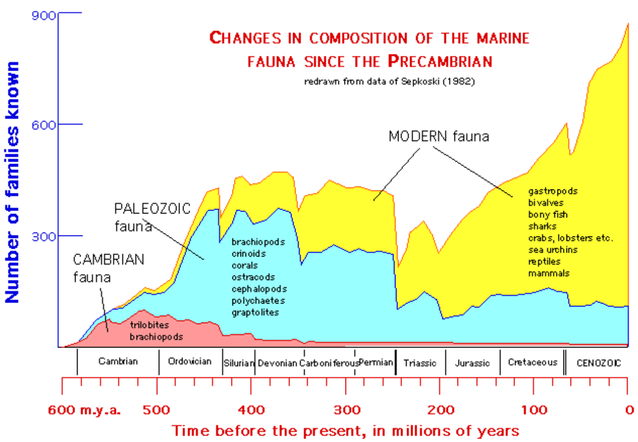
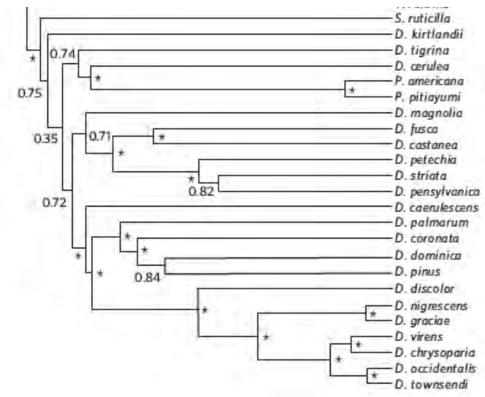
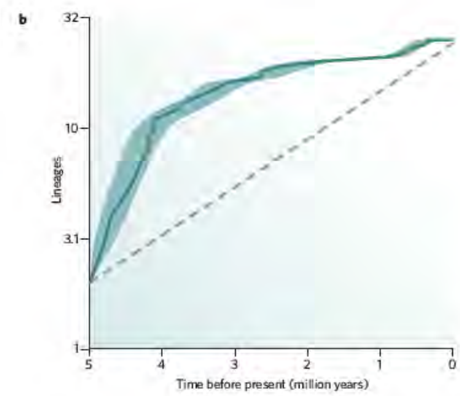
Phenotypic Diversity in Macroevolution

Patterns of taxonomic diversity through time

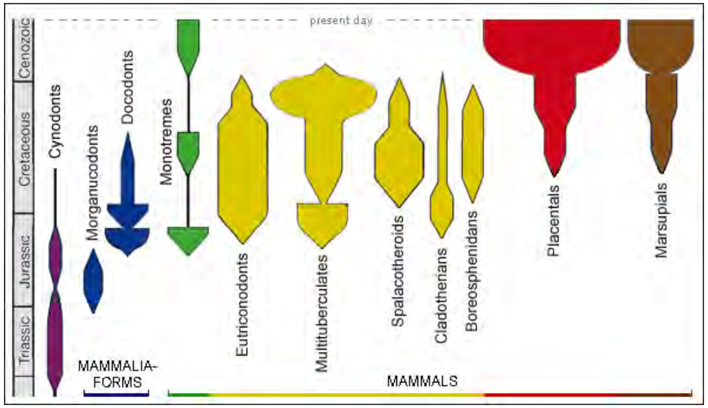


after Sepkowski (1982)





Reznick and Ricklefs 2009

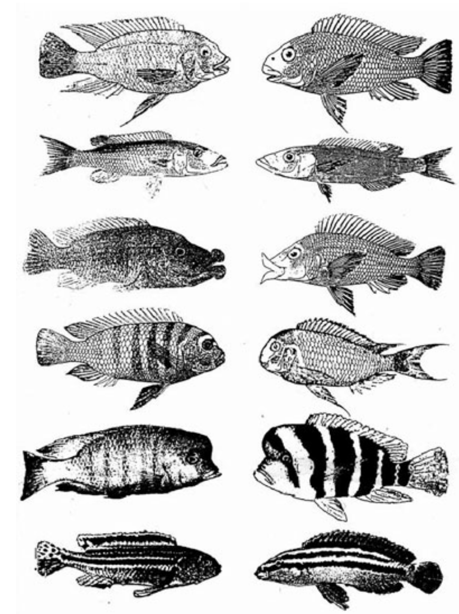


Luo (2007)

Phenotypic Diversity

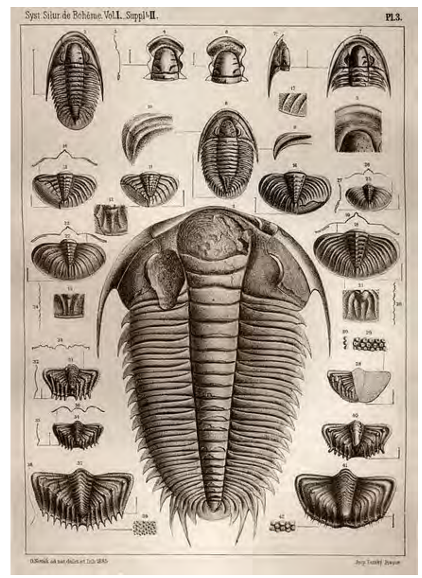
What about phenotypic diversity?

www.ucmp.Berkeley.edu/taxa/inverts/Mollusca/gastropoda.php



Kocher et al. (1993)

dbs.umt.edu/research_labs/fishmanlab



Wikimedia: from Barrande (1852)

-Understanding trends requires a quantification of phenotype

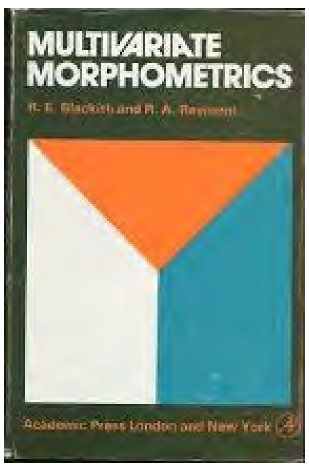
Challenge:

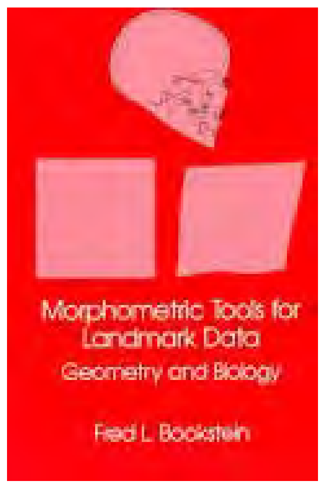
-How do we quantify morphology & phenotypic diversity?

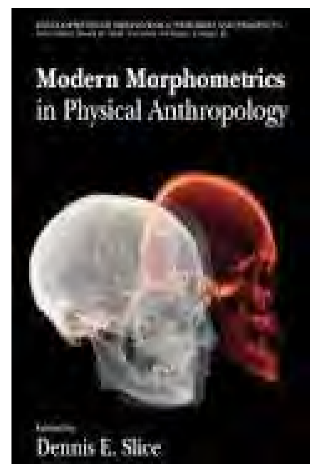
Morphometrics (*morpho* = form; *metrics* = measure)

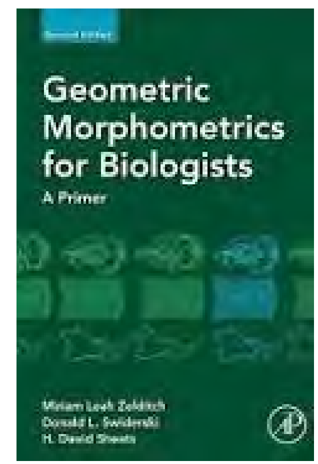
-The quantification of morphology

-The study of phenotypic variation and covariation









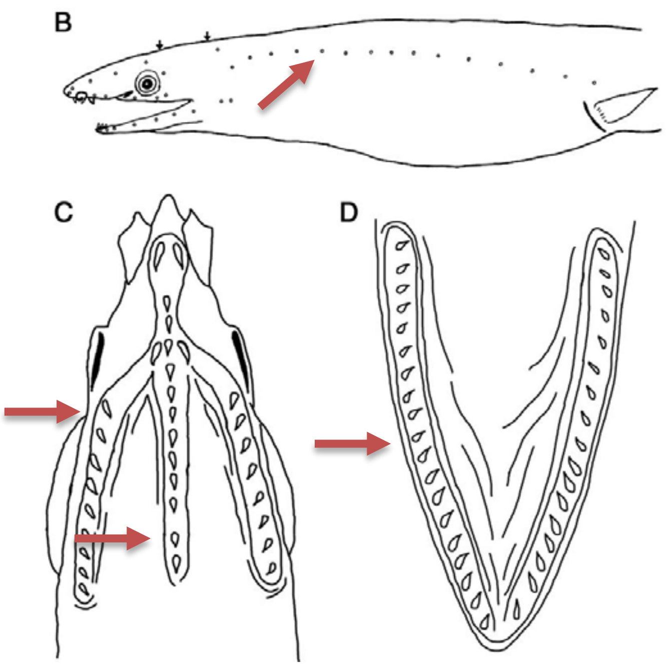
Different types of variables (and methods) have been used

Images from google

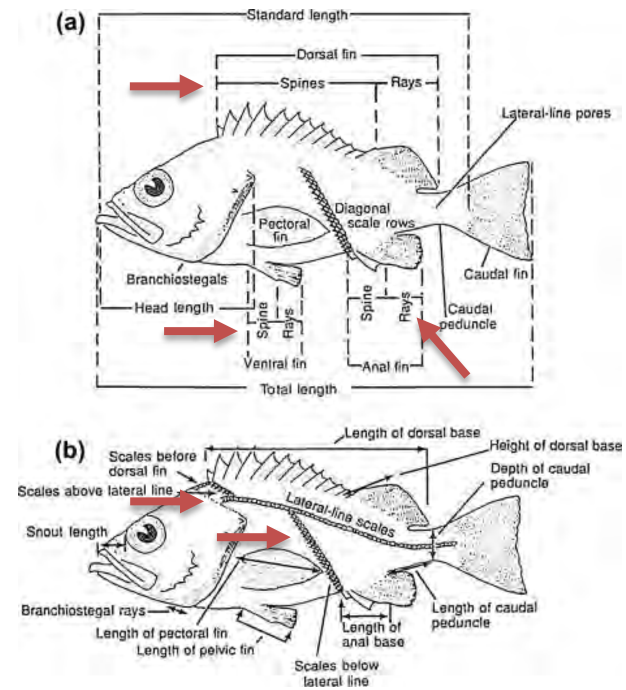
Common Morphometric Data

Meristic count data*

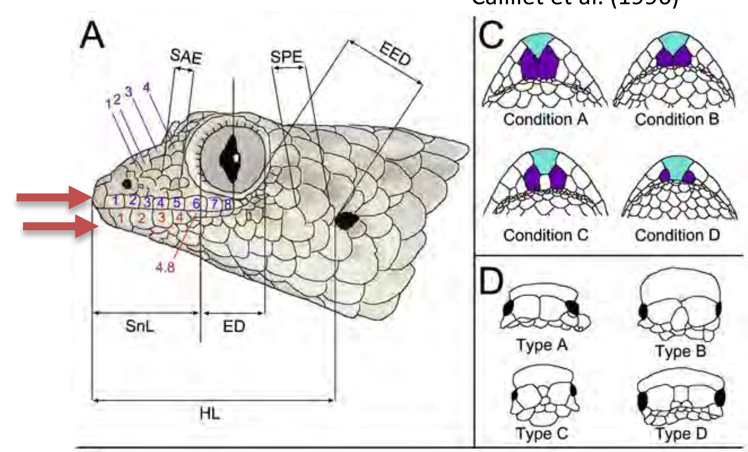
-#teeth, pores, fin rays, scales, etc.



