

# **Phylogenetic Biology**

# **Character Evolution**

Biology 1425

Professor: Casey Dunn, [dunnlab.org](http://dunnlab.org)

Brown University

# Front matter...

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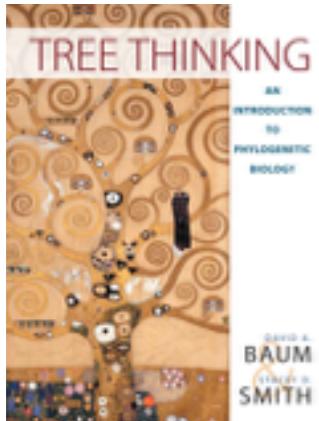
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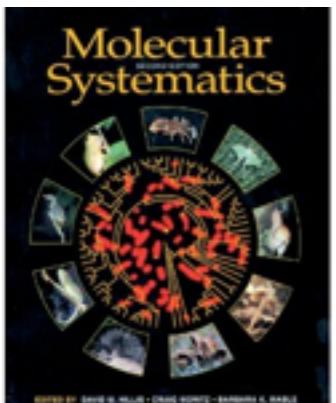
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# Sources

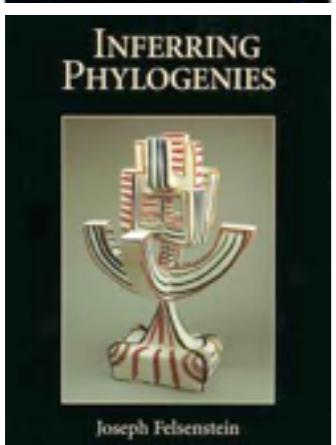
Some non-original content is drawn from:



Baum, D and S. Smith (2012) Tree Thinking: and Introduction to Phylogenetic Biology. Roberts and Company Publishers. ISBN 9781936221165



Swofford, D. L., Olsen, G. J., Waddell, P. J., & Hillis, D. M. (1996). Phylogenetic inference. In: Molecular Systematics, Second Edition. eds: D. M. Hillis, C Moritz, & B. K. Mable. Sinauer Associates. ISBN 9780878932825



Felsenstein, J. (2003) Inferring Phylogenies. Sinauer Associates. ISBN 978-0878931774

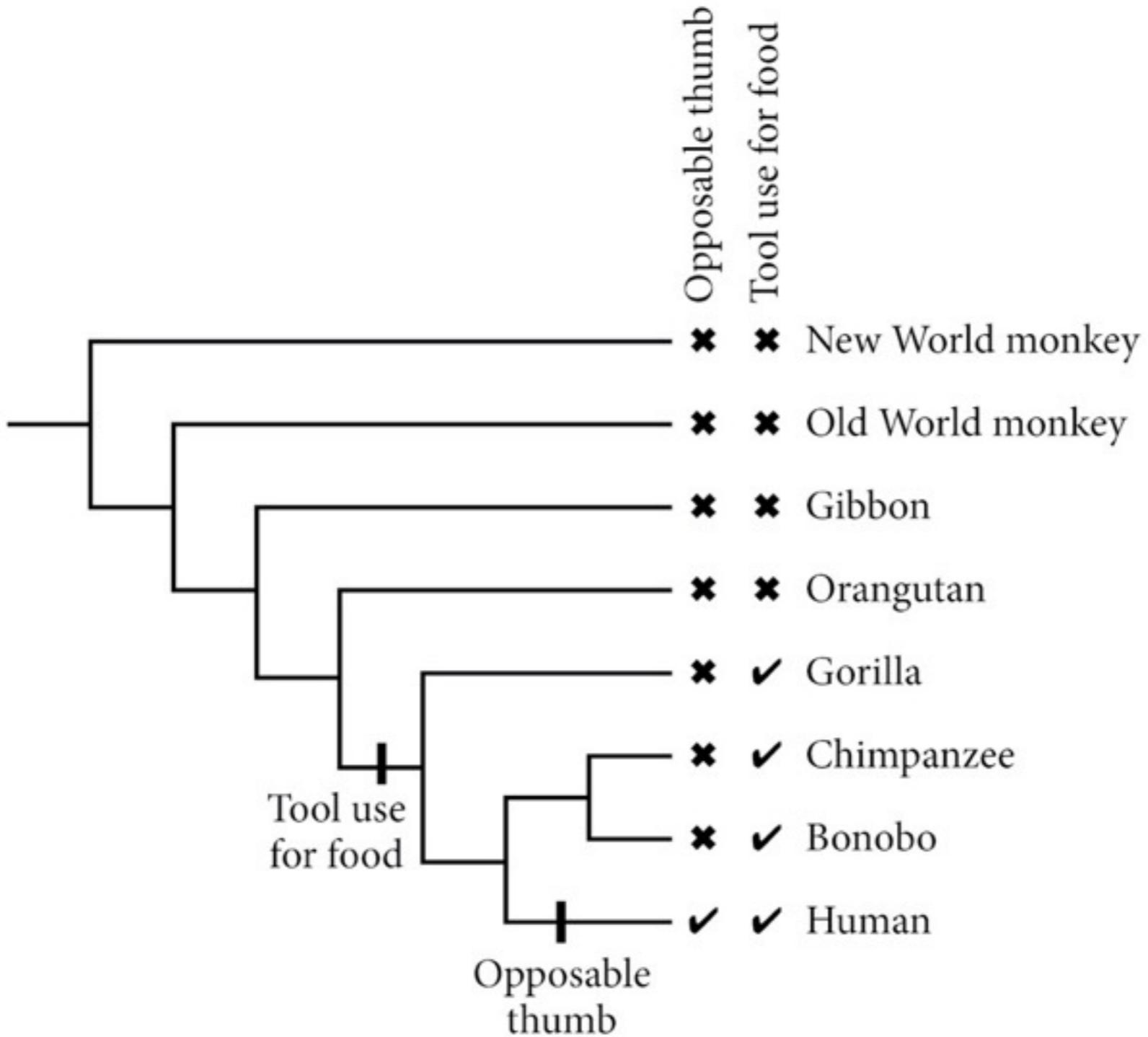
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**Phylogenies are chronicles** - they tell us who, what, when, where...

We often want **narratives** - the why. For example, does a change in one character facilitate change in another character?

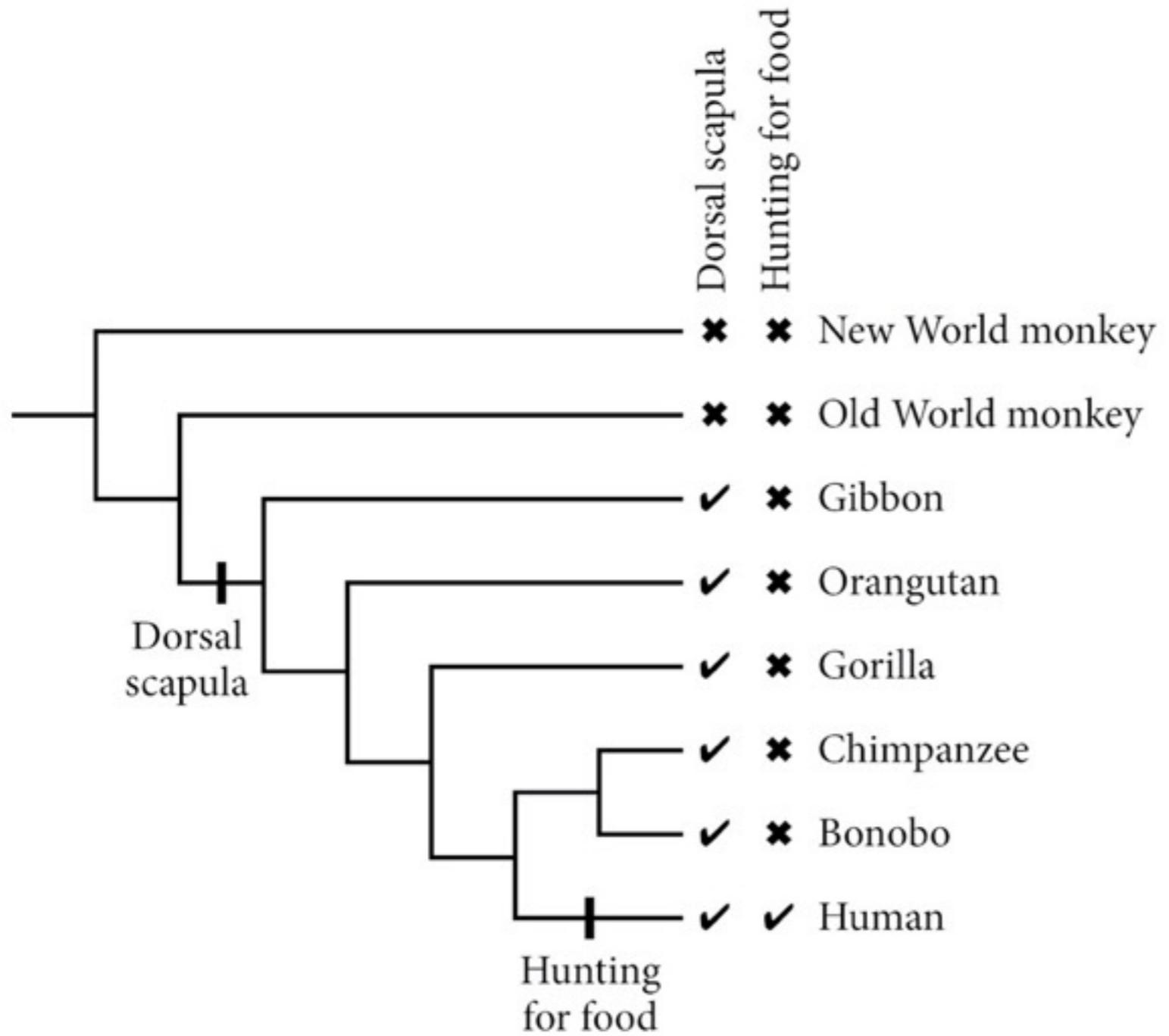
You need to know the chronicle  
before you can test ideas about  
the narrative

Is an opposable thumb an  
adaptation for more effective tool  
use?



Tool use evolved prior to opposable thumb,  
consistent with this hypothesis.

Is the dorsal scapula an  
adaptation that improves hunting  
for food with projectiles?



