and new discoveries from developmental genetics have exposed the complexity involved with the origin of novel taxa. This complexity tells us much about how evolution works. As Clack demonstrates in the book, the tetrapod limb provides a major example of such evolutionary transformations. The simple view would hold that the origin of tetrapods is associated with the invasion of land by vertebrates, the transformation of fins into limbs, and the origin of the first fingers and toes. Clack shows that the relation among these three aspects is loose at best: primitive tetrapods are aquatic, primitive limbs can be very flipper-like, and digit-like structures appear in parallel in at least one other lineage of Devonian fish. Indeed, transitional taxa are often mélanges of structures, genes, and functions seen in a variety of different primitive groups. These mélanges are the result of parallel evolution and the disparate patterns of ecological and anatomical change. The features that characterize important new groups often arise in several different primitive species independently. In addition, major anatomical shifts can precede ecological ones. In the case of tetrapods, key features evolved in fish living in aquatic ecosystems, and only later were they used to exploit terrestrial environments. There are general lessons to be gleaned from this new view of tetrapod origins: the complex relation among parallel evolution, ecological change, and evolutionary diversification is likely to pertain to other evolutionary transitions as well.

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EVOLUTION AND DEVELOPMENT

Evolution as Frozen Music

Jeffrey S. Levinton

Johann Wolfgang von Goethe, the great poet, amateur musician, and biologist, saw architecture as "frozen music." His metaphor can be extended to the development of organisms under the influence of the previous history of the evolutionary process. As I listened the other night to Van Cliburn playing a piano concerto, I heard Beethoven's score transformed into a highly structured phenotype of sound. The music was influenced by the pianist's forceful hand; by the localized and organized sounds that flowed from the conductor's motions to the double bases one moment, to the violins another; and perhaps even by the windy evening's gusts and the patter of raindrops. The biological phenotype is no less shaped by its DNA score, though we have much to learn about the role of the environment in shaping its development and about how a variety of developmental branching points can lead to different outcomes of frozen music. Evolutionary biologists have, in the service of theoretical convenience, visualized a population of heritable scores from which some are selected—by differential mortality and reproductive success, which lead to increased fitness—to play the best tune; their focus has generally been on how genes and traits propagate or are lost. In *Developmental Plasticity and Evolution*, Mary Jane West-Eberhard addresses the crucial question of how novel forms arise.

Developmental Plasticity and Evolution
by Mary Jane West-Eberhard

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West-Eberhard, an evolutionary biologist at the Smithsonian Tropical Research Institute, is a specialist in the natural history, behavior, and evolution of social wasps. Inspired by the perception of a "failure of evolutionary biology to deal effectively with complex adaptive plasticity," she offers a new synthesis of development and evolution. Her complete theory incorporates the effects of the environment on plastic phenotypic responses, the ontogeny of organized alternative phenotypes turned on by developmental switches, the mechanisms by which environmental influences initially maintain these phenotypes and then increase their frequencies, and, finally, the evolutionary incorporation of these frequency shifts.

West-Eberhard bases her theory on three major precepts. First, because of phenotypic plasticity and the common amplification of environmental effects by behavioral responses, environmental induction often initiates adaptive evolutionary change. For example, she cites well-known effects of changes in food concentration on the form of skeletons and ciliary bands of larval sea urchins. She also resuscitates James M. Baldwin's theory, which argues

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that the behavior of appropriately responding individuals can accelerate their exposure to new environments, exposure that (if they are genetically distinct) enhances their role as players in evolutionary change.

Second, the organized nature of development produces, through phenotypic plasticity, quantally distinct new phenotypes. West-Eberhard considers genes to be followers, not leaders, in evolutionary change. She sees developmental switches as a source of evolutionary creativity. Instead of constraining change, they produce distinct alternative phenotypes, whose deleterious pleiotropic effects are fewer than previously thought. Negative pleiotropy can be further reduced by "character release." Owing to an environmental shift, the new, plasticity-induced phenotype becomes dominant in the population, and subsequent evolutionary rearrangement of genetic modifiers then increases its independence from other aspects of the phenotype. The theory depends on a notion of "extreme modularity," which "leads to extreme developmental independence of the parts, and, consequently, to a capacity for extreme specialization of traits." Switches are the plasticity-induced focal point for evolutionary change. Because plasticity can induce the new phenotypes, the problem of the loss of rare mutants due to stochastic factors is greatly reduced and the probability that the change will spread in a population is increased. The storehouse of developmental potential is always at the ready. The induction of alternative phenotypes may be predictable, which could lead to recurrent appearances of a trait throughout the history of a clade. The theory is not Lamarckian, because the induced phenotypes must have some genetic distinctiveness in order to be recruited into the evolutionary process.

