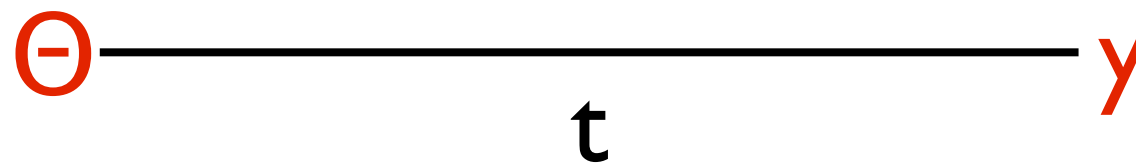


Other Models for Continuous Characters



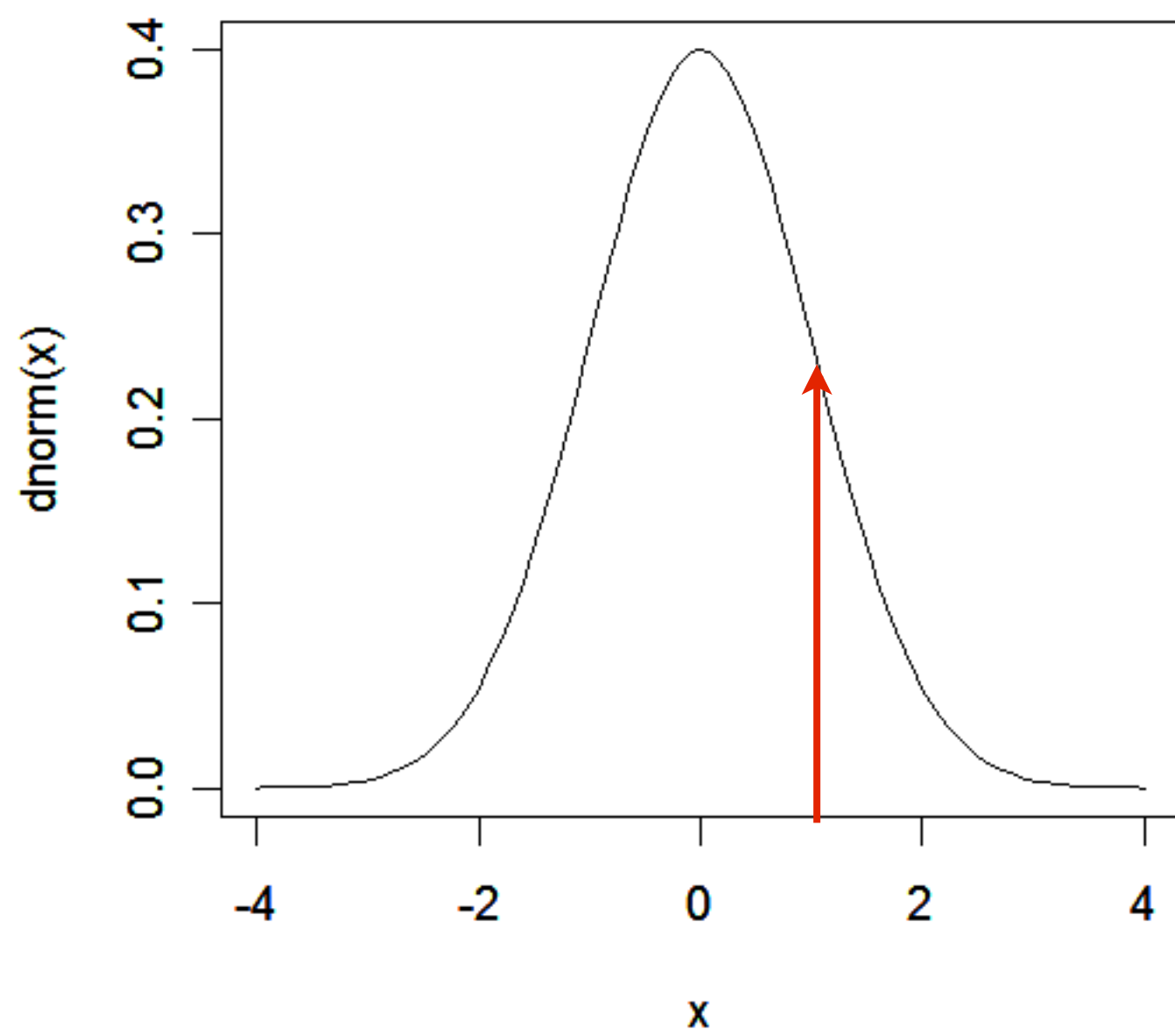
Likelihood for a single character

Brownian motion

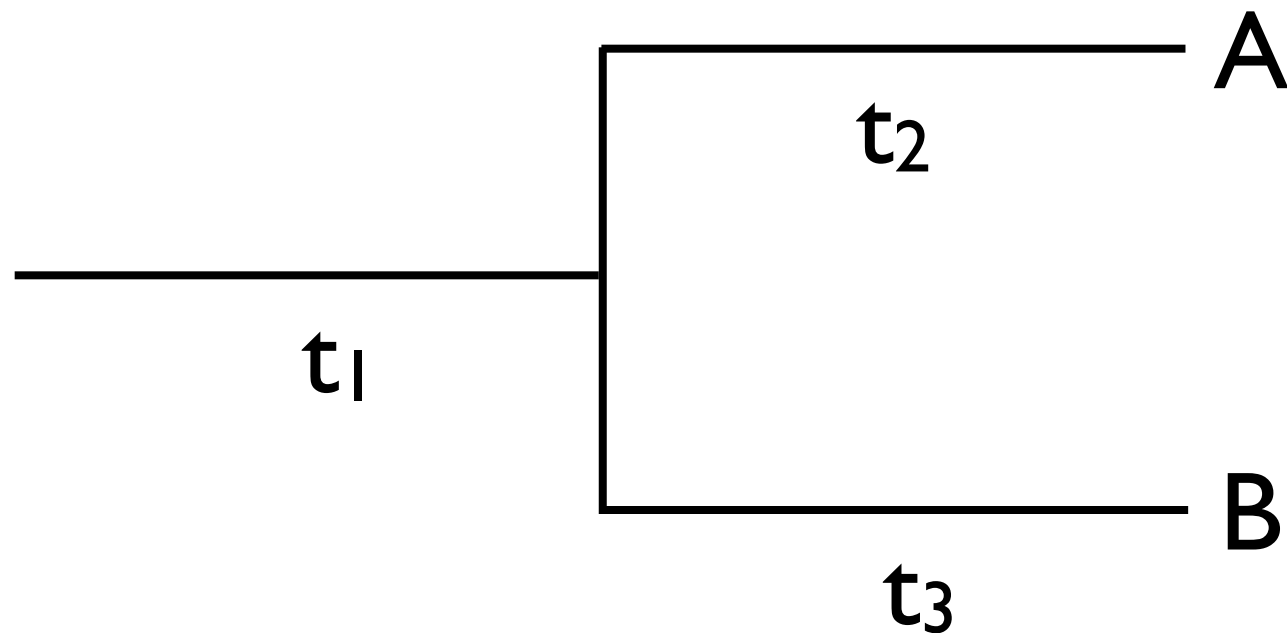


$$y \sim N(0, \sigma^2 * t)$$

$$\Pr[y = x] = \frac{1}{\sigma\sqrt{2\pi t}} \exp\left(-\frac{(x - \theta)^2}{2\sigma^2 t}\right)$$



