March 28, 2016**. Evolution and development - heterochrony**

The last frontier in our understanding of biological forms is an understanding of their developmental origins. Much of the ultimate control of form resides in the genome, yet much also resides in the environment (at levels from the internal cellular environment to the external habitat). The highly interactive and complex nature of developmental processes make it impractical to deduce phenotype from genotype based on first principles. The phenotype is an emergent property and its origin can be studied most efficiently by backtracking from the phenotype itself to its structural, physiological, developmental and genetic causes. Development and morphology will remain a rich source of information for systematics and for evolutionary biology.

Today we'll talk about patterns as seen on phylogenies using ancestral state reconstruction, and Friday we'll talk about developmental processes relating to evolution.

1. Ontogeny and phylogeny.

The relation between ontogeny and phylogeny has been of longstanding interest to biologists, and continues to be a timely topic. It is important of course to take a comparative approach to development, within a phylogenetic framework. Our aims are to reconstruct both the developmental pathway taken by a given species for a given structure, and the manner in which the developmental system evolved. Some terminology:

Heterotopy -- evolutionary change in the position of development

Heterochrony -- evolutionary change in the timing of development (more later in the class)

Peramorphosis (Hypermorphosis vs. Acceleration vs. Predisplacement)

Paedomorphosis (Progenesis vs. Neoteny vs. Postdisplacement)

See next page for illustrations.

From: William L. Fink, The Conceptual Relationship Between Ontogeny and Phylogeny. *Paleobiology*, Vol. 8, No. 3. (Summer, 1982), pp. 254-264.

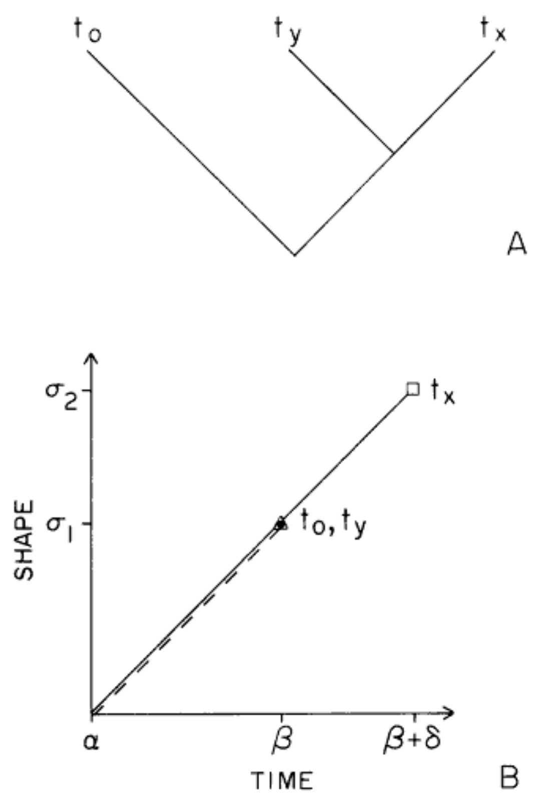


FIGURE 3. Example of the model of Alberch et al. (1979) for describing heterochronic development, modified for the examination of ontogenetic trajectories of sister taxa rather than ancestors and descendants. A. The given phylogenetic hypothesis. B. Projections of ontogenetic trajectories of shape (σ) in three taxa. In this case, development of σ in t_x proceeds along a trajectory similar to those of t_o and t_y but the offset time is positively displaced relative to that of the latter two taxa. The result is formation of σ_2 through hypermorphosis. Parameters (e.g., α, β) defined in text.