Third, phenotypic plasticity can facilitate evolution by accommodating, and even exaggerating, changes in the production of new phenotypes. Shifts in the environment, for example, can result in the dominance of a phenotype that was formerly present, though in lower frequency. Thus, the traditional standing genetic polymorphism that figures so prominently in most population-level models of evolution is seen as secondary in importance (though not absent). Nevertheless, the model is quintessentially one that operates at the population level. Although speciation may separate a new evolving line, the evolutionary transition does not require speciation for change. Indeed, West-Eberhard posits a continuity in the evolutionary process from below the level of species to above it.

West-Eberhard is arguing for a development-centered approach to the investigation of phenotypic variation. As she notes, "The causal chain of adaptive evolution…begins with development." This claim is exactly on the mark, but it seems to me that evolutionary biologists have, to a large extent, already abandoned the notion that mutations are always random and have accepted development as the correct framework for the search for mutants and population-level evolutionary change. Therefore, this part of the author's argument crashes through an open door, even if that door has only recently been opened wide by evolutionary developmental biologists and geneticists.

What will be regarded as novel is West-Eberhard's belief that environment-induced variation, guided by the predictability of development that produces alternative phenotypes, is the major stuff of evolution. One exciting outcome of this theory is the possibility of investigating major evolutionary change at the population level. (However, some changes may have been lost in the early history of organisms when some fundamental new phenotypes—such as the arthropod exoskeleton—were incorporated.) West-Eberhard bolsters her argument with many examples that suggest how environmental effects on phenotypic plasticity might cause organized, quantum leaps in evolutionary change and how (owing to the organized nature of development) these leaps might predictably recur in a phylogenetic history. Yet many of these examples are little more than well reasoned and mildly convincing conjecture, and many are also open to interpretation by means of the more traditional, mutation-followed-by-selection arguments.

Those skeptical of West-Eberhard's theory will ask for answers to a number of crucial questions and tests. Most important, known phenotypic plasticity will have to be examined carefully. Is such plasticity generally a source of evolutionary creativity? Or is it normally only a product of previous gradual adaptive evolution? Do behavioral responses usually follow Baldwin's theory? Or is behavior more frequently a buffering factor, one that acts largely as a centripetal force in evolution? Especially needed is an algebraic formulation that will allow researchers to evaluate the frequency of plasticity and behavioral accommodation to environmental change, the phenotypic costs of developmental variation, and the competition between these processes and genetically based variation.

Image not available for online use.

Site-shifting? Did the crown feathers of the sulfur-crested cockatoo (*Cacatua galerita*) evolve by gradual elongation of ancestral head feathers? Or did they arise when the developmental program of wing feathers was transplanted onto the head? (In which case, they are an example of heterotopy—evolutionary change in the site of expression of a phenotypic trait.)

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Also necessary is an unbiased consideration as to whether organized developmental alternative phenotypes actually appear so frequently and predictably without strong negative pleiotropies. The multiple paths known to operate in similar evolutionary changes (for example, in neoteny of salamanders) suggest that organized phenotypes may be ad hoc affairs and not inevitable alternative outcomes of development. Are developmental switches so readily available to generate novel phenotypes? Or did they evolve to turn on particular developmental processes with occasional and unpredictably strong negative consequences when altered? After all, in sea squirts the *manx* gene appears to cause the loss of the tail and other characters involved in phylum-level change (*1*); whereas in cats the *Manx* locus dominant *M* allele reduces tail length as a heterozygote (*Mm*), but leads to death in utero when homozygous (*MM*). The character of pleiotropy is clearly not predictable at present.

In addition, researchers will have to determine whether genetic organization can be ignored so readily as West-Eberhard manages to do. The example of *Hox* genes argues that we must be careful in ignoring gene arrangement, and the dominant role of gene regulation in morphology is a story that has yet to be told completely (*2*). Will developmental phenotypes typically involve a set of interactive enhancers that are tissue-specific and genetically localized? Only careful genetic analysis will be able to answer such questions.

Despite these many challenges to West-Eberhard's provocative explanations, *Developmental Plasticity and Evolution* is a forceful volume. Filled with an impressive repetoire of examples and strong imaginative lyrics, it demands a careful examination with an open mind.

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