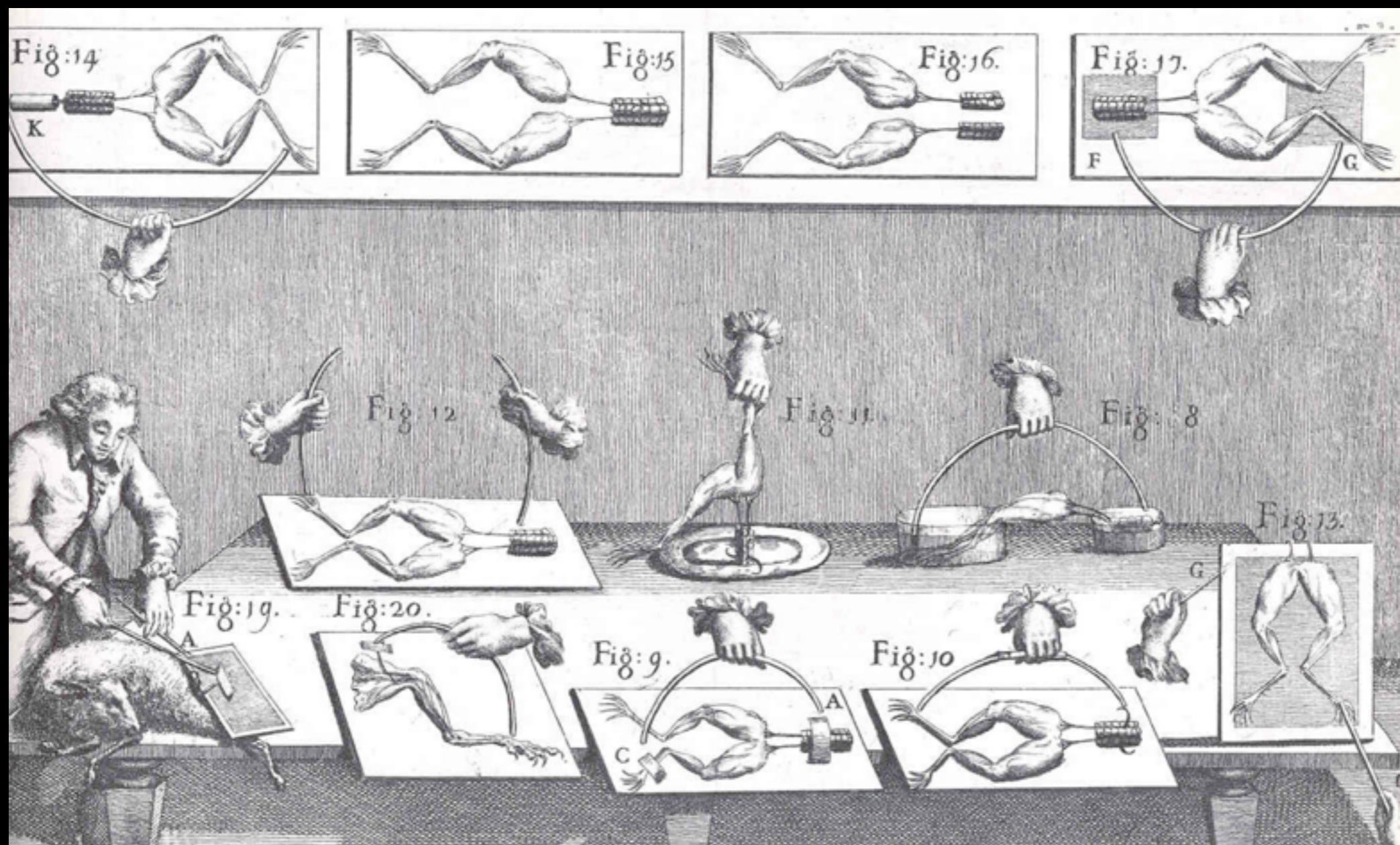
The order of character changes is not consistent with this hypothesis.

