Integrative Biology 200 "PRINCIPLES OF PHYLOGENETICS" Spring 2020
University of California, Berkeley D. Ackerly

April 8, 2020**. Tempo and mode in macroevolution: trait-dependent diversification and extinction**

Reading:

Maddison et al. 2007. Estimating a binary character's effect on speciation and extinction. 56: 701-710

Goldberg, E.E., et al. 2010. Species selection maintains self-incompatibility. Science 330: 493-495

Considering fossils (and therefore morphological characters) is critical 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:

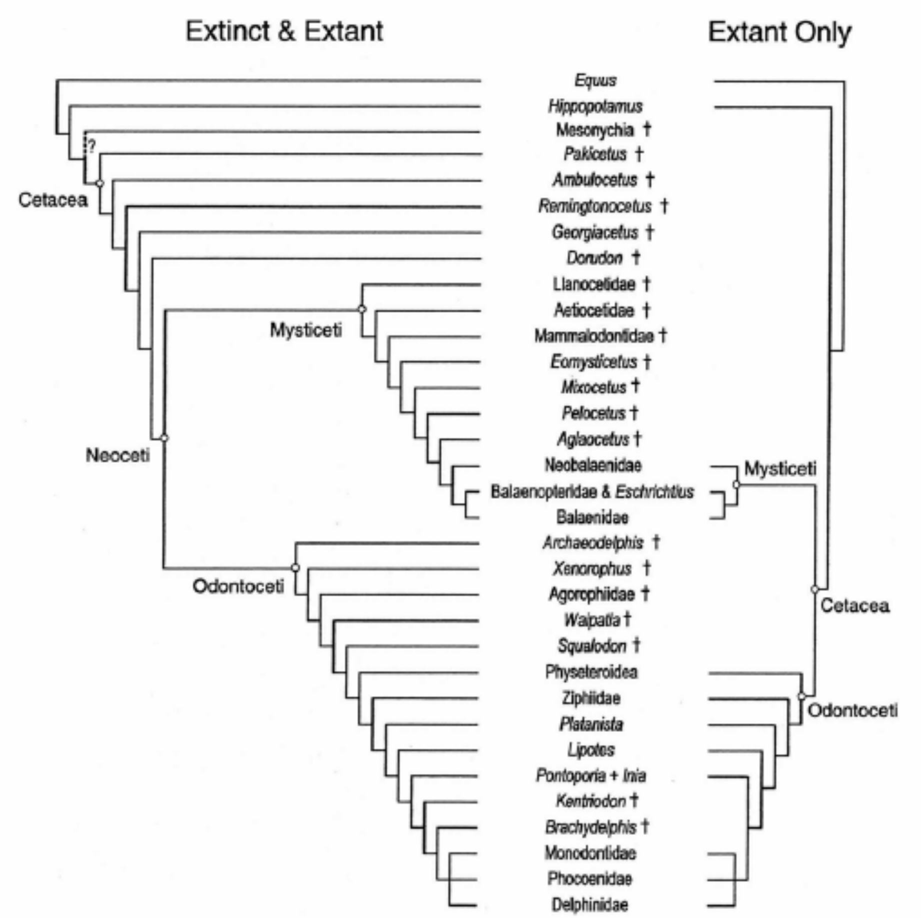


FIGURE 7.1. Composite phylogeny of the Cetacea based on morphological (Kimura and Ozawa 2002; Geisler and Sanders 2003; Uhen 2004) and molecular (Arnason et al. 2004) analyses. Outgroup relationships modified from Gatesy and O'Leary (2001).