Multivariate Normal



variance-covariance
matrix

$$\sigma^2 \begin{bmatrix} t_1 + t_2 & t_1 \\ t_1 & t_1 + t_3 \end{bmatrix}$$

$$\text{var}(A) = \sigma^2(t_1 + t_2)$$

$$\text{cov}(A, B) = \sigma^2(t_1)$$

$$\text{var}(B) = \sigma^2(t_1 + t_3)$$

C

Two dimensions (x, y) correspond to tree with n=2

$$f(x, y) = \frac{1}{2\pi\sigma_x\sigma_y\sqrt{1-\rho^2}} \exp\left(-\frac{1}{2(1-\rho^2)}\left(\frac{x^2}{\sigma_x^2} + \frac{y^2}{\sigma_y^2} - \frac{2\rho xy}{(\sigma_x\sigma_y)}\right)\right)$$

More dimensions gets more complicated
Easy to do with computers

Other Models for Phenotypic Evolution

- Brownian Motion (BM)
- Early Burst (EB)
- Ornstein-Uhlenbeck (OU)

Brownian Motion (BM)

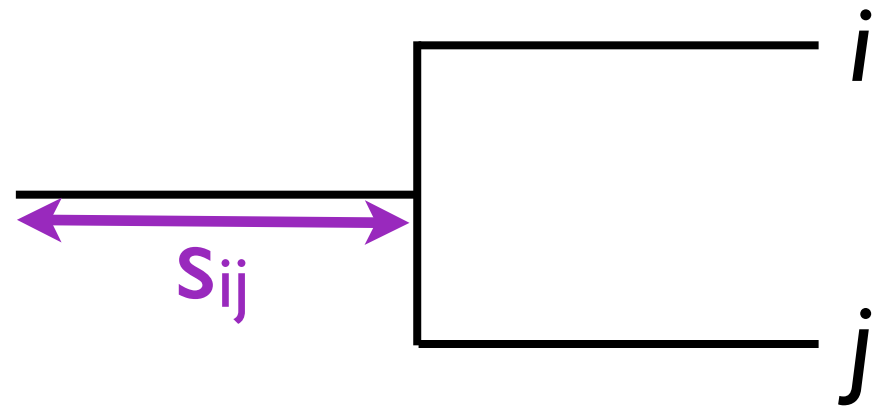
- Brownian motion model with a constant rate of evolution
- Two parameters: starting value (Θ) and rate (σ^2)

Early Burst Model (EB)

- Rate of evolution slows through time
- Highest rate at the root of the tree
- Three parameters: starting value (Θ), starting rate (σ_0^2), and rate change (r)

$$r(t) = \sigma_0^2 e^{rt}$$

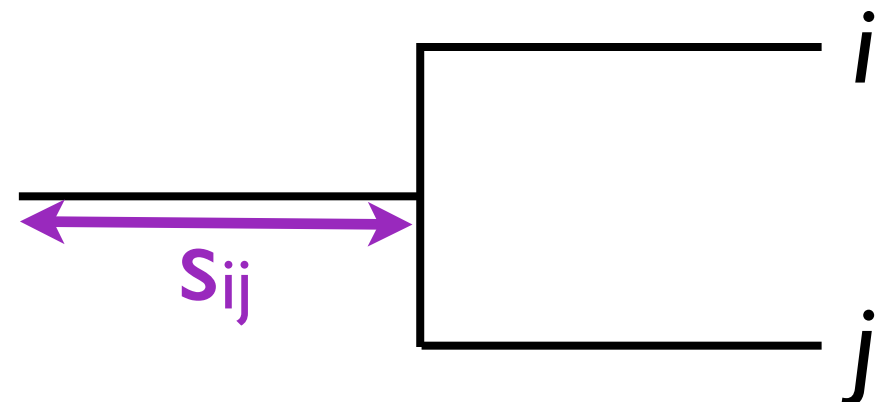
$$V_{ij} = \int_0^{s_{ij}} \sigma_0^2 e^{rt} dt = \sigma_0^2 \frac{e^{rs_{ij}} - 1}{r}$$



Ornstein-Uhlenbeck Model (OU)

- Evolution has a tendency to move towards some medial value
- “Brownian motion with a spring”
- Three parameters: starting value (Θ), rate (σ^2), and constraint parameter (α)

$$V_{ij} = \frac{\sigma^2}{\alpha} e^{-2\alpha(T-s_{ij})} (1 - e^{-2\alpha s_{ij}})$$



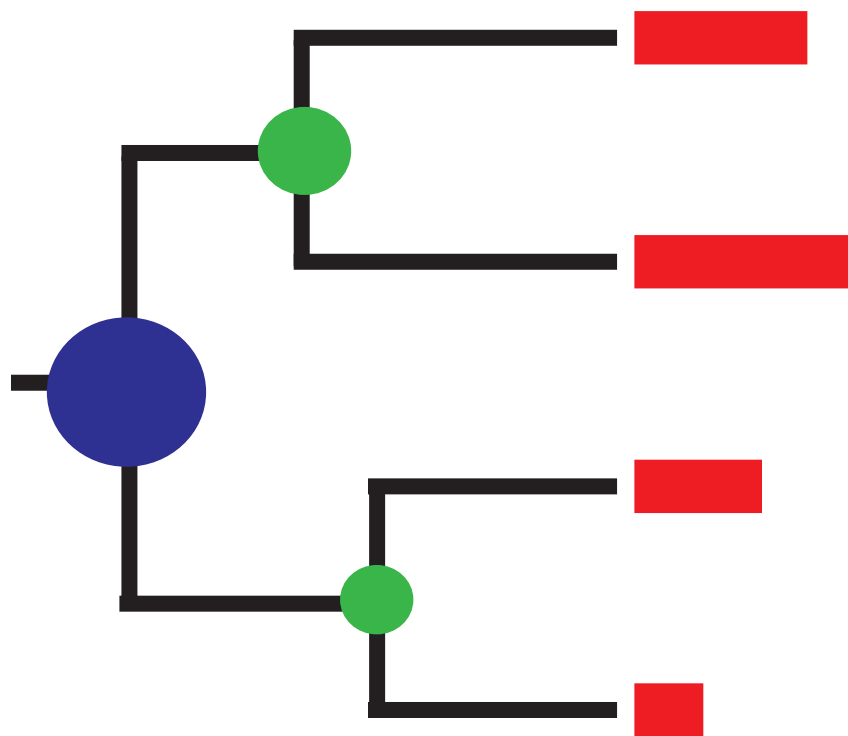
T = total tree depth

Why these three?

