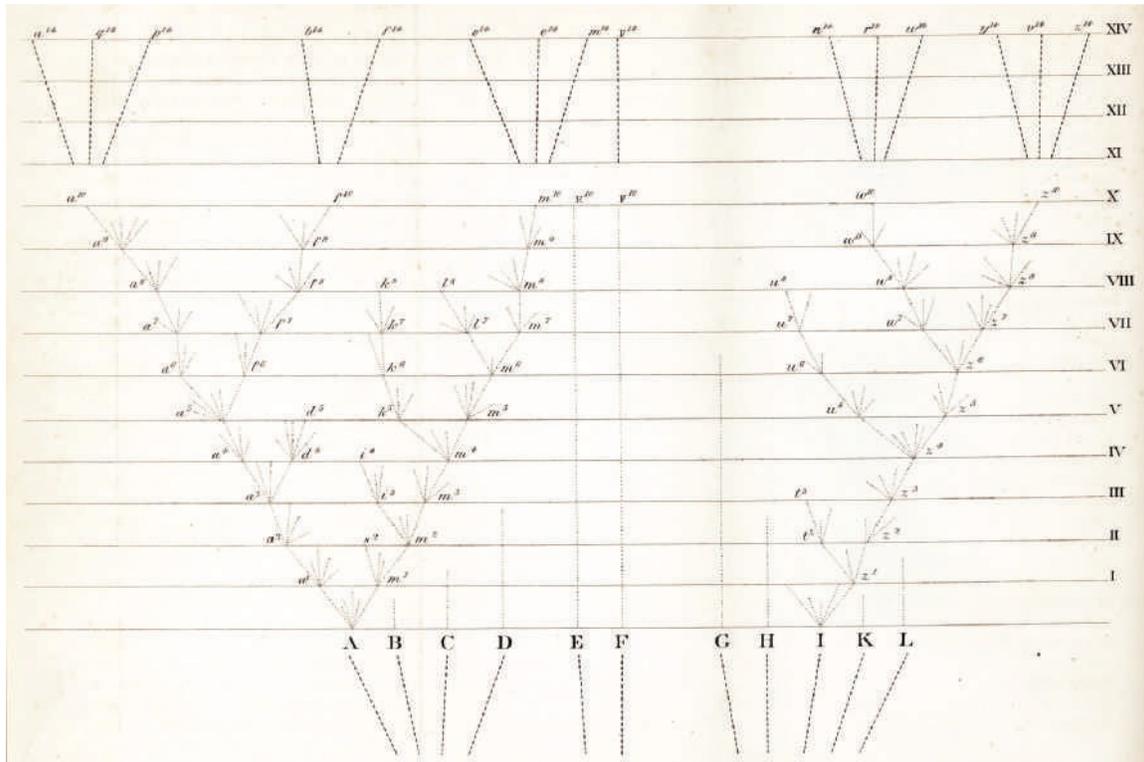


Modes of Macroevolution

Macroevolution is used to refer to any evolutionary change *at or above the level of species*.

Darwin illustrated the combined action of descent with modification, the principle of divergence, and extinction in the only figure in *On the Origin of Species* (Fig. 1), showing the link between microevolution and macroevolution.

The New Synthesis sought to distance itself from the ‘origin of species’ (= macroevolution) and concentrated instead on microevolution - variation within populations and reproductive isolation.



“Darwin’s principle of divergence derives from what he thought to be one of the most potent components of the struggle for existence. He argued that the strongest interactions would be among individuals within a population or among closely related populations or species, because these organisms have the most similar requirements. Darwin’s principle of divergence predicts that the individuals, populations or species most likely to succeed in the struggle are those that differ most from their close relatives in the way they achieve their needs for survival and reproduction.” (Reznick & Ricklefs 2009. Nature 457)

Macroevolution also fell into disfavor with its invocation for hopeful monsters in development as well as its implication in some Neo-Lamarckian theories. Interest in macroevolution revived by several paleontologists including Steven Stanley, Stephen Jay Gould and Niles Eldredge, the latter two in the context of punctuated equilibrium. They proposed that what happens in evolution beyond the species level is due to processes that operate beyond the level of populations – including species selection. Niles Eldredge, in particular, has written extensively on the macroevolutionary hierarchy.