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

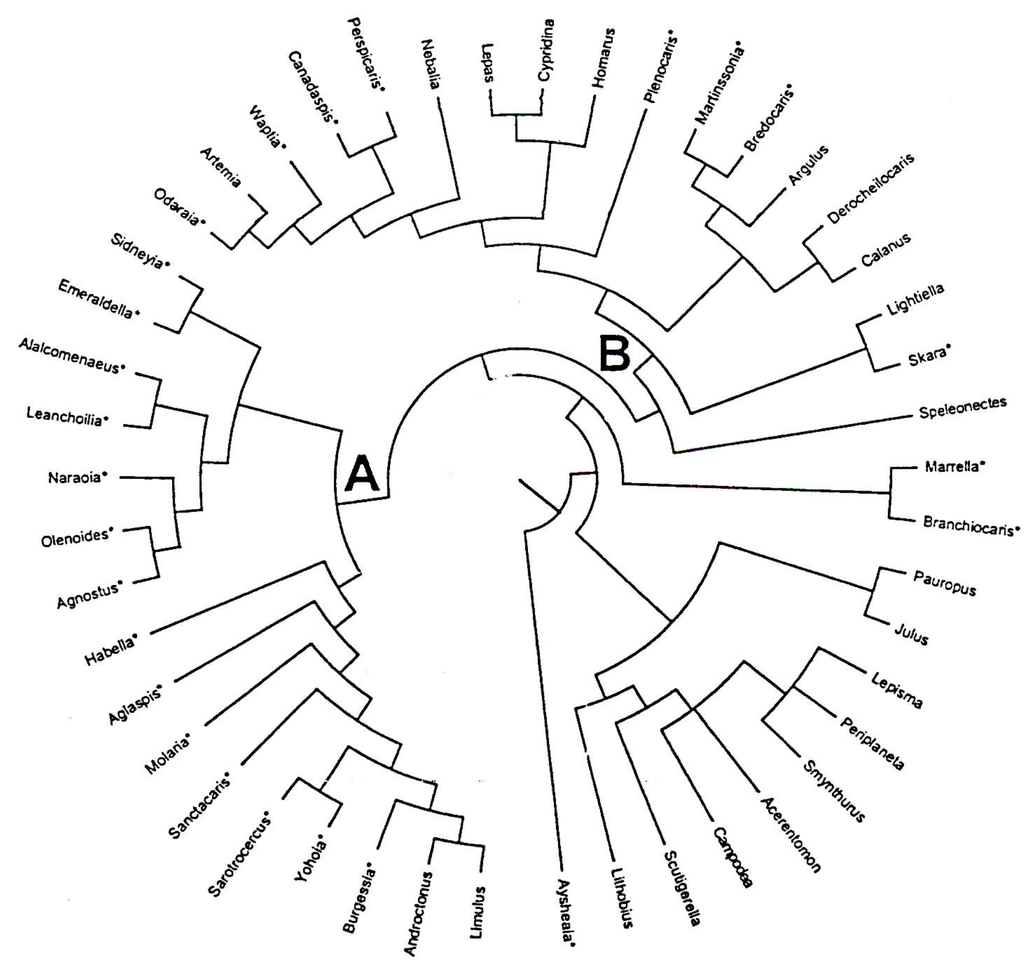
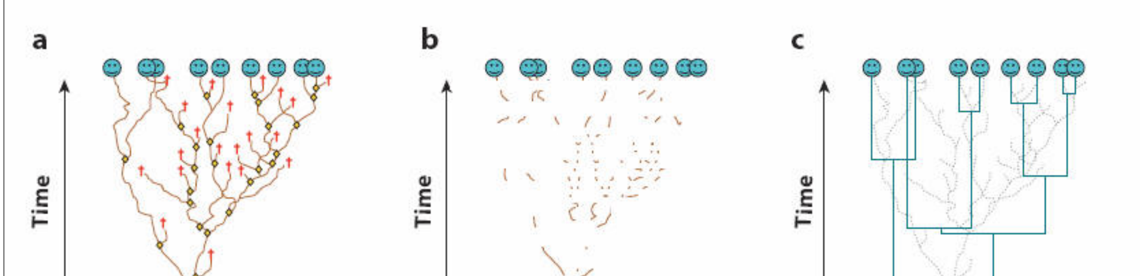
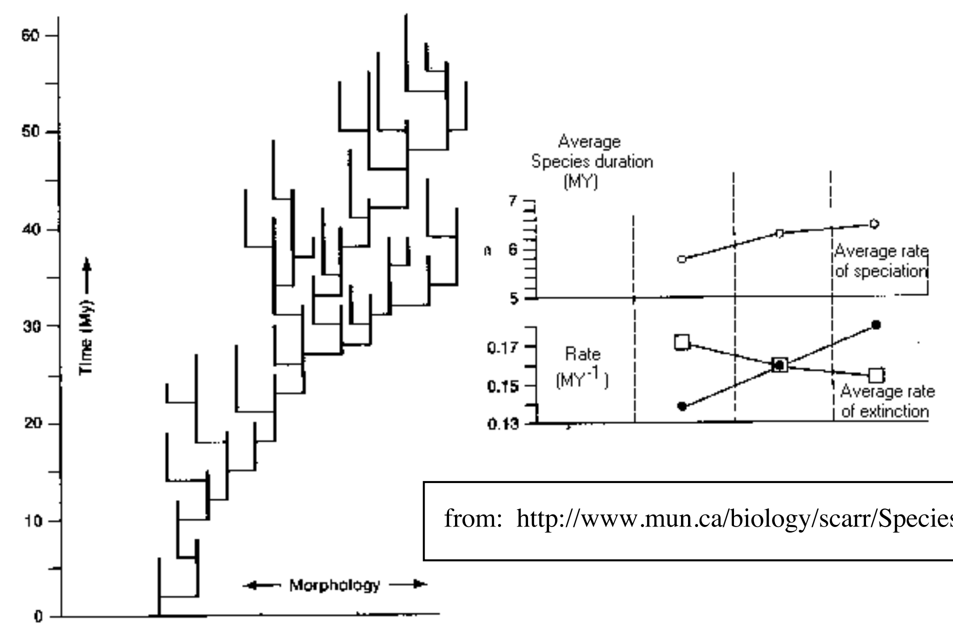


