Evolutionary Patterns in Fossil Lineages

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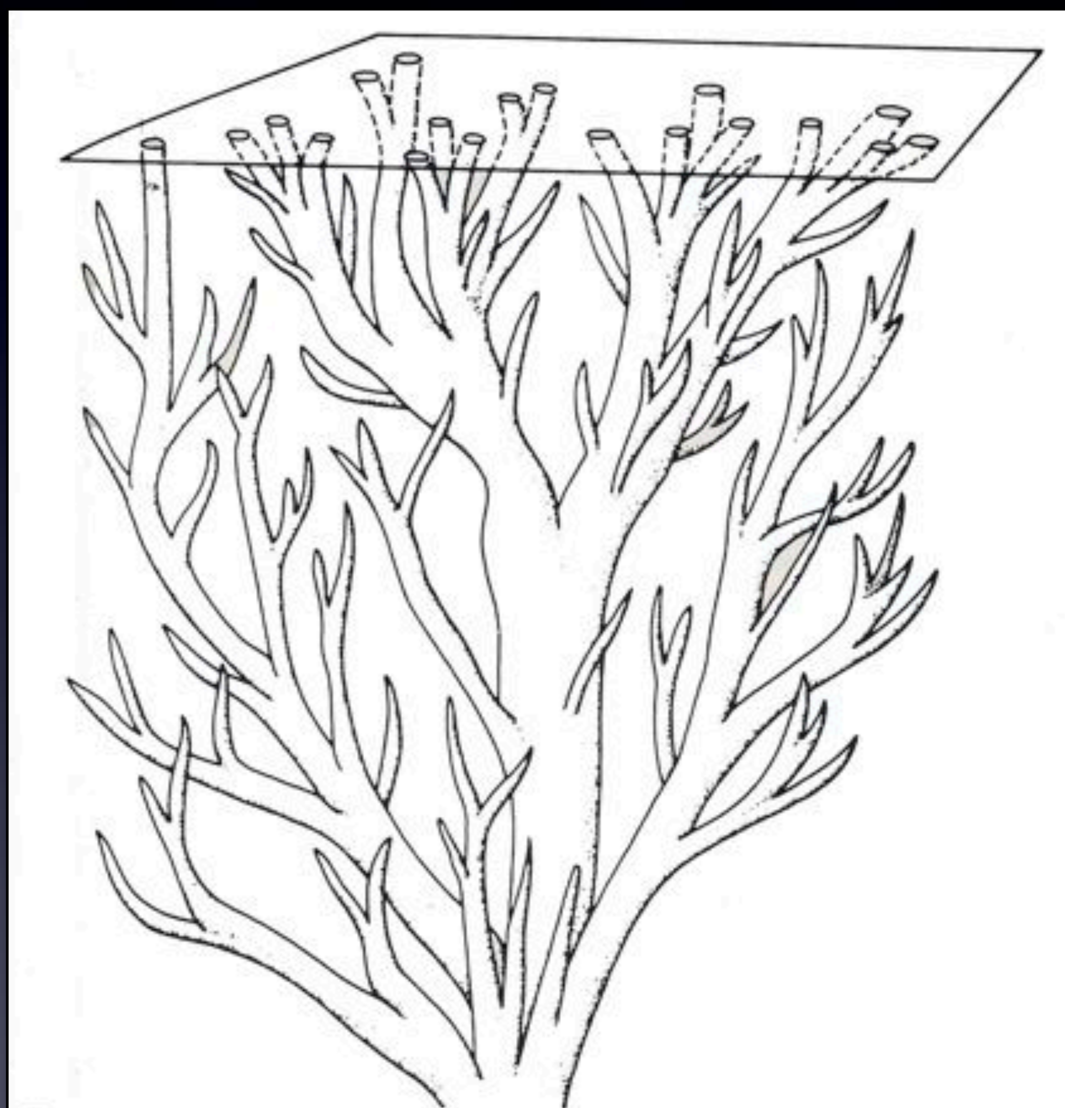
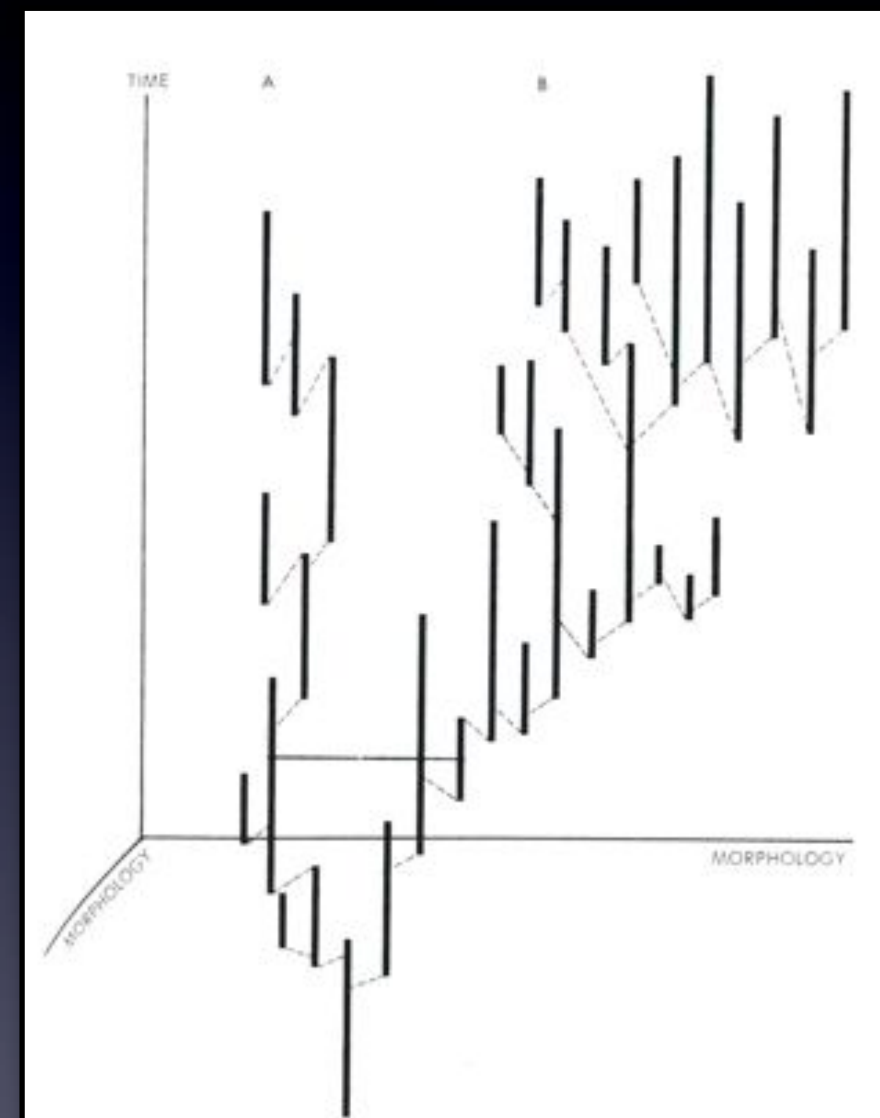
Two Paradigms

Eldredge & Gould (1972)

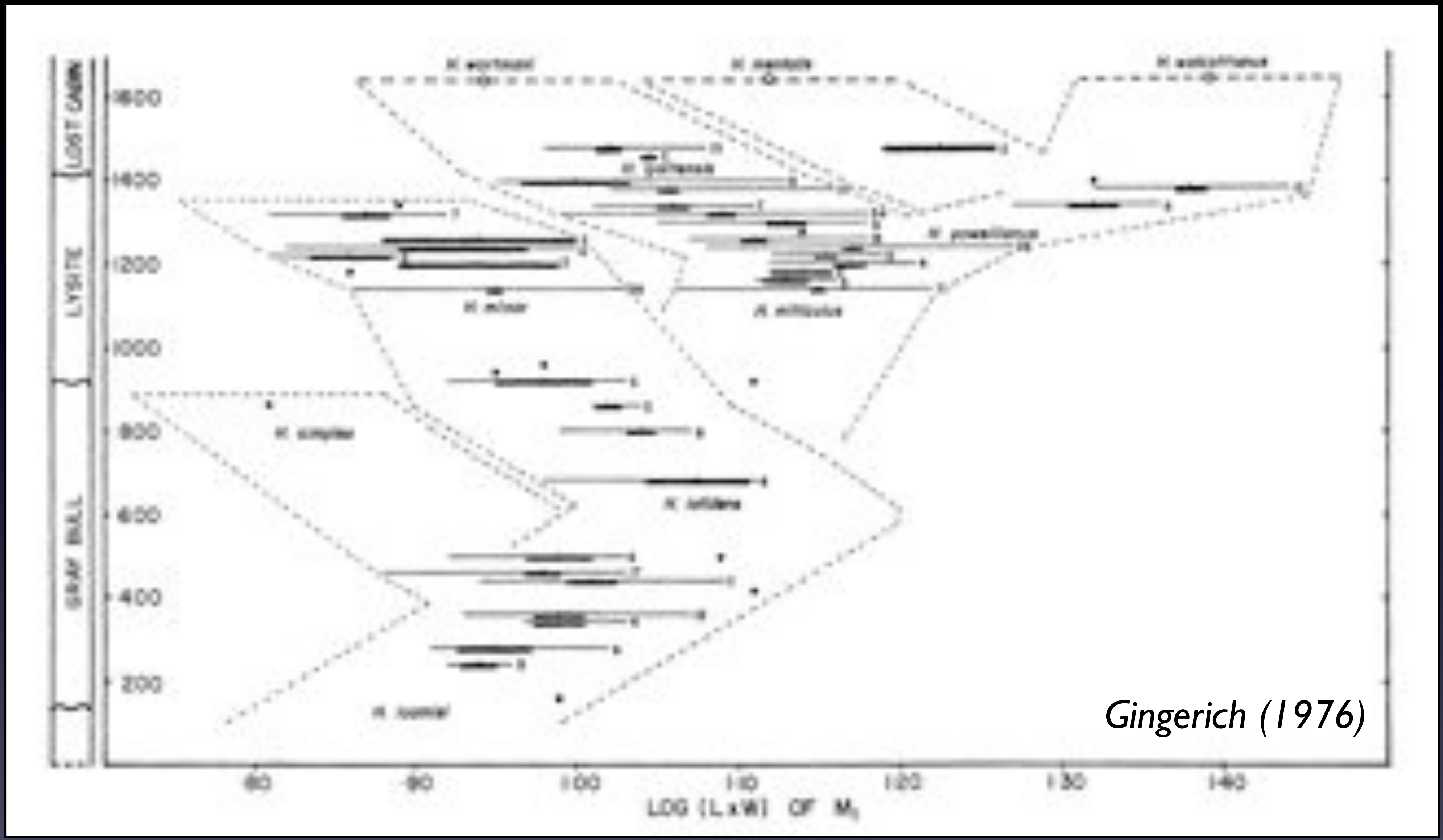


Phyletic Gradualism



Punctuated Equilibria

Disputed Interpretations



Gingerich (1976)

- Same data interpreted in conflicting ways
- Inadequacy of verbal models
- Led to incompatible summaries of the subject