Macroevolutionary Hierarchy

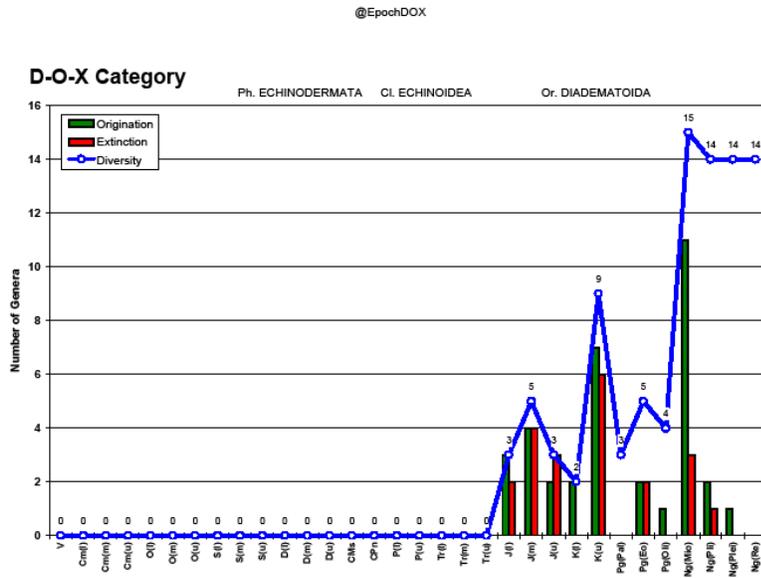
Type	Resolution	Mechanism	Causality	Direction	Process	Label
Macro ₂	Highest Taxa (Family, Order, etc.)	External (Abiotic?)	Stochastic (Non-deterministic, Non-random)	↑ Environmental Constraints	Faunal Replacement, Mass Extinction, Punctuation	Non-Darwinian
Macro ₁	Mid-Taxa (Genus, Species, etc.)	Taxon Sorting	Broadly Contingent (Deterministic & Non-deterministic Processes)	↑ Species (Group) Selection	Differential Species/Genus Survival	Semi-Darwinian
Micro ₂	Population	Natural Selection	Deterministic	↑ Organism Selection	Individual Organismal Survival	Darwinian
Micro ₁	Individual	Genetic Drift and Mutation	Stochastic (Non-deterministic, Non-random)	↑ Gene Selection	DNA Recombination	Ultra-Darwinian
Cellular	Cytoplasmic	Selection on Replication Rates	Contingent	↑ Selection of Cytoplasmic Elements	Genomic Conflict	Genomic
Molecular	Molecular	Biochemistry	Deterministic	↑ Molecular Configuration	Chemical Bonds	Chemical
Atomic	Atoms	Physics	Stochastic	↑ Quantum Uncertainty	Quantum Mechanics	Physicalist

From Sepkoski (2007)

Species selection - Species selection in the broad sense – also termed species sorting – shapes evolutionary patterns through differences in speciation and extinction (emergent fitness of clades) that arise by interaction of intrinsic biological traits with the environment. Macroevolution supposedly occurs when those biotic traits, such as body size or fecundity, reside at the organismic level. Elizabeth Vrba’s effect hypothesis – speciation rates vary between taxa producing differential representation, but trait reducibly to the individual. Strict-sense species selection occurs when those traits are emergent at the species level, such is geographic range or population size. Jablonski (1987) presented evidence of geographic range as species selection.

Species extinction is both a key process throughout the history of life and central to macroevolutionary theory.

1. Extinction rates and severities (background vs. mass)
2. Phylogenetic nonrandomness of extinction
3. Testing of hypotheses relating extinction-proneness to attributes of organisms or species.



Recent studies by John Alroy have shown that two biotic mechanisms have hastened recoveries from mass extinctions and confined diversity to a relatively narrow range over the past 500 million years (Myr). First, a drop in diversity of any size correlates with low extinction rates immediately afterward, so much so that extinction would almost come to a halt if diversity dropped by 90%. Second, very high extinction rates are followed by equally high origination rates. His data also show that extinction and origination rates both declined through the Phanerozoic.

