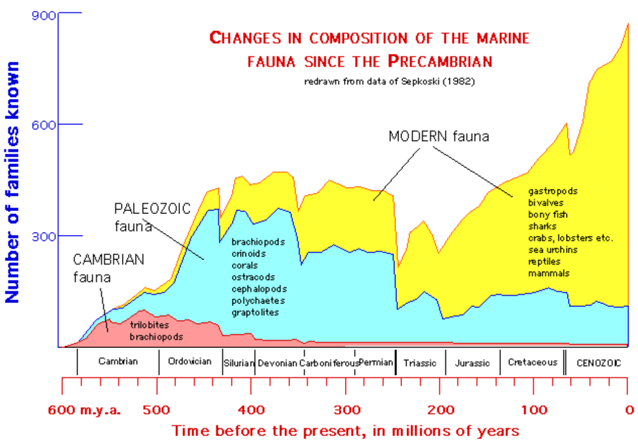
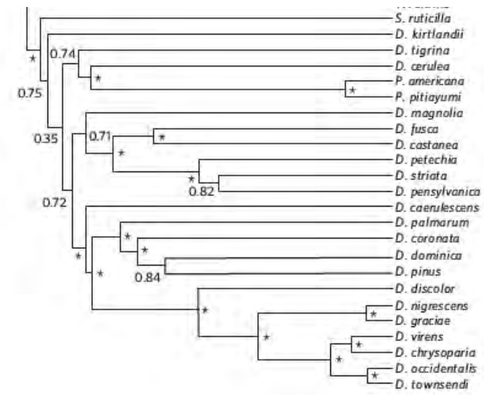
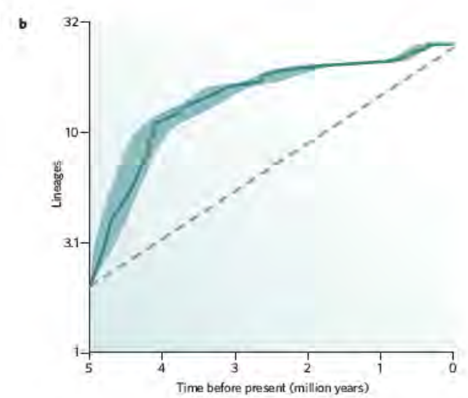
The Evolutionary Synthesis and Macroevolutionary Extensions

Patterns of taxonomic diversity through time

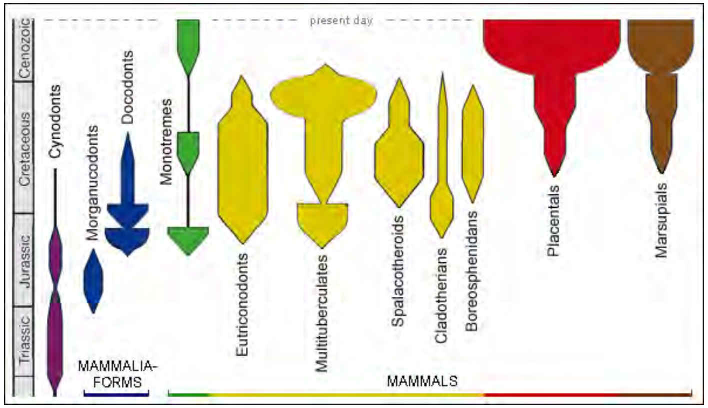


after Sepkowski (1982)





Reznick and Ricklefs 2009



Luo (2007)

Patterns of phenotypic diversity through time

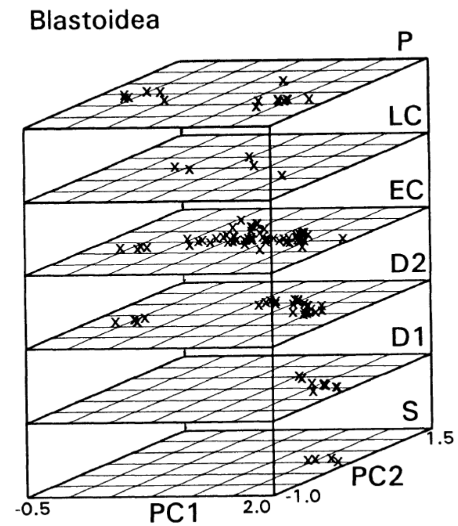


FIGURE 2. Temporal pattern of morphospace occupation in Blastoidea. Note overall increase in range of morphospace occupied. Early Carboniferous taxonomic di-

Foote (1993)

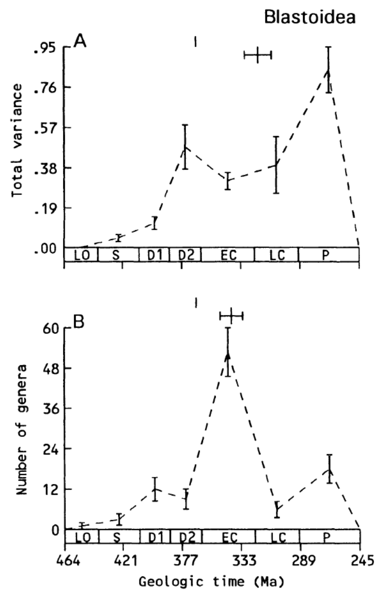
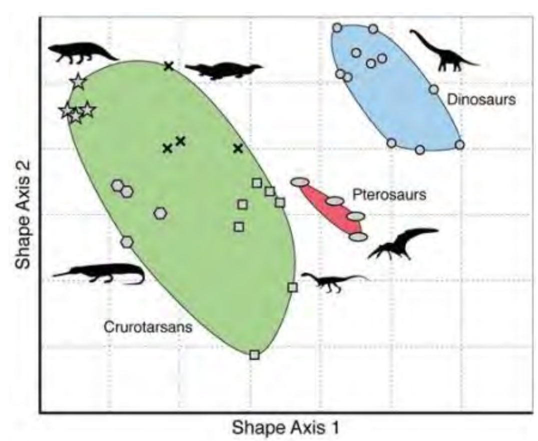
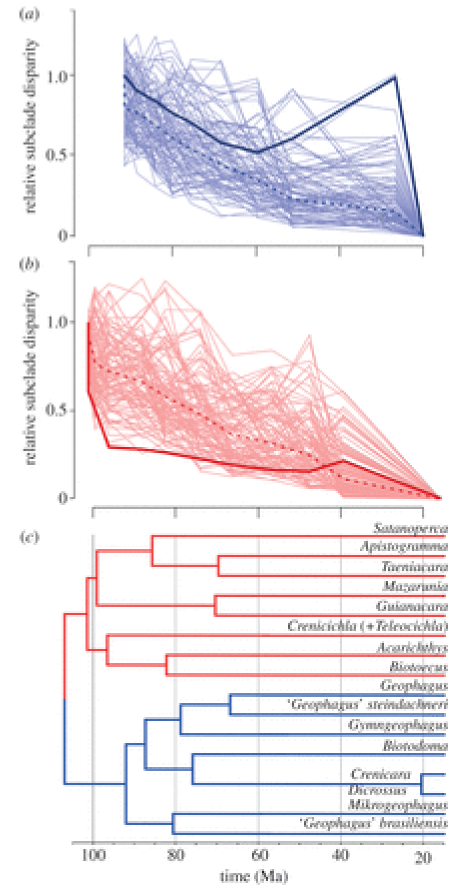


FIGURE 3. Comparison of morphological and taxonomic diversity in Blastoidea. Morphological diversity in this



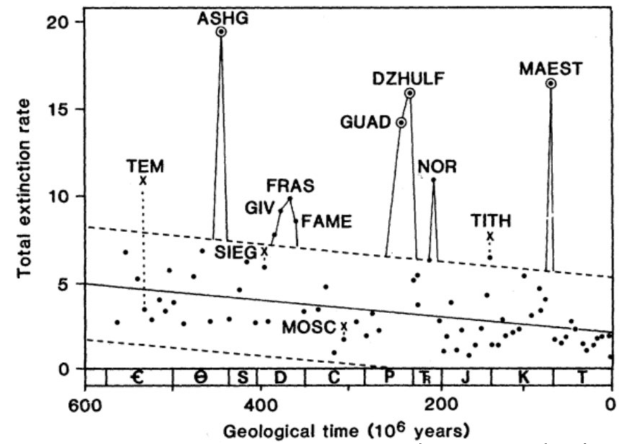
Brussatte et al. (2008)