Ho et al. (2012)



Cailliet et al. (1996)



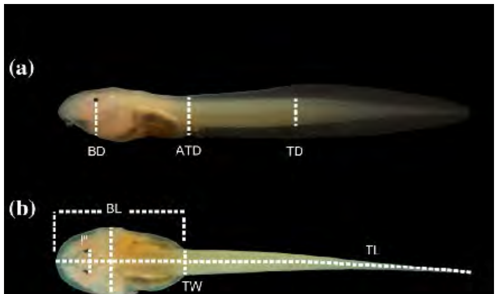
Scherz et al. (2017)

*Frequently used for taxonomy and classification

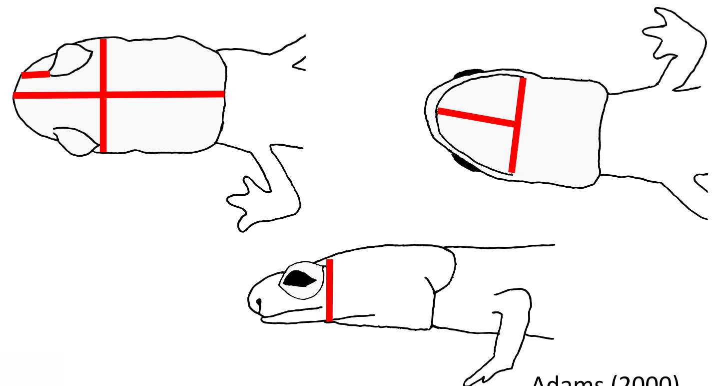
Common Morphometric Data

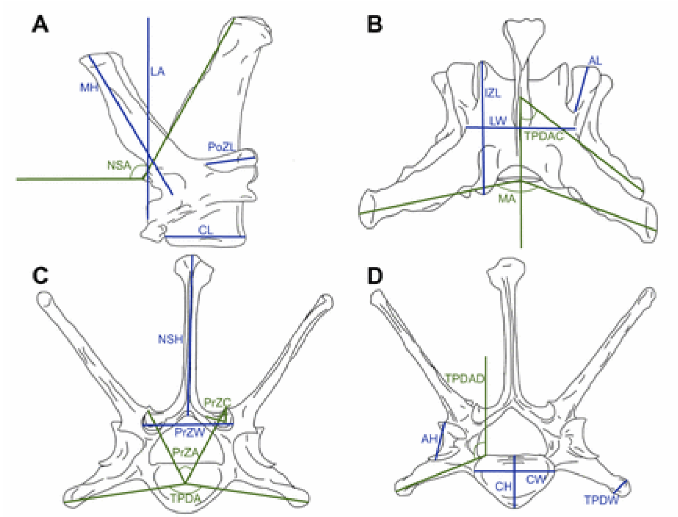
Linear measurements*

-Extents of, distances between, and angles among structures

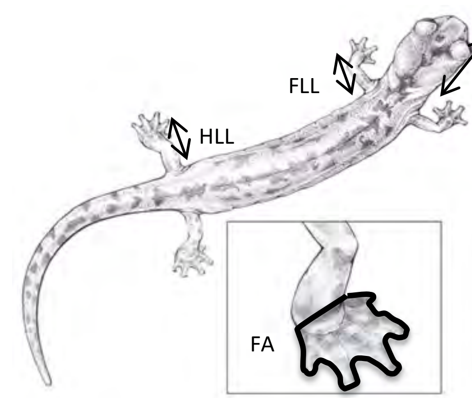


Martín-Torrijos et al. (2016)


Adams (2000)



Oliver et al. (2016)



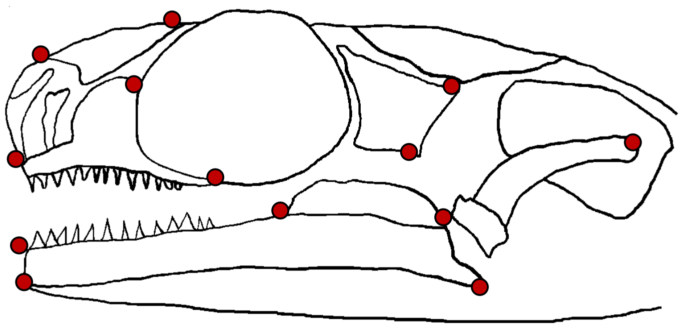
Adams et al. (2017)

*Often called multivariate morphometrics

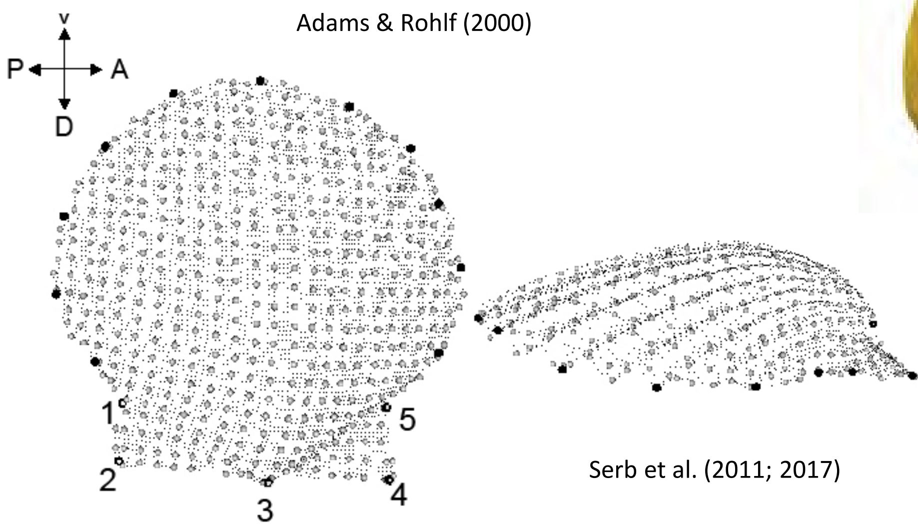
Common Morphometric Data

Geometric morphometrics*

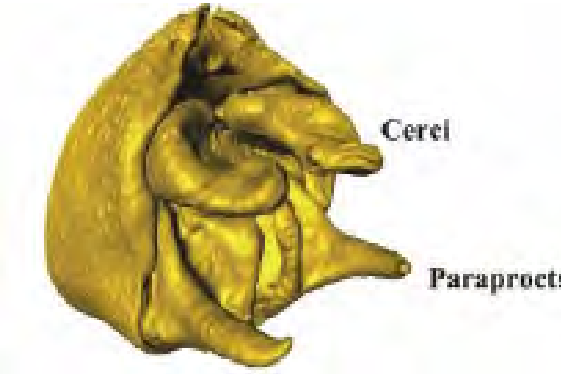
-Shape data from geometric variables



Adams & Rohlf (2000)



Serb et al. (2011; 2017)



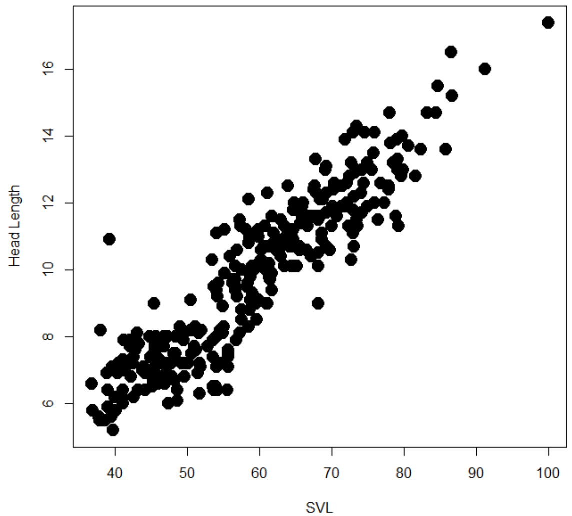
McPeek et al. (2008)

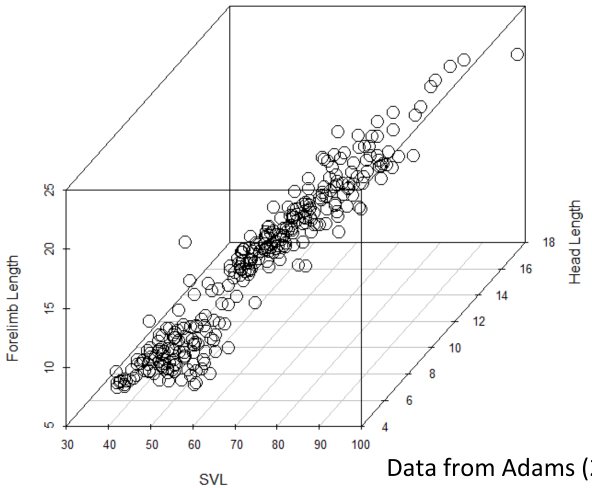
*Highly multivariate, multi-dimensional data

Morphospaces

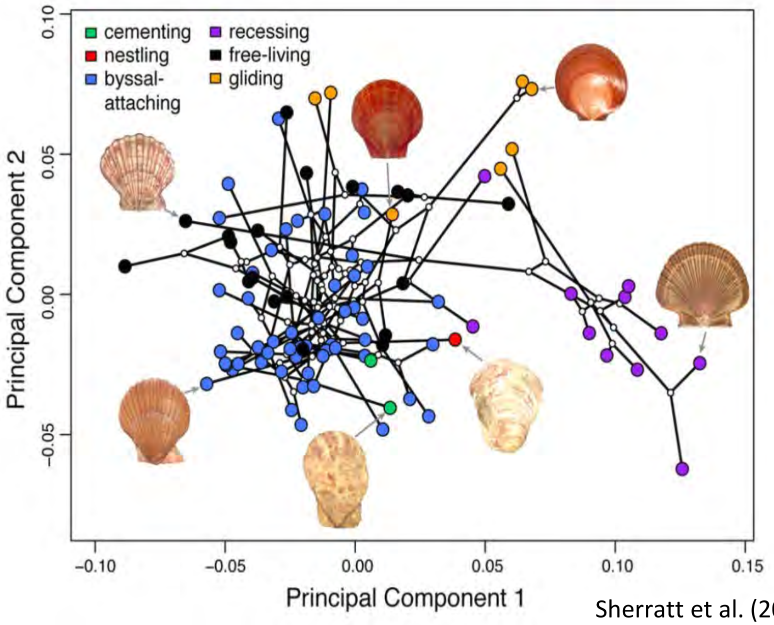
What does one do with these variables?

-Morphospace: Dataspace summarizing morphological variables*





Data from Adams (2000)

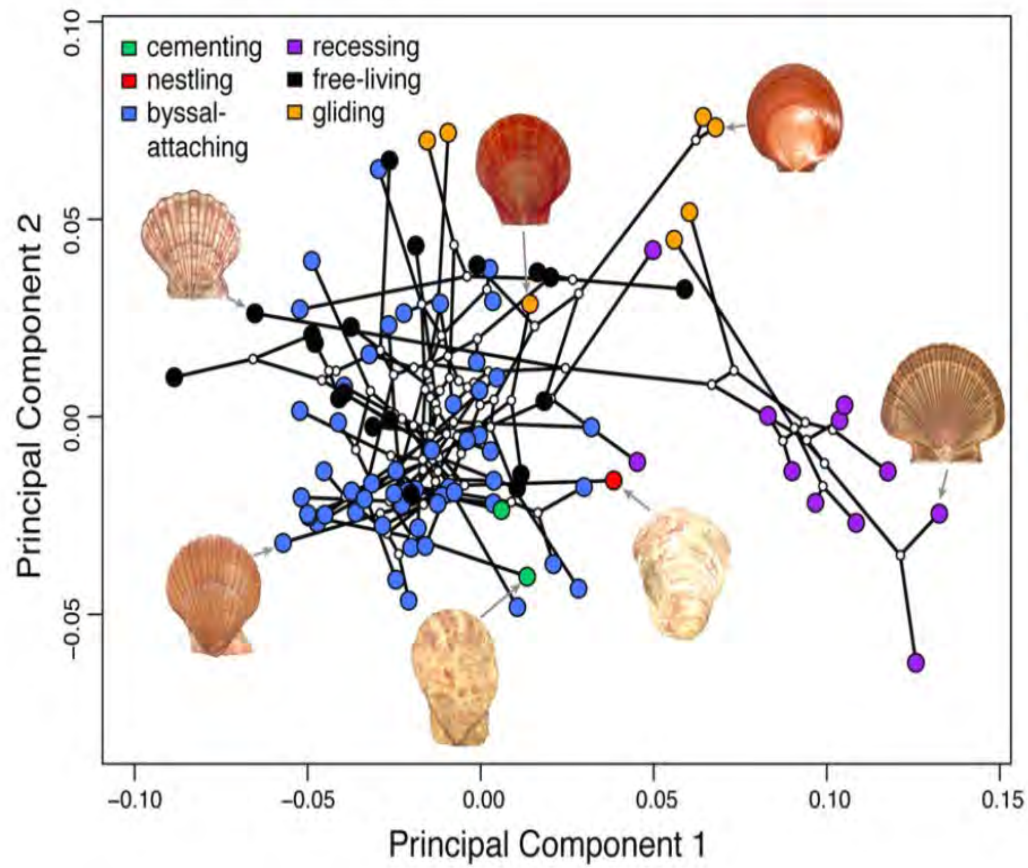


Sherratt et al. (2016)

*PCA: principal components analysis often used to view space

Phylomorphospaces

Morphospace with phylogeny superimposed

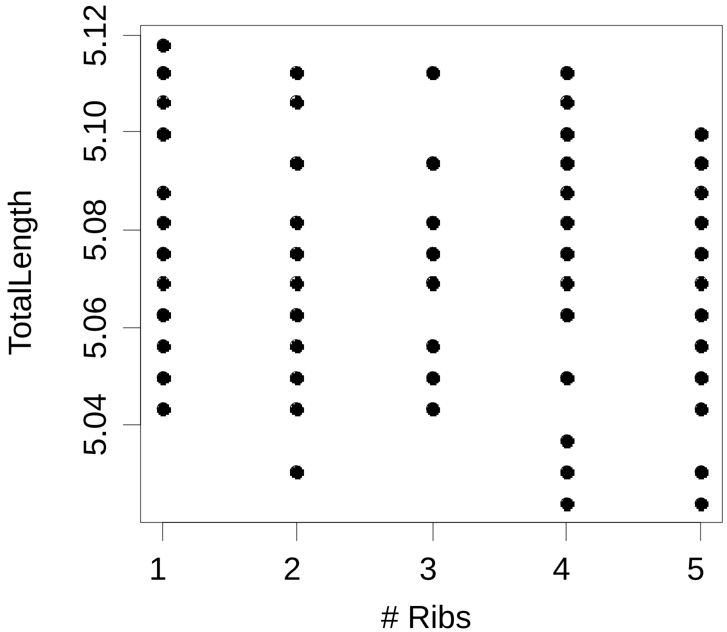


Sherratt et al. (2016)

-EXTREMELY useful for visual inspection of convergence, directional evolution, etc.