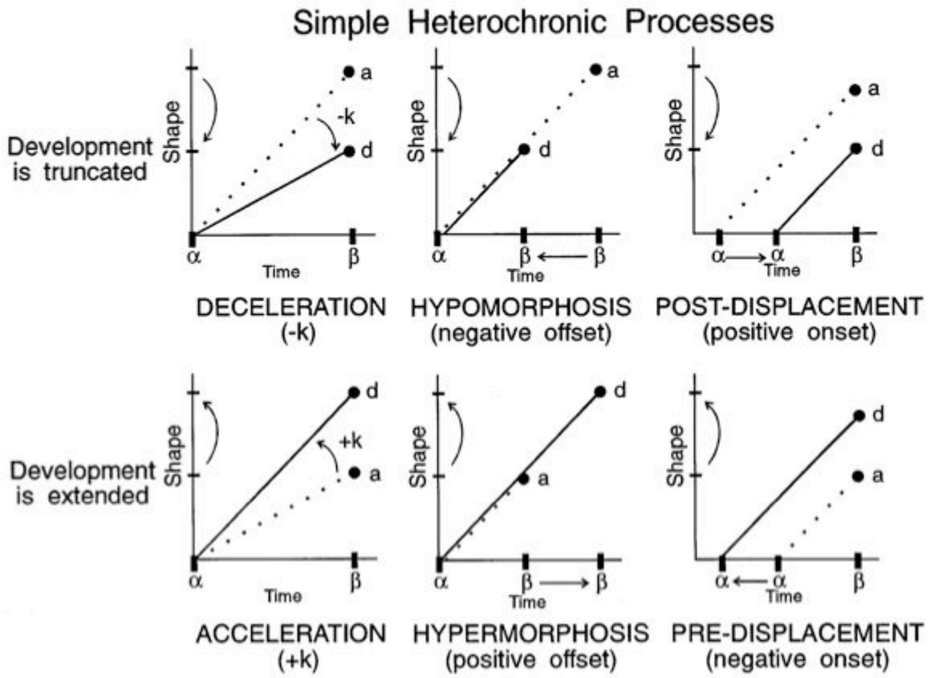


Figure 1. Six simple heterochronic processes identified by comparing ontogenetic trajectories of ancestral (a) versus descendant (d) ontogenies. Ontogenetic trajectories are defined by rate of shape development (k) from age of onset of growth (α) to the age when the offset shape is attained (β). Arrows on the shape axis indicate patterns of truncated (top) or extended (bottom) development. The terms deceleration and hypomorphosis are formally proposed to replace the inappropriate terms neoteny and progenesis, respectively, used by Alberch *et al.* (1979). Although originally defined for comparing species (Alberch *et al.*, 1979) this scheme can be used to categorize both inter- and intraspecific heterochronic phenomena.

http://www.usm.maine.edu/bio/courses/bio205/Lab_3.html

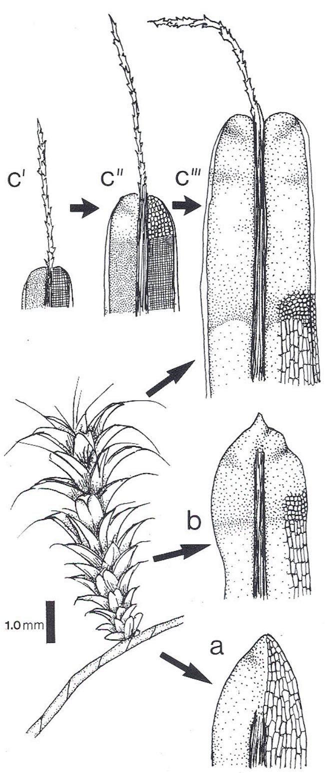
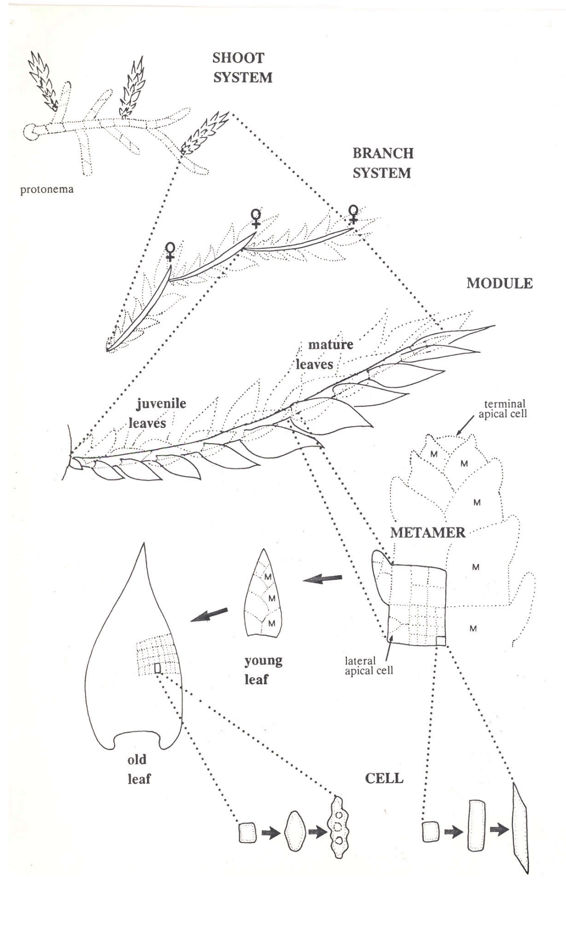
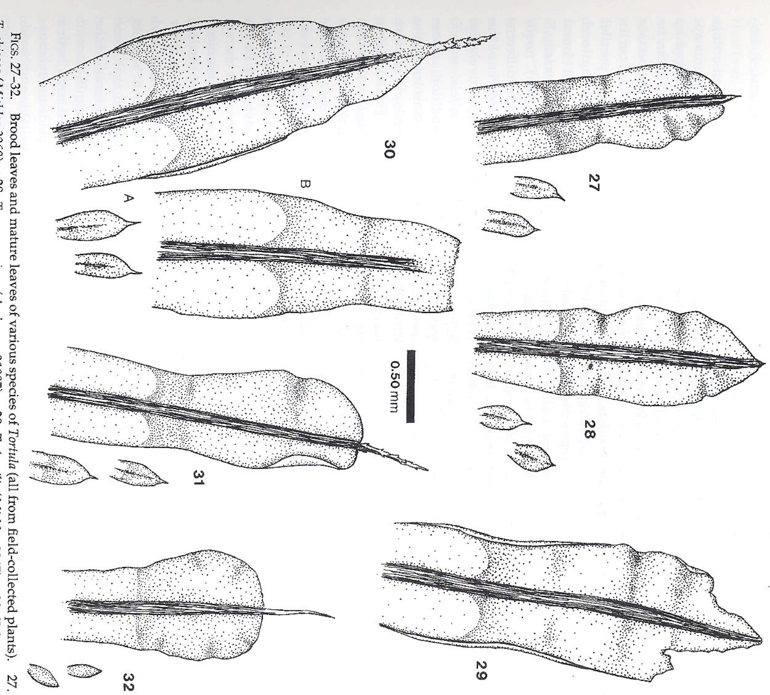