Arbour and López-Fernández (2013)

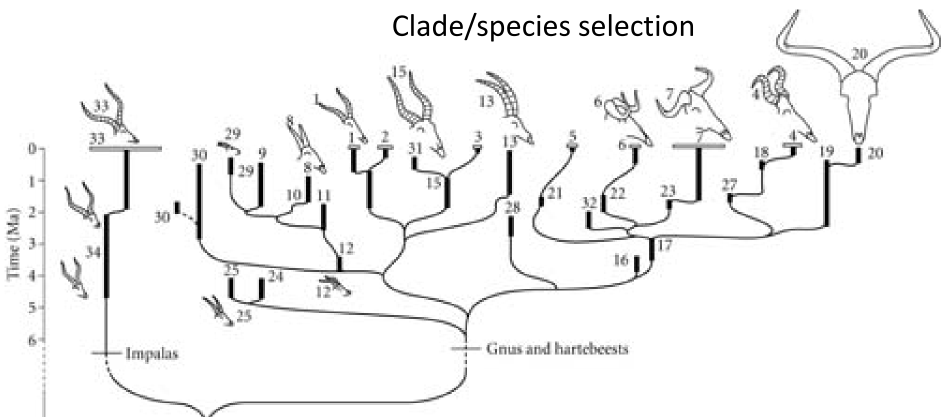
Numerous other topics common in macroevolutionary studies

Heterochrony & developmental 'channeling'
Wikimedia Commons



Mass extinctions and non-gradual trends
Raup & Sepkowski (1982)

Clade/species selection



Benton & Harper (2009)

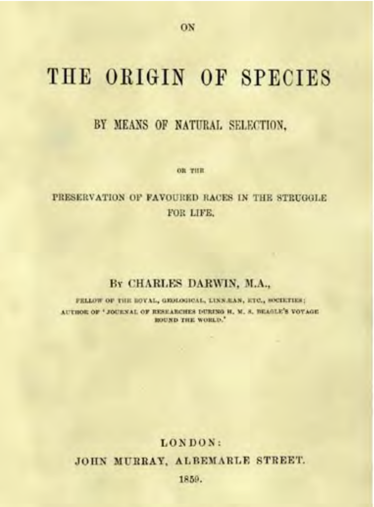
How/why did these lines of inference arise?
How do they fit in the standard evolutionary paradigm?

History of Evolutionary Thought

Recall Darwin (1859)
-Two key concepts
1) Evolution by Natural Selection
2) Descent with Modification

Species change over time (microevolution)
-Natural selection can generate adaptations and population discontinuities
Lineages split to form new species (speciation)
New life forms derive from older life forms (macroevolution)

View espouses that microevolution + time = macroevolution



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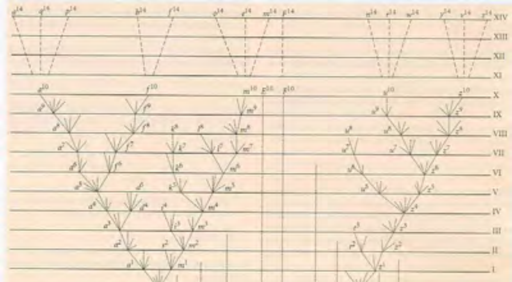

From Darwin (1859)

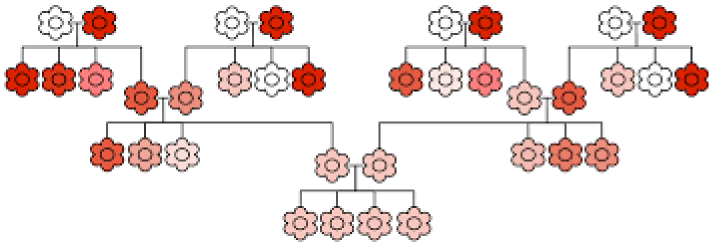
*Note: a partial history, related to macroevolution

Variation and Inheritance

Natural selection requires variation to operate

Mechanism of inheritance unknown to Darwin in 1859

-proposed *blending inheritance*



Wikimedia Commons

PROBLEM: blending inheritance would ameliorate variation over time, not generate it!

-So where did variation, and thus evolutionary change, come from?

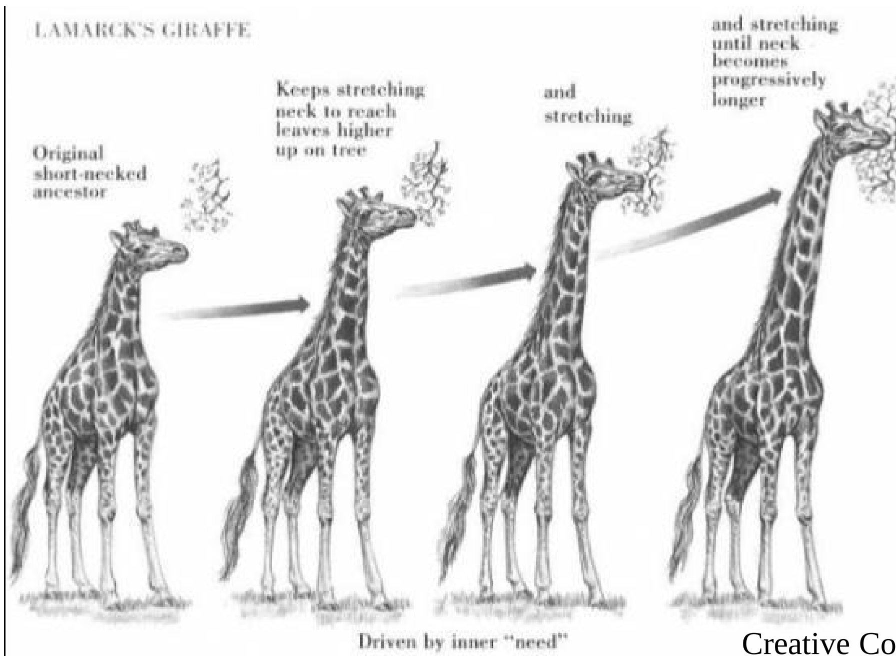
Alternatives: Neo-Lamarkism

Late 19th century alternatives to Darwinian evolution

1: Neo-Lamarkism

Resurgence of intra-generational inheritance

-Modifications within an organism's lifetime were inherited



-Weismann's rat experiments refuted this notion*

*Weismann cut off tails, next generation had tails (evidence that current environment alone did not generate evolutionary change)

Alternatives: Orthogenesis

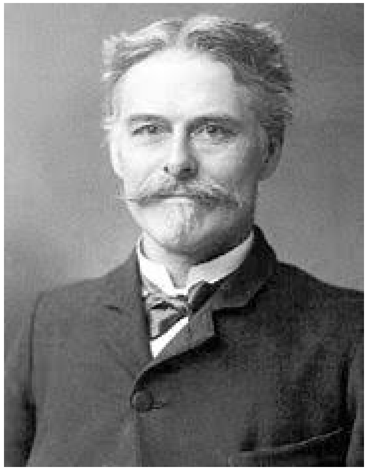
Late 19th century alternatives to Darwinian evolution

2: Orthogenesis

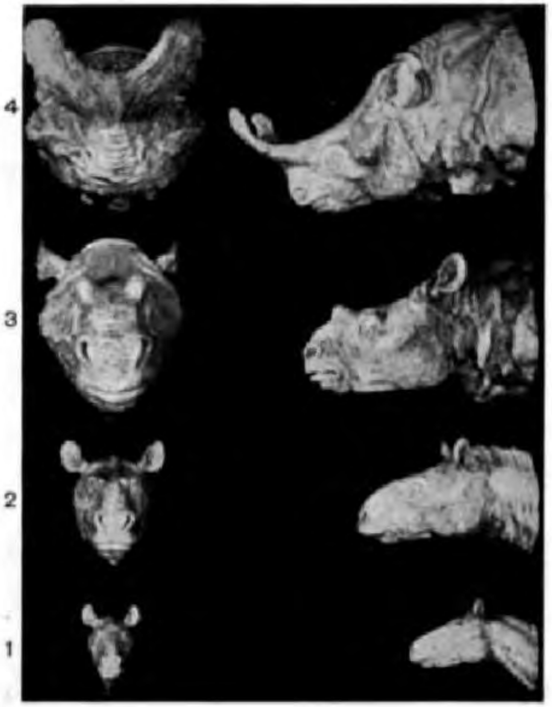
Straight line evolution:

- -Variation arising in pre-determined direction
- -*Internal drive* of change, ***NOT*** selection

-No mechanism for this drive ever proposed



Cope: Wikimedia Commons



From Osborne (1918)
Wikimedia Commons

Alternatives: Saltation and Mutationism

Late 19th century alternatives to Darwinian evolution

3: Saltation: large, instantaneous changes important

"Monstrosities become founding fathers of new species by instantaneous transformation" Saint-Hilaire

Observed discontinuities between forms taken as evidence of macromutations*

de Vries: work on primrose: new phenotypes arise by mutation

De Vries: Wikimedia Commons

Wikimedia Commons

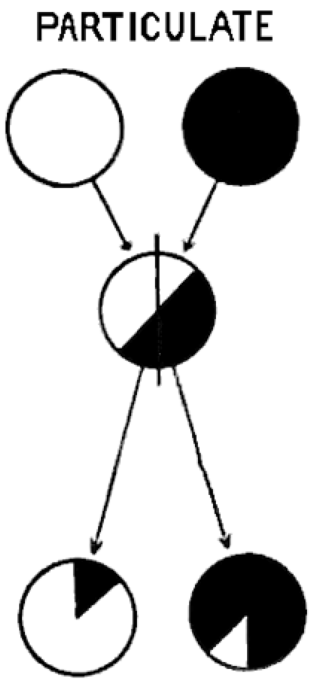
Saint-Hilaire: Wikimedia Commons

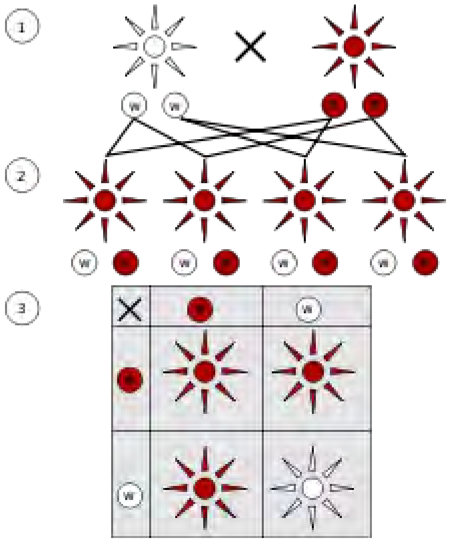
*Much of this proposed *BEFORE* Mendel's work rediscovered

Mendel: Particulate Inheritance

Mendel (1865, 1866) discovered particulate inheritance
-Proposed laws of segregation

Provides mechanism for variation to be passed across generations





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Evolutionary importance unappreciated for nearly 40 years!

Mendelians vs. Biometricians

Early 20th century: two biological schools of thought

1: Mendelian tradition
- -Saltationist/Mutationist view + Mendelian inheritance
  - -Genetic inheritance discrete
  - -Phenotypic changes based on mutations, which are discrete

Bateson: Wikimedia Commons

2: Biometric tradition
- -Much of variation is continuous
- -Advocated gradual changes to traits

Resolution: Genetic experiments of Morgan, Castle etc.
Continuous variation could be generated and inherited by (multiple) discrete genetic changes*

Pearson: Wikimedia Commons

*Yule 1902 showed mathematically that multiple discrete factors could generate continuous variation
(This result has mathematical links to the normal distribution, Galton's 'quincunx' machine, Brownian motion, etc.).

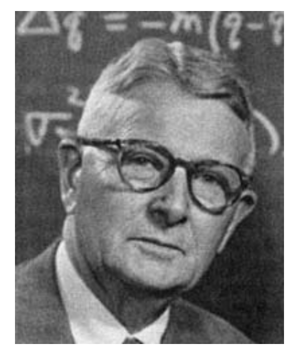
Evolutionary Synthesis

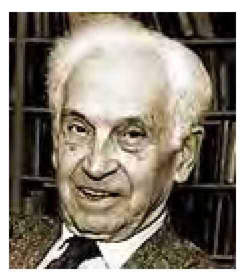
Synthesis of evolutionary thought: ~1918-1950

1: Reconciled Darwin’s theory with genetics
- -Fisher, Haldane, Wright: mathematical population genetics
  - Mutation + Nat. Sel. = Adaptive evolution
- -Chetverikov, Dobzhansky, Stebbins: Genetic variation & change in natural populations; hybrid speciation

2: Mayr: Allopatric speciation & NS in local populations

3: Simpson: Paleontology, evolutionary trends

*A partial list; other contributed as well

Wikimedia Commons

Evolutionary Synthesis

Tenets of the evolutionary synthesis

1: Genetic variation underlies evolutionary change

2: Adaptations result from natural selection operating on genetic variation in traits

3: Mutation generates variation; gene flow, genetic drift, and selection drive evolution within species (microevolution)

4: Given sufficient time, these processes account for origin of new species and major differences among higher taxa (macroevolution)

*Note: Evolutionary synthesis linked Darwin's ideas with various contemporary disciplines related to evolution, but also a way of rallying consensus around this perspective relative to alternative hypotheses (e.g., neo-Lamarkism, orthogenesis, etc.).

-The Evolutionary synthesis was a persuasive argument from a philosophical and conceptual viewpoint

Post-Evolutionary Synthesis

In subsequent decades, research largely reified the synthesis

Neo-Darwinian paradigm was _hardened_ (sensu Gould)

Three core principles of neo-Darwinism emerged:

1: Natural selection operates at the level of the individual*

2: Natural selection is *the* creative force in evolution (generates adaptations)

3: Microevolution + time = macroevolution

"*All evolution is due to the accumulation of small genetic changes, guided by natural selection, and that trans-specific [=macro] evolution is nothing but an extrapolation and magnification of the events that take place within populations and species*".

Mayr (1963). *Animal species & evolution*. P. 586.

*Results in changes in frequency at the population level

Back to Macroevolution

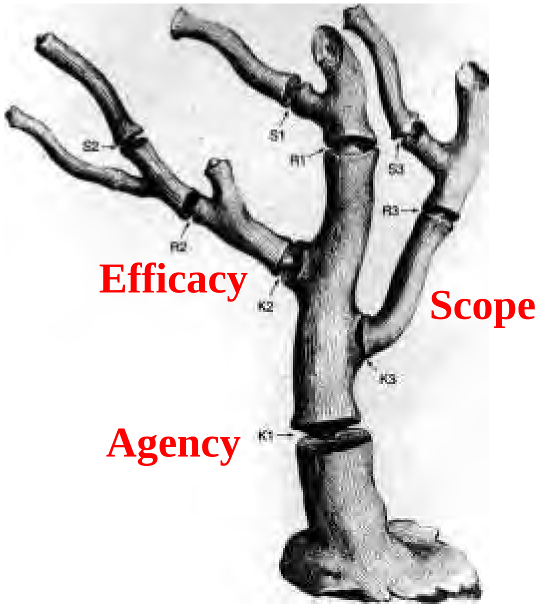
Gould (2002) summarized macroevolutionary challenges to neo-Darwian paradigm

The pillars of neo-Darwinism

1: **Agency:** Natural selection operates at level of individual
2: **Efficacy:** Natural selection is *the* creative evolutionary force
3: **Scope:** Microevolution + time = macroevolution

Argued macroevolution provides evidence that cuts these pillars

Suggested that evidence supports a re-thinking and expansion of evolutionary thought



From Gould (2002)

1: Agency: Levels of Selection

Paradigm: Natural selection operates at individual level

Natural Selection: Differential survival and reproduction of entities (typically individuals within a population) due to differences in phenotype

-When acting on heritable variation, natural selection can result in evolutionary change

Natural Selection: Any consistent difference in fitness among different classes of biological entities (Futuyma & Kirkpatrick 2017)

-Entities display variation, and this variation is passed on differentially

Could this broader definition apply to other biological units?