**The comparative method -  
looking across species for  
statistically significant  
associations between traits**

**Biological insight  
requires biological**

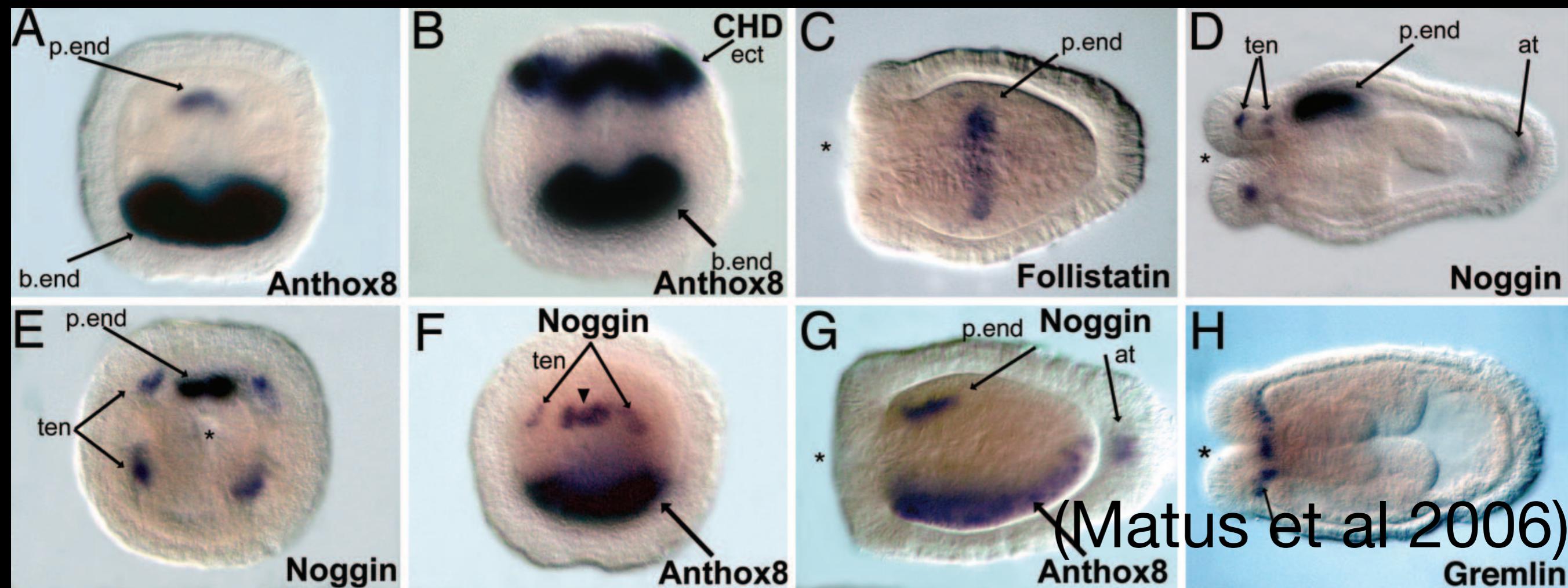
# Experiments

Induce variation through  
perturbation of organism function



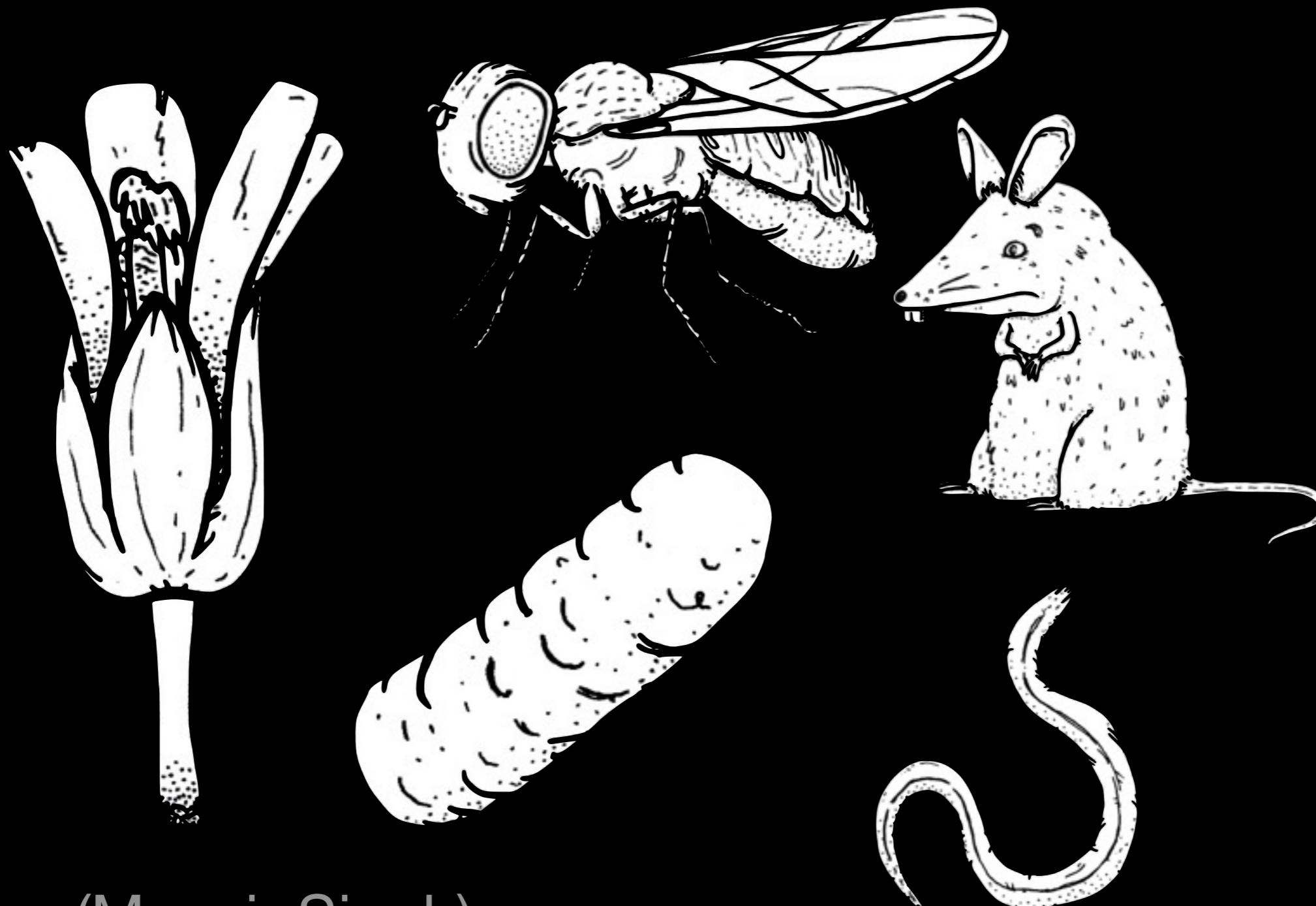
# Within-organism

Variation between cells, tissues,  
organs, development, environment,  
behavior



# Mutant screens

Induced genetic variation



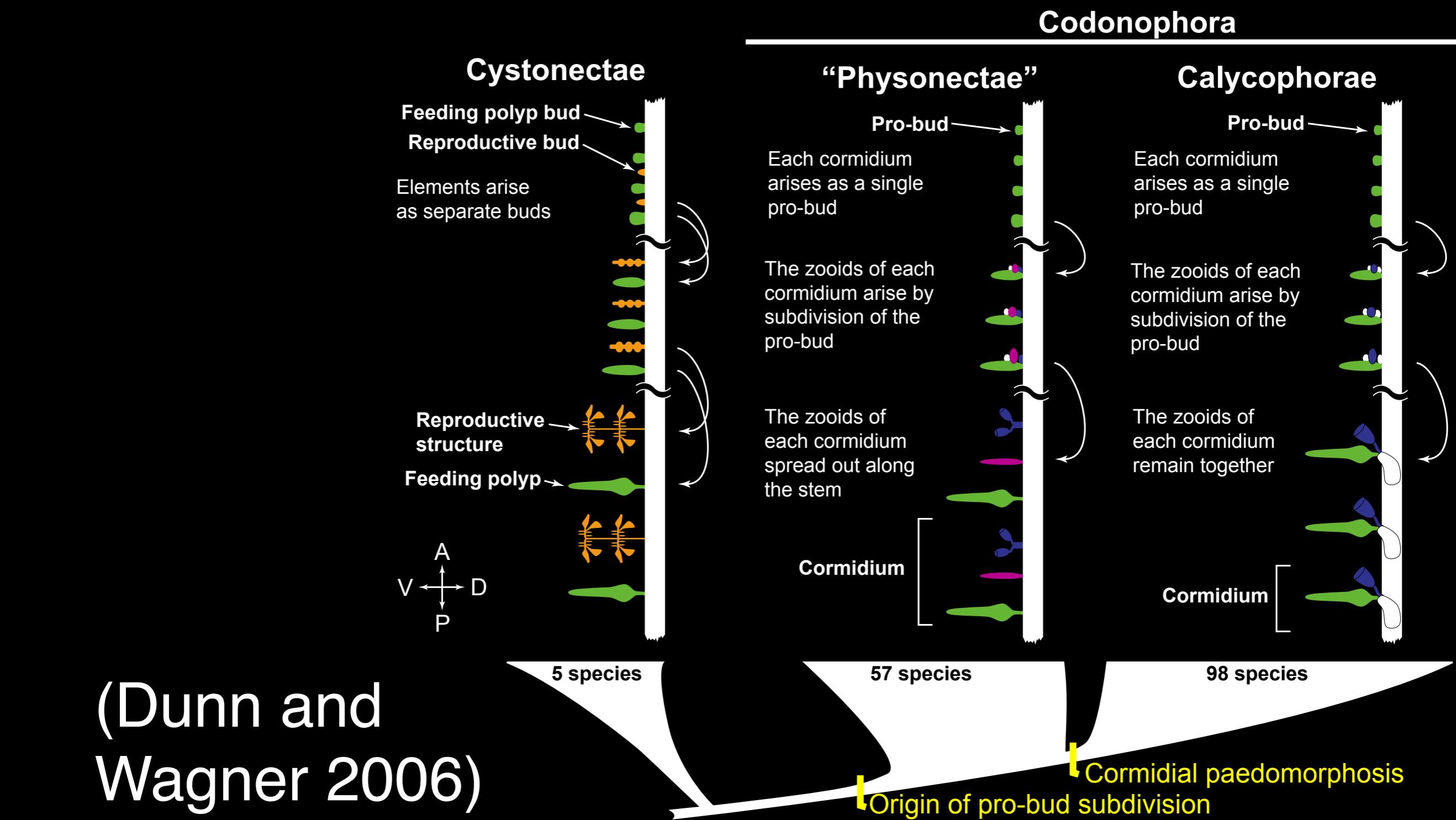
(Manvir Singh)

# Population genetics

Standing heritable variation in a population

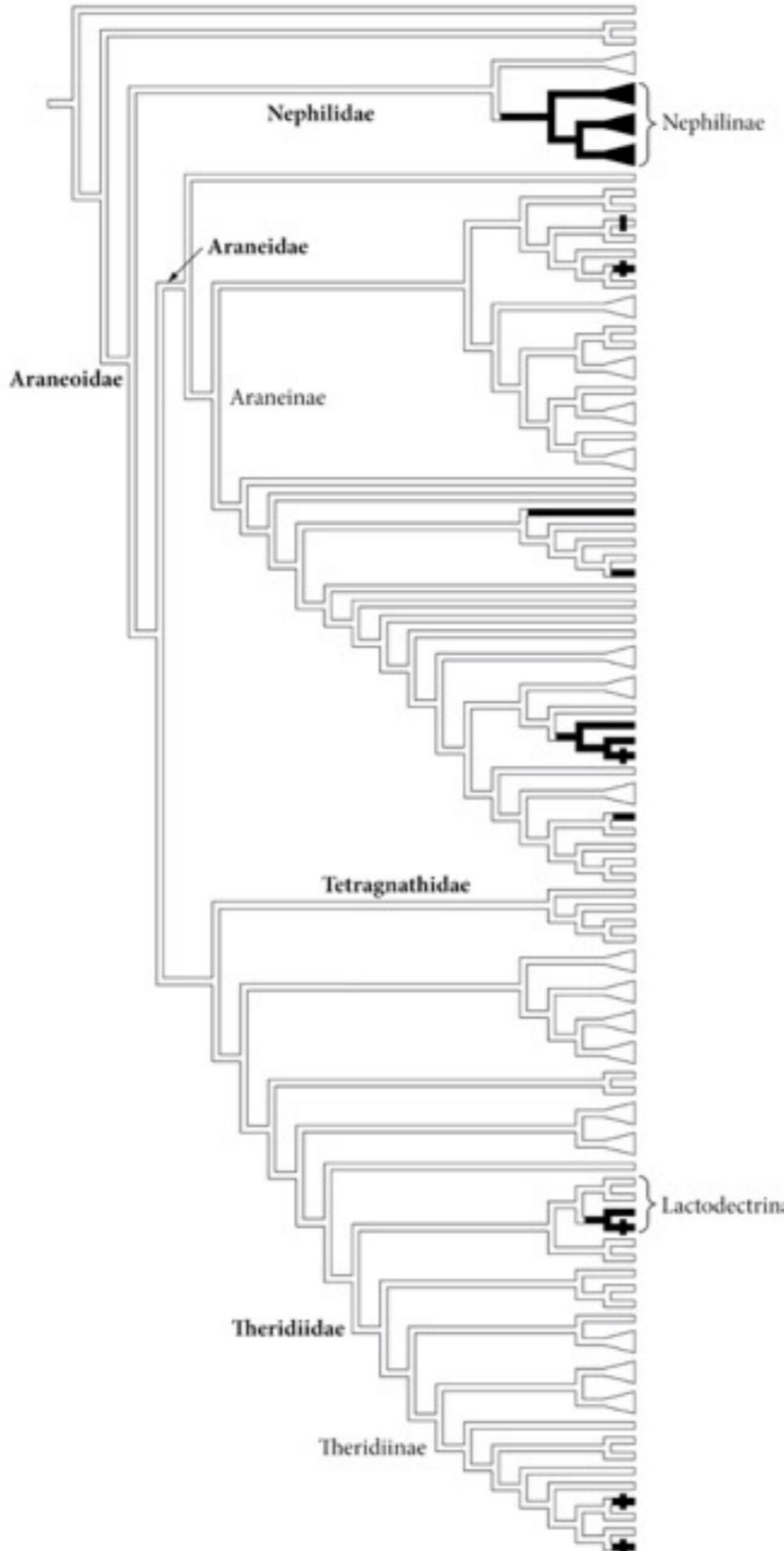
# Comparative Biology

## Variation between species



# **Investigating patterns in character evolution**

# **Concentrated change - a parsimony approach to testing the association between a selective regime and changes in a character of interest**



Black branch - male  
genital mutilation

Black bar - male sacrifice  
to females

Origin of male sacrifice  
enriched in lineages with  
genital mutilation

# Model-based approaches to character evolution

# Equal rates

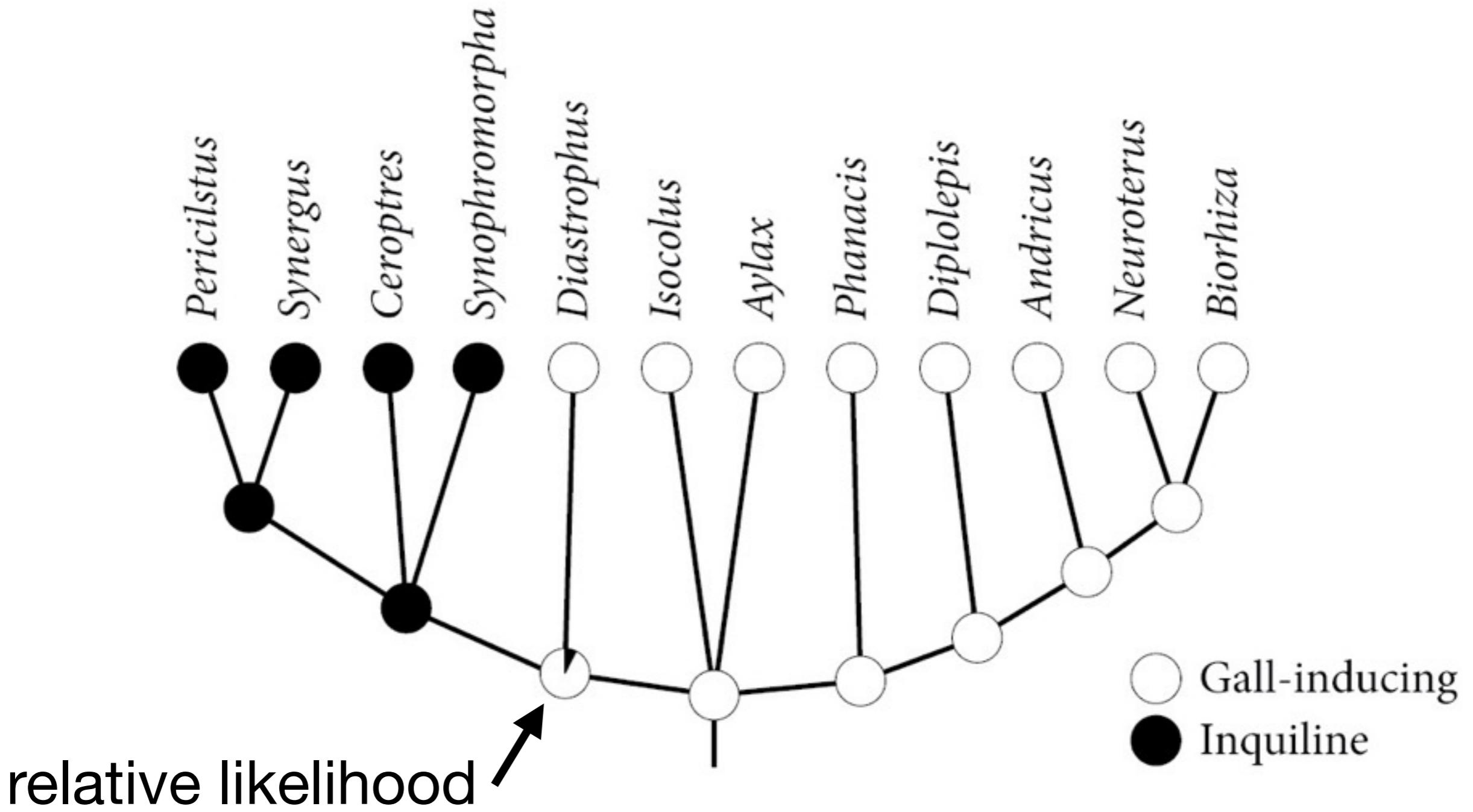
TABLE 10.2 Symmetric rate matrix  
for a binary character

