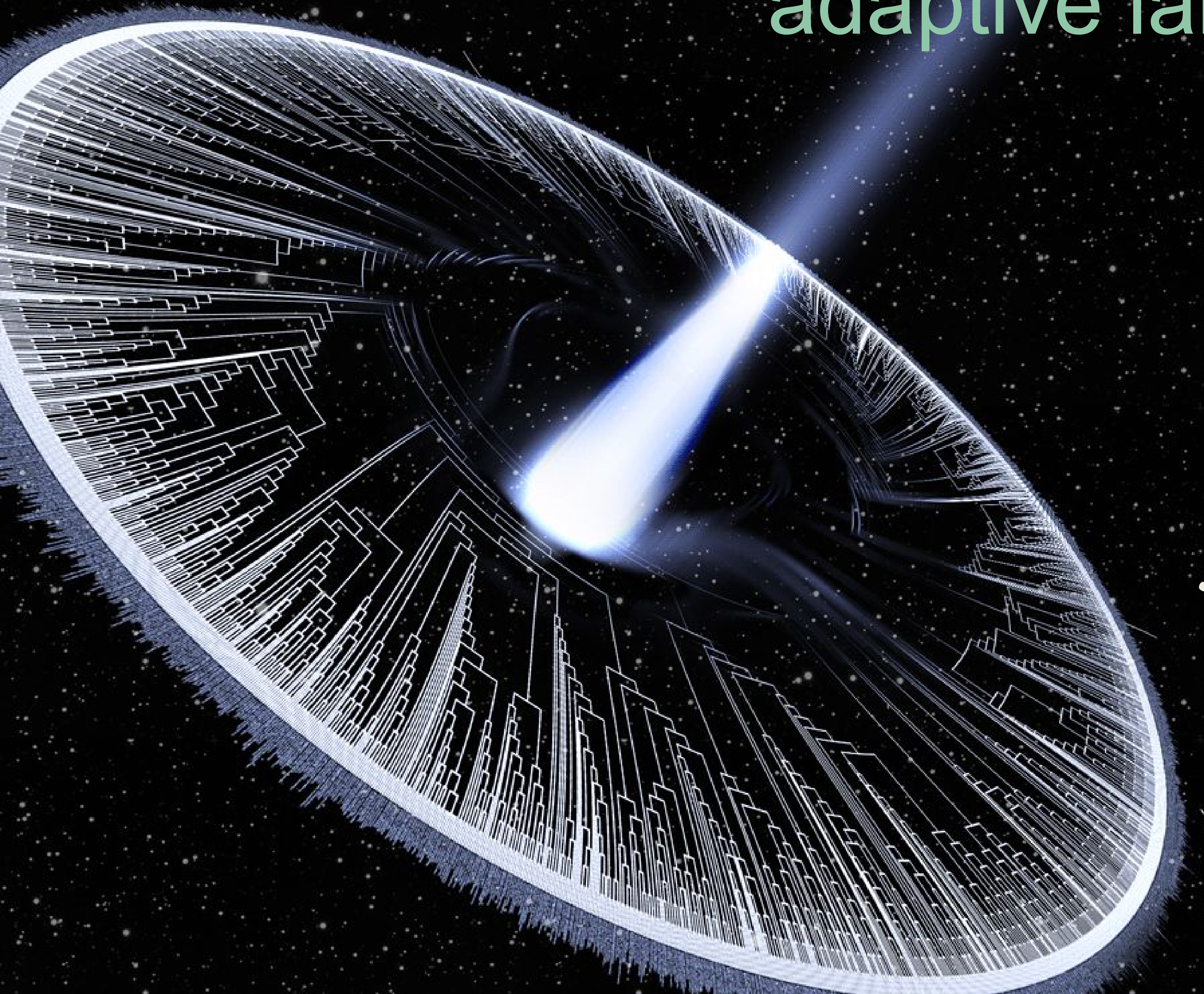
The macroevolutionary dynamics of adaptive landscapes

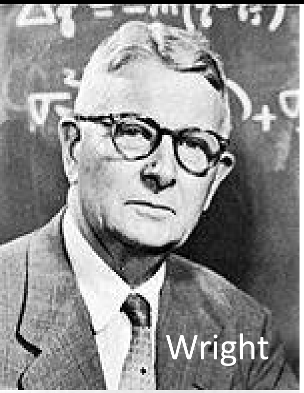


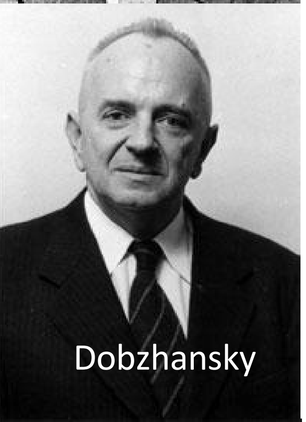
Josef C Uyeda

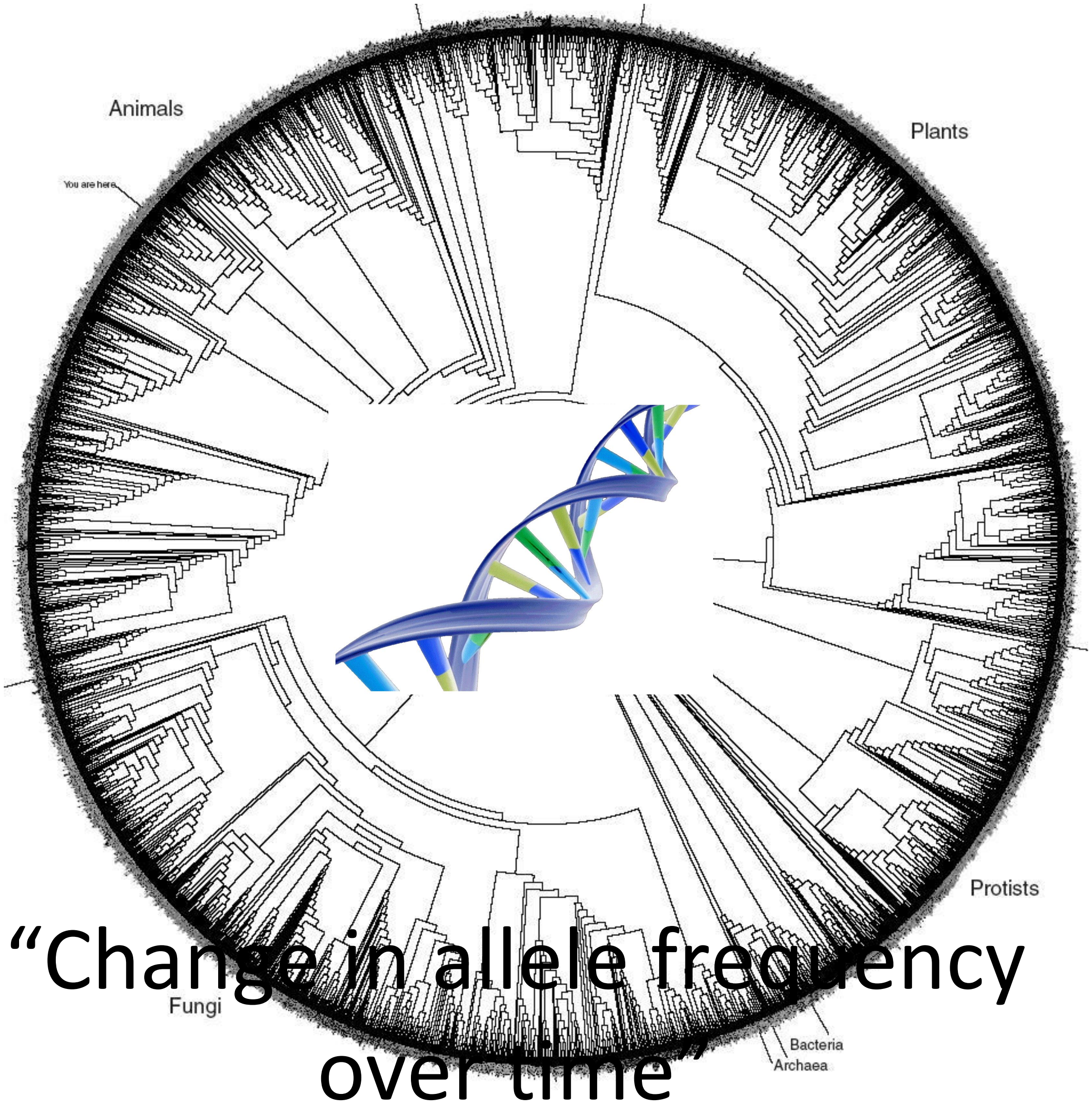
Postdoctoral Fellow

University of Idaho

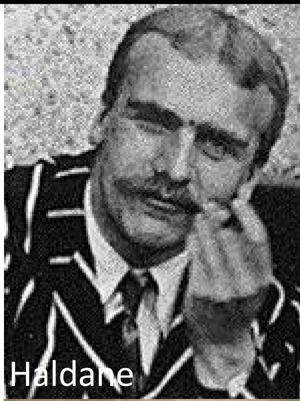
Reductionism & the Modern Synthesis

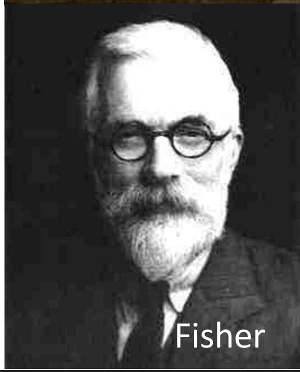






“Change in allele frequency over time”





Outline

- Are micro and macroevolution are in conflict?
- How can we study macroevolution using realistic models of adaptation and evolution?
- Using bayou

Microevolutionary patterns

We now know that we can study evolution in real time

16.06 g (1976) → 17.13 g (1978)

Response to selection

6.7% Δ body size in 1 generation (2 years)

Let's assume only 1% is evolutionary

(Grant and Grant, 2002)

Let's do the calculations:

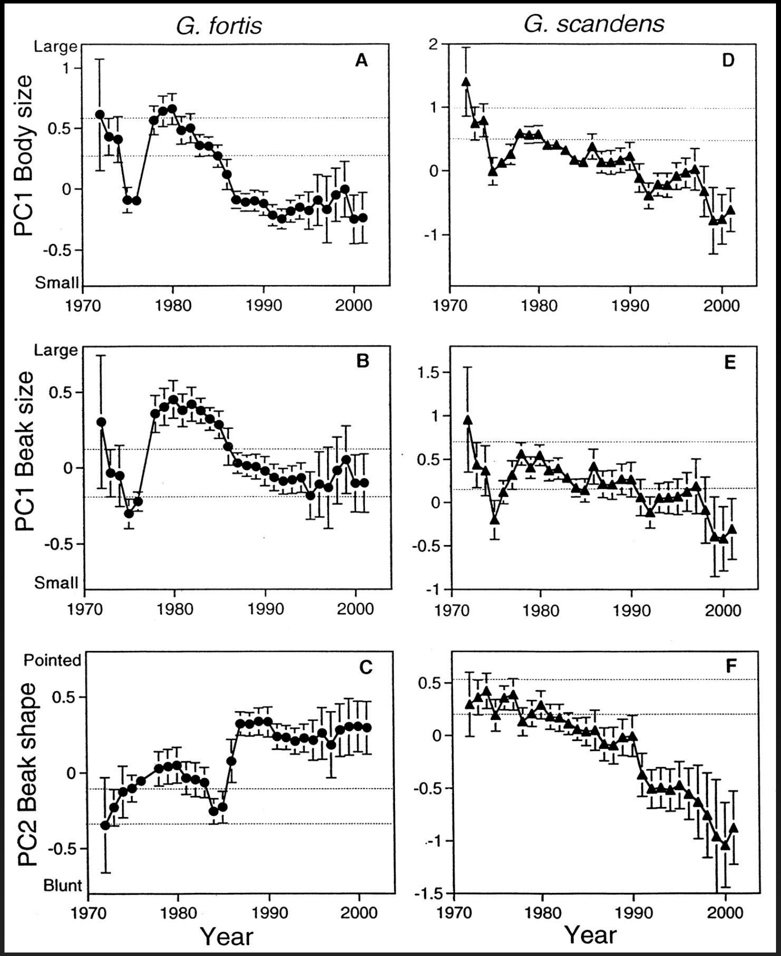
If a population increased by 1% every generation starting from ~16 g:

In 200 years →	43 g
In 500 years →	193 g
In 1,000 years →	2.3 kg
In 2,000 years →	335 kg
In 10,000 years →	6.47×10^{19} kg

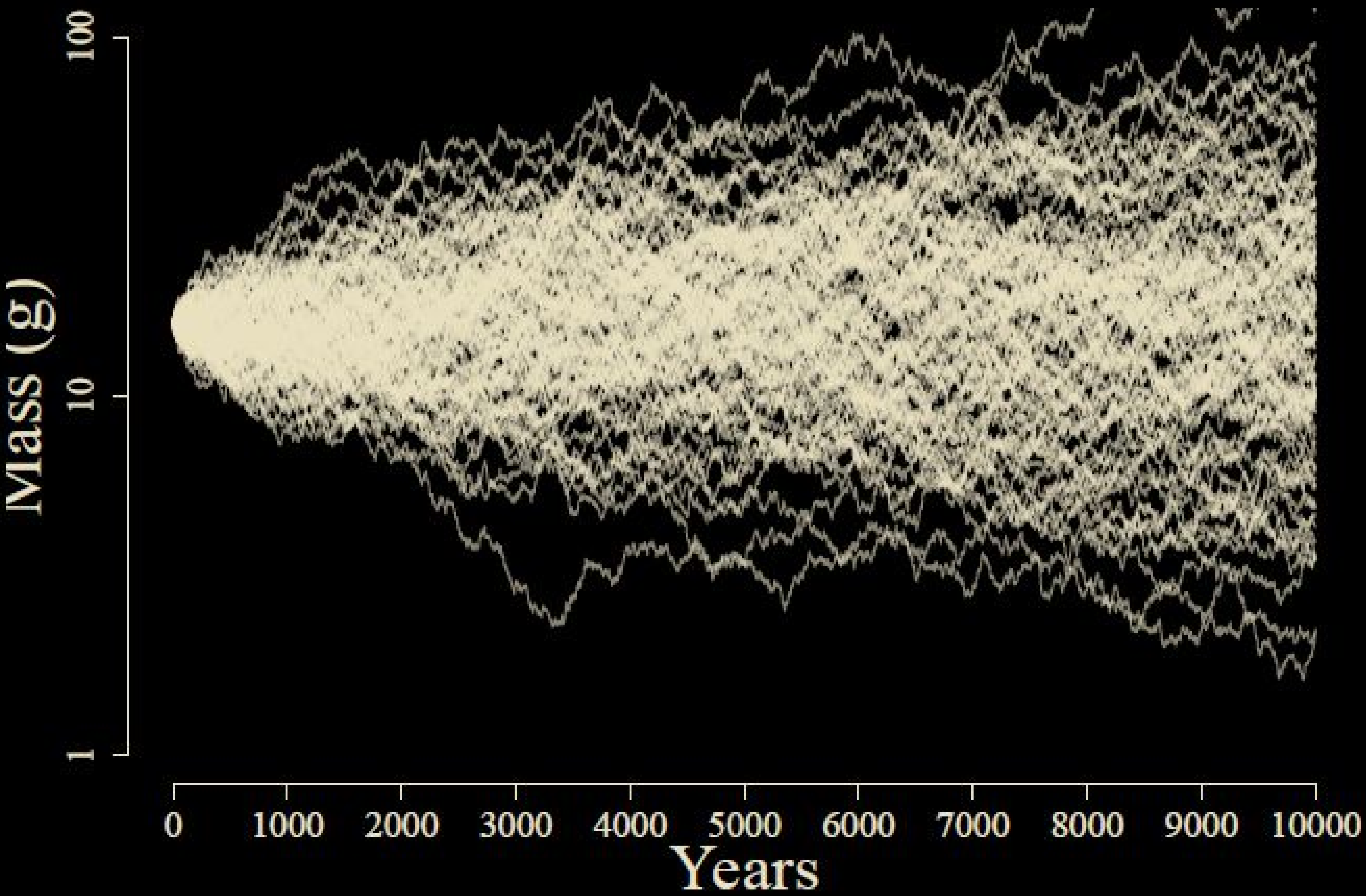
But evolution often reverses itself!

Let's instead simulate going up or down randomly

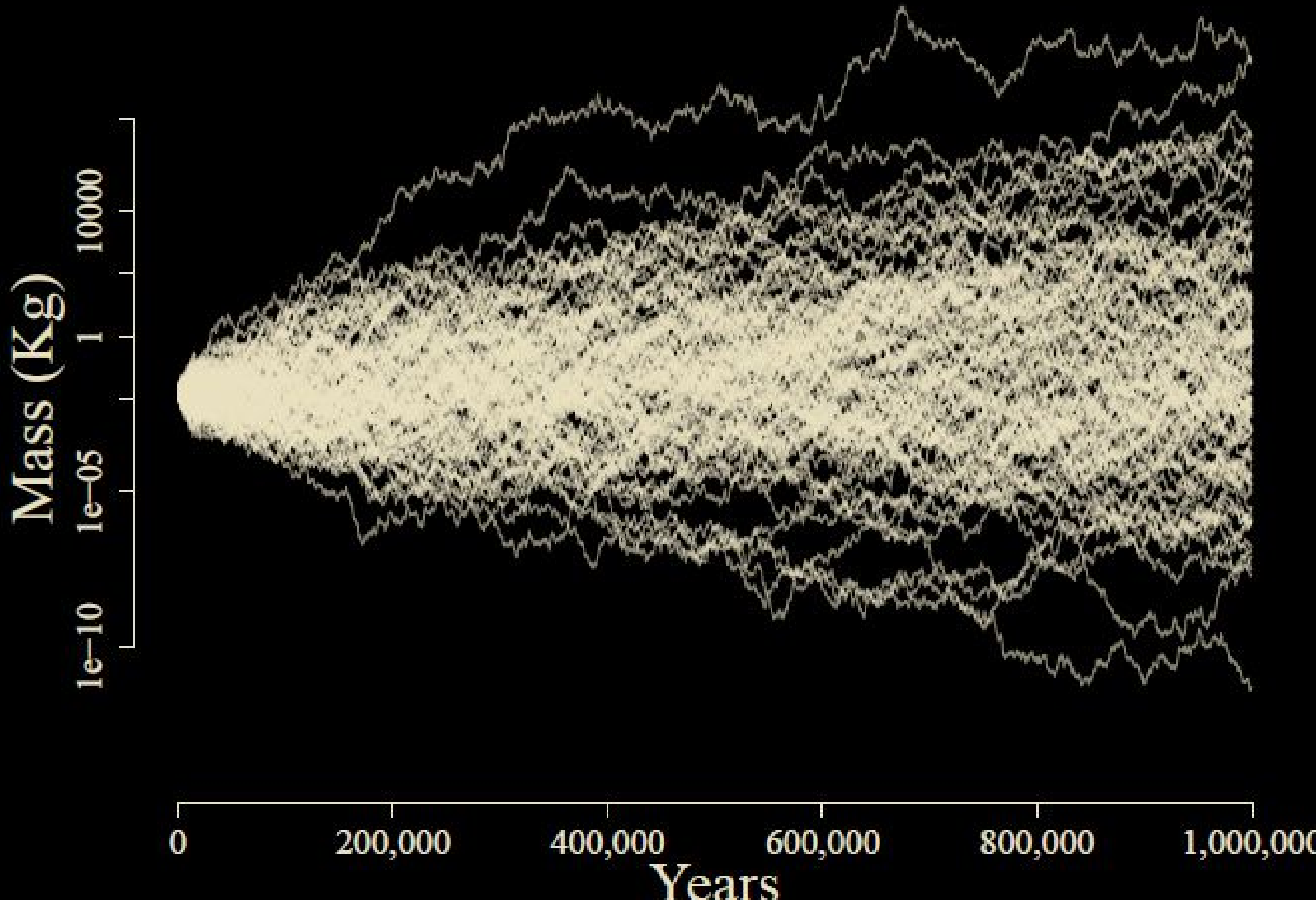
(*Brownian motion*)

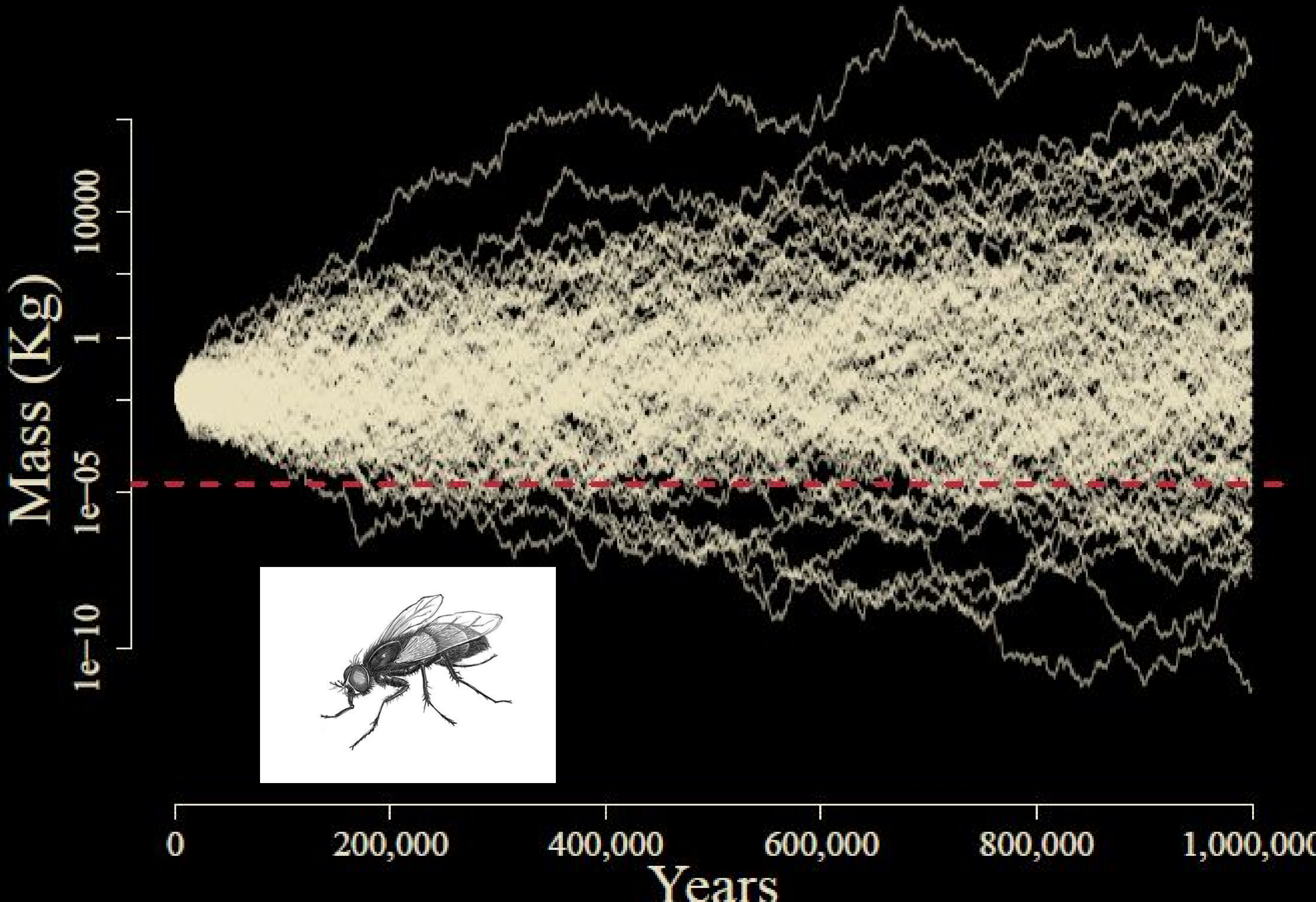


(Grant and Grant, 2002)