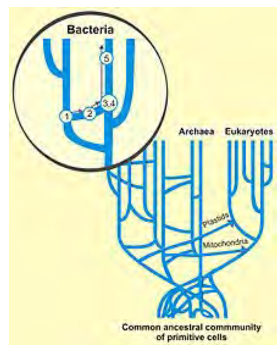
"The generality of the principles of natural selection means that any entities in nature that have variation, reproduction, and heritability may evolve. ...the principles can be applied equally to genes, organisms, populations, species, and at opposite ends of the scale, prebiotic molecules and ecosystems." (Lewontin, 1970)

1: Agency: Genic Level Selection

Selection at level of gene operates when some genotypes differentially replicate and proliferate

-Often termed *selfish genes* (Dawkins 1976)

-Transposable elements are transmitted at ↑ rate than other genic components



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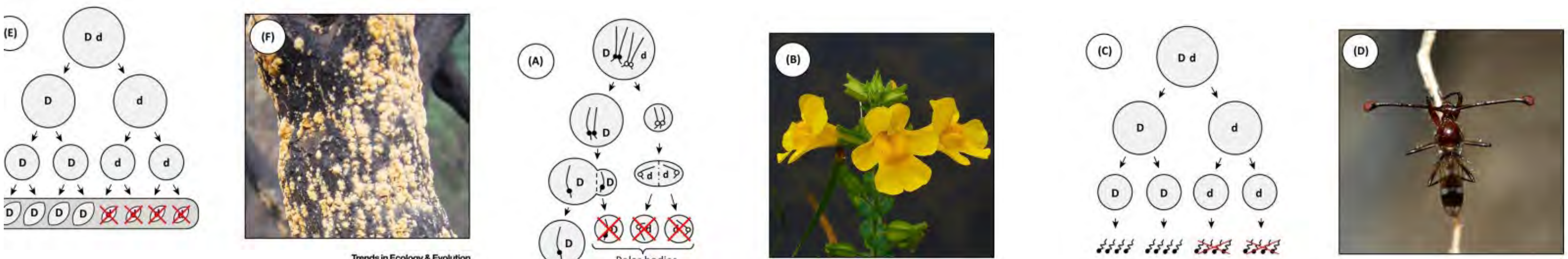
-Meiotic drive: elements that manipulate production of gametes and increase their rate of transmission



Lindholm et al. (2016)

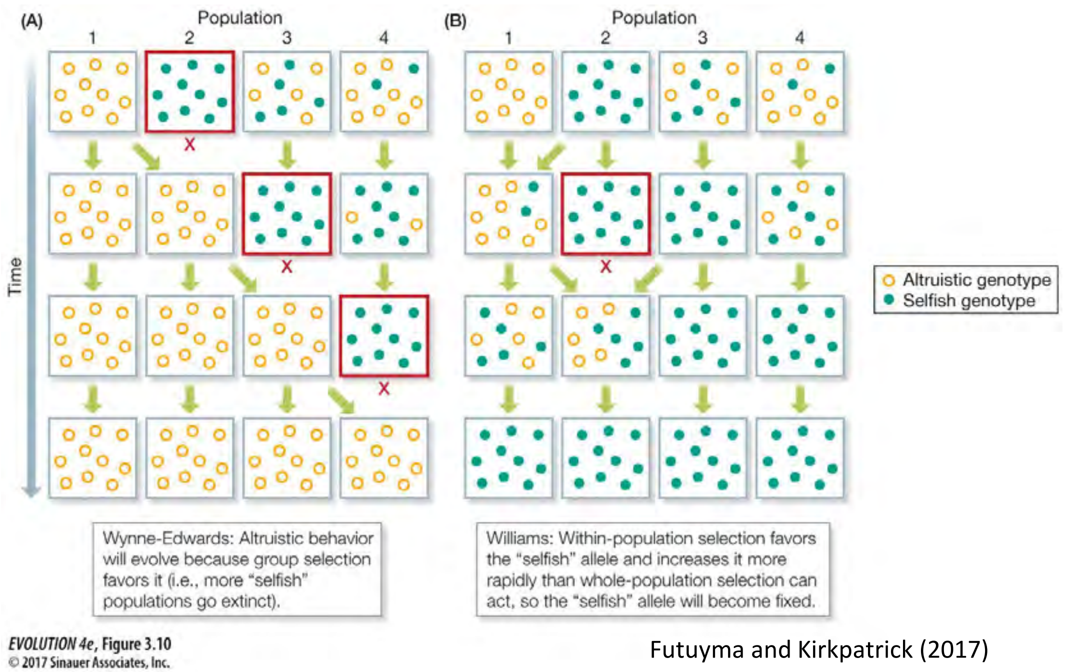
1: Agency: Group Selection

Selection of groups: differential survival and reproduction of groups

-Can occur, e.g., when groups have differing genetic composition

-Evolution of altruism via inclusive fitness possible example

Altruism dominates (group selection) Selfish behavior dominates (individual)



Futuyma and Kirkpatrick (2017)

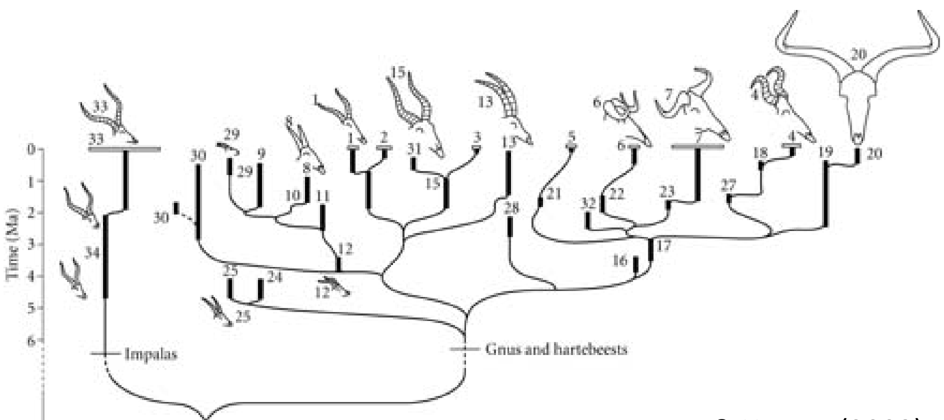
More challenging, as it must outweigh individual-level selection

*Historical note: Many early group selection examples were strongly discredited (Williams 1966 and others). More recent evidence suggests under certain conditions group selection is viable (e.g., Wilson and Sober 1994; Eldakar and Wilson 2012).

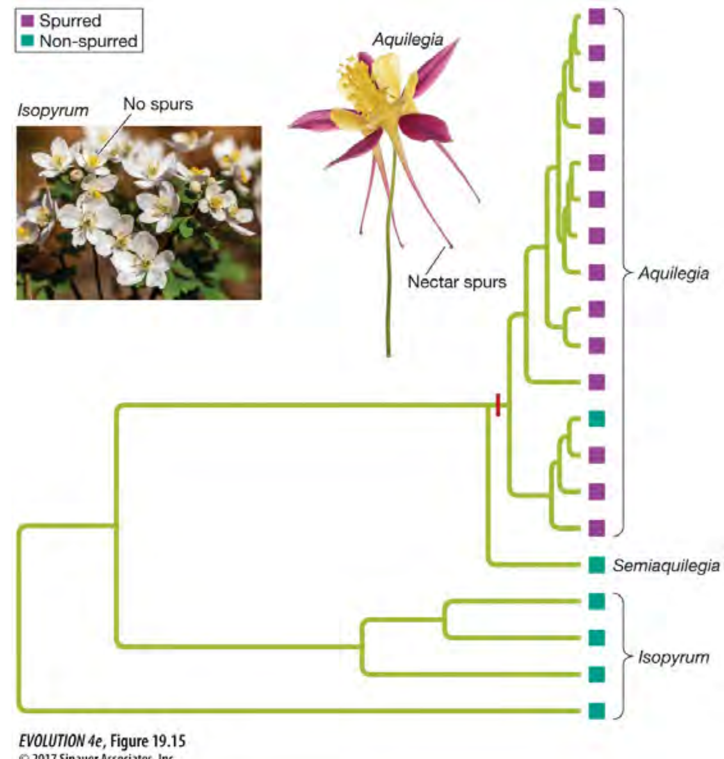
1: Agency: Clade/Species Selection

Clade Selection: differential survival and reproduction of species

-Differential speciation and extinction rates can lead to differences in clade disparity



Benton & Harper (2009)



From Futuyma and Kirkpatrick (2017)

-If associated with a trait (often a *key innovation*), can lead to phenotypic disparity differences

*Difficult to determine if this is selection ‘on’ clades, or selection for traits, with diversification differences resulting

Parting Thoughts

-Selection does operate on individuals
-Multi-level selection theoretically possible

-Gene level: some evidence (transposable elements, meiotic drive)

-Group level: less evidence (altruism?)