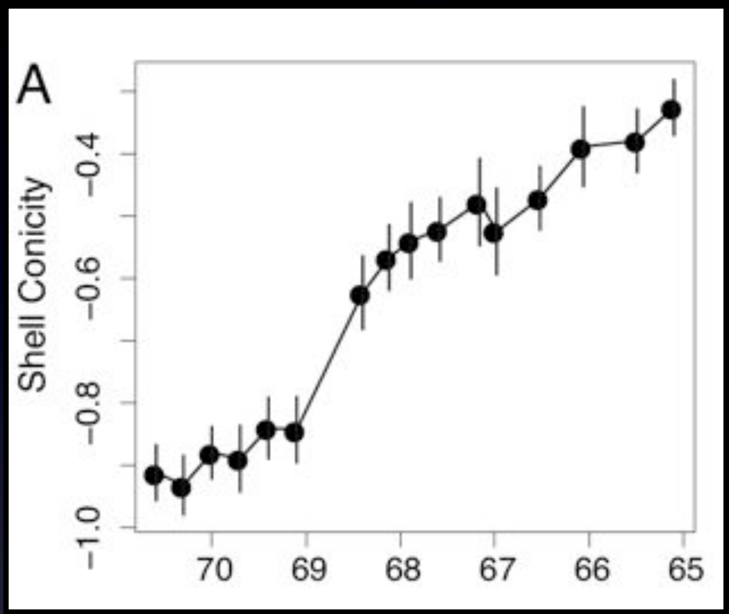
Evolution in Fossil Lineages

I. Fitting Statistical (not Verbal) Models

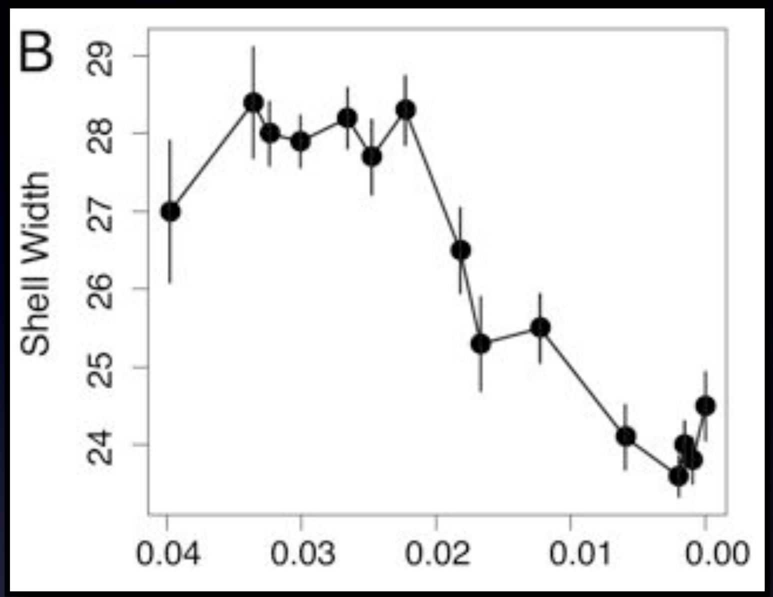
II. Applications

1. Evolutionary Modes
2. Tempo
3. Punctuations
4. Process Models

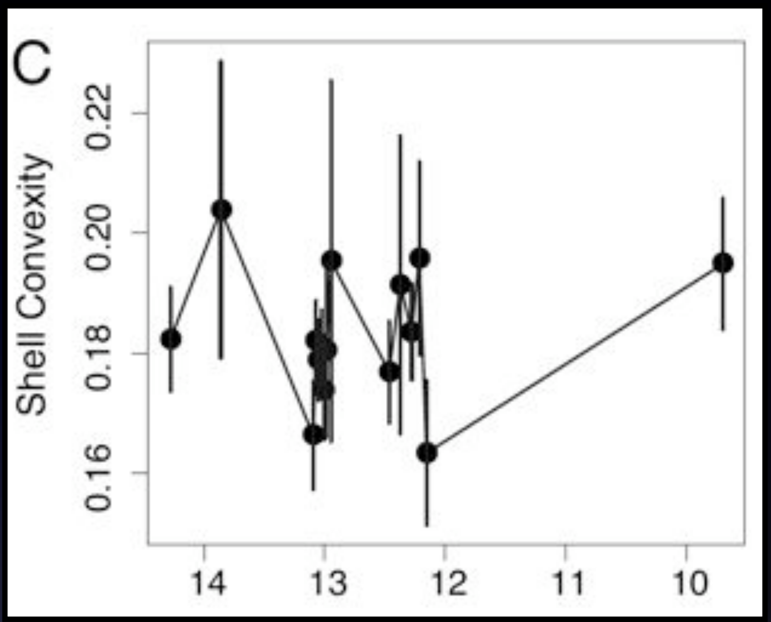
Evolutionary Modes



Directional change



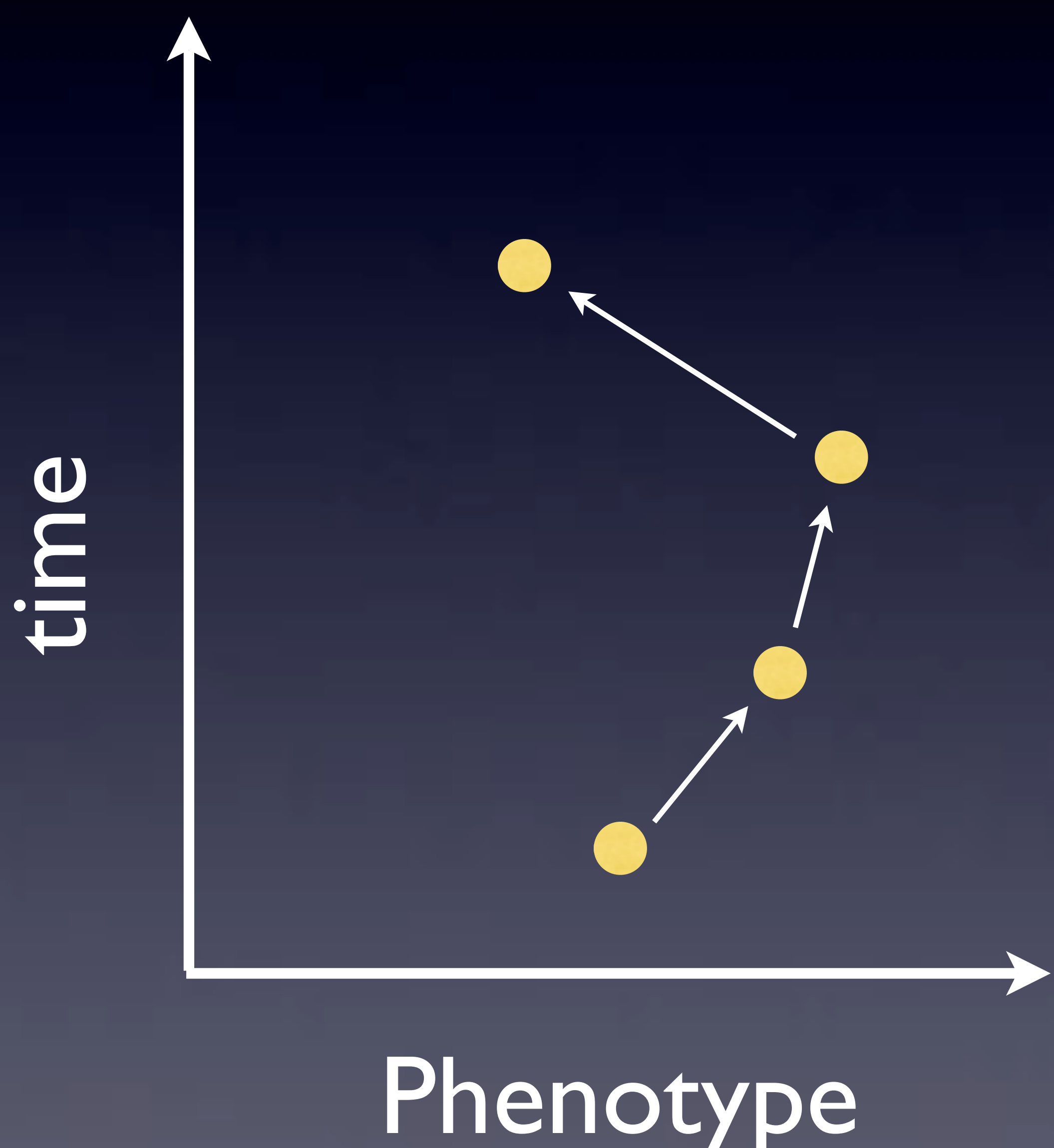
Random walk



Stasis

- Methods proposed to sort out different modes of evolution (e.g., Raup 1977, Bookstein 1987, Gingerich 1992, Roopnarine 2001)
- Generally rely on Random Walk as a null model