Mass (g)
100
10
1
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
Years

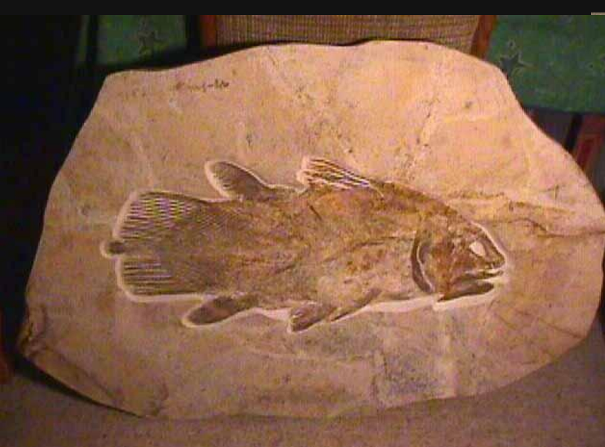

Mass (Kg)
1e−10
1e−05
1
10000
0
200,000
400,000
600,000
800,000
1,000,000
Years

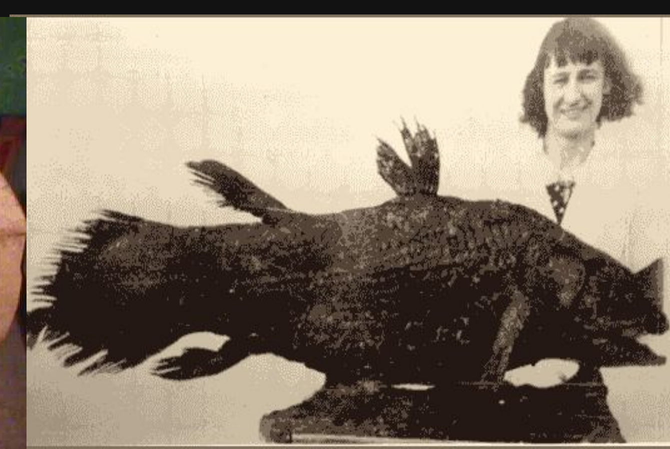


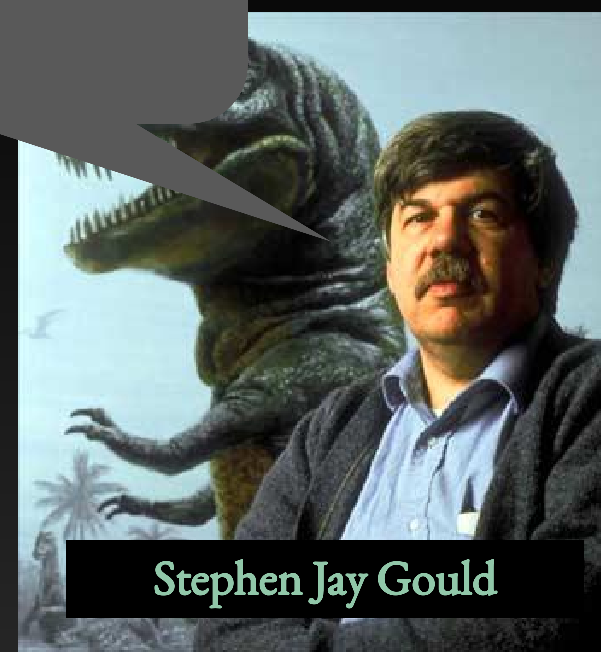
Mass (Kg)
10000
1
1e−05
1e−10
0
200,000
400,000
600,000
800,000
1,000,000
Years

What does the fossil record say?

The pattern is stasis







The Paradox of Stasis (Hansen & Houle 2004):

Organisms seem to be able to evolve far more than they ever do

Empirical studies often find:

- Strong (and often persistent) directional selection

  (Hereford et al. 2004, Morrissey & Hadfield 2012)

- High levels of additive genetic variance

  (Mousseau & Roff 1987, Houle 1992)

- Rapid evolutionary rates

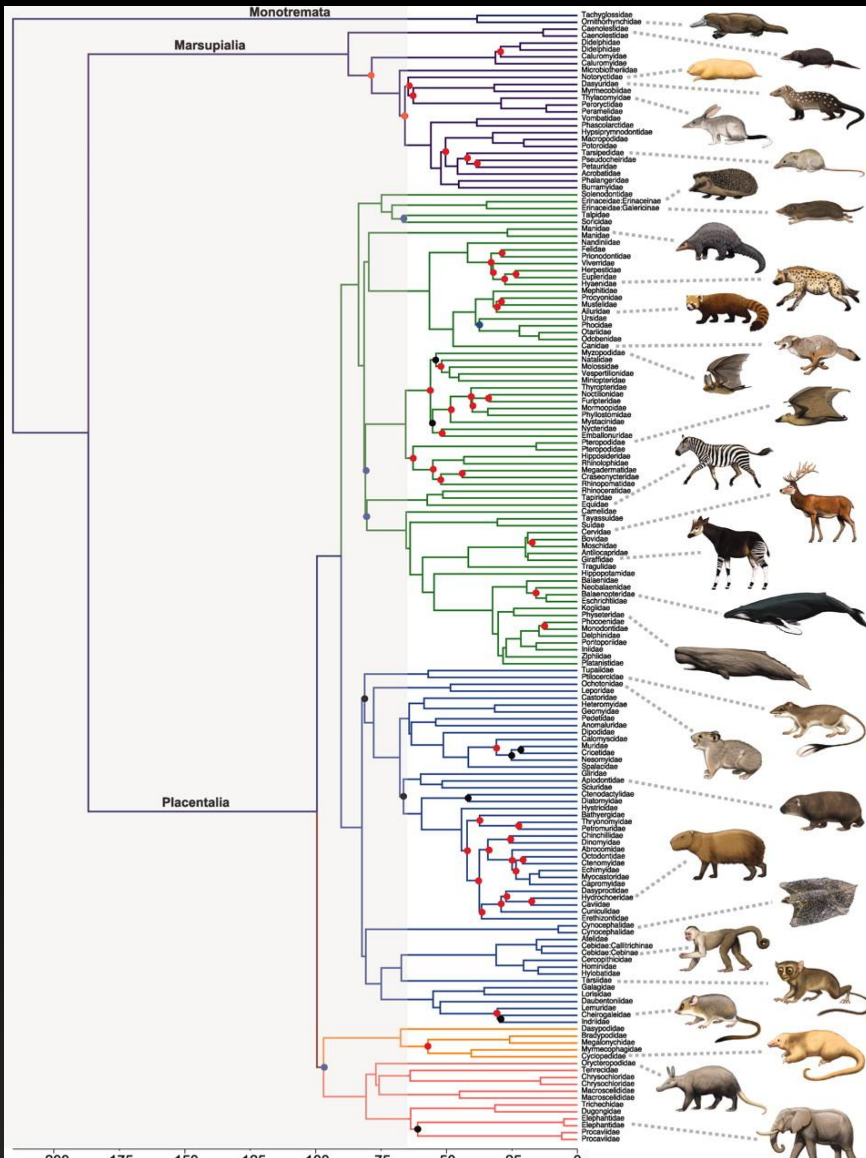
  (Hendry & Kinnison 1999, Kinnison & Hendry 2002)

...yet stasis in the fossil record

(Gingerich 1983, 2002)

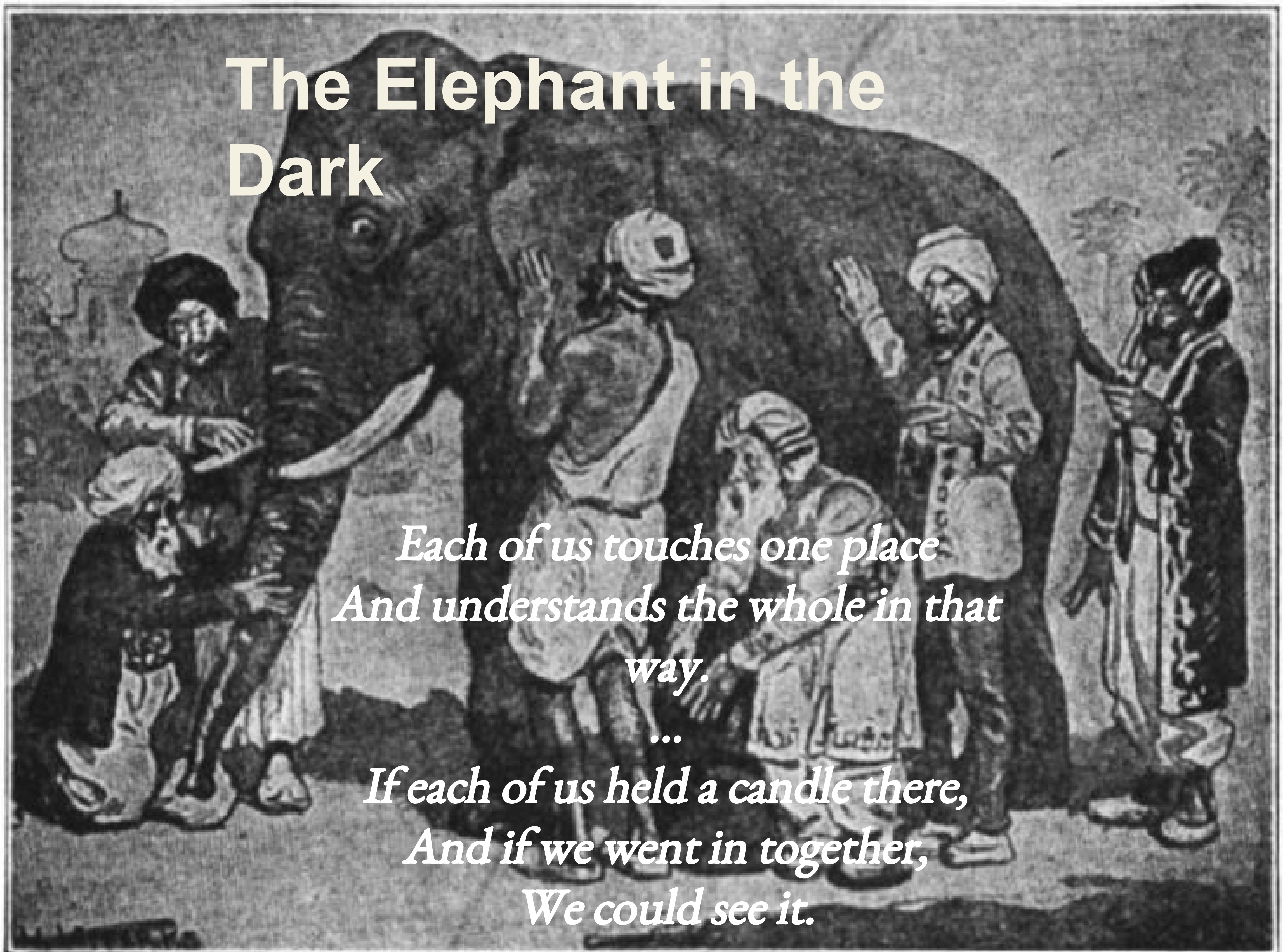
Does microevolution even matter for long-term change?

Patterns in phylogenetic comparative data



So what do comparative biologists use to model evolution on a phylogeny?

Gradual Brownian motion!

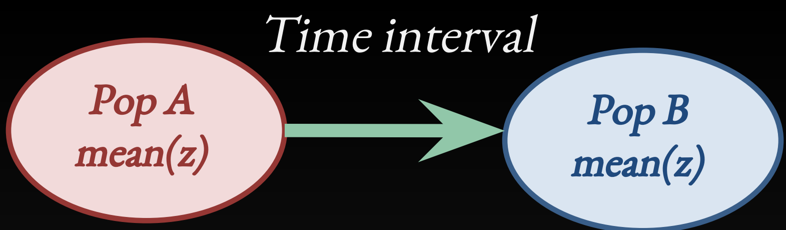


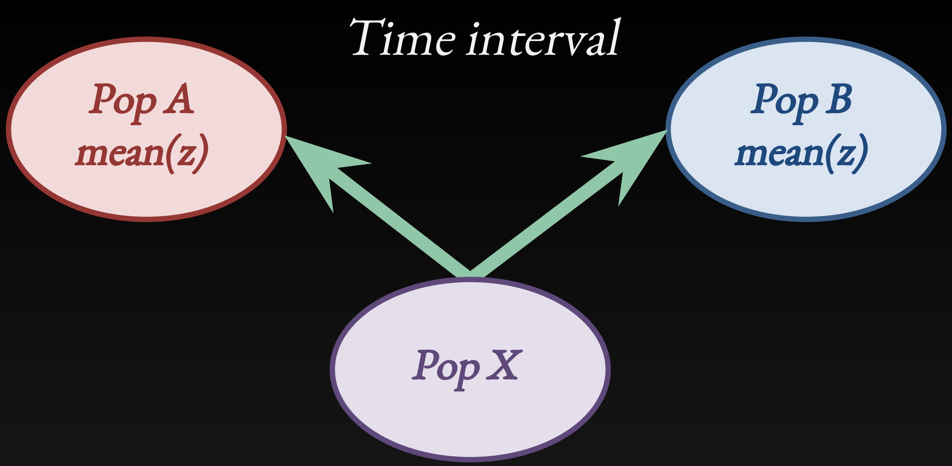
The Elephant in the Dark

Each of us touches one place
And understands the whole in that way.
...
If each of us held a candle there,
And if we went in together,
We could see it.

How can we see the pattern across scales of time?

All studies of phenotypic evolution measure comparable quantities

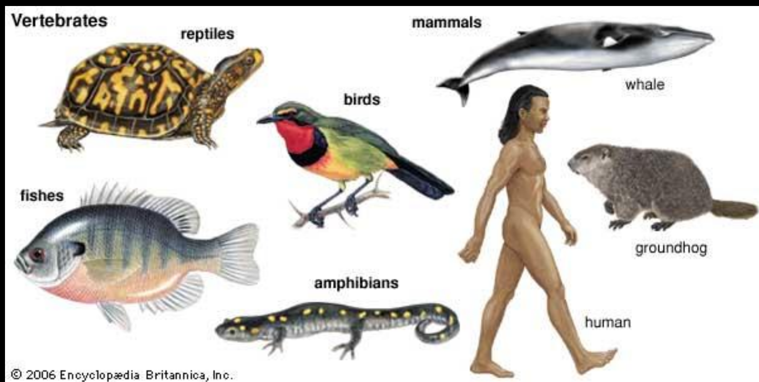




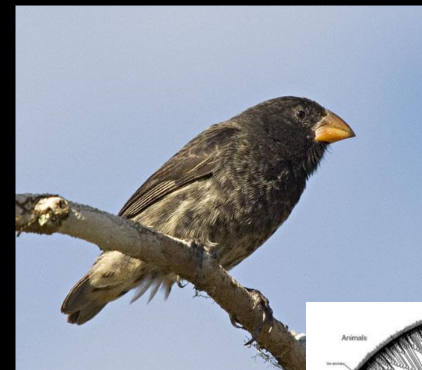
We measure two quantities:
(1) "time for evolution"
(2) Δ mean body size

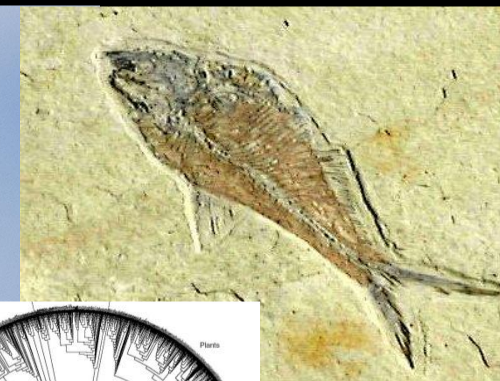
Phenotypic divergence database

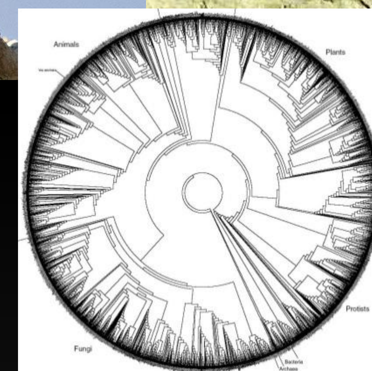
(Uyeda, Hansen, Arnold & Pienaar, 2011. *PNAS.*)



Only animals, mostly vertebrates, but also some inverts





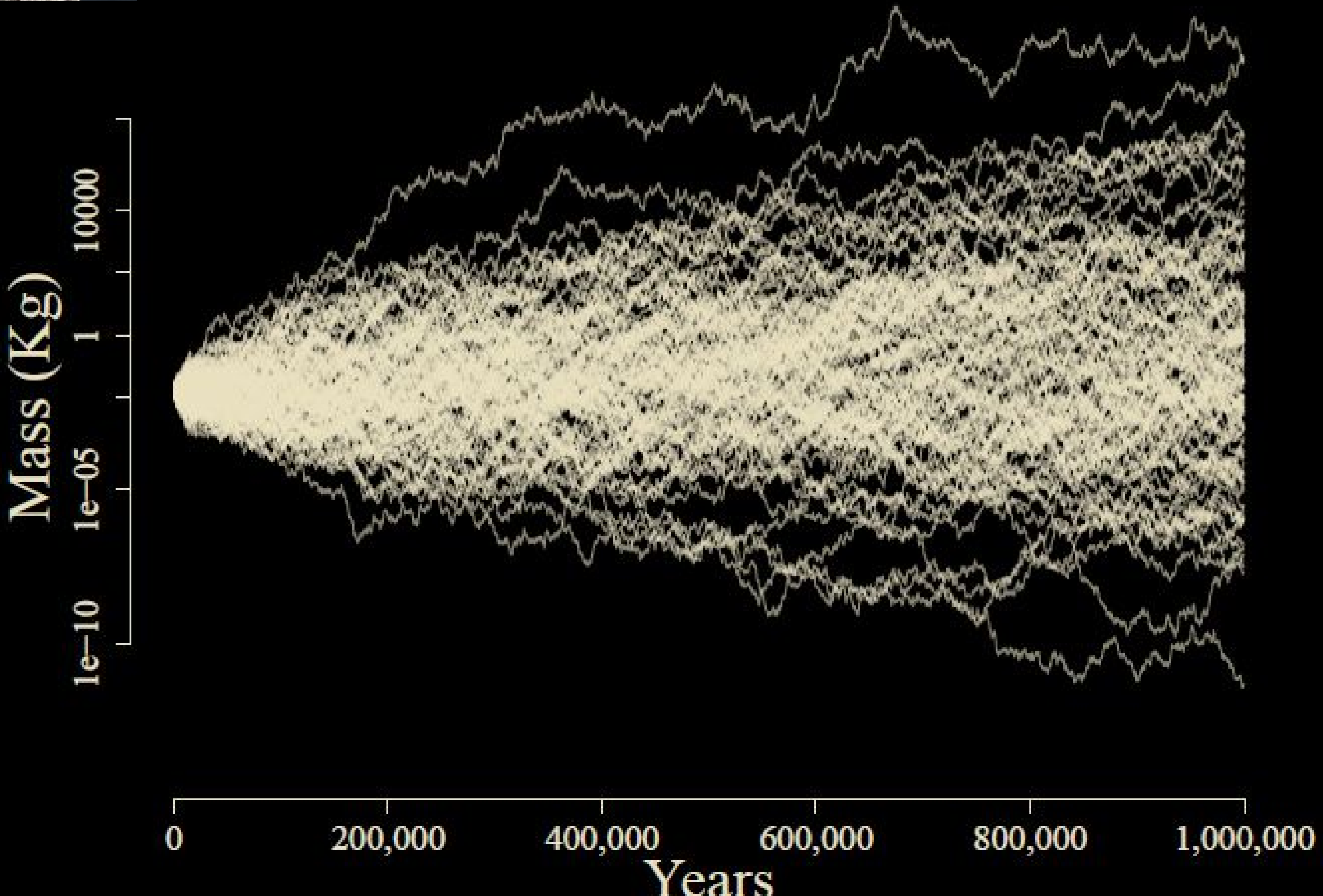


Only traits related to linear body size change

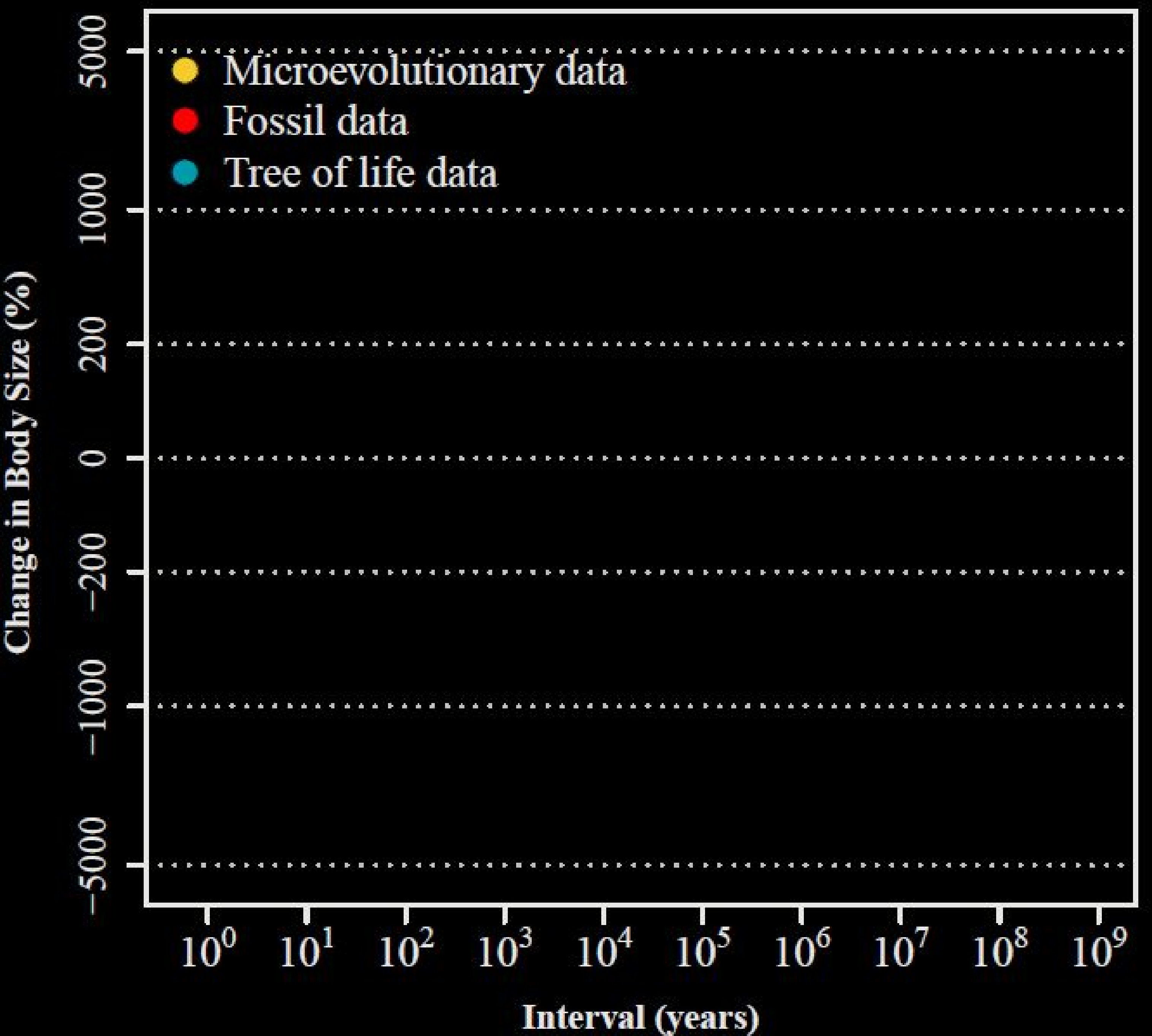
Field, Fossil and Phylogenetic comparative data