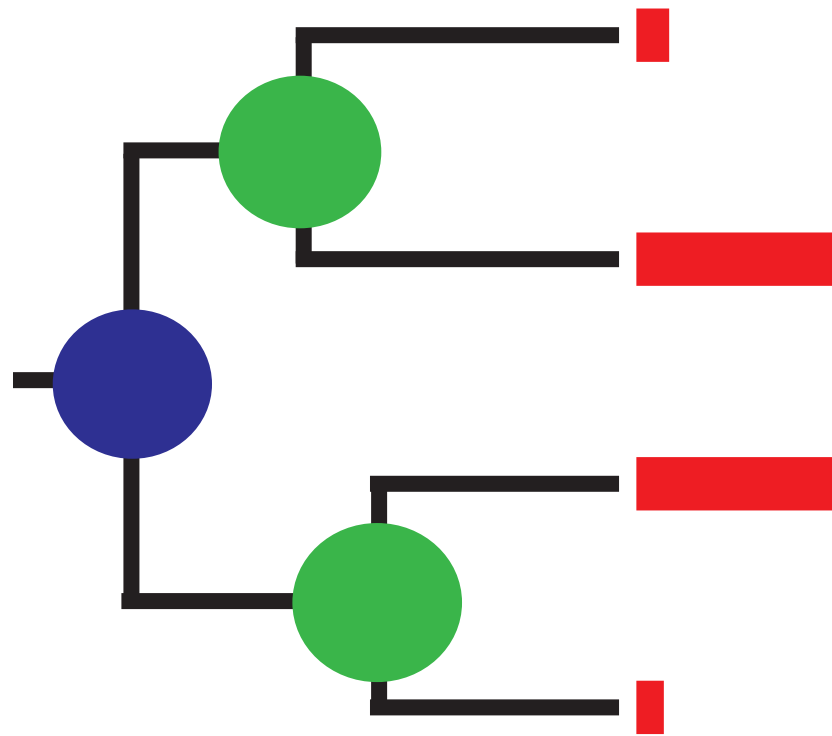
- BM is assumed by almost all phylogenetic comparative methods
- EB corresponds to one idea of adaptive radiation
- OU may capture the importance of constraints on evolution

How do we tell these models apart?