Morphospaces: Careful in Application!

Axes of morphospace ***<u>MUST</u>*** be in commensurate units



-Technically, this is a morphospace
(all variables are numeric)
-but is total GIGO!!!

-Why? Axes are incommensurate units & scale

-Variances, covariances, disparity, distances, etc. have no meaning in this space

-Morphospaces should only be constructed with data in commensurate units!!!

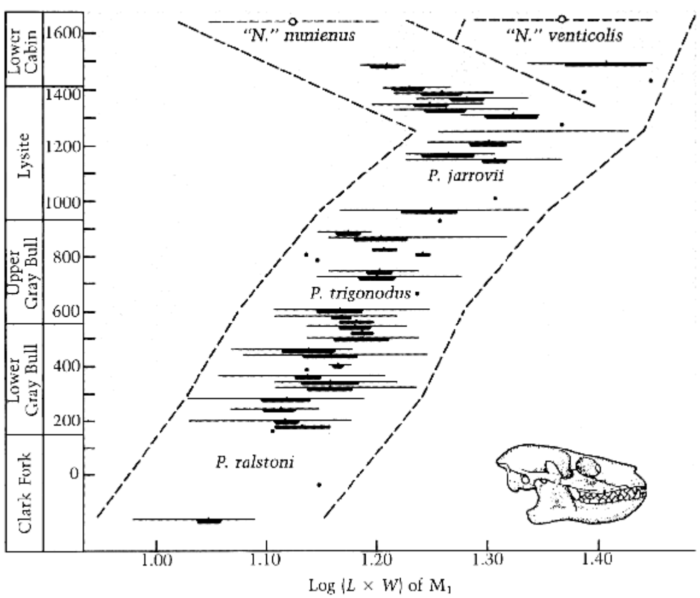
See: Adams and Collyer (2019)

Some Phenotypic Trends

Phenotypic Trends: Gradualism

Phyletic gradualism

- H_0: evolution is slow and gradual (ala Darwin's suggestion)
- Small changes accumulate over time
- Speciation from gradual accumulated divergence



Data from Gingerich (1976)
Image: Gould & Eldredge (1977)

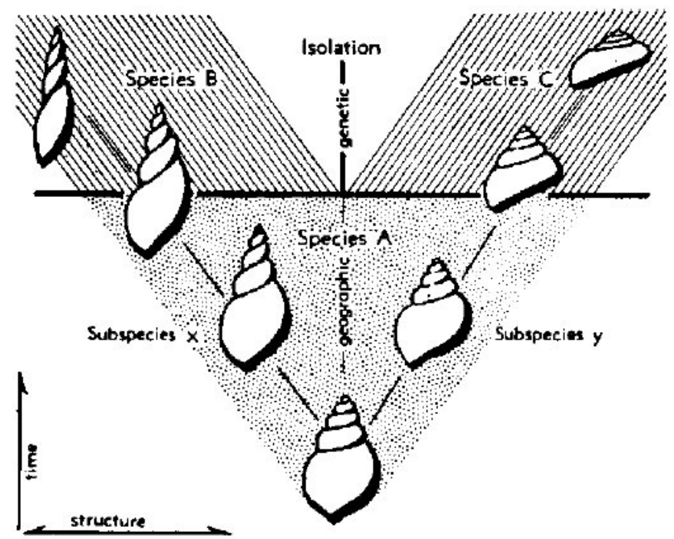


Figure 5–3:
A hypothetical case of geographic speciation viewed from the perspective of phyletic gradualism—slow and gradual transformation in two lineages.
From Moore, Lalicker, and Fischer, 1952; figure 1–15.

Phyletic Gradualism: Anagenesis

Anagenesis: Phenotypic change within species over time

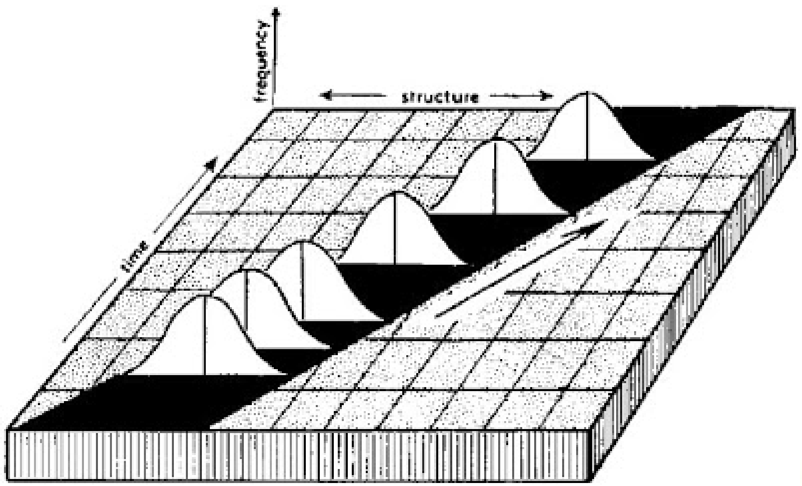
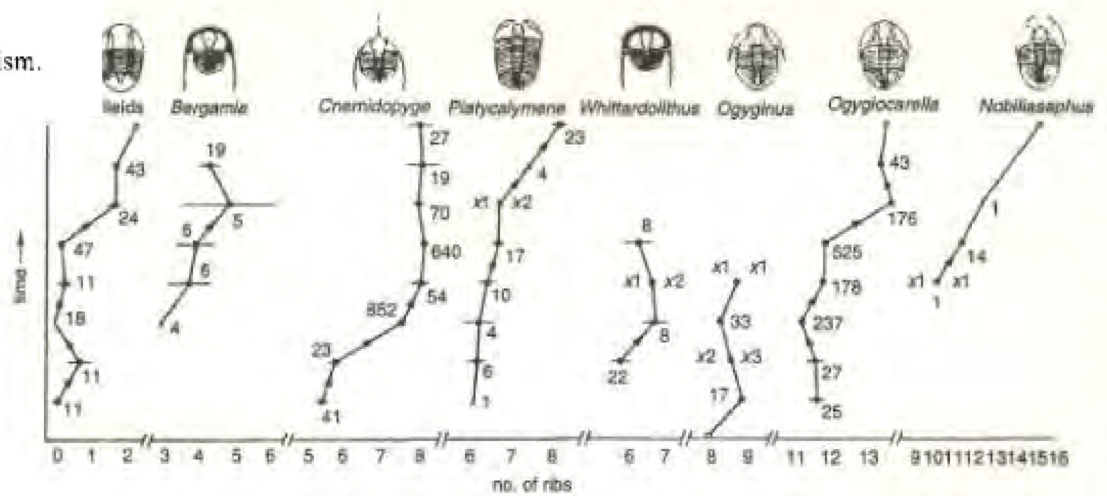


Figure 5–2:
A standard textbook view of evolution *via* phyletic gradualism. From Moore, Lalicker, and Fischer, 1952; figure 1–14.



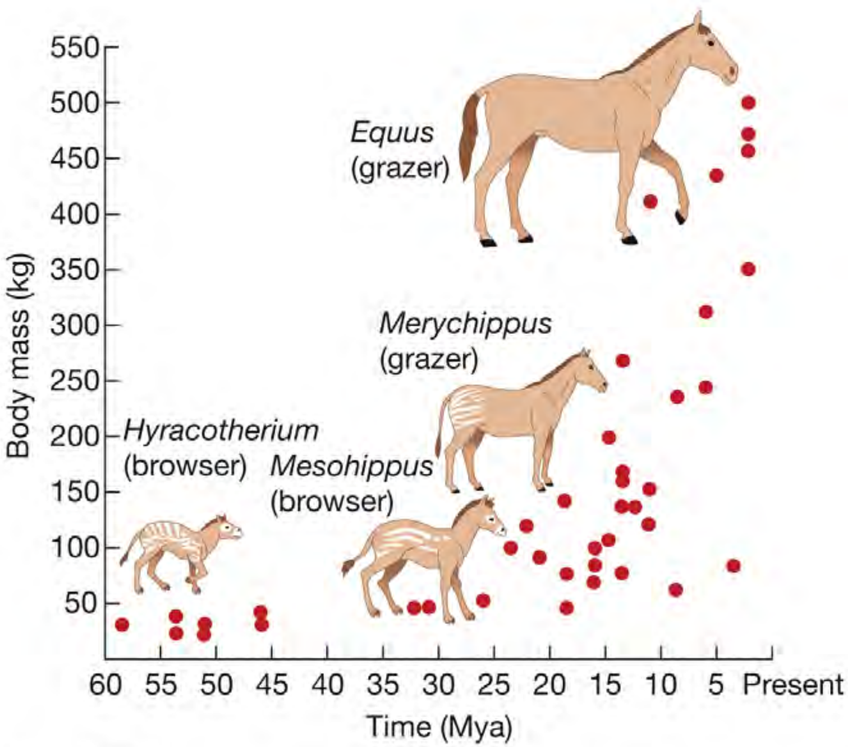
Trilobites: Sheldon (1987)

