

Feb. 14, 2008. **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.

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)

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 over)

 Paramorphosis (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.

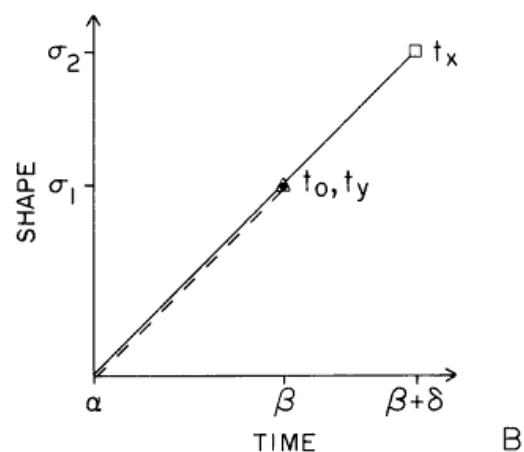
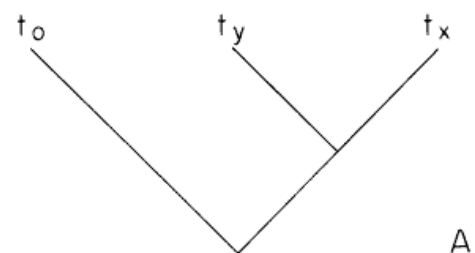


FIGURE 3. Example of the model of Alberch et al. (1979) for describing heterochronic development, modified for the examination of ontogenetic trajectories of sister taxa rather than ancestors and descendants. A. The given phylogenetic hypothesis. B. Projections of ontogenetic trajectories of shape (σ)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

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; Mabee 1989). 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.

Differences of plant development, as compared to animals:

- 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

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).