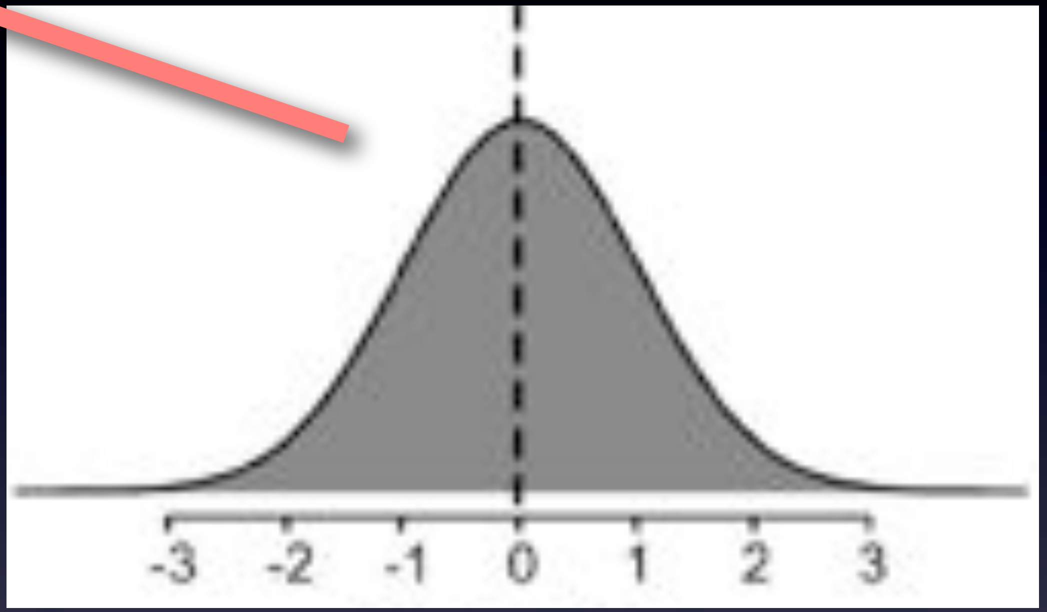
General Random Walk



+1.2

+0.1

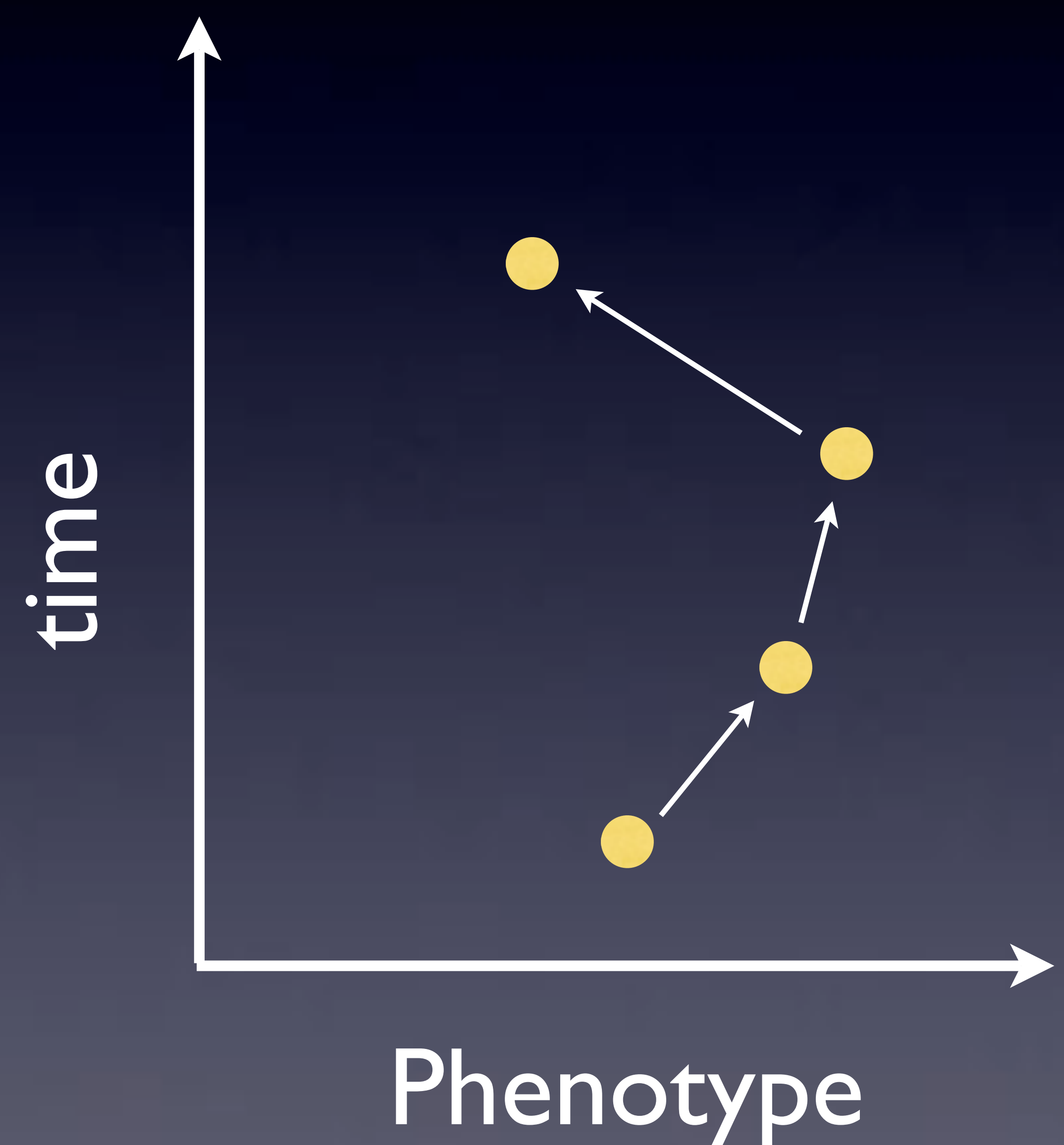
−1.5

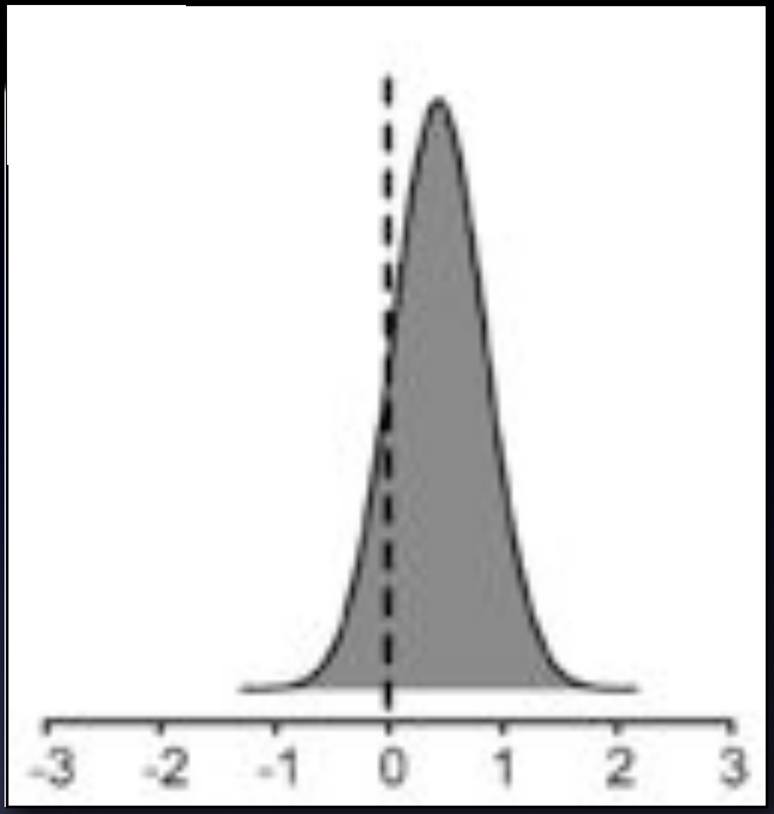


Evolutionary "steps"

step mean (μ_s) = **directionality**
step variance ($\sigma^2{}_s$) = **volatility**

General Random Walk



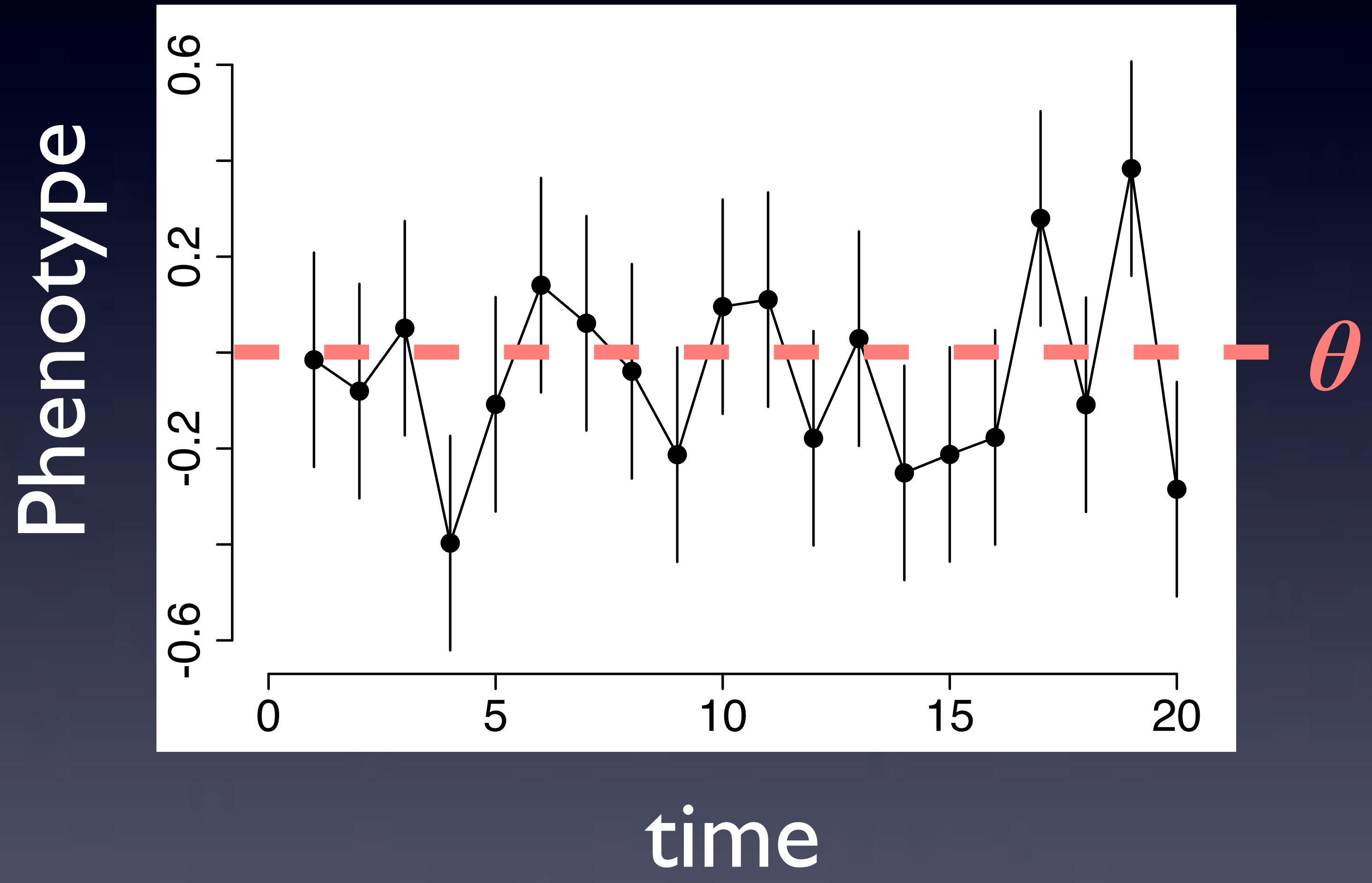


Evolutionary "steps"

step mean (μ_s) = **directionality**
step variance (σ^2_s) = **volatility**

Modeling Stasis

- Simple white noise
  (Sheets & Mitchell 2001)
- Optimum at θ, with variance of ω

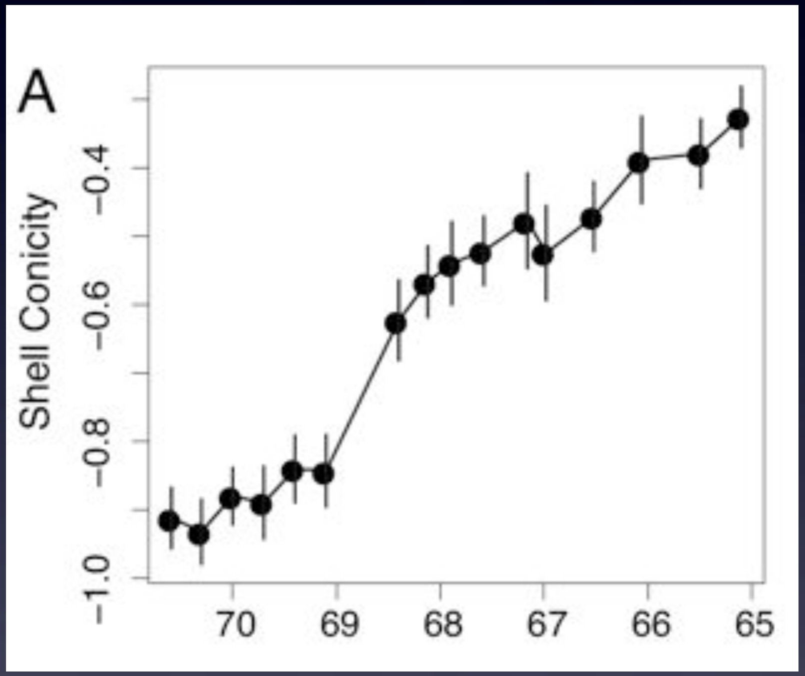


Statistical Inference

- Expected change in phenotype is normally distributed, with mean and variance determined by model parameters & age model
- Allows calculation of likelihood = **Pr[data | model]**
- Maximizing likelihoods gives best parameter estimates