>8000 data points from
> 150 studies

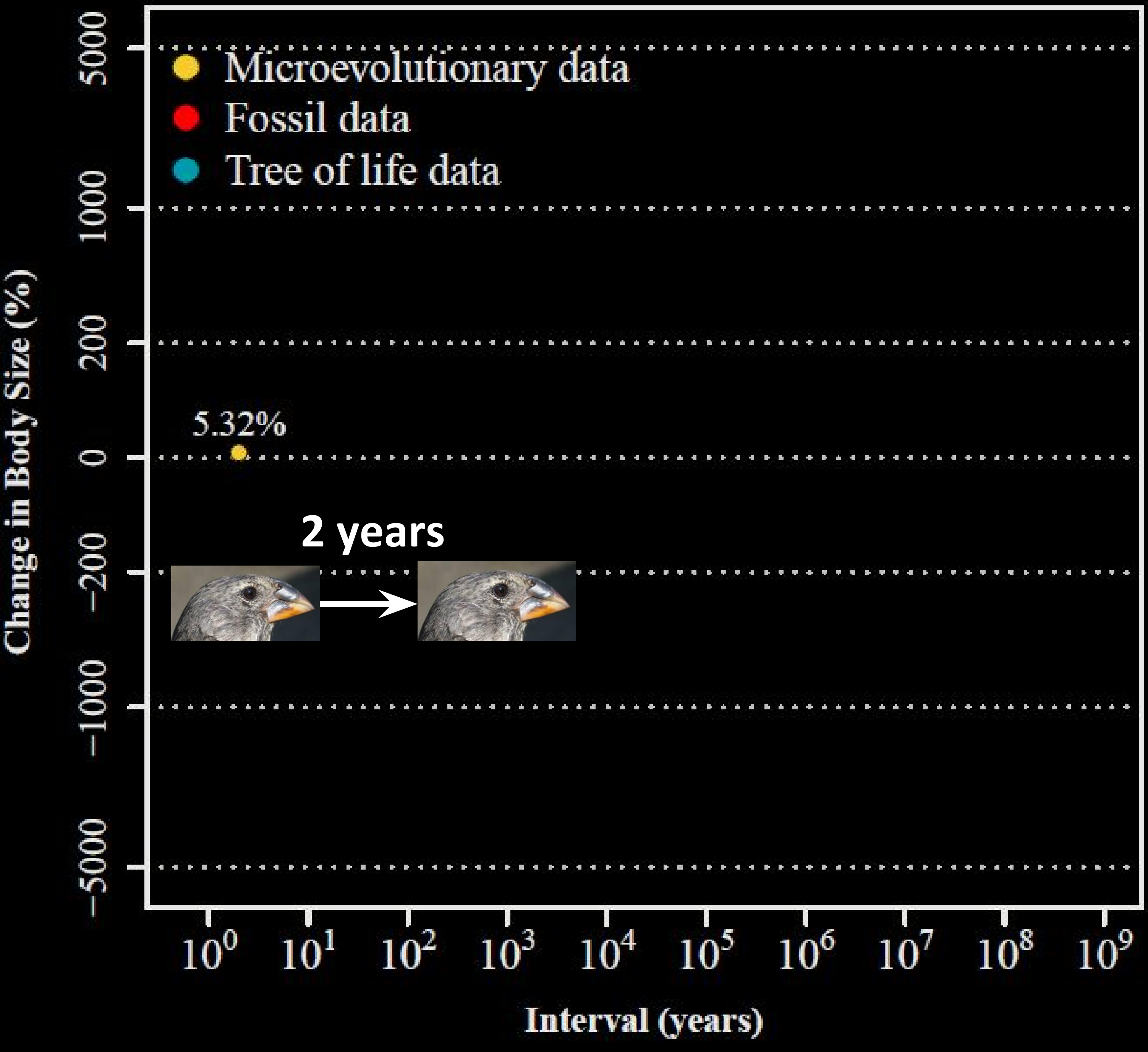
Intervals from < 1 yr to
360 my



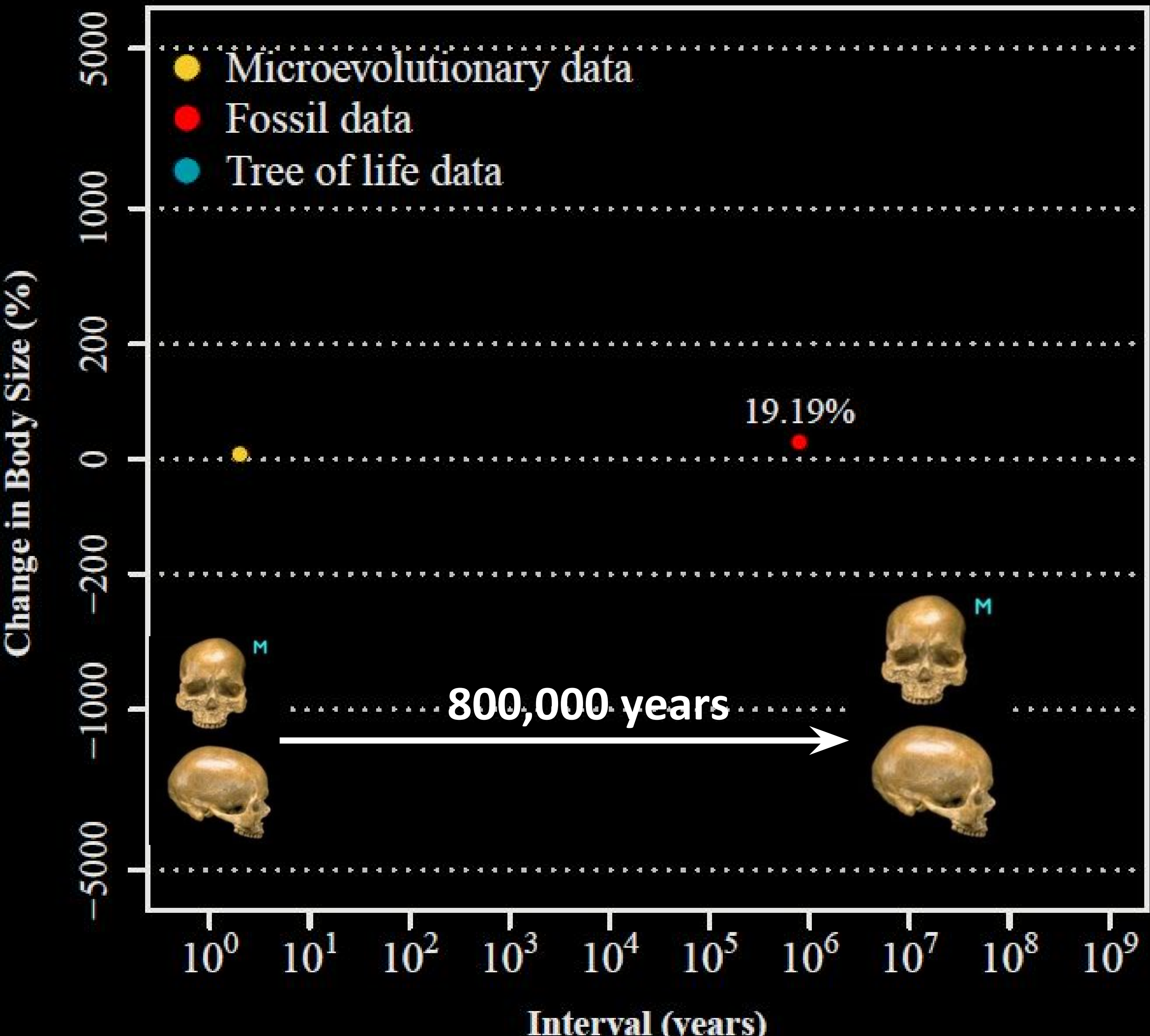
Mass (Kg)
10000
1
1e−05
1e−10
0
200,000
400,000
600,000
800,000
1,000,000
Years



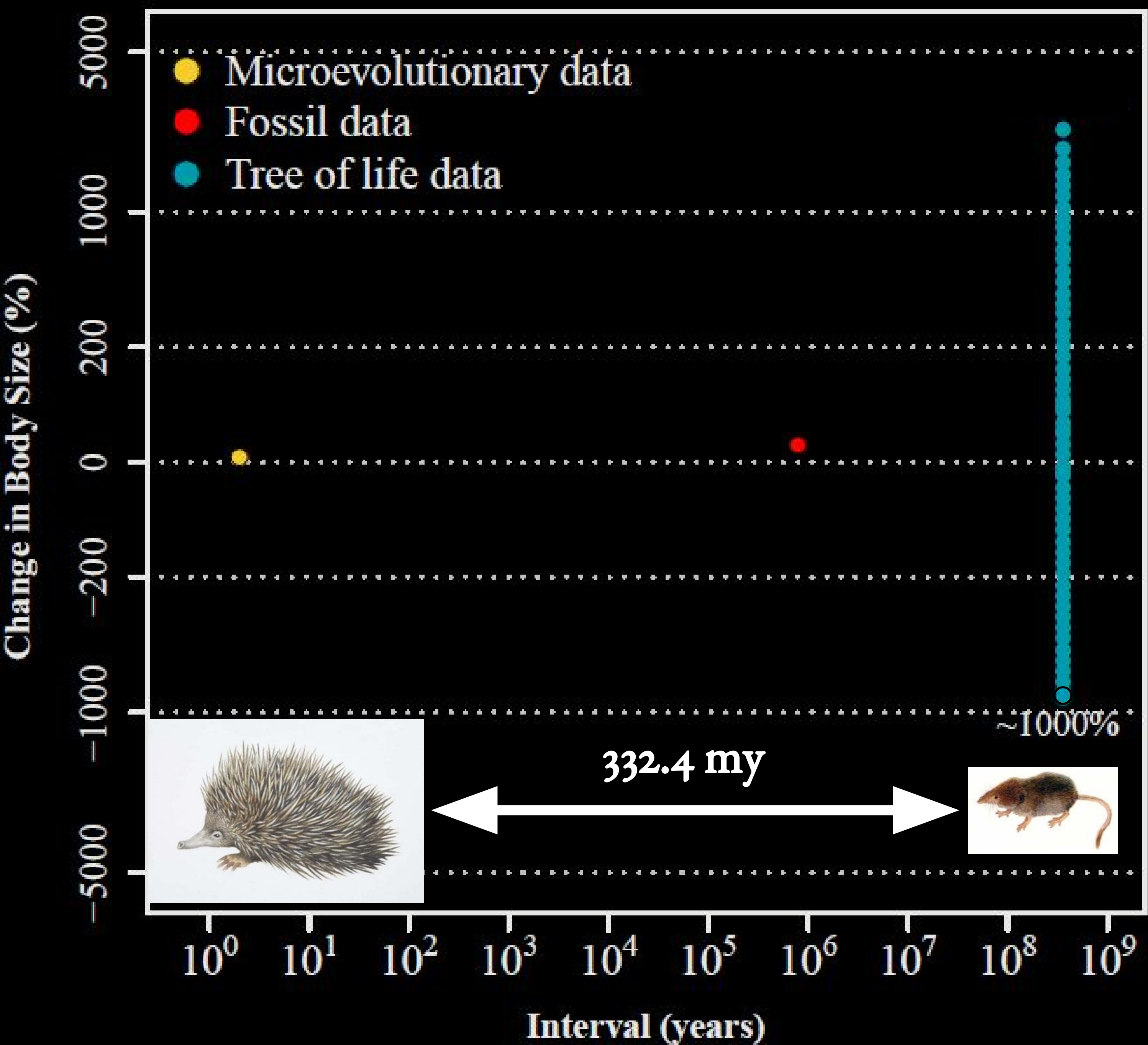
Uyeda et al., *PNAS*, 2011



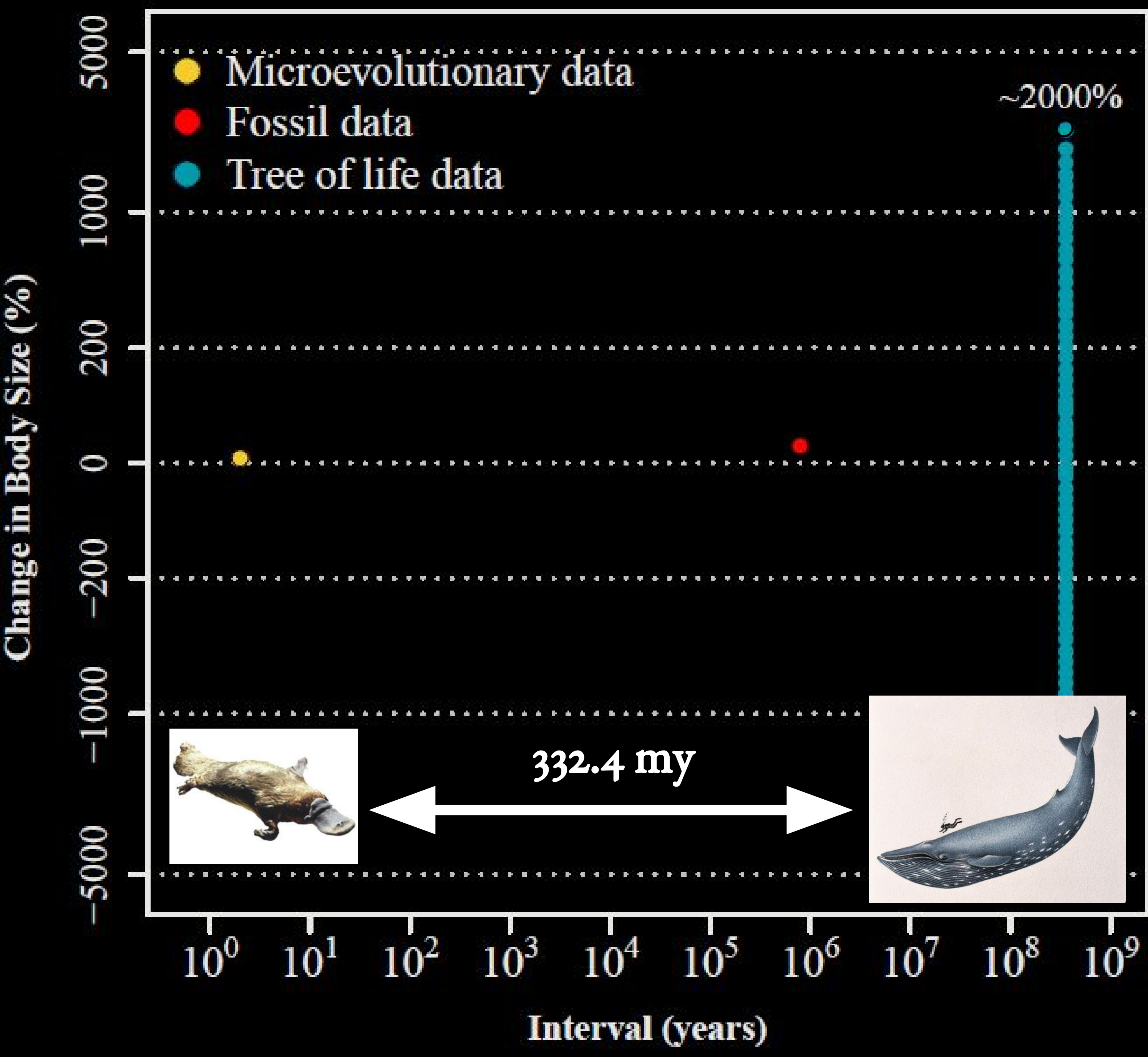
Uyeda et al., *PNAS*, 2011



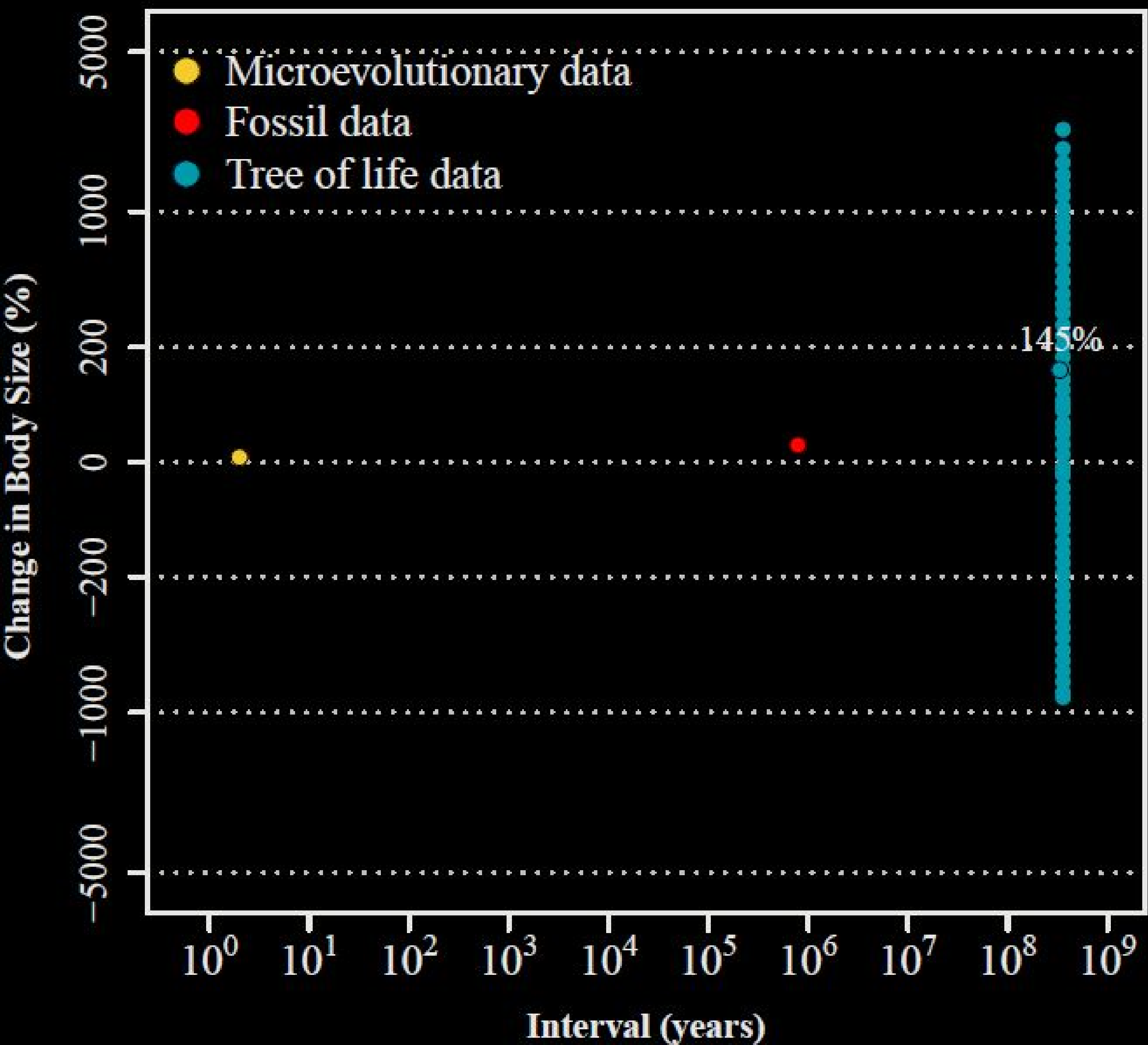
Uyeda et al., *PNAS*, 2011



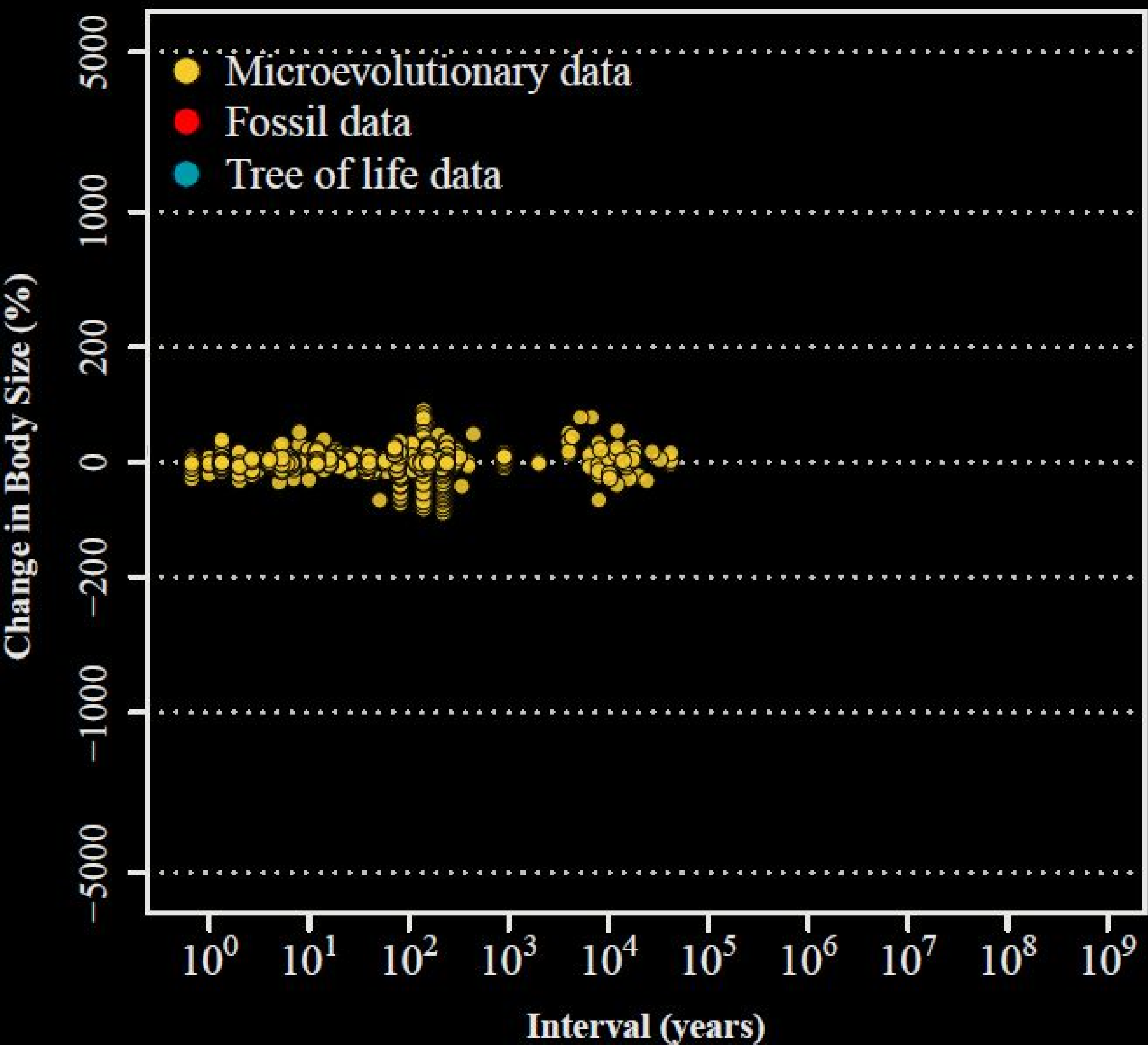
Microevolutionary data
Fossil data
Tree of life data
Change in Body Size (%)
5000
1000
200
0
−200
−1000
−5000
~1000%
332.4 my
Interval (years)
10^0
10^1
10^2
10^3
10^4
10^5
10^6
10^7
10^8
10^9