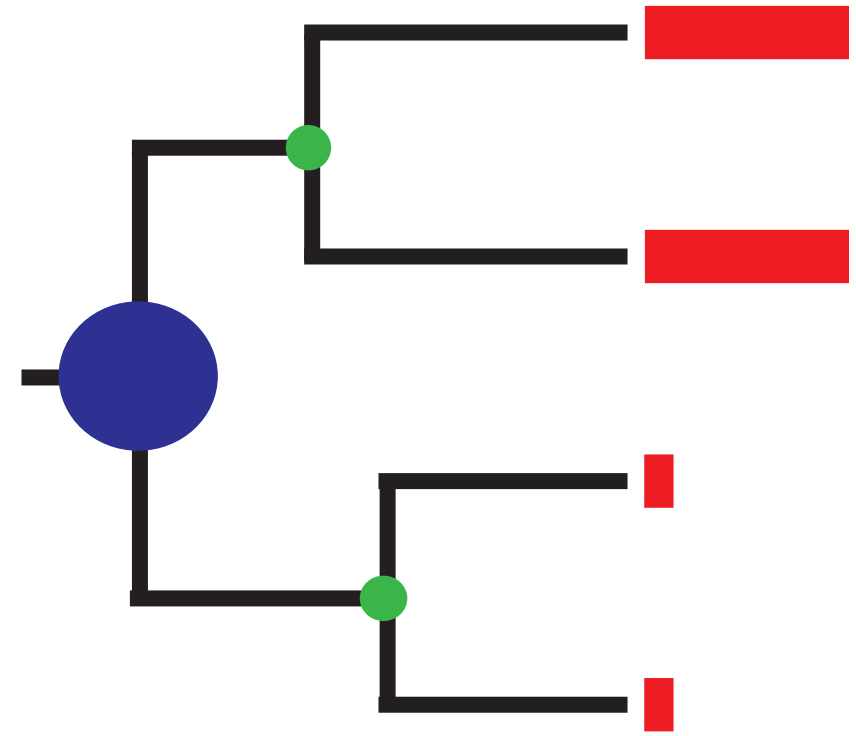
BM



CC



EB



~~Brownian motion =
drift~~

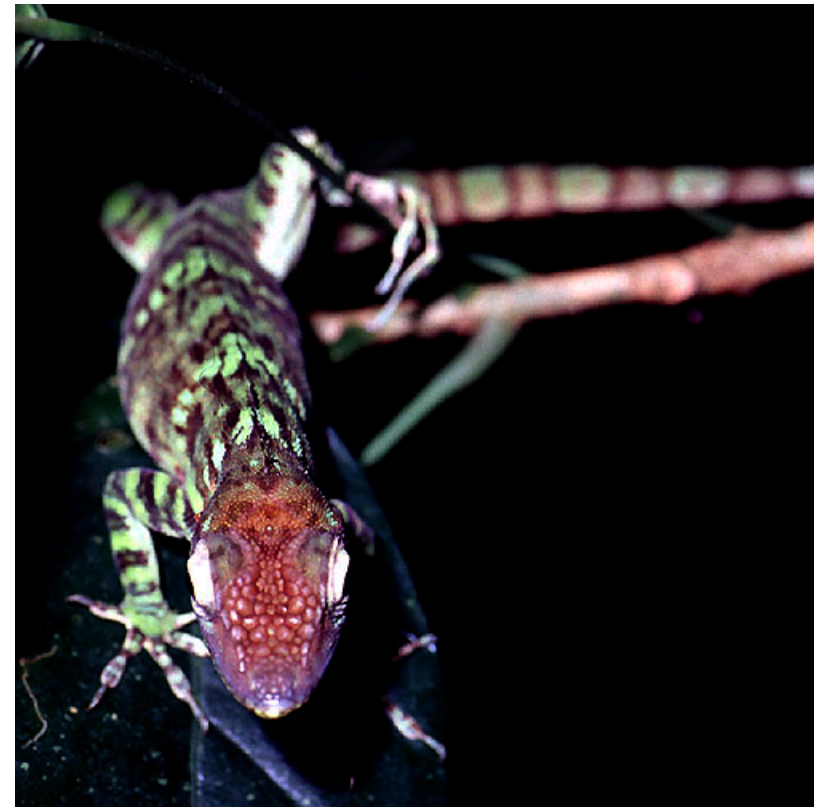
~~OU =
stabilizing
selection~~

Brownian motion =
drift or many other
processes

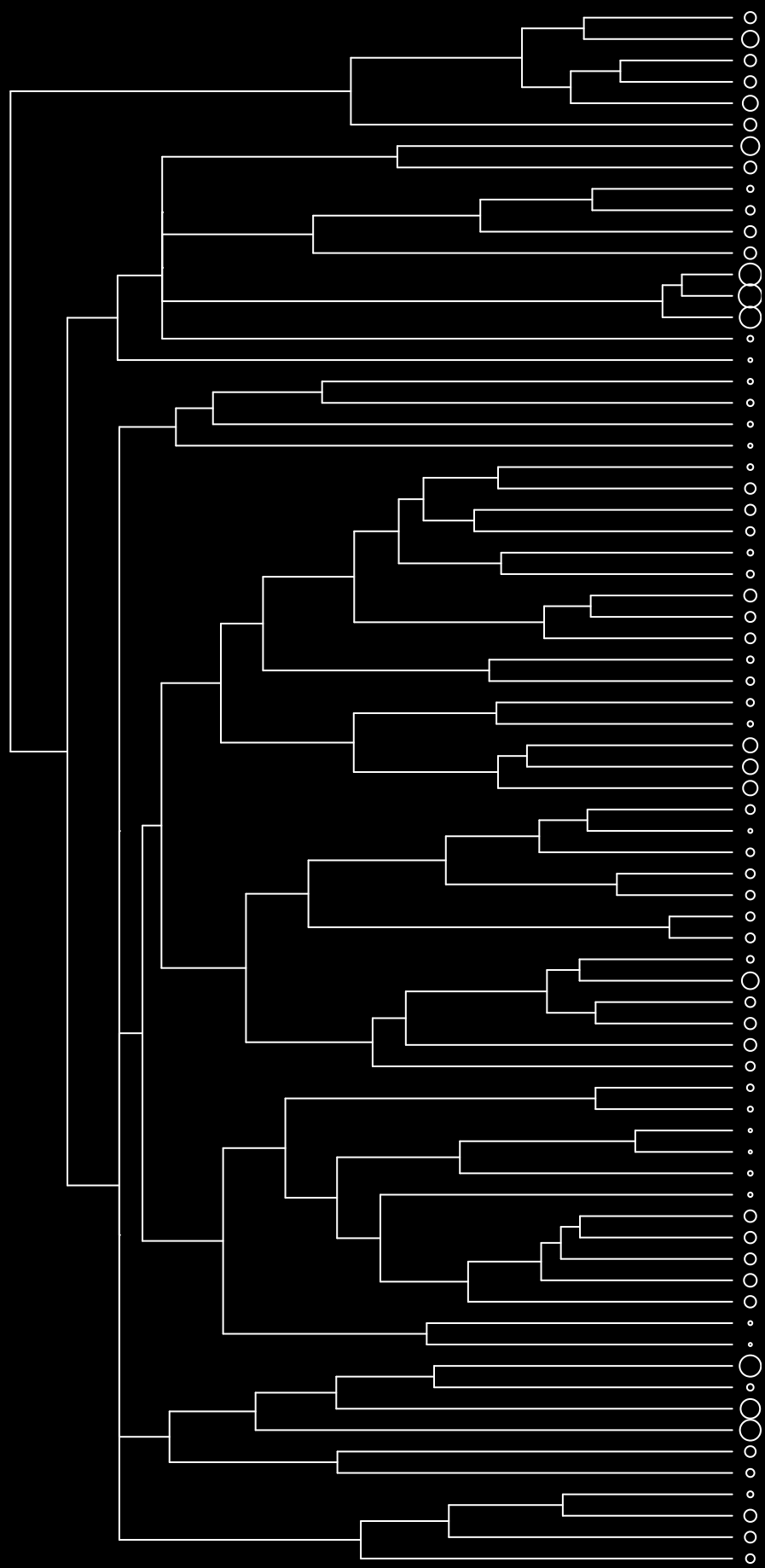
OU =
stabilizing
selection or many
other processes

