Feb. 7, 2012**. Morphological data IV -- ontogeny & structure of plants**

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.

1. Uses of ontogeny in systematics:

1) A source of new characters in juvenile phases
2) a source of clarifying homologies and defining character states in mature phases
3) a source for determining transformational homology among character states within a character (ordering)
4) a source for hypothesizing evolutionary directionality among character states within a character (polarization)

2. 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 (see Humphries 1988 for details):

Heterotopy -- evolutionary change in the position of development

Heterochrony -- evolutionary change in the timing of development (see next page)

Peramorphosis (Hypermorphosis vs. Acceleration vs. Predisplacement)

Paedomorphosis (Progenesis vs. Neoteny vs. Postdisplacement)

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

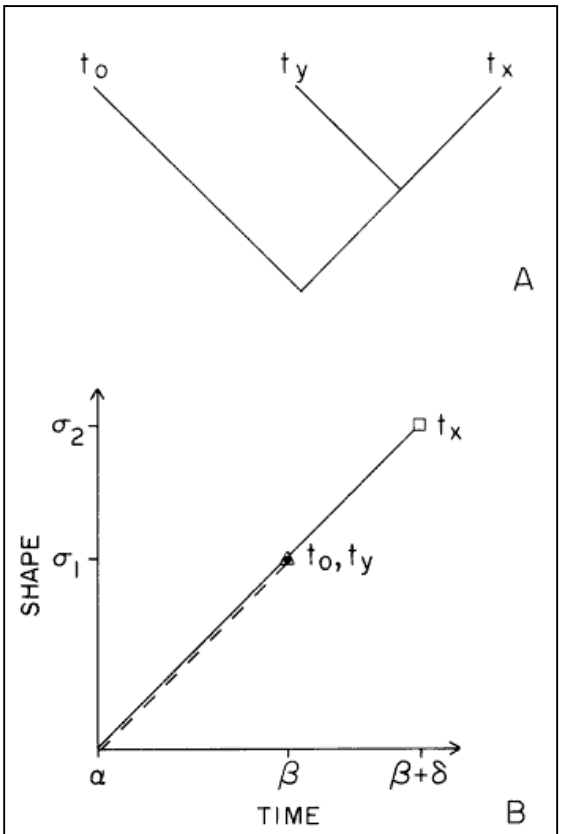


FIGURE 3. Example of the model of Alberch et al. (1979) for describing heterochronic development, modified for the examination of ontogenetic trajectories of sister taxa rather than ancestors and descendants. A. The given phylogenetic hypothesis. B. Projections of ontogenetic trajectories of shape (σ) 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.

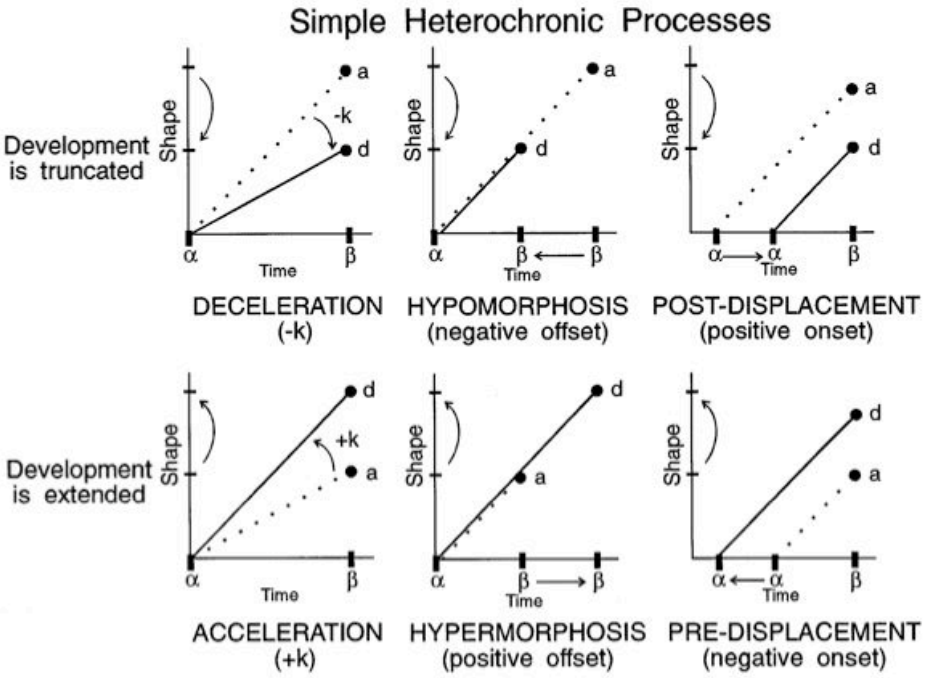


Figure 1. Six simple heterochronic processes identified by comparing ontogenetic trajectories of ancestral (a) versus descendant (d) ontogenies. Ontogenetic trajectories are defined by rate of shape development (k) from age of onset of growth (α) to the age when the offset shape is attained (β). Arrows 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

A number of workers have evaluated and tested the proposition that character polarities can be reliably inferred through direct observations of developmental (ontogenetic) character transformation (Lundberg 1973; Mishler 1986, 1988; Mabee1989). The consensus of these authors is that while terminal addition (thus recapitulation) is often seen, other patterns are common as well, thus the "ontogeny criterion" for polarity determination is suspect. So even though there are some limitations for use in systematics, there are few sources of data more rewarding to an evolutionary biologist than the study of ontogeny.

