8 Developmental Constraints

8.1 Forms of Asymmetry

There are three forms of asymmetry. For simplicity we'll consider differences between the right (R) and left (L) sides of paired structures, but the same principles hold for other kinds of symmetrical structures.

Directional asymmetry Consistent bias of a character within a species toward greater development on one side of the body than on the other. Characterized by a distribution of $R-L$ differences with a mean significantly different from zero (e.g. coiling and anatomical asymmetry in snails).

Antisymmetry Non-directional deviation from bilateral symmetry characterized by a bimodal (or broad peaked) distribution of $R-L$ differences about a mean of zero (e.g. the oversized signalling claw in male fiddler crabs occurs with approximately equal frequency on both the R and L sides in nearly all species)

Fluctuating asymmetry Non-directional deviation from bilateral symmetry characterized by a normal distribution of $R-L$ differences with a mean of zero.

8.2 Inheritance of Acquired Characteristics

As an organism develops, it acquires many individual characters, due to its particular environment and history. Jean-Baptiste de Lamarck believed, as did many of his contemporaries (including Darwin), that such acquired modifications could be inherited by an individual's offspring. Lamarck proposed that evolution resulted from the accumulation of such modifications over time. Note, however, that it is historically inaccurate to attribute the idea of inheritance of acquired characters to Lamarck.

Modern genetics has generally refuted Lamarckian inheritance. Furthermore, Waddington showed that natural selection can produce the "illusion" of inheritance of acquired characters.

8.3 Constraints

Developmental constraints Biases in the production of variant phenotypes or limitations on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system[1].

Generative constraints Constraints that limit or bias the production of certain phenotypes during development. Therefore, generative constraints result in the non-random production (or non-production) of phenotypic variants on which natural selection can act[2].

Selective constraints Constraints arising from natural selection during development[2]; also known as *internal selection*[3]. Selective and generative constraints are difficult to distinguish in practice.

Genetic constraints Constraints caused by lack of genetic variation for a given phenotype. These may result from lack of mutations, lack of standing variation within a population, or genetic correlations.

8.4 Correlations

Many phenotypic traits are correlated within populations. The phenotypic correlation between two traits (r_P) is a function of the heritabilities of the traits, and of the additive genetic (r_A) and environmental (r_E) correlations between the traits. When traits are genetically correlated, selection on one trait will result in a correlated change in the second trait (correlated response). Genetic correlations may be caused by linkage disequilibrium or pleiotropy.

8.5 Next Lecture

The next lecture will be replaced by a seminar by Prof. Günter Wagner on "The Role of Hox Gene Cluster Duplications in Vertebrate Evolution" (4:00 – 5:00 PM, 102 HSC).

8.6 Literature Cited

1. Maynard Smith, J. *et al.* Developmental constraints and evolution. *Q. Rev. Biol.* **60**, 265–287 (1985).

2. Richardson, M. K. & Chipman, A. D. Developmental constraints in a comparative framework: A test case using variations in phalanx number during amniote evolution. *J. Exp. Zool. (Mol. Dev. Evol.)* **296B**, 8–22 (2003).

3. Arthur, W. *The origin of animal body plans: a study in evolutionary developmental biology* (Cambridge University Press, Cambridge, UK, 1997).