-Clade/Species Selection: theoretically possible
    -Little evidence (hard to distinguish from selection on individuals)

*Considering distinct levels of selection sometimes useful

2: Efficacy: Primacy of Natural Selection

Paradigm: Natural selection is *the* creative evolutionary force
-Thus selection generates adaptations

Adaptation: an organismal feature that has become prevalent in a population (or species), owing to its functional role

Outcome of this perspective: ***Everything*** was seen as an adaptation

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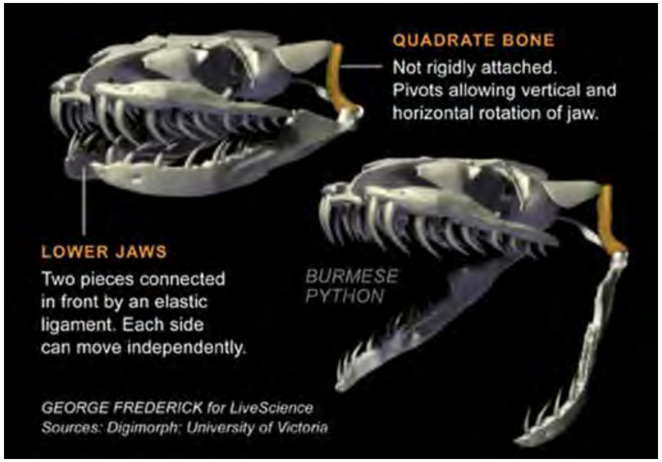


LiveScience (George Frederick)

Problem: not everything is an adaptation

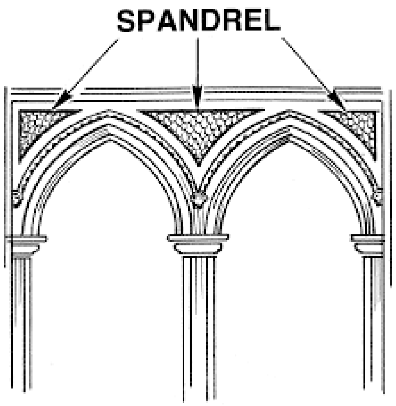
"Adaptation is a special and onerous concept that should be used only where necessary." (Williams 1966)

2: Efficacy: By-Products & Structural Constraints

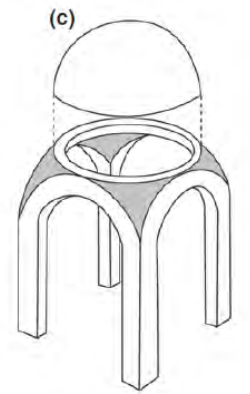
Spandrels and by-products (Gould and Lewontin 1979)

Spandrels are architectural by-products of mounting domes on arches

They are often decorated with mosaics, but were NOT created for that purpose



Blog.stephens.edu



Olson (2012)

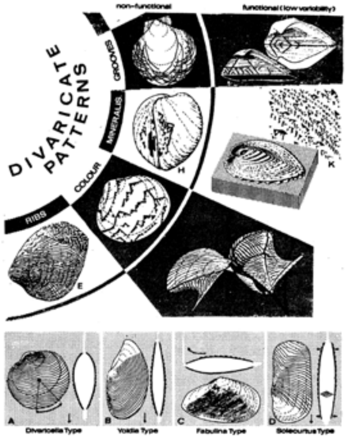

Spandrel in St. Marks
Wikimedia Commons

Some traits are by-product of evolution of other characteristics

Over-atomizing traits may erroneously lead to an adaptive story-telling for traits that may be spandrels

-blood is not adapted to be red; that is a by-product of selection for hemoglobin, which is red

-Divarticulate patterns in mussels are architectural requirements, not adaptive difference between taxa



Seilacher (1972)

Structural/architectural constraints should be considered

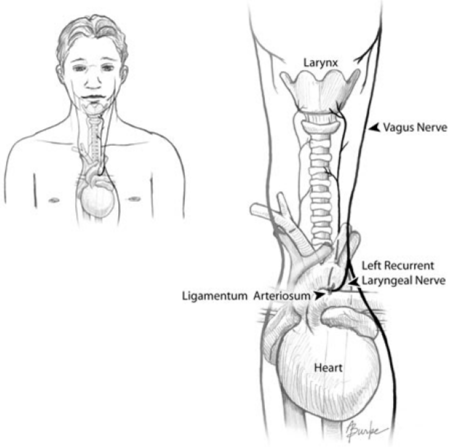
2: Efficacy: Vestiges and Design Limitations

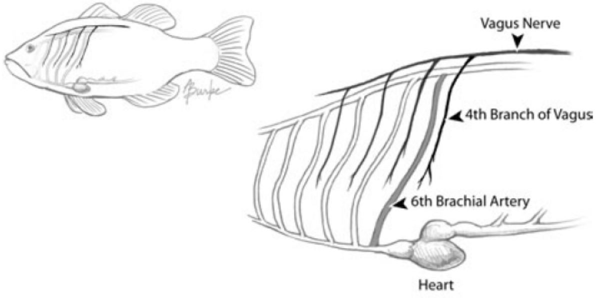
Vestiges: Retention of traits no longer in use

Eyes degenerated, but still present: Wikimedia Commons

Sub-optimal design: traits with obvious historical baggage

Result of 'evolution by tinkering' and design limitations



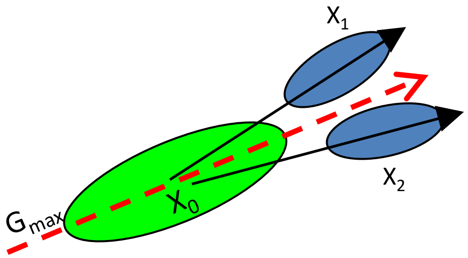


Human vagus-laryngeal nerve path: from Coyne (2009)

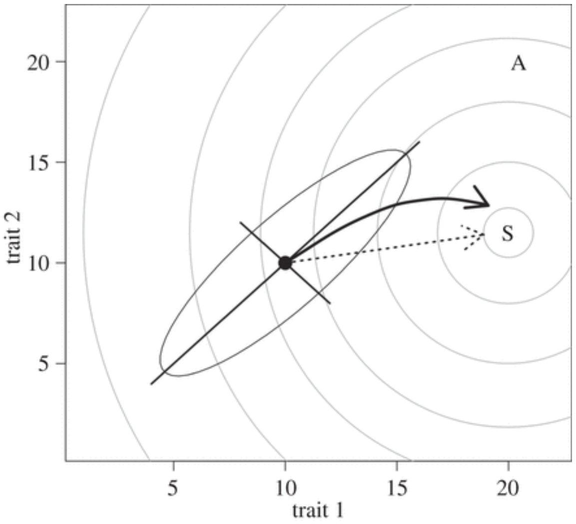
These are clearly not adaptations

Genetic covariation can constraint path of selective change

Genetic: 'lines of least resistance'

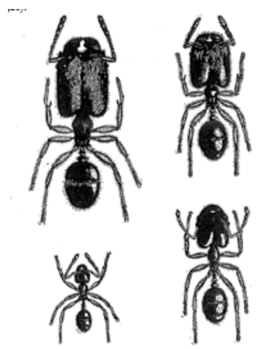


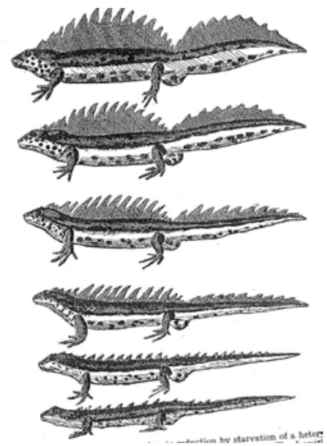
After Schluter (1996)



Pitcher et al. (2014)

