

published in 1994. These include I. Barber's authoritative chapter on host–parasite interactions, a chapter by I. Katsiadaki on the stickleback as a model system for ecotoxicology studies, and a pair of chapters on reproductive endocrinology. This latter pair of chapters (Chapter 7 by B. Borg, and Chapter 8 by I. Mayer and M. Páll) could well have been combined to reduce redundancy and to provide a clearer overview of the control of reproduction, but are valuable in that they provide authoritative reviews of the topic.

A personal favorite among the chapters is that by D. McLennan, in which she discusses the sensory world of threespine sticklebacks. Although this topic was covered in W. Rowland's thorough summary of literature on reproductive behavior and color in threespines in the 1994 volume, significant advances have occurred since that time and McLennan interprets them in the context of earlier literature in a well-written chapter. Her beautiful description of color changes in males of many populations during reproduction is alone worth the read. The chapter on speciation in the threespine stickleback radiation (J. W. Boughman) summarizes in careful detail insights garnered by J. D. McPhail and subsequent researchers, whereas the chapter on reproductive behavior (S. Östlund-Nilsson) is less successful because of an incomplete coverage of many topics. This chapter, like the chapter on antipredator defenses (F. Huntingford and S. Coyle) justifies partial coverage of the stated topics as a description only of advances in the field since 1994; however, the result is somewhat misleading if the chapters are not paired with earlier volumes, an effect that may be frustrating for some readers.

***Evolution in Four Dimensions: Genetic, Epigenetic, Behavioral and Symbolic Variation in the History of Life.*
Eva Jablonka and Marion Lamb.**

Cambridge, MA: MIT Press, 2005. 462 pp. 58 illustrations. ISBN-10:0-262-10107-6 (cloth), \$34.95.

This book is written, as if from across a great divide, by explorers with feet firmly planted on new terrain. The perceived conceptual framework of evolutionary theory, the neo-Darwinian Modern Synthesis, accounts for all inherited phenotypic change by the selection of genetic variation produced in a manner that is entirely blind to biological function. For most of the 20th century, the notion that heritable variation

This volume clearly provides a new resource for those interested in exploring the value of threespine sticklebacks for research in a diversity of areas. Although most of the chapters begin with the recognition that freshwater populations comprise an adaptive radiation, most (excluding those by Mattern, Barber and Kingsley, and Peichel) are weakened by forgetting this diversity, and instead interpreting information from single or a few populations as if characteristic of the entire *G. aculeatus* complex. This is a serious flaw and should be kept in mind by readers looking for guidance on the value of the radiation for evolutionary study. Nevertheless, I am sure I will reach for this volume frequently as a source of information—especially in those areas not previously covered by earlier reviews, or in which there have been substantial advances in the field.

References

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may be generated in response to organismal requirements or experience, and more, that the medium of such inheritance may be something other than DNA, was considered a Lamarckian heresy. While this constricted view retains its hold in most textbooks and popular accounts of evolutionary change, it has had little influence on basic research in gene regulation, developmental and behavioral biology, or linguistics, the main areas reviewed by Eva Jablonka and Marion Lamb. By teasing out the implications of this newer work for evolutionary mechanisms across this vast landscape of knowledge, the authors show that trans-generational phenotypic effects have multiple origins and channels of transmission, and even those elements of the phenotype that are most strictly conveyed by the genes do not necessarily start out that way.

Jablonka's and Lamb's "four dimensions" of evolutionary change, as announced in the book's subtitle, are the genetic, epigenetic, behavioral, and symbolic. Even when discussing the first, and to evolutionary biologists, most familiar, of these, they emphasize the dynamic and interactive nature of the relevant mechanisms. After a brief discussion of alternative splicing, for example, they conclude:

Clearly the relationship between genes and visible traits is very different from the way in which it is usually presented to the public. The idea that a gene is a sequence of DNA that codes for a product and variations in the DNA sequence can cause a difference in the product and hence in the phenotype, is just too simplistic. Coding sequences are only a small part of DNA, and DNA is just part of the cellular network that determines which products are produced. When and where these products are produced depends on what goes on in other cells and what the environmental conditions are like.

The authors draw on recent research to show that gene mutations, far from occurring exclusively in a fashion that is indifferent to context and need, can be directed (e.g., spurred by stress), and even "interpretive" (i.e., biased by evolutionary history), an ultimate form of which is the "evolved genetic guess." The latter mode of targeted mutation is familiar from the way antibodies are generated in vertebrates, but allied phenomena in other systems across a range of taxonomic groups are also presented.

If function-related targeting of inherited change can exist in the genetic dimension, it is all the more possible in the epigenetic dimension, where the rules of information transmission are even more flexible and context-dependent. Jablonka and Lamb include among the epigenetic inheritance systems gene-regulatory networks, which can have multiple states depending on externalities, macromolecular structural templating, as in cortical inheritance in ciliates and functionally useful prions in yeast, chromosome marking systems, imprints and the like, such as employed in the differentiation of animal cells and RNA interference.

