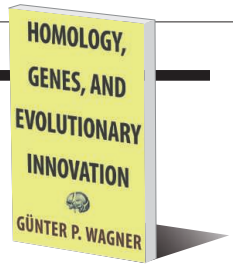
BOOKS *ET AL.*

EVOLUTION AND DEVELOPMENT

Enriching macroevolution

By **Carl Simpson** *and* **Douglas H. Erwin**

Homology, Genes, and Evolutionary Innovation
Günter P. Wagner
Princeton University Press, 2014. 494 pp.



What drives evolutionary innovation? This question has become a central focus of evolutionary biologists over the past decade as comparative evolutionary developmental biology ("evo-devo") has established a mechanistic basis for understanding the evolution of form and, increasingly, the evolution of developmental processes themselves. The challenge has been to build a conceptual framework that makes sense of the facts of development and explains how development can evolve while producing viable offspring. Prior to the codification of evo-devo, heterochrony was invoked for this purpose (*1*). Heterochrony produces new phenotypes by varying the rates of somatic and reproductive maturation, and for a time it was a promising conceptual organizer of developmental evolution. But heterochrony can only modify existing allometric variation and thus cannot explain the origin of novel traits—and the history of life is strung with novel traits.

State for a character identity. The elytra (protective cover) of beetles, such as this glorious scarab (*Chrysina gloriosa*), is a character state of insect forewings.

This issue of the developmental origin of novel traits is the central focus of Günter Wagner's rich and insightful *Homology, Genes, and Evolutionary Innovation*. Wagner, an evolutionary biologist at Yale, has been studying evolutionary novelty empirically and conceptually for over two decades. This deep engagement is evident in the rigor of his arguments for a new approach to the study of developmental evolution. In the book, Wagner addresses the mechanisms that allow the generation of new morphological novelties, in contrast with others who have focused on innovation in networks of DNA, RNA, or proteins (*2*). Wagner emphasizes the primacy of traits that require a substantial but specific genetic change: the origin of novel character identity networks (ChINs). ChINs are self-regulatory networks of genes associated with a morphologic character and occurring in an intermediate position within gene regulatory networks. Serving to produce characters that share identity even if they are dissimilar or in another place on the body, ChINs thus generate homologous traits. [ChINs are conceptually very similar to the kernels discussed by Eric Davidson and one of us (*3*, *4*), indeed more similar than Wagner acknowledges.]

Homology is conceptually messy because traits change both as morphological features—a bat's wings are homologous to a frog's arms—and at the developmental level, where different processes can generate a homologous character. The challenge is to understand how traits can share identity while similarities at the phenotypic and genetic levels dissipate over evolutionary time.

Wagner argues that homologous characters need share only a common ChIN: neither a character's embryological origin nor its outward form are relevant. This powerful idea focuses our attention on one important type of organismal characteristic out of the many in the developmental fray. When homologs first evolve, they and their associated ChINs are novelties: new and unique characters and gene networks. The structure produced by a ChIN can be of any complexity, and, importantly, the parts of a homologous structure are not automatically homologous themselves. Previous notions of homology are hierarchical: limbs and the digits within are each homologous among tetrapods. Wagner's notion does not recognize digits as being homologous unless they are generated by a separate ChIN from the one that initiates the limb. ChINs allow a precise operational distinction between character identity and character state. Homologous traits have a shared identity that evolves by the origin of a novel ChIN, and they indicate specific ways in which development evolves. In contrast, character states are variations of a homologous trait. As Wagner distinguishes between the two kinds of entities: "[T]here are character identities—for example, forewings and hind wings of insects. [And] there are various character states that insect wings can assume; the forewing can be a wing blade or an elytra or even a haltere … and the hind wing can be a wing blade or a haltere."

Missing from the modern synthesis, development has had an uneasy relationship with the rest of evolutionary biology. It has never been clear how evolutionary changes in development can be encompassed within a population genetic framework. Ron Amundson (*5*) noted that population genetics focuses on vertical transmission of genetic information, while evo-devo is more concerned with the generation of form within an individual and how developmental mechanisms evolve over time. By using ChIN-based homology, Wagner takes a different approach, establishing the developmental circumstances where population genetics directly applies and what limits development places on the remit of population genetics. This boundary characterizes systems where little heritable variation exists until new genetic elements are introduced into a gene network (most dramatically with the origin of a new ChIN). Given a specific and stable gene network population, genetic methods can measure a population's ability to evolve and adapt to environmental changes by microevolution. The origin of novel ChINs alters the structure of gene networks substantially and thus imposes nonuniformitarian evolutionary changes. Consequently, this limits our ability to extrapolate population genetic methods to macroevolutionary timescales. Another issue that will challenge some readers is Wagner's explicit and welcome defense of developmental types, long the bête noir of right-thinking

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microevolutionists. Wagner argues that these represent "suites of characters actively maintained through developmental or functional constraints."

Wagner's articulation of the ChIN framework and its application to homology and evolutionary novelty occupies the volume's first half. After an interregnum that addresses some of the philosophical issues raised by this conceptual framework, the final five chapters provide in-depth case studies of its application to some well-studied examples: the origin of cell types; skin and derivatives such as feathers; limbs; digits; and flowers.