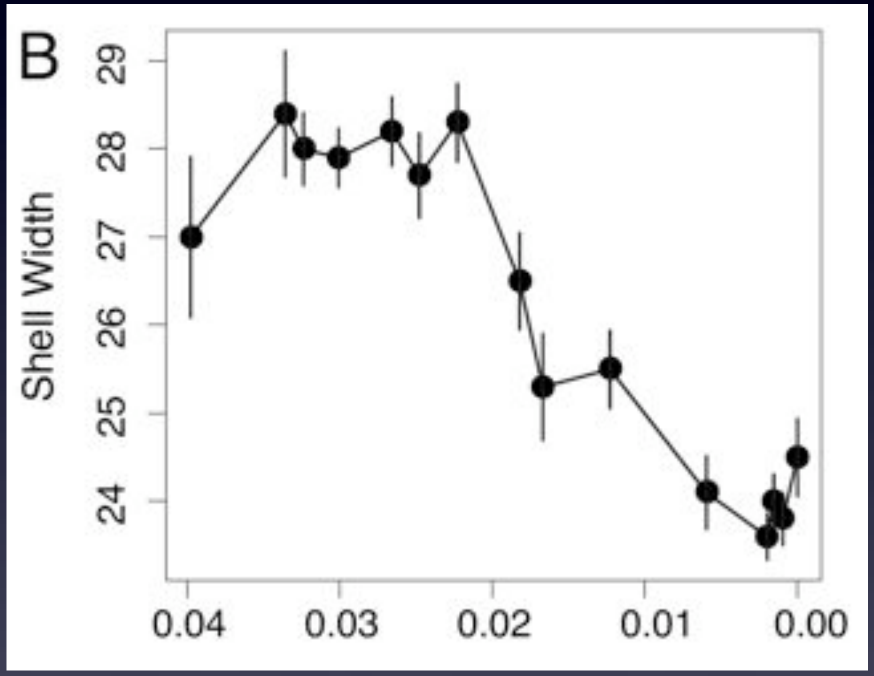
Models of Evolution

Directional change



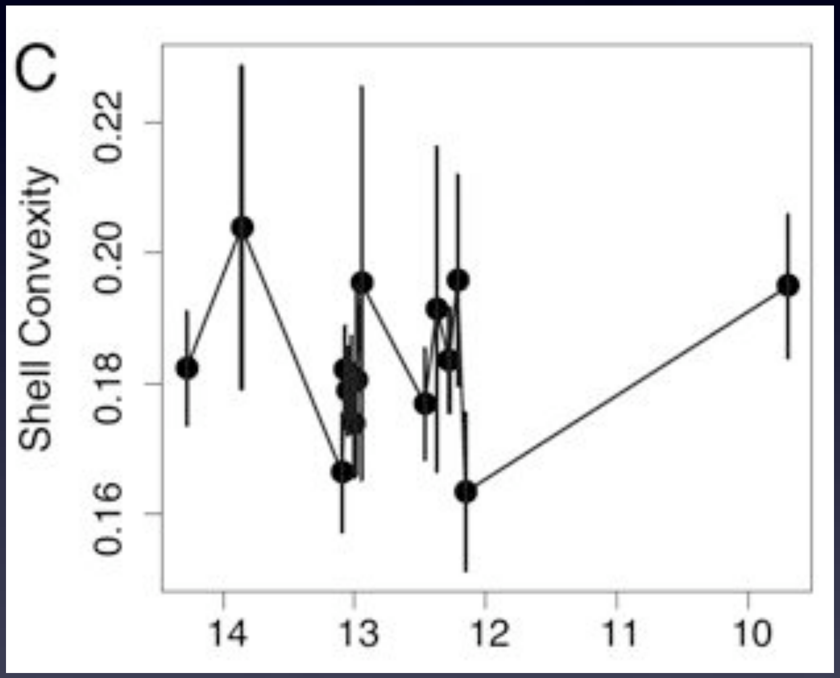
2 parameters

Random walk



1 parameter

Stasis



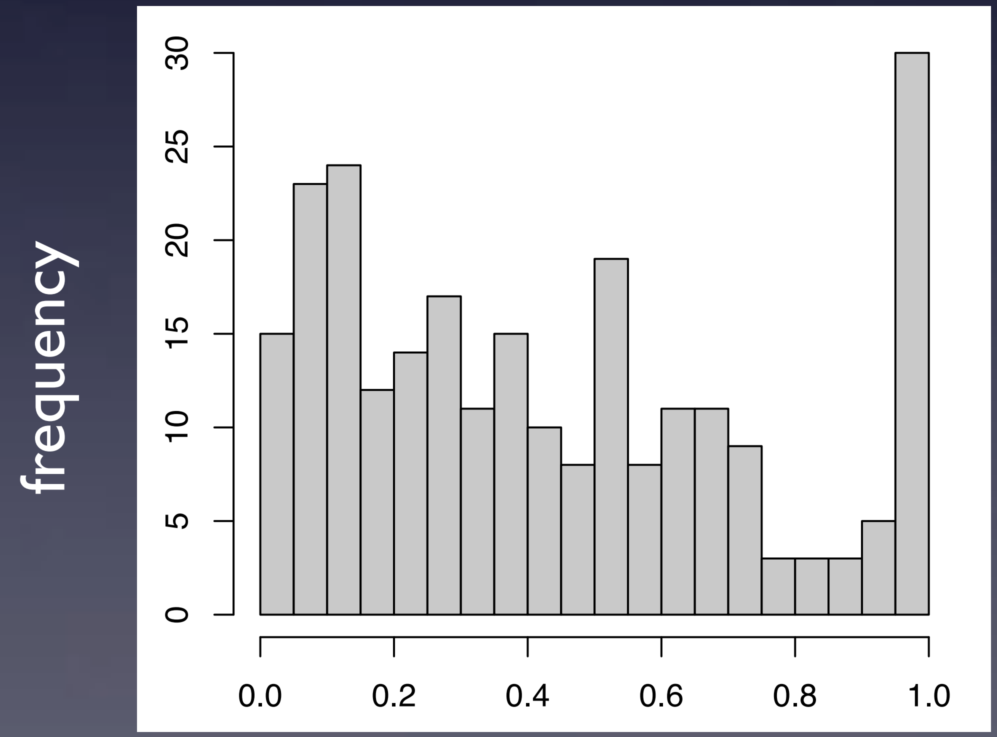
2 parameters

Comparing Models

- Models differ in complexity (# parameters)
- More parameters → higher log-likelihood
- AIC = -2(logL) + 2K
- Bias-corrected form, AICc, is better
- Akaike weights represent relative support among models

Advantages

- There is no null model
- Powerful and flexible machinery
- Sampling error is correctly handled



Proportion Morphological Variance from Sampling Error

Mean = 44%

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Evolutionary Modes

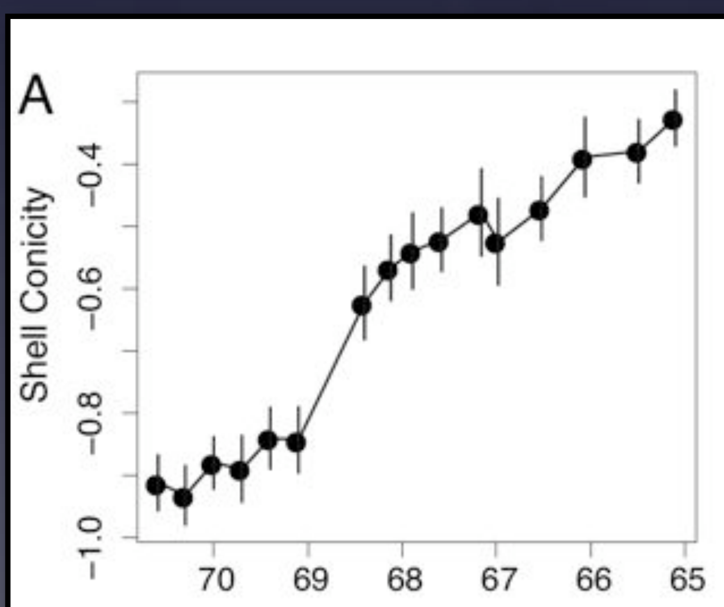
Gradualism dominates

Stasis/Punc. dominates

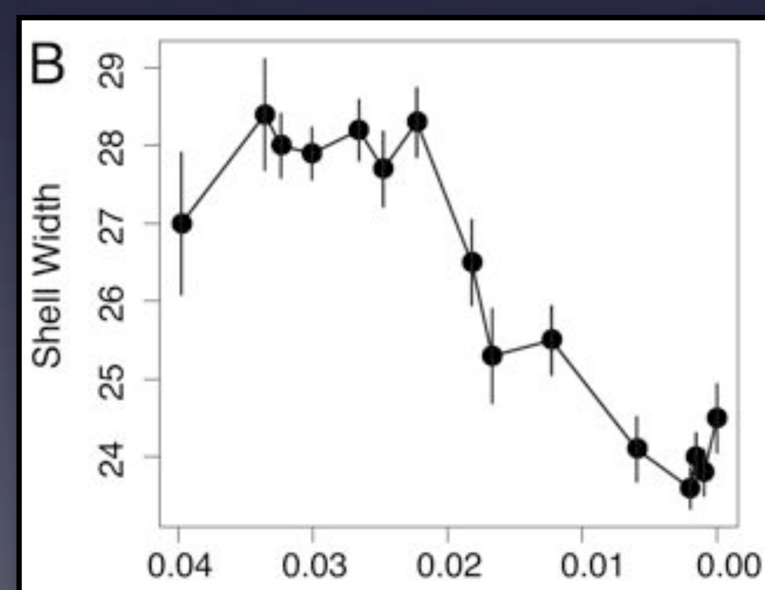
Levinton (2001)
Gingerich (1985)

Erwin & Antsey (1995)

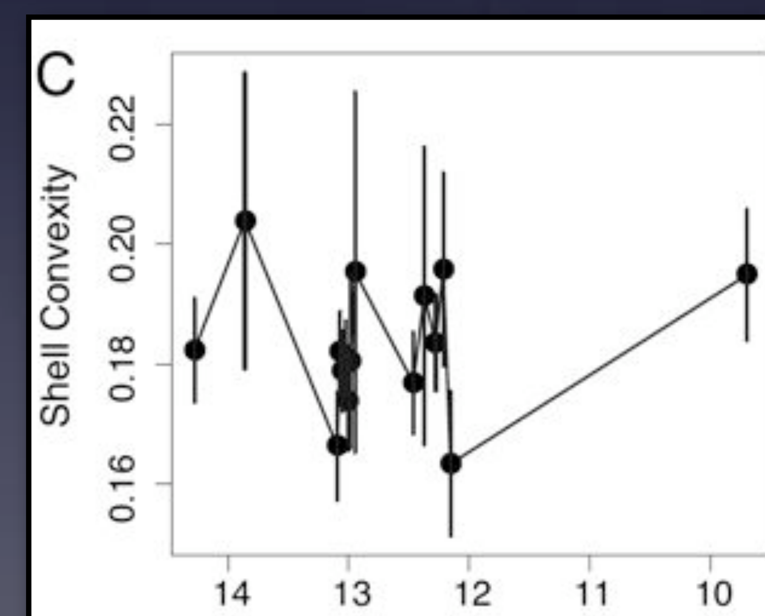
Gould (2002)
Jablonski (2000)
Jackson & Cheetham (1999)



Directional change



Random walk



Stasis

Data

- 251 time-series from 53 lineages
- 6 - 114 samples per time-series
- See Hunt (2007) *PNAS* 104(47).