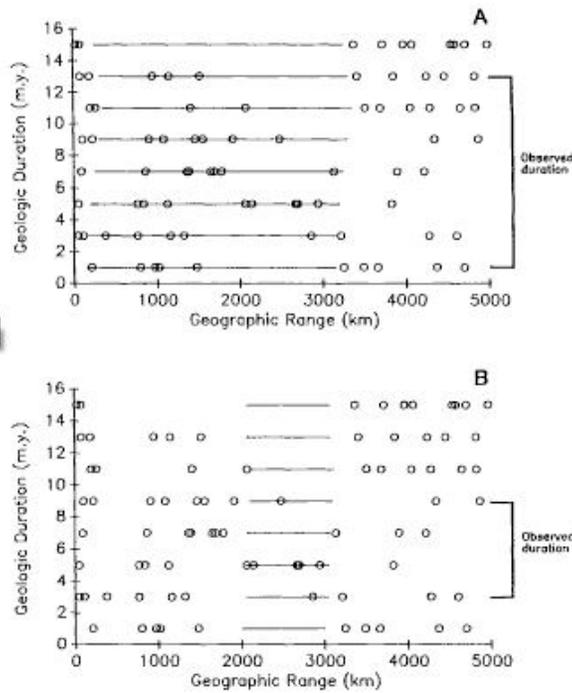


FIGURE 1. The geographic range of a species (X-axis) is represented as a horizontal line in the eight stratigraphic horizons (Y-axis). The circles represent fossil localities. Although there is no difference in the actual durations of the long-ranging (A) and short-ranging species (B), there is a difference in the observed durations. For the geographic range and geologic duration simulations, each plot represents a point along the species or Z-axis of the matrix.