3. Differences between plant development and animal development:

Modular growth, at several hierarchical levels
Growth from an apical meristem (or single apical cell)
Cells don't move (rigid cell wall)
Plants do not have a segregated germ line

4. An example from mosses in the genus *Tortula*

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 heteroblastic 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).

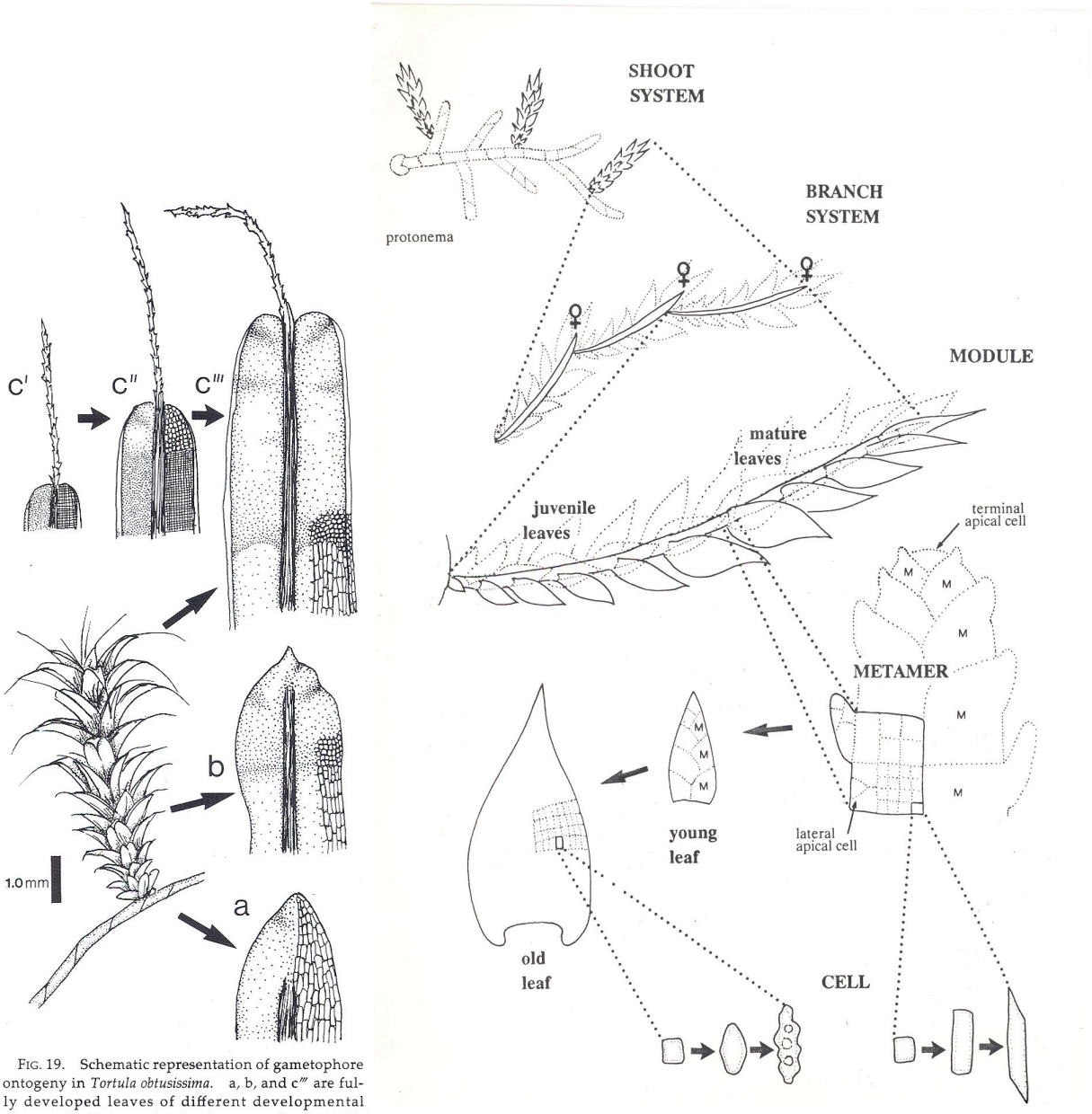


FIG. 19. Schematic representation of gametophore ontogeny in *Tortula obtusissima*. a, b, and c‴ are fully developed leaves of different developmental stages; c′–c‴ shows the development of an individual mature leaf.

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).

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.

