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From Embryology to Evo-Devo: A History of Developmental Evolution

Author: Bolker, Jessica A.

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Size Matters

Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Daphne J. Fairbairn, Wolf U. Blanckenhorn, and Tamás Székely, eds. Oxford University Press, New York, 2007. 280 pp., illus. $110.00 (ISBN 9780199208784 cloth).

A book titled *Sex, Size and Gender Roles* certainly grabs the attention of potential readers—even a fellow passenger on an airline flight seemed interested—but the volume's subtitle, *Evolutionary Studies of Sexual Size Dimorphism,* captures the book's contents much better. The book focuses on morphological differences between males and females, with a major emphasis on overall body size as the dimorphic trait of interest.

The 20 chapters of this edited work are divided into three sections. The first six chapters on "macro-patterns" contain very useful reviews and analyses of dimorphism in mammals, birds, reptiles, amphibians, insects, and spiders. Although some may cry, "Where are the fishes!" (and likewise for some other neglected taxa), as a whole, this section serves as a greatly needed, updated reference work. It also introduces much of the adaptive reasoning that is the subject of closer scrutiny in the second section, this one on "micro-patterns." This section contains eight case studies covering one or a few species each, ranging from the dimorphic plant *Silene latifolia* to eight hartebeest subspecies. Finally, the book closes with five chapters on some of the proximate mechanisms that underlie sexual size dimorphism.

Edited volumes are typically tough to compile. Researchers tend to be an opinionated bunch of people. Even after a workshop—and this book is based on one—it can be hard to ensure that they speak a common language. It is a merit of *Sex, Size and Gender Roles* that the boundaries between the sections are rather fluid. For example, adaptive explanations for observed patterns can be found in all of the sections, despite an initial (incorrect) warning that they will be absent in the last section of the book. Even so, it took me too long to figure out the common framework that underlies all the studies. In hindsight, I wish I had read the chapters in a different order—the book eventually clarifies some of the issues on selection that I struggled with initially, but it took time.

The best and most influential books might be those that do not solve all the problems they describe. If you need food for thought that requires some chewing, I can absolutely recommend this book.

Why did I have trouble piecing some of the arguments together? To answer the question, "Why are males smaller [or bigger] than females in species X?" many chapters explain that a smaller size makes males more agile (which is beneficial when mate searching), or that a larger size confers an advantage during male combat, or that fecundity selection acts on females to make them larger. But whether these advantages should be reflected in selection currently favoring small or large males or females is a different question. Why? In chapter 9, by Daphne Fairbairn, readers are reminded that if both sexes have reached their optimum size, one expects stabilizing selection, not directional selection, around the mean size of each sex. If, on the other hand, size does not evolve independently in the two sexes because of genetic correlations, we expect genetic conflict to prevent the two sexes from reaching their optima (a point that is further clarified in chapter 18 by Stéphanie Bedhomme and Adam Chippindale). If so, we can indeed expect to find directional selection, as the average individual of neither sex reaches its optimal size.

But why did I have to read until chapters 9 and 18 (and other chapters toward the end of the book) before this issue became clear? Admittedly, the introduction before the first section mentions this point briefly, but I would have understood it sooner if the chapters had been offered in a different order. Readers would do well to start with the later chapters. It is there that we learn about adaptive theories together with proximate mechanisms, which are intimately linked issues in a field where genetic constraints can have a major impact on evolutionary outcomes. Only after one is armed with this knowledge can the single-species studies (section 2)—and finally the wider taxonomic patterns (section 1)—be understood.

To mention another example, Wolf Blanckenhorn's statement that "data do not support the differential-equilibrium model of SSD" (chapter 10) means, in the simpler language of Fairbairn, that selection is directional rather than stabilizing. Only after figuring this out could I accept Blanckenhorn's claim that since "net sexual selection on males is stronger than fecundity selection on females, current selection can explain why males are larger" (pp. 110–111). At first, this statement appeared to conflict with Fairbairn's prediction that at equilibrium, one does not necessarily expect directional selection at all.