Allometry (relative growth) describes consistent trends





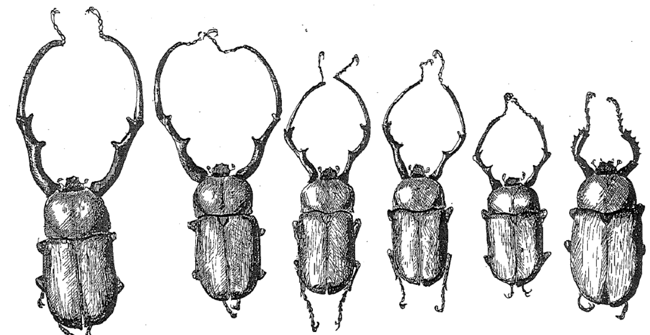
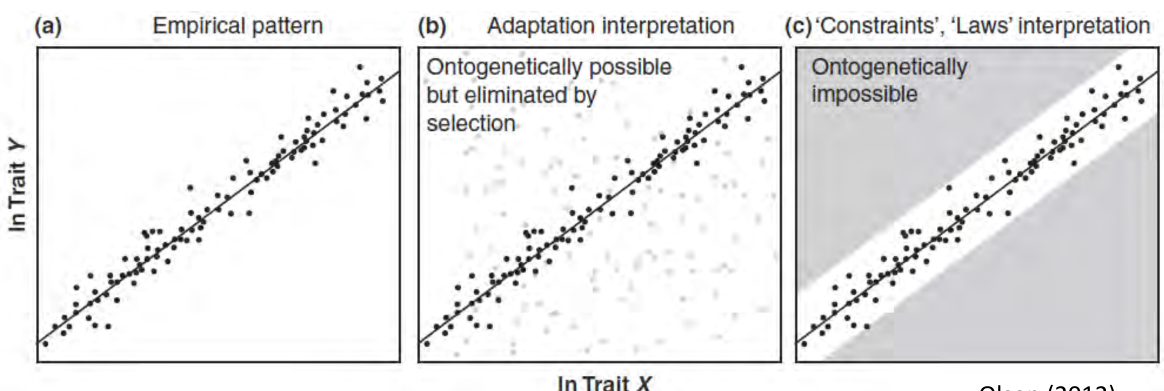


FIG. 33.—Heterogony of the male fore-limb of the beetle *Euchirus longimanus*.

Huxley (1932)

Allometry can be seen as channeling variation; a *pull* of the direction of correlated trait change

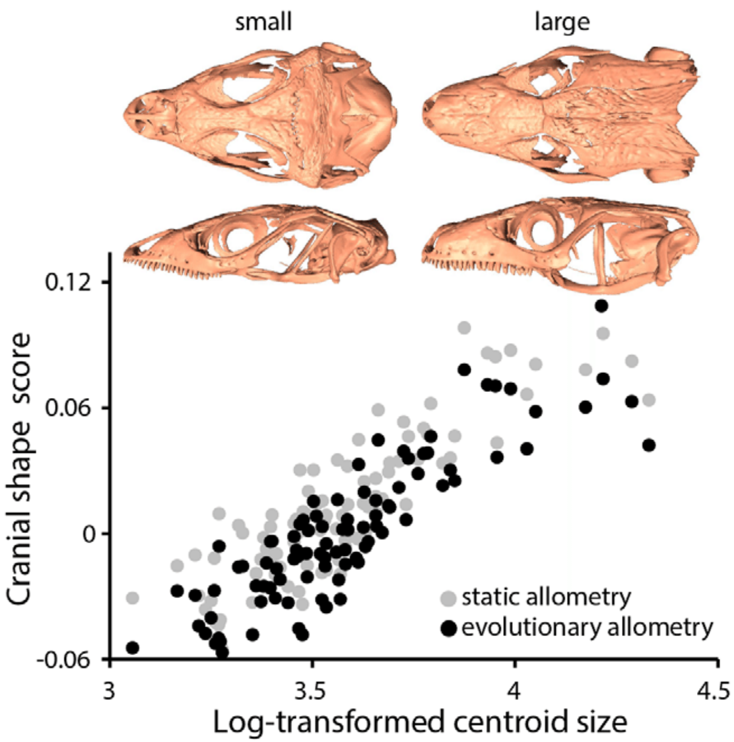


Olson (2012)

Evolutionary Patterns of Allometry

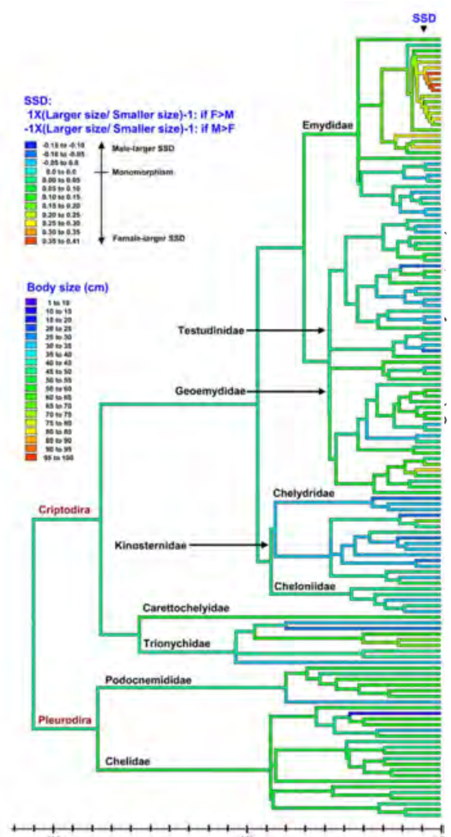
At macroevolutionary scales, allometric patterns are pervasive and demand explanation (e.g., is it channeling or selection along the allometric trajectory?)

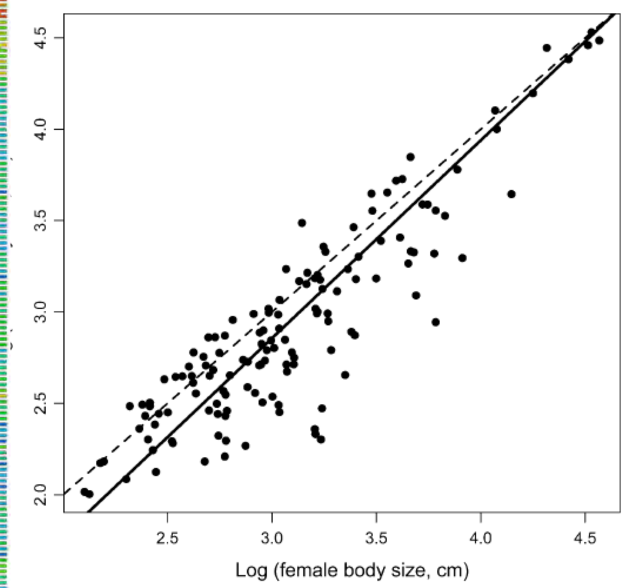
Shape allometry



Hipsley and Müller (2017)

Size allometry **(here, SSD: sexual size dimorphism: Rensch's rule)**

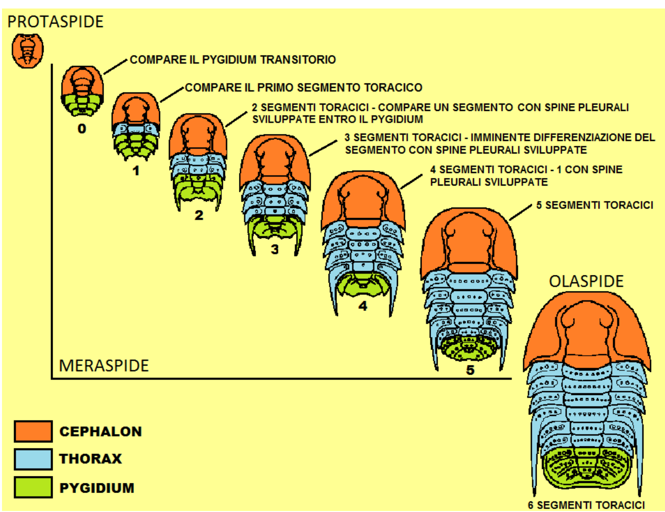




Ceballos, Adams, Iverson, Valenzuela (2013)

Consistent trends of progression of developmental stages

Haeckel (1866) suggested this reflected phylogeny (biogenetic law*)



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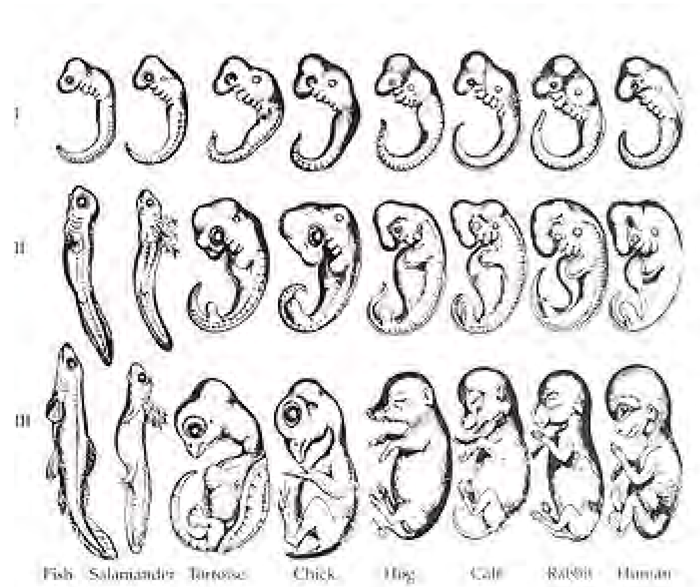

