

sian czar and czarina. The editor's own contribution to the volume describes the forensic analysis of a mummified head found in a pawn shop, and uses toolmark and elemental analyses to place the head into a temporal context. Gill-King describes using facial superimposition, among other techniques, to identify the skeletal remains of a young girl. The identification of the girl was fairly straightforward, but Gill-King met with two ethical dilemmas and concerns along the way. He presented the case in a clinical and scientific manner to a group that he assumed consisted of law enforcement officers and their pilot, only to learn that the "pilot" was the girl's father. Further, while analyzing the remains, he had noted some indicators of mixed ancestry. This led Gill-King to remind the reader that sometimes forensic anthropologists need to refrain from speaking about findings that are not directly related to the issues at hand.

The last section in this volume presents case studies that demonstrate the expansion of the field into the arenas of human rights issues, mass-fatality incidents, and the recovery and identification of America's war dead. Some of the work done by the Disaster Mortuary Operational Response Teams is described in reference to cemetery flooding (Sledzik and Willcox). Bunch and Shine tell the story of an Air Force officer lost in Vietnam, the impact that this loss had on his family, and how the science of anthropology was used both to recover his remains and ultimately identify this US service member, this husband and father, whose status had been unknown for 25 years. That one of the authors of this contribution (Shine) is the daughter of the officer

described brings an added depth to the piece, and serves as a poignant reminder to all forensic anthropologists of who it is we actually serve. Lastly, Doretti and Snow provide a detailed description of human rights work done in Argentina, including the formation of the *Equipo Argentino Antropologia Forense* (Argentine Forensic Anthropology Team). An example of how the team worked to identify some of the "disappeared" in Argentina is presented, as are examples of human rights work in El Salvador and Ethiopia.

This edited volume meets its stated purpose of presenting case studies that are both technical and revealing of interpretative problems met by anthropologists while conducting analyses. *Hard Evidence* serves experienced anthropologists by keeping them informed about the current activities and cases of their peers, and it is also a great book to supplement forensic anthropology textbooks in a classroom setting. Students will benefit by reading about some of the current applications of forensic anthropology in a real-world setting.

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DOI 10.2002/ajpa.20219

Published online 13 May 2005 in Wiley InterScience  
(www.interscience.wiley.com).

DEVELOPMENTAL PLASTICITY AND EVOLUTION. By Mary Jane West-Eberhard. New York: Oxford University Press. 2003. 794 pp. ISBN 0-19-512235-6. \$49.95 (paper).

Where do new tissues, organs, behaviors, and species come from? How does a zygote "know" to develop into an elephant or a saguaro? Where do genes originally come from? Population geneticists, community ecologists, evolutionary biologists, and creationists would, of course, give seemingly different yet, conceptually, disturbingly similar answers. Whether the *cause* of development is placed in the concept of gene, weather fluctuations, or the mind of a benevolent inhabitant of a cloudy sky, as long as it is seen as preexisting and uncoupled from the phenotype's development, it does little to uncover life's origin and complexity. It has long been noted that conventional evolutionary thinking skips a crucial step in organic evolution—the actual production of phenotype—and, as such, decouples the causes of within-generation variation from the causes of among-generation variation (Lewontin, 1983). Yet the reason for skipping developmental processes is not an accidental oversight of unexamined research programs, but rather an unfortunate legacy of the modern interpretation of the Darwinian evolutionary synthesis that states explicitly that internal organismal factors (e.g., genes) that cause variation operate independently of external factors (e.g., selection) that delete or retain these variants.

Coupled with tremendous advances in molecular developmental biology and superimposed on sophisticated

models of population genetics, the updated version of synthesis states that the complexity of life is produced by modifications of a preexisting genetic toolkit for the regulation of developmental processes, sorted out, at the end of the production line, by population-level quality controls, such as natural selection. Very much alive is the general notion that Darwinian evolution requires a strict separation and independence of *preexisting* inherited form and *created* acquired form. Several major dogmas are, thus, deeply embedded in the context of modern biology: that the preexisting genes are the *cause* of organismal form, that the evolution of everything, from novel migratory routes to extra digits, ultimately depends on the spontaneous generation of random genetic variation, that a barrier exists between generations penetrable only by genetic inheritance and only at certain times, that organisms are vehicles for carrying replicators, and, most importantly, that any adaptations acquired by the vehicles are irrelevant to the information coded in replicators and inherited by the next generation of vehicles. The result is that fascinating scientific advances in our understanding of developmental processes, a growing catalog of soon-to-be-completely-described genomes and functions of model laboratory organisms, and sophisticated population genetics techniques for predicting variation in populations of organisms, currently coexist with embarrassingly vague notions about the *origin* of these forms, the nature of deterministic forces in development, and, most importantly, the *origin* of genes.

