M. Birkmann

A wild canary. From *A Brand-New Bird.*

refused to entertain the possibility that red plumage—even (as it later proved) the siskin's—could depend on diet to any degree. In his view, a blood-red canary should be red by blood alone.

Duncker's first flaw, an absolute dependence on the primacy of genes over environment, led to his second—fatal hubris. The historian of modern biology or of Germany in the 1920s and 1930s will find it no surprise, but to Birkhead, who has invested a great deal in the purity of Duncker's biology, it comes as a "terrible shock" and "bitter blow" that Duncker's views on canary breeding coincided largely with his eugenical views on human breeding, which led him in turn into collusion with the Nazis. He was director of the local chapter of the Society for Racial Hygiene, arranged lecture programs for local National Socialist party members and gave enthusiastic public lectures on eugenics. He had also by the late 1930s grown a "Hitleresque" mustache. During his de-Nazification inquisition after the war, Duncker insisted that he had, at some detriment to his career, resisted becoming a party member himself until 1940 (true), but he nevertheless refused to apologize for his previous actions or views.

Birkhead derives from Duncker's ambitions and failures a moral lesson on the subject of nature and nurture: Duncker's downfall came from feeling too strongly that "creating a red canary by breeding rather than feeding was a matter of personal pride, coupled with an unshakable belief in the inheritance of color." In Birkhead's view, this failure to appreciate the complex interdependence of genes and environment crippled both Duncker's biological views and his political views. We happy inheritors of a modern biological paradigm are wiser, Birkhead implies in the closing pages, because a sociobiology has triumphed that through integration of nature and nurture proposes a new eugenics. Based on "our enormous strides in understanding the genome and in developing reproductive technologies," it shows "great promise for improving the quality of life." If scientists are allowed proper control this time, he believes, this new eugenics will be free of the poisons introduced in the past by "politicians and regulators." Future historians will judge.—*Abigail J. Lustig, History, University of Texas, Austin, and Max Planck Institute for the History of Science, Berlin*

BIOLOGY

Putting Genes in Perspective

Developmental Plasticity and Evolution. Mary Jane West-Eberhard. xx + 794 pp. Oxford University Press, 2003. $49.95.

An unfortunate outgrowth of the modern revolution in genetics is the widespread belief that the genes of an individual organism determine its appearance, physiology and behavior. The genome does not, of course, completely determine how an organism is constructed: The environment is an essential partner. Nowhere is this point more clearly illustrated than by the principle of developmental plasticity—the tendency for genetically identical organisms to differ in response to various environmental stimuli, or for individuals to vary over time as the result of changing conditions in their surroundings. For example, in many reptile species, incubation temperature determines gender. Likewise, certain insects develop wings only if they live in crowded conditions (and hence are likely to run out of adequate food). Indeed, environmentally mediated developmental flexibility is so ubiquitous that it can be regarded as a universal property of living things.

In *Developmental Plasticity and Evolution*, Mary Jane West-Eberhard, an evolutionary biologist at the Smithsonian Tropical Research Institute and a member of the National Academy of Sciences, undertakes to explain how developmental plasticity fits within a genetic theory of evolution. She believes (with considerable justification) that evolutionary and developmental biologists have failed to incorporate developmental plasticity into their framework for understanding the living world. For example, although most evolutionary biologists recognize the environment as an important source of individual variation, many regard environmental responsiveness as simply developmental "noise" that has no long-term evolutionary consequences. Moreover, the emerging field of evolutionary developmental biology ("evo-devo") has not yet produced a synthetic view of the evolutionary process, because it largely ignores speciation, developmental plasticity, and variation and selection within populations.

West-Eberhard seeks to correct these oversights. Obtaining the complete picture, she believes, will require reassessment of virtually every major question in evolutionary biology. Her approach in this massive 31-chapter treatise (which is aimed primarily at biologists interested in evolutionary theory) resembles Darwin's in *On the Origin of Species* in that she marshals an impressive array of evidence to support her arguments.

The book has two major themes. The first concerns the relation between genetics and environment in the evolution of organismal design—that is, "nature versus nurture." Contrary to the prevailing viewpoint, West-Eberhard argues that the two influences are *equally* important, both in development and in evolution. This claim will be controversial; evolutionary biologists are particularly likely to view it skeptically. Most of them believe that the phenotypic similarity between parents and offspring depends on the continuity of information passed solely through the germ line; environmental effects are not thought to persist across generations. Yet West-Eberhard notes that

> Individual development always begins with an *inherited bridging phenotype*—a responsive, organized cell, or a set of cells that springs entirely from the previous generation, is adapted for survival and interaction in the gametic and embryonic environment, and is the active and organized field upon which the zygotic/offspring genome products and subsequent environments eventually act.