The epigenetic dimension is home to a broad class of determinants that include physical mechanisms of morphogenesis and pattern formation to which all chemically excitable viscoelastic materials, including multicellular aggregates, are subject. Although not discussed in the book, such mechanisms introduce a needed element of "inherency" to the history of life, accounting for why organisms assume a particular, delimited range of forms.

What is important in these examples is that context-dependence implies plasticity of outcome, and this means, in turn, that the genotype does not uniquely determine the phenotype. Nonetheless, since genetic evolution never ceases, any nonprogrammed element of the phenotype is always potentially available for capture by a genetic routine that can make its development more reliable. Here, Jablonka and Lamb make good use of the concept of "genetic assimilation" put forward by C. H. Waddington in the mid-20th century. This important mechanism is one of several related ones (Baldwin's "organic selection," Schmalhausen's "stabilizing evolution") that were neglected or marginalized in relation to organismal development and its evolution during the ascendancy of molecular genetics, but which have re-entered this discourse with the rise of evolutionary-developmental biology in more recent years. Jablonka's and Lamb's discussion is one of the best available on the centrality of "phenotype-first" evolution at all organismal levels.

Behavioral evolution is one area in which neo-Lamarckian scenarios have not been in as bad repute as they have been in the evolution of morphology. Since behavior is obviously flexible and context-dependent, transmission by social and cultural means, at least in humans and nonhuman primates, is uncontroversial. Jablonka and Lamb take this further, though, describing "animal traditions" of food preference in rabbits and even insects. If an acquired phenotype can be propagated to subsequent generations, it can be the target of natural selection and hence eventually assimilated into the DNA-dependent inheritance system.

The last of the authors' evolutionary dimensions, the symbolic, is one they suggest to be confined mainly to the human species. What they have in mind are languages, fashions, and styles, and they make a strong case that the degree of abstraction involved separates this mode of social transmission from those like food preference that move through the "behavioral" channel. I would suggest, however, that a form of symbolic transmission of information exists wherever an entity plays a role in which it stands in for something else. In this sense, the nucleotide triplets are a form of symbolism, since they represent amino acids. This is not a deficiency in Jablonka's and Lamb's scheme, though, since the genetic mode of transmission already occupies its own dimension. Physiological and developmental signals, however, can also serve as symbol. The role of cyclic AMP as a second messenger for certain hormones, for example, has less to do with its chemical structure or reactivity than with its evolved role as an arbitrary marker in a system of signs.

Furthermore, it is difficult to see why the “waggle dance” of honeybees, whereby these insects communicate the direction and distance of food sources by stereotypical body motions, would not be considered symbolic transmission of information according to Jablonka’s and Lamb’s definitions. It would have been interesting to see the authors’ take on this phenomenon.

In any case, the chapter on symbolic inheritance is one of the richest in the book, containing spirited critiques of meme theory (which is formally identical to the most elemental neo-Darwinism, with cultural informational modules playing the role of genes) and evolutionary psychology (not quite as reductive, but still unnecessarily gene centered). A separate chapter on genes and language contains an informative discussion of the ongoing debates between the Chomskian generative grammarians and the functionalist school, focusing on the question of the manner and extent to which the facility for human language is inherited or innate, and what “innate” might actually mean. Again, genetic assimilation plays a key role in their suggested reconciliation of these views. To an informed nonspecialist in the cognitive sciences, the authors’ discussion of these subjects is compelling, well earned based on what has preceded it, and of a degree of subtlety well beyond that found in the writings of others (Richard Dawkins and Steven Pinker come to mind), who have taken up related questions.

A few words must be said, finally, about the manner in which the material and arguments are presented. The book is gracefully written, in a tone that is unusually relaxed and confident given the complexity

and broad range of its subject matter and the iconoclastic ideas of the authors. Jablonka and Lamb make extensive use of vivid thought experiments, a venerable tradition in physics but one rarely encountered in biology. They subject their ideas to intensive criticism in the form of an invented character, an “educated layperson” they call *Ifcha Mistabra* (I. M., for short), which is Aramaic for “the other conjecture.” I. M. appears at the end of each chapter, and in a long chapter at the end, in a dialogue with the authors, in which he rakes them over the coals and forces them to sharpen and amplify their ideas. This device permits the initial exposition to flow in an unobstructed fashion, while forthrightly presenting the extent to which the views of the authors and allied thinkers continue to stir controversy. Then, there are the amazing illustrations. Drawn by Anna Zeligowski, they are slightly reminiscent of the charming pictures by which the 20th-century author Munro Leaf taught several generations of children “How to Behave and Why” and that “Manners Can be Fun.” Their unique style and symbolic language are well suited to the memorable rendition of complex ideas, making them an ideal match for this intellectually daring book.

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