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Evolvability, Plausibility, and Possibility

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Evolvability, Plausibility, and Possibility

Resolving Darwin's Dilemma. Marc W. Kirschner and John C. Gerhart. Yale University Press, New Haven, CT, 2005. 314 pp., illus. $30.00 (ISBN 0300108656 cloth).

Judgments of plausibility involve the appearance of truth or reasonableness, which is always a function of background knowledge. What anyone will countenance is conditioned by what they already know (or think they know). Marc Kirschner (professor of systems biology at Harvard) and John Gerhart (professor of molecular and cell biology at the University of California–Berkeley) aim to show that molecular, cellular, and developmental processes relevant to the generation of phenotypic variation in anatomy, physiology, and behavior demonstrate how evolutionary processes, especially the origins of novelty, are plausible. The outstanding question for Kirschner and Gerhart concerns not the modification of structures but their origination—a question unanswered by the theoretical framework of the modern synthesis.

Two different audiences are in view: scientific researchers interested in the structure of evolutionary theory and the skeptical (but open-minded) public attuned to controversies over the adequacy of evolutionary theory. Kirschner and Gerhart adopt a mediating tactic between these audiences by keeping technical jargon to a minimum (and supplying a useful glossary) while locating their commitments within the broad space of alternatives seen in the history of evolutionary theorizing. The backbone of their argument is that the plausibility of evolution is conditioned by the possibilities of phenotypic variation available to natural selection. These possibilities of variation are underwritten by a set of conserved core processes that contribute to the increasing evolvability of life on this planet. The book is tightly argued and highly readable despite a wealth of biological detail (all effectively chosen and succinctly presented with illustrations). It synthesizes contemporary research and expands on the authors' earlier joint publications emphasizing the significance of molecular and cellular development for comprehending evolutionary dynamics.

That plausibility increases with a widening of the space of possibilities relates directly to complaints about the inability of evolutionary theory to explain the origins of novelty. If there are many ways to generate variation in components relevant to eyes, for example, then the plausibility of selection seizing on those variations to cumulatively produce varieties of complex optical structures is enhanced. In the background are three necessary conditions for the operation of natural selection—variation, fitness differences, and heritability—each uncontroversially present in nature. Variation is observed for most phenotypic features to which fitness differences readily attach. Heritability usually comes via genetic material, which presumes a connection with phenotypic variation through random genetic mutation. The missing link concerns how genetic variation translates into phenotypic variation via ontogeny. This is where the authors seek to fill the gap in evolutionary theory, or "resolve Darwin's dilemma," by explaining how phenotypic variation originates. It is a gap long recognized, and recent discoveries of deep genetic similarity across taxa, with no correlation between gene number and organismal complexity, have made it more conspicuous.

The explanation offered by Kirschner and Gerhart is "facilitated (phenotypic) variation." Although facilitated *genetic* variation (whereby mutation is biased to be viable, to give functional outcomes, and to be relevant to ecology) is not empirically supported, random genetic variation can lead to biased *phenotypic* variation as a consequence of the properties of core cellular processes (e.g., transcription) operating during development. These properties include weak regulatory linkage (easily modified connections among components), exploratory behavior (developmental selection), and compartmentation (localization of components or activities). The processes are highly conserved by selection because they confer robustness, flexibility, and versatility on ontogeny but make possible a multitude of phenotypic variations through recombination during development at different times and places, and in differing amounts. These regulatory capacities are manifested in the organism's ability to physiologically adapt within each generation as well as in developmental plasticity (e.g., insect polyphenisms). Thus, phenotypic variation will tend to be viable, to give functional outcomes, and to increase genetic diversity, which means that selective processes will be facilitated to produce evolutionary change. On a larger scale, the history of life is punctuated by the emergence and stabilization of new core processes (e.g., multicellularity) followed by the exploration of new possibilities emerging from the consequent facilitated phenotypic variation.

