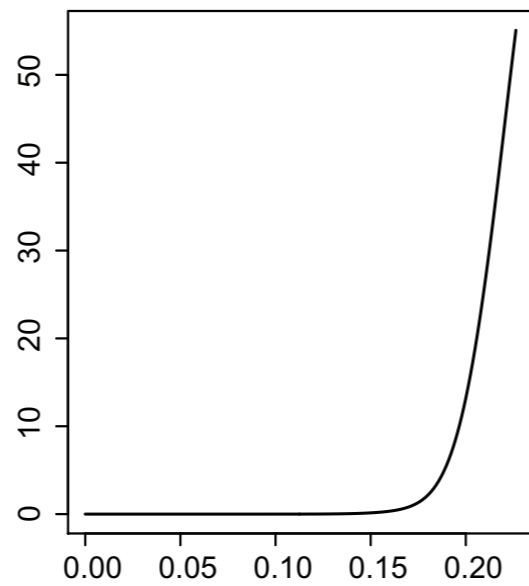
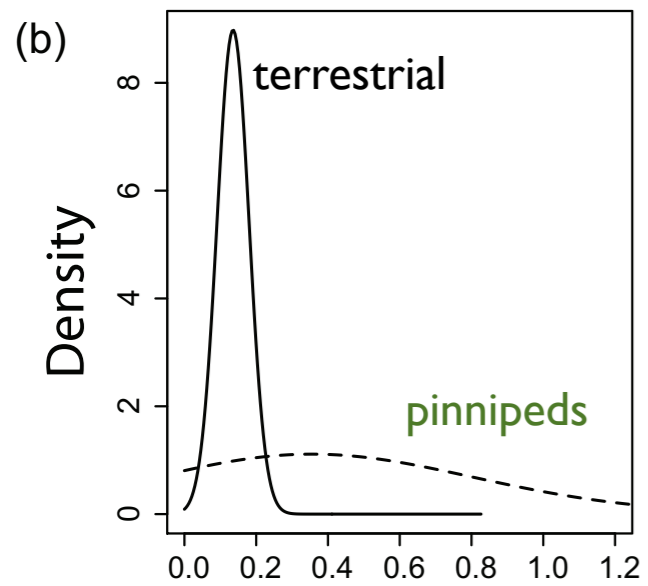
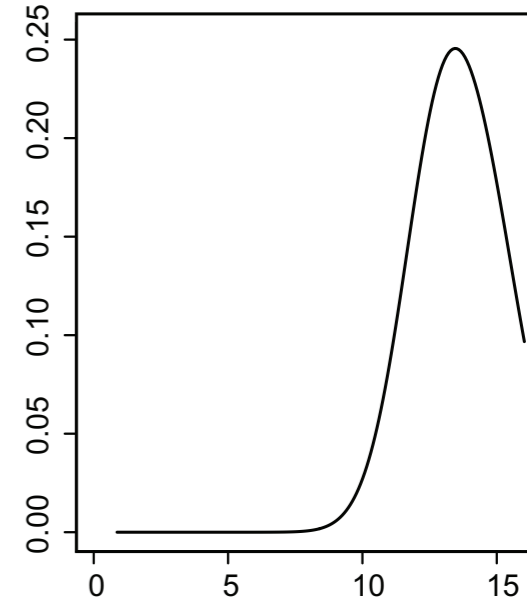
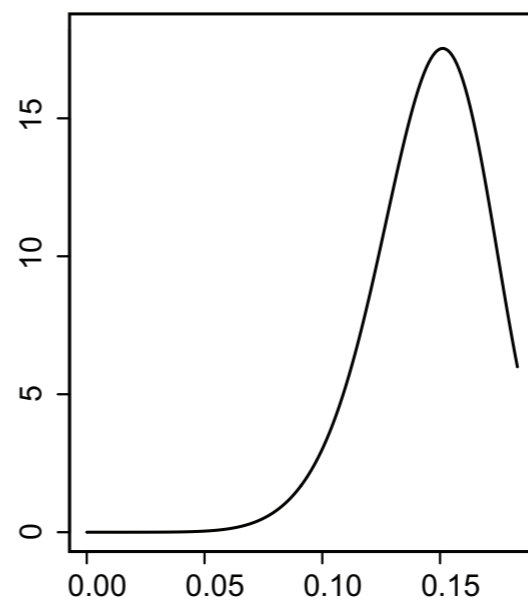
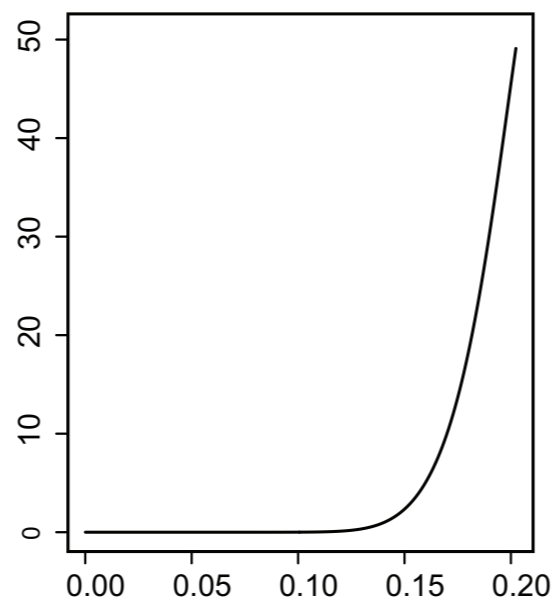
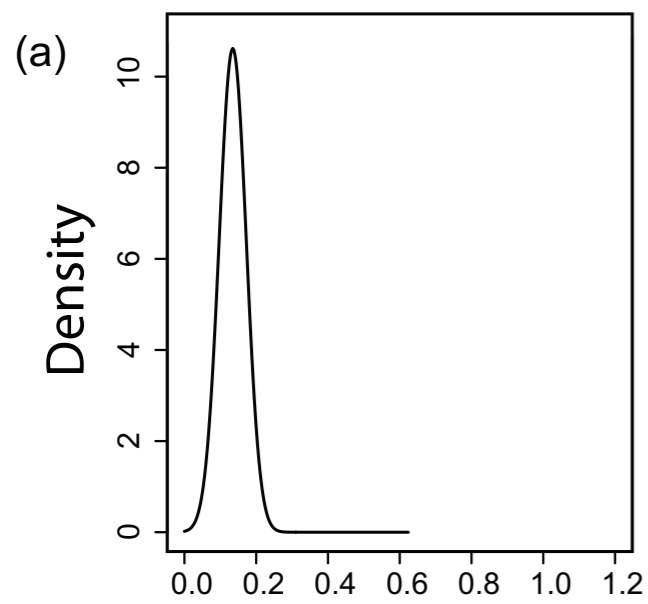
$\lambda$