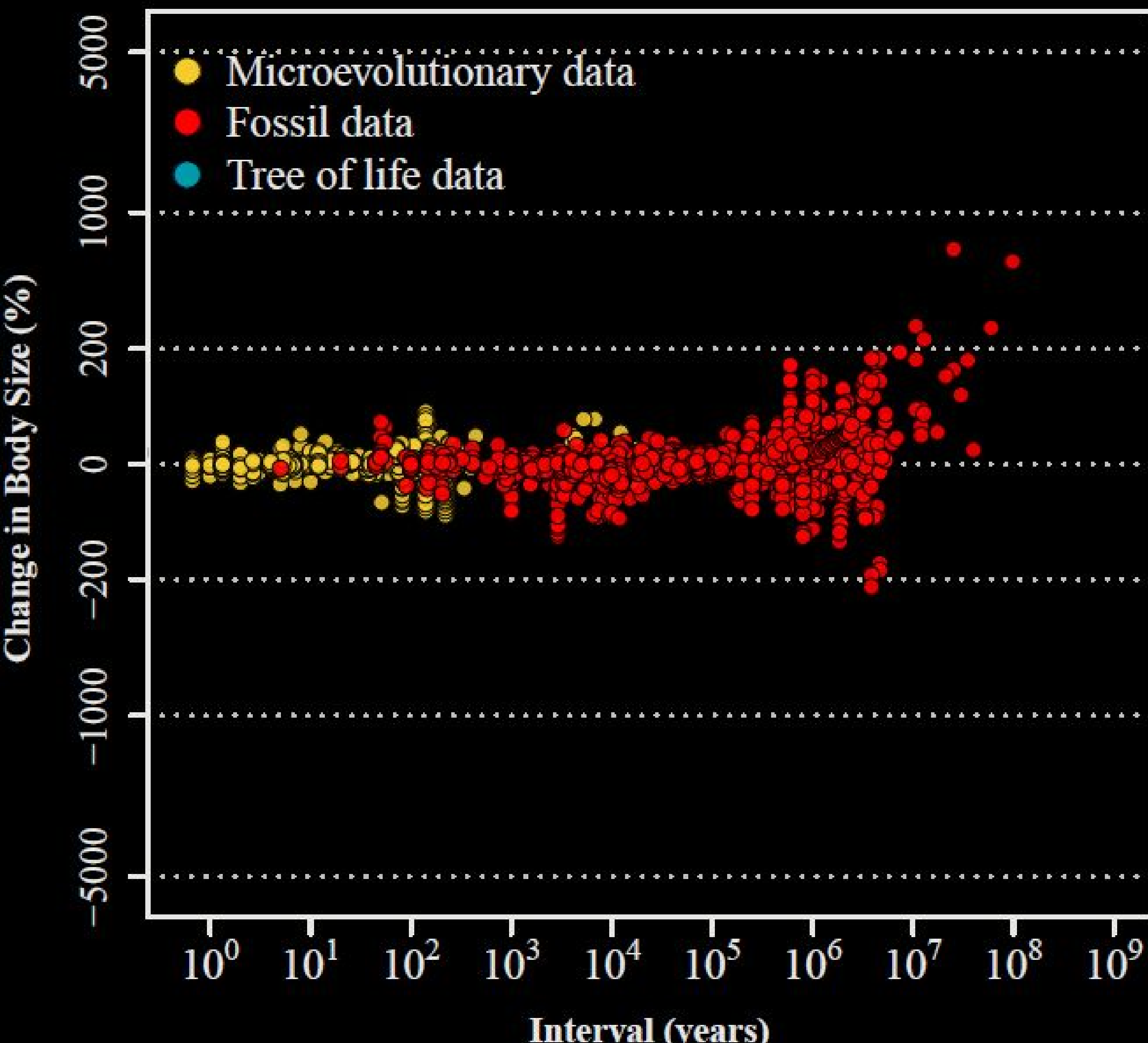
Uyeda et al.,
PNAS, 2011



Uyeda et al., *PNAS*, 2011



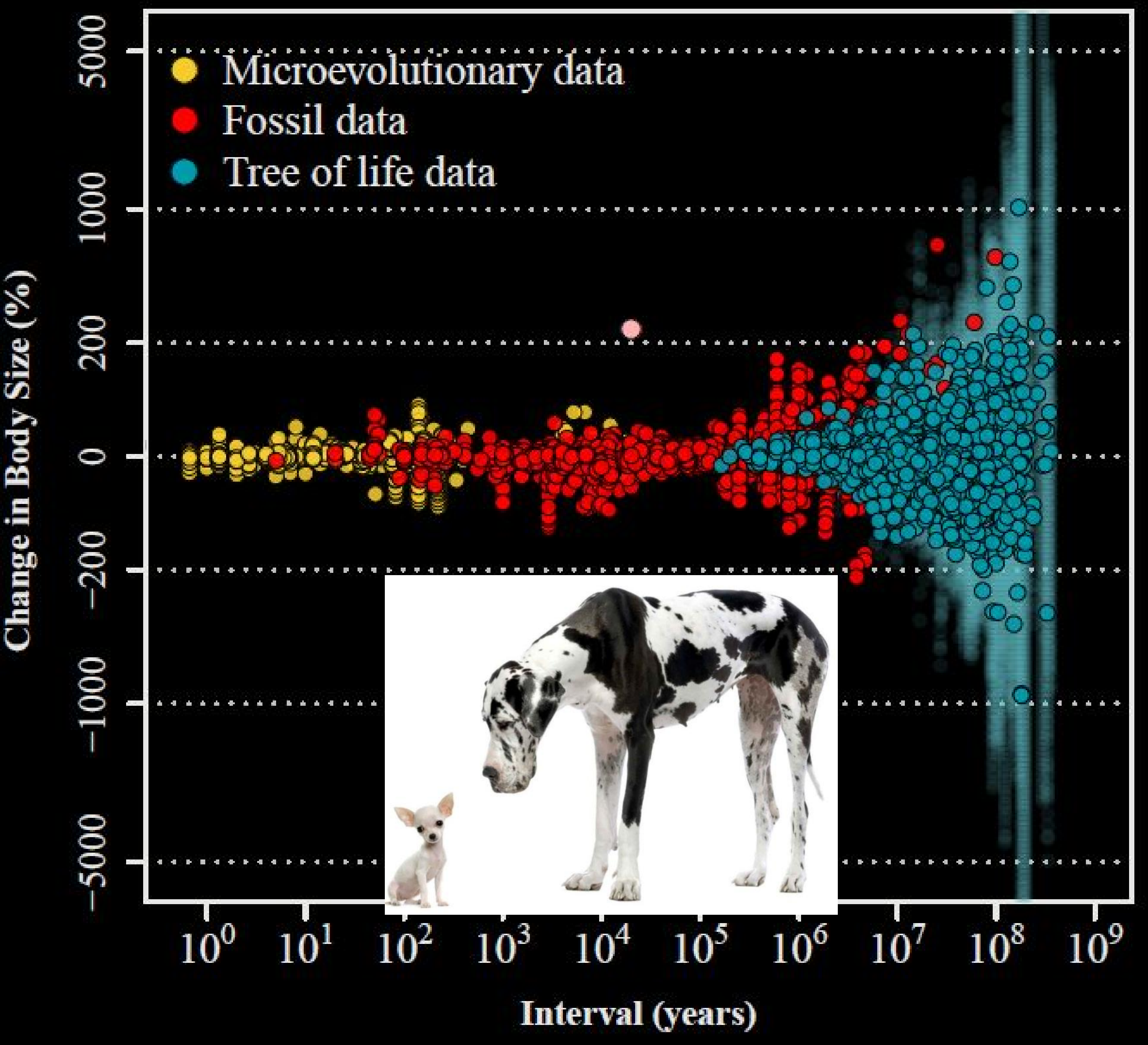
Uyeda et al., *PNAS*, 2011



Uyeda et al., *PNAS*, 2011

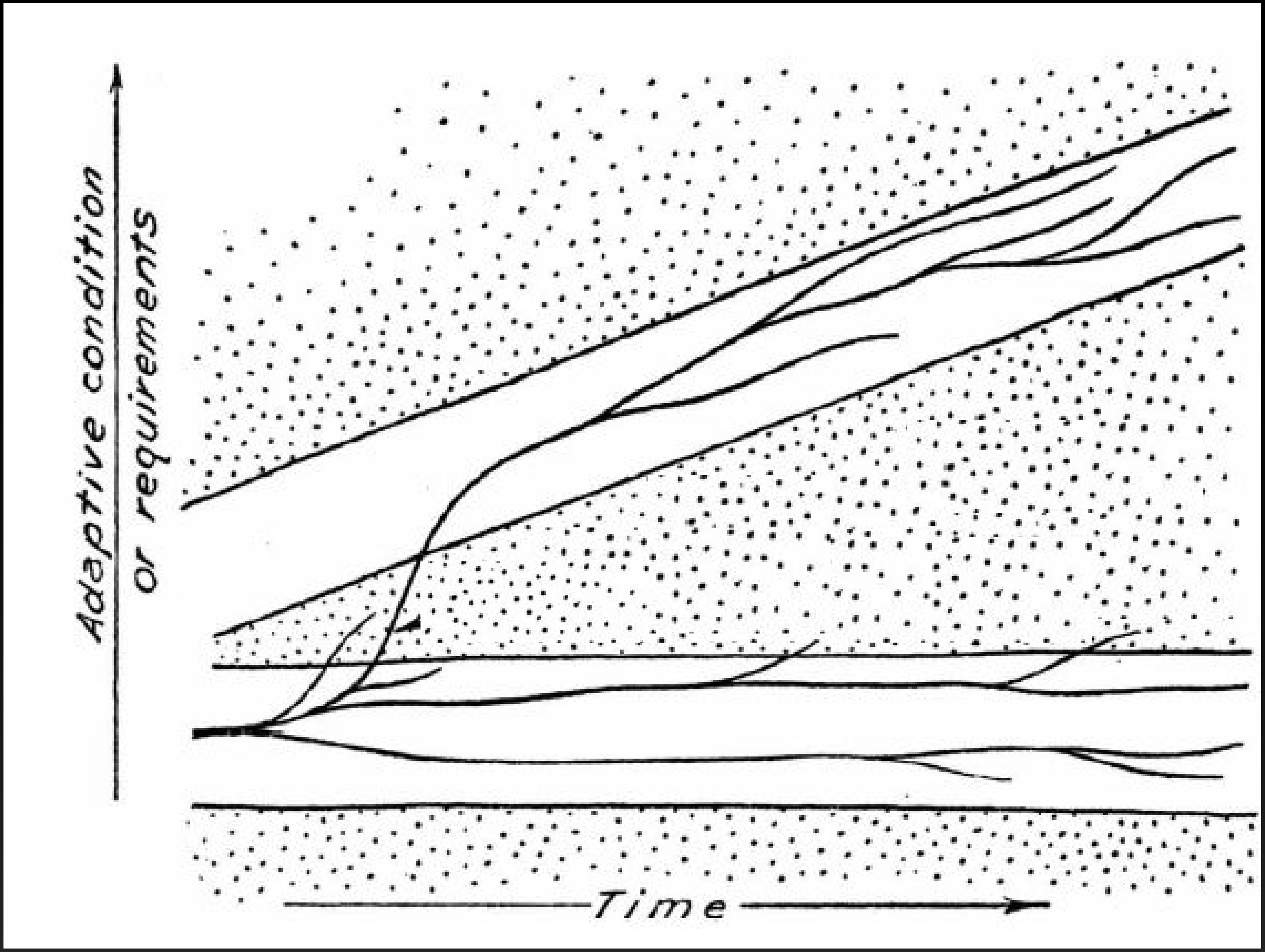
“The Evolutionary Blunderbuss”

Uyeda et al., *PNAS*, 2011

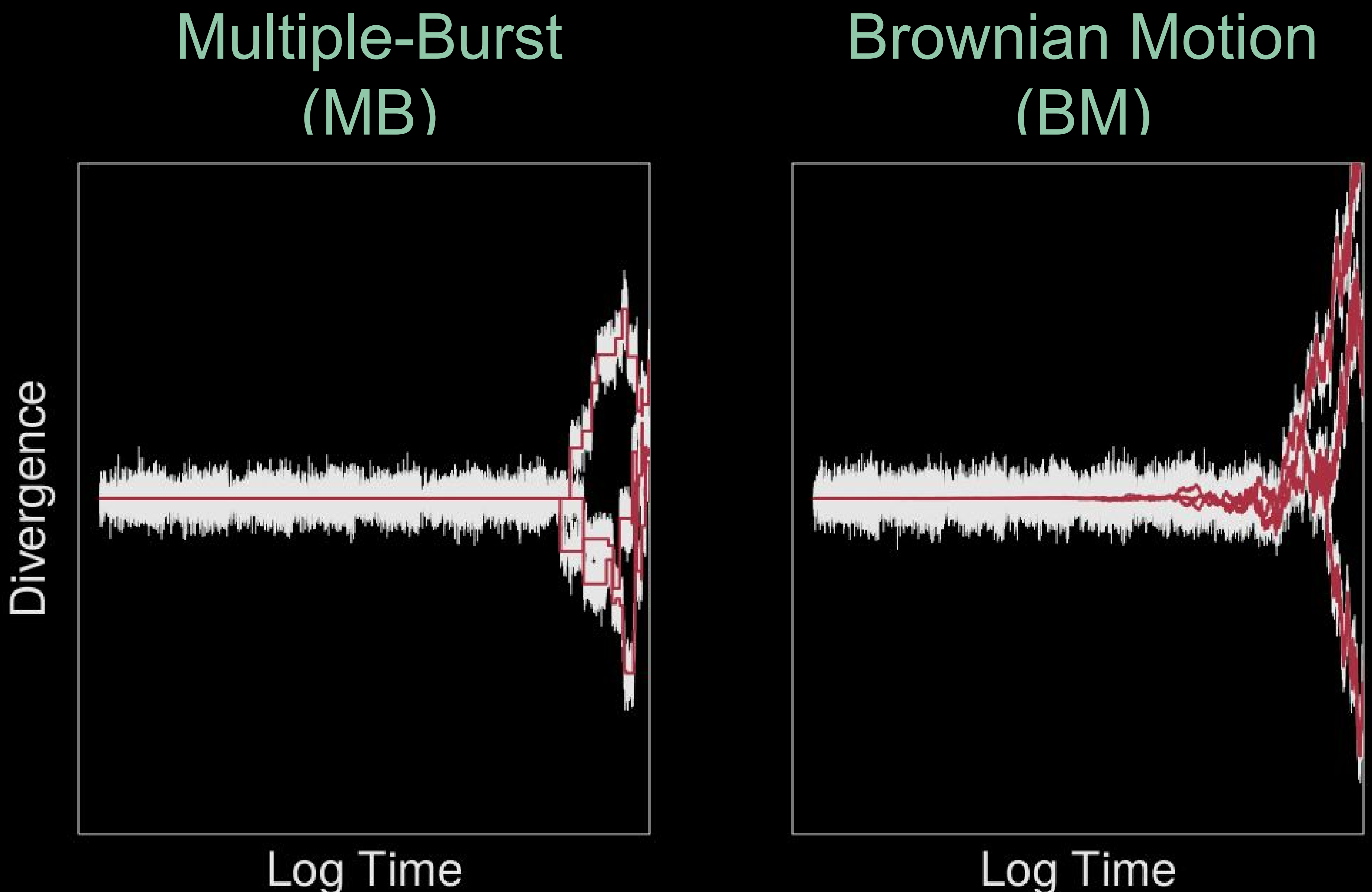


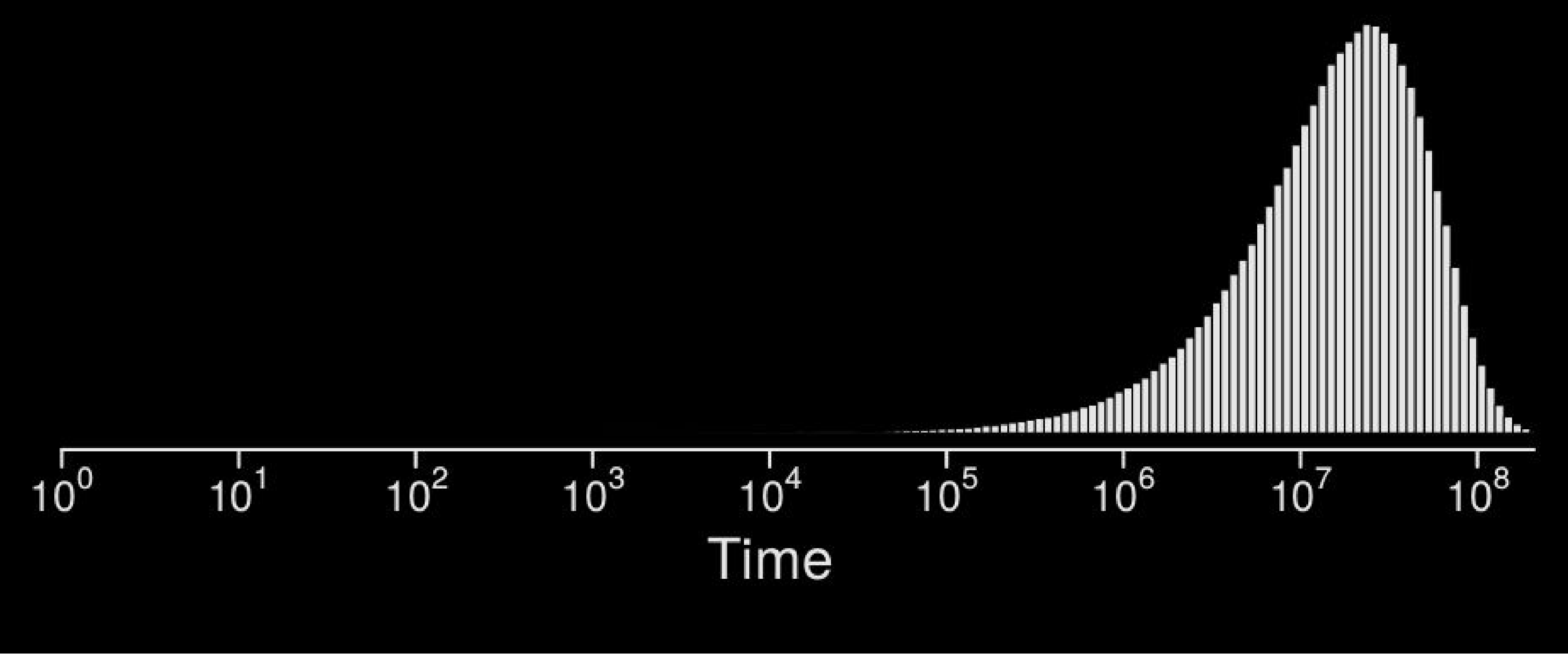
Uyeda et al., *PNAS*, 2011

Simpson's Adaptive Zones



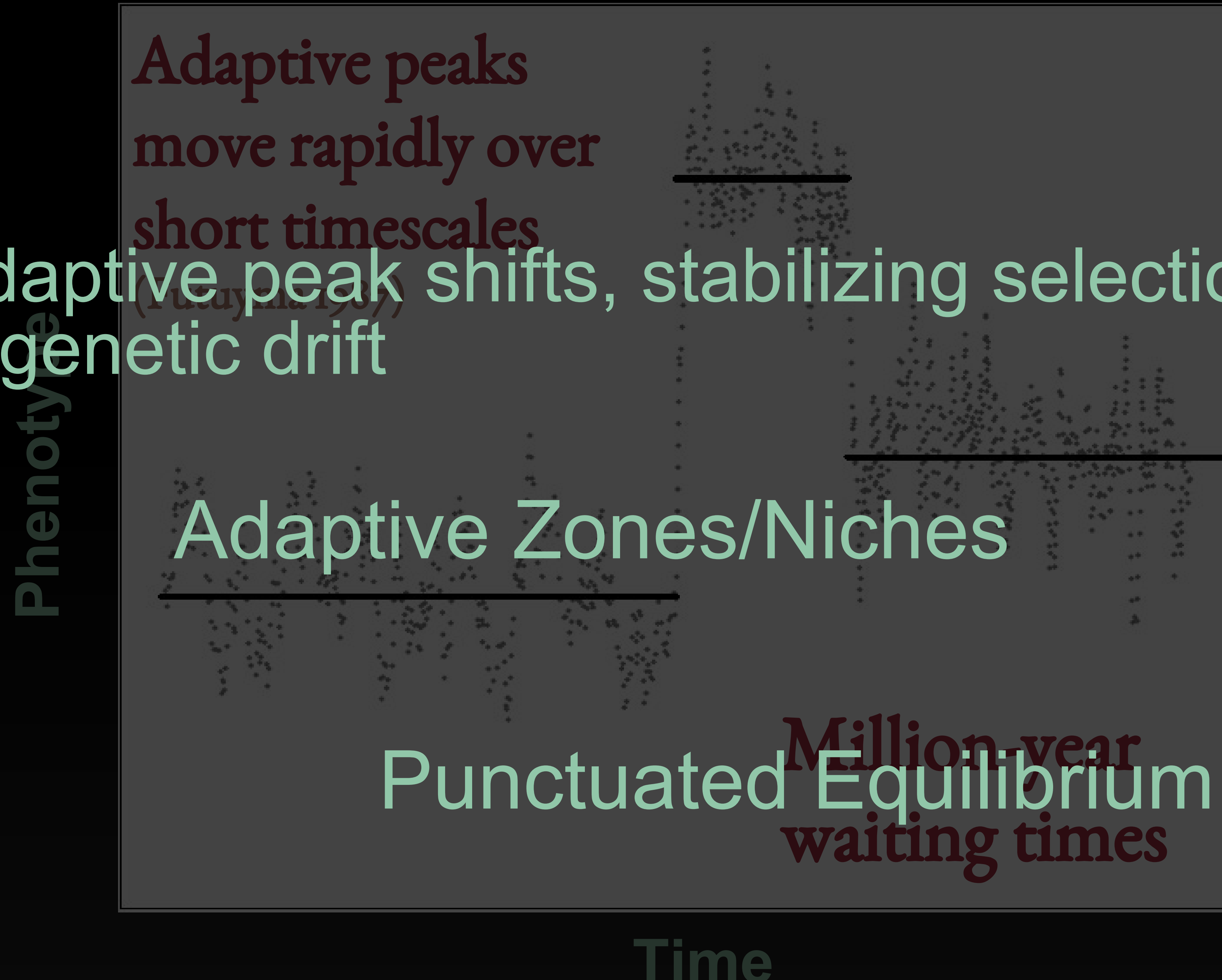
Model fits


Multiple-Burst
(MB)
Brownian Motion
(BM)
Divergence
Log Time
Log Time



Dataset	Parameter Estimates		
	Stasis SD	**Burst SD**	**Ave. burst time**
Whole dataset	= 0.096	= 0.27	25.0 my
Microevolutionary & Fossil	= 0.087	= 0.25	1.5 my
Phylogenetic	= 0.086	= 0.22	21.8 my

Adaptive peak shifts, stabilizing selectio
& genetic drift



Adaptive Zones/Niches

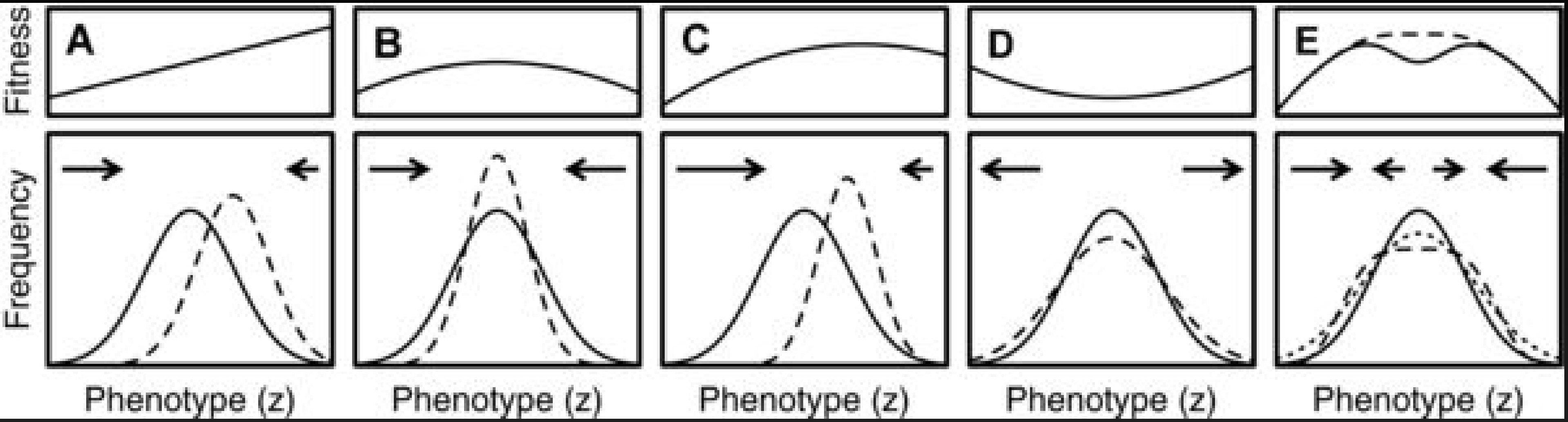
Punctuated Equilibrium

Pennell, Harmon & Uyeda. 2013. Is there room for Punctuated Equilibrium in Macroevolution? *TREE*.