There were multiple prior attempts to breach this gap and to integrate explicitly the production of phenotype within a generation with its change among generations. Some addressed this problem by pointing to the crucial inconsistencies in the philosophical background of current evolutionary theory (Oyama, 2000), and others by carefully documenting, beyond any doubts, growing empirical evidence that calls for a wider conceptual framework of evolution (Jablonka and Lamb, 1995). Mary Jane West-Eberhard's *Developmental Plasticity and Evolution* is the most comprehensive, authoritative, and novel synthesis of evolution and development to date. Few books rival its tremendous and immediate impact: within a mere year since publication, it has become an irreplaceable component of research programs, the subject of numerous seminars and discussions groups, and an integral part of dissertations in areas as diverse as psychology and molecular biology. But there are several reasons why, over the long term, this book will come to be regarded as one of the most important, (if not the most important) landmarks of a long-awaited evolutionary synthesis.

First, the central theme of the book is the most pressing and unresolved issue of modern biology: the origin of deterministic forces in development. No one will argue that there are multiple "inputs" into development, from learning to genes, yet, whereas volumes were written about the relative contributions of these inputs, this is the first comprehensive biological treatment of the *origin* of developmentally relevant information. Second, West-Eberhard proposes a consistent and novel framework that solves many conceptual difficulties of current biology. She thoroughly evaluates the notion of environmental induction as a major initiator of adaptive changes and introduces genes as "followers in evolution," meaning that the present-day relationship between genes and organismal form, especially the linear and additive relationships between genotype and phenotype required by statistical assumptions of transmission genetics, is a highly derived product, not precondition, of evolution. Genes, then, are either "suppliers of building blocks without direct influence on the outcome" or, more importantly, are "an outcome of recurrent organism-environment interactions." West-Eberhard provides a comprehensive treatment, complete with illuminating empirical examples, of the evolutionary sequence from environmental induction of developmental plasticity, through phenotypic and genetic accommodation facilitated by developmental complexity and extended inheritance, to the evolution of genes and genetic inheritance as guarantors of the most recurrent and consistent organism-environment interactions (i.e., fitness). The central theme is that evolutionary novelty always involves reorganization of preexisting phenotypes and the incorporation of environmental factors, and thus developmental plasticity strongly influences the direction and pattern of evolutionary change. The notion that what actually evolves among generations is ontogeny is not, by itself, new. What is new is the thorough biological treatment of phenotypic and genetic accommodation as the bridge between recurrent environmental induction and the genetic inheritance of novelty. Third, in an unprecedentedly wide-ranging application of this framework, West-Eberhard critically reevaluates major biological fields, from molecular evolution to sociobiology. The result is an elegant and long-sought resolution of several conceptual and empirical paradoxes. The book goes well beyond documenting the role of development in evolution, or advocat-

ing a wider conceptual framework that now includes development, but instead delivers a novel, comprehensive, and informed evolutionary synthesis that provides a clear and testable framework for biological research. And that is what sets it apart from the recent proliferation of books on developmental evolution.