$\mu$



$\theta$

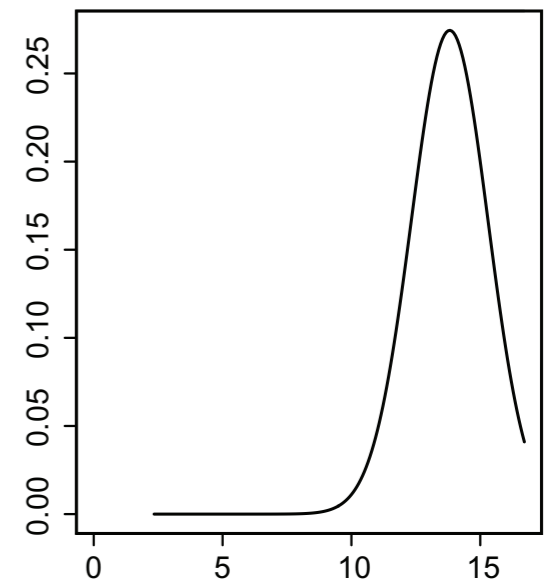
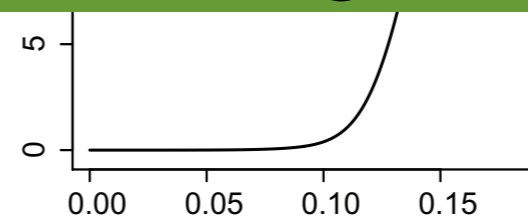
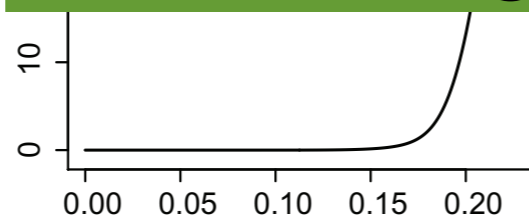
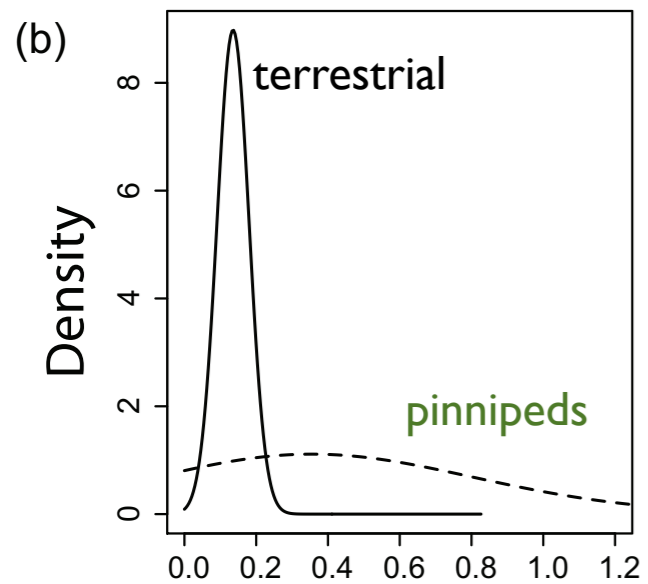
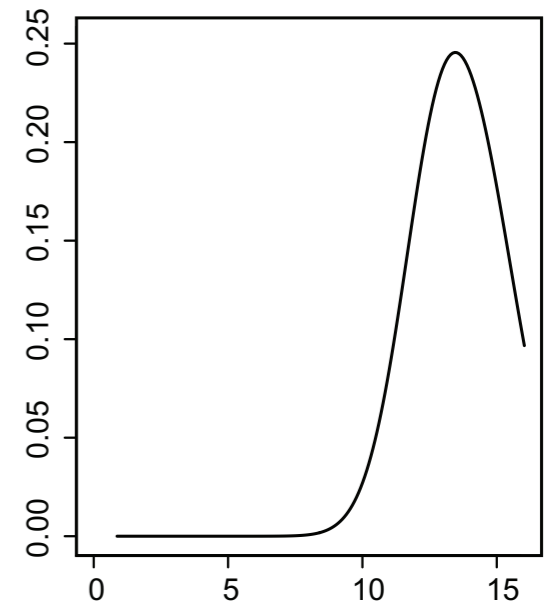
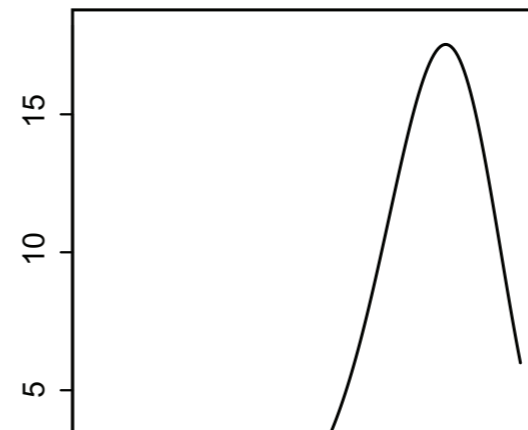
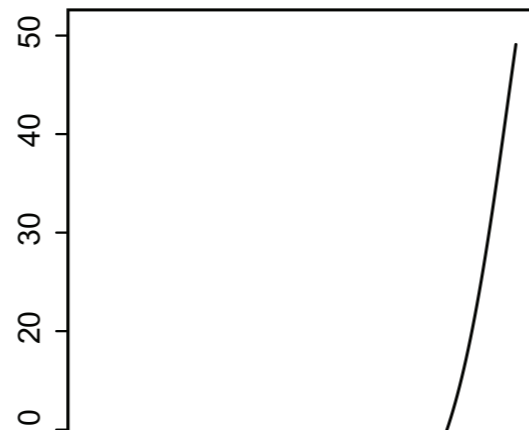