Some recent proposals

Intraspecific competition

Haller & Hendry. 2014. *Solving the paradox of stasis: Squashed stabilizing selection and the limits of detection, Evolution*



Populations vs. lineages

Bartoszek et al. *The Ornstein-Uhlenbeck process with migration: evolution with interactions, arXiv*

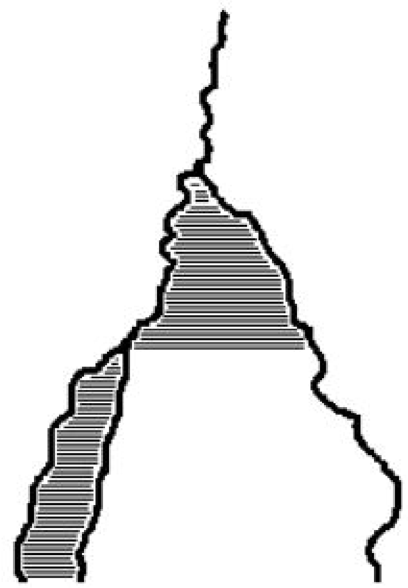
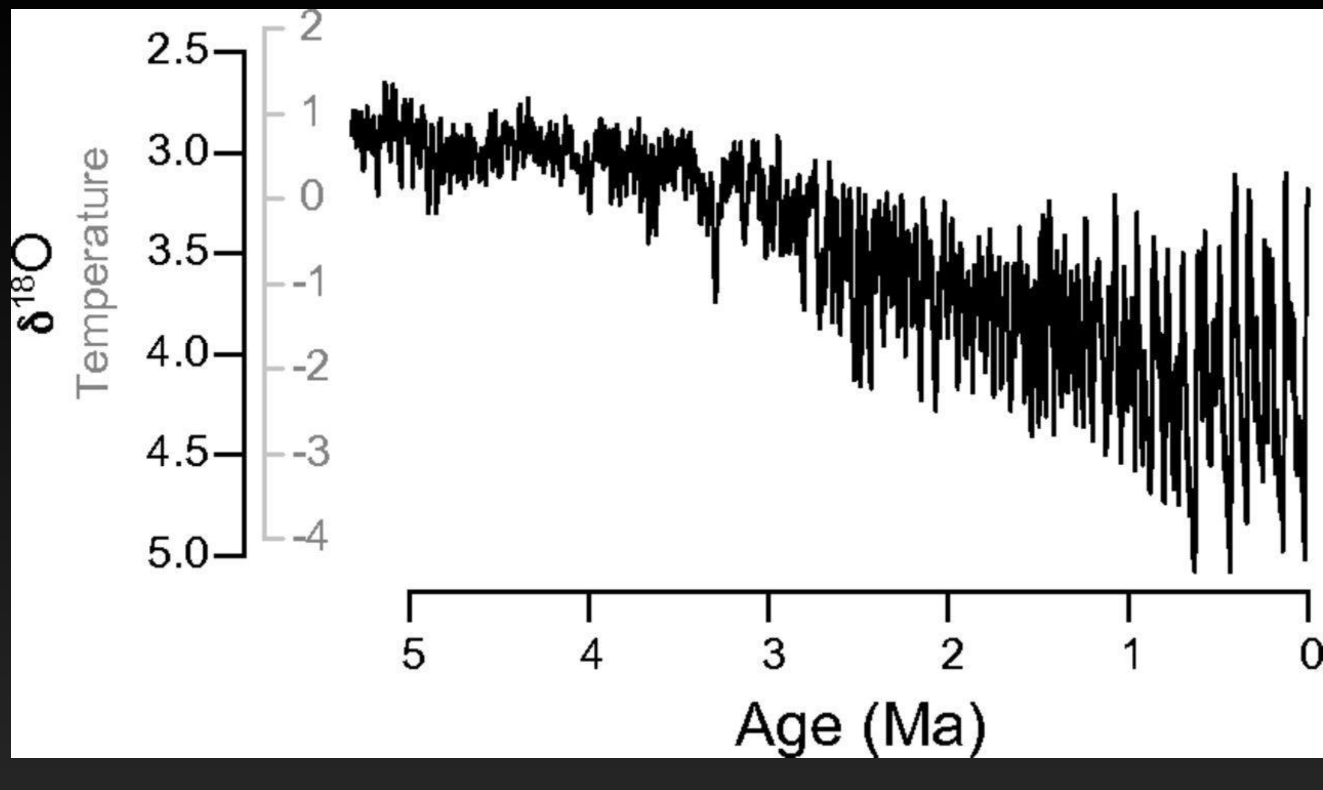


Figure 2: An evolving trait on a phylogenetic tree with migrations indicated, by horizontal lines.

Temperature tracking

Hunt et al. 2015. *Simple vs complex models of trait evolution and stasis as a response to environmental change, PNAS*



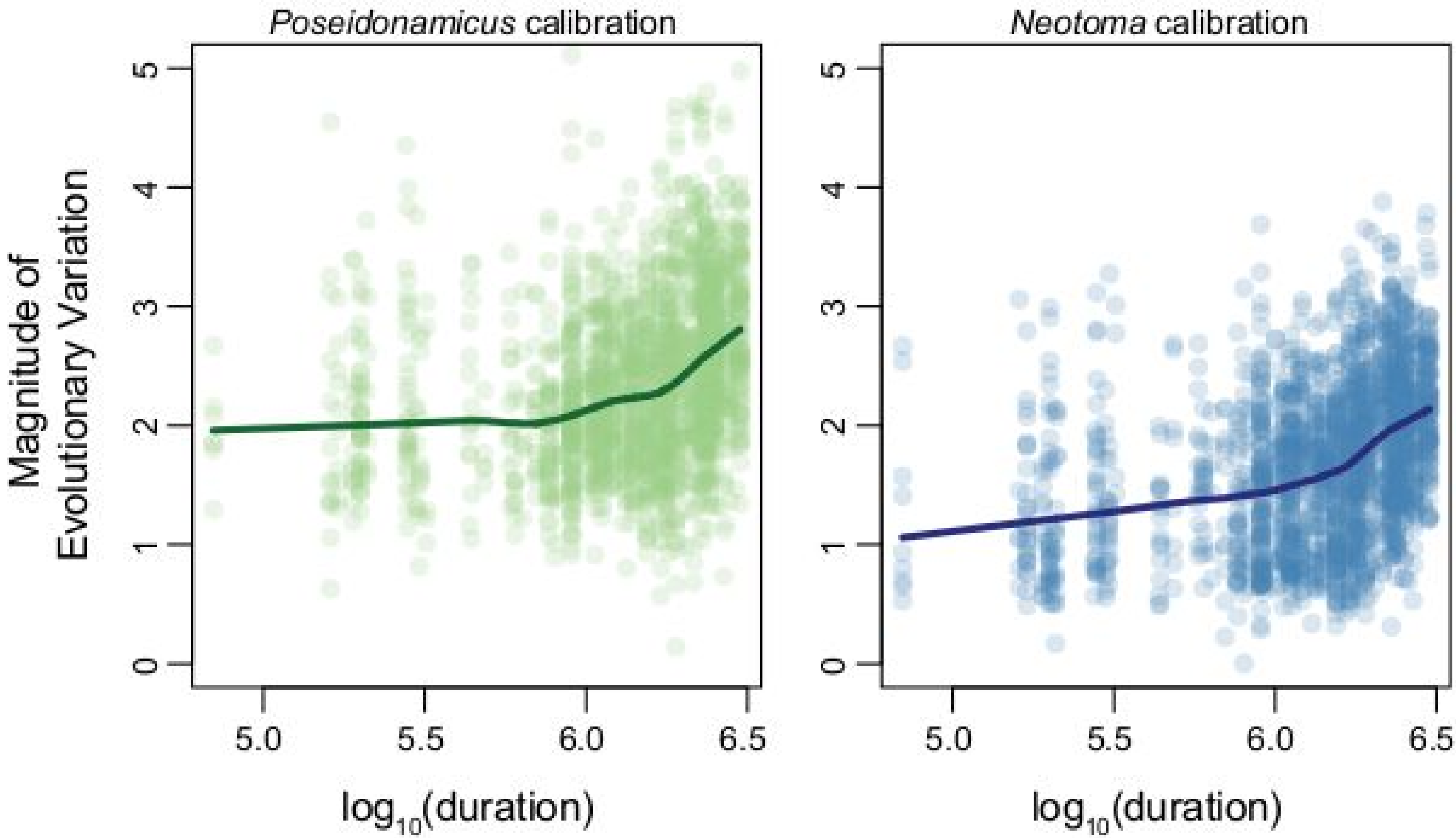
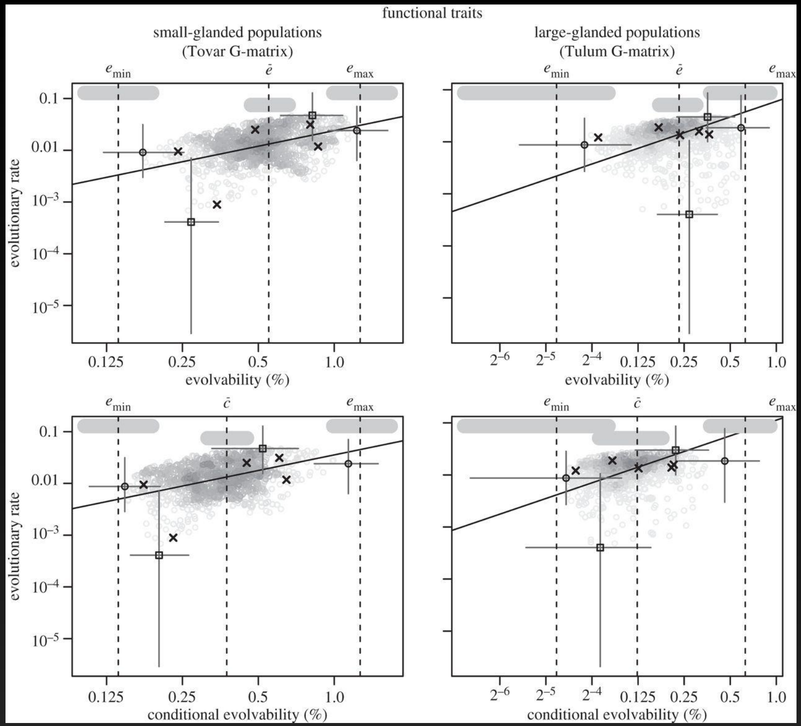
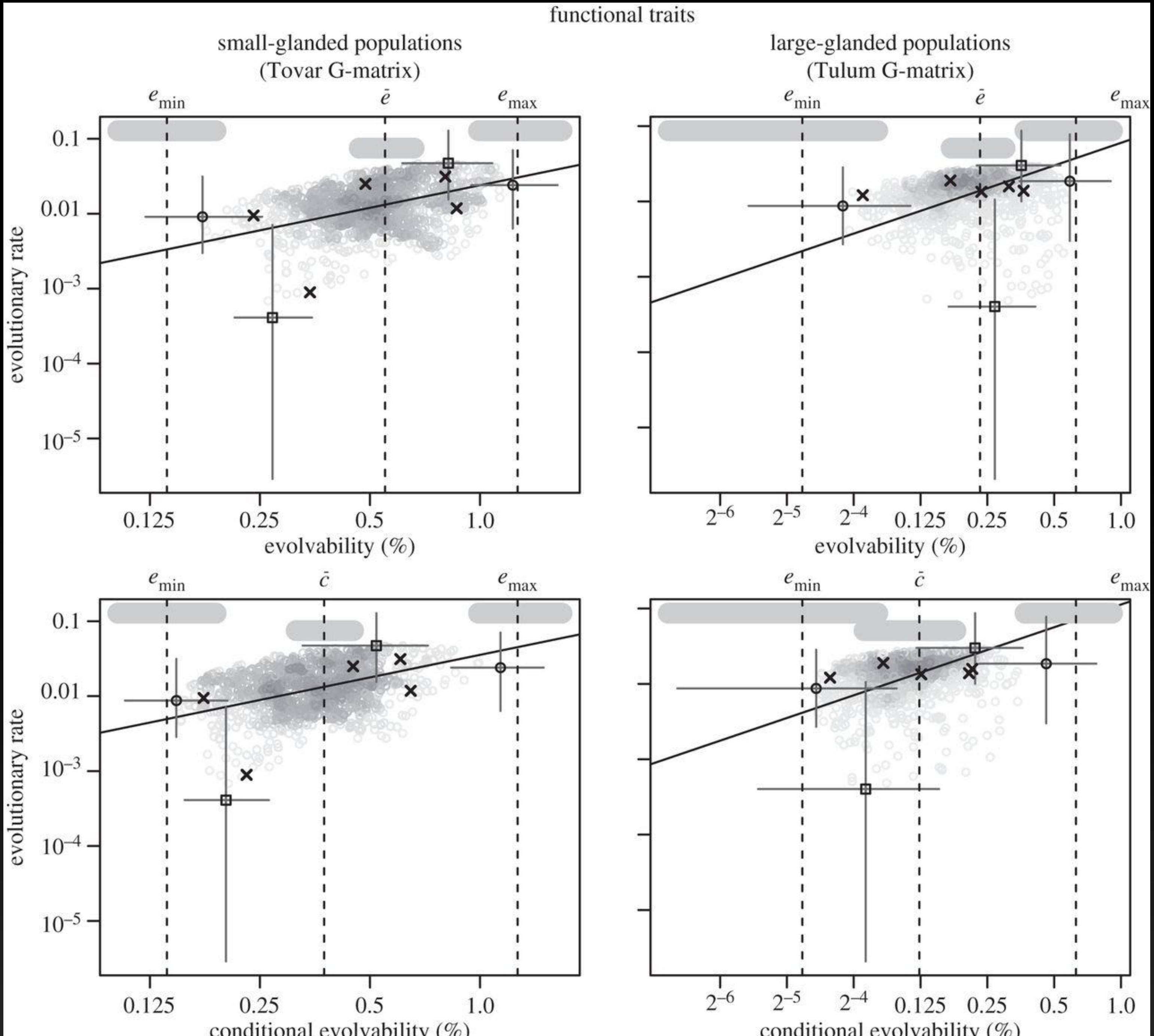


Figure S6. Results of simulations from the temperature-tracking model, calibrated by *Poseidonamics major* (left) and *Neotoma cinerea* (right). Vertical axis is magnitude of evolutionary variation measured as the standard deviation of samples in a sequence, with the contribution from measurement error removed (see Methods). Horizontal axis is sequence duration, in years and on a $\log_{10}$ scale (a value of 6 is 1 Myr). Points are semi-transparent and lines represent locally weighted (lowess) regressions with a smoother span = 0.5.

Multivariate genetic constraints

Bolstad et al. 2014. *Genetic constraints predict evolutionary divergence in* Delachampia *blossoms.* Phil. Trans. B.





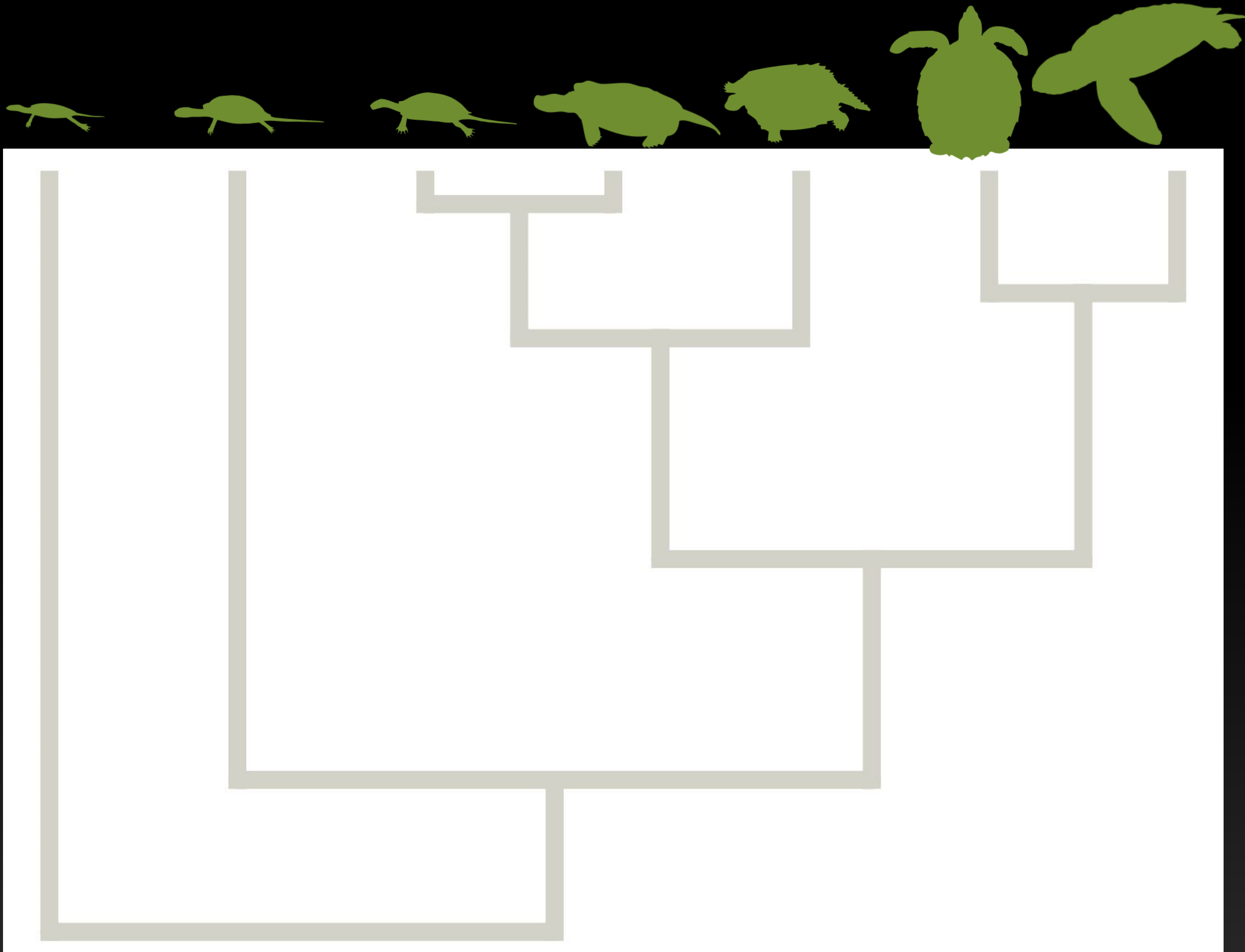
functional traits
small-glanded populations
(Tovar G-matrix)
large-glanded populations
(Tulum G-matrix)
e_{min}
$\bar{e}$
e_{max}
$\bar{c}$
0.1
0.01
10^{-3}
10^{-4}
10^{-5}
evolutionary rate
0.125
0.25
0.5
1.0
2^{-6}
2^{-5}
2^{-4}
evolvability (%)
conditional evolvability (%)

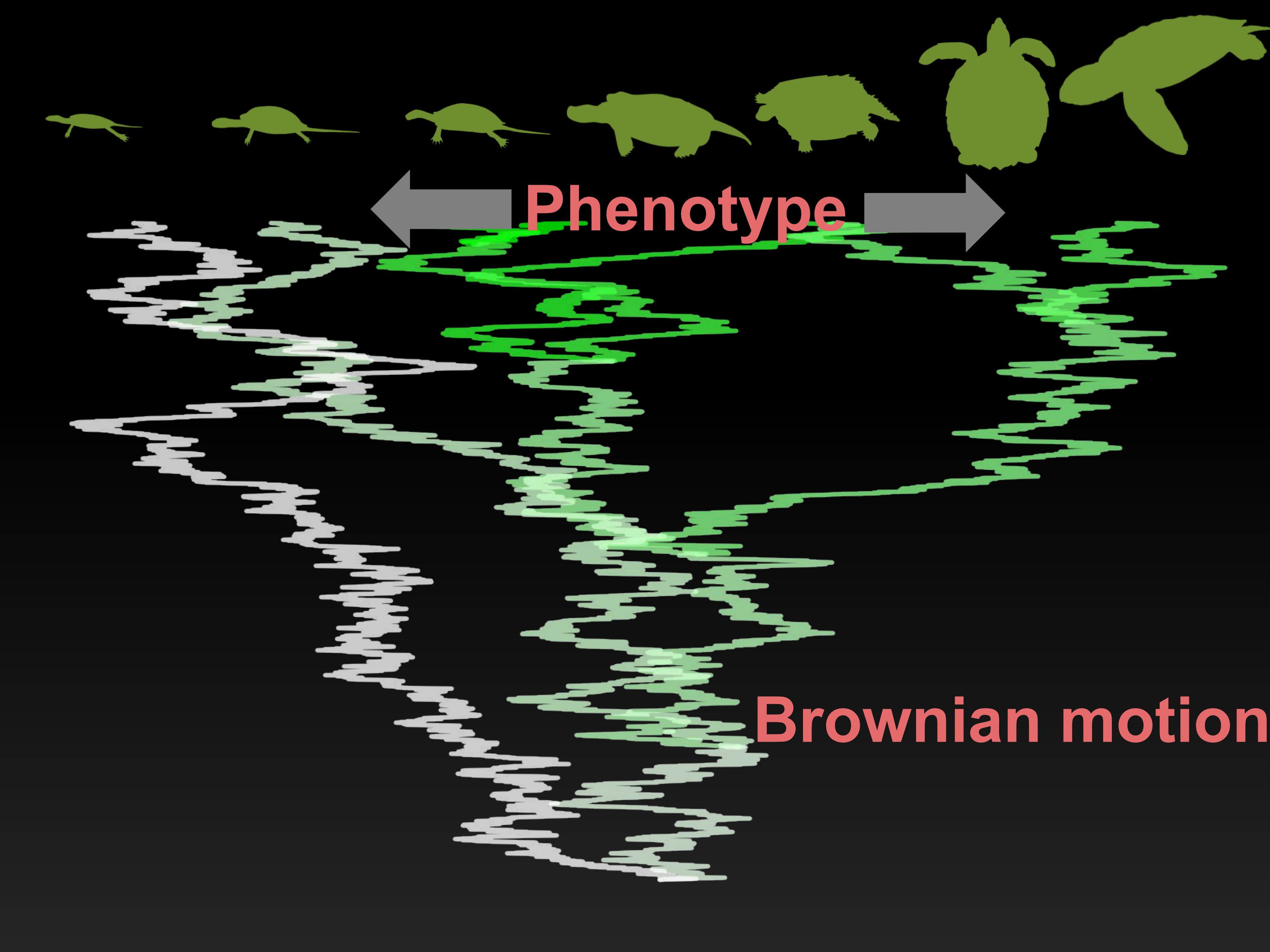
All of the above?

