April 14, 2014**. Tempo and mode in macroevolution: patterns of diversification and extinction**

To return to a point discussed earlier in the class, there is a vital need to consider fossils (and therefore morphological characters) in order to understand the full set of evolutionary processes operating on the tree of life. We should not expect to be able to understand these using only the biased sample of organisms that happen to alive today.

Check out this Cetacean phylogeny from Lindberg & Pyenson (2006), and look what we would miss if we did not know about the fossils:

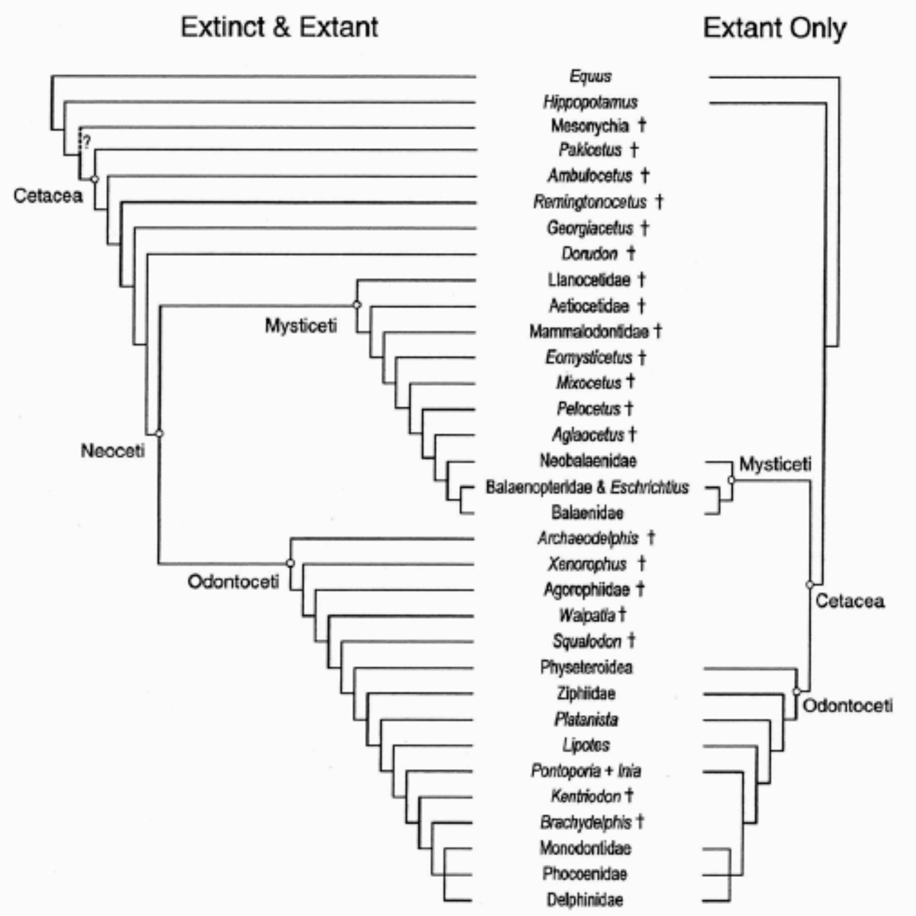


FIGURE 7.1. Composite phylogeny of the Cetacea based on morphological (Kimura and Ozawa 2002; Geisler and Sanders 2003; Uhen 2004) and molecular (Arnason et al. 2004) analyses. Outgroup relationships modified from Gatesy and O'Leary (2001).

Also note the phylogeny of the Burgess Shale Arthropods on the next page, which tells the same story.