How well does facilitated variation address the plausibility concerns of those outside the scientific community? The answer is mixed. Because plausibility rests on background knowledge, and facilitated variation relies on much of existing evolutionary theory (it is technically a completion of existing natural selection theory, not a genuinely new evolutionary theory), its persuasiveness will be conditioned by the degree to which these other ideas are assimilated (arguably a major part of the problem in the first place). And yet it is clear that the origins of novelty have been a consistent irritant surrounding the adequacy of evolutionary theory. Therefore this book successfully broadens the space of possibilities through appeal to how actual molecular, cellular, and developmental processes produce phenotypic variation. Exploratory behavior in the formation of the vascular and nervous systems goes a long way

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toward addressing how multiple changes occur simultaneously during the origins of novelty. It is also a reminder that organismal "parts" are multifunctional and therefore disanalogous in many ways to the parts of artifacts such as watches.

How well does facilitated variation address plausibility concerns among scientists? The answer here too is mixed. Whereas those not specifically working in evolutionary biology are likely to find that facilitated variation augments the plausibility of evolutionary transformations, many researchers intimately associated with standard evolutionary theory will not be so easily moved. For example, some population biologists welcome findings from molecular developmental biology but have already begun arguing that these results do not warrant revamping evolutionary theory. This highlights diversity in the background knowledge of biological researchers, which is due to differing areas of expertise. The plausibility of a particular conception of evolutionary theory has often been directly connected to the methods favored by those offering the conception. Background knowledge is not equally distributed among biologists, and this affects plausibility judgments pertinent to evolutionary theory and the acceptance of the empirical results canvassed by Kirschner and Gerhart.

Although I am sympathetic to the argument that facilitated variation confers a higher plausibility on both the pattern and the process of evolutionary change, this argument has another, less conspicuous consequence. The possibilities of phenotypic variation that increase the plausibility of the origin of novelty simultaneously raise issues of how to discriminate between these possibilities. We want explanations that pin causal responsibility on one or more of the plausible mechanisms, especially for historical phenomena for which we lack experimental access. Paraphrasing the 19th-century philosopher of science John Herschel, identifying "true causes" for the origin of natural phenomena requires a demonstration of their existence, capability, and responsibility. Existence and capability are fully documented in this book. Discriminating which possibility is responsible for the origin of variation relevant to particular novelties, however, goes beyond plausibility and remains part of nascent research in evolutionary developmental biology.

Several outstanding issues remain. For example, Kirschner and Gerhart indicate a commitment to reductionist methodology: "To understand novelty in evolution, we need to understand organisms down to their individual building blocks, down to the workings of their deepest components" (p. ix). But many challenges to the completeness of evolutionary theory have arisen from those holding that a hierarchical conception of evolutionary (and developmental) processes better explains life's diversity. Whether evolvability has been selected *for* is also contentious, and hierarchy emerges here as well, because the authors' rationale includes selection at multiple levels (individual, population, group, clade). Other slippery notions permeating the text are "complexity" and "novelty," which can have different meanings for biological researchers, as well as for the public. This affects the authors' interpretation of empirical cases, such as the evolution of direct development in echinoids. But the judicious temperament and comprehensive nature of Kirschner and Gerhart's presentation of facilitated variation should serve not only as a plank in the case for the general plausibility of evolutionary processes but also as a key


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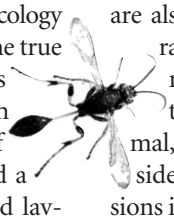
point of departure for exploring evolutionary possibilities more thoroughly, including the nature of evolvability.

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POISONS, SPRAYS, AND GLUES

Secret Weapons: Defenses of Insects, Spiders, Scorpions, and Other Many-Legged Creatures. Thomas Eisner, Maria Eisner, and Melody Siegler. Belknap Press, Cambridge, MA, 2005. 372 pp., illus. $29.95 (ISBN 0674018826 cloth).

Whereas the general public is keenly aware of very obvious chemical defenses such as the venomous stings and bites of insects and related creatures, even many biologists are unaware of the full arsenal of defenses that insects and other arthropods use for protection from predation or parasitism. These defenses can assume a wide variety of forms, from passive defenses such as maintaining toxic compounds in the blood (or on the cuticle) to active defenses such as noxious stews of chemicals that are sprayed or wiped onto attackers. The origins of defensive compounds also vary widely, with some being sequestered or derived from host plants, whereas others are probably synthesized de novo. Overall, the literature on chemical defenses in arthropods is rather scattered, and so a single volume that presents a broad overview of the subject is long overdue. No one is better equipped for the task of assembling such a volume than Thomas Eisner, J. G. Schurman Professor of Chemical Ecology at Cornell University and one of the true pioneers in the field. He and his wife, Maria Eisner, along with neurobiologist Melody Siegler of Emory University, have produced a highly readable, entertaining, and lavishly illustrated book that presents a nice general summary of the subject.