From	To	
	0	1
0	$-q$	$q$
1	$q$	$-q$

TABLE 10.3 Substitution probability matrix  
for a binary character

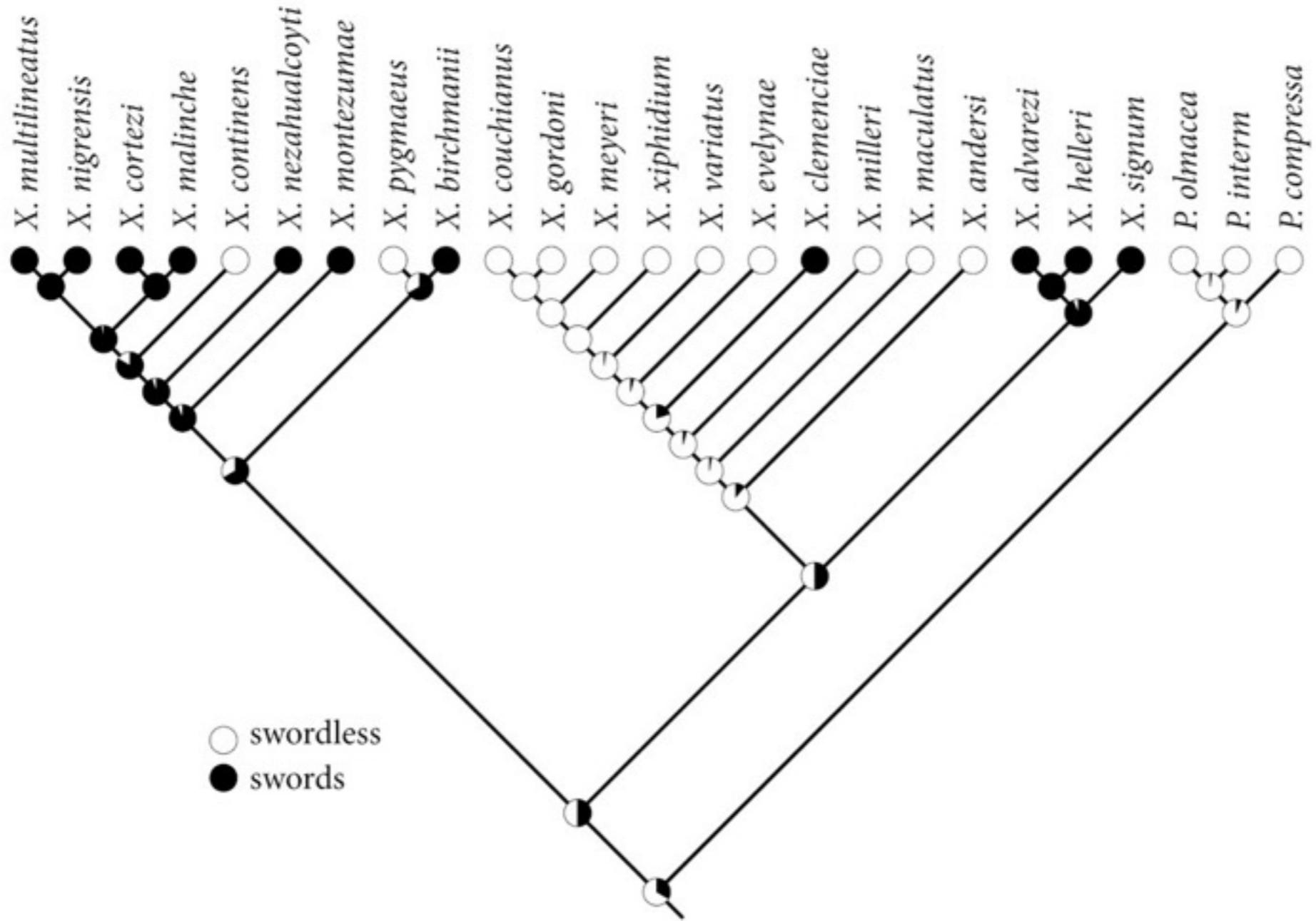
From	To	
	0	1
0	$\frac{1}{2} + \frac{1}{2}e^{-qt}$	$\frac{1}{2} - \frac{1}{2}e^{-qt}$
1	$\frac{1}{2} - \frac{1}{2}e^{-qt}$	$\frac{1}{2} + \frac{1}{2}e^{-qt}$

$$0 \xleftrightarrow[q]{} 1$$



Is this study consistent with a high or low rate?

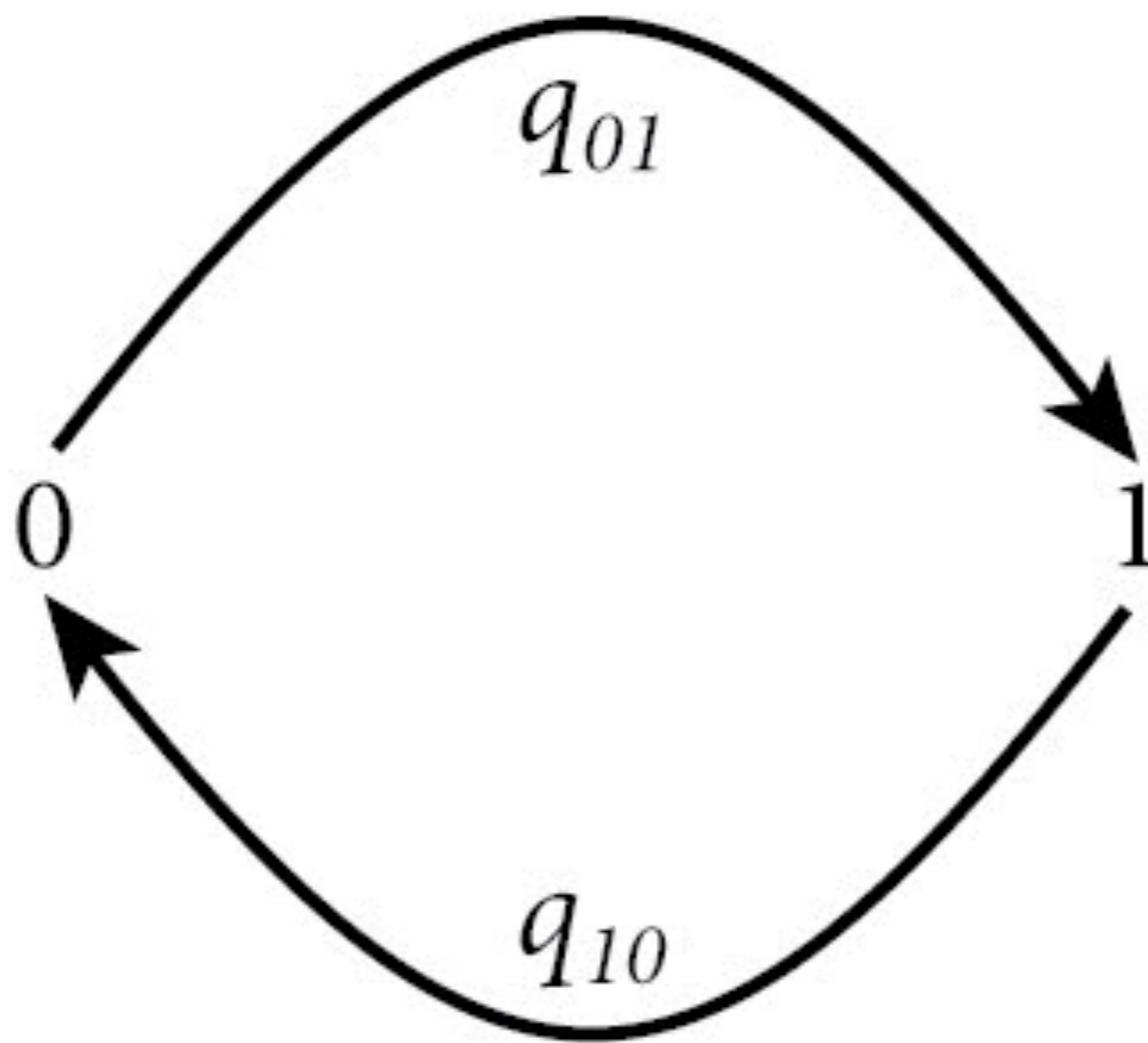
Low.



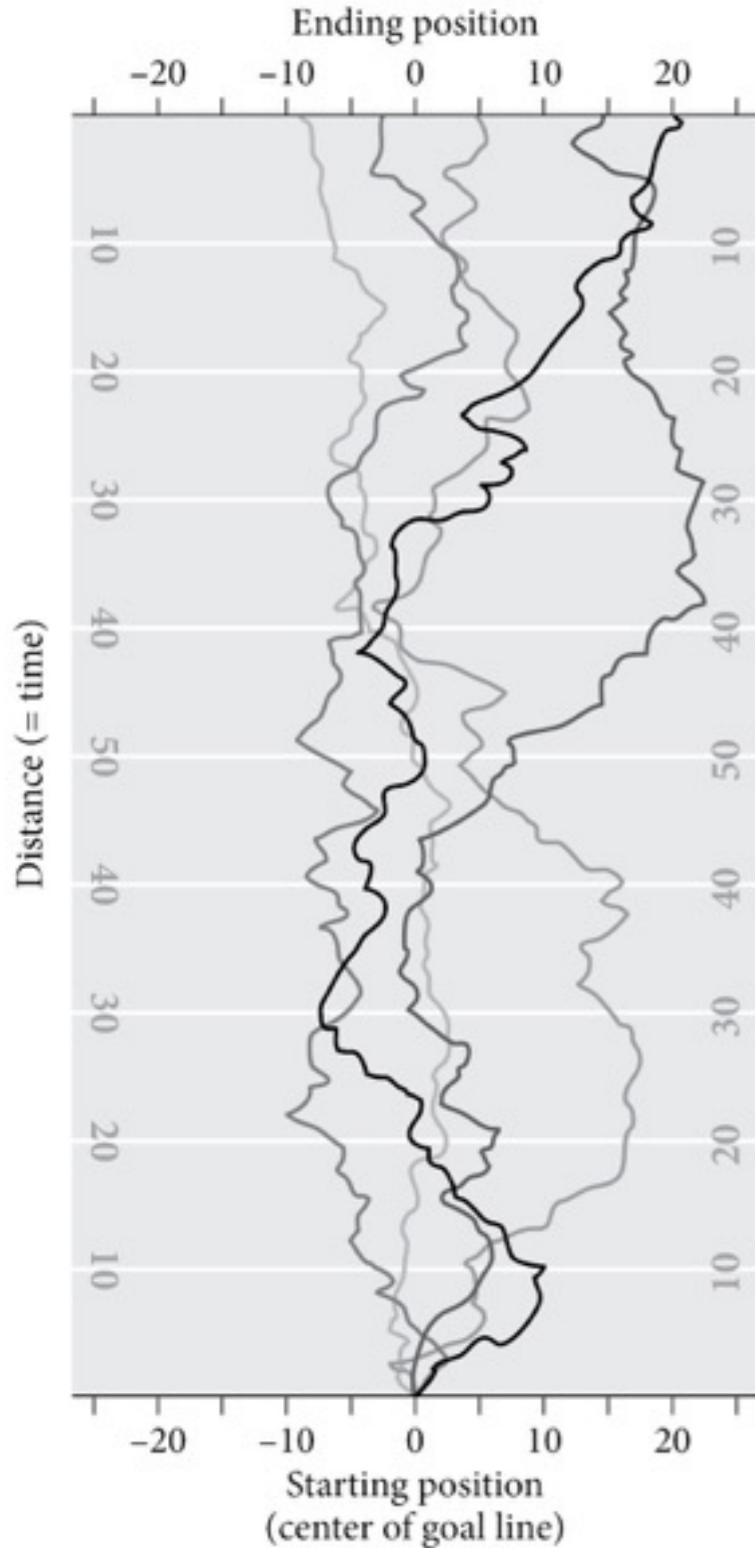
Is this study consistent with a high or low rate?

High.