The book is organized into four parts. Part I (Chapters 1–9) outlines the overall conceptual framework of the origin of genes and phenotypes and the role of development and selection in evolution. It explicitly establishes the key concepts used throughout the book: the concept of cross-generational continuity that combines the notion of extended inheritance with flexible boundaries between generations; the concept of recurrent environmental induction of developmental variation as the origin of an adaptive novelty; and the concept of the interchangeability of environmental and genotypic influences (reinforcing the point that both are a part of a temporal continuum) accomplished by phenotypic and genetic accommodation. This framework is then used to clarify the relationship between morphology and behavior, between phenotypic and genetic accommodation, and between developmental canalization and constraint. Plasticity is recast as somatic selection, started anew each generation, and it is shown how such plasticity enables phenotypic accommodation and, ultimately, evolutionary change, often without genetic change. There is also an extensive discussion of how modularity facilitates mosaic evolution, adaptive modifications, and specialization without compromising organismal functioning. Overall, the conceptual framework of the chapters in Part I illustrates how organisms can produce, accommodate, and retain environmentally induced variations between generations, and how phenotypic flexibility directs and facilitates adaptive evolution.

There are a number of far-reaching implications of this framework. First, genetic assimilation (trait fixation due to a genetic change in regulation) is elevated from one of the most misunderstood and neglected phenomena, a subject of taboos "rivaling those of group selection and sympatric speciation," to a process that is involved in most, if not all, cases of adaptive evolution, especially of complex phenotypes. Second, it shows that both of the prerequisites for evolution by natural selection (recurrence of organism-environment interactions and their heritability) are possible through either phenotypic or genetic accommodation. Third, it draws attention to the evolutionary importance of the constraining effects of homeostasis and organismal integration, advocating the view that evolutionary capacitance (i.e., the ability to accumulate unexpressed variation) is a by-product of organismal complexity, and not a prerogative of specially evolved structures. Fourth, it provides a mechanism for the similarity among individuals in environmentally induced modifications, and demonstrates that the evolution of phenotypic novelty does not require genetic novelty. Fifth, it calls attention to the fact that all sources of variation must be expressed by the same developmental pathways, thus accounting for their interchangeability. Finally, West-Eberhard reminds us of our "collective amnesia" of the original work of Darwin, whose theory of inheritance included concepts of continuity of phenotypes and transmission of traits' expression, views that today would be considered anti-Darwinian by some evolutionary biologists.

Part II (Chapters 10–19) introduces a major developmental framework for the origin of novelties that expli-

citly uses the evolutionary principles of Part I to reexamine research programs ranging from combinatorial molecular evolution to exploratory foraging behaviors. It introduces the notion of phenotypic recombination (interplay between evolutionary and ontogenetic reorganization of preexisting phenotypes), including the evolution of allometric relationships and life-history trade-offs, which is enabled by phenotypes' modular structure and accomplished by the establishment of developmental switchpoints. Discussing the evolutionary importance of duplication, deletion, and reversal in development, West-Eberhard demonstrates that the loss or acquisition of life stages, intermediate phenotypes, and sex-specificity is most often accomplished by regulatory developmental modifications of genotype by phenotype (e.g., as in sequential development), and not vice versa, as commonly assumed. Similarly, the author shows that one of the major paradoxes in evolutionary biology—the common occurrence and rapid evolution of sexual dimorphism in traits with shared genetic determination between sexes—is not really a paradox, since sex-specific expression is commonly accomplished by developmental regulation that does not alter the shared genetic determination. West-Eberhard takes this concept a step further and shows that the sex-specific expression of shared developmental programs (that are shielded from selection in one sex) is a common source of evolutionary novelty, especially in behavioral and morphological traits. Calling the interface between developmental molecular biology and Darwinism “the Wild West of evolutionary biology,” she provides some insightful suggestions for studies of evolution at the molecular level, especially relevant to those interested in molecular aspects of modularity and complexity.

Part III (Chapters 20–23) provides a thorough account of the interaction between development and evolution by showing how alternative phenotypes can facilitate adaptive evolution and retain developmental modifications. West-Eberhard extends the ideas of previous chapters to show that conditionally expressed phenotypes are favored by selection on developmental switchpoints, which are often under genetic control. The selective expression of alternative phenotypes in distinct functional contexts strongly facilitates adaptive evolution by maintaining consistent divergent selection. She further examines the population maintenance of alternative phenotypes, presenting a novel perspective that explains, albeit only partially, the “enigmatic” maintenance of genetic polymorphism in the absence of equal fitness of alternative phenotypes. Chapter 23 is a masterpiece that addresses the evolutionary importance of environmental assessment—a topic of crucial importance to the understanding of phenomena as diverse as the evolution of a stress response, learning, mate choice, and habitat selection. Remarkably, despite an abundance of mate choice and habitat selection studies, there are very few satisfactory explanations of the origin and evolution of such phenomena.