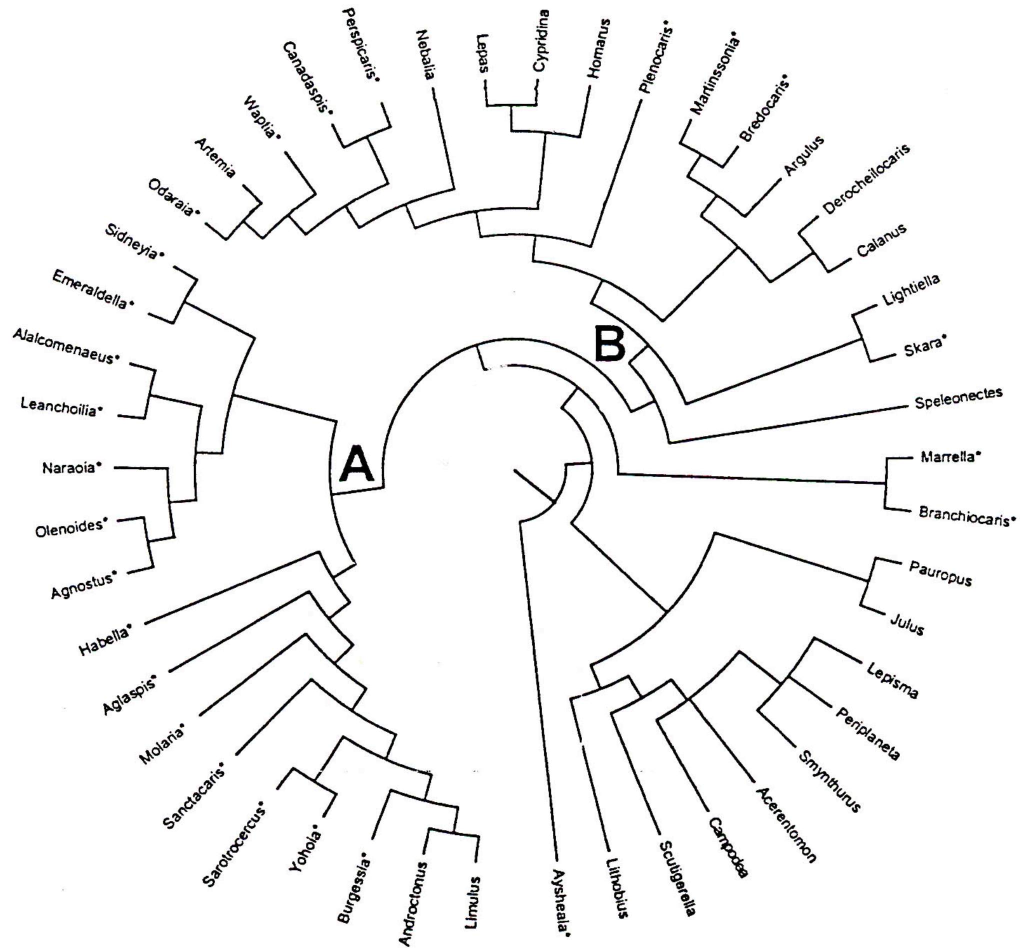


Figure 2 Cladogram of Cambrian and living arthropods. Cambrian arthropods are marked with an asterisk. In subclade A 87.5% of the taxa are extinct Cambrian taxa; in subclade B only 44.4% of the taxa are extinct. Differential extinction rates in different subclades exacerbate patterns of disparity. After Briggs et al (1992).

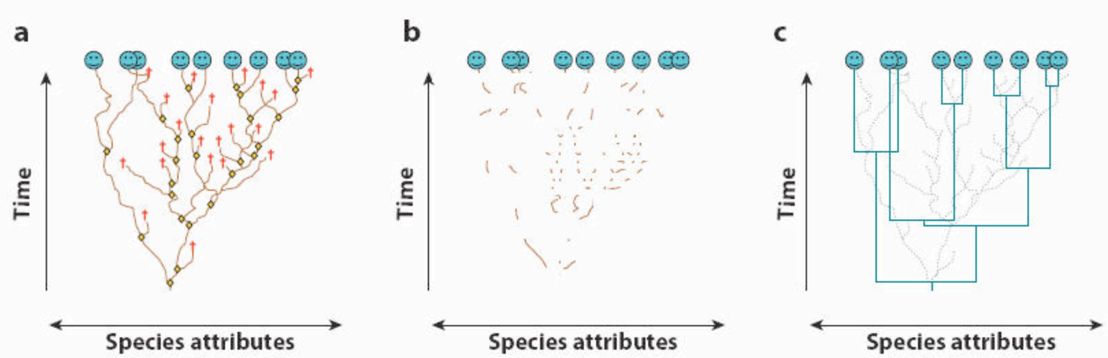


Figure 1

(*a*) The ideal data set for testing hypotheses about extinction, with all speciations (*diamonds*), extinctions (*crosses*), and character states (*x* axis) recorded. Species' attributes can be correlated against fates. (*b*) The information that might more typically be available in the fossil record. (*c*) The best information obtainable from the phylogeny of extant species. Modified after Purvis et al. (2008).