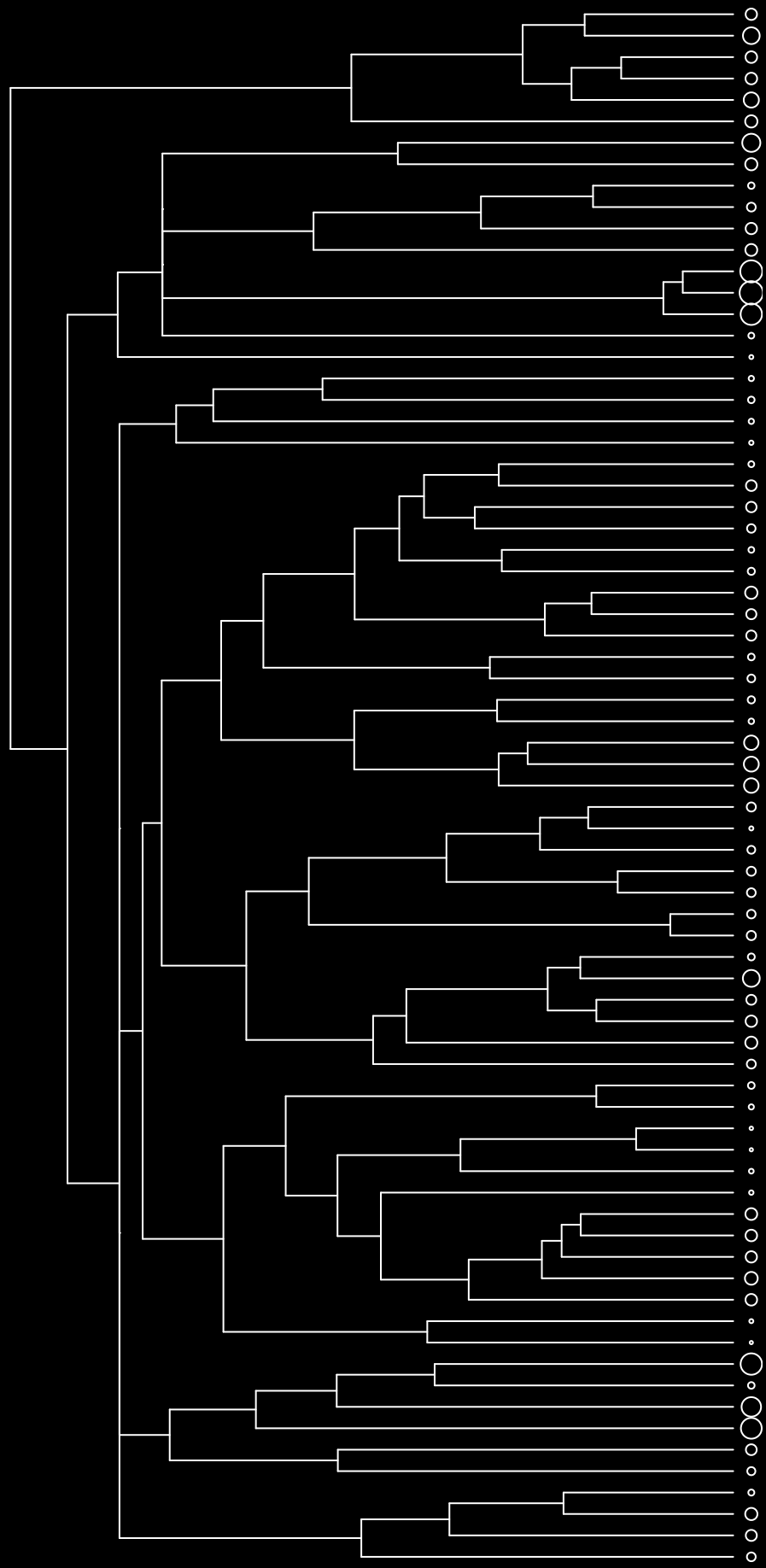
Example: *Anolis* lizards

- Lizards on Caribbean islands
- Phylogenetic and body size data for 73 species (out of ~140 total)