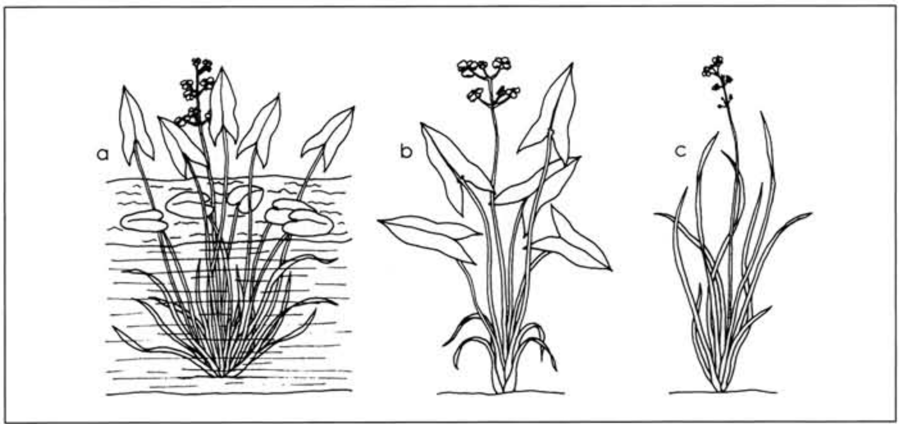
A particular gene may appear to be entirely responsible for a certain trait because the trait does not occur in its absence. But as she points out,

> it has this decisive effect only because there is a structure that is poised by the peculiarities of its organization to respond in the observed way. The impact of gene expression at every stage of the life cycle depends on the presence of a structure susceptible to change.

She goes on to discuss the maternal role in building a cross-generational bridging phenotype, giving examples of the influence of the maternal environment. For example, West-Eberhard observes that in a typical insect egg, the total amount of genetic information—including messenger RNA, ribonucleoproteins, enzymatic proteins, ribosomes and mitochondria—constitutes only about 1 percent of the mature egg volume; the rest, in the form of nutrients to fuel growth, "comes via the hemolymph of the maternal soma" and can reflect environmentally influenced variables such as crowding or diet. And she notes that genes "are packaged in phenotypes as eggs, spores, pollen, or sperm and sometimes vegetative fragments built by a parent," pointing out that "The survival and frequency of genes in a population depends on the packaging—the properties of phenotypes that reproduce." Furthermore, the notion that genes are mapped onto the phenotype is "too flat an image," she says.

> It would better evoke the events of development to ask, "How do environmental supplies, partially ordered by the genome, affect the highly reactive phenotype that exists before they arrive?" . . .
>
> With the responsive phenotype at the center of development, it becomes clear that the provenance of impinging stimuli—whether environmental or genomic—is of little developmental consequence. This is the death knell of the nature-nurture controversy, for it puts genes in perspective without detracting from their importance.

West-Eberhard argues that information about the environment can, through the inherited bridging phenotype, be transmitted across generations through epigenetic means—for example, through maternal effects and cultural transmission. Natural selection favors those inherited bridging phenotypes that best provide specific genetic *and environmental* information that enhances development and survival of the offspring.



The phenotype expressed by the marsh plant *(Sagittaria sagittifolia)* depends on its environmental circumstances: It shows highly dissociable independent expression in its leaf forms depending on whether it is *(a)* partially submerged, *(b)* completely terrestrial, or *(c)* completely submerged. From *Developmental Plasticity and Evolution.*

The book's second major theme concerns the role of developmental plasticity in the evolutionary origins of novel traits. West-Eberhard's central claim is that most phenotypic evolution begins with environmentally mediated developmental change, and that genes are often followers—not leaders—in phenotypic evolution.

She envisions that adaptive evolution involves four steps: First, a distinctive developmental variant is produced when some new input—such as a mutation, a new genetic combination (due to drift or a recombinational event) or an environmental stimulus—affects an existing responsive phenotype, causing a phenotypic change or reorganization.

Second, *phenotypic accommodation* improves on the newly reorganized phenotype through "adaptive mutual adjustment among variable parts during development without genetic change."

Third, the initiating factor recurs, producing a subpopulation of individuals who express the trait.

Fourth, "genetic accommodation"—a sort of adaptive refinement—may follow, in which gene frequencies change due to selection on the regulation, form or side effects of the novel trait in that subpopulation. Genetic accommodation can occur whether a novel trait is mutationally or environmentally induced. After all, accommodation depends on genetic variation at numerous loci that are exposed to a new selective regime by the induced phenotypic change.

West-Eberhard predicts that environmentally triggered novelties may have greater evolutionary potential than mutationally induced ones, for at least two reasons. First, an environmental factor tends to affect large groups, whereas a mutation initially affects only one individual. Such intraspecific "recurrence" enables the trait to be tested in many different genetic backgrounds. Second, an environmentally triggered novelty is automatically associated with a particular environmental situation—the one that induced it. Therefore, such traits are more subject to consistent selection and directional modification than are mutationally induced novelties, whose expression is more likely to be random with respect to environment. (It is also worth pointing out that many environmentally triggered phenotypes are selectively favored in the particular environment that triggered them.)

