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Mechanisms of Life History Evolution: The Genetics and Physiology of Life History Traits and Trade-Offs edited by Thomas Flatt and Andreas Heyland

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as medical professionals, becoming regional experts at the expense of studying the head in its entirety. This is where Lieberman's book comes in, and it is why this volume will be viewed as an important contribution to the anatomical and anthropological literature for years to come.

*The Evolution of the Human Head* is an engaging synthesis of anatomy, evolutionary biology, developmental biology, and paleontology in an effort to understand the evolution of our distinctive skull. Lieberman's thesis is that, precisely because of the skull's integration and overall complexity, relatively small changes during development ("tinkering") have cascading consequences and result in relatively large changes in the overall form of the human head. The author argues for just these sorts of changes during human evolution, and he connects these small developmental changes to selective advantages for walking and running bipedally, chewing and processing different types of food items, and increasing brain size. Add these small changes up over five to seven million years and Lieberman illustrates that it is not terribly difficult for natural selection to transform a chimpanzee-like head into one as unique as our own. In fact, as the author demonstrates, many aspects of fossil hominin crania hint at periods in time when some of these developmental changes were occurring. All in all, this is an amazing review of human cranial anatomy, development, and integration that allows a broader perspective on how the skull evolved.

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PLASTICITY, ROBUSTNESS, DEVELOPMENT AND EVOLUTION.

By Patrick Bateson and Peter Gluckman. Cambridge and New York: Cambridge University Press. \$115.00 (hardcover); \$45.00 (paper). ix + 156 p.; ill.; index. ISBN: 978-0-521-51629-7 (hc); 978-0-521-73620-6 (pb). 2011.

As encapsulated in their concluding sentence, which extends Dobzhansky's famous quote to "[n]othing in biology makes sense except in the light of evolution and development" (p. 132), Bateson and Gluckman's short book is a plea for biologists to more seriously consider developmental processes, moving away from gene-centric views of individuals and evolution. This volume argues that the nature-nurture dichotomy, and the metaphor of the "genome as a blueprint," are impediments to scientific progress. They replace such dichotomies and metaphors with a clear framework that articulates how integrated and functional phenotypes arise from genomes in the face of environmental variation and perturbation. The authors argue that genes and

environment cannot (and should not) be separated when studying phenotypic evolution; indeed, the genotype-by-environment interaction is a tool to study sources of variation in populations, not a conceptual framework to approach development. Similarly, there are no genes "for" a trait; instead, hundreds of genes may underlie the development of a trait, while a handful of genetic differences may explain variation in a trait. They discuss how robustness and plasticity are not separate, but intertwined, given that plasticity often underlies robust phenotypes, and many induced, plastic phenotypes are robust. The authors also clearly lay out the links between development and evolution, reviewing the importance of robustness and plasticity for the survival of organisms and stabilization of phenotypes in novel and changing environments until a phenotypic change is fixed through selection on development. Throughout the book, the authors clarify a long list of concepts—such as robustness, plasticity, and modularity—integrating them and clearly illustrating their diverse mechanistic bases, such as epigenetic-induced changes in gene expression. Bateson and Gluckman's complementary perspectives result in clear, powerful, and accessible arguments. The framework developed in this volume is timely, refreshing, informative, and easy to read for not only biologists and doctors, but also the general public.

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MECHANISMS OF LIFE HISTORY EVOLUTION: THE GENETICS AND PHYSIOLOGY OF LIFE HISTORY TRAITS AND TRADE-OFFS.

Edited by Thomas Flatt and Andreas Heyland. Oxford and New York: Oxford University Press. \$144.00 (hardcover); \$79.95 (paper). xxv + 478 p.; ill.; index. ISBN: 978-0-19-956876-5 (hc); 978-0-19-956877-2 (pb). 2011.