Cope's Rule

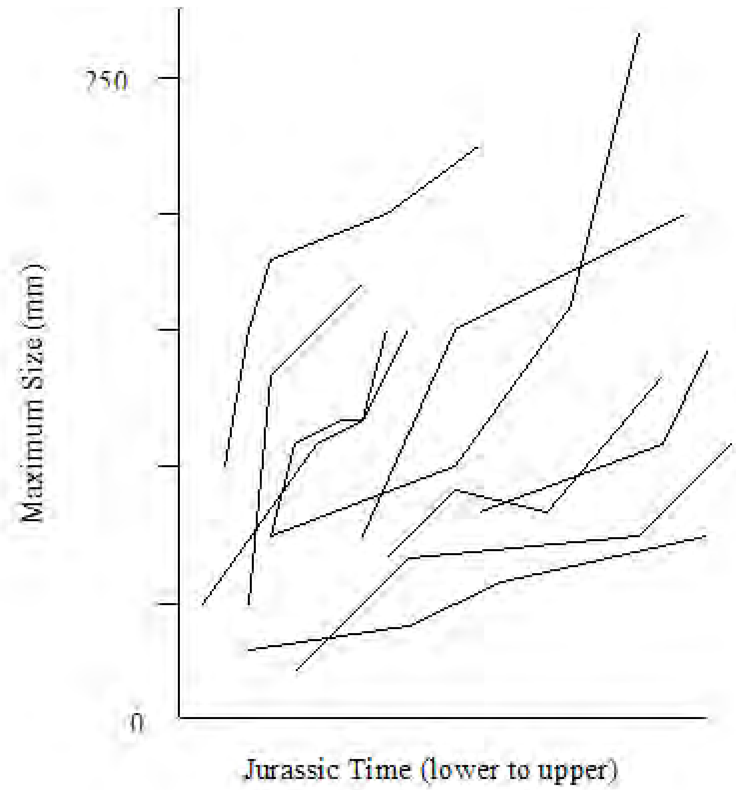
Cope's rule

-Increase in body size in clade over time

-Frequently linked with gradualism

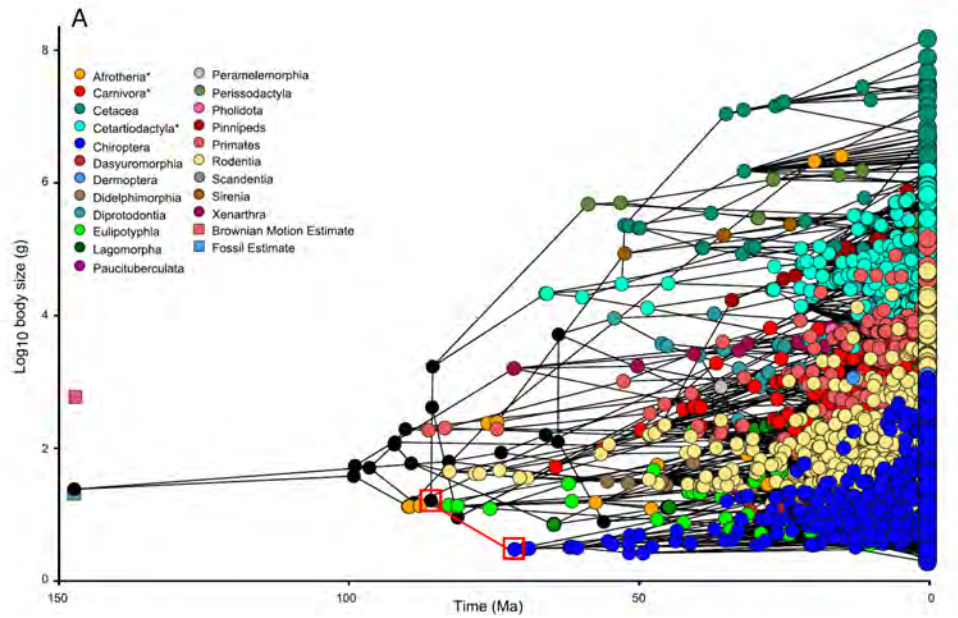


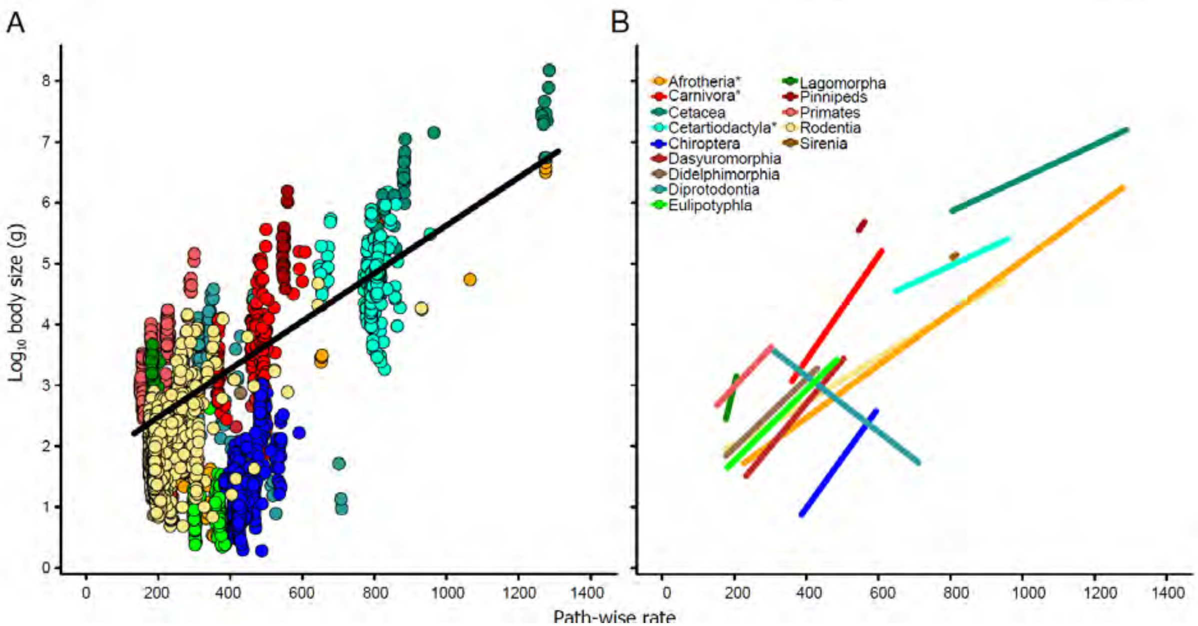
EVOLUTION 4e, Figure 20.13



Bivalves: Hallam (1975)

A neontological example

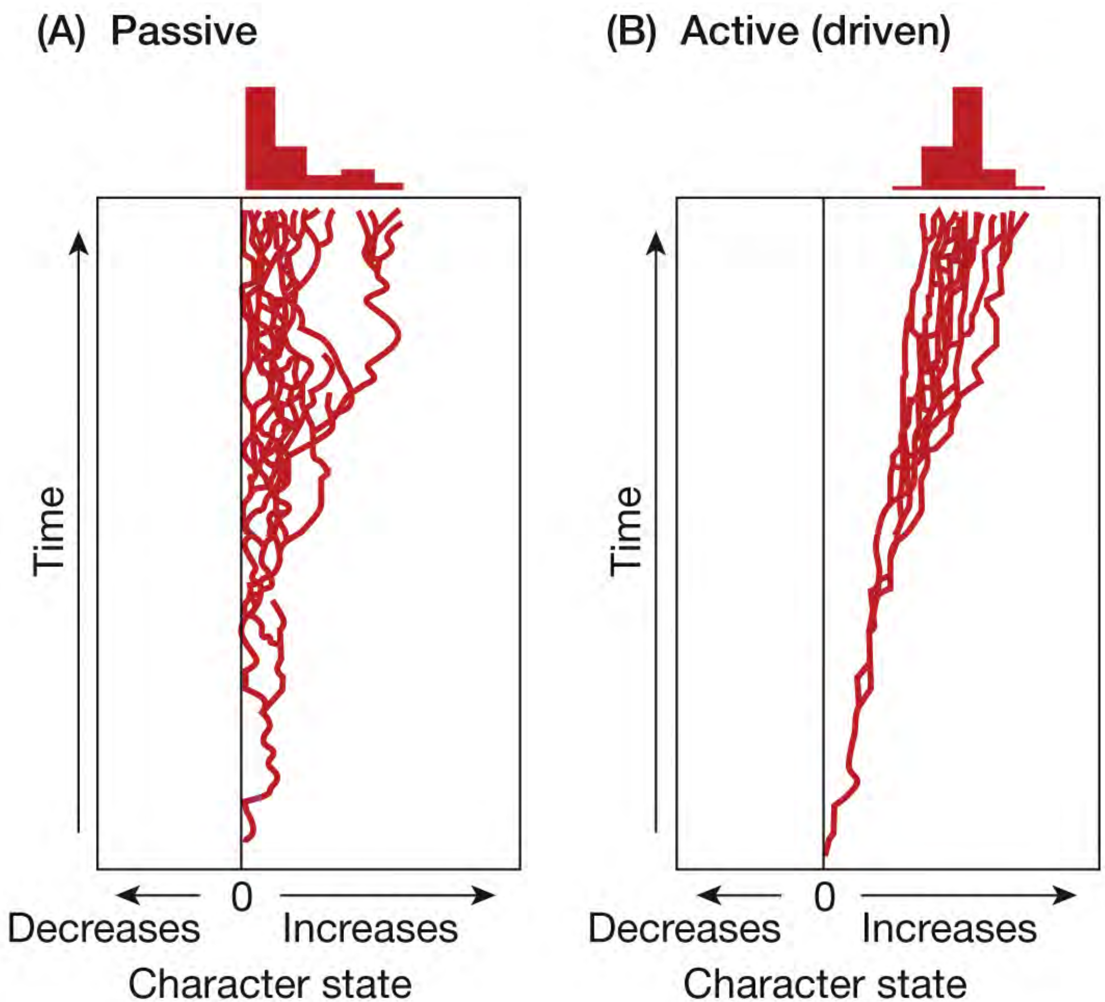




mammals: Baker et al. (2015)

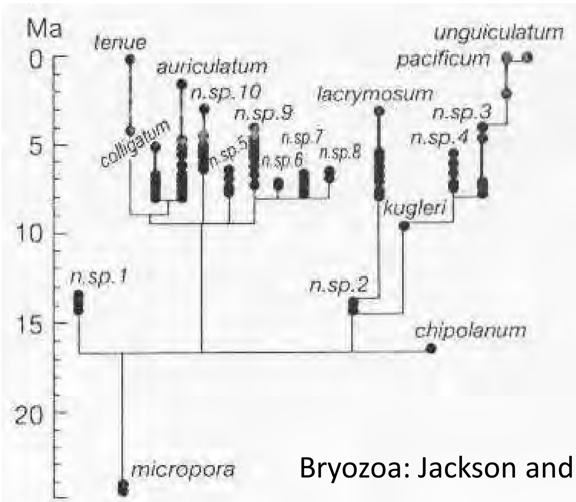
Note that directional trends may take two forms: active and passive

(the latter when trait value 'bump' into some limit over time)

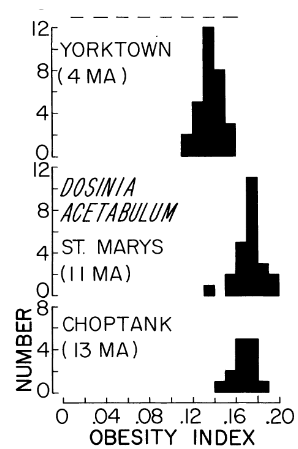


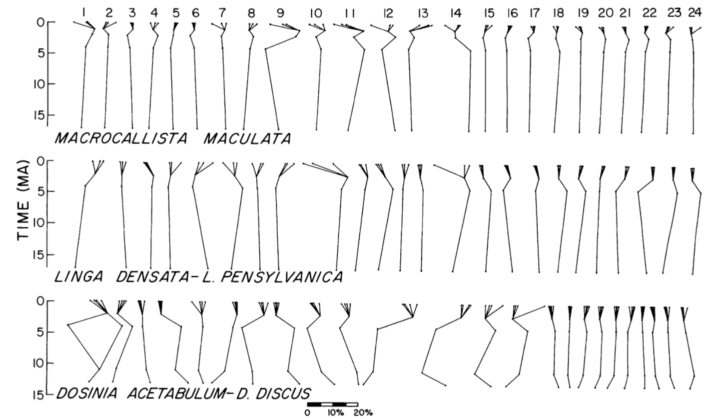
EVOLUTION 4e, Figure 20.21

Stasis: Much of fossil record shows little change



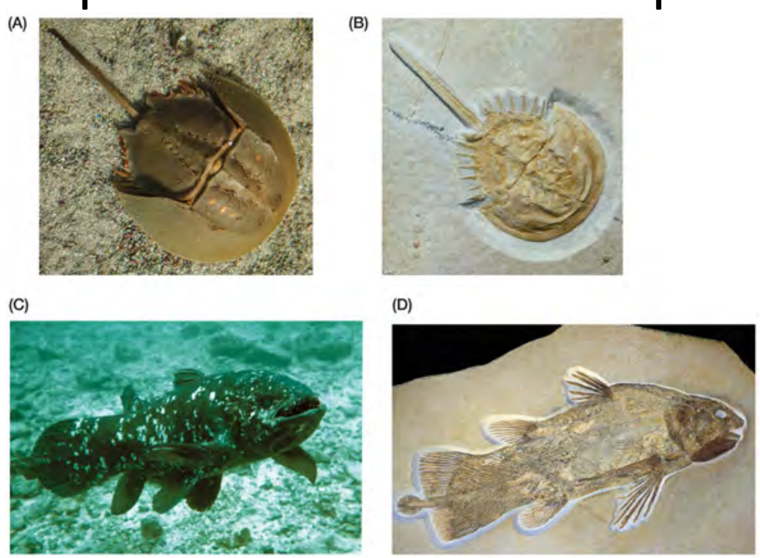
Bryozoa: Jackson and Cheetham (1994)





Bivalves: Stanley and Yang (1987)

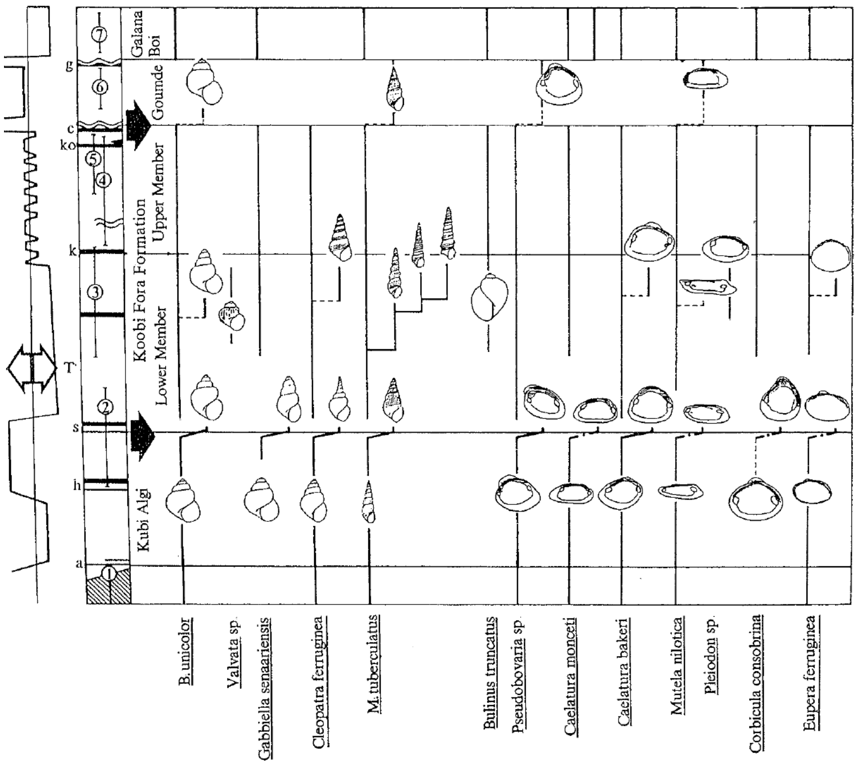
So called "Living fossils" provide another example



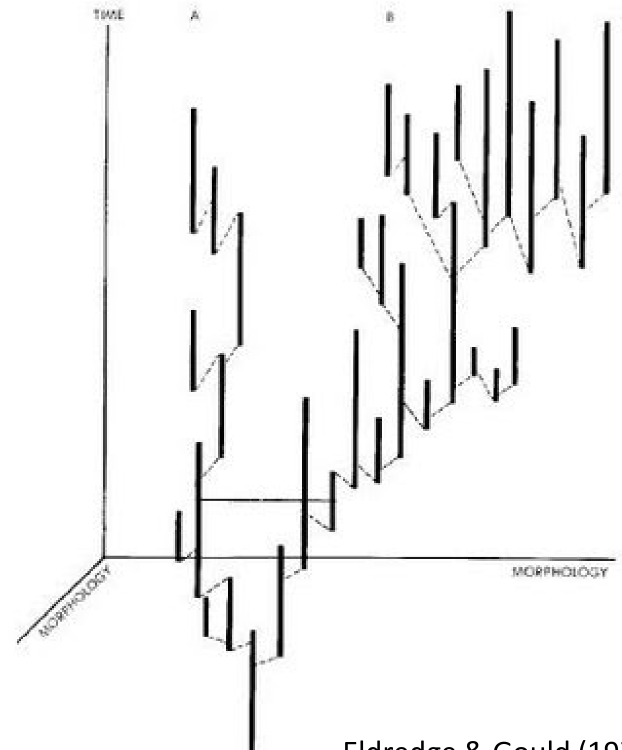
EVOLUTION 4e, Figure 20.14

Punctuated Equilibrium: Stasis followed by rapid change

-Gould & Eldredge (1972) argued PE better explains many fossil trends



Williamson (1981)



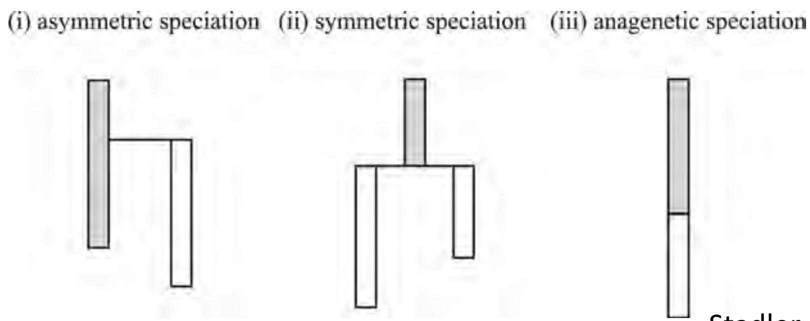
Eldredge & Gould (1972)

*Note manner in which branching in phylogeny is depicted!