Planktonic Microfossils
foraminifera [23]
radiolaria [9]
conodonts [9]

Benthic Microfossils
foraminifera [37]
ostracodes [60]

Macrofossils
mollusks [70]
trilobites [1]
mammals [40]
fish [2]

Relative Importance of Evolutionary Modes

Gradualism dominates ⟵ ⟶ Stasis/Punc. dominates

Levinton (2001)
Gingerich (1985)

Erwin & Antsey (1995)

Gould (2002)
Jablonski (2000)
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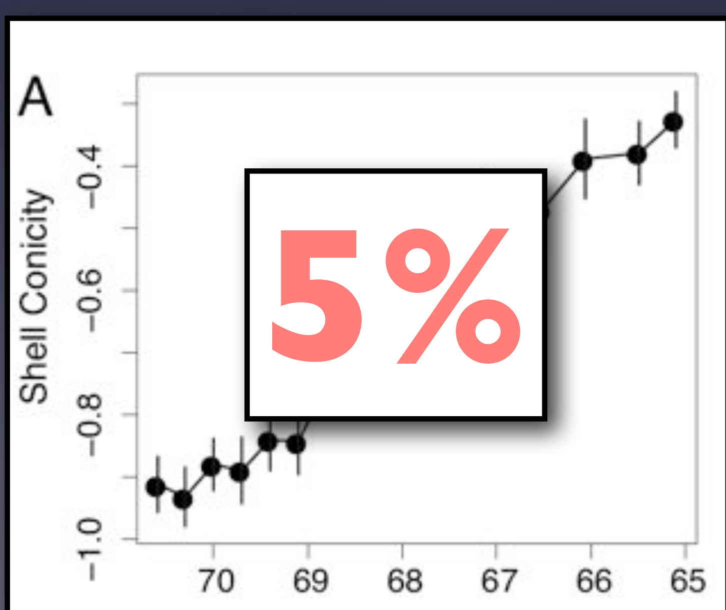
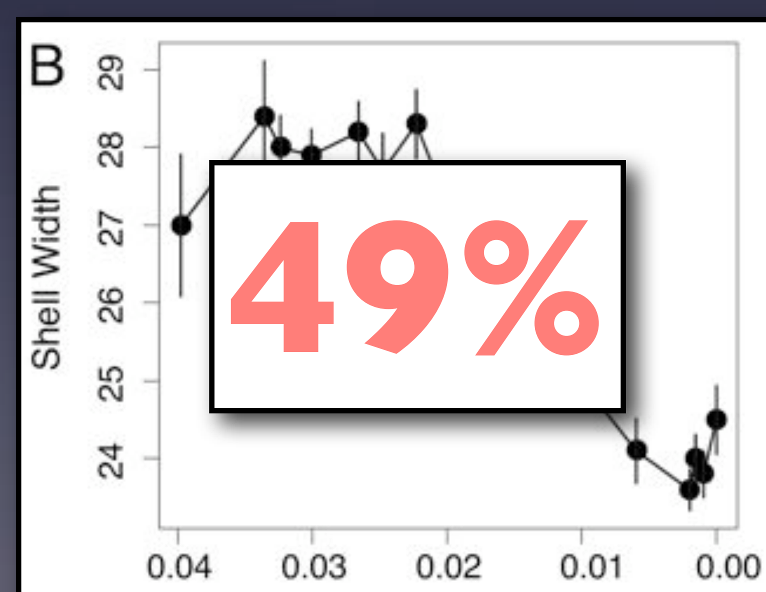
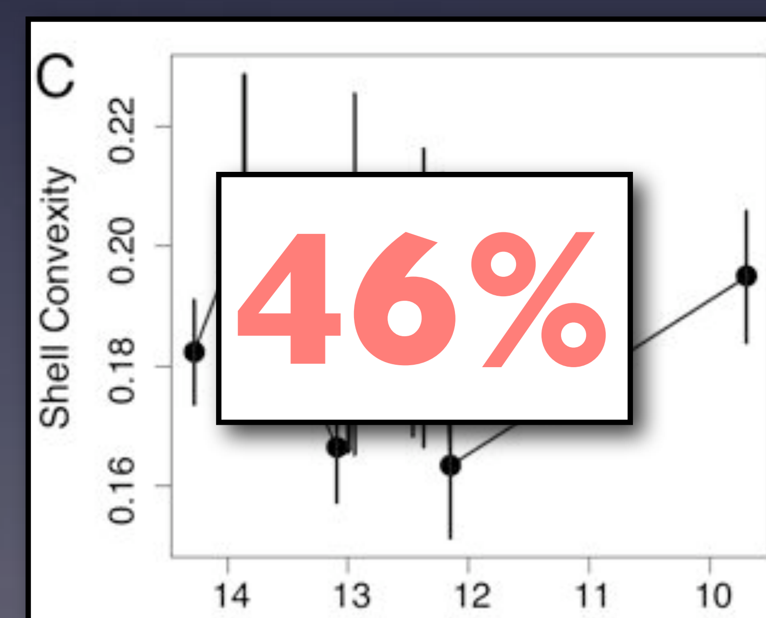


Directional change



Random walk



Stasis

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Rates of Evolution

Parameter of the Random Walk (step variance) is useful as a rate metric:

1. uncorrelated with interval length for true random walks
2. known range of values under drift (Lynch 1990)
3. can be measured from A-D or phylogeny

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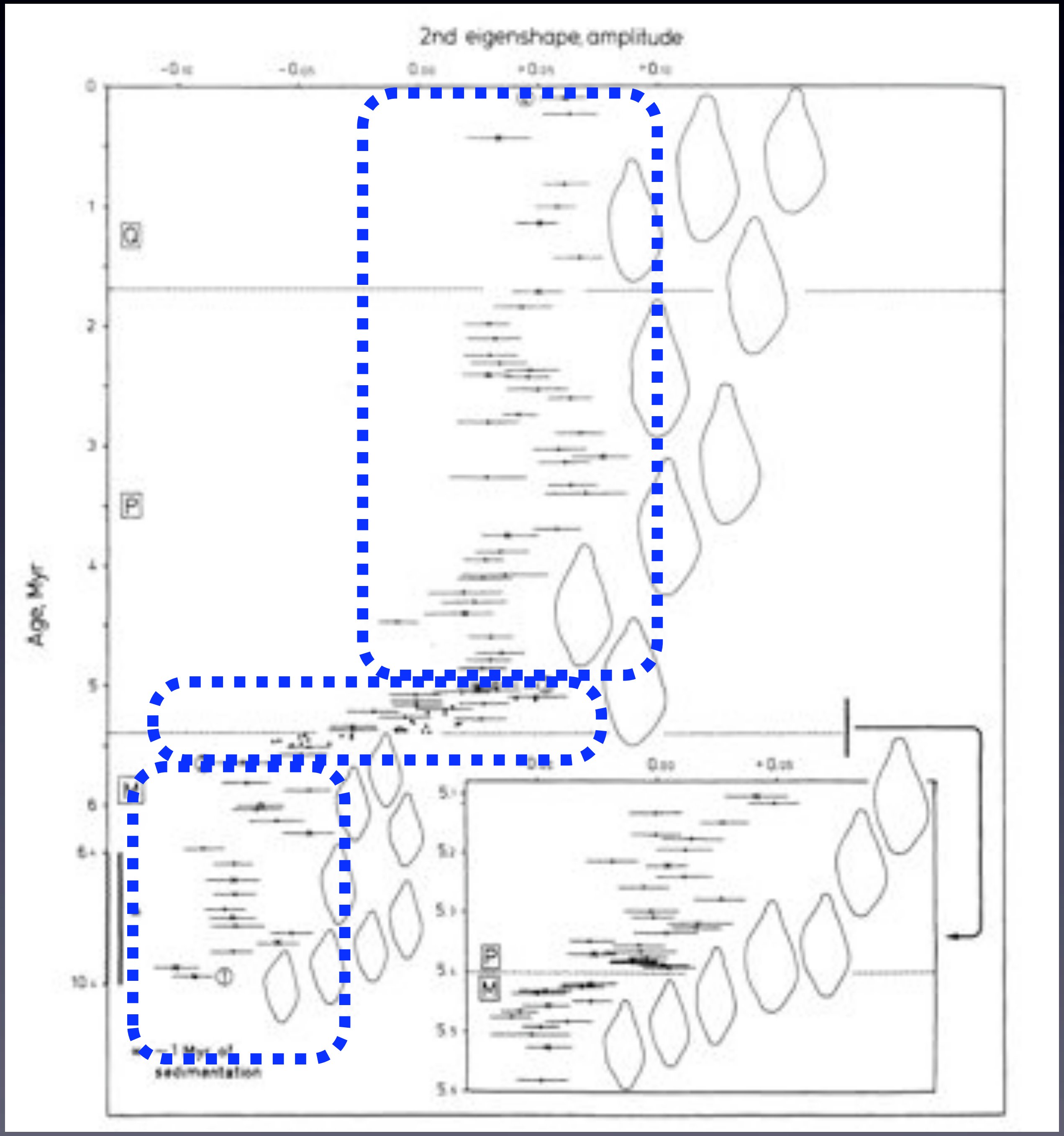
Punctuations

Malmgren et al. (1983)



- General form:

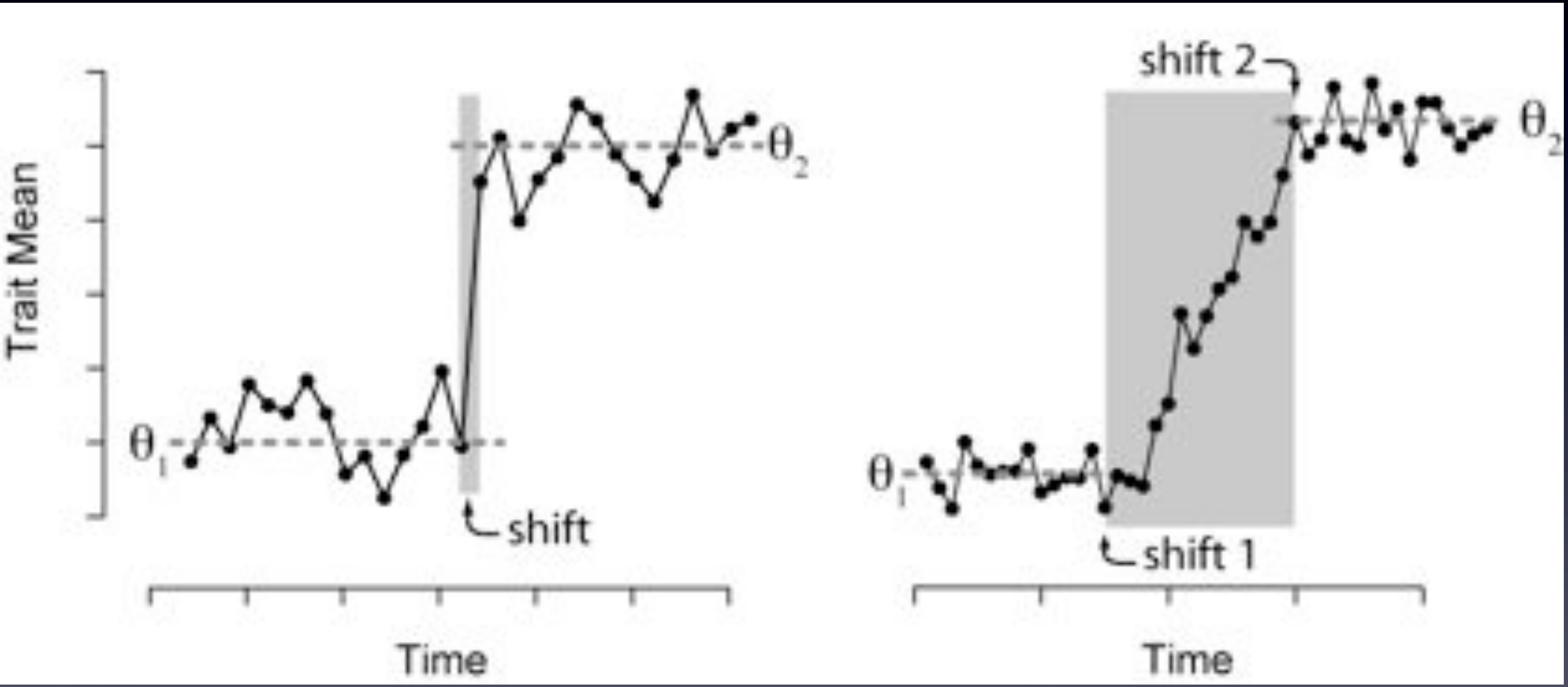
  stasis - change - stasis

- Class of models in which evolutionary dynamics shift over time

Does improved fit of punctuated models outweigh their greater complexity?

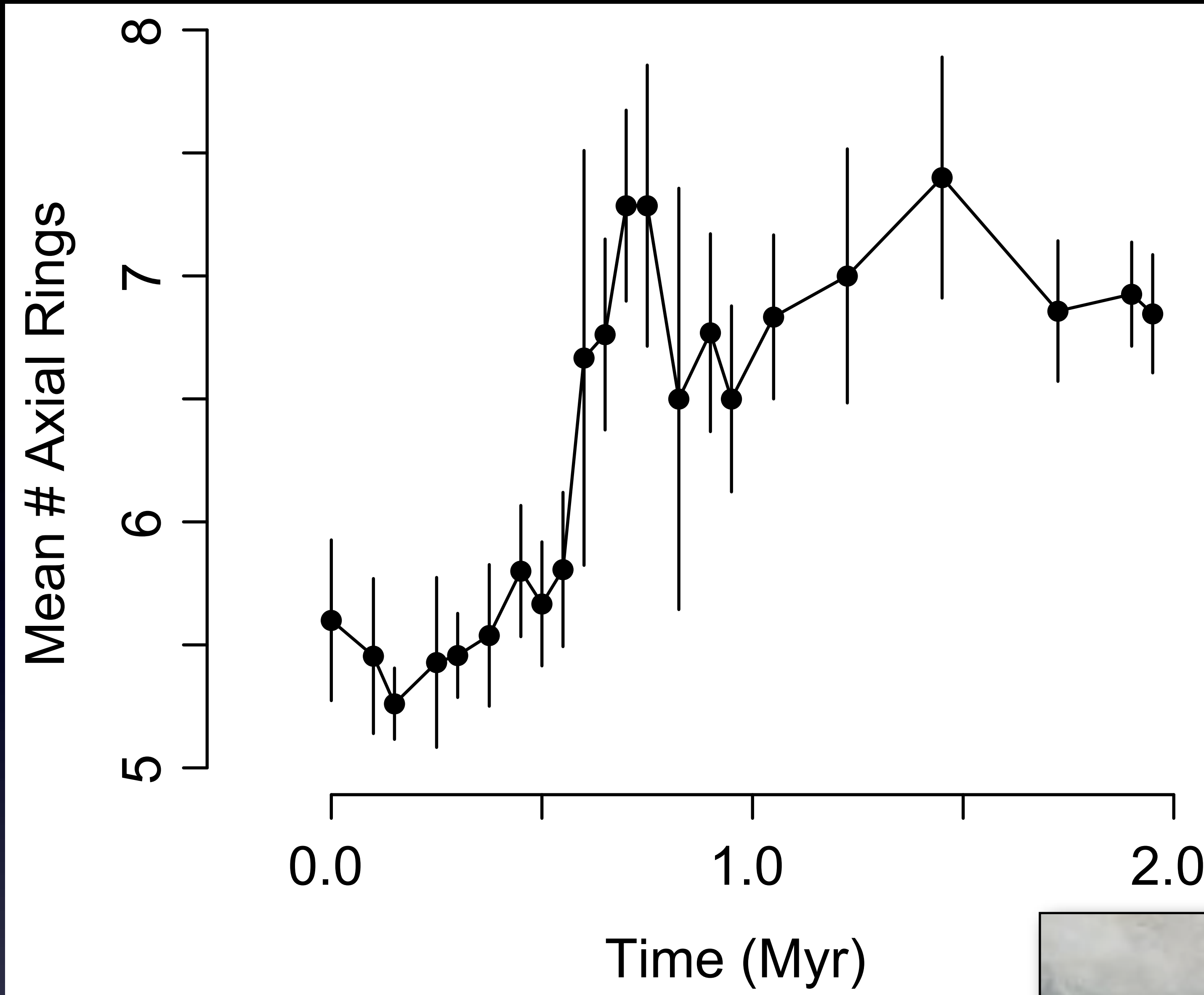
Two kinds of punctuations

Unsampled | Sampled



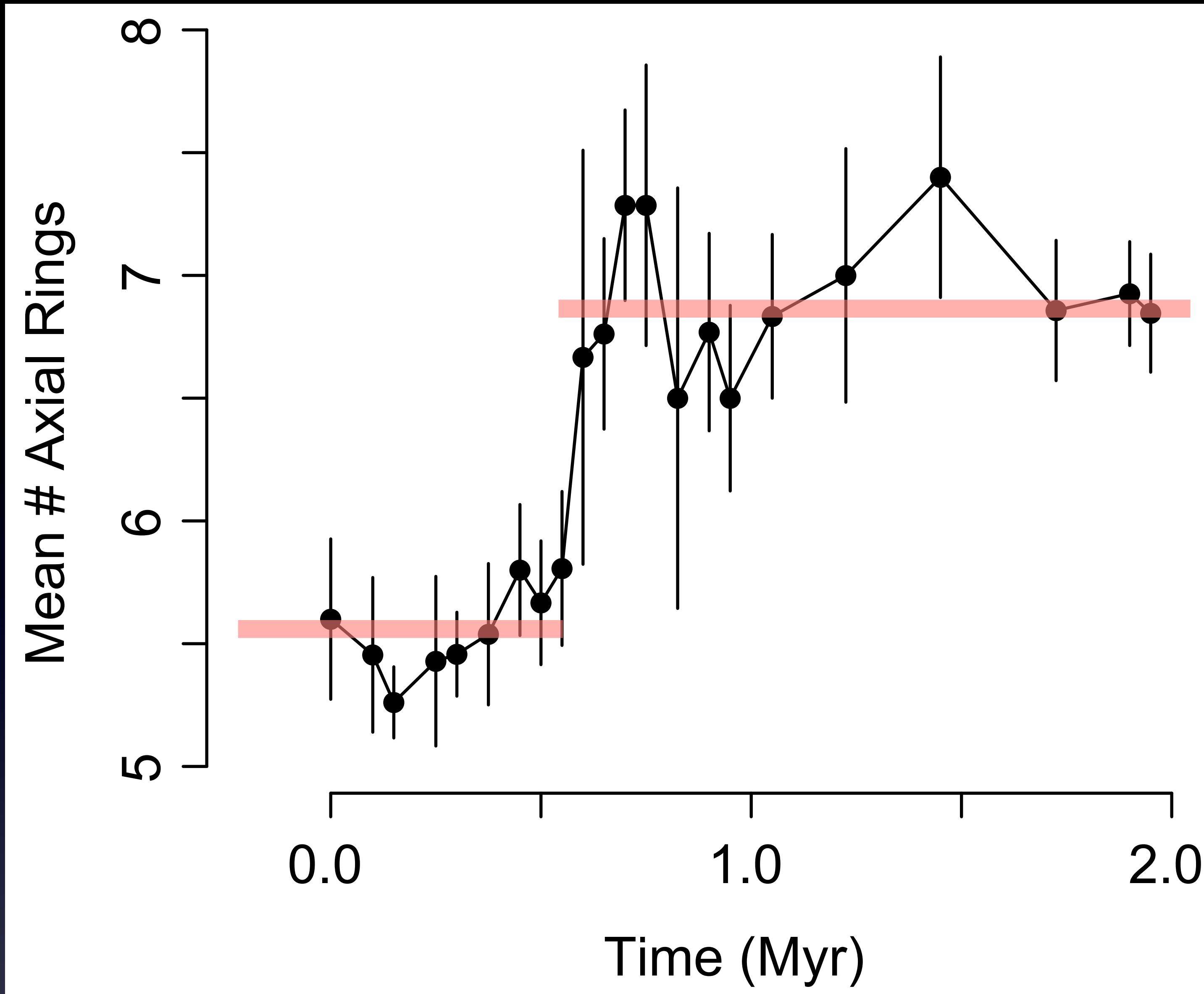
5 parameters | *8 parameters*

Use AIC$_C$ scores to weigh model support



- Cisne et al. (1980) documented pulsed change in trilobite *Flexicalymene*
- Levinton (2001) cited it as an example of gradual change

Hunt (2008) Paleobiology 34:360.