Figure 2 Cladogram of Cambrian and living arthropods. Cambrian arthropods are marked with an asterisk. In subclade A 87.5% of the taxa are extinct Cambrian taxa; in subclade B only 44.4% of the taxa are extinct. Differential extinction rates in different subclades exacerbate patterns of disparity. After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



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!]



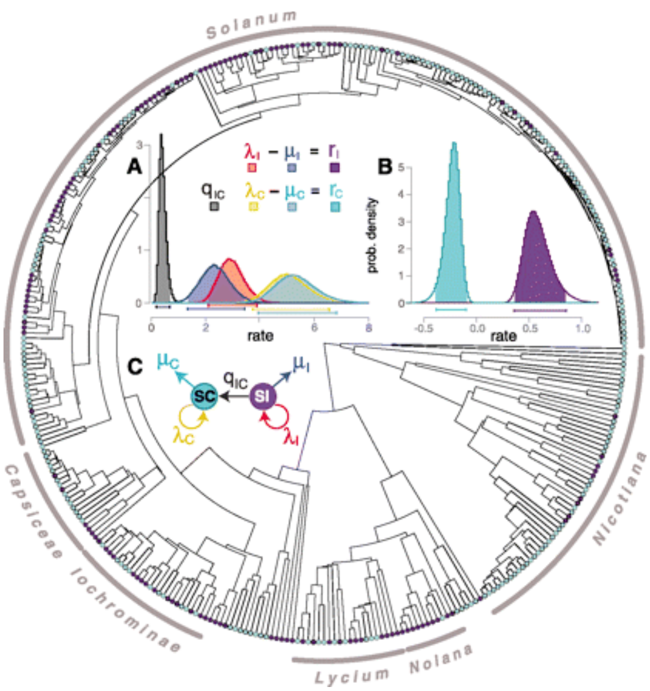
from: http://www.mun.ca/biology/scarr/Species_Selection.htm

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.

Maddison (2006) noted that trait-dependent speciation may look like asymmetric character change, and vice versa. Maddison et al. 2007 introduced BiSSE, a full ML model to simultaneously estimate six parameters: binary character evolution (forward and reverse rates), and state-dependent speciation and extinction rates. Simulations show the method is quite effective to estimate speciation rates, though much less so for extinction and character change rates.

An early application of the model addressed the paradox of the maintenance of self-incompatibiligy. Self-compatible (or asexual) organisms have a two fold advantage in reproduction, as only one parent is needed. Yet sexually reproducing lineages are prevalent. Plants with self-compatibile and self-incompatible breeding systems, which vary within clades, offer an opportunity to test underlying dynamics. Goldberg et al. (2010) applied BiSEE to Solanaceae and detected higher speciation AND extinction rates in SC lineages, with the result that net diversification was higher in SI lineages. Assuming that character evolution is one-way towards SC, they show that the higher diversification of SI is sufficient to outweigh the switch to SC with subsequent high extinction, thus maintaining SI over evolutionary time.



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 ($q_{IC} \ll \mu_I < \lambda_I \ll \lambda_C < \mu_C$). (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).

BiSSE models can also be used to model effects of climate and biogeography simply by coding these as characters in the tree. Character evolution is used to model niche shifts or biogeographic range shifts. Lagomarsino et al. (2016) offer an elegant example of diversification in Andean Campanulaceae, showing that net diversification is higher in: Andean compared to non-Andean lineages; high elevation compared to low elevation lineages; lineages with berries vs. capsules; and vertebrate pollinated vs. invertebrate pollinated lineages.