# Unequal rates



# Continuous models



## Brownian motion

- random walk
- The probability of direction doesn't depend on where you are

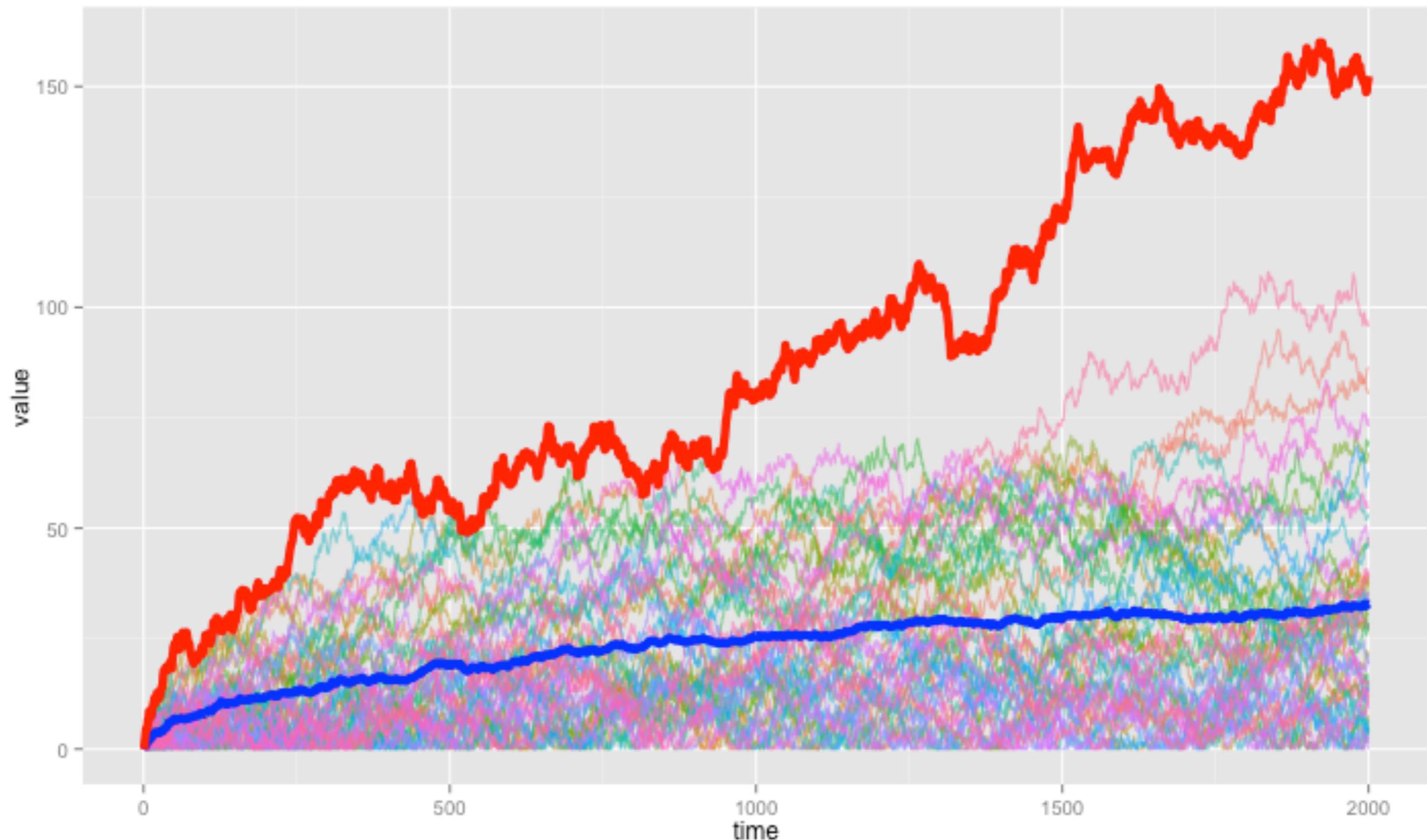
# Continuous models

## Brownian motion

- Often a reasonable approximation of evolutionary processes
- Very useful for establishing null expectation in absence of directionality

Is increasing “complexity” through time evidence of selection that favors complex traits?

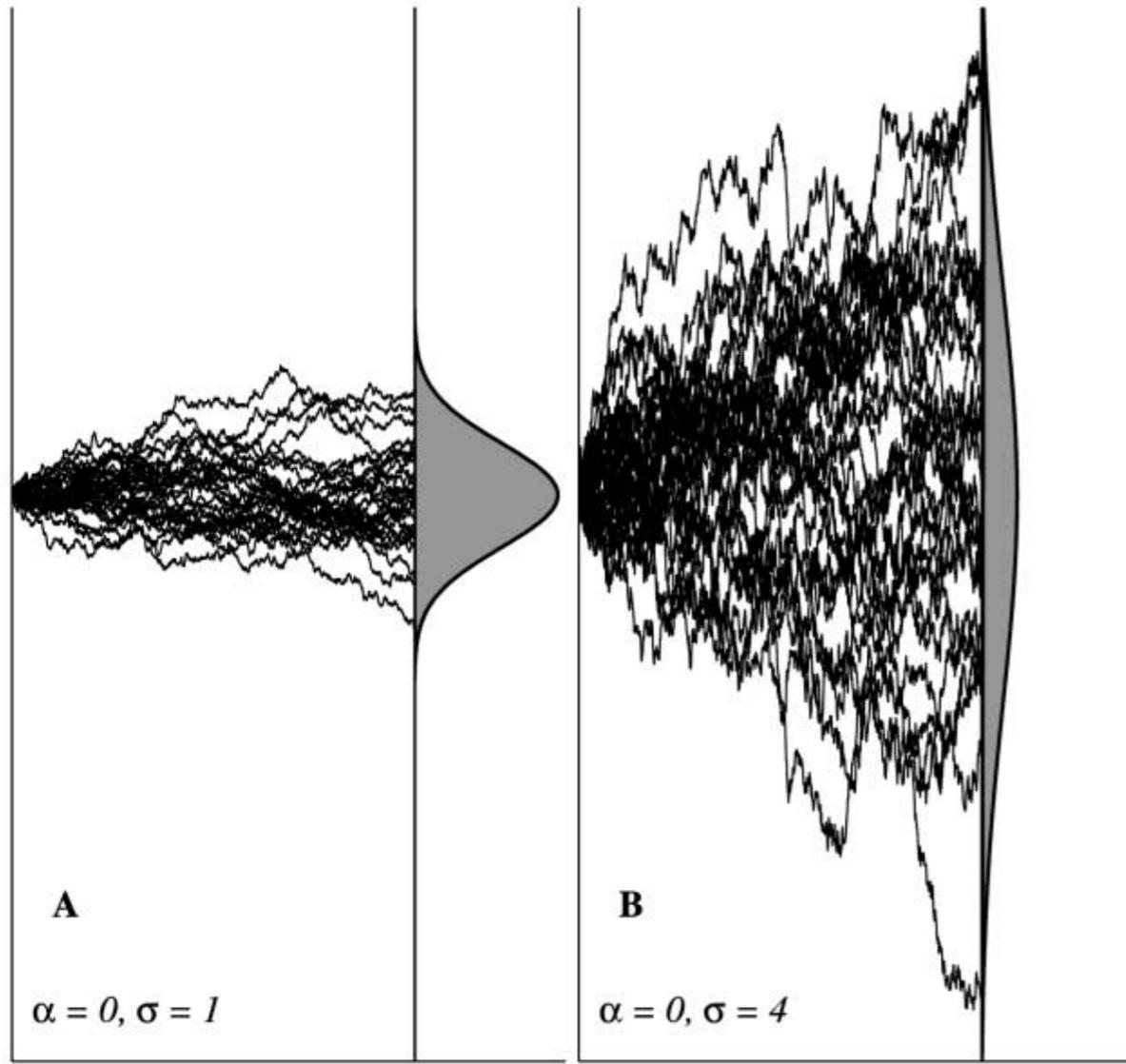
# Brownian motion



[http://htmlpreview.github.io/?https://github.com/caseywdunn/random\\_walk/blob/master/randomwalk.html](http://htmlpreview.github.io/?https://github.com/caseywdunn/random_walk/blob/master/randomwalk.html)

# Continuous models

## Brownian motion



$\alpha$  Selection  
 $\sigma$  Step size

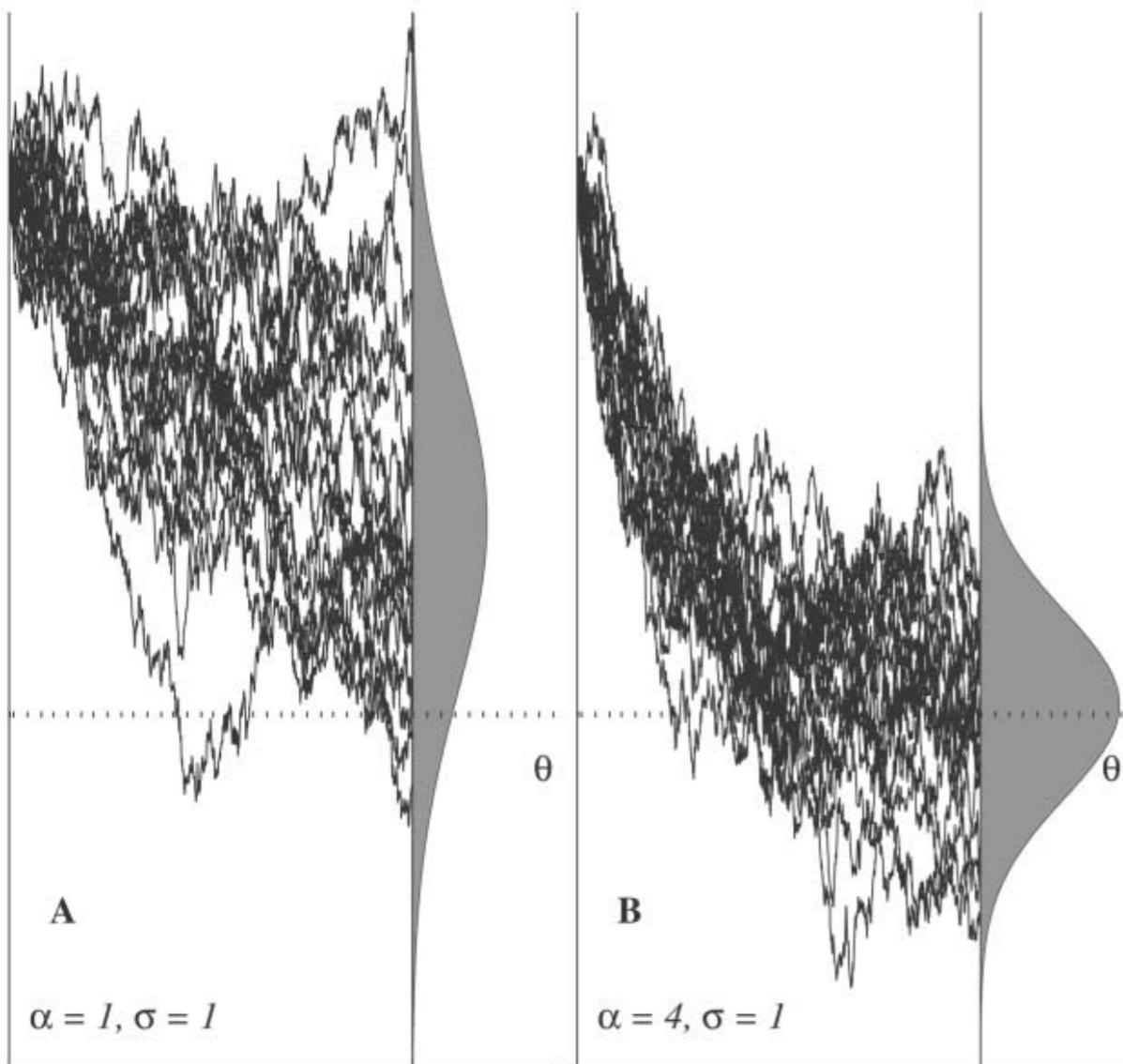
# Continuous models

## Ornstein–Uhlenbeck

- random walk
- The probability of direction depends on how far you are from mean