Many of the taxonomic overviews near the beginning of the book take it as more or less granted that current directional selection pressures—for example, estimates of sexual selection or fecundity selection—can be used to explain current differences in the mean body sizes of males and females. This might indeed be a sensible null expectation, because females and males share the same genome (give or take one or a few sex chromosomes). As pointed out by Turk Rhen (chapter 16), a shared

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genome creates a massive constraint that prevents us from seeing wholly independent evolutionary trajectories that would lead to optimal sex-specific body sizes and the disappearance of directional selection. This is a clearly expressed point, one that might shed light on a question that receives relatively little attention in this book: Why don't males and females more often evolve separate niches, freed of their initial similar-size constraints? Yet the next chapter, by Russell Bonduriansky, appears to offer a somewhat different explanation for why there can be directional selection at equilibrium: condition-dependence of sexual traits.

Bonduriansky's style of argumentation will be familiar to researchers interested in traits subject to female choice. In that context, the lek paradox asks why there is still female choice for traits that should no longer show heritable variation after generations of directional selection resulting from female choice. The same question is relevant for sex-specific body size, or indeed any trait that has important fitness consequences and is subject to directional selection. Why are some males still small if larger ones always win fights? Bonduriansky tackles this question with clarity, but I wish that the authors of other chapters had paid more attention. The book does not describe how condition-dependence is related to the other approaches taken to explain how current selection for larger or smaller body size can persist. Instead, the chapter immediately following Bonduriansky's simply notes, "apparently, even with every opportunity to adapt, the average fitness of individuals often remains low relative to the fittest."

Of course, a somewhat suboptimal ordering of chapters doesn't mean that one cannot eventually assimilate everything on offer. Perhaps my quibbles should be interpreted as a sign that there are still unresolved issues in this field, which in turn makes it an exciting one. Take, for example, Rensch's rule. This is an allometric rule formulated in several different ways throughout the book, but Lukás Kratochvíl and Danile Frynta expressed it simply in chapter 15: in small species, females tend to be larger; in large species, males do. The pattern applies in some taxa more consistently than in others. If we understood why, we would probably have a beautiful sequence of ideas from basic theory to explanations within and across species, taxon-specific where required, but with an understanding of why the exceptions exist. My impression is that we are not quite there yet, but the journey toward that goal is already offering some very rewarding views.

The best and most influential books might be those that do not solve all the problems they describe. If you need food for thought that requires some chewing, I can absolutely recommend this book. It might be best enjoyed, however, if, like an eager young child, you eat the dessert first and then work your way toward the inspiring taxonomic variety of the starters.

HANNA KOKKO
Hanna Kokko (e-mail: hanna.kokko@helsinki.fi) is a professor at the Laboratory of Ecological and Evolutionary Dynamics in the Department of Biological and Environmental Sciences at the University of Helsinki, Finland.

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DEVELOPING A HISTORY OF EVO-DEVO

From Embryology to Evo-Devo: A History of Developmental Evolution. Manfred D. Laubichler and Jane Maienschein, eds. MIT Press, Cambridge, MA, 2007. 577 pp., illus. $55.00 (ISBN 9780262122832 cloth).

From Embryology to Evo-Devo originated in a 2001 Dibner Institute workshop organized by the book's editors. Manfred D. Laubichler is an assistant professor of biology and an affiliated assistant professor of philosophy at Arizona State University; Jane Maienschein is Regents' Professor and Parents Association Professor at the same university, where she also directs the Center for Biology and Society. Both are long-time observers of, as well as participants in, the modern emergence of evolutionary developmental biology, or "evo-devo." As they note in the introduction, we continue to confront "a rather old cluster of scientific problems of embryos, development and evolution," and struggle with how to think about them and what to do about them in the lab. The quest to articulate how ontogeny and phylogeny fit together, and to achieve some kind of conceptual continuity that unifies their disparate timescales and explanatory modes, is a long-standing one. This volume, an anthology of essays, combines a history of these efforts with attempts to move the project forward.