Among the book's many great strengths is the virtual absence of a disquisition on the term homology. Wagner clearly defines homology in terms of the development of ChINs, but he disposes of the debate over the term with a few sentences. Although we suspect that those who enjoy wallowing in arguments over homology will fault Wagner, we view this as an inspired decision as it frees him to focus on the power of his conceptual framework.

Readers will find obvious extensions to the author's framework; Wagner identifies some, such as arthropod appendages, himself. Major evolutionary transitions provide another opportunity for extending the framework. There, Wagner's focus on the individuation of characters through the structure of regulatory networks could be applied to the study of new evolutionary individuals.

Homology, Genes, and Evolutionary Innovation makes a seminal contribution to evolutionary biology. As Wagner argues, his view provides an opportunity for a major research program on the study of novelty as distinct from adaptation. This means focusing research on the various mechanisms that generate variation in character identity rather than the consequences of changes in character state. The benefits of such research will prove as substantial as the study of speciation has been to macroevolution and microevolution. There is new biology to be discovered in macroevolution now that we know where to look. ■

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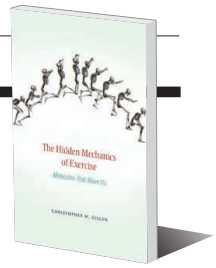
EXERCISE PHYSIOLOGY

See how we run

By **Stephen D. R. Harridge**



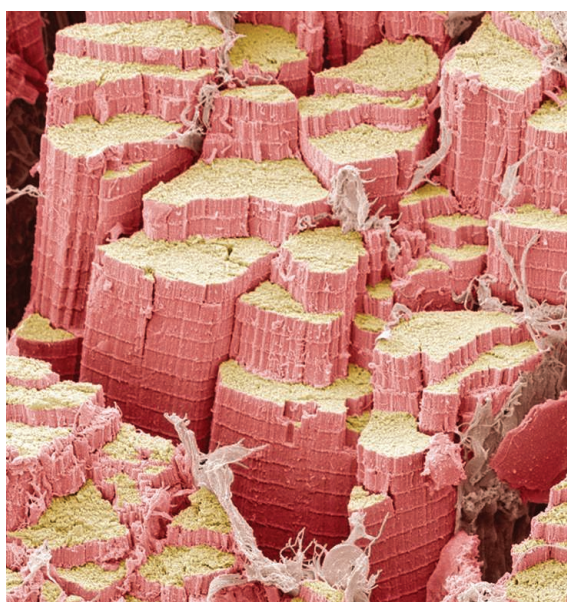
The Hidden Mechanics of Exercise: Molecules That Move Us
Christopher M. Gillen
Harvard University Press, 2014. 352 pp.

Exercise is an essential component of the study of human physiology. The world faces enormous healthcare challenges from diseases (e.g., cardiovascular disease, obesity, and type 2 diabetes) inextricably linked to a lack of physical activity. Thus the need to understand how our bodies move and adapt to exercise has never been more relevant.

Insufficient exercise is clearly not a personal issue for Christopher Gillen—runner, physiologist (Kenyon College), and author of *The Hidden Mechanics of Exercise*. Despite its title, the book doesn't focus on whole-body joints and moment arms. Instead, Gillen's enjoyable account emphasizes the molecules and protein structures that allow us to move, run, jump, control fuel use, and regulate adaptations to exercise training.

Using analogies to make the science accessible, Gillen takes readers through critical systems of the human body, from the molecular protein structures that allow us to store and reuse elastic energy in our tendons to the processes by which hemoglobin molecules bind and release oxygen. He effectively integrates traditional physiology with more recent developments in cell and molecular biology and genetics. He links together topics ranging from the molecular chain of events in the brain that cause us to initiate movement to the behavior of myosin (the molecular motor protein in skeletal muscle that produces force and ultimately generates movement). Refreshingly, Gillen approaches the subject from the system down rather than the molecule up. Throughout the book, he emphasizes how tiny changes in protein structures scale up to produce whole-body movements.

Gillen comes to the topic with the perspective of a long-distance runner (he has completed 10 ultramarathons) and not that of a power athlete. Thus he can be forgiven for some confusion regarding hyperplasia in the hypertrophic response of whole muscle to high-resistance strength training. Satellite cells may well proliferate, but that does not mean that the number of functioning muscle fibers increases. His description of proteins "morphing" also becomes a little irksome after a while, but that should not detract from the enjoyable way he takes us through the different biological systems, linking each with various aspects of physical and sports performance.



Force producer. Colored scanning electron micrograph of a freeze-fractured skeletal (striated) muscle.

Overall, Gillen offers exercise enthusiasts wishing to understand the science behind their training an interesting read. The book also serves as an engaging primer for exercise-science students who want to begin to understand some of the underlying molecular mechanisms. *The Hidden Mechanics of Exercise* introduces concepts that make the step to the specialized textbook or research article easier. At the same time, researchers studying the behavior of the individual molecules may find Gillen's account enlightening in regard to the functional implications of their work at the whole-body level. ■

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