# Continuous models

## Ornstein–Uhlenbeck

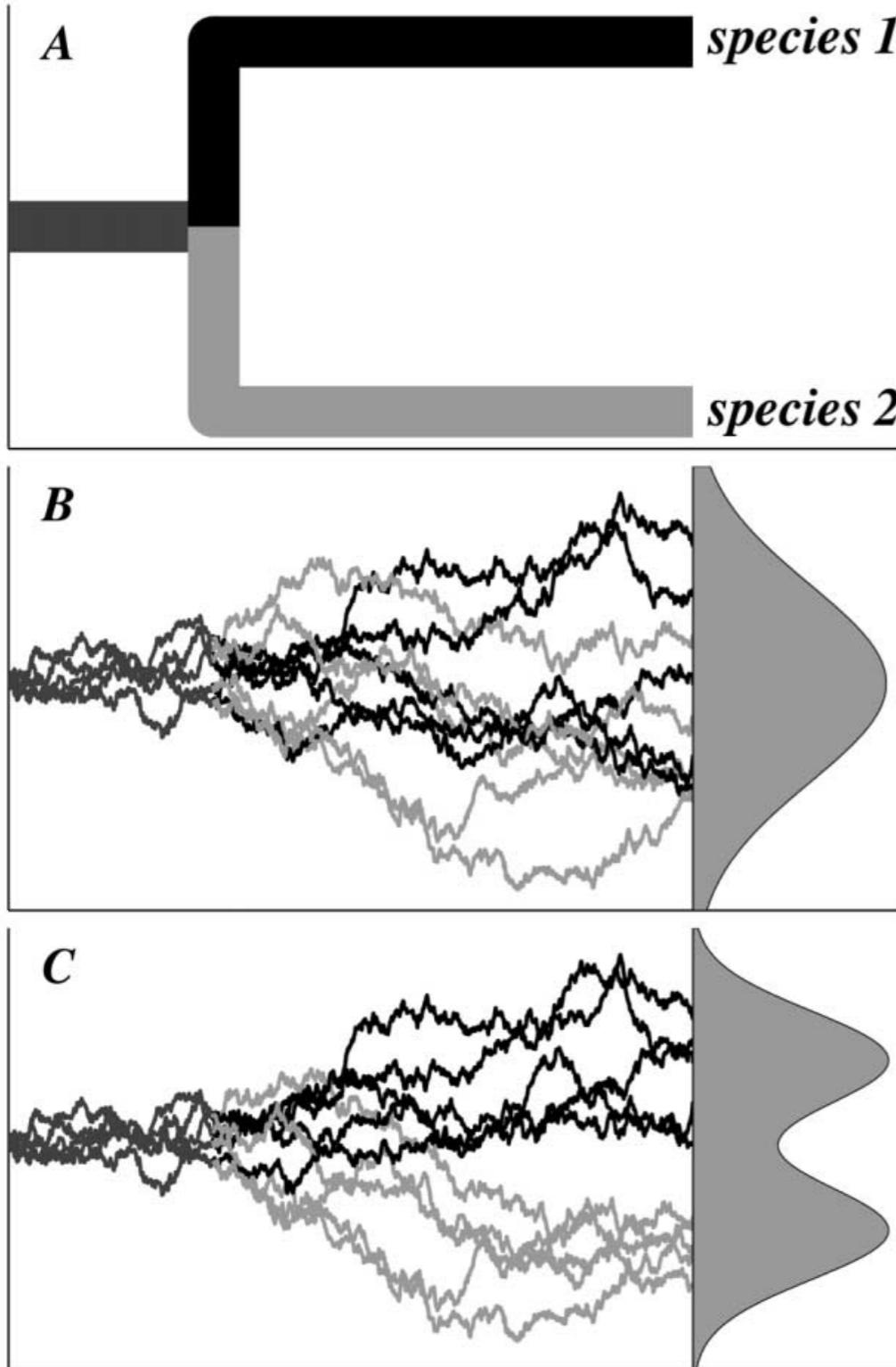


$\alpha$  Selection

$\sigma$  Step size

$\theta$  Optimum

# Continuous models



Phylogeny

Brownian

OU  
with different selection  
regimes after speciation

Buttler and King, 2004

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Vol. 125, No. 1

The American Naturalist

January 1985

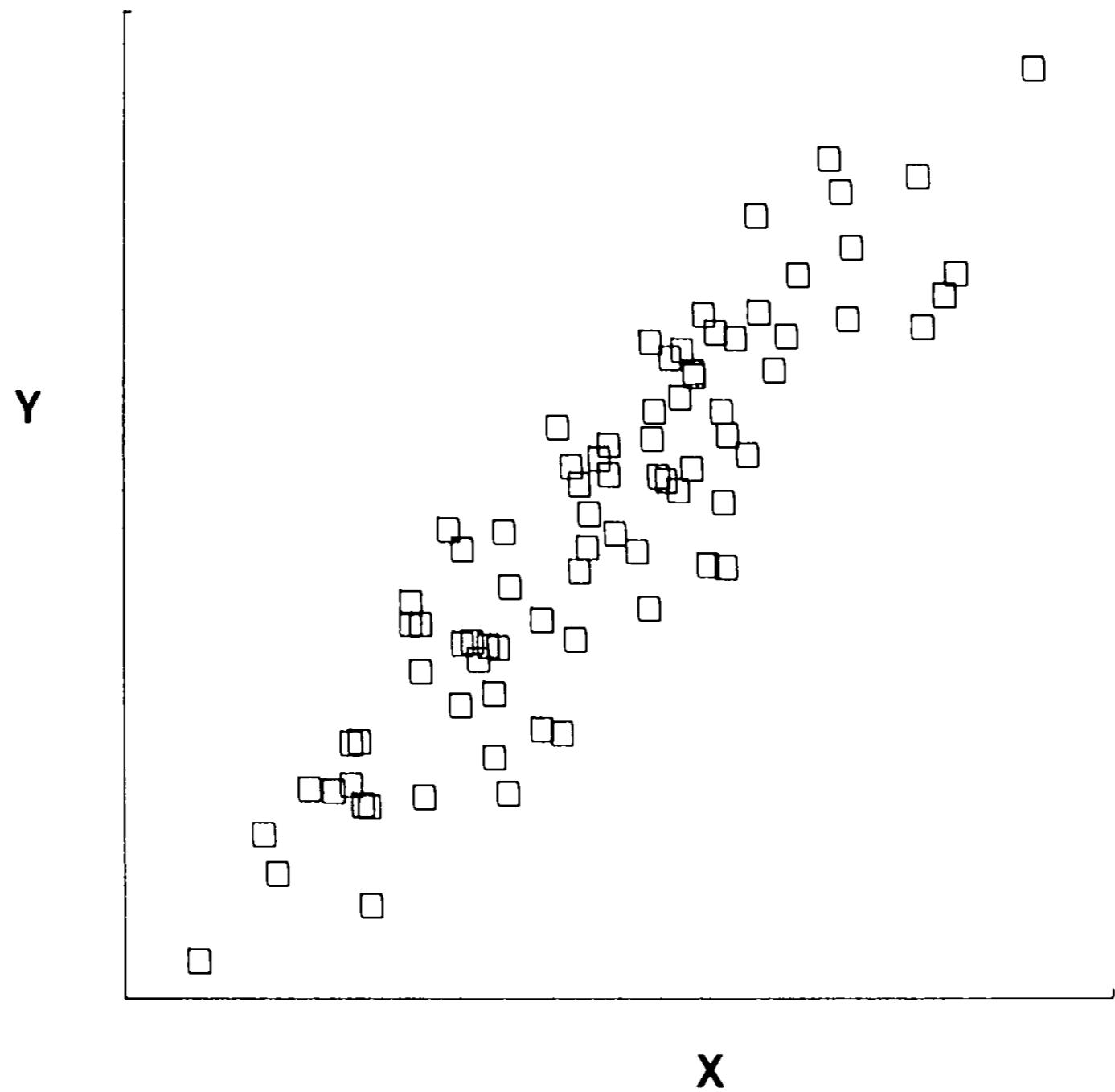
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## PHYLOGENIES AND THE COMPARATIVE METHOD

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*Submitted November 30, 1983; Accepted May 23, 1984*



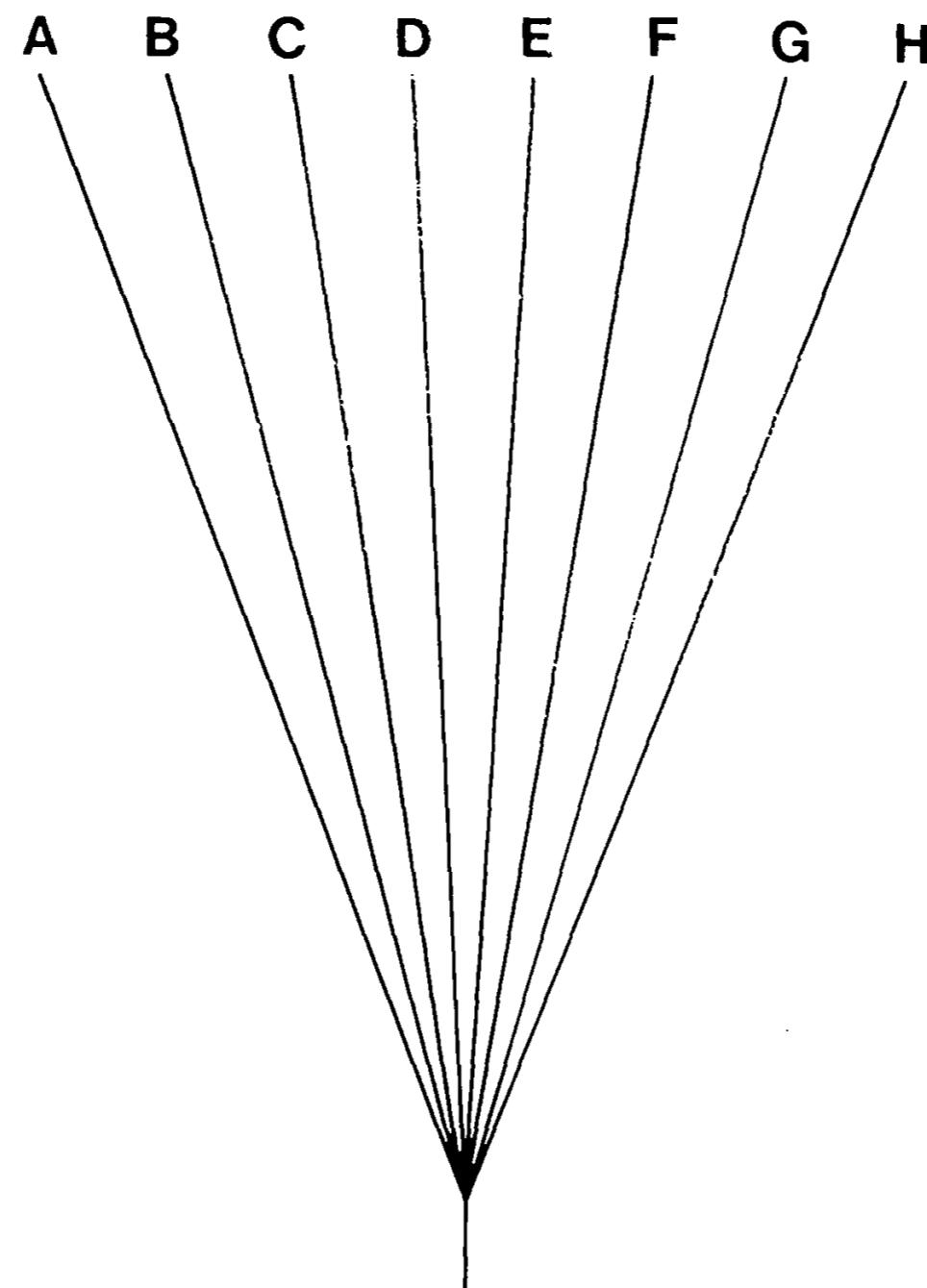


FIG. 2.—One phylogeny for the 8 species, showing a burst of adaptive radiation with each lineage evolving independently from a common starting point.