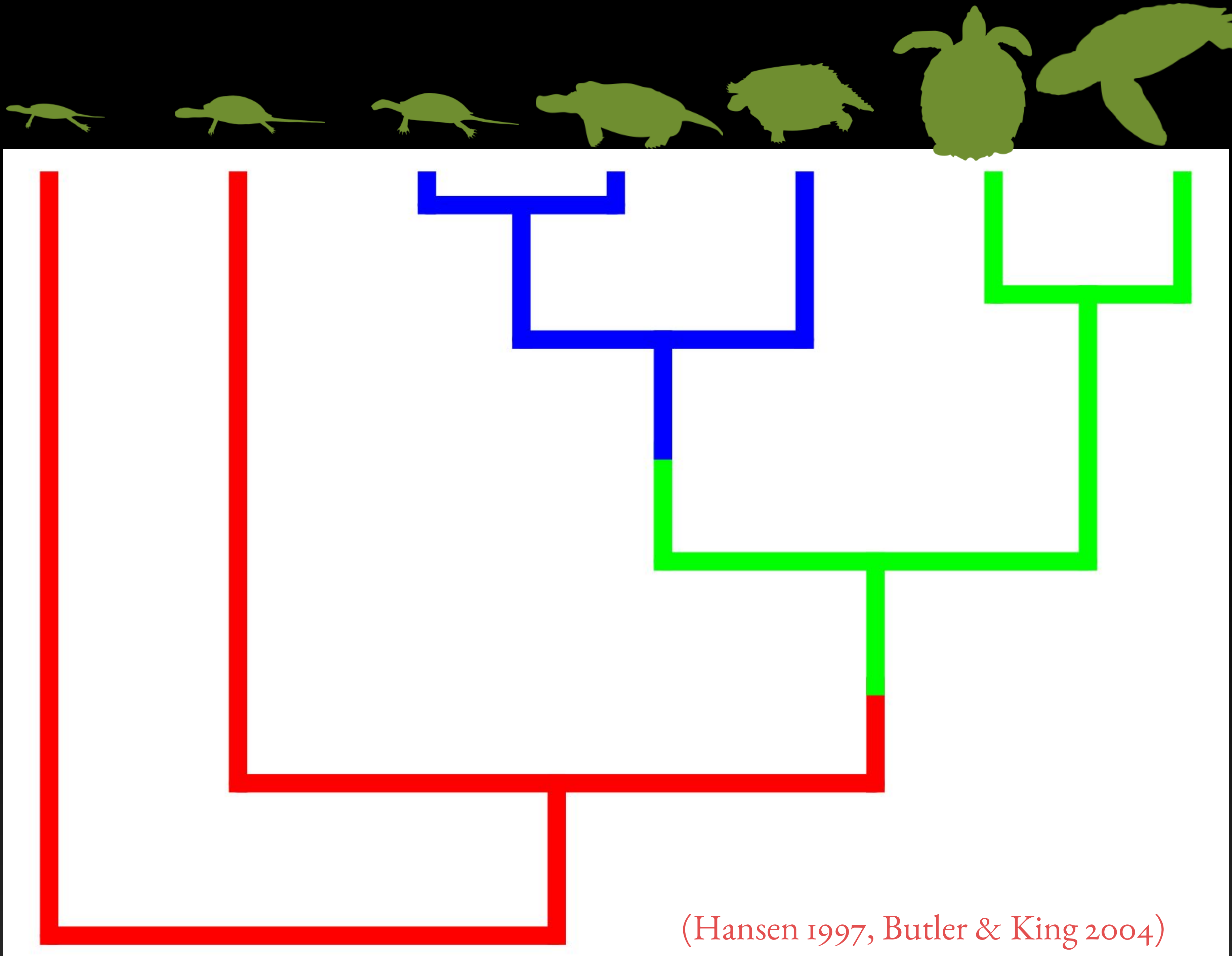
Most of Hansen & Houle's criticisms of these ideas still hold

...but it's hard to imagine that they don't all contribute

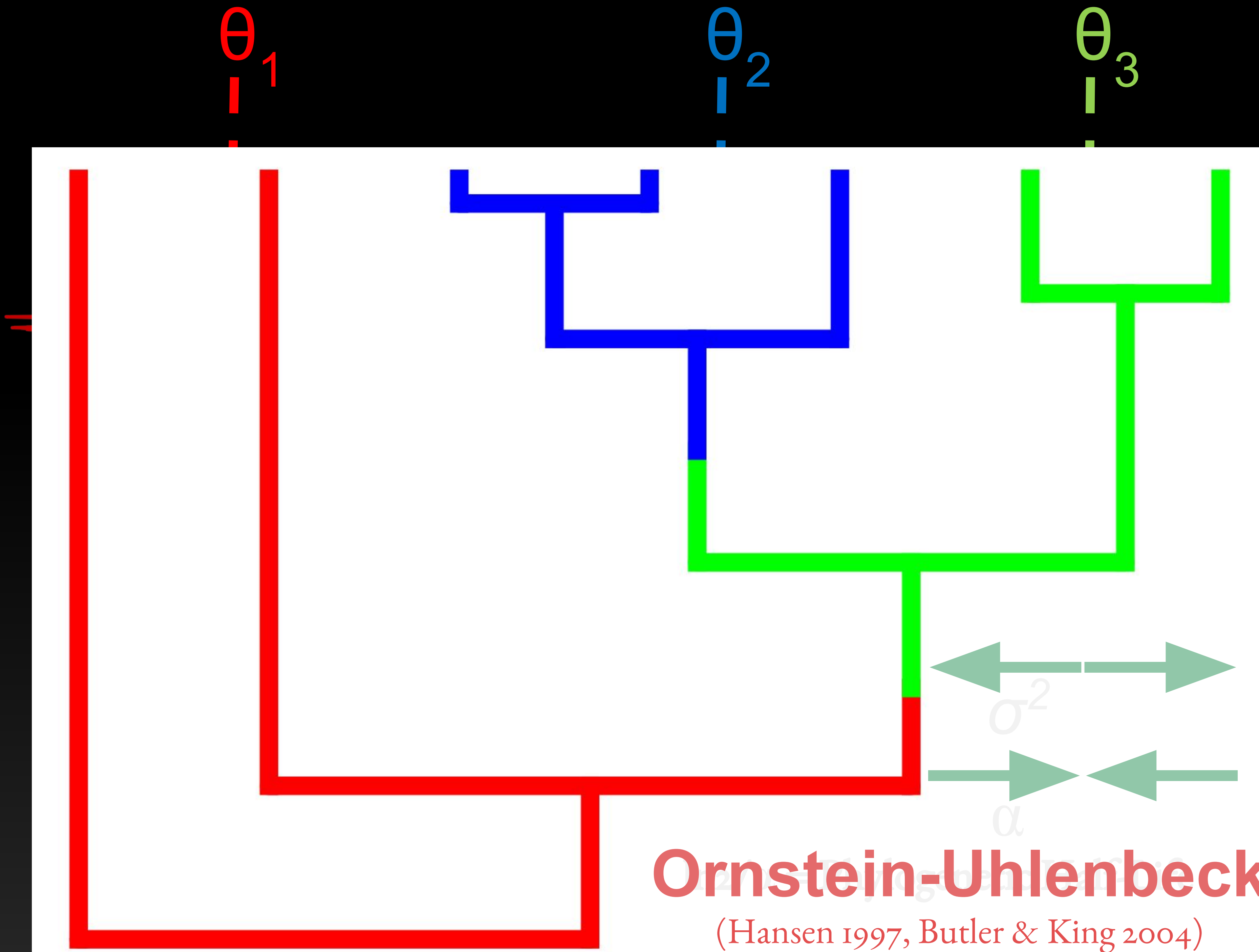
The phylogenetic comparative method




Phenotype
Brownian motion



(Hansen 1997, Butler & King 2004)



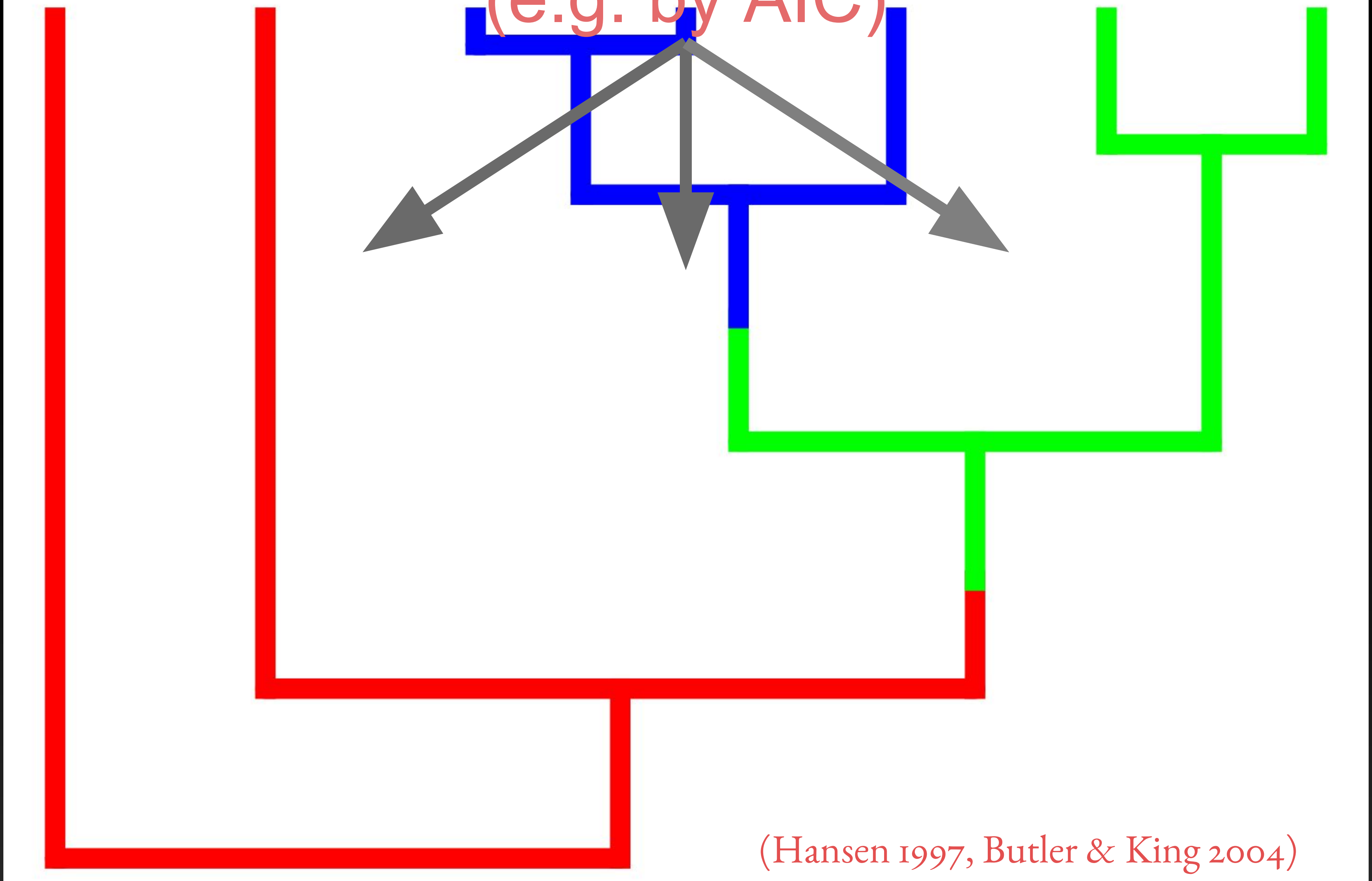
Ornstein-Uhlenbeck

(Hansen 1997, Butler & King 2004)

Compare models

Best Model

(e.g. by AIC)

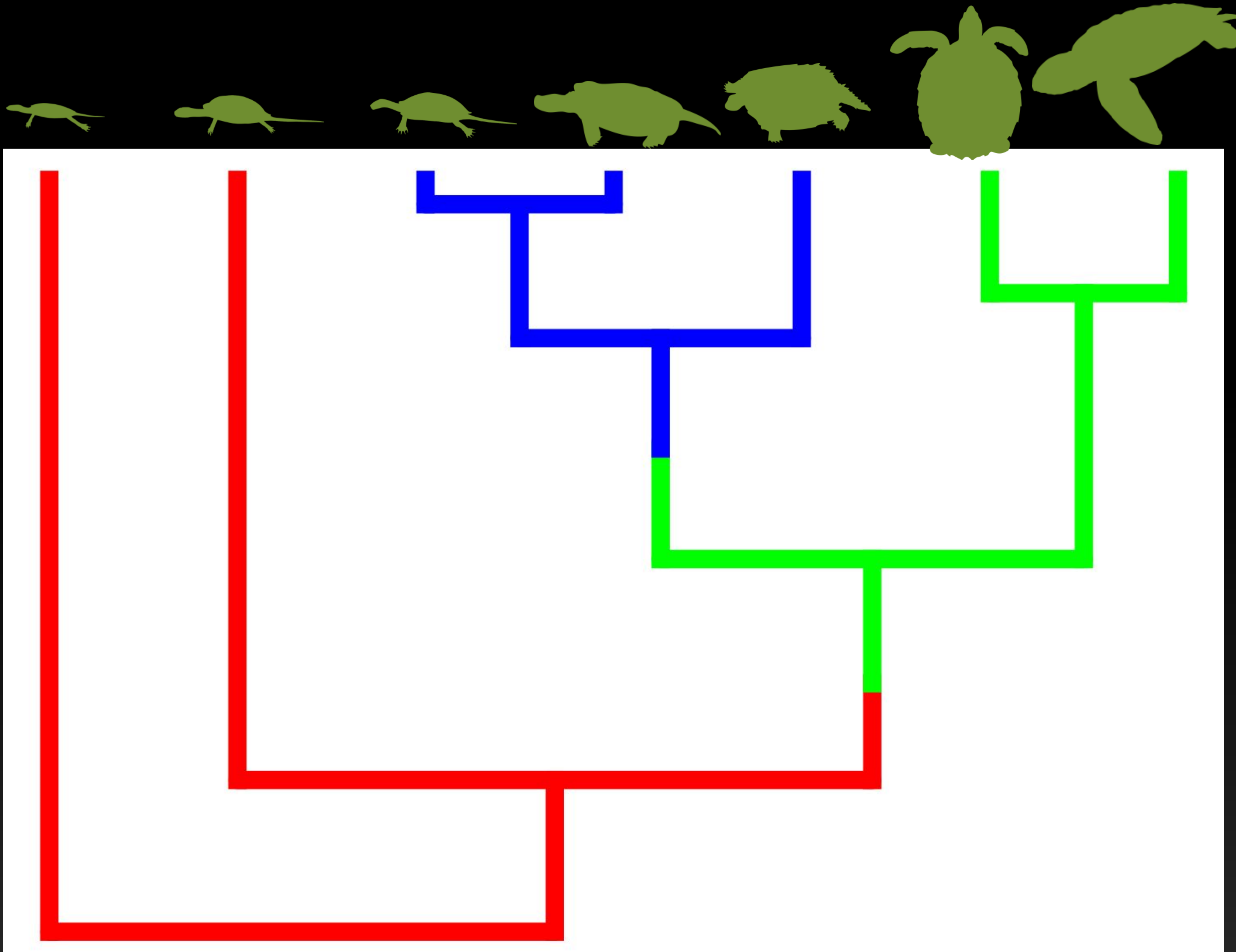


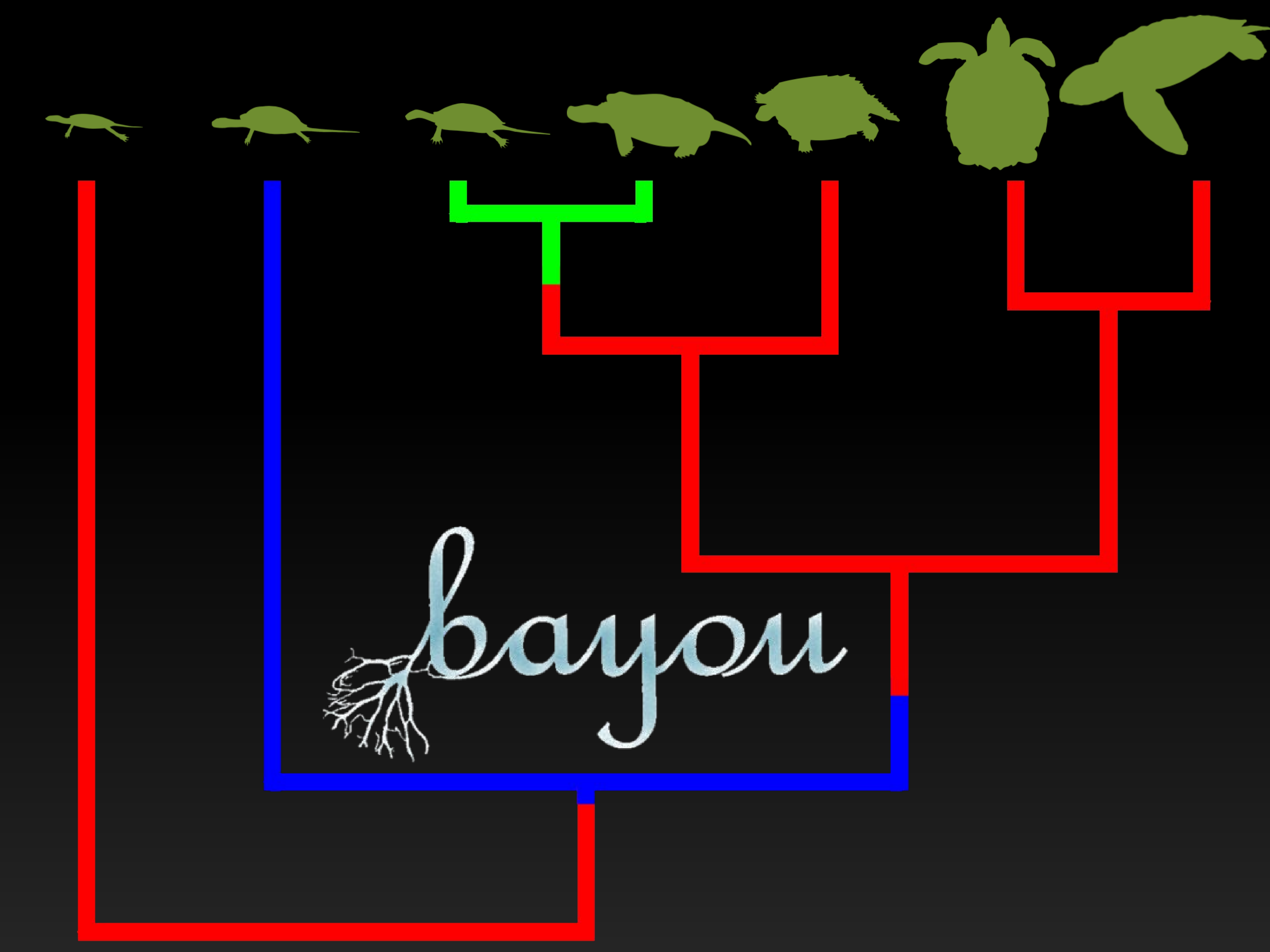
(Hansen 1997, Butler & King 2004)

Two issues

1. Best model may still be bad

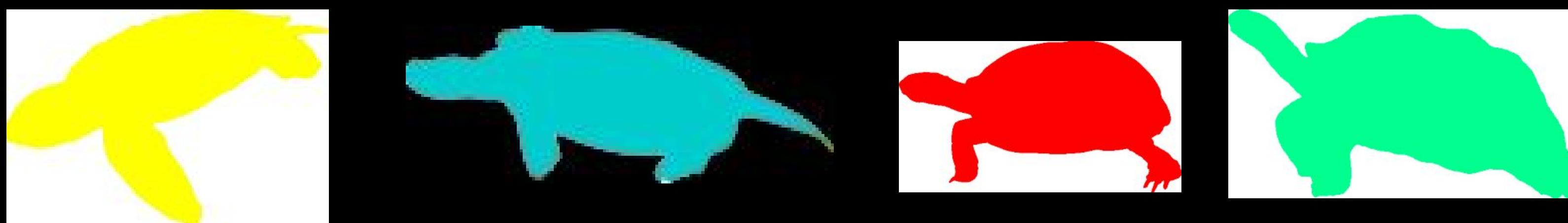
2. Model has biological meaning – but may be lost when applied to comparative data



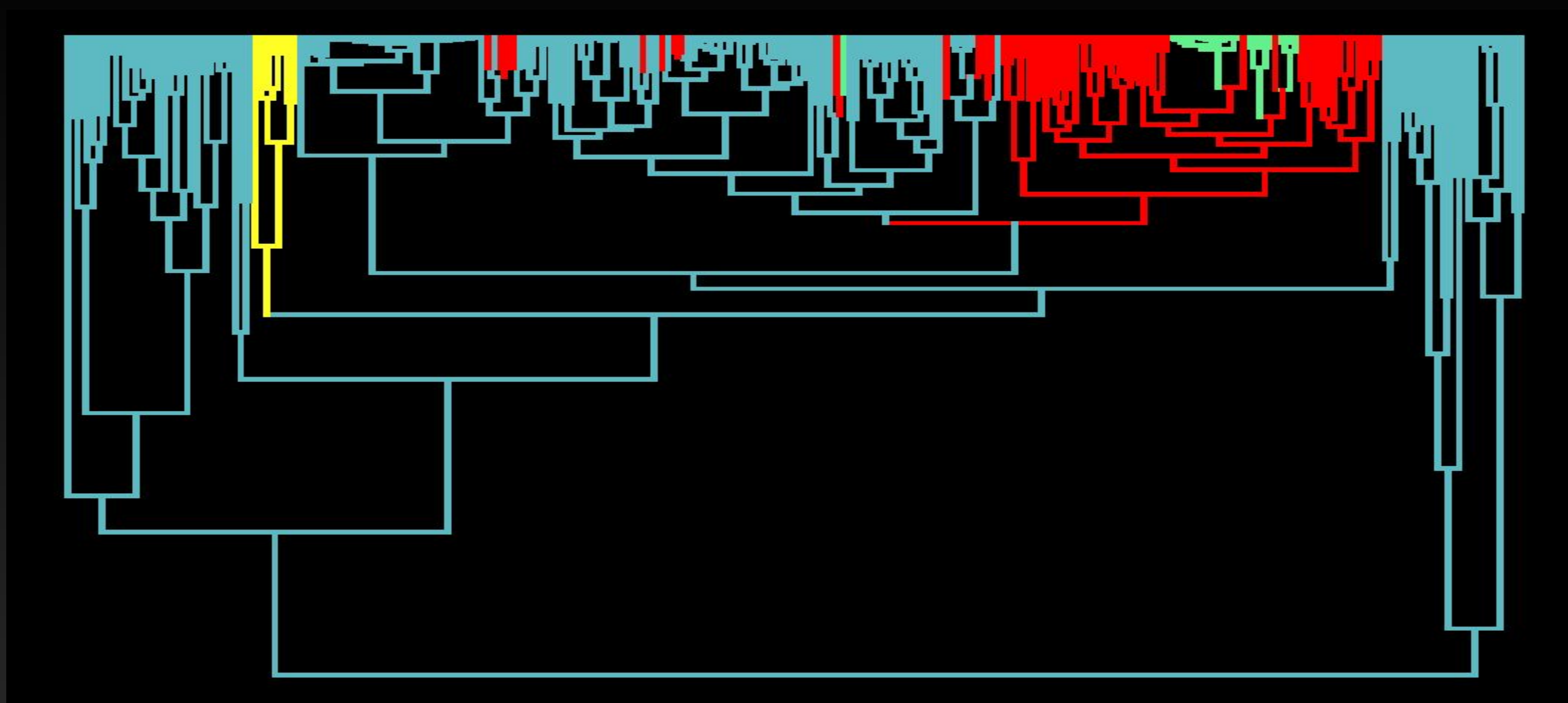

bayou

Turtles and Tortoises

(Jaffe et al. 2011)