FIG. 19. Schematic representation of gametophore ontogeny in *Tortula obtusissima*. a, b, and c‴ are fully developed leaves of different developmental stages; c′–c‴ shows the development of an individual mature leaf.

<u>2. An example from mosses.</u>
B.D. Mishler. *1986*. Ontogeny and phylogeny in *Tortula* (Musci: Pottiaceae). *Systematic Botany* 11: 189-208.

The morphology of the leaves of mosses changes as the plant ages in such a way that "juvenile" leaves near the base of a stem are radically different in structure from leaves near the tip of a mature stem, and these juvenile leaves resemble the mature leaves of more primitive species. This prolonged <u>heteroblastic</u> series of leaf-types that is produced as a moss stem matures apparently lends itself to heterochronic evolution, and has potential relevance to reproductive ecology (since asexual reproduction through fragmentation and regeneration is the primary means of dispersal in these plants).





FIGS. 27–32. Brood leaves and mature leaves of various species of *Tortula* (all from field-collected plants). 27. *T. chisosa* (*Mishler 3269*). 28. *T. ammonsiana* (*Anderson 21897*). 29. *T. fragilis* (*Mishler 3047*). 30. *T. bogotensis.* A, from an atypical population with brood leaves (*Bell 110*); B, from a typical population, with fragile leaf tips (*Mishler 3373*). 31. *T. laevipila* var. *laevipiliformis* (*Rilstone, s.n.*). 32. *T. pagorum* (*Mishler 3065*).