Felsenstein, 1985

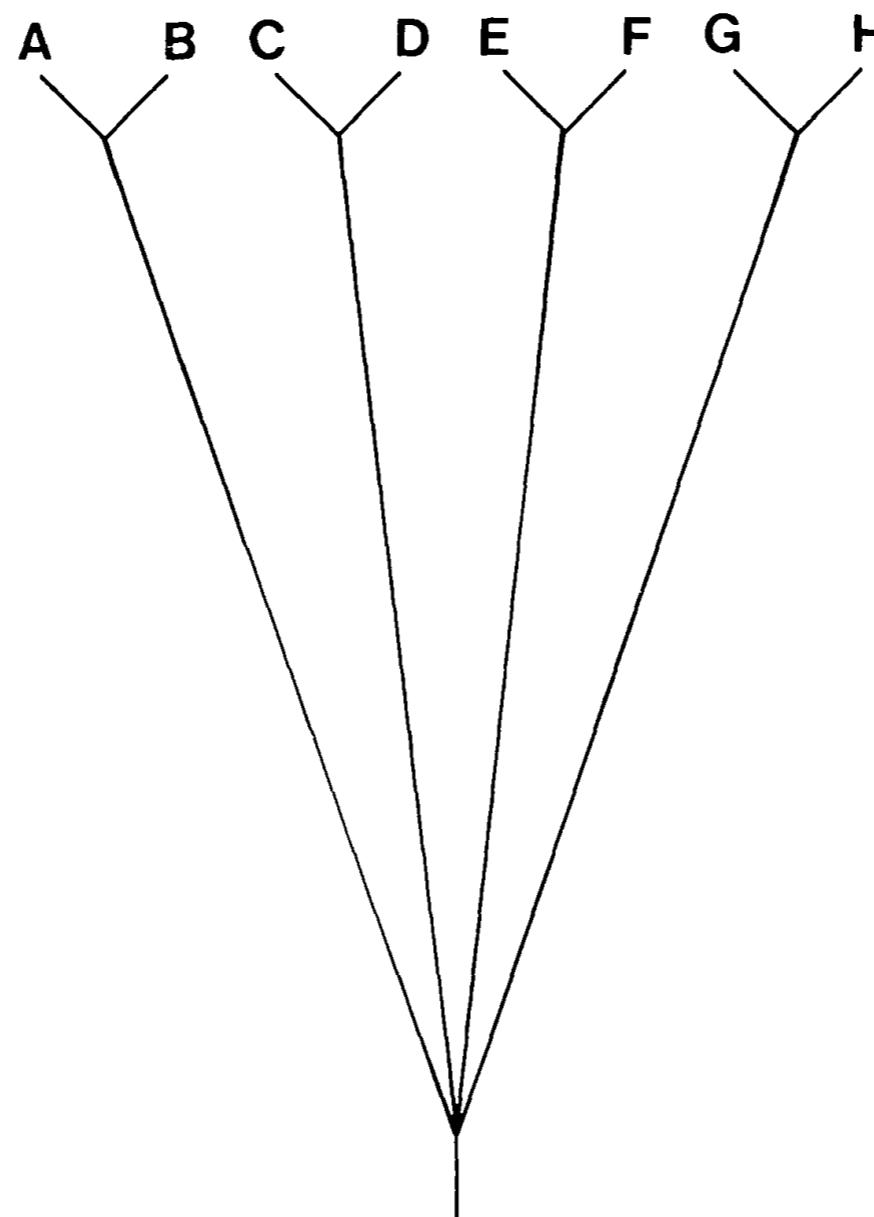


FIG. 3.—Another phylogeny for the 8 species, showing a radiation that gives rise to 4 pairs of closely related species.

Felsenstein, 1985

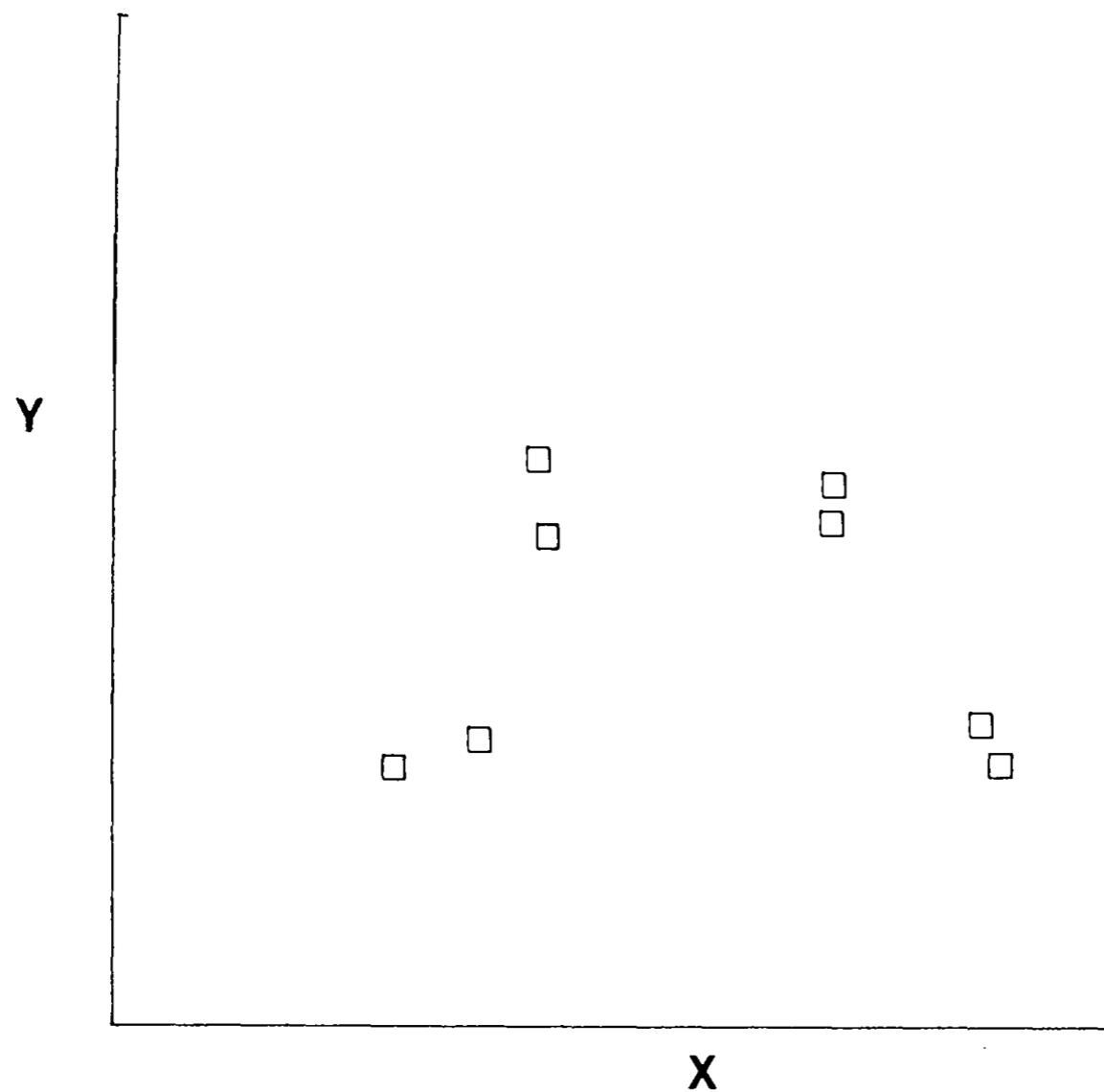


FIG. 4.—A data set simulated using the phylogeny of fig. 3, under a model of random, normally distributed, independent change in each character, where the change in each branch is drawn independently from a normal distribution with mean zero and variance proportional to the length of the branch.

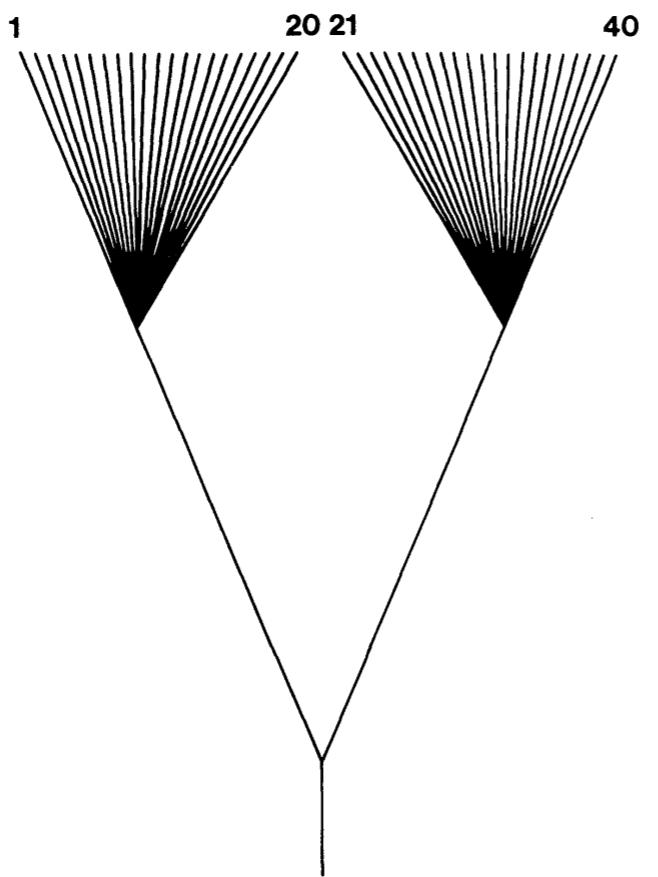


FIG. 5.—A “worst case” phylogeny for 40 species, in which there prove to be 2 groups each of 20 close relatives.