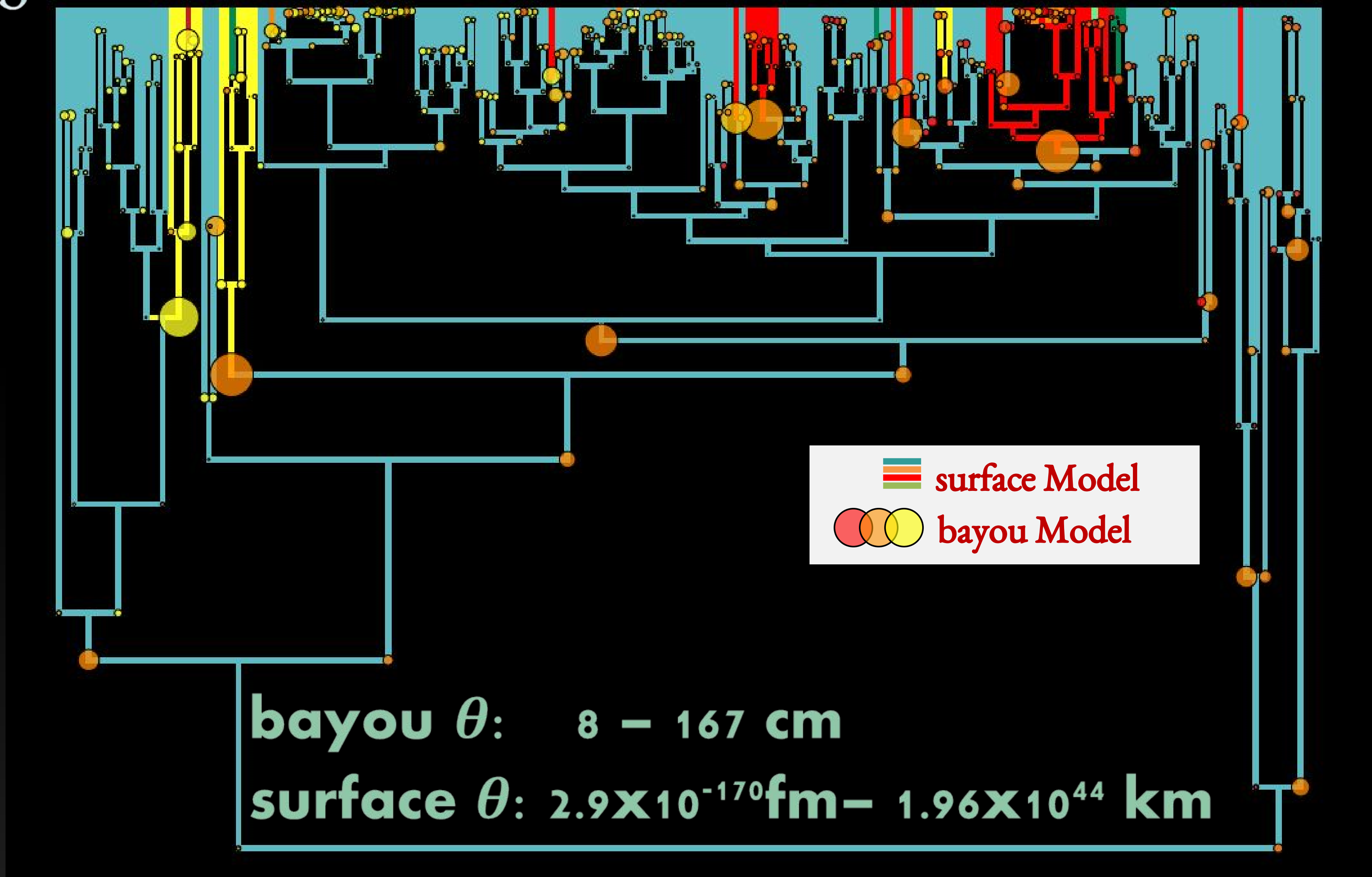


Marine Freshwater Terrestrial Island



bayou

(Uyeda and Harmon, 2014)

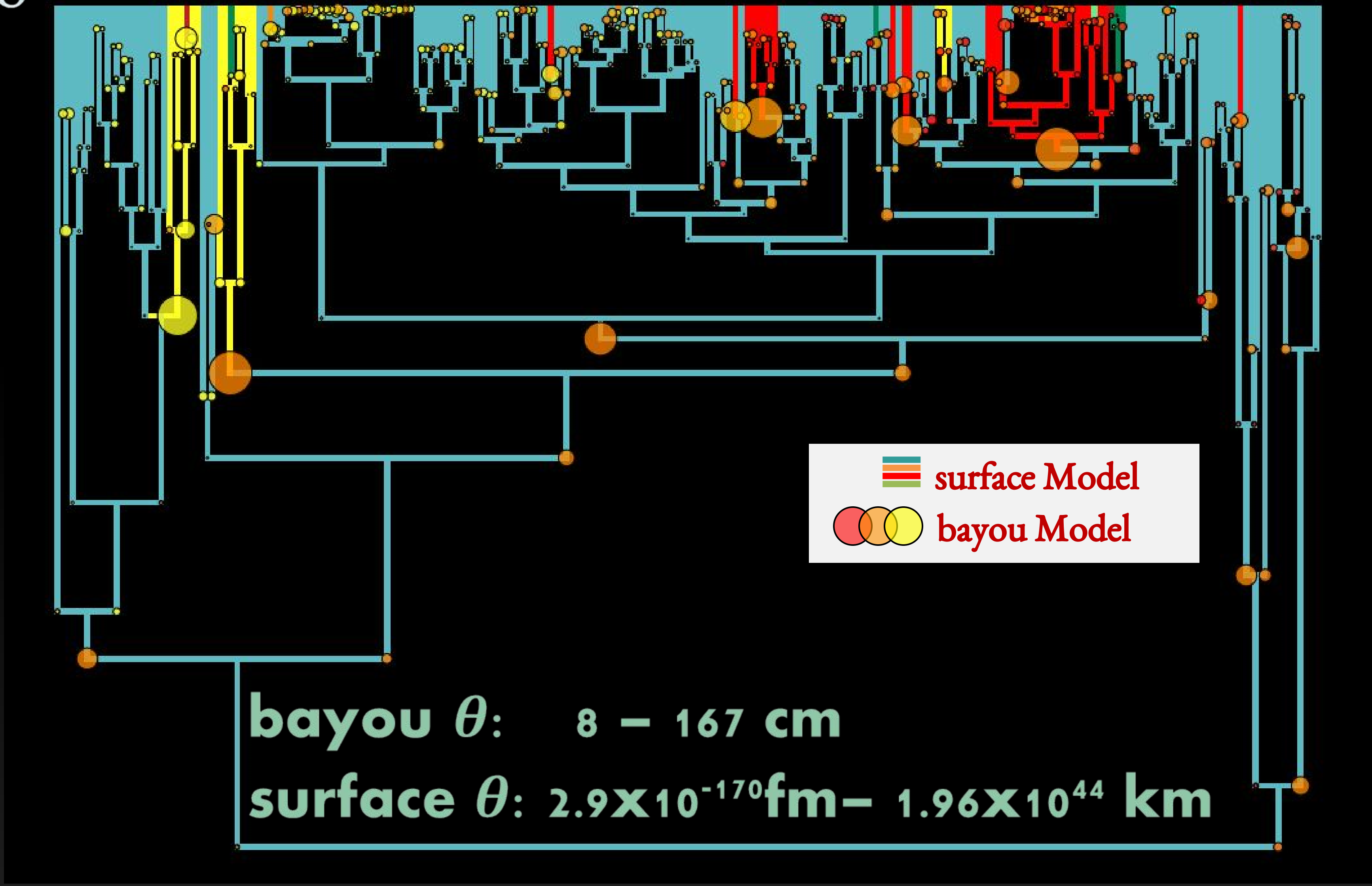


surface

(Ingram & Mahler, 2012)

bayou

(Uyeda and Harmon, 2014)



bayou phy. half-life = 3.94 million years
surface phy. half-life = 92 million years

We can generate better hypotheses

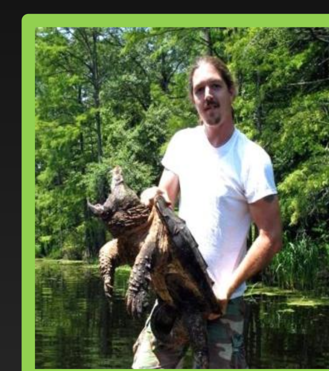
Jaffe et al. (2011)

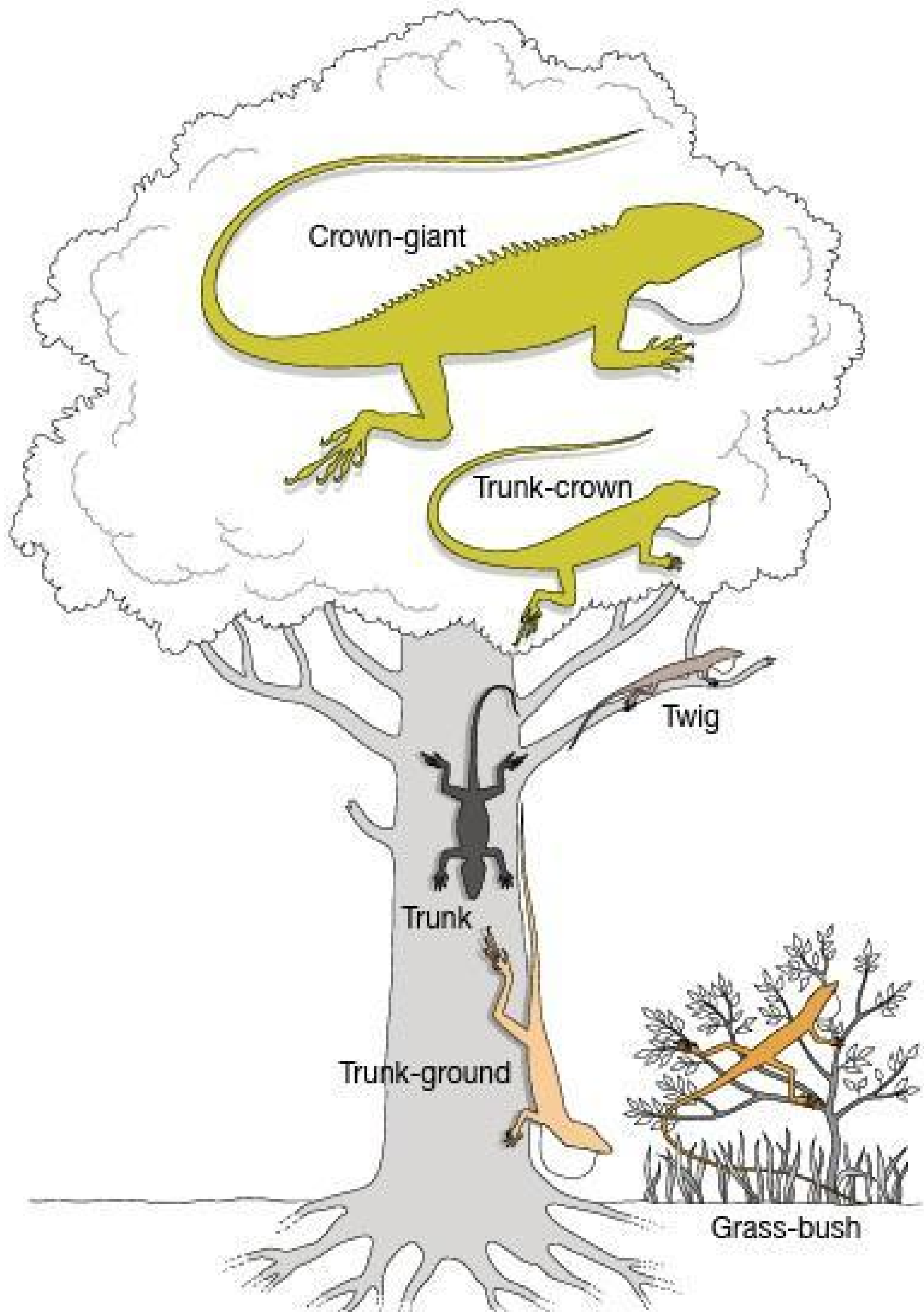
Marine, Freshwater, Terrestrial and Island

Of those, only Marine was found by bayou.

Better hypothesis?

Aquatic life history + high environmental temperature



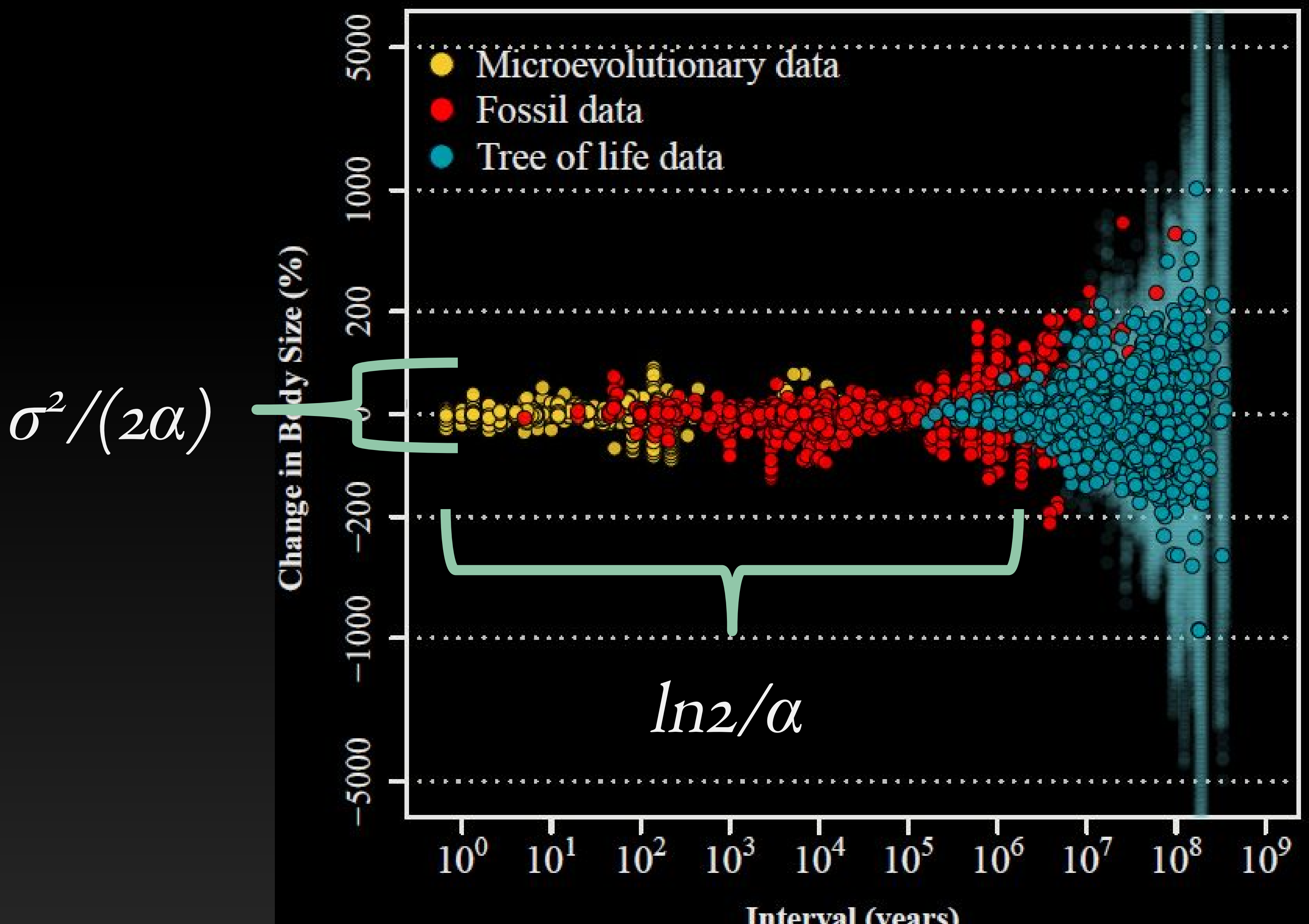


Anolis

bayou

- 85 taxa
- Body size (SVL)
- Use 3 different priors:
  - Weakly informative (Free)
  - Blunderbuss model (Stasis shifts)
  - Quantitative genetic model (Peak shifts)

“Blunderbuss” Parameterization



Quantitative Genetics Parameterization

(Lande 1976)

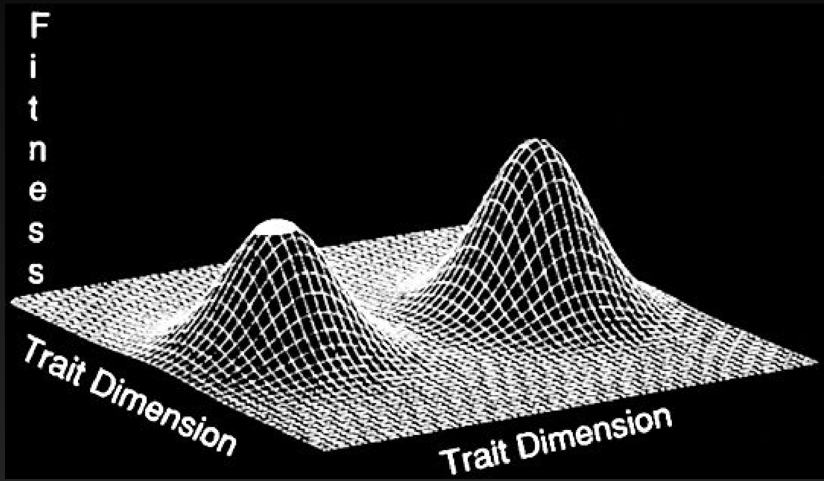
$$dZ_t \quad -\alpha\left(Z_{t-1} - \quad \right)dt + \sigma dWt$$