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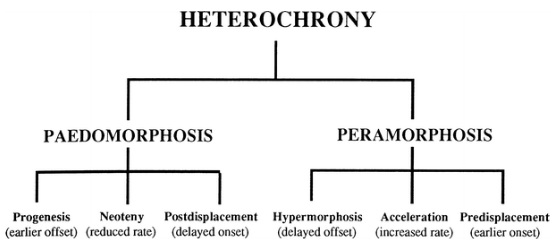
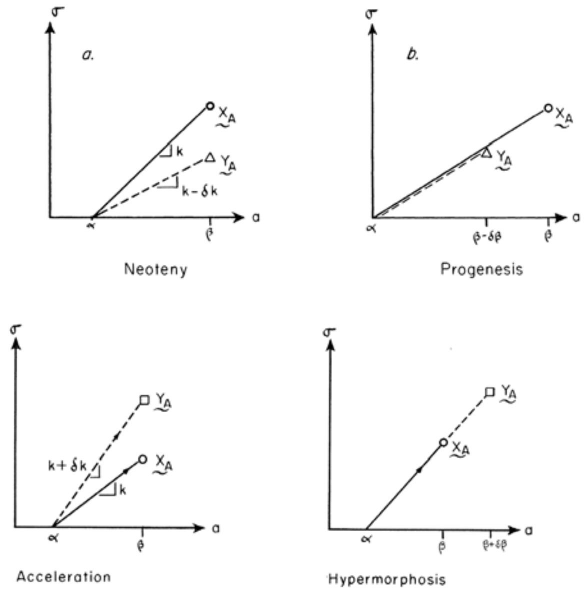
*Largely defunct, though there are clear trends in ontogeny across related taxa

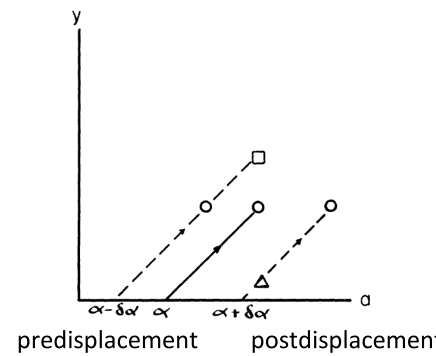
2: Efficacy: Heterochrony

Developmental changes in rates and timing of events (relative to ancestral condition)



McNamara (2012)





Alberch et al. (1979)

Can generate large phenotypic differences*

Neoteny: Wikimedia Commons

Peramorphosis: Wikimedia Commons

*NOTE: selection of course may operate on rates and timing of events!

2: Efficacy: Primacy of Natural Selection

Parting Thoughts

-Not all traits are adaptations
-Phenotypic evolution may be channeled by one or more constraints
(structural/architectural, genetic, allometric, ontogenetic, etc.)
-Heterochronic patterns evident in many clades

-Understanding phenotypic variation requires pluralistic approach

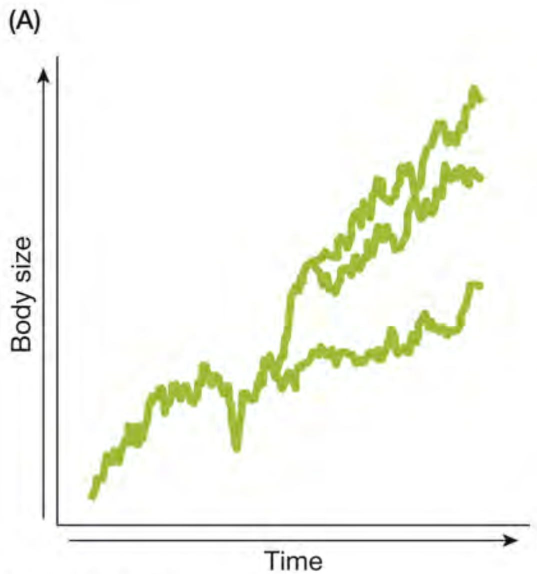
-Appreciating that selection may operate within allometric/ontogenetic/developmental channels is hugely important

*None of these invalidate importance of selection, but remind the biologist to investigate alternatives (rather than assume adaptation!)

3: Scope: Explaining Macroevolution

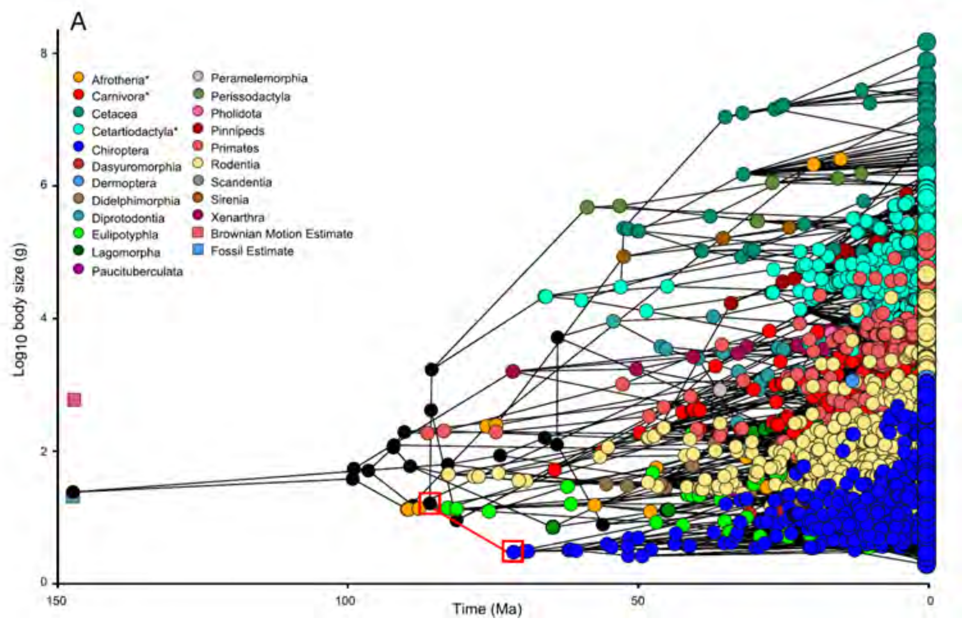
Paradigm: Macroevolutionary trends explained by microevolution + time

Implies continuous, often gradual changes over time



EVOLUTION 4e, Figure 20.22 (Part 1)

Futuyma and Kirkpatrick (2017)



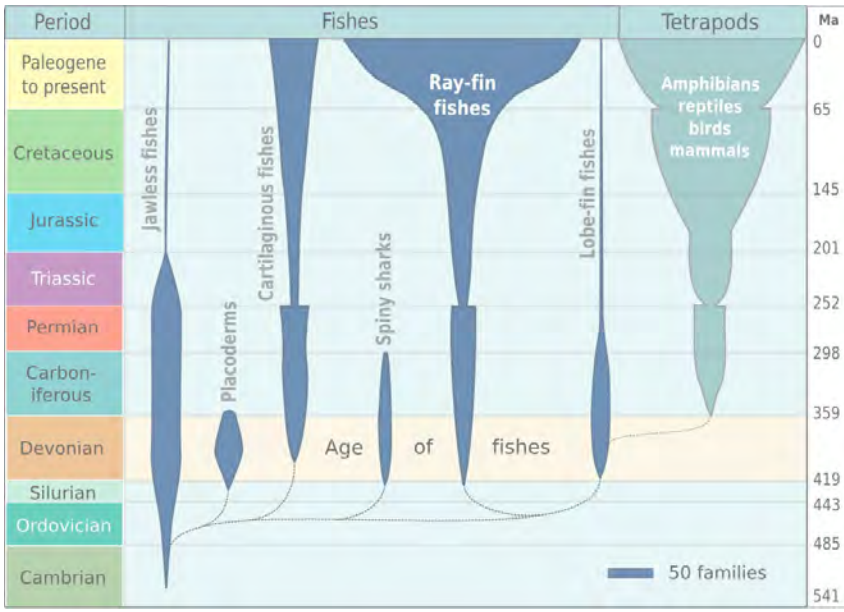
e.g., Baker et al. (2015)