The book presents workshop participants' attempts to record the history of evo-devo—or a series of interrelated histories—and also tries to make the case that this history is important to the field's present and future. The first objective is certainly achieved: the collection offers a multifaceted construction of the history of evo-devo. The second task meets with less success, however: by the end of the book, it is not clear exactly how or why evo-devo's history matters to its current practice or practitioners. The volume will certainly be of interest to historians, both for its immediate content and for the variety of historiographic approaches it comprises. Although it will not engage all evo-devo biologists, it will appeal to those interested in the origins of their discipline.

There are many different ways to construct history, whether of evo-devo or anything else: one can focus on individuals, institutions, or central questions. Each of these approaches is represented in this anthology. The first step, of course, is to decide what one is constructing a history *of*—in this case, the biological discipline (or subdiscipline, or interdiscipline) of evolutionary developmental biology. Evo-devo is variously construed as an overlap between two otherwise independent fields, a set of questions, or an attempt to fill "explanatory gaps" in or between evolutionary and developmental biology.

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Although Brian K. Hall cautions that "the title [of the book] is, obviously, not meant to be taken literally," some contributors do in fact view evo-devo as the lineal successor of comparative (evolutionary) embryology. One topic of discussion is whether, or to what extent, "modern" evo-devo is finally getting somewhere with the classical questions of comparative embryology—as well as precisely which of those questions were the central ones in the first place. (Amundson [2007] focuses on this issue in his review of the book, contrasting it with the 1980 volume *The Evolutionary Synthesis,* edited by Mayr and Provine.)

Two things about this historical project are particularly interesting. The first is the timescale: this is very recent history (the 2001 workshop focused on the interval between the 1920s and the 1970s), and writing the history of a field at so short a temporal remove raises some important questions—for instance, how well can we judge in the present the likely future significance of particular questions, institutions, or individuals? As is clear by the end of the volume, we do not even necessarily agree on their past significance.

Second, scientists were engaged in the historiographic project alongside historians of science. One unusual aspect of modern evo-devo is that a number of the key scientific players are also seriously interested in, and knowledgeable about, the history of their field (although it is not clear that this interest materially affects the direction of their biological research programs). Günter P. Wagner reports that a colleague compared his attending a workshop about the history of his own field with being a "bird…at a meeting of ornithologists" (p. 525). Nevertheless, the participation of scientists in addition to that of historians clearly brought much to the project.

But what do the birds get out of it? That is, what can this volume offer to other scientists in or entering evo-devo—especially those who might not be historians on the side? One answer is an appreciation of history within a field. For example, history may be particularly useful in explaining why certain people and ideas become very influential while others remain on the sidelines, as well as why some individuals are honored as intellectual progenitors of the modern discipline while others are deemed irrelevant (or worse). Marsha L. Richmond, Stuart A. Newman, William C. Wimsatt, Alan C. Love, and others discuss the roles played by the likes of Richard B. Goldschmidt, Patrick Bateson, Rupert Riedl, and D. Dwight Davis. In the most detailed example, James Griesemer describes how geneticists have retrospectively claimed the contributions of Gregor Mendel—though read another way, those contributions could equally well be considered "developmental," and Mendel himself did not make the distinction at all.

Evo-devo has achieved substantial mainstream success and recognition, including all the essential paraphernalia of an established discipline (dedicated journals, National Science Foundation funding, etc.). Now that the discipline is mature, we have to guard against stodginess; one way to do that may be to resist defining the field too carefully or insisting on a single version of its history.

A second important message for scientists is that the complexity of constructing the history of evo-devo, let alone projecting its future, is increased by the field's fluid boundaries and shifting focus. Yet these very characteristics are largely responsible for its dynamism, excitement, and promise. It is clearly impossible to erect a rigid retrospective definition of evo-devo, or unambiguously identify its intellectual parentage (although there are multiple, and not mutually consistent, attempts to do so in this volume). It would certainly be a mistake to make such an attempt prospectively—that is, to develop a strict description of what "counts" as evo-devo, or a limited list of questions considered its proper concern. Evo-devo has achieved substantial mainstream success and recognition, including all the essential paraphernalia of an established discipline (dedicated journals, National Science Foundation funding, etc.). Now that the discipline is mature, we have to guard against stodginess; one way to do that may be to resist defining the field too carefully or insisting on a single version of its history.