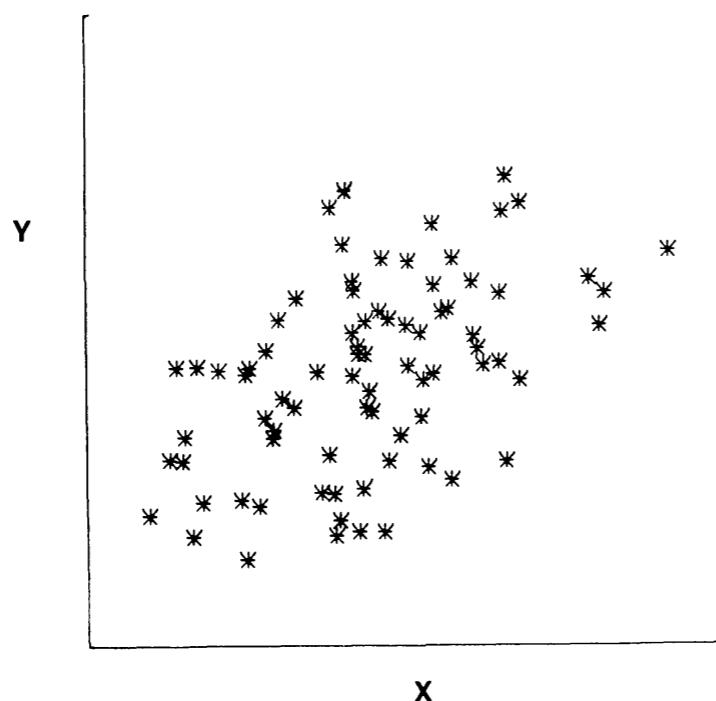


FIG. 6.—A typical data set that might be generated for the phylogeny in fig. 5 using the model of independent Brownian motion (normal increments) in each character.

Felsenstein, 1985

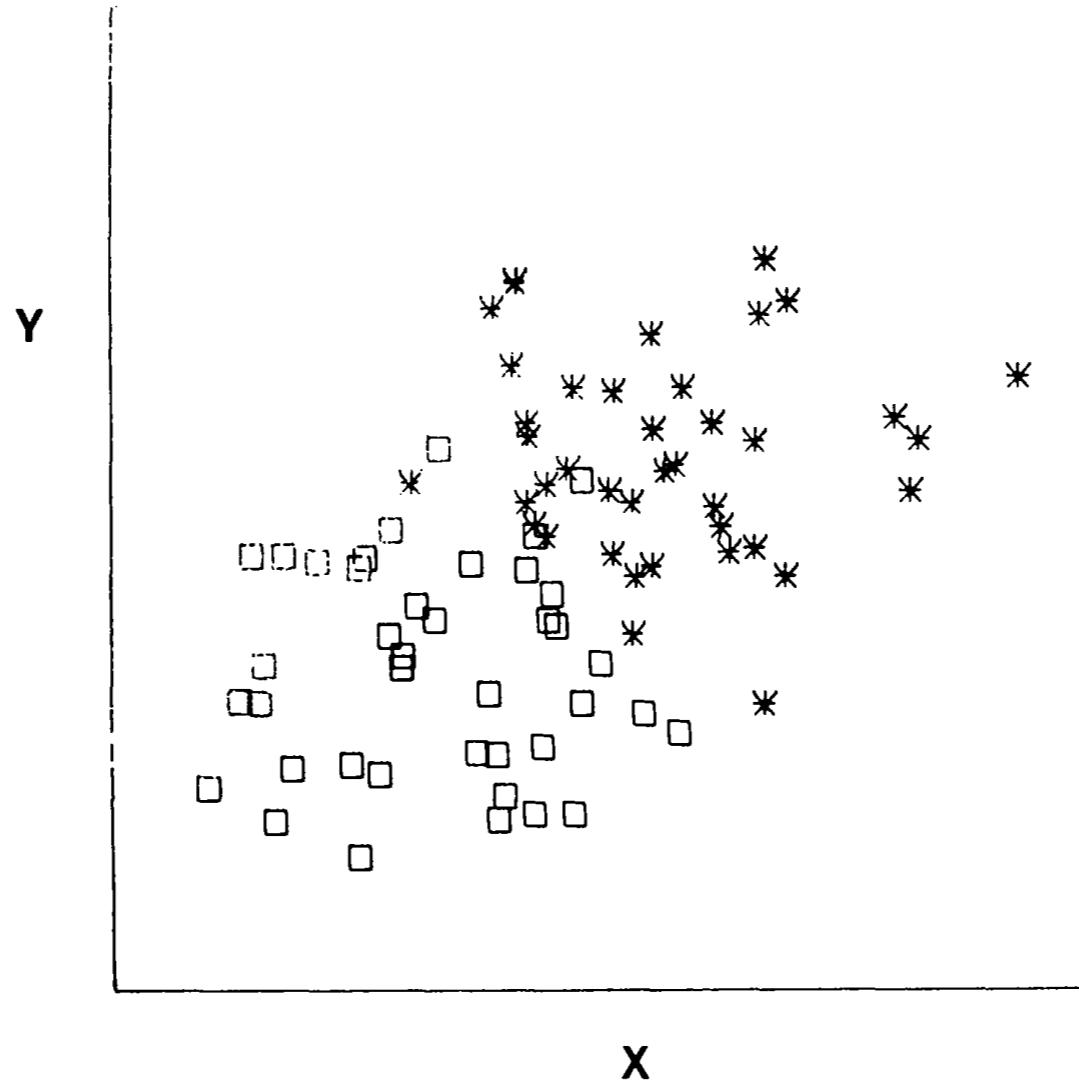


FIG. 7.—The same data set, with the points distinguished to show the members of the 2 monophyletic taxa. It can immediately be seen that the apparently significant relationship of fig. 6 is illusory.

Observations across species are not independent, but contrasts across internal nodes are

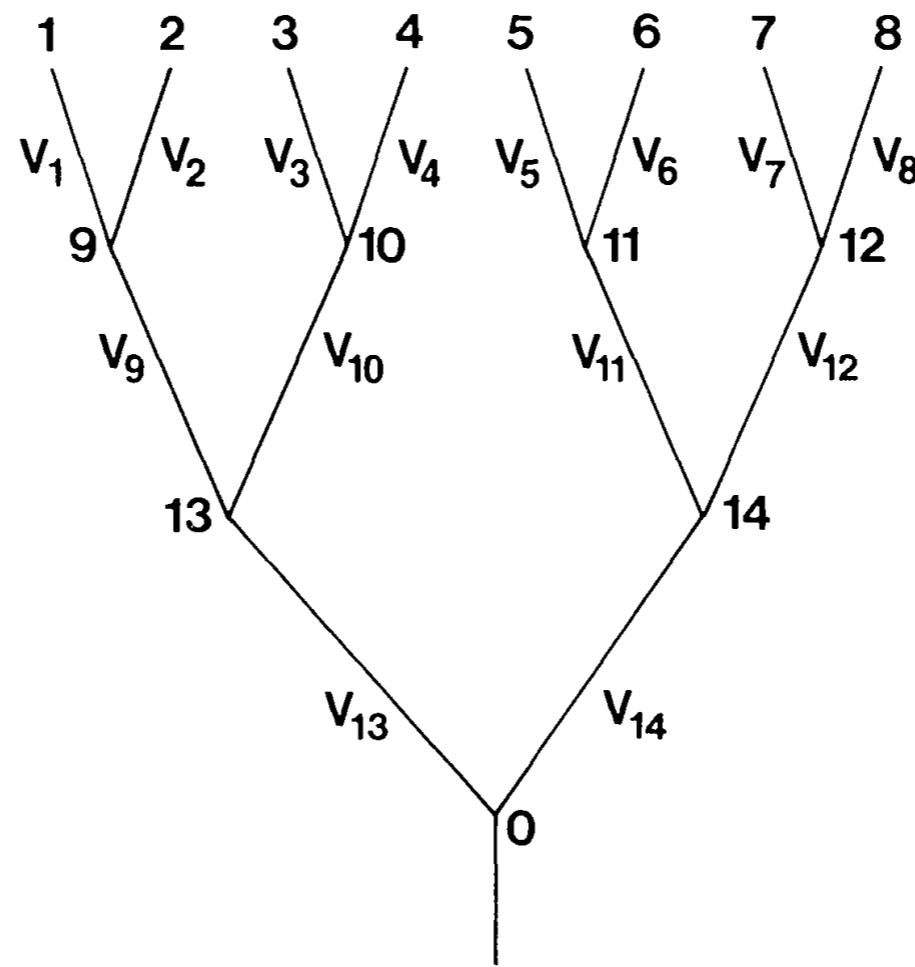


FIG. 8.—An example of a phylogeny, assumed known, from which we can define independent contrasts between taxa. This tree is highly symmetric, so that  $v_1 = v_2 = v_3 = v_4 = v_5 = v_6 = v_7 = v_8$ ,  $v_9 = v_{10} = v_{11} = v_{12}$ , and  $v_{13} = v_{14}$ .

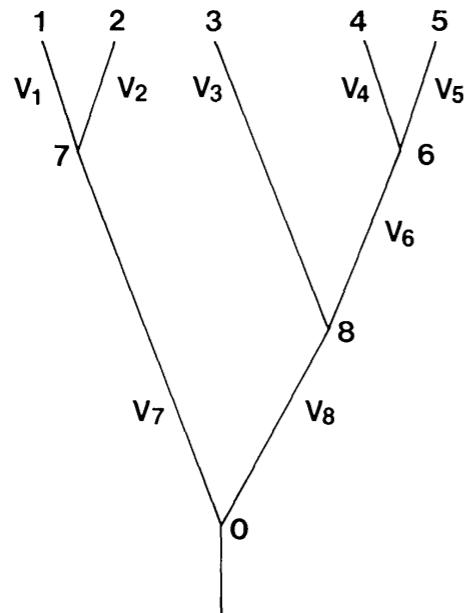


FIG. 9.—A less symmetrical phylogeny. The independent contrasts for this phylogeny are given in table 1.

TABLE 1  
THE FOUR CONTRASTS EXTRACTED FROM THE PHYLOGENY SHOWN IN FIGURE 9, EACH WITH ITS VARIANCE, ALL COMPUTED USING STEPS 1–4 IN THE TEXT

CONTRAST	VARIANCE
$X_1 - X_2$	$v_1 + v_2$
$X_4 - X_5$	$v_4 + v_5$
$X_3 - X_6$	$v_3 + v'_6$
$X_7 - X_8$	$v'_7 + v'_8$

where

$$X_6 = \frac{v_4 X_5 + v_5 X_4}{v_4 + v_5}$$

$$v'_6 = v_6 + v_4 v_5 / (v_4 + v_5)$$

$$X_7 = \frac{v_2 X_1 + v_1 X_2}{v_1 + v_2}$$

$$v'_7 = v_7 + v_1 v_2 / (v_1 + v_2)$$

$$X_8 = \frac{v'_6 X_3 + v_3 X_6}{v_3 + v_6}$$

$$v'_8 = v'_7 + v_3 v'_6 / (v_3 + v'_6)$$

## *What if We Do Not Take the Phylogeny into Consideration?*

Some reviewers of this paper felt that the message was “rather nihilistic,” and suggested that it would be much improved if I could present a simple and robust method that obviated the need to have an accurate knowledge of the phylogeny. I entirely sympathize, but do not have a method that solves the problem. The best we can do is perhaps to use pairs of close relatives as suggested above, although this discards at least half of the data. Comparative biologists may understandably feel frustrated upon being told that they need to know the phylogenies of their groups in great detail, when this is not something they had much interest in knowing. Nevertheless, efforts to cope with the effects of the phylogeny will have to be made. Phylogenies are fundamental to comparative biology; there is no doing it without taking them into account.

# Phylogenetic Least Squares

*Phil. Trans. R. Soc. Lond. B* **326**, 119–157 (1989) [ 119 ]

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## THE PHYLOGENETIC REGRESSION

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*(Communicated by W. D. Hamilton, F.R.S. – Received 13 February 1989)*

# Phylogenetic Least Squares

- A special instance of generalized least squares (GLS)
- Can use multiple models, not just Brownian
- When you use Brownian, it is equivalent to Independent contrasts