

THE EVOLUTION OF GASTROPOD SHELL FORM: A DEVELOPMENTAL MODEL ILLUSTRATING THE ROLES OF HETEROCHRONIC AND NON-HETEROCHRONIC CHANGES

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The shape of an isometric gastropod shell can be described completely by specifying the pattern of shell secretion around the aperture (relative to aperture size) and the growth rate of the aperture itself. These descriptors provide a "natural" morphometric in that they correspond to the specific biological processes involved in constructing the shell.

Describing shell form in this way allows us to specify what developmental changes must occur during the transition of one shell form to another. In particular, we can distinguish between transitions that can occur through purely heterochronic processes (changes in growth rate) and those that require a change in the specific pattern in which cells of the mantle lay down shell. We can also investigate just what changes occur during the ontogeny of non-isometric shells.

Any change in either the pattern of shell secretion or the growth rate of the animal leads to changes in a number of classical morphometric measures, such as apex angle and whorl expansion rate. Those transformations resulting from changes in growth rate, however, are much more predictable than those resulting from changes in the pattern of shell production. A slight increase in the growth rate of the animal, for instance, produces a correspondingly slight increase in the apex angle and the rate of whorl expansion. By contrast, the consequences of a slight change in the pattern of shell production are highly sensitive to just how that change was achieved.

Data from 8 genera of marine snails show that the variance within each genus, relative to the variance among all genera, is smaller for measures of aperture shape (which can only be altered through a change in the pattern of secretion of shell material) than for characters that can change through heterochronic transformations (such as apex angle). Furthermore, the shell forms of a number of non isometric shells can be described by a constant pattern of shell production and a variable growth rate.

Heterochronic changes thus appear to be the preferred mechanism for changing phenotype in gastropod shells. Those characters that can only be altered by changing the pattern of shell production around the mantle, such as aperture shape, appear to be more conservative than those that can be changed through purely heterochronic transitions. This is consistent with the idea that mutations which alter many characters in a highly correlated manner have a higher probability of being favored by selection than those with relatively unpredictable consequences.