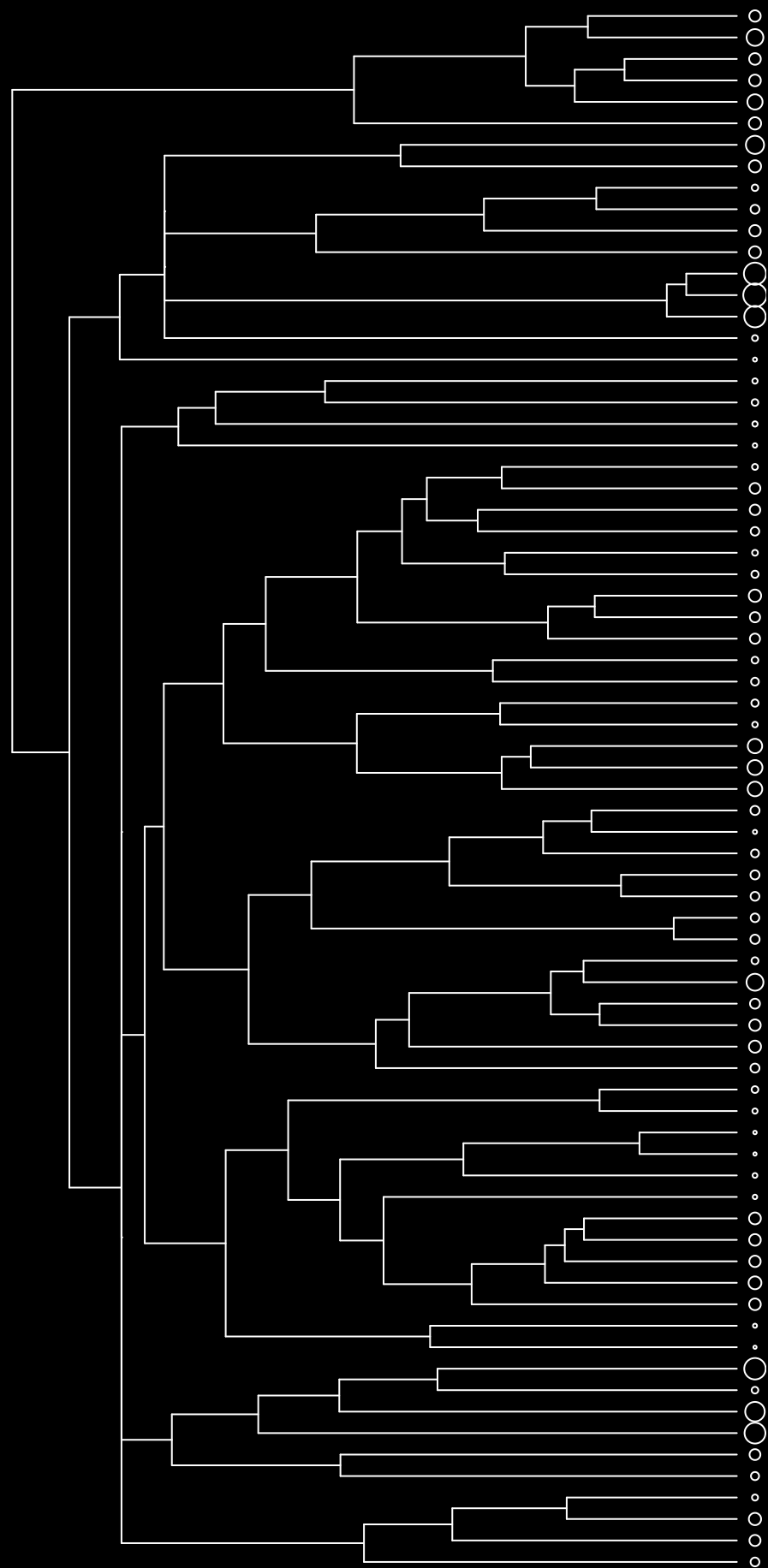


Anolis baleatus



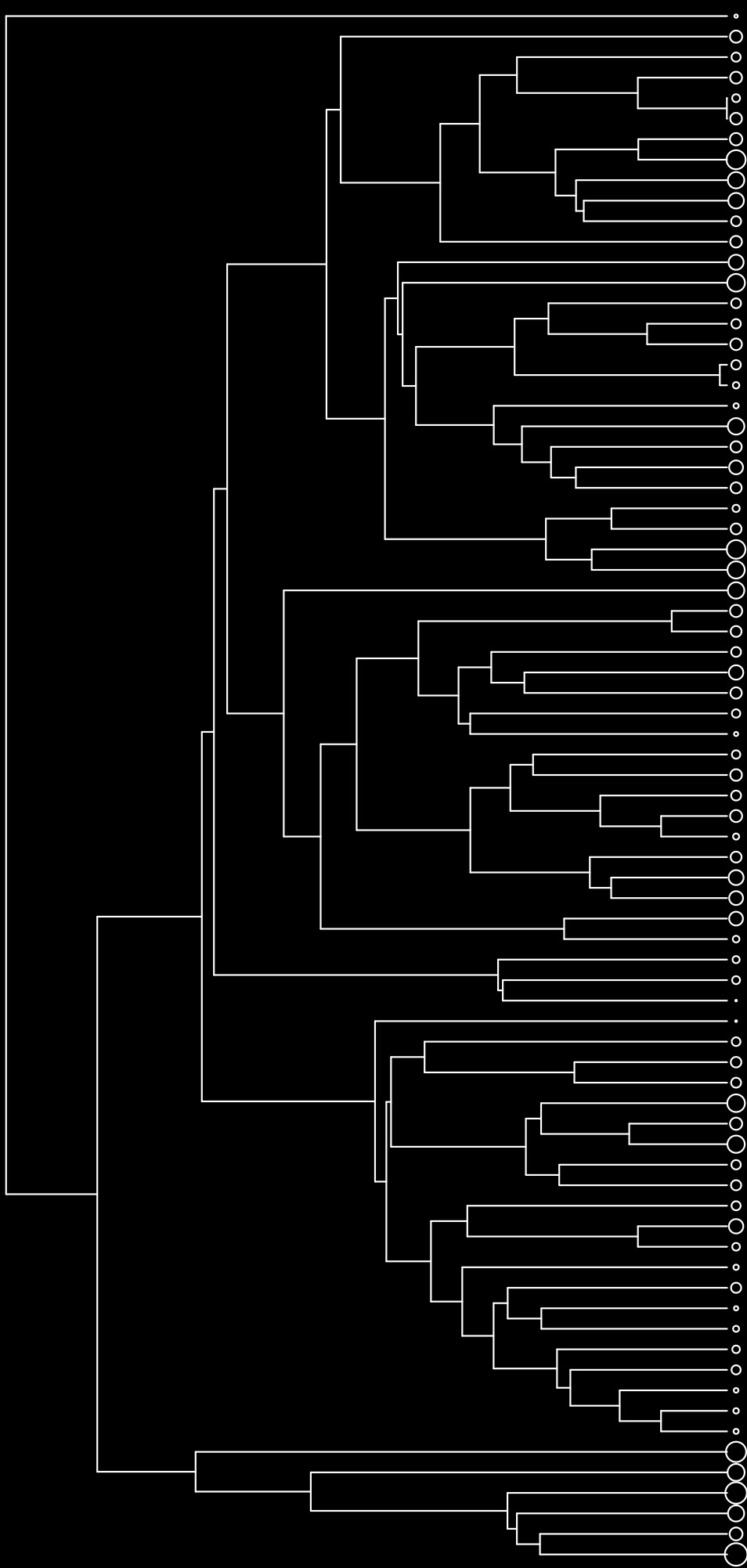


Model	Parameter estimates	lnL	Akaike weight
BM			
EB			
OU			

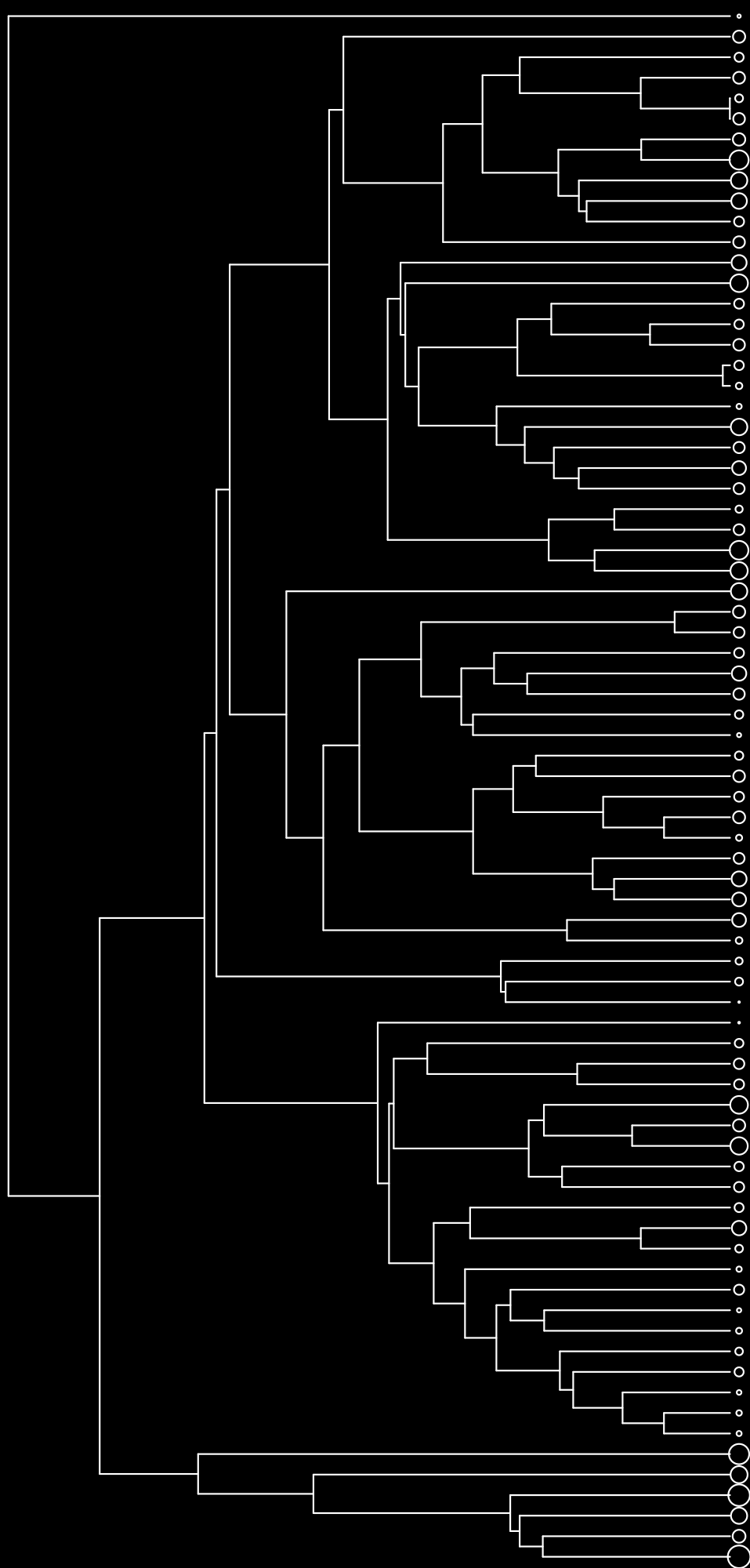


Model	Parameter estimates	lnL	Akaike weight
BM	$\sigma^2 = 0.004$	-18.2	0.58
EB	$\sigma^2 = 0.006$ $r = -0.01$	-18.1	0.2
OU	$\sigma^2 = 0.004$ $\alpha = 0$	-18.2	0.22