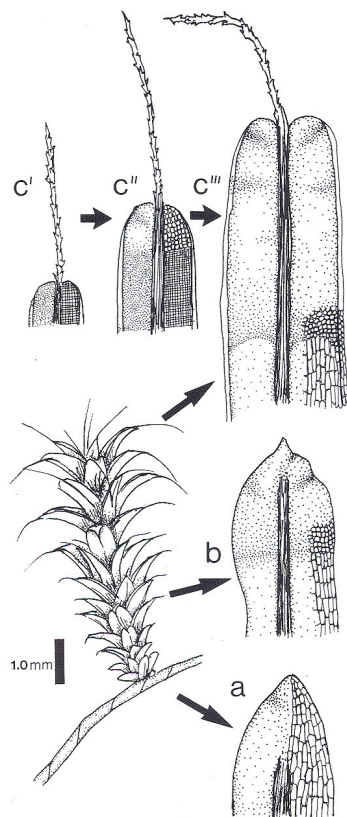
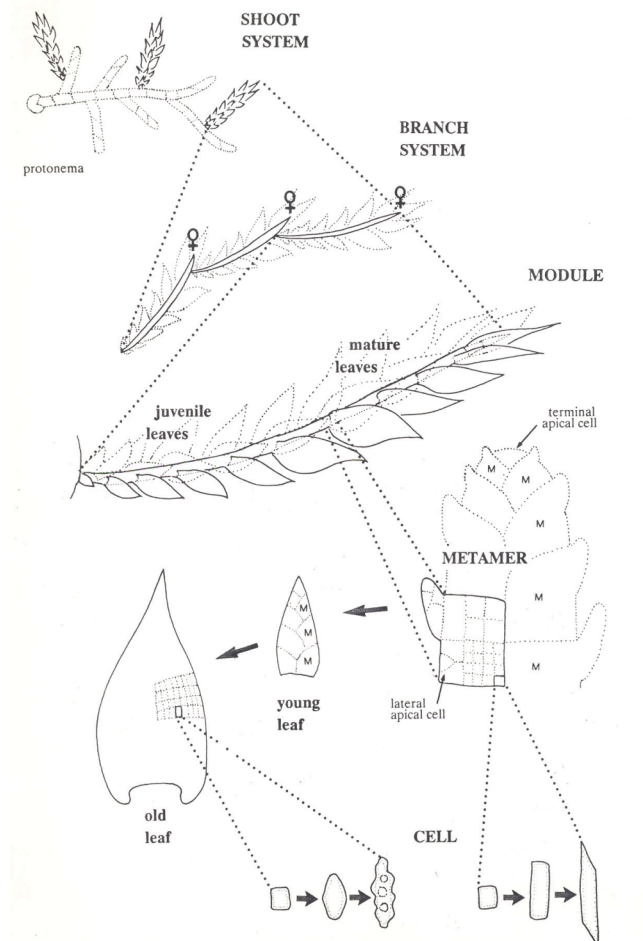
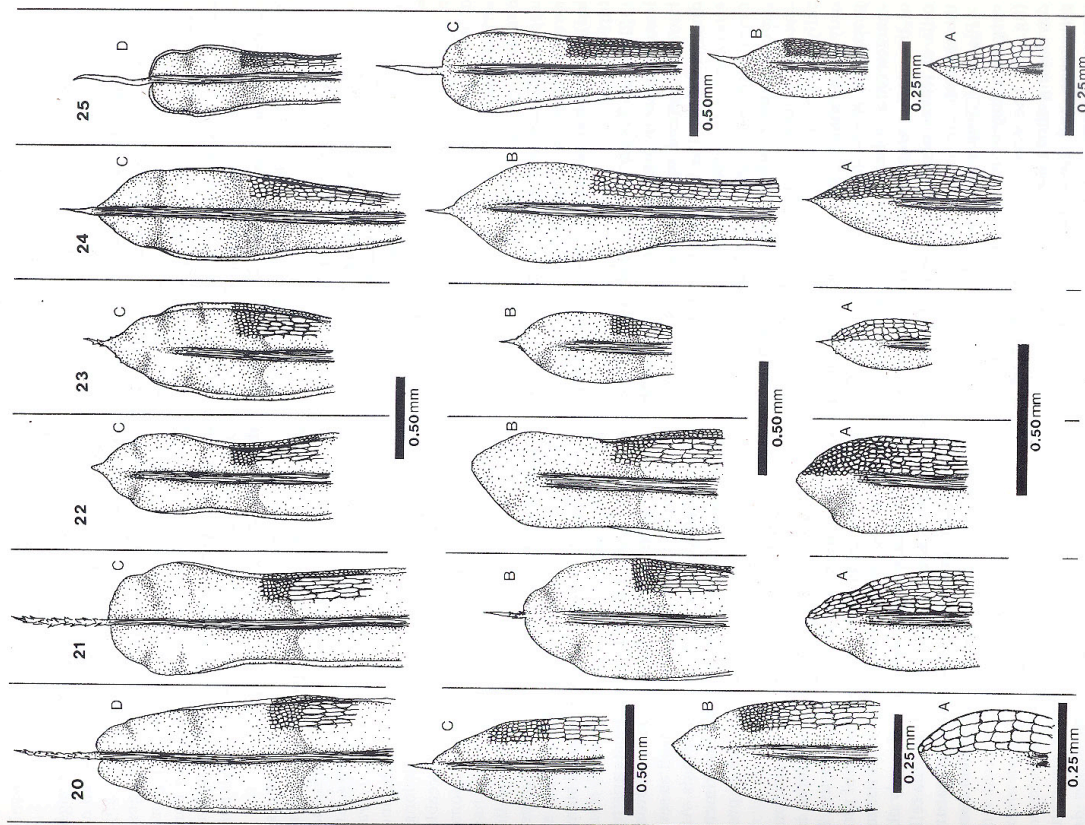
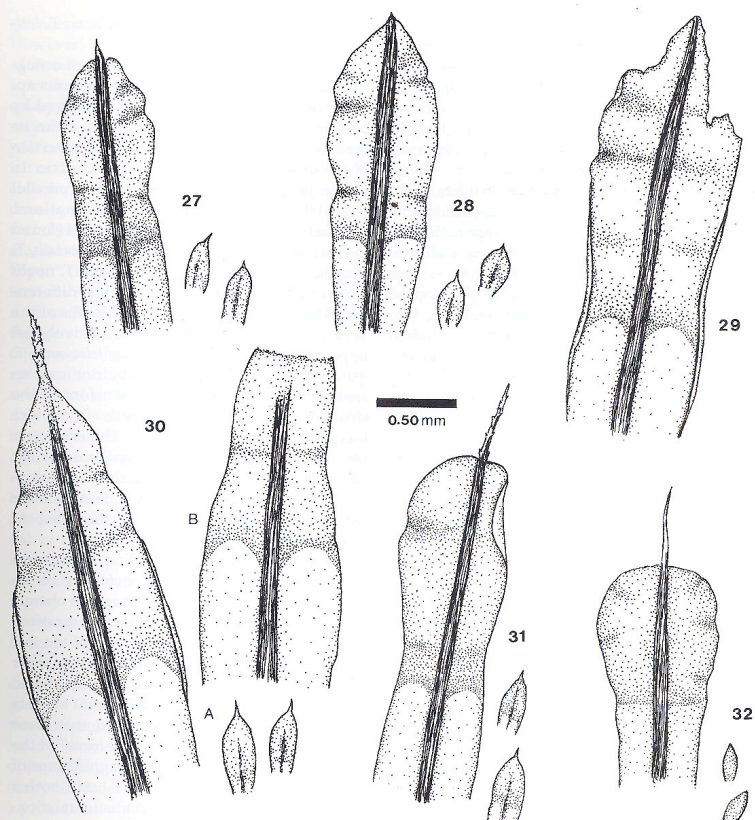