This underplays the importance of contingency in evolution (Gould)

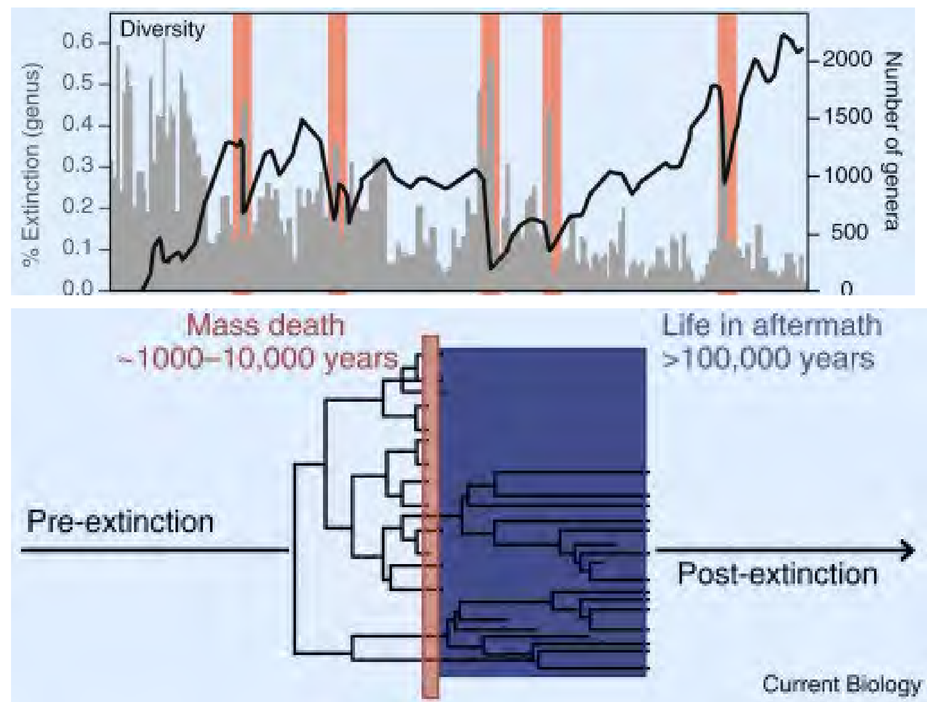
3: Scope: Mass Extinctions & Faunal Turnover

Mass extinctions generate major faunal turnover

-Catastrophic events shift evolutionary paths



Benton (2015)



Hull (2015)

-Challenge gradual and uniformitarian viewpoints

-Challenging to predict winners and losers (or direction)

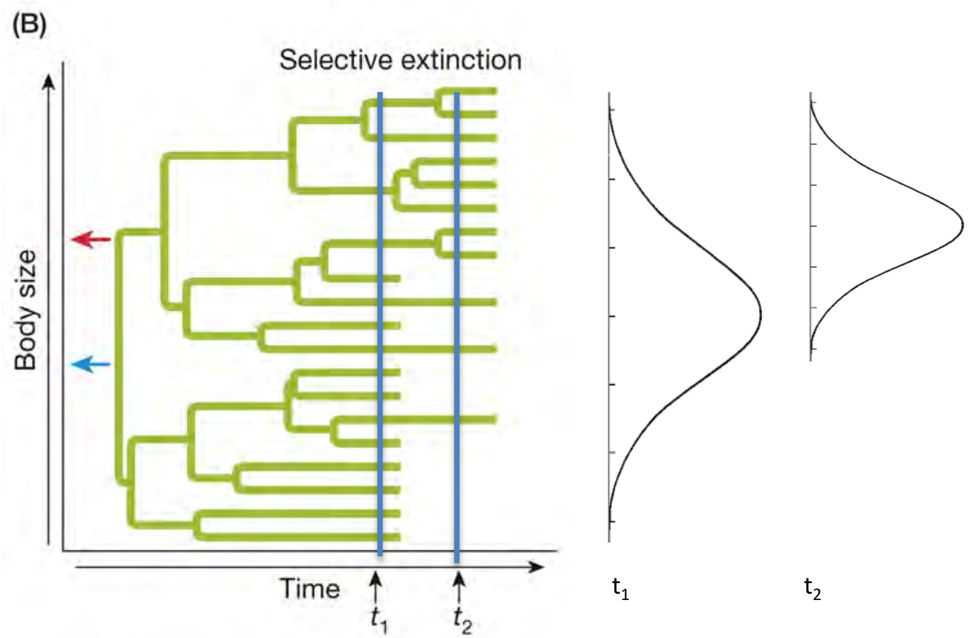
3: Scope: Species Sorting

Taxon survival based on trait values

Evolution of trait variation in surviving taxa shifted relative to original

(e.g., a selective filter at extinction that is size based: only species of certain size classes survive)

-Can enhance prior selective trend or be in opposition to it



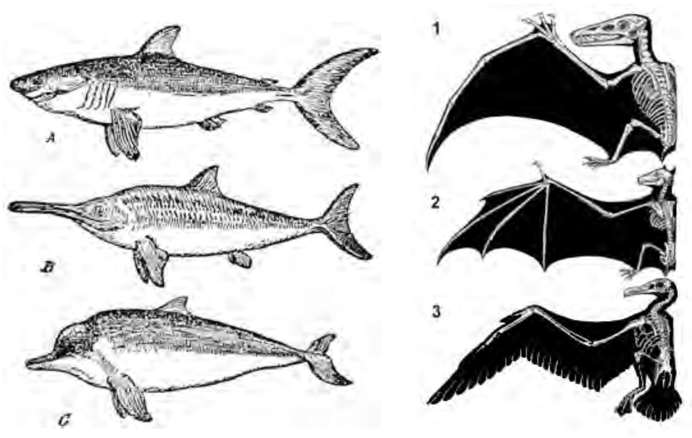
EVOLUTION 4e, Figure 20.22 (Part 2)

Futuyma and Kirkpatrick (2017)

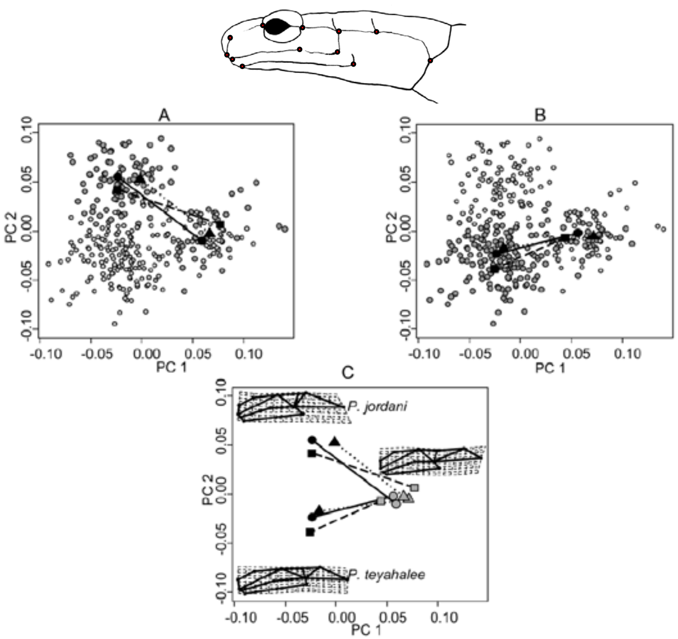
3: Scope: Contingency Versus Repeatability

If the tape of life were replayed, would the same result evolve?

-How *repeatable* is evolution? How important is contingency?



Convergent evolution: Wikimedia commons



Convergent outcomes: Adams (2010)

Examining convergence (or lack of it): a major research theme

"The divine tape recorder holds a million scenarios, each perfectly sensible. Little quirks at the outset, occurring for no particular reason, unleash cascades of consequences that make a particular feature seem inevitable in retrospect. But the slightest early nudge contacts a different groove, and history veers into another plausible channel, diverging continually from its original pathway. The end results are so different, the initial perturbation so apparently trivial". Gould (1989)

Parting Thoughts

Contingency is important in macroevoution

- -Alters community composition, faunal turnover
- -Alters dispersion of trait values (species sorting)
- -Contingency vs. repeatability/convergence a major research area

*Macroevoutionary trends better understood when contingency *AND* selection are examined and tested