Cichlids in Lake Tanganyika



Cichlids in Lake Tanganyika



Model	Parameter estimates	lnL	Akaike weight
BM	$\sigma^2 = 0.02$	-62.3	0
EB	$\sigma^2 = 0.02$ $r = 0$	-62.3	0
OU	$\sigma^2 = \dots$ $\alpha = \dots$	-33.3	1

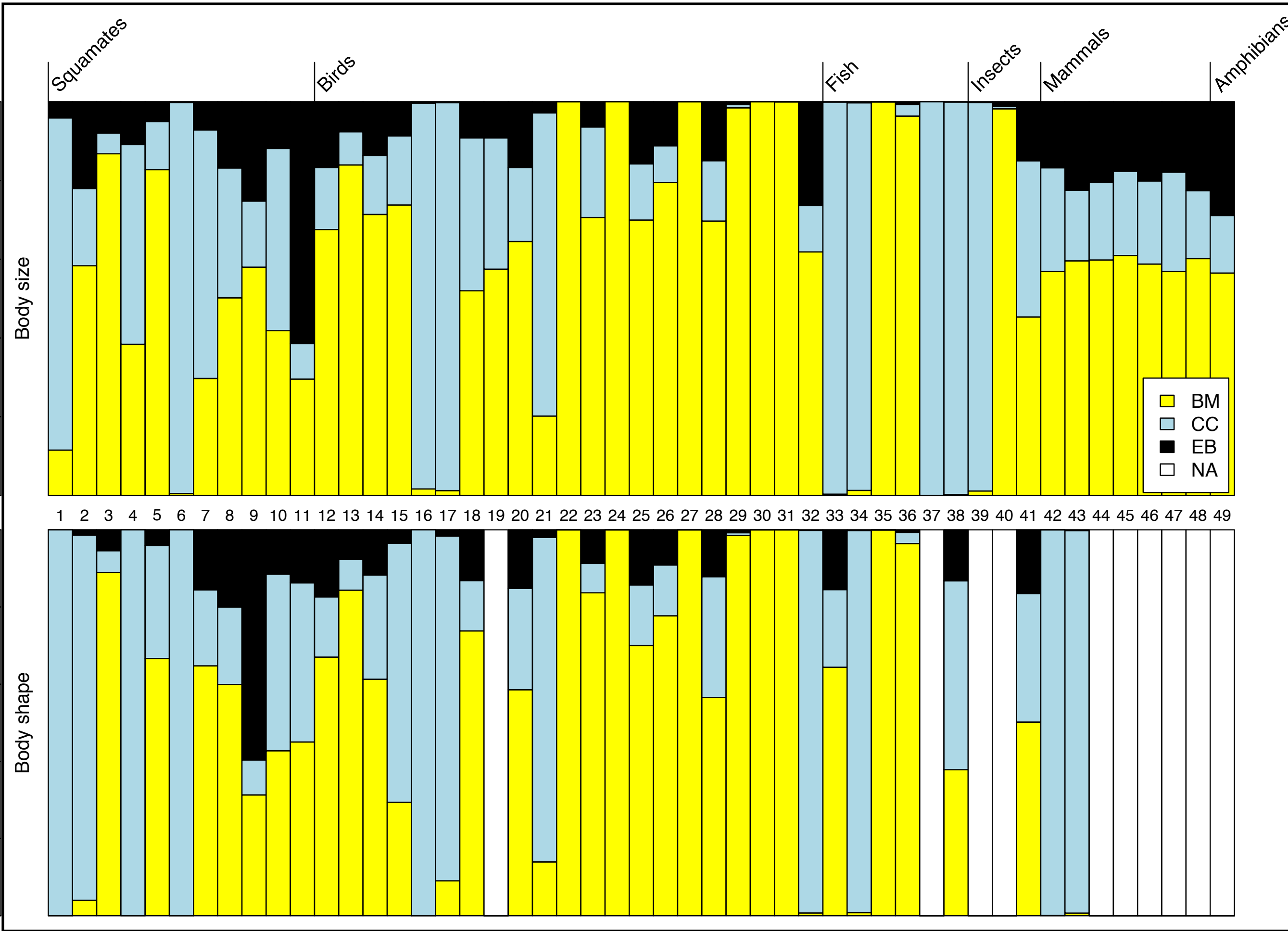
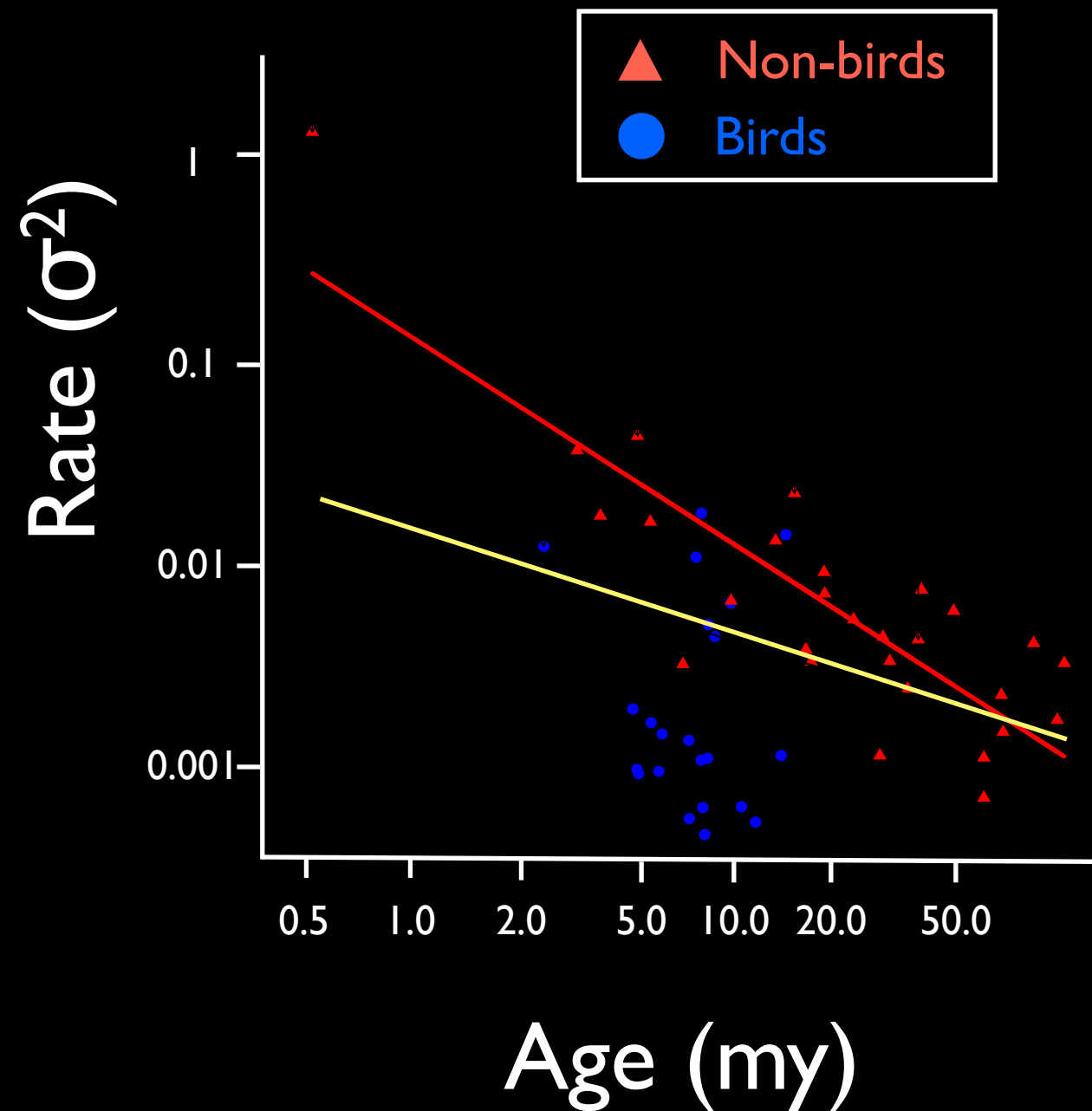