-Subtle implications: 1) change is punctuational; 2) speciation is ‘budding off’ from ancestor, not 2 new descendants

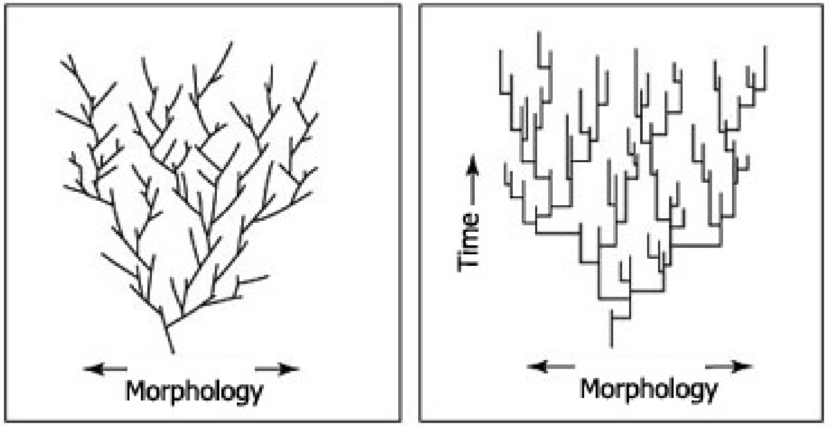
Speciation in the Fossil Record

As fossil species are defined phenotypically, linking trait change and lineage diversification results in distinct speciation modes



Stadler et al. (2018)
after Foote (1996)

Neontologists & paleontologists often depict speciation differently (has implications for how we view phenotypic trends)

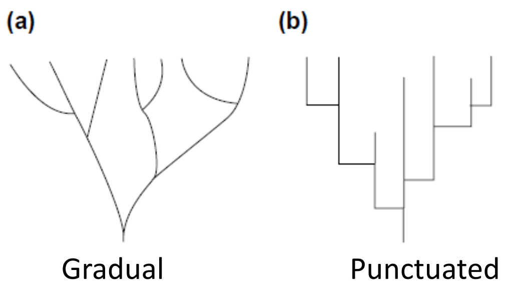


Freeman & Herron (1998)

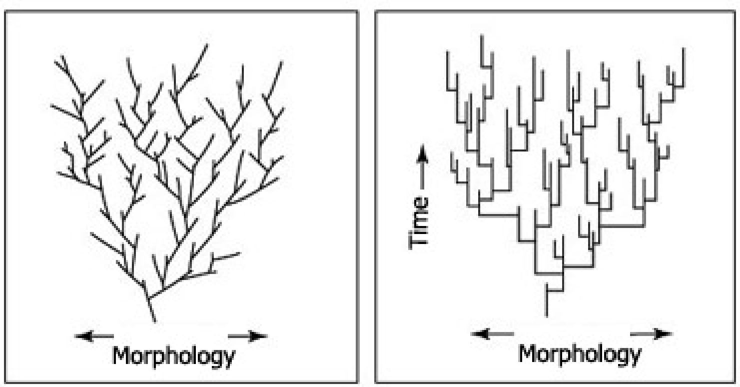
Distinguishing PE from Gradualism

Interpreting the fossil record can be challenging

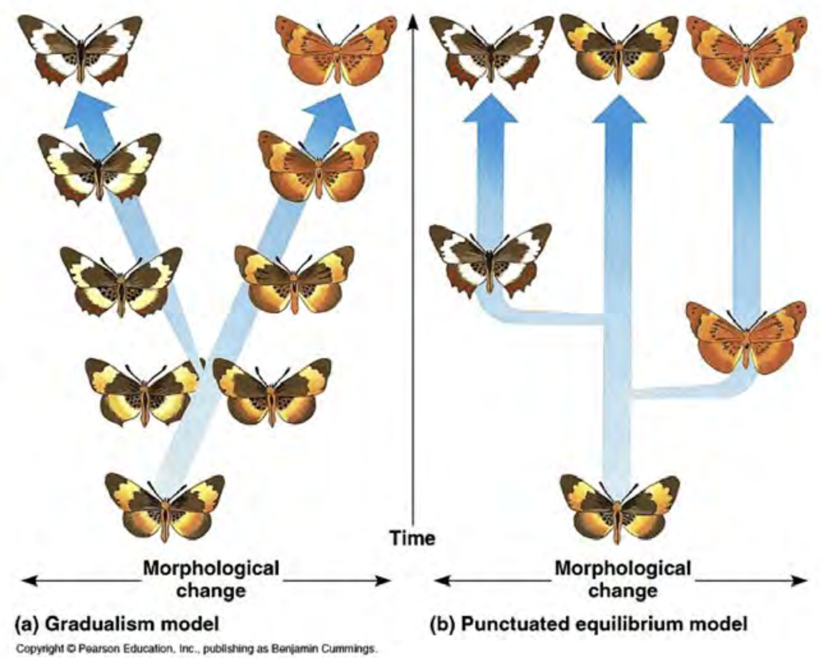
-Is the pattern punctuational or gradual?



Benton & Pearson (2001)

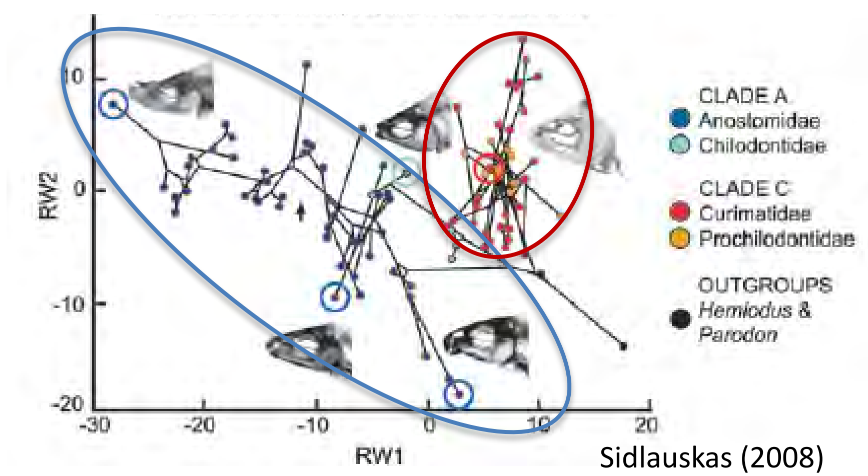


Freeman & Herron (1998)

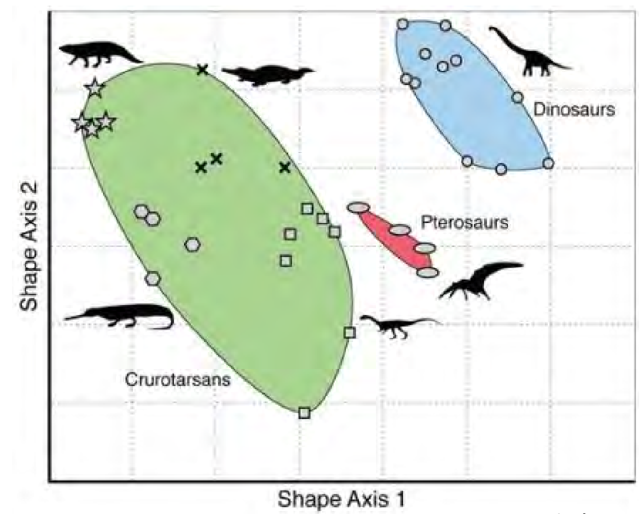


Morphological Disparity

How much phenotypic diversity does a lineage display?



Sidlauskas (2008)



Brussatte et al. (2008)

-Some lineages seem to occupy more of morphospace

Why? Hypotheses include:

-Constraints (competition, niche filling, biomechanical, etc.)

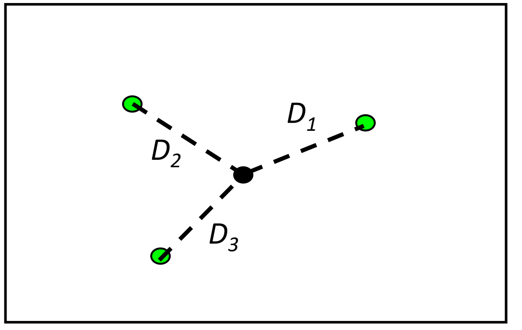
-Ecological release

-Can this be quantified and compared?

Morphological Disparity: a measure of phenotypic diversity*

$$MD = \frac{\sum D_j^2}{N-1}$$

D_j: Distance from j[th] object to centroid



Foote (1990; 1993)

MD is a measure of variance (for 1 trait it *IS* the variance)

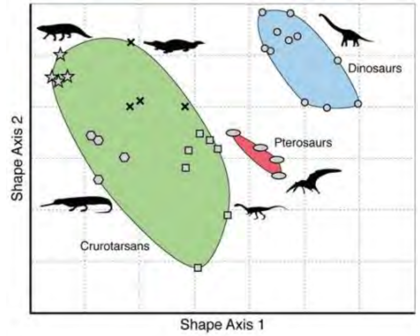
Recall: $$\sigma^2 = \frac{\sum\left(Y_j - \bar{Y}\right)^2}{N-1}$$

$\sqrt{\left(Y_j - \bar{Y}\right)^2} = D_j$ so $\left(Y_j - \bar{Y}\right)^2 = D^2_j$

*One can obtain MD using pairwise distances among objects using SS → distance equivalency
Gower, (1966); Anderson (2001); Adams (2014)

Comparing Disparity

For multiple groups, which group displays greater MD?