FIG. 19. Schematic representation of gametophore ontogeny in *Tortula obtusissima*. a, b, and c''' are fully developed leaves of different developmental stages; c'-c''' shows the development of an individual mature leaf.





D). 20. *Tortula muralis*, from a protonematal bud (Mishler 2850, cultured plant). 21. *Tortula muralis*, from a branch bud (Mishler 3614, field-collected plant). 22. *Tortula canini*, 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. chisos* (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).

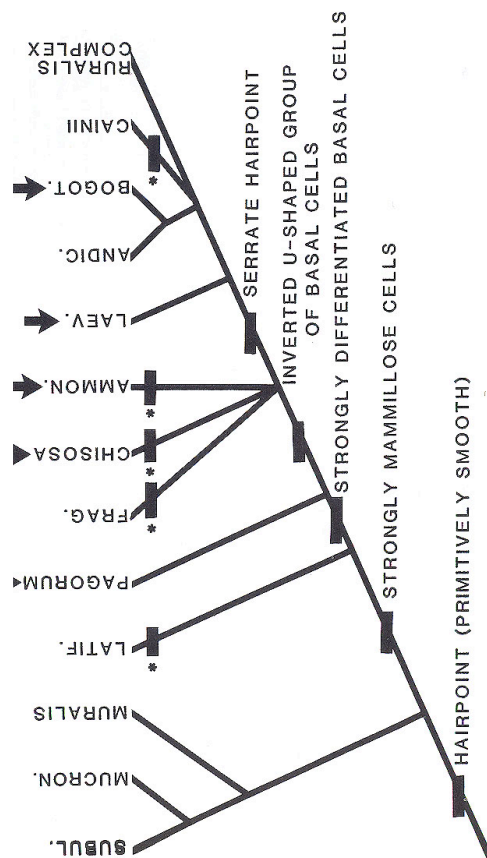


FIG. 26. A cladogram summarizing postulated phylogenetic relationships of species of *Tortula* discussed in this paper, based on information in Mishler (1984). Species belonging to the *T. muralis* complex are indicated in the Appendix. Note that only selected apomorphic characters are shown and that 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.