Thus the most important role of genetic mutations in evolution, according to West-Eberhard, may be to contribute not so much to the origin of phenotypic novelties as to the pool of genetic variation that makes genetic accommodation possible. She envisions the four-step process as being important not only in microevolution (evolution within populations) but also in macroevolution (the origin of major new structures and new taxa).

The last step in West-Eberhard's process, genetic accommodation, is redolent of the theory of *genetic assimilation,* or trait fixation due to quantitative genetic change in regulation, which British geneticist Conrad Waddington developed in the 1950s to explain some curious experimental results. He noted that if he selected for a trait that was initially produced only in response to change in external conditions, he could, through evolutionary time, produce lineages in which the new trait remained *even in the absence of the environmental influence*. In order to explain this result, Waddington hypothesized that genotypes differ in their susceptibility to the influence of the environment—that is, they differ in their degree of "canalization," such that some are more easily deflected into an aberrant developmental pattern. Selection for this pattern favors alleles that canalize development into the new pathway. As such alleles accumulate, less and less environmental stimulus is needed to produce the novel phenotype. Eventually the new phenotype is produced even in the absence of the environmental stimulus. West-Eberhard characterizes genetic assimilation as "genetic accommodation carried to an extreme," but she also notes that the two concepts differ in important ways. For example, genetic accommodation may *increase* phenotypic susceptibility to environmental influences, rather than decreasing it, as occurs in genetic assimilation, and may actually prevent genetic assimilation.

West-Eberhard's claim that adaptive novelty frequently begins as environmentally mediated developmental change challenges our modern view of evolution. One of the major tenets of the Modern Synthesis of evolutionary biology (the understanding forged in the 1930s and 1940s aimed at reconciling Darwin's theory of natural selection with the facts of genetics) is that environmental factors do not preferentially direct the production of new variants that would be favorable in the organism's specific environment; that is, mutations are assumed to be random with respect to what is favored by natural selection. If, however, novel phenotypes begin with environmentally initiated change (and if most of this change is adaptive), then a mechanism is in place to generate favorable variants for an organism's specific environment.

Some readers may note gaps and inconsistencies in some of West-Eberhard's arguments. For instance, by defining evolution as "cross-generational change in phenotypic frequencies or dimensions involving change in gene frequencies," she misses an important opportunity to develop a comprehensive view of evolution that incorporates both genetic and nongenetic sources of inherited information (as E. Jablonka and M. J. Lamb attempted to do in their 1995 book *Epigenetic Inheritance and Evolution*, which West-Eberhard cites). Moreover, a thorough discussion of the possible genetic mechanisms involved in genetic accommodation would have been helpful. For example, recent work on the heat shock protein and molecular chaperone Hsp90 may provide a molecular framework to explain Waddington's theories of canalization and genetic assimilation, and possibly genetic accommodation as well. Finally, throughout much of the book, West-Eberhard seems to assume that unexpressed alternative phenotypes will persist indefinitely, thereby providing a ready source of adaptive variation if the environment were to change. Yet in chapter 27, on speciation, she assumes that unexpressed alternative phenotypes are readily lost. Such losses, she argues, may lead to reproductive isolation: That is, populations that maintain the ability to express all phenotypes may become unable to breed with those that become more highly canalized.

Despite the above criticisms, the book contains much that is of value. These gaps merely reveal how little we actually know about the role of developmental plasticity in evolution and point to the need for further research. Indeed, we currently lack answers to the most basic questions; for example, we don't actually know whether West-Eberhard is correct in arguing that genetic and environmental influences are equally important, both in development and in evolution.

In conclusion, *Developmental Plasticity and Evolution* is an important book of immense scope that must be taken seriously by anyone who seeks to understand how living things are built, function and evolve. At its heart is a remarkable and thoroughly researched account of some of the most important ideas in the history of science. West-Eberhard's book is a vital contribution to the ongoing search for the missing link between developmental and evolutionary processes.—*David W. Pfennig, Department of Biology, University of North Carolina at Chapel Hill*

Potted Histories

Botanist, taxonomist and plant collector Sandra Knapp has put together an eclectic coffee-table–sized history of plants, flowers and botanical exploration illustrated with glorious color reproductions of paintings from London's Natural History Museum. ***Plant Discoveries: A Botanist's Voyage Through Plant Exploration*** (Firefly Books, $60) profiles 20 plant families, including peonies, poppies, roses, irises, tulips, cacti, conifers and daffodils. The coast banksia *(Banksia integrifolia)* below was collected at Botany Bay by Joseph Banks and Daniel Solander on Captain Cook's expedition in the 1770s. At left is a fan palm *(Livistona Humilis)* sketched by Ferdinand Bauer in January 1803 at Blue Mud Bay in Australia's Northern Territory.