This book is not a comprehensive scholarly tome, nor is it intended to be. Rather, the authors state in their prologue that *Secret Weapons* "is intended as an illustrated guide to the defenses of insects and their kin." This idea works very well, particularly as the authors have personally worked on many of the species described, and thus can provide both spectacular photographs of the study organisms and all sorts of interesting details about various arthropods and their defensive systems. Within the context of this entertaining and readable format, the authors have provided key factual information about each system, including the full taxonomic names of the organisms, the names and chemical structures of the bioactive compounds, and pertinent references to the scientific literature. Thus, the book should appeal to a wide variety of audiences, from high school students in search of homework projects to biologists and research professionals seeking a general overview of the chemistry, tactics, and strategies of arthropod defense.

The book is organized primarily along taxonomic lines, rather than by the function of the defense (e.g., protection of eggs) or by classes of chemicals. It consists mainly of 69 brief chapters—each describing the chemical defenses of a particular species—bookended by a short prologue and epilogue, and a brief summary on the equipment and methods for studying insects and other small arthropods. Each chapter is essentially a vignette, giving a concise description of each organism, the chemicals that are found in its defensive secretions or sprays, and the mechanical, morphological, and behavioral adaptations that enable it to use its defenses effectively. The simple bioassays that the authors have developed for illustrating the nature of the chemicals involved in particular defenses are also nicely described. Throughout, rather than using the rather dry formalism of the scientific literature, the authors have adopted an informal, storytelling style, sprinkled with sidebar comments and brief digressions into discussions of related systems and examples. To some extent, it is like listening to an off-the-cuff narrative, with the authors' accumulated knowledge and experience leading to all sorts of fascinating parallels and connections as each story unfolds and leads into the next. Overall, this style draws the reader into the book; I could hardly wait to finish one example so that I could go on to the next.



However, what really makes each vignette come alive is the lavish use of color photographs, showing each animal in all its vivid glory. Even more remarkable are photos showing some of the various defenses in exquisite detail, such as droplets of secretions on the ends of glandular hairs, or the egg of a lacewing laid on a stalk, with the egg protected from predation by droplets of noxious secretions on the stalk (chapter 32). The latter example goes a step further by showing a subsequent photo of a newly hatched lacewing larva descending the stalk, imbibing the droplets as it goes for use in its own defense. (Nature is nothing if not parsimonious!) The clarity and vivid colors of the photographs of these tiny organisms, and the numerous other equally spectacular photos, would by themselves warrant purchase of this book. That they are intimately tied in with the factual text as illustrative examples of particular tactics and strategies only increases their worth.

The book is nicely indexed, with taxonomic names, common names, and chemical names all included, so that information about particular species, or the use of a specific chemical by one or more species, can be found readily. The text is well written, and virtually free of the typographical errors or other irritating mistakes that one sometimes sees in less professional volumes. To my knowledge, the factual information presented is accurate, with the single exception of the case of volicitin (chapter 57), which is described as a caterpillar salivary component that attracts parasitic wasps. The function of volicitin is actually more complicated, because it acts as an elicitor, inducing plants that are being attacked by herbivores to produce volatile chemicals that attract parasitic wasps, rather than being an attractant in its own right. It would also have benefited the reader to have citations supporting factual infor-

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mation in the text tied to the relevant articles, rather than simply listing all the articles used in developing each chapter at the end of that chapter. However, these are minor quibbles that do not seriously detract from a terrific book.

Overall, it is astonishing that the authors and publisher have been able to produce this remarkable volume in hardcover for a list price of under $30, particularly given the large number of photographs in brilliant colors. I highly recommend *Secret Weapons* as a good read for any organismal biologist, ecologist, or natural products chemist—or, for that matter, anyone with an interest in natural science. Volumes such as this, which bridge the gap between the general public and professional scientists, are both scarce and sorely needed. Given its content, quality, and relatively inexpensive cost, this book should find its way onto numerous bookshelves in both libraries and personal collections.