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Hunt (2008) Paleobiology 34:360.

model	segments	# par	AICc	weight
Random Walk	1	1	8.01	**0.375**
Directional	1	2	10.31	0.119
Stasis	1	2	49.48	0.000
1 Punctuation (unsampled)	2	4	7.42	**0.505**

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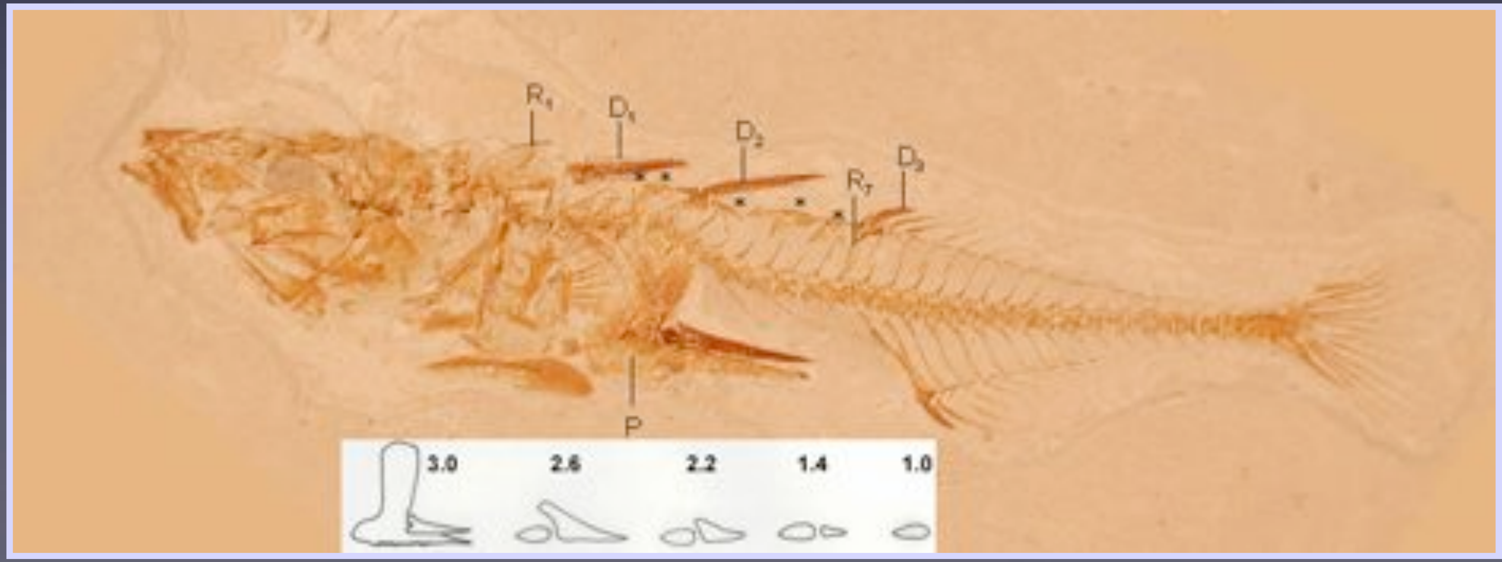
Other Kinds of Models

Process-based models

1. Causal drivers (e.g., Temperature tracking)
2. Adaptive evolution

Selection in Fossil Lineages

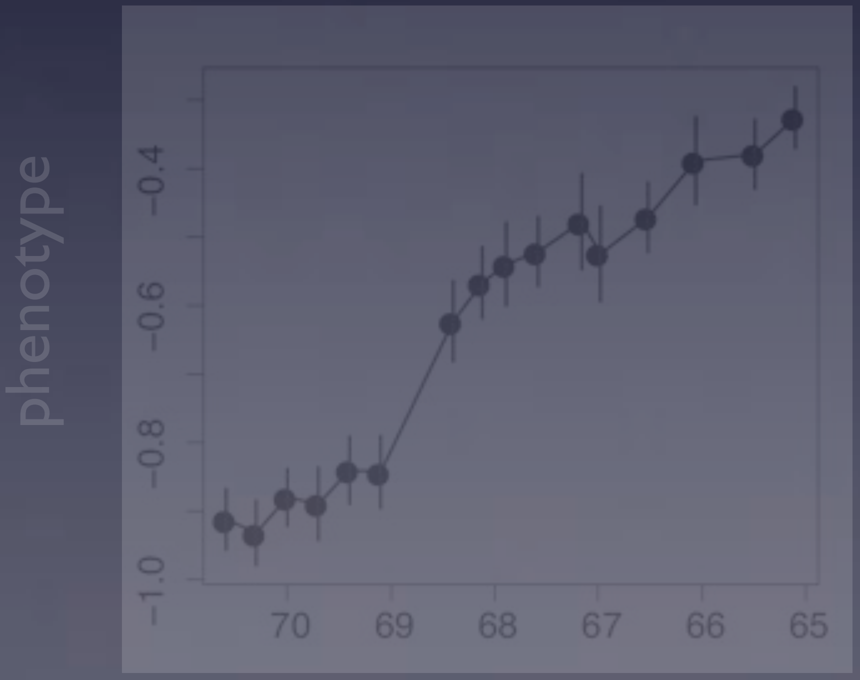
- Originally, Directional mode thought to be indicative of natural selection
- Rareness of clearly Directional was disconcerting
- Best test case: stickleback from varved lakes (Bell et al. 2006)



What should adaptive evolution look like?

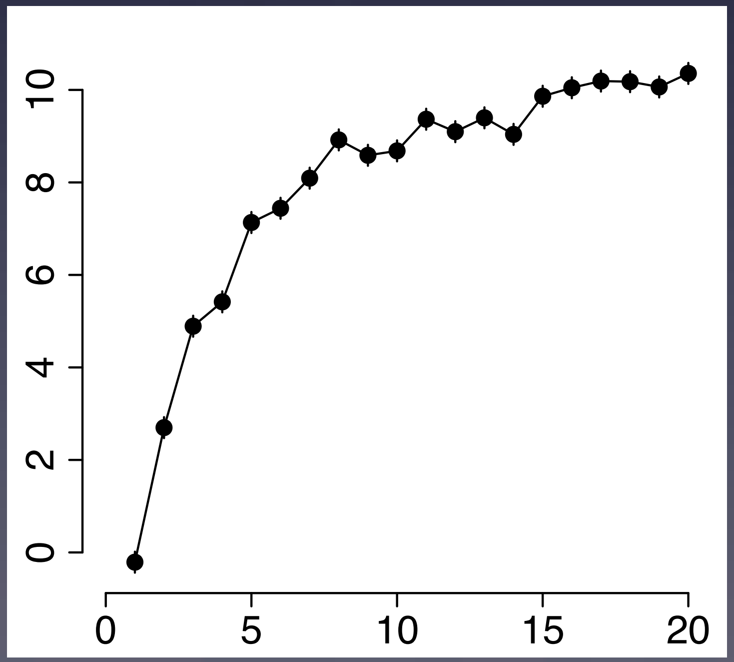
Scenario: Environment shifts, population is dislocated from an adaptive peak

Directional change?



time

Orstein-Uhlenbeck process (Lande 1976)