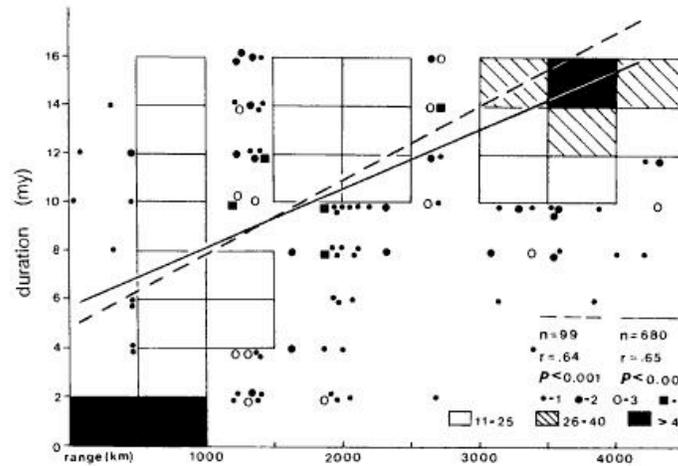
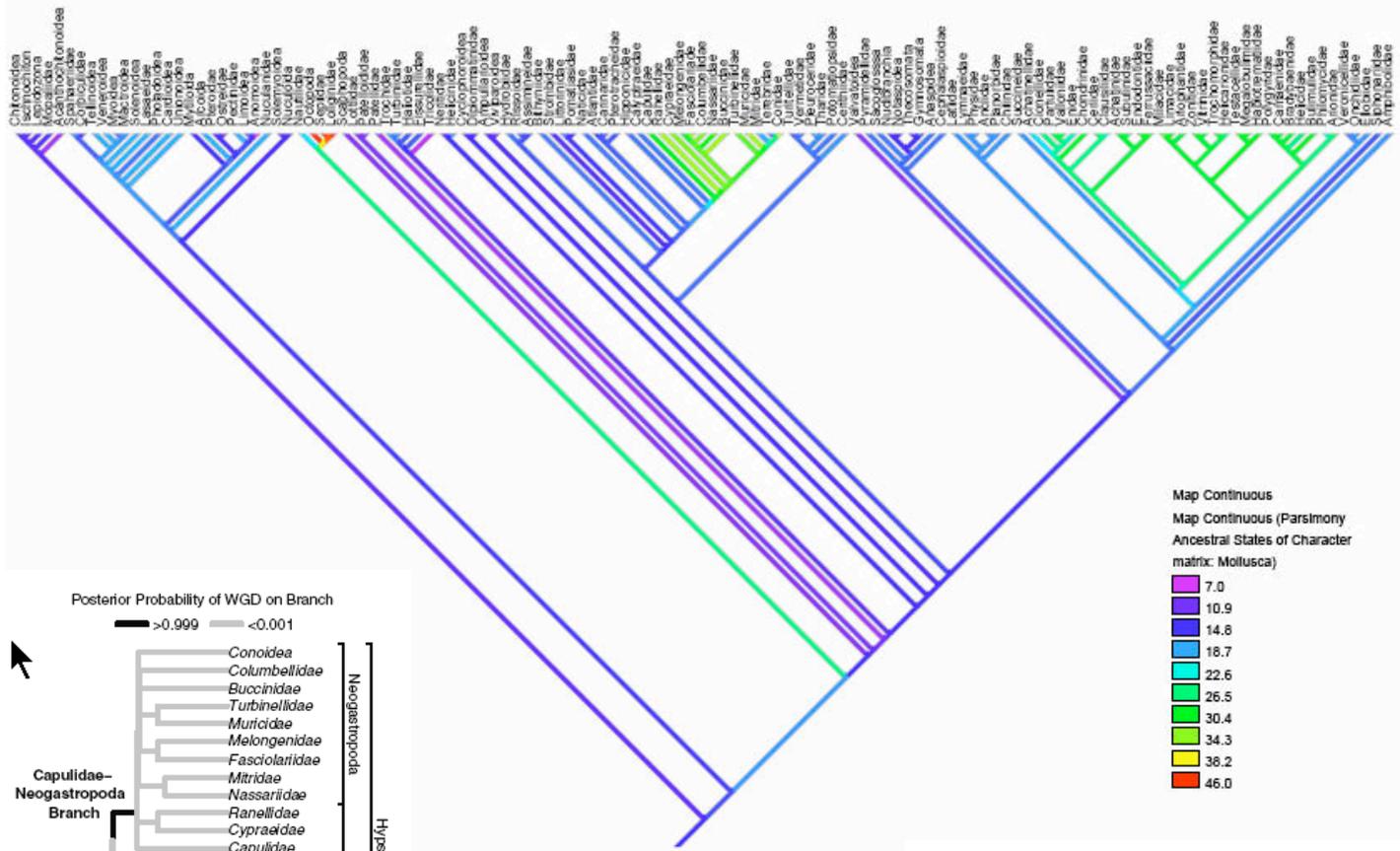


FIGURE 6. Scatterplot and regression of the results of our simulation using systematic sampling and a 1% resolution level (solid line). Dashed line is the regression obtained from plotting duration on range for a published set of prosobranch gastropod data from the Cretaceous of North America (Jablonski 1986: table 1. Duration = $0.0015 \times \text{Range} + 2.44$, $N = 99$, $r = 0.64$, $P < 0.001$). The two slopes are not significantly different ($P < 0.05$, t -test: Sokal and Rohlf 1981).