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BUILDING A BASELINE FOR PLANT CONSERVATION

Plant Conservation: A Natural History Approach. Gary A. Krupnick and W. John Kress, eds. University of Chicago Press, Chicago, 2005. 344 pp., illus. $75.00 (ISBN 0226455122 cloth).

What is the role of natural history in contemporary conservation science? With the increasing focus on mechanisms of extinction, experimental adaptive management, and restoration, today's students of conservation may be forgiven for not considering the question. Yet that is precisely what we are forced to ponder when reading *Plant Conservation: A Natural History Approach,* edited by Gary Krupnick and W. John Kress (Department of Botany, National Museum of Natural History, Smithsonian Institution). The book, to which some 48 authors contributed, attempts to address this broad issue and advocate for its importance by exploring the state of our understanding of biological diversity, drawing on the expertise and botanical resources available in herbaria, museums, and botanical gardens.

The theme of natural history reflects the premise that conservation is a truly global concern, and protecting biological diversity or the evolutionary processes on which it depends cannot advance with more models and experimental investigations if we cannot comprehend the magnitude, dynamics, and history of biological diversity itself. The strength of herbaria, museums, and botanical gardens in this regard rests on their collections (living and preserved) of diversity, their skills in interpreting evolutionary history, and their sources of plant material for restoration programs. As this book attests, these institutions are making significant contributions toward reversing the deficit of natural history information. In the foreword, tropical biologist Dan Janzen provides a compelling justification for natural history as an instrument for conservation, and promotes the role of herbaria and gardens in democratizing knowledge of biological diversity through emerging tools such as DNA barcoding. Increasing access to basic natural history information may be the most significant method for building awareness and fostering debate about the need for conservation and the methods for accomplishing it.

The main body of the book is organized into four broad sections, roughly corresponding to (1) large-scale variation in diversity, (2) diversity in specific habitats and taxonomic groups, (3) causes of plant extinction, and (4) conservation implications. Each section is subdivided into three to five chapters, each of which is composed of several short accounts written by various authorities. The target audience is never explicitly identified, so readers may either appreciate or dislike the format depending on their motivations. Readers with only a basic knowledge of conservation or interest in a broad overview will like this structure. I found the short essays well written and surprisingly cohesive, but there is necessarily a trade-off with depth in some topics. With 26 of its 48 contributing authors

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from the Smithsonian Institution, the book presents a broad but somewhat idiosyncratic perspective on diversity, with heavy emphasis on the neotropics and subtropics.

The first section ("Plant Diversity: Past and Present") sets the stage with discussions of historical and large-scale patterns of plant diversity and extinction. The first chapter, on the evolution of diversity of plant form in geological time, is succinct and enlightening, although a schematic illustrating the timeline of body plan evolution in plants would have helped to clarify the complex patterns discussed. The remaining chapters are also succinct and provide valuable summaries of patterns of diversity and extinction. I especially appreciated the authors' critical analysis of the methods and reliability of current biodiversity knowledge, which contrasts dramatically with the seemingly absolute estimates often given in the popular media. The essential message communicated is that, even for plants, we are only in the early stages of documenting patterns of biological diversity on a global scale.

The second section ("Plant Diversity: Habitats and Taxonomic Groups") is a series of case studies, each of which describes plant diversity in select geographic regions and taxonomic groups. Chapter 4 focuses on tropical and subtropical ecosystems, areas that are often rich in plant diversity and have high rates of endemism. Overall, the case studies provide detailed glimpses into specific tropical regions that will not be familiar to most readers. The analyses of individual taxonomic groups (chapter 5) seemed less useful. The specific groups highlighted were rather idiosyncratic, and often there were extensive accounts of the basic biology of a particular group, but with few linkages to conservation issues. At times, the perspective was quite narrow. For example, the description of lichens focused on one particular species, with little discussion of the patterns of diversity and concerns associated with lichens as a whole. In general, this section missed an opportunity to explore ways in which contemporary methods can advance the conservation of certain taxa. It might have been useful to ask "In how many cases of conservation (even in the United States) is recovery hampered by taxonomic confusion?" and "How have studies of systematics and phylogeography helped to resolve the appropriate scale of conservation attention?"