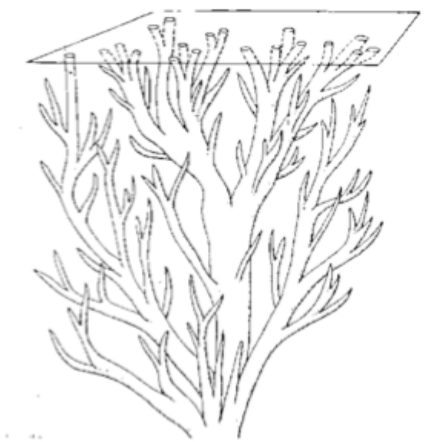
Diversity versus disparity

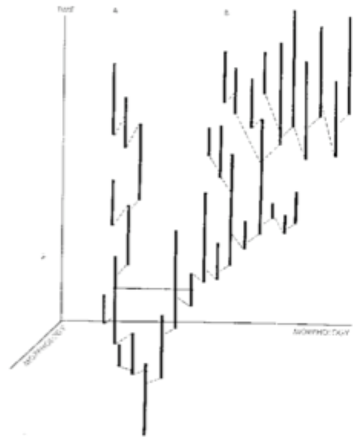
Diversity = the number of lineages present at a given time

Disparity = the amount of morphospace or ecospace filled at a given time.

Punctuated equilibrium versus gradualism

What is the mode of change?





George Gaylord Simpson: pointed out that not only does the tempo, or rate, of evolution differ greatly from group to group, but groups apparently have rapid and relatively slow periods in their evolution.

Eldredge and Gould: proposed theory of punctuated equilibria in 1972. Evolution occurs in spurts, creating a "punctuation" in the fossil record; the norm is long periods without change (stasis) punctuated by spurts of relatively rapid change. Their hypothesis of punctuated equilibrium held that evolution proceeds relatively rapidly during speciation when a peripheral population splits off and evolves rapidly into a new species. Punc Eq does not have to be linked with splitting, of course.

Although the morphological changes are perhaps always continuous in the sense of passing through many intermediate stages, the changes when they occur have been so rapid that the fossil record presents the appearance of a discontinuous change.

Living fossils: species that morphologically have changed little from their fossil ancestors in the distant past, e.g., lungfish, horsehoe crabs. At the DNA level, "living fossils" usually show as much genetic variation, and molecular evolution, as other species. What are living fossils, really? What process(es) gives rise to this pattern.