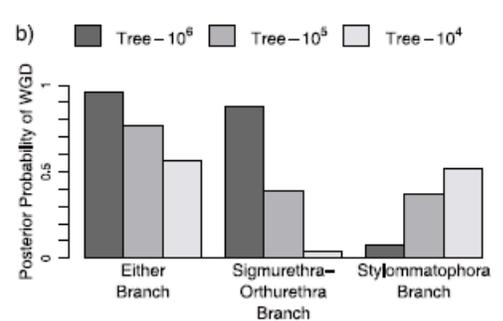
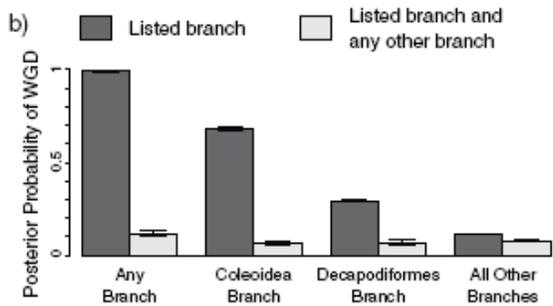
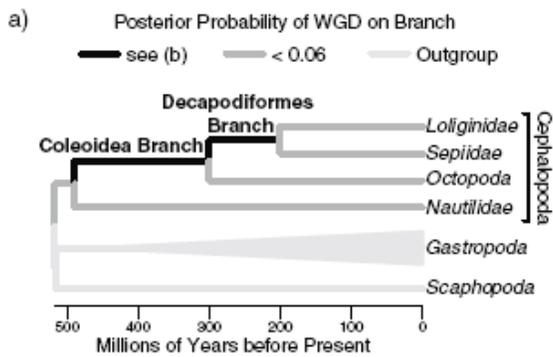
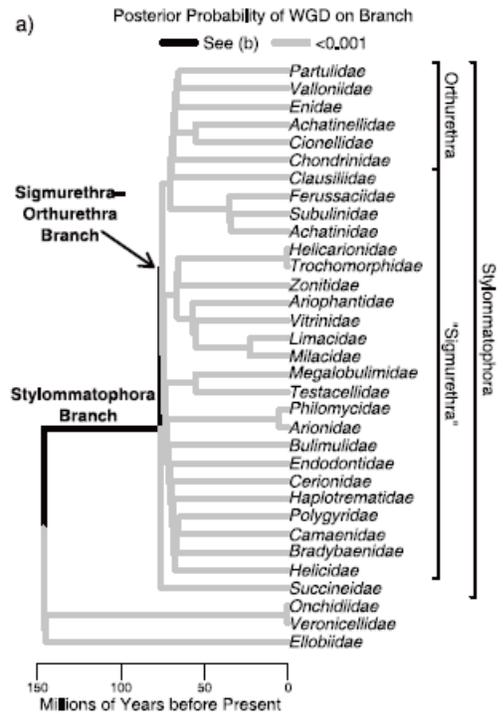
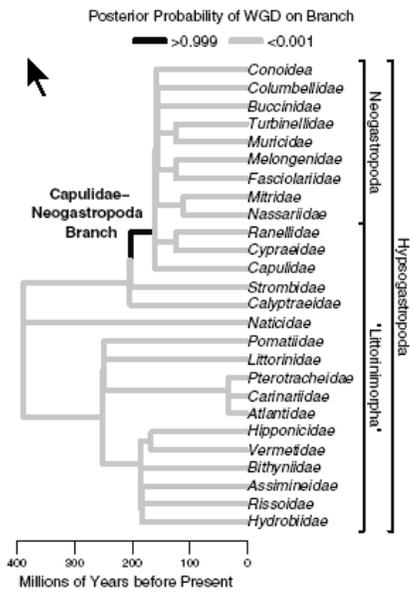
Sorting among taxa is widely accepted in principle as an evolutionary mechanism, but detailed analyses are scarce; if geographic range or population density can be treated as traits above the organismic level, then the paleontological and macroecological literature abounds in potential raw material for such analyses. Even if taxon sorting operates on traits that are not emergent at the species level, the differential speciation and extinction rates can shape large-scale evolutionary patterns in ways that are not simple extrapolations from short term evolution at the organismal level.

Genomic – (e.g. lateral gene transfer, gene or genome duplications, chromosomal rearrangements, co-option of gene products for new functions, changes in regulatory networks, paedomorphism, hybridization, etc.). Gene duplication has been postulated as a way to acquire new functions in macroevolution; this view has been reinforced by the knowledge derived from the sequencing and comparison of genomes from a wide range of living organisms. Such gene duplication allows one of the copies to maintain its original function, while the other copy may thus accumulate mutations and eventually gain a new function.

Gene duplication is thought to be a source of genetic novelty in vertebrate evolution, and both continuous small-scale and discrete large-scale duplication likely played crucial roles in vertebrate evolution - one or two successive rounds of large-scale duplication are placed at the early origin of vertebrates.