Brussatte et al. (2008)

Compare MD statistically with permutation test

1) obtain MD_1, $MD_{2,}$ etc.
2) calculate difference score: $S = | MD_1 - MD_2 |$
3) Randomly assign taxa to groups, obtain MD and S_{perm}
4) proportion $S_{perm} > S_{obs}$ is level of significance

<u>**NOTE: This MD test evaluates differences in *DISPERSION* (variance). Tests of *LOCATION* are performed using MANOVA!**</u>

e.g., Foote (1990); Adams and Rohlf 2000

Taxonomic and morphological disparity: Balstoidea and Trilobita

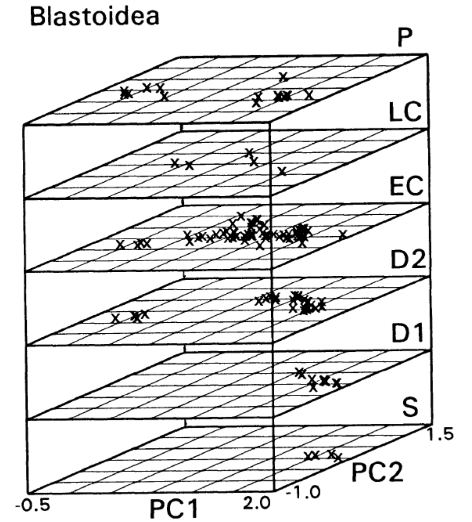


FIGURE 2. Temporal pattern of morphospace occupation in Blastoidea. Note overall increase in range of morphospace occupied. Early Carboniferous taxonomic di-

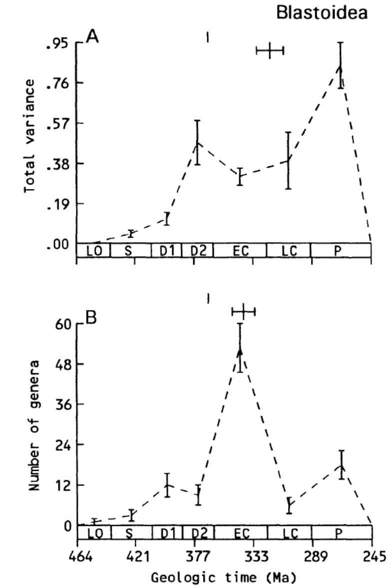
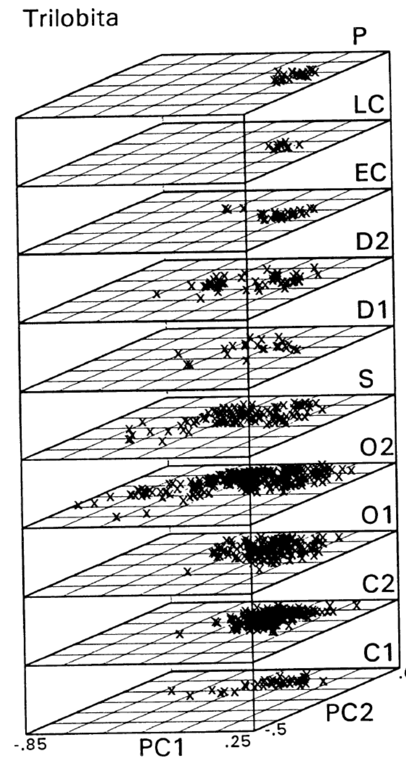


FIGURE 3. Comparison of morphological and taxonomic diversity in Blastoidea. Morphological diversity in this



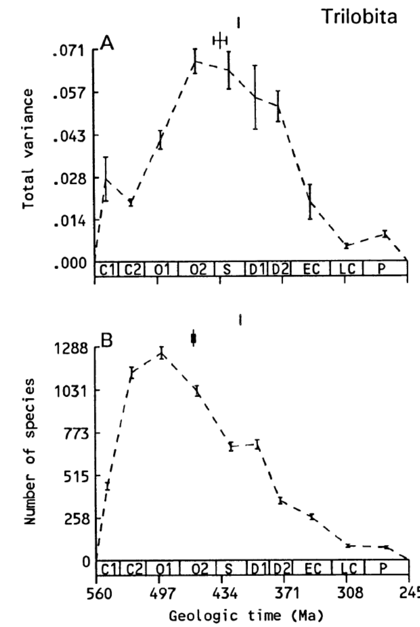


FIGURE 5. Comparison of morphological and taxonomic diversity in Trilobita. Morphological diversity is displaced forward in time relative to taxonomic diversity,

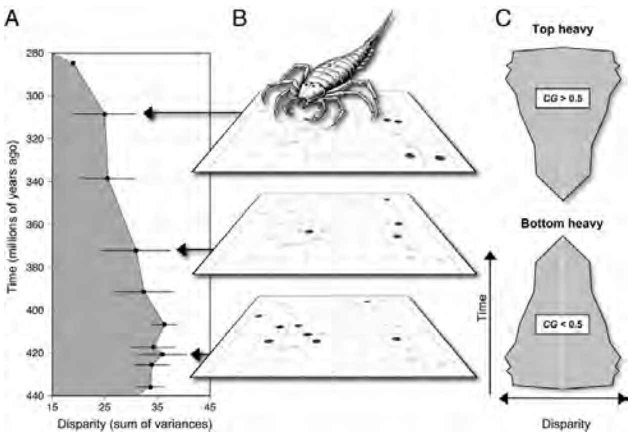
Foote (1993)

Disparity Examples

Is there a common pattern of MD accumulation across time or taxa?

-H_0: ↑MD from Cambrian → recent, and early in lineage history

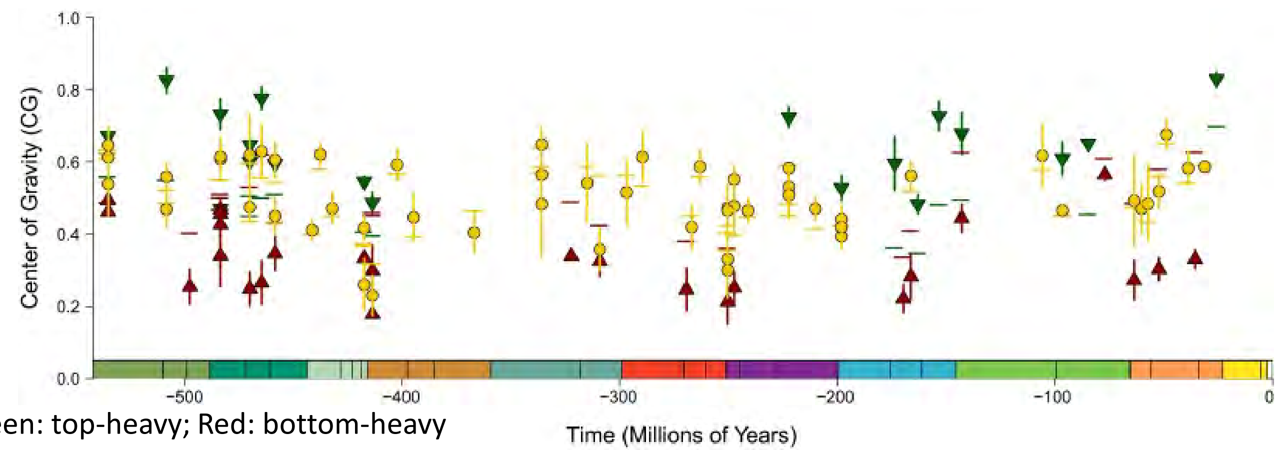
-Analysis of 98 metazoan datasets; most reach peak disparity early



No general trend Cambrian → recent

Most clades bottom-heavy

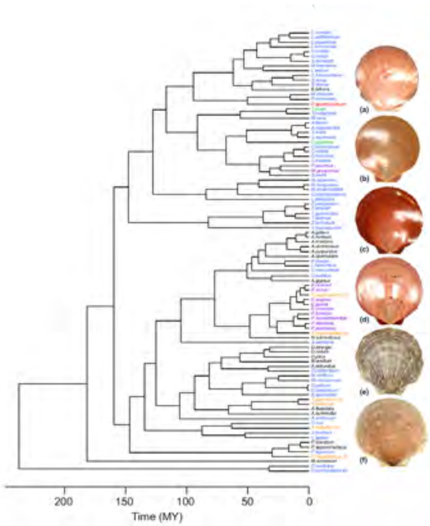
-latter consistent with EB-type radiation models

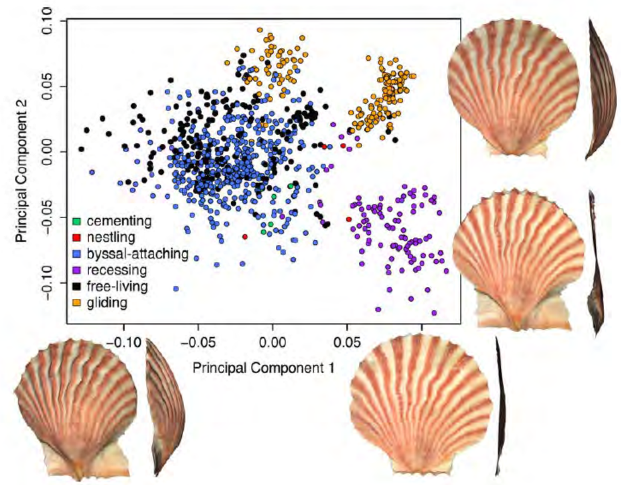


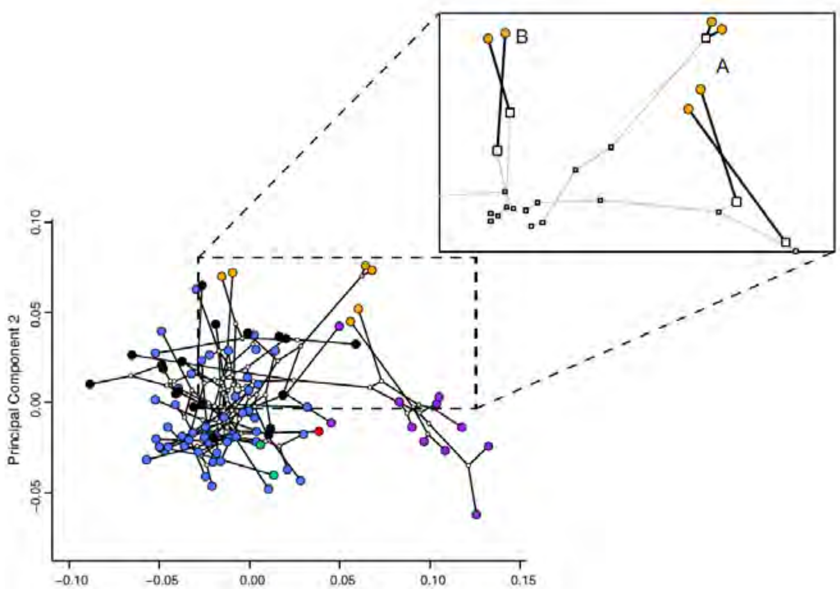
Green: top-heavy; Red: bottom-heavy

Hughes et al. (2013)

MD differs across scallop life habit eco-groups





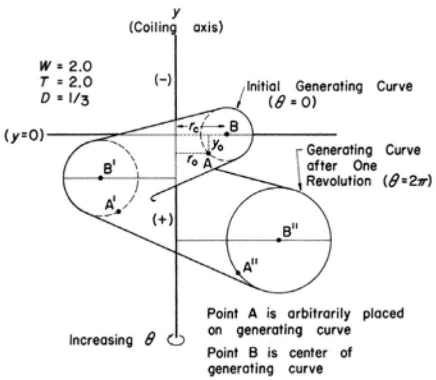


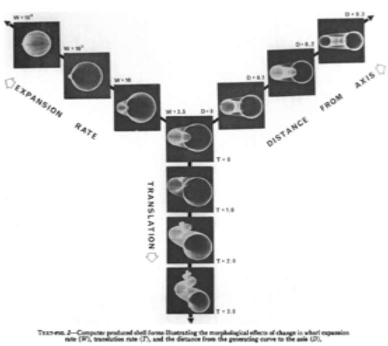
-Gliders display less MD
-Evidence of convergence

Serb et al. (2017)

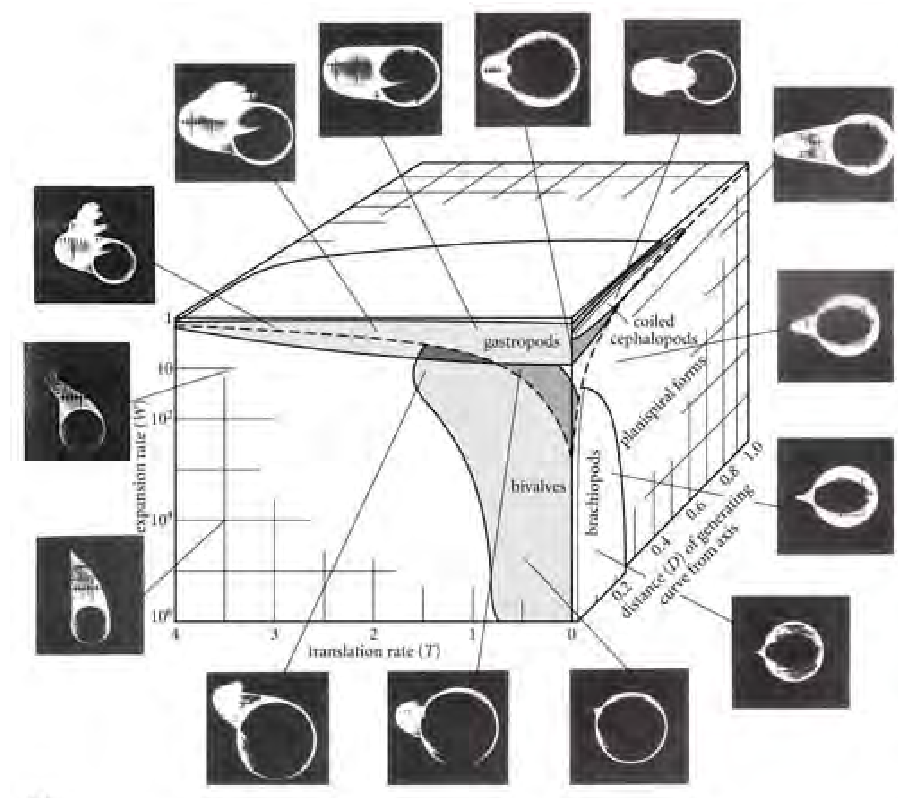
Theoretical Morphospace

Generate morphospace from mathematical rules





3 variables of coiling shell:
-Expansion whirl
-Distance from axis
-Translation



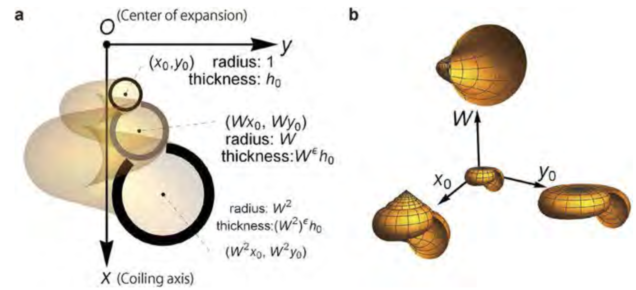
Resulting morphospace with
500 MYA of shell evolution
superimposed

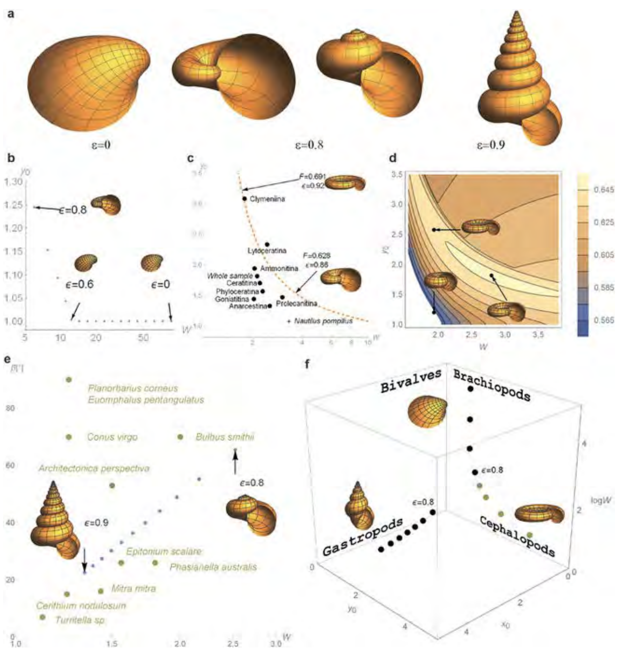
-Helpful to understand structural limits to macroevolutionary change

(Why have certain morphologies not evolved?)