Stabilizing Selection

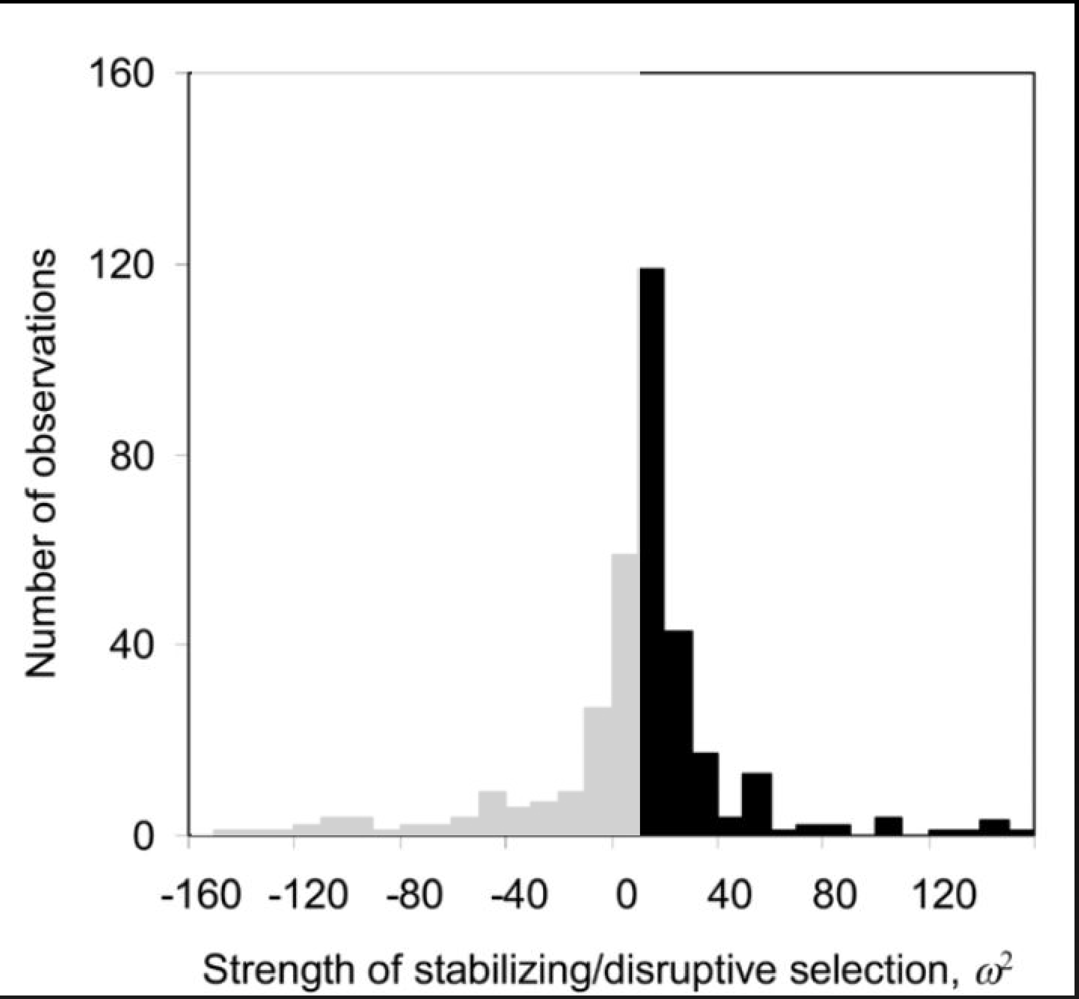
$$\alpha = h^2 V_P / (V_P + \omega^2)$$

Genetic Drift

$$\sigma^2 = h^2 V_P / N_e$$



QG model priors

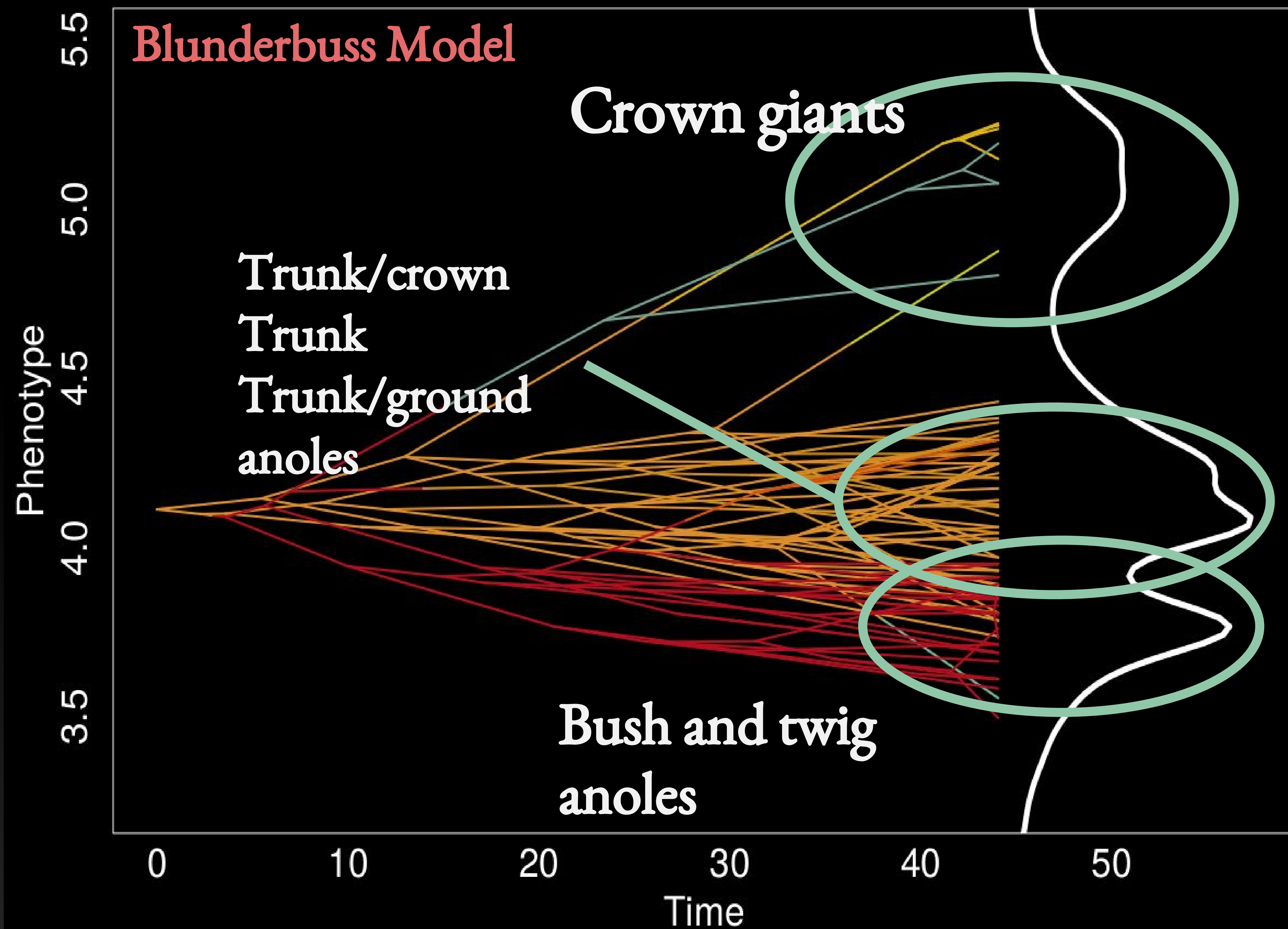


h^2 =estimated in anoles to be ~0.55 for body size

V_P=estimated from the data

Ne = 99% CI between 1000 and 400,000 (mean 22,000)

ω^2= Stabilizing & directional selection gradients estimated from wild populations


Blunderbuss Model
Crown giants
Trunk/crown
Trunk
Trunk/ground
anoles
Bush and twig
anoles
Phenotype
5.5
5.0
4.5
4.0
3.5
0
10
20
30
40
50
Time

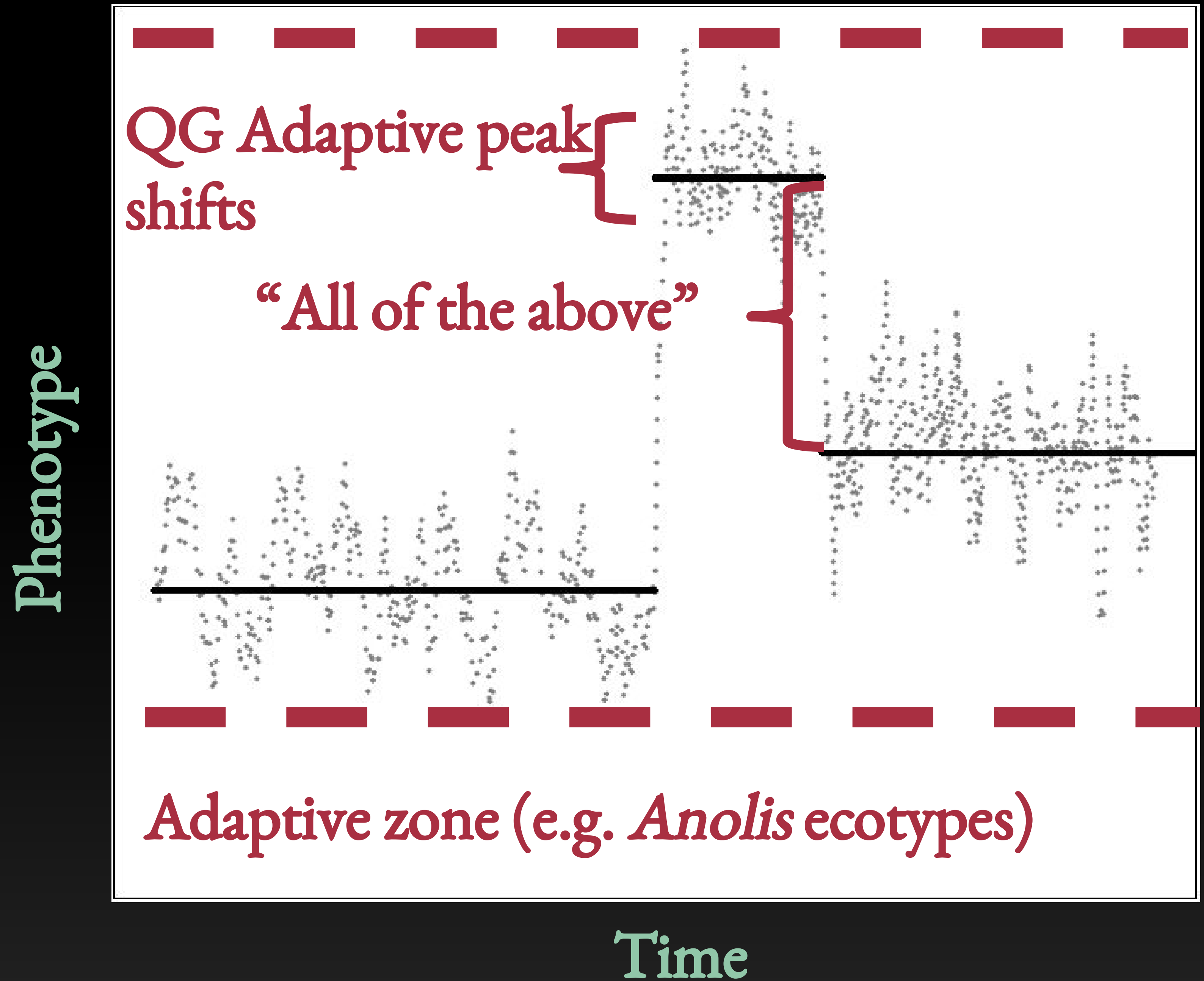
Both Blunderbuss and Lande models perform much more poorly than free parameterization

Parameterization	Marginal lnL	2 ln BF: Free vs. ______
Free	-16.4	0
Blunderbuss	-24.9	17.0
Lande (QG)	-37.7	21.3

Can also combine these interpretations with ecotype-based hypotheses.....

Convergent, Ecotype-based regimes fit tree best, but should not be interpreted as either Blunderbuss or Lande model

Regimes	Parameterization	Convergence	Marginal lnL
Fixed- Ecotype	Free	Yes	9.83
Fixed- Ecotype	Blunderbuss	Yes	2.73
Fixed- Ecotype	Free	No	-3.62
Fixed- Ecotype	Lande (QG)	Yes	-6.70
Fixed- Ecotype	Blunderbuss	No	-14.16
Free	Free	No	-16.41
Fixed- Ecotype	Lande (QG)	No	-18.66
Free	Blunderbuss	No	-24.93
Free	Lande (QG)	No	-37.73


QG Adaptive peak shifts
"All of the above"
Adaptive zone (e.g. *Anolis* ecotypes)
Phenotype
Time

Conclusions

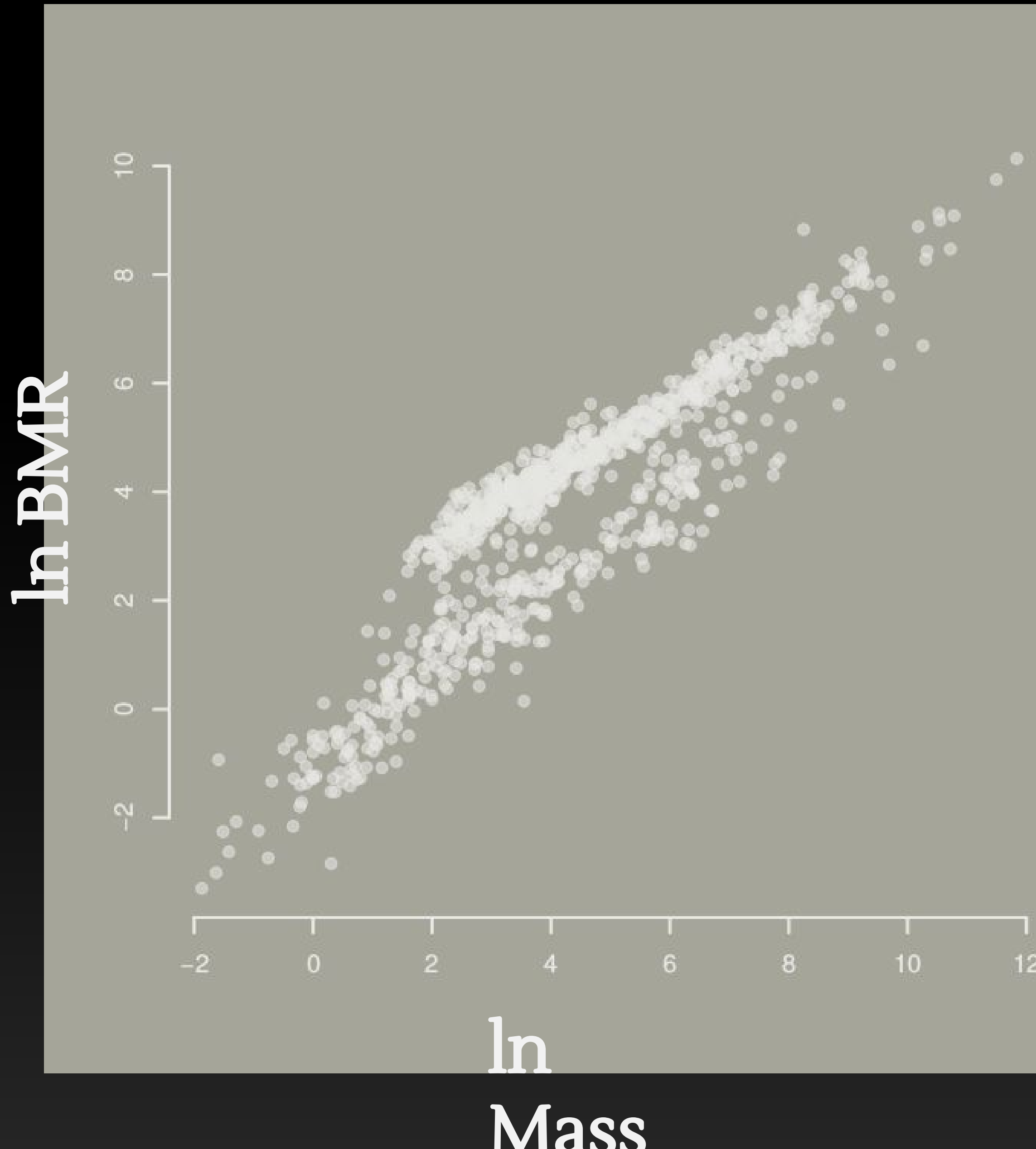
All datasets point toward a common pattern with million-year thresholds

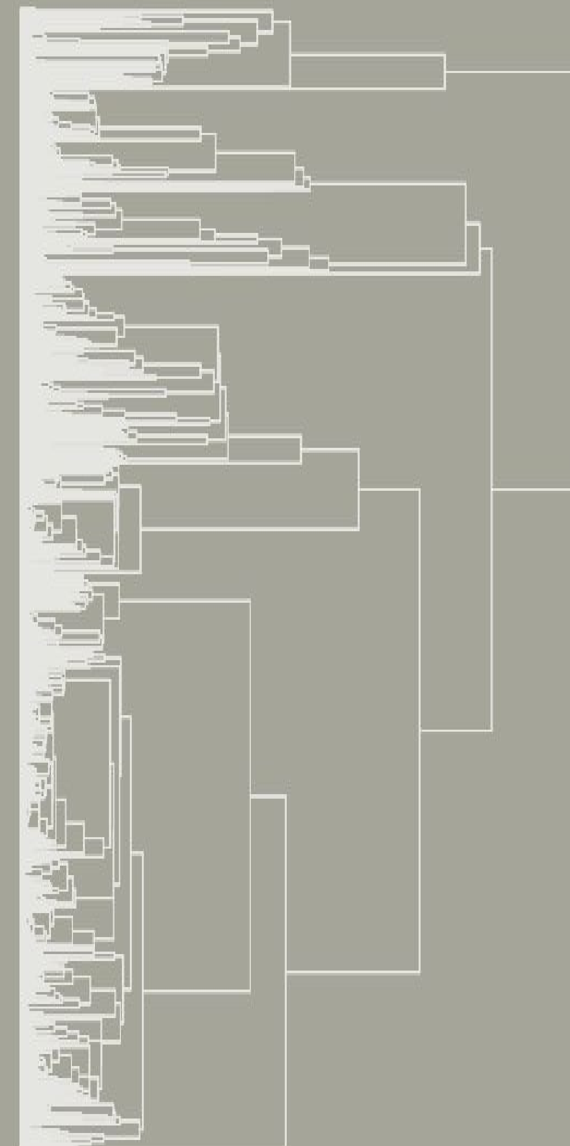
(but why remains...)

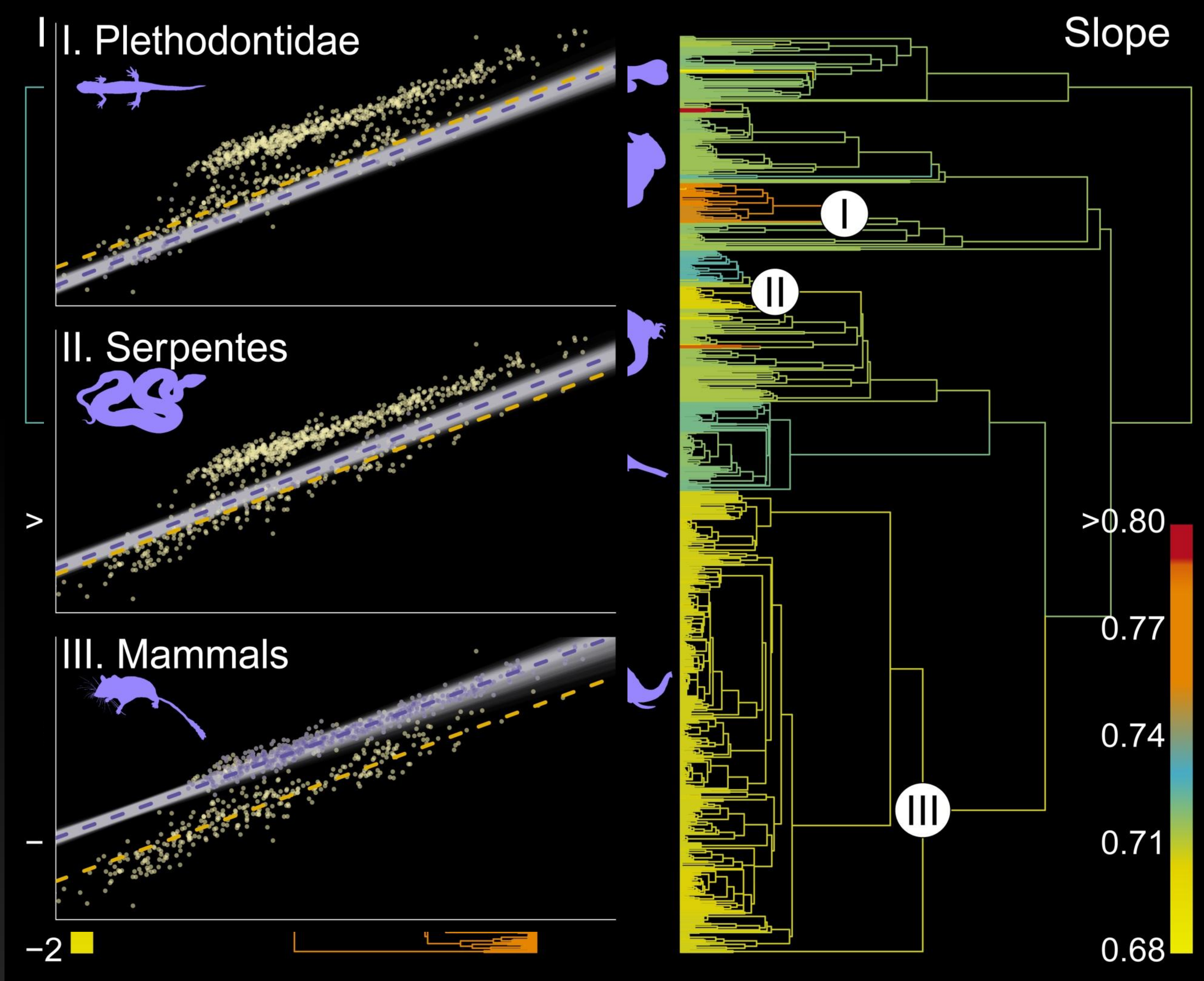
We can understand the causes of adaptive shifts by using biologically realistic Bayesian models – Analyze data jointly across scales

Just the beginning....

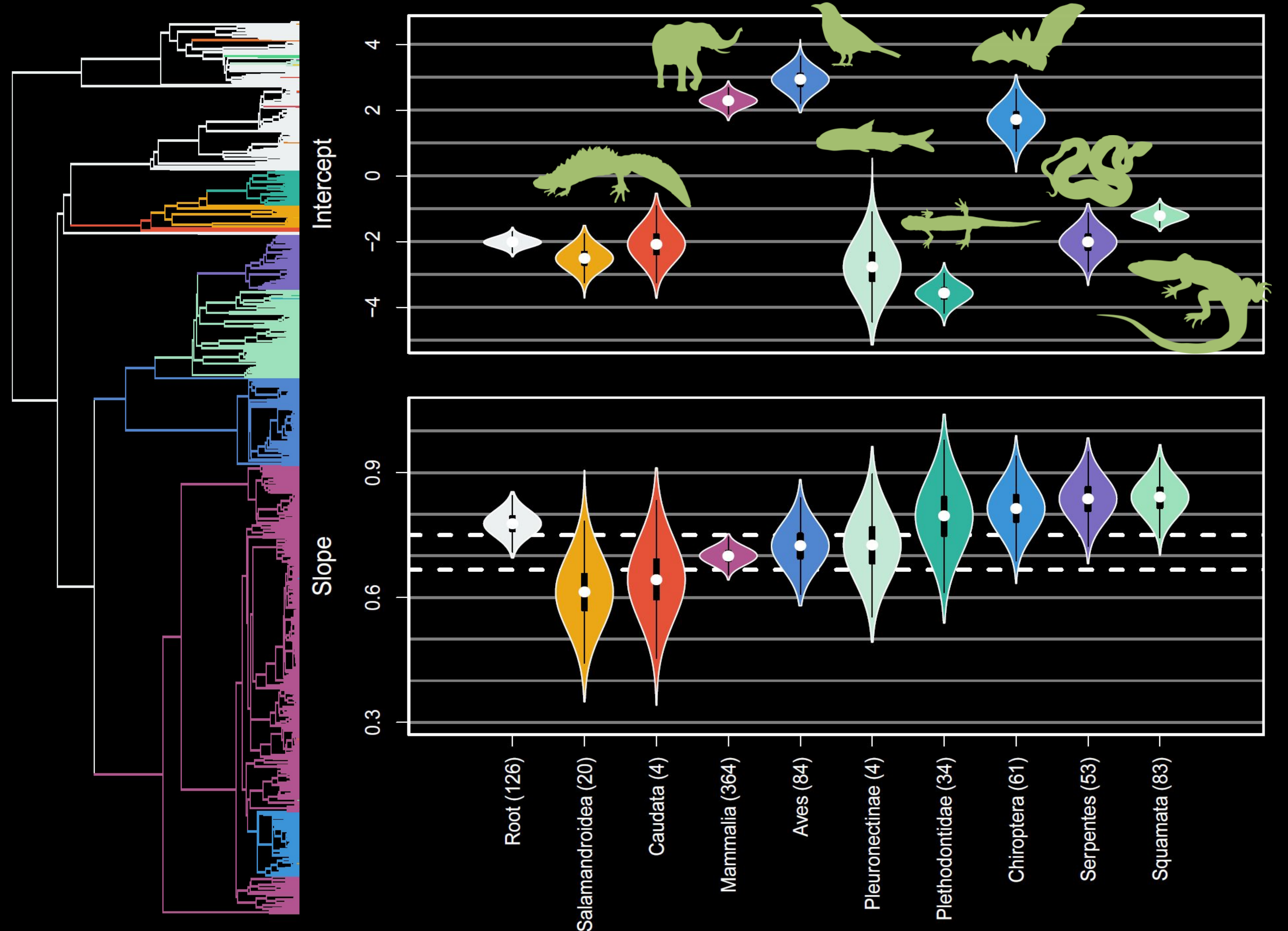
Basal Metabolic Rates







I. Plethodontidae
II. Serpentes
III. Mammals
Slope
I
II
III
>0.80
0.77
0.74
0.71
0.68
−2



Intercept
4
2
0
-2
-4
Slope
0.9
0.6
0.3
Root (126)
Salamandroidea (20)
Caudata (4)
Mammalia (364)
Aves (84)
Pleuronectinae (4)
Plethodontidae (34)
Chiroptera (61)
Serpentes (53)
Squamata (83)

bayou v2.0-alpha

- Reversible-jump & Fixed models
- Flexible prior specification
- Alternative OU parameterizations
- Flexible model implementation (including regression models)
- Impute missing predictors using BM
- Model comparisons using Bayes Factors

Warnings

- bayou tends to be conservative
- Convergence can be difficult
- Identifiability of shift configurations
- Identifiability of shift numbers
- Bayes Factors are influenced by priors
- Cannot yet do RJ + convergent regimes

Tomorrow: *bayou* computer exercise

Have a working development environment:

Mac: Install Xcode

Windows: Install Rtools

Install R packages:

devtools, treeplyr

You are encouraged to run through the posted code ahead of time, and use tomorrow's time to develop and analyze your own question

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Questions?