In Part IV (Chapters 24–31), West-Eberhard shows that the debate about gradualism (the theoretically expected, but typically not observed, small and continuous changes in evolution) follows from the incorrect assumption that evolution depends crucially on the spontaneous introduction of random small changes. When one considers instead the role of development in directing and amplifying adaptive change, the observable large and distinct changes become the rule, not the exception.

Moreover, environmental modifications of development can accomplish concordant changes in many individuals simultaneously and thus explain such phenomena as the evolution of stress-response and the heritable incorporation of environmental components into an organism's ontogeny (such as ingestion of rocks for food processing in bird gizzards following the evolutionary loss of teeth, the origin of vitamin catabolism, and the incorporation of externally obtained pigments into sexual displays). In the rest of Part IV, the developmental perspective is used to address major unresolved issues in such fundamental themes of evolutionary biology as speciation, macroevolution, and the maintenance of sexual reproduction.

There are several ways to read this large book. Perhaps the best way to grasp the entire content of this major work, and to appreciate the completeness, intellectual rigor, and implications of this synthesis, is to read the entire book at once. The book's clear and engaging style makes it hard to put down, but I suspect that few people would be able to allocate enough time to go through its almost 800 pages in one go, although I hasten to add that the time allocated to this book (and the airlines' excess baggage fees accumulated in the process) is a negligible investment compared to the time and money saved from pursuing trivial and unexamined research programs. The author suggests reading individual chapters independently. Indeed, the first chapter in each part is usually a preview and conceptual summary of the subsequent chapters. Yet, after reading the entire book twice, some chapters many times, and still discovering new information from the few remaining nonunderlined passages, I suggest a different approach. First, read Part I to get the complete perspective on the conceptual framework. Then make use of the index, and not the table of contents, to find subchapters relevant to a particular topic. For example, an excellent treatment of the evolutionary importance of stress is spread among several subchapters, and is only directly assessable through the index. Once you are done with specific topics, read the whole book anyway.

Since it was published a year ago, this book has drawn much praise but also some criticism. In my experience, some of the criticism comes from people who have actually not read the book: the inability to incorporate development into evolutionary thinking, and the deeply embedded resistance to even try, often stem from the lack of a coherent conceptual framework that this book now provides. So these people stand to benefit from this book the most. Another line of criticism deals with the perceived lack of mechanisms and empirical evidence for proposed concepts. Ironically, this critique comes from the same group of scientists, that routinely, for statistical convenience, impose such unrealistic assumptions as genetic additivity, linearity of phenotype-genotype interactions, and distinct and nonoverlapping generations. On the contrary, each proposed mechanism in this book is thoroughly, sometimes slightly excessively backed by empirical evidence. The final line of criticism states that the inability of the modern evolutionary synthesis to keep up with advances in empirical fields proves that concepts are not necessary for scientific progress in biology. Yet conceptual issues are not separable from empirical studies. It is concepts that are used to design experiments, recognize empirical patterns as meaningful, and write laboratory protocols. *Developmental Plasticity and Evolution*, with its unmatched combination of conceptual strength, empirical breadth, and illuminating and



powerful insights, is a major landmark in biology that will shape evolutionary thinking for many years.

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### LITERATURE CITED

1. Jablonka E, Lamb MJ. 1995. Epigenetic inheritance and evolution: the Lamarckian dimension. Oxford: Oxford University Press.

2. Lewontin RC. 1983. Gene, organism and environment. In: Bendall DS, editor. *Evolution: from molecules to men*. Cambridge: Cambridge University Press. pp. 273–285.
3. Oyama S. 2000. *The ontogeny of information: developmental systems and evolution*. Durham, NC: Duke University Press.

DOI 10.1002/ajpa.20220

Published online 13 May 2005 in Wiley InterScience  
(www.interscience.wiley.com).