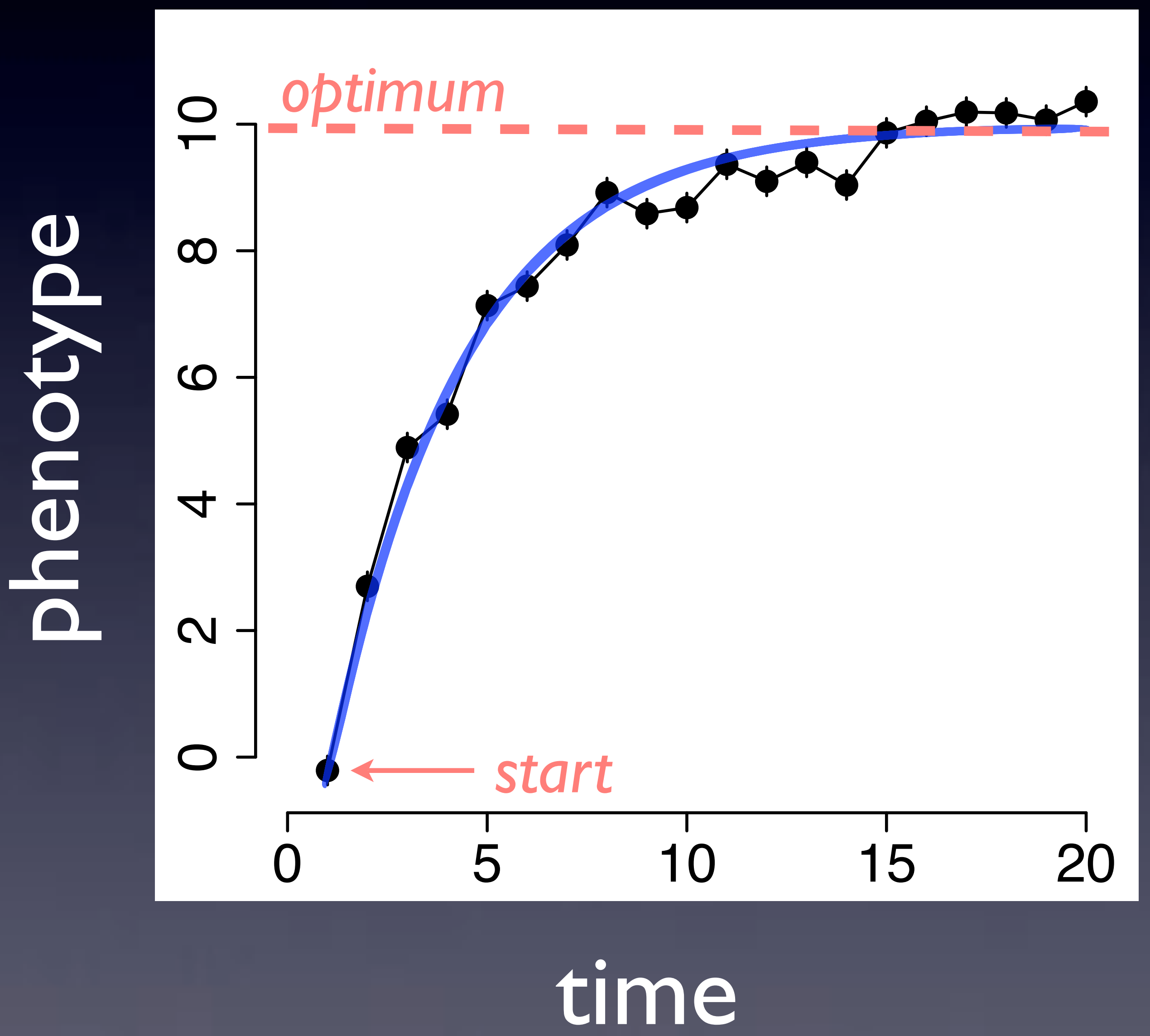


time

Adaptive (OU) Model

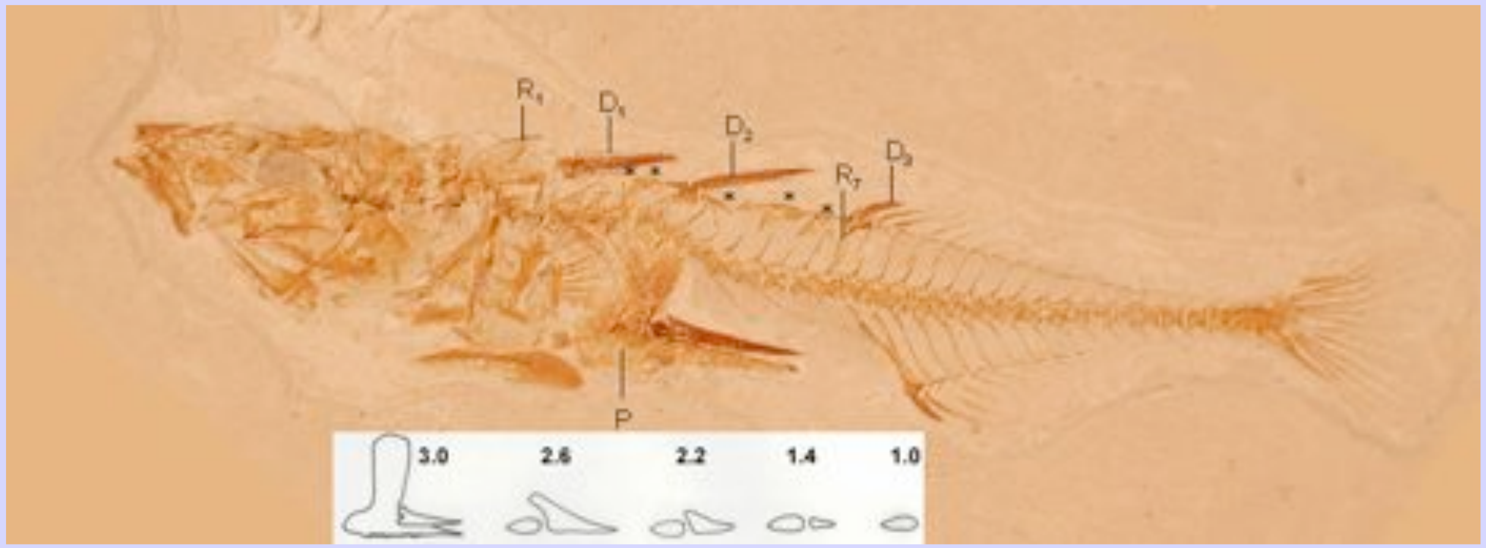
Four key parameters

- starting phenotype
- optimal phenotype
- strength of selection
- step variance (drift)



Bell's stickleback

- ~5,000 stickleback fish from diatomite mine
- Countable yearly varves
- Resolution = 250 yrs

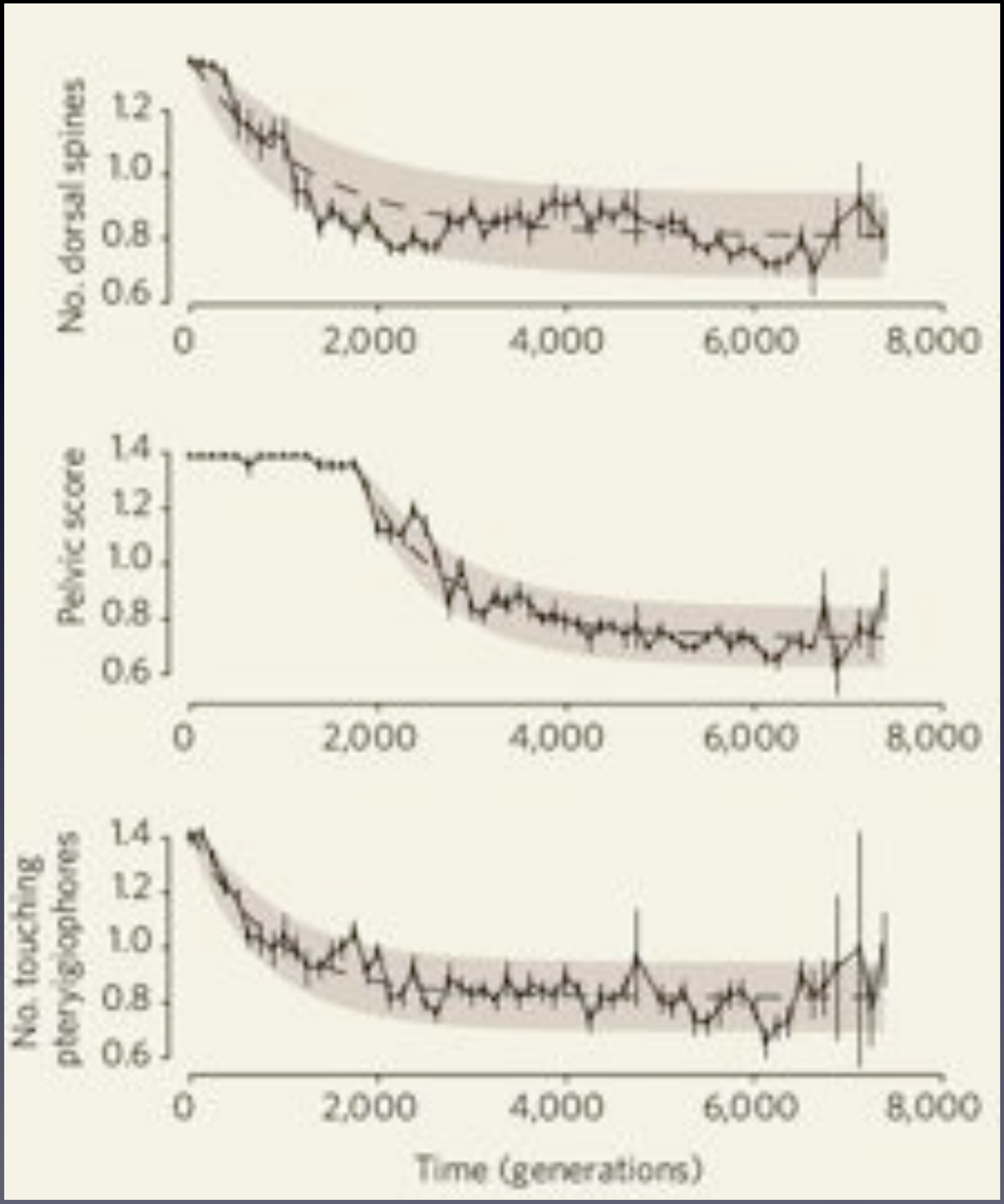


- Counted dorsal spines, pterygiophores, scored pelvis
- Independent evidence for selection for reduced armor

Numerous tests failed to find selection (directionality)

Re-analysis

- Fit adaptive (OU), and neutral drift (Random walk) models
- Adaptive models conclusively beat neutral ones ($w > 0.99$)



Hunt et al. (2008) Evolution 62:700.

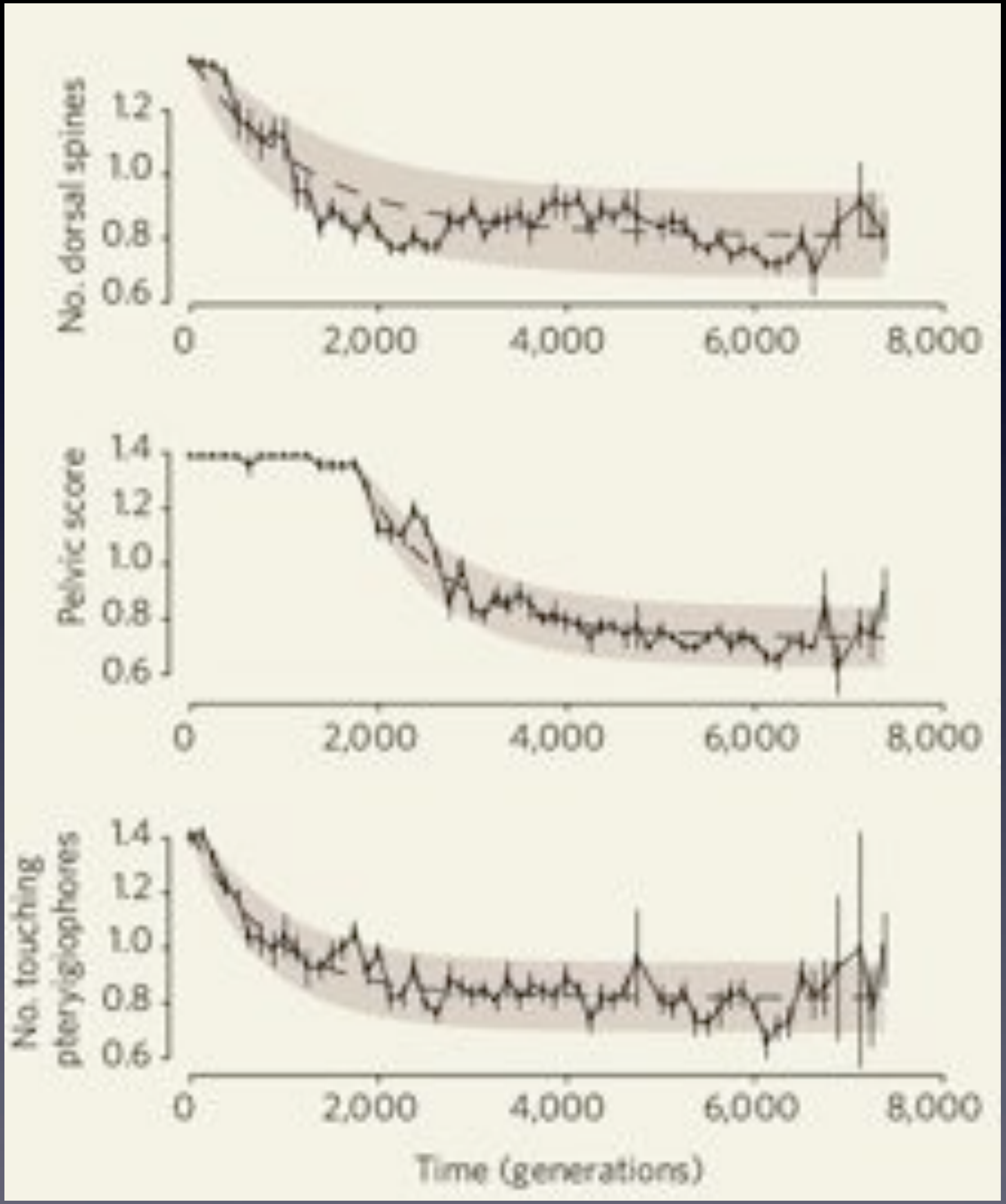
Implications

- Consistency check: all models imply reasonable N_e

trait	Ne
dorsal spines	575 – 4,023
pelvic score	889 – 6,222
pterygiophores	851 – 5,957

- Weak selection: fitness differences ≈ 1 - 5% or less

- With coarser resolution, this would look like unsampled punctuation



Conclusions I

1. Banish the word ‘gradual.’ Evolution can be:
    - directional or not
    - homogeneous or heterogeneous
2. Directional evolution is rarely observed
3. Heterogeneous dynamics are not uncommon
4. Skeletal reduction in sticklebacks was adaptive

Conclusions II

There are many advantages to formulating evolutionary interpretations as statistical models:

- unambiguous model comparisons
- parameters are evolutionary informative (rates, directionality, natural selection)

Acknowledgments

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- Mike Bell's field crew