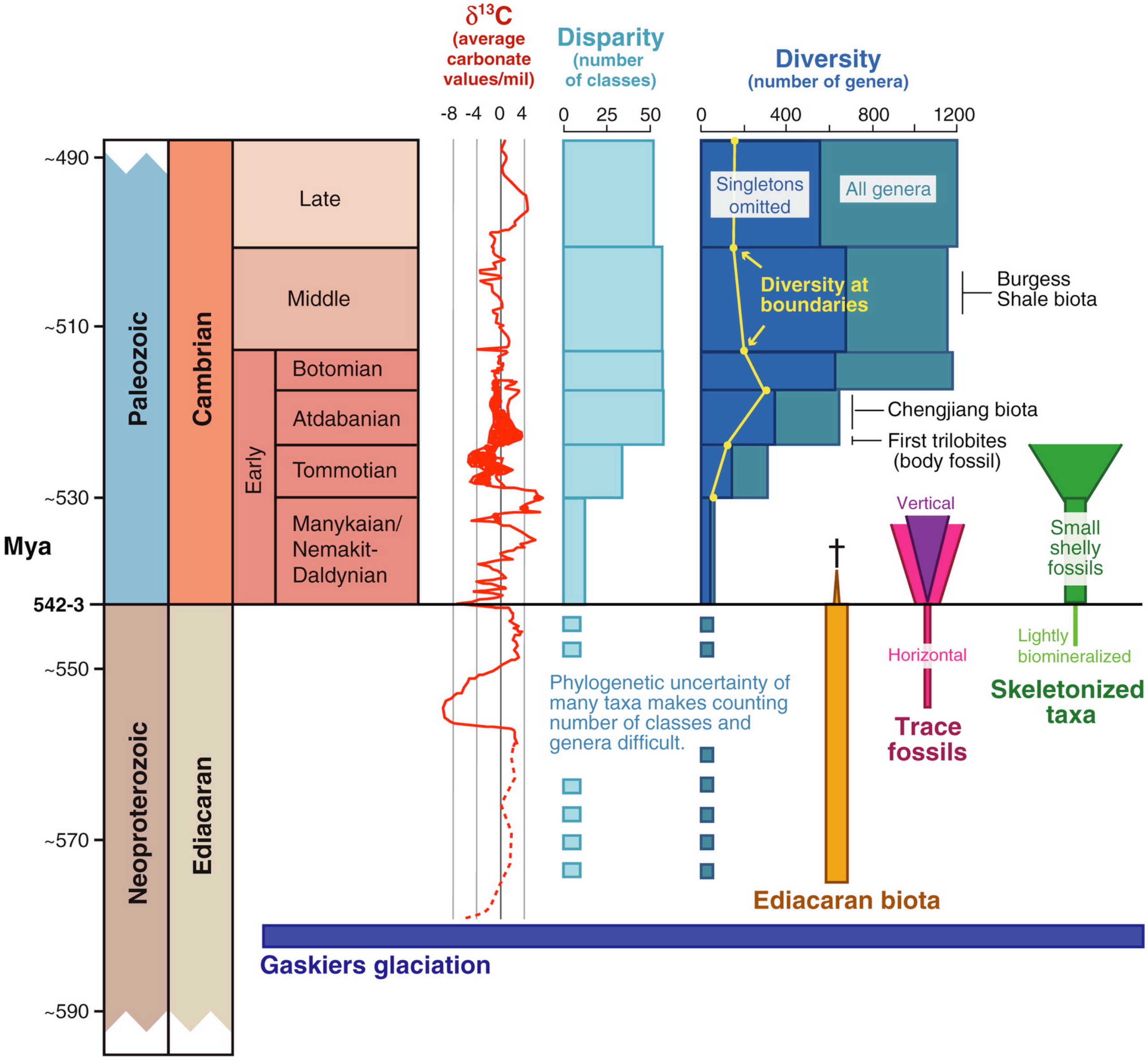
Mass extinction versus background extinction

Periods of time in earth history when major events triggers huge die-off.

Is extinction non-random? Are there intrinsic traits affecting extinction-proneness?

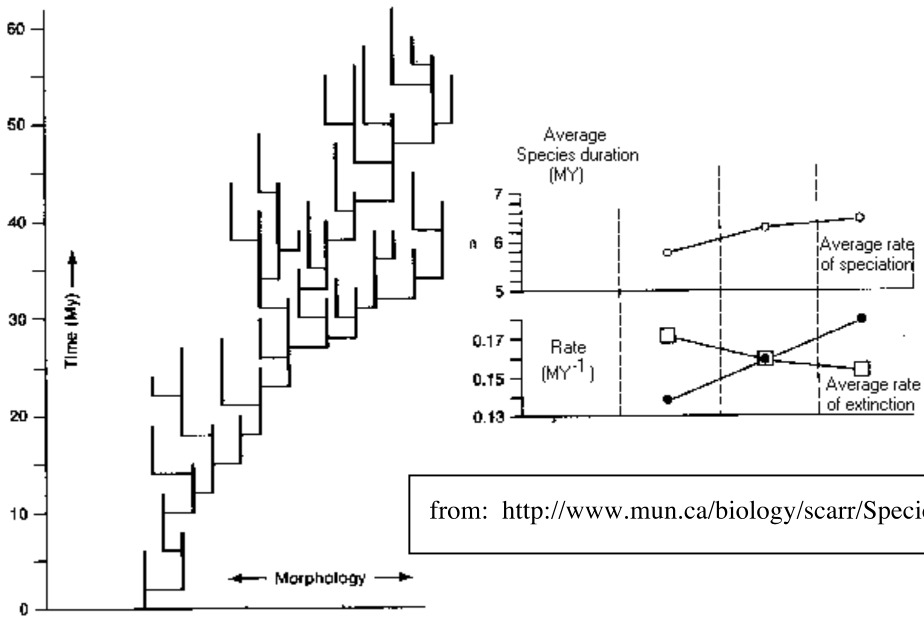
Are the same traits adaptive for surviving mass extinction as normal, background extinction? Jablonski (1987) presented evidence of geographic range as a trait with trade-offs at these two level of extinction.