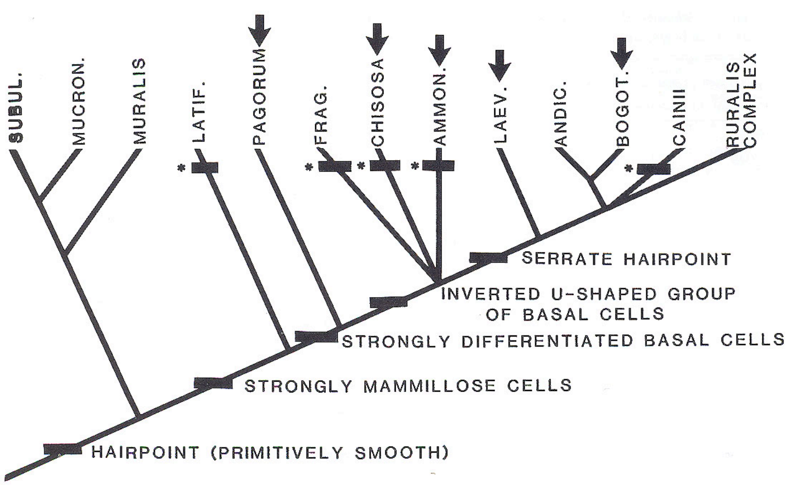
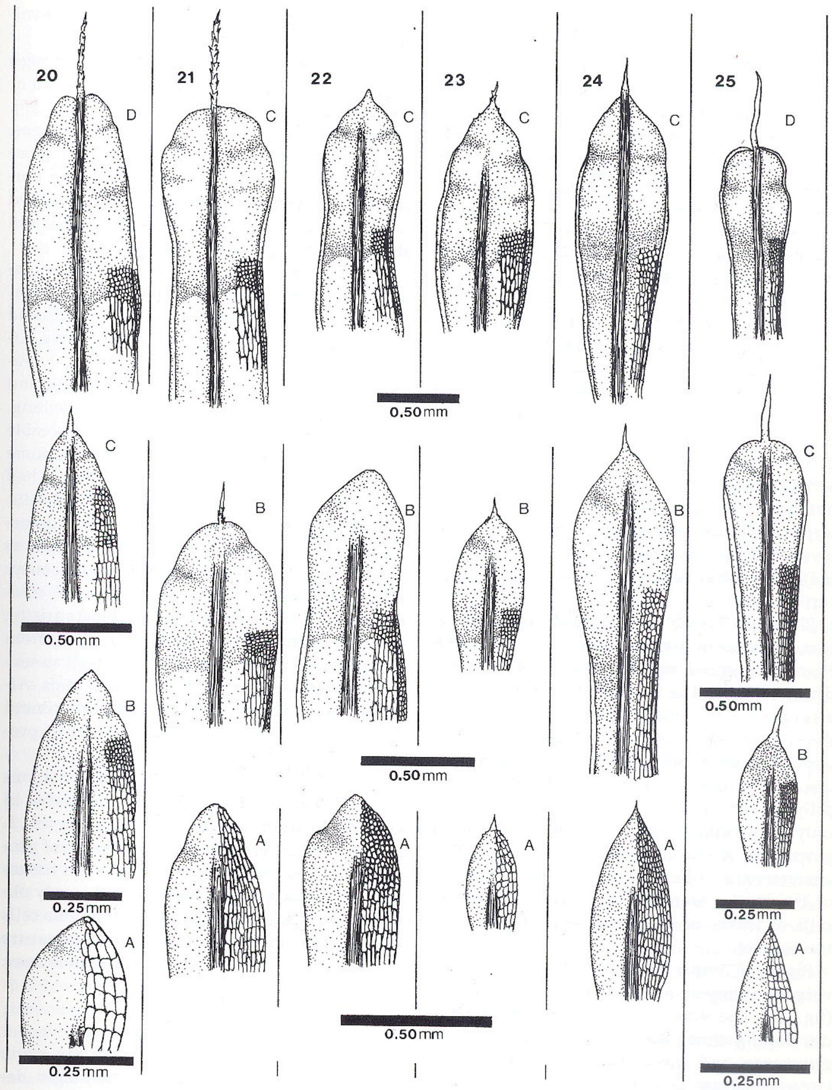
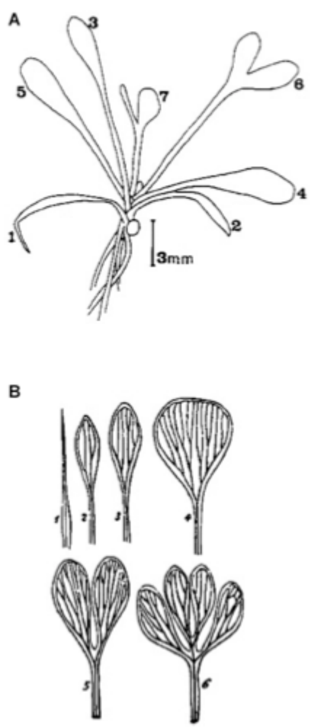