Life-history theory successfully explains why different species live the lives they do. It has been powerful in showing that the diverse life histories of different species can be understood as the result of one underlying evolutionary process. That said, how, mechanistically, life histories are controlled (and so how they evolve) is not known. Life-history theory can proceed apace without knowing these mechanisms, although this theory does use conceptual mechanisms all the time; for example, recognizing that there are constraints to, and trade-offs between, life-history traits. This book, a collection of 28 multiauthor chapters is an ambitious, first attempt to capture the state of the art of progress in understanding mechanisms of life-history traits. The volume has an impressive range (covering animals and plants, although taxonomically, the arthropods dominate), arranged into seven parts, with the central five sec-

tions focused on key aspects of life-history biology: growth; reproduction; lifespan; plasticity; and trade-offs. The editors do an impressive job of bringing coherence to the structure of every chapter as well as an introduction to each section. The book is topped and tailed by an introductory call to arms and a concluding critique.

Although this book is the state of the art of understanding mechanisms of life-history biology, it makes clear the difficulties for this field. I think there are at least four. First, life-history traits are complex, and so will be their underlying genetics. Genetics and genomics have, to date, sought to explain how genes control phenotypes. It has done this successfully, but only for simple traits, simple in the sense that there is a clear one gene-one trait relationship. Our ability to now collect genome sequence data (and ever more quickly and cheaply) has made clear that we have very little idea what most of an organism's genes are doing. This is fair enough because these are early days in this endeavor. To my taste, it seems that we keep busy collecting ever more genome sequence data so as to avoid having to think about what to do with it to gain biological insight. The justifications often seem to be that, perhaps, if we have just a bit more data then clarity may dawn (why?), or this will be a good community resource (but for what?), but that we need better taxonomic representation (ok, but what for?). Moreover, for even slightly complex traits, it is combinations of genes in networks that are relevant, and these are much harder to study (Banta and Purugganan's Chapter 9 gives an idea of how these studies might look). Life histories are complex traits; in fact, they are likely a complex of subtraits and need to be treated as such. Treating them in this way might clarify whether or not apparently analogous traits among species are, indeed, the same or not. For example, diapause in some form occur in many taxa, but are insect diapause really the same as mammalian hibernation? Therefore, correct identification of the subtraits of life histories and recognizing that they will have complex genetic control will be key to progress.

Second, candidate gene approaches, but what about the rest of the genome? We know that all life is related, so it is clear that often similar genes will be performing similar processes in related species. It is relatively easy to generate data consistent with such ideas, although often the extent of the proof is less than one would like. Candidate gene approaches (i.e., starting from a well-studied gene in species 1, find the homologous gene in species 2 and seek to show conserved function) are biased because they are effectively ignoring most of the genome. Even for the most thoroughly studied model organisms (*D. melanogaster*, *C. elegans*) we have no idea

of what most of the genes do (the full range of genes may be computationally predicted, and their similarity to genes in other organisms known, none of which really helps with understanding function). These neglected genes are hard to work on, but it has to be that many of them will be involved in these two complex traits in which we are interested. More generally, this argues that a quantitative genetic approach to life-history traits is needed. These approaches are unbiased in their search for genetic control and are bound to illuminate dark corners of genomes.

Third, a confusion between studying the signal and the information content of the signal. Many of the chapters of this book look at hormonal control of traits, leading to the superficially attractive conclusion that hormones are key mediators of life-history traits. Really? Hormones are the means by which large multicellular organisms pass information around their bodies. If you take a computer to pieces, you will find it is full of electricity—this is how information is moving around your computer. Hormones/electricity are the messengers, not the message. The key to understanding the mechanisms of life histories is to know what those hormones are saying, to whom and when. Therefore, surely the question becomes when is a hormone signal turned on and off, and where, and when and where is that signal received and what is the consequence?

Finally, let us study resource allocation—properly. Trade-offs and constraints are key to almost all our thinking about life-history traits. These are most often thought of as questions of resource allocation, for example, the Y-model where limited energy (bottom of Y) can go to reproduction or survival (the two tips of Y; Lancaster and Sinervo's Chapter 25 explores this extensively). This is a conceptually important and clear mechanism that can be tested. Therefore, tracing energy/micronutrients from organismal acquisition to use for a trait would seem to be the most direct and powerful approach to use. This approach is barely being used (Zera and Harshman's Chapter 24 being a notable exception), but should this not become mainstream?

Are these reasons to give up and be downhearted? Absolutely not, it is a reason to redouble our efforts, but recognizing that investigating and understanding mechanisms of these important, complex life-history traits is a major intellectual challenge (and more so intellectual than technological) that may be the next great leap forward in biology. So remember, it started here first with this book.

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