NEANDERTHALS AND MODERN HUMANS. AN ECOLOGICAL AND EVOLUTIONARY PERSPECTIVE. By Clive Finlayson. Cambridge: Cambridge University Press. 2004. 255 pp. ISBN 0-52182-087-1. \$85.00 (cloth).

Let it be clear from the beginning that this is an interesting and enlightening book, densely packed with information. Being a biologist, it was a pleasure to see the question of the evolution of Neanderthals and modern humans treated from the more general perspective of population biology, evolutionary ecology, and biogeography, instead of, say, paleogenetics. For example, in his discussion of the continuously changing distributional patterns for human populations, Finlayson refers to metapopulation theory, a tool that has to some extent been introduced into paleoanthropology, but deserves even more attention as an alternative or supplement to the “big-bang” Out-of-Africa model.

Finlayson's main thesis is that the demise and extinction of the Neanderthals is, at most, indirectly related to the migration of modern humans into Eurasia (although it is not always easy to disentangle an unequivocal definition of the term “modern humans”). While he acknowledges that the presence of modern humans could have contributed to the final disappearance—the coup de grace—of the Neanderthals, climatic changes were more important. In particular, deterioration, from a Neanderthal perspective, pushed these so-called Archaic people into a number of South European areas, too small for the population(s) to survive. In contrast, modern humans were able to cope with the temperate Eurasian plains, presumed hostile to the Neanderthals. True or not, Finlayson's hypothesis is a reminder of the fact that hominid extinction is not necessarily caused by a failure to win or at least obtain a draw in the competition with other hominids, but can be the consequence of an inability to respond properly to other ecological challenges, a possibility already posed a long time ago concerning the extinction of the robust australopithecines vs. the survival of gracile hominins.

Whether or not Finlayson's hypothesis is tenable is still an open question. One obvious problem is that the book appears to be an example of an umbrella hypothesis, a hypothesis that explains a lot of phenomena based on one or a few causes: in this case, climatic change. This approach is open to several angles of attack. On the other hand, the story told must be coherent, and this goal is largely achieved, with some assumptions taken for granted. The chronological coincidence of Neanderthal extinction and modern human expansion in the same area is a pro-

blem for Finlayson's hypothesis. The way he poses the combination of climatic changes and adaptations of the two groups of humans makes the hypothesis difficult to test definitively based on present evidence. However, the hypothesis would appear to be falsified if or when we have certain evidence for the temporal and geographical overlap of the two populations up to the time when the Neanderthals disappeared. In this case, the two groups' ecological niches would largely overlap, despite differences in resource exploitation patterns. Another problem with Finlayson's hypothesis is the premise that Neanderthals were not cold-adapted, whereas modern humans were (at least culturally). Even if there are still unresolved questions concerning Neanderthal morphology, not to speak of the disputes over the interpretation of their peculiarities, the general impression is still that the Neanderthals were morphologically well-suited for living in a cold climate. Furthermore, the contention that the combination of anatomy and foraging behavior predicts that Neanderthals would find the relatively open Eurasian plain unpleasant, cold or not, is not very convincing.

One refreshing aspect here is that Finlayson is obviously a skeptic concerning traditional viewpoints, and rightly so. For example, he questions the simplistic assumption of a single worldwide pattern for the transition from Archaic to modern humans, and reintroduces the possibility that replacement could be the pattern in Europe, with continuity the pattern in East Asia. Furthermore, he insists on the fact that the most recent dates for Neanderthals are “terminus post quem” dates, and not actual extinction dates. This last truism could result in a backlash, however, as it is related to the problem mentioned above: if the Neanderthals actually died out later than the latest known dates, then the probability of coexistence and competition with modern humans is even greater.

In an attempt to look forward from the time when the Neanderthals disappeared, Finlayson draws attention to studies that found an apparent difference in group behavior patterns, foraging strategies, and home range sizes. These differences are often attributed to morphology and cognitive capabilities. Thus, he connects neuroanatomy to the larger ecological picture, be it theoretical or empirical. One conclusion is that modern humans were better at dealing with unpredictable environments, but the argument that such environments were actually significantly more prevalent 50,000–30,000 years ago than earlier is not completely compelling. However, an interesting and important conclusion is that the large (but also restructured) brain of modern humans was the