5. Concluding thoughts on the roles of morphology

Why morphology in this day and age? Does it have any role? Some workers (e.g., Scotland, Olmstead, and Bennett, 2003) have argued that the active use of morphology in phylogenetic reconstruction is dead, and that phylogenies should be based solely on molecular data, relegating morphological characters to be passively mapped onto phylogenies later.

Such an argument unwisely downplays the value of morphological characters (as being too subjectively defined and evolutionarily plastic) while conveniently forgetting that molecular characters are subject to the same uncertainties about homology and character analysis, and may be quite homoplastic as well. It is much better to take a hard look at the advantages and disadvantages of each kind of data, according to the criteria we discussed last time. First, let's start with the roles that morphological characters can play, and do the same for molecular data later (next lecture).

Brent's Top Ten reasons to include morphological characters in phylogenetics:

10. Their greater complexity may allow better homology assessments. Unlike DNA sequences, which are often one-dimensional strings (unless you have secondary structure), morphology is complex and three-dimensional, plus has ontogeny (more on that topic next time).

9. They have many potential character states. As we will see later in the semester, an important parameter determining whether your data might be subject to "long-branch attraction" problems is the number of potential character states. False reconstructions are only a problem when parallel changes to the same character state happen, a phenomenon that is most frequent with binary data and rare with many available states.

8. **Data can be gathered from *many* specimens, cheaply and quickly.** A systematist can base their conclusions on samples from thousands of semaphoronts.

7. We need to be able to identify lineages easily in the field. Morphological apomorphies are easier to apply in field keys and in photo IDs guides.

6. Discovering morphological apomorphies. We need to have a real analysis to show what the apomorphies at a particular level are. It is not rigorous to inspect a purely molecular tree and hang morphological characters onto branches intuitively.

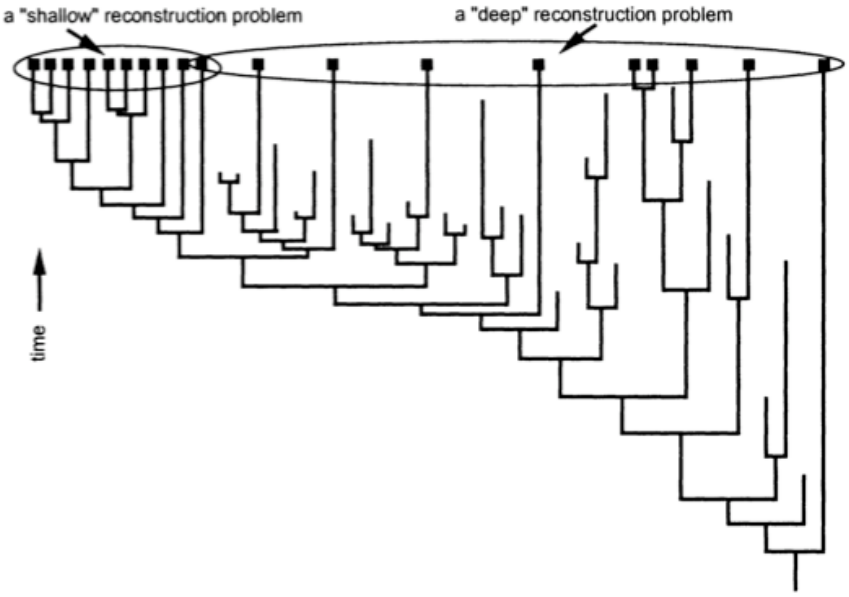
5. Morphology gives you another independent data set, distinct from your organellar and nuclear genes. Comparing the topology of morphological datasets to those derived from specific genes can help you discover reticulation, lineage sorting, etc.

4. Morphological characters might actually help you get the best-supported answer! Even in cases where the topology of the total evidence tree is the same as with the molecules alone,

support values such as bootstrap values often go up. And sometimes, the total-evidence topology has novel, highly-supported branches, synergistically supported by the combined data.

3. Episodic patterns of change. Despite common misconceptions to the contrary, clock-like markers are actually undesirable for reconstructing deep, short branches. Such markers continue to click along, changing at a regular rate until all the signal marking the deep branch is gone. The best marker for such deep branches is like the clock on the *Titanic* -- ticks once and stops forever. Slow change with long periods of stasis works best for these cases, i.e., the pattern shown by some morphological and anatomical features.

2. Better sampling of the tree of life. As we'll study later, good sampling is extremely important for reconstructing the correct tree. We need to break down those long branches. 99%+ of the lineages that have existed on the tree of life are extinct, and the only feasible way to get information about them is by adding fossils, which in turn requires morphology.



1. Studies of molecular clocks and dating of lineages. In order to include fossils. we must have morphological characters in the matrix, and therefore optimized to the cladogram. The fossils do not come with a taxon ID in the fossil record; they just come with some morphological characters. The fossil must therefore be attached to the cladogram based on its characters, then (and only then) can we infer that its sister group is at least as old as the age of the fossil.

☞ **The Bottom line:** you have to have a rigorous morphological character matrix to achieve most of the goals of phylogenetics, including incorporating information from fossils in phylogenetics, getting the tree right, and interpreting character evolution rigorously.