Raup (1966)

Theoretical Morphospaces

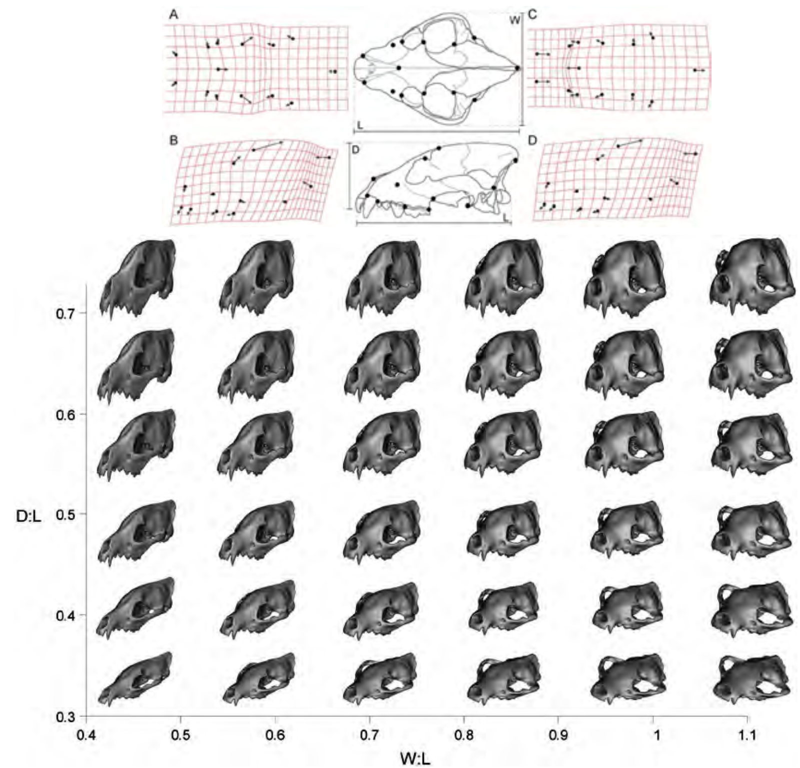


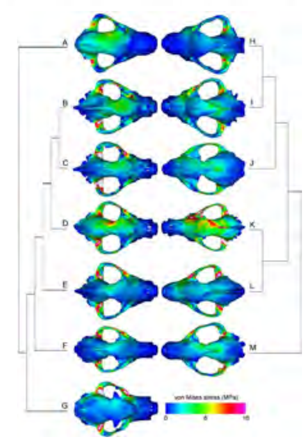


Bivalves, gastropods, cephalopods

Coiling→morphospace→diversity

Okabe and Yoshimura (2017)





Hypercarnivores and Bite force

Shape→morphospace→function

Tseng (2014)

"How fast, as a matter of fact, do animals evolve in nature?" Simpson (1944)

Rates of phenotypic evolution

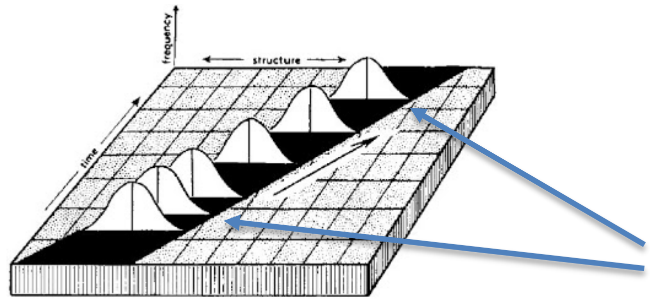


Figure 5–2:
A standard textbook view of evolution *via* phyletic gradualism.
From Moore, Lalicker, and Fischer, 1952; figure 1–14.

-*Darwins*: $r_D = \frac{(\ln Y_1 - \ln Y_2)}{\Delta T}$ common for fossils; ΔT typically in MYA

-*Haldanes*: $r_H = \frac{\left(\ln Y_1 / \sigma^2_{Y_1} - \ln Y_2 / \sigma^2_{Y_2} \right)}{T_1 - T_2}$ common for extant; t-generations

NOTE: these are lineage-specific (tree-based rates discussed later in semester)

Evolutionary Rates

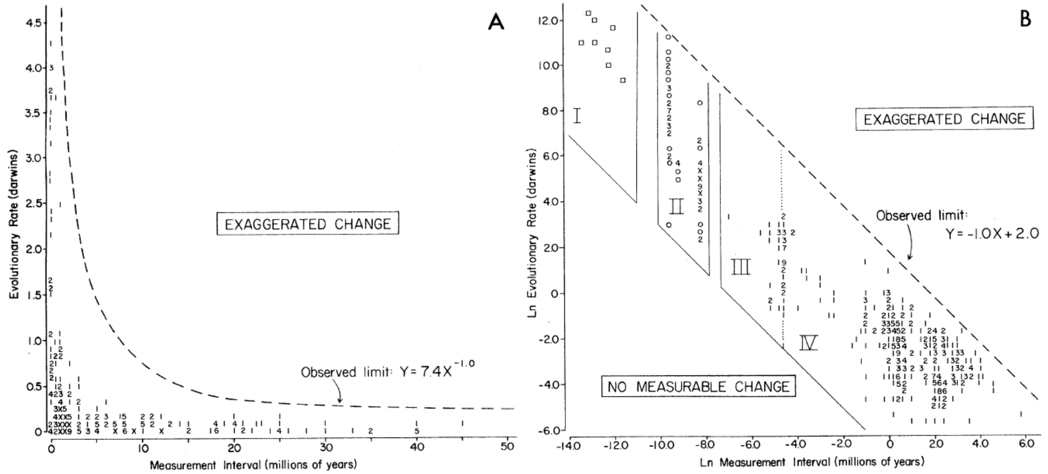


Fig. 1. Inverse relationship of evolutionary rates and interval of time over which rates were measured. (A) Central portion of distribution of 521

Paleontological studies
Rates are slow
Gingerich (1983)

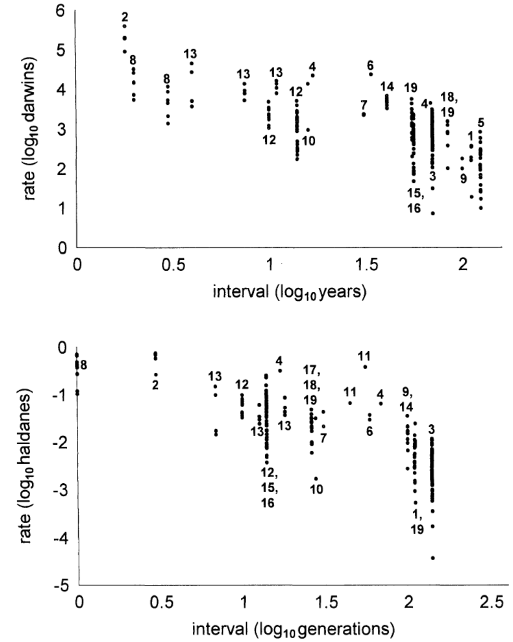
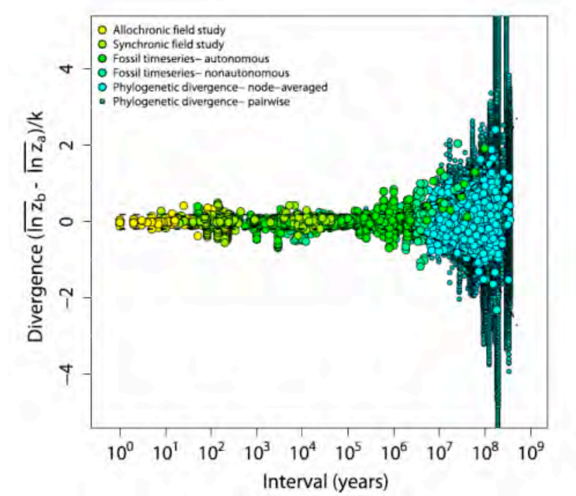


Fig. 4. Distribution of evolutionary rates in darwins (top panel) and haldanes (bottom panel) for the studies summarized in Table

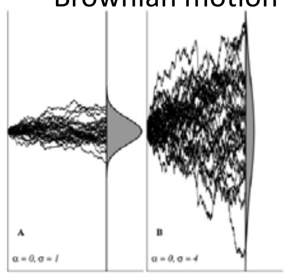
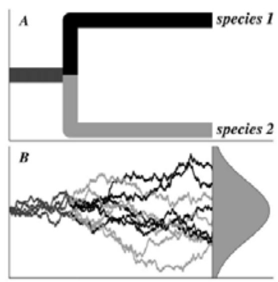
Neontological studies
Rates are fast
Hendry & Kinneson (1999)



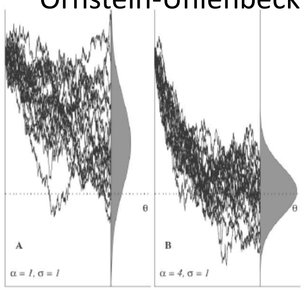
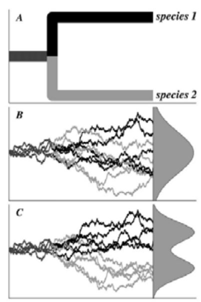
Major change ~ 1 MYA
Uyeda et al. (2011)

The mode of evolution: the manner in which disparity accumulates

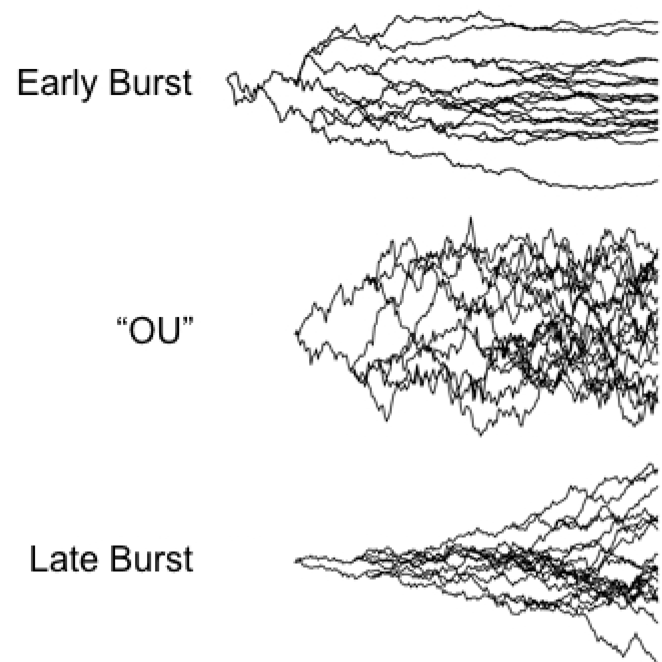
Brownian motion

Ornstein-Uhlenbeck

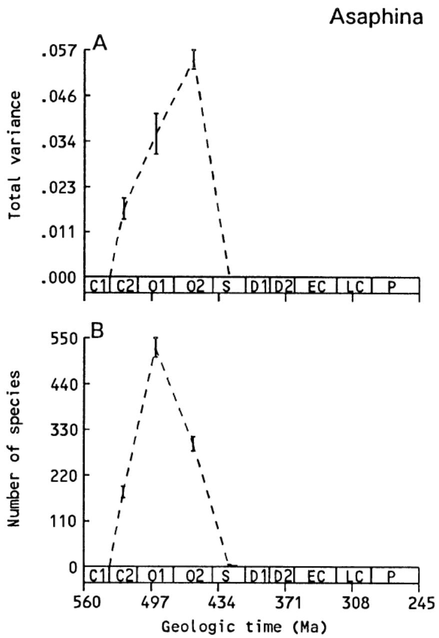
Butler and King (2004)