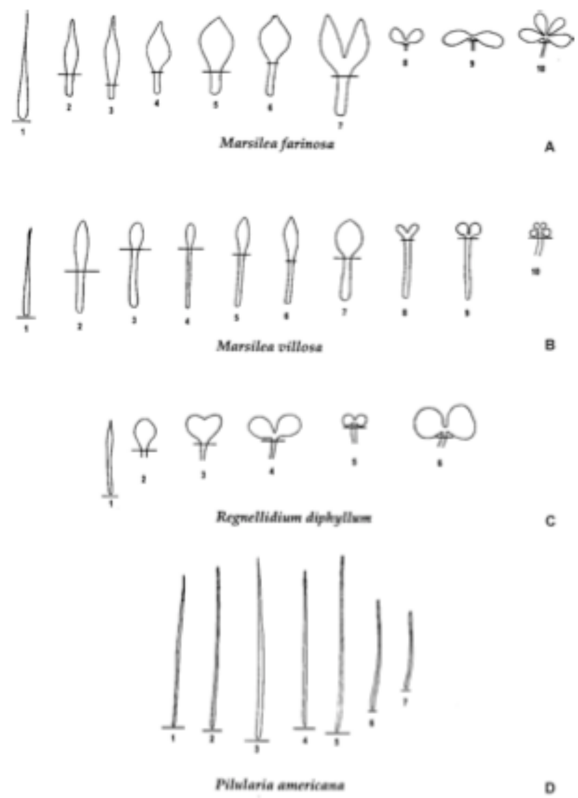
FIG. 26. A cladogram summarizing postulated phylogenetic relationships of species of *Tortula* discussed in this paper, based on information in Mishler (1984). Species belonging to the *T. ruralis* complex are indicated in the Appendix. Note that only selected apomorphic characters are shown and that a number of species within this clade have been omitted (see Mishler 1984). Asterisks indicate the secondary loss of hairpoints; arrows indicate species possessing specialized brood leaves.



D). 20. *Tortula ruralis*, from a protonematal bud (*Mishler 2850*, cultured plant). 21. *Tortula ruralis*, from a branch bud (*Mishler 3614*, field-collected plant). 22. *Tortula cainii*, from a branch bud (*Mishler 2335*, cultured plant). 23. *Tortula andicola*, A–B, from a protonematal bud (*Mishler 3560*, cultured plant); C, a mature leaf from a branch bud (*Mishler 3560*, cultured plant). 24. *Tortula mucronifolia*, from a branch bud (*Mishler 1935*, cultured plant). 25. *T. muralis*, from a branch bud (*Mishler 2161*, cultured plant).

<u>3. An example from the water ferns, family Marsiliaceae.</u>
Pryer, K.M. and D.J. Hearn. 2009. Evolution of leaf form in Marsileaceous ferns: evidence for heterochrony. *Evolution* 63: 498-513.





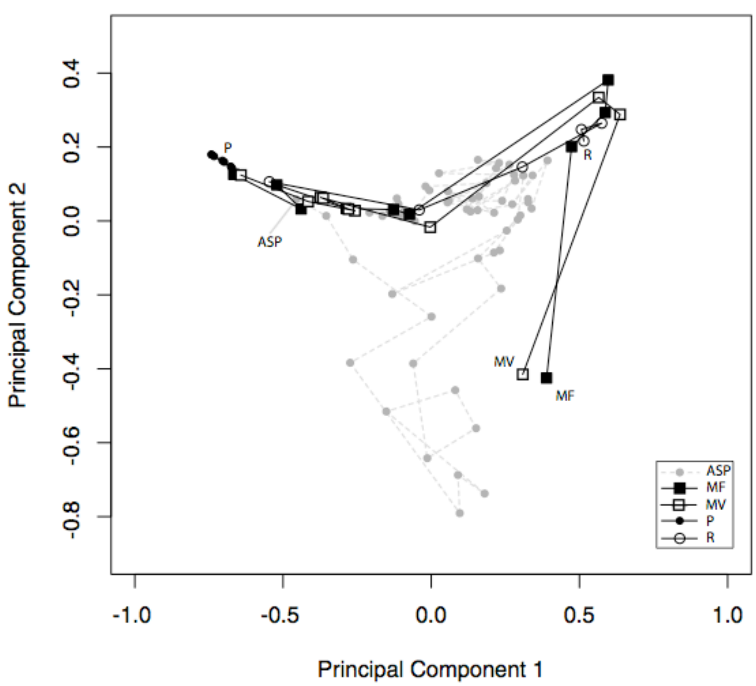


Figure 7. Principal components analysis of elliptic Fourier coefficients for harmonics 1 through 20 for ontogenetic leaf shape sequences of *Pilularia* (P), *Regnellidium* (R), *Marsilea farinosa* (MF), *M. villosa* (MV), and *Asplenium* (ASP). The points represent 7, 6, 10, 10, and 59 leaves for each taxon, respectively, and they are connected with a line in their ontogenetic order. The first leaf of *Pilularia* is found in the center of the cluster of its points and the label "P" is next to the last leaf of the sequence. First leaves for *Regnellidium* and both species of *Marsilea* are in the upper left corner and their labels "R," "MF," and "MV" are next to the last leaf of each sequence. First leaves for *Asplenium* are clustered close to the intersection of PC 1 and PC 2 axes and the label "ASP" is next to the last leaf of that sequence. The last leaf of each sequence indicates a final or adult leaf shape; thereafter little or no changes in leaf shape occur.