Cambrian Example (Marshall 2006) – Marshall provided a framework for integrating environmental, ecological, and developmental into a single model for the Cambrian explosion – perhaps the first and biggest divergence event in the history of life (as we know it).



Marshall CR. 2006.
Annu. Rev. Earth Planet. Sci. 34:355–84

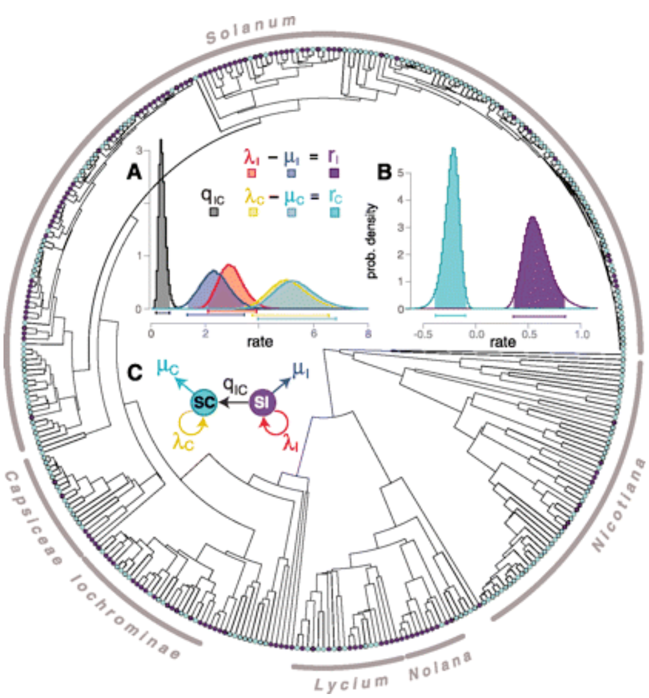
Could intrinsic traits affecting propensity for lineage splitting, or for resisting extinction, resulting in selection? Let's return to the levels of selection question. What conditions would have to be met for "clade selection" to occur? [This is sometimes known as "species selection," but we know species are at best just one particular level of clade!]



from: http://www.mun.ca/biology/scarr/Species_Selection.htm

Species Selection

Suppose that larger-bodied species lineages tend to speciate more rapidly, and that the average rate of extinction (the inverse of the species duration) is also less for larger species. Over time, this will result in a **species trend**, in which the clade becomes more speciose and each species on average larger. Careful examination of the clade shows that (*a*) speciation events that produce smaller-bodied species are equal in number to those that produce larger, and (*b*) that they contribute the same total amount of morphological change, so that the direction of speciation plays no role in the formation of the trend.



From: *Science* 22 October 2010:
Vol. 330 no. 6003 pp. 493-495. **"Species Selection Maintains Self-Incompatibility"**
Emma E. Goldberg, Joshua R. Kohn, Russell Lande, Kelly A. Robertson, Stephen A. Smith and Boris Igić.

Fig. 1. Maximum likelihood tree of phylogenetic relationships among 356 species of Solanaceae. Higher ranks are indicated around the perimeter of the tree. Purple and turquoise tip colors denote SI and SC extant species, respectively. The root age is 36 million years. Inset panels display posterior probability distributions and 95% credibility intervals of reconstructed rates of character evolution (the time unit is millions of years). (A) BiSSE estimates of transition, speciation, and extinction parameters ($q_{IC} << \mu_I < \lambda_I << \lambda_C < \mu_C$). (B) Net diversification rate—the difference between speciation and extinction rates—associated with each state. (C) Schematic summary of estimated rate parameters. For methods, species names, character states, and further results, see (19).