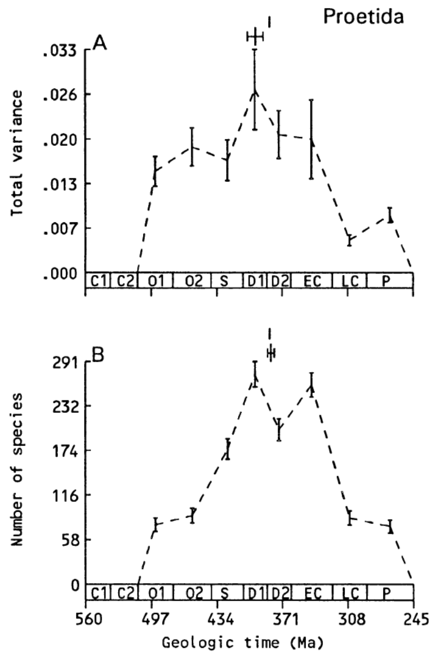


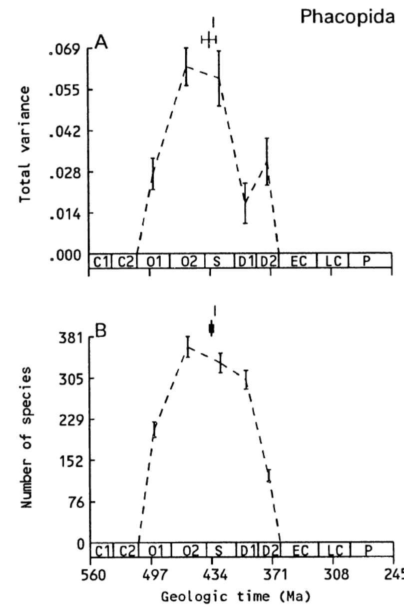
T. Ingram: www.anoleannals.org

-We will discuss this later in the semester

When are diversity and disparity associated?

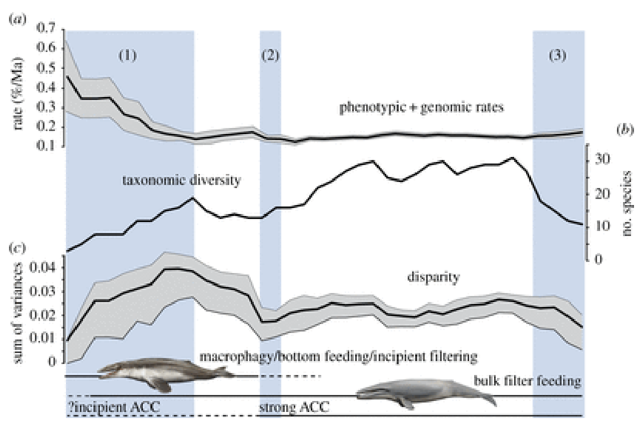






Diversity & disparity
Correlated through time

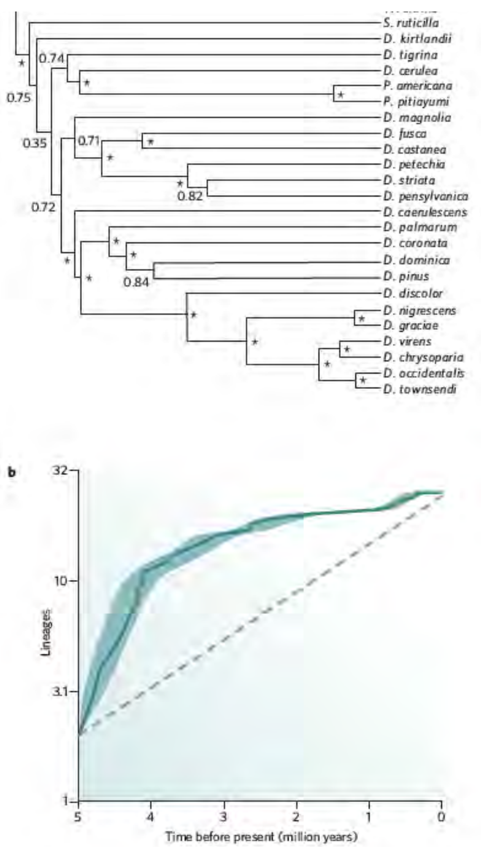
Foote (2015)



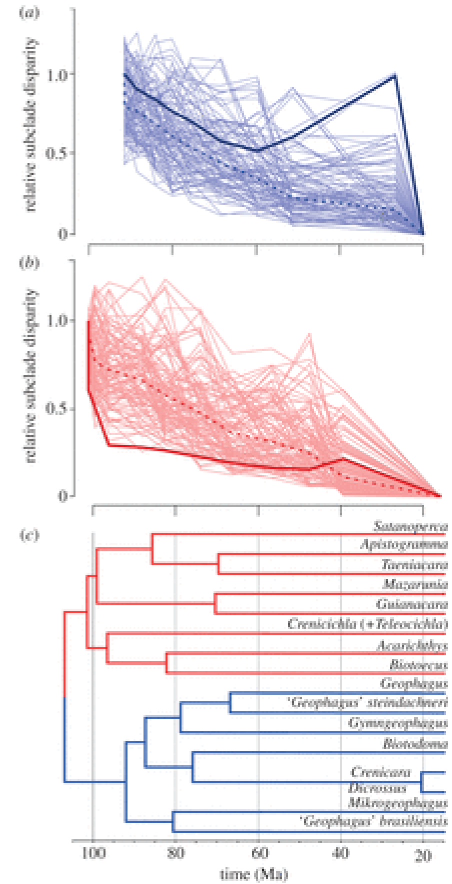
Diversity & disparity
Decoupled through time

Marx & Fordyce (2015)

How do taxonomic & phenotypic diversity accumulate over time?



Reznick and Ricklefs (2009)



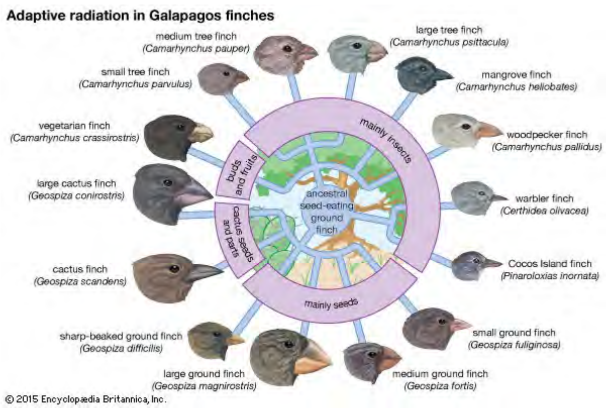
Arbour and López-Fernández (2013)

LTT plot

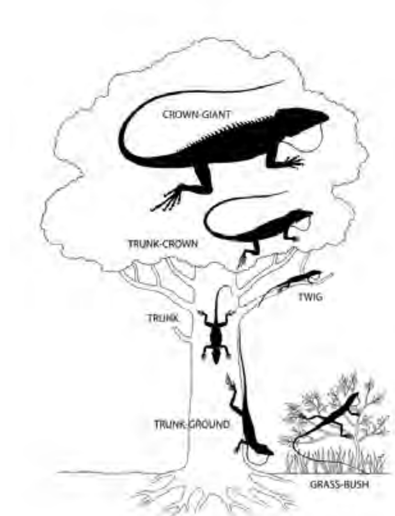
*NOTE: convention for DTT is opposite LTT, because measured as MD BETWEEN sub-clades which must decrease over time (began with Harmon et al. 2003)

DTT plot

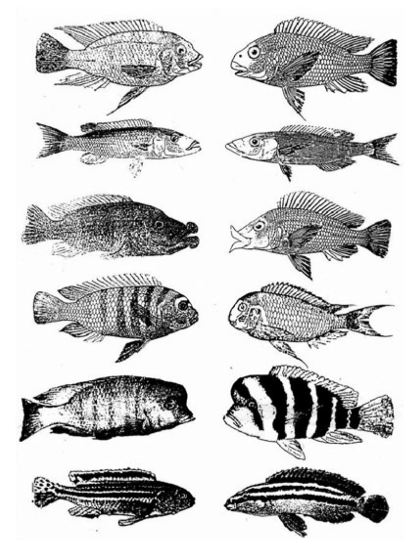
Phenotypic and taxonomic diversification; exploiting new niches



Encyclopaedia Brittanica, Inc (2010)



Losos (2009)



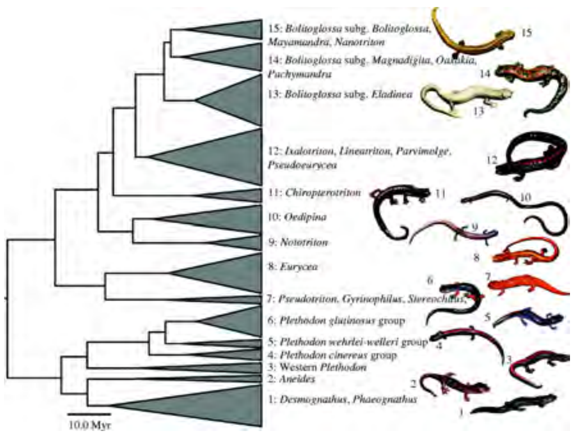
Kocher et al. (1993)

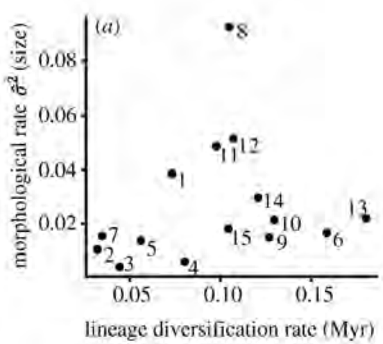
Predictions from AR hypothesis:

-Disparity follows early-burst (EB)
-Diversity: LTT plot shows EB
-Diversity and disparity *rates* expected to be coupled

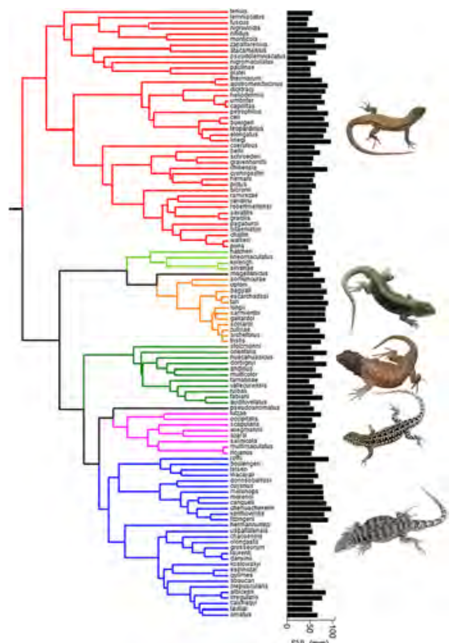
~~Adaptive~~ Radiations

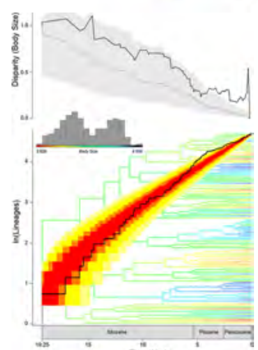
Sometimes, it's just a radiation…



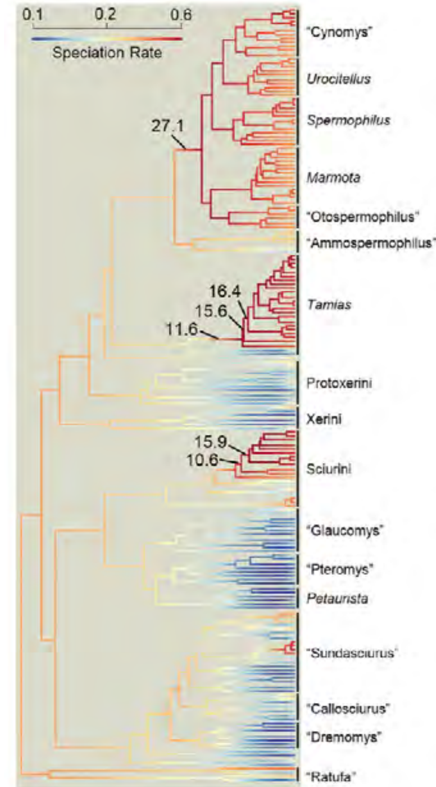


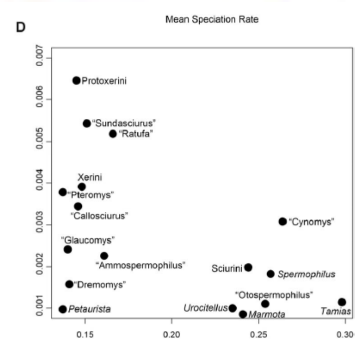
Plethodontids
 -Rates not correlated
Adams et al. (2009)





S. Amer. *Liolaemus* lizards
 -LTT & DTT: not EB
Pincheira-Donoso et al. (2015)





Sciuridae rodents
 -Rates not correlated
Zelditch et al. (2015)