It might have been useful to ask "In how many cases of conservation (even in the United States) is recovery hampered by taxonomic confusion?" and "How have studies of systematics and phylogeography helped to resolve the appropriate scale of conservation attention?"

An analysis of the causes of extinction, the topic of the third section ("Contemporary Causes of Plant Extinction"), seemed, at first, peripheral to the natural history theme. However, this section distinguishes itself from ecological references on conservation by focusing, in chapters 6 and 8, on the kinds of extinction pressures unique to different ecosystems and taxa as well as the potential consequences of these pressures. In contrast, chapters 7 and 9 attempt to summarize more general causes of endangerment: invasive species and loss of genetic diversity. While each of these chapters does an admirable job with the space available, these more theoretical topics seemed at odds with the field-based, natural-history observations of other chapters. They are also not as well suited to the short essay format, as they cannot encompass the current expansive literature on such mechanisms, nor compete with the detailed theoretical and empirical summaries covered in other references. Moreover, for a book devoted to natural history, there is an imbalance between attention to genetic diversity and the limited consideration of ecology. This perpetuates a prevalent view that extinction risk can be evaluated or resolved with marker genes, and without consideration of the demographic and ecological context of species.

The fourth section ("The Conservation of Plant Diversity: Assessment, Management Strategies, and Action") provides a sense of how data on biodiversity are used to make conservation decisions—specifically, to set priorities for conservation action. It makes a compelling argument for the value of herbarium collections in developing maps of species diversity and in collecting and documenting diversity in lesser-known areas. This would have been an ideal place to summarize the challenges of sampling and estimating species diversity, and to offer methods for proceeding when resources are less than adequate. In addition, methods for predicting distributions and diversity using geographic information systems required more than just a passing mention. The chapter on phylogenetic considerations made reference to several topics that could have been expanded considerably. The discussions were thought-provoking and highlighted the complexities of prioritizing conservation targets. However, using phylogeographic criteria for identifying target geographic regions and predicting risks of hybridization are areas in which herbaria and botanical gardens can provide much leadership, and hence was worthy of expanded treatment in the book. A chapter on assessing conservation status summarized current methods for evaluating diversity at the genetic, species, and community levels. While a summary is useful to the novice, more emphasis on the criteria used in these analyses (e.g., in IUCN Red List designations) and critical evaluation of the quality of the data that result would have been a valuable addition. For example, the essay on molecular diversity is mostly a summary of kinds of genetic markers. However, it isn't apparent what the relationship is between molecular diversity and the ecological fate of populations, or when demographic and ecological factors may be of more immediate concern and a better predictor of extinction risk than the rate of heterozygosity at some arbitrary DNA segment.

With the increasing availability of genetic markers and ecological models, one

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could argue that conservation biology is focused on remedies and is losing sight of the basic knowledge of diversity on which the field is based. This book, although superficial in places, reveals a wealth of information about the organization of biological diversity from a global perspective and demonstrates the important contributions that herbaria, botanical gardens, and museums are making to this effort. In the process, it reveals how little we know about the very problem so many are trying to address, and highlights the importance of scientifically sound information as a baseline and an impetus for future research and conservation action through management, restoration, and policy development.

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The Cell: A Molecular Approach. 4th ed. Geoffrey M. Cooper and Robert E. Hausman. Sinauer, Sunderland, MA, 2006. 840 pp., illus. $107.95 (ISBN 9780878932191 cloth).

Conservation and Biology of Small Populations: The Song Sparrows of Mandarte Island. James N. M. Smith, Lukas F. Keller, Amy B. Marr, and Peter Arcese. Oxford University Press, New York, 2006. 274 pp., illus. $59.50 (ISBN 0195159365 cloth).

Conservation Education and Outreach Techniques. Susan K. Jacobson, Mallory D. McDuff, and Martha C. Monroe. Oxford University Press, New York, 2006. 496 pp., illus. $49.50 (ISBN 0198567723 cloth).

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