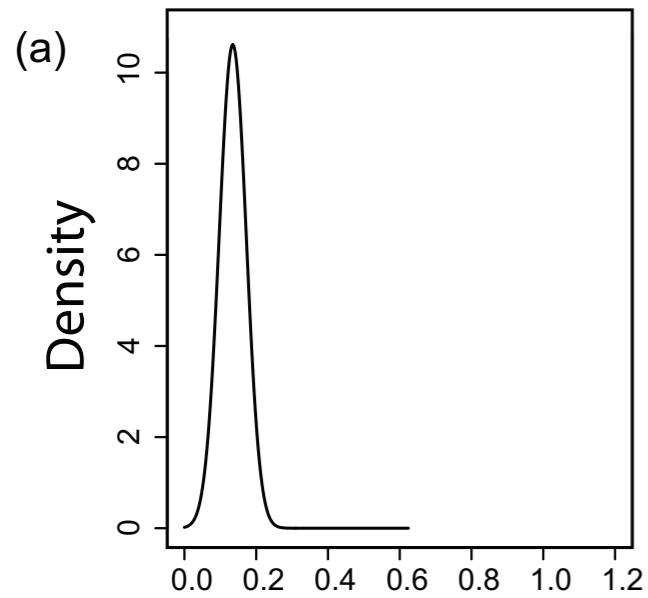


$\sigma^2$

$\lambda$

$\mu$

$\theta$



**MECCA**

Can fit models of lineage diversification and character evolution together using ABC

$\sigma^2$

$\lambda$

$\mu$

$\theta$

# Goal:

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