Hallinan & Lindberg (2011)



Development – Although the macroevolutionary exploration of developmental genetics has just begun, considerable progress has been made in understanding the origin of evolutionary novelty in terms of the potential for coordinated morphological change and the potential for imposing uneven probabilities on different evolutionary directions. Global or whole-organism heterochrony, local heterochrony (affecting single structures, regions, or organ systems) and heterotopies (changes in the location of developmental events), and epigenetic mechanisms (which help to integrate the developing parts of an organism into a functional whole) together contribute to profound nonlinearities between genetic and morphologic change, by permitting the generation and accommodation of evolutionary novelties without pervasive, coordinated genetic changes.

“Developmental constraint and its converse constraint release are significant concepts in understanding pattern and process in macroevolution. The purpose of this paper is to propose a two-step method for identifying constraints and constraint release. The first step is a phylogenetic optimization procedure to identify which trait/process is primitive and which is derived. The primitive trait is inferred to be the constraint and the convergently derived trait the release. The second criterion uses sister-clade asymmetry. Clades diagnosed by the constraint will have fewer taxa than clades diagnosed by the release. As an example, we use the process of germ cell specification, in which there are three modes of specification. Our results corroborate previous conclusions that the induced mode is the constraint and the predetermined mode is the release and we speculate on the importance of these two processes in terms of robustness and evolvability.” [Crother et al. (2007)]

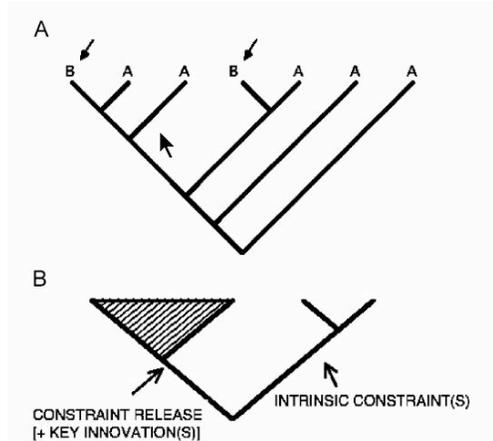


Fig. 1. Illustrations of the proposed criteria for identifying developmental constraint and constraint release. (A) Distribution of characters A and B, where A is basal and primitive and B is convergent and derived. Character A is interpreted as a constraint and character B as a release. (B) Cartoon of an unbalanced tree with asymmetrical sister clades. The depauperate clade indicates the presence of a constraint whereas the speciose clade indicates the release from the constraint that allows the development of key innovations. See text for further discussion.

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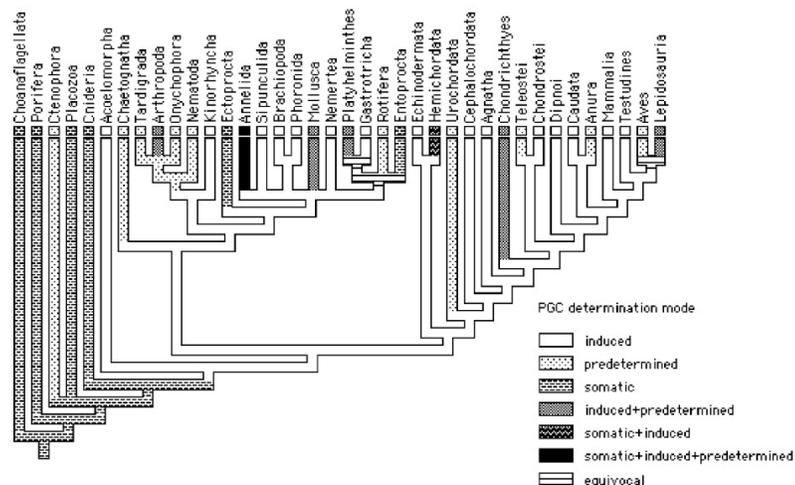


Fig. 3. Distribution of PGC determination mechanisms among metazoans. The evolution of germ cell determination mode was inferred by parsimony optimization in MacClade (v. 4.0, Maddison and Maddison, 2000). See the legend in the figure for character types. Some clades are presumed to exhibit both modes (e.g. in the Lepidosauria, snakes are presumed to have the predetermined mode whereas iguanids have the induced mode (Hubert, 1985) and are shown here. Branch lengths are arbitrary and not intended to indicate evolutionary distance. See the text for further explanation.