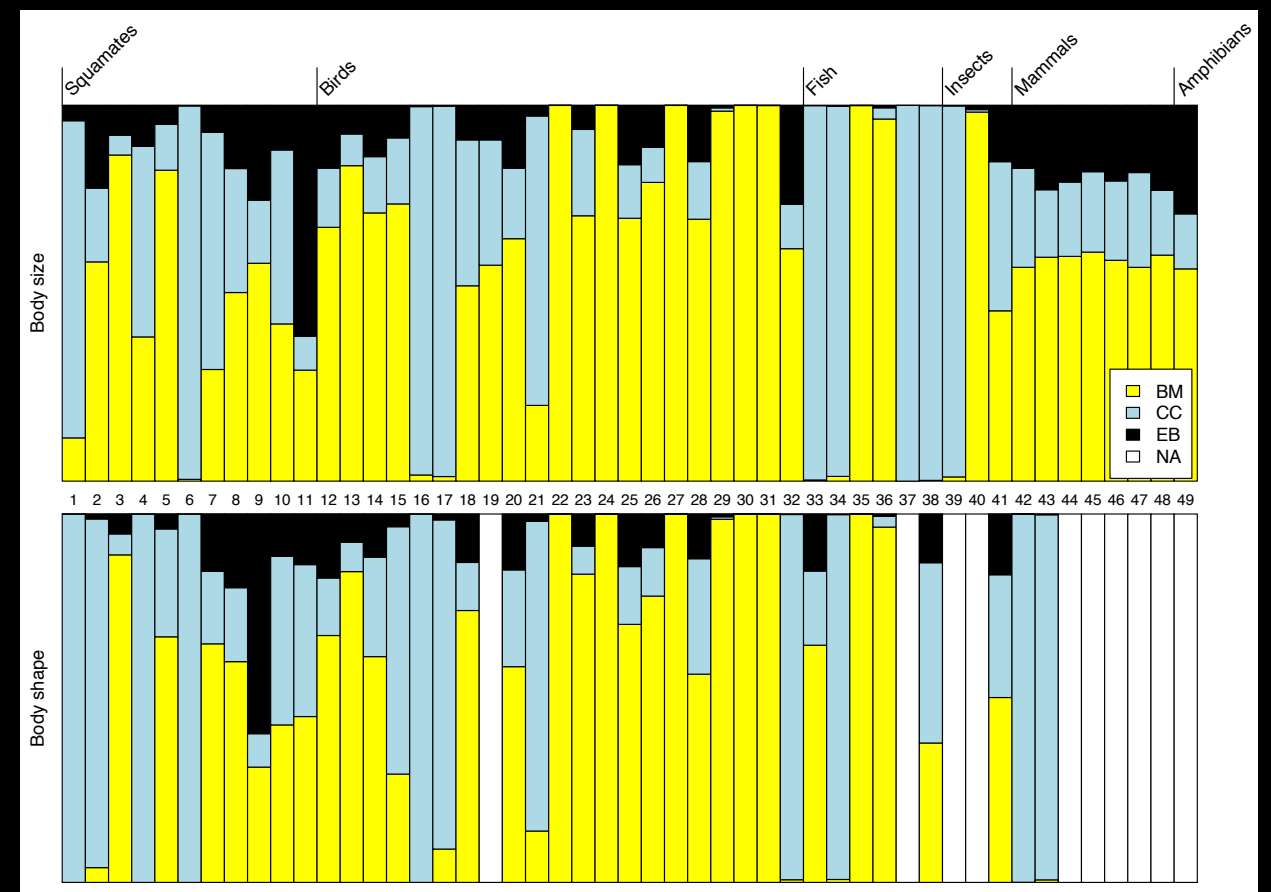
Table 1. Number of clades and subclades showing support for each of the three models (BM, CC, EB) for body size and body shape. We count both the number of clades with the highest AICc values for a particular model (“maximum w”) and those with weights greater than 0.95 (“w > 0.95”).

Clades	Data set	n	Criterion	BM	CC	EB
All full clades	Body size	49	Maximum w	35	13	1
			w > 0.95	9	8	0
	Body shape	39	Maximum w	24	14	1
			w > 0.95	8	8	1
All subclades	Body size	284	Maximum w	200	74	10
			w > 0.95	0	22	0
	Body shape	205	Maximum w	99	101	5
			w > 0.95	0	41	0

Brownian “Rates” Scale with Time



- “Adaptive radiation” pattern very rare in this data set
- Constraints dominate over long time periods
- Brownian motion is sometimes a poor fit to real data



What about “phylogenetic signal”?

“Phylogenetic signal”

A pattern where closely related species on a phylogenetic tree have trait values that are more similar than expected by chance.

1. We expect phylogenetic signal under a wide range of evolutionary models.

- Brownian motion
- OU with small α
- multi-peak OU
- early burst

2. Phylogenetic signal is a pattern, not a process

3. Phylogenetic signal is NOT a constraint

In fact, unconstrained models (like BM) create lots of phylogenetic signal, while constrained models (like OU) can result in very little phylogenetic signal

Measuring Phylogenetic Signal

- Blomberg's K statistic (comparison to BM)
- Pagel's lambda (branch length transformation)