Griesemer maintains that "the representational openness of 19th-century unifiers…facilitated the diversification of subsequent lines of research" (pp. 400–401). Such openness is equally essential to modern evo-devo if it is to fulfill its ambitious promise of building conceptual continuity from ontogeny through phylogeny: this can occur only through a uniquely broad synthesis of data, ideas, and methodological and epistemological approaches. No one set of tools—not even molecular genetics—will suffice.

Müller contrasts the "explanatory force" of evo-devo with that of traditional evolutionary approaches to some key issues. Moving beyond such direct comparisons, it is clear that the most radically synthetic piece of evo-devo is its attempt to combine two explanatory modes (with very different timescales and notions of causality) in order to address a series of questions that have been important to both evolutionary and developmental biology but addressed adequately by neither (Müller offers a list on pp. 509–510). Modern evolutionary biology, even after the synthesis with genetics, still lacks the "generative component" and "projectability" needed to explain phenomena such as morphological novelty; but without an evolutionary context, no amount of *Entwicklungsmechanik,* or developmental genetics, can even discern novelty, let alone explain how it occurs or why it matters.

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The ultimate ambition or "promise" of evo-devo is to achieve full conceptual continuity between evolutionary and developmental mechanisms and explanations—that is, to generate "a conceptually continuous narrative that connects the molecular processes which create genetic variation, the developmental processes which lead to phenotypes, their function, and the population genetic processes which ultimately effect evolutionary change" (Wagner, p. 539). But close examination of the canonical examples, such as Hox genes or vertebrate limbs, reveals critical gaps. We know a lot about limb development and a lot about the pattern of the fin-limb transition, but we still do not know exactly what embryological changes were directly responsible for evolutionary changes in morphology, and we lack direct "proof of the mechanistic efficacy of the identified molecular changes" (p. 532). More fundamentally, we are not in agreement on what would count as evidence for specific developmental changes serving as direct causes of particular evolutionary variations.

Especially challenging—Wagner suggests it may even be impossible—is combining the radically different timescales and conceptions of causality from evolutionary and developmental biology. The handful of beautiful examples we now have offers some hope that this synthesis is possible, and some models of how to go about it (I'd add finch beaks [Abzhanov et al. 2006] to Wagner's list on pp. 530–531, which includes *Drosophila* microevolution, quantitative trait locus analysis of stickleback skeletal evolution, and angiosperm phytochromes). But we need more, and that is going to require a combination of groundbreaking ideas and extraordinary technical expertise.

It is also going to require people who are both trained and inclined to make connections well beyond the borders of their own traditionally defined field. Griesemer suggests that the reunification of evolution and development into a coherent whole depends most critically on "instigating [a] realignment of perspectives" (p. 414). This will require both individual polymaths and interdisciplinary collaborations. Even as we struggle to assimilate an overwhelming flood of new information from an ever-broader range of fields, any or all of which might turn out to be important for the evo-devo project, we need to maintain some space for serendipity—like Wallace Arthur's pulling the wrong volume off the shelf and getting Garcia-Bellido and colleagues' work (1979) instead of Kimura's (1979) (an incident described by Wimsatt on p. 333). And having the birds put in a word or two at the ornithology conference may be another way to open up the conversation.

JESSICA A. BOLKER
Jessica A. Bolker (e-mail: jbolker@cisunix.unh.edu) is an associate professor in the Department of Zoology at the University of New Hampshire in Durham.

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SIX LEGS BEST?

Six Legs Better: A Cultural History of Myrmecology. Charlotte Sleigh. Johns Hopkins University Press, Baltimore, MD, 2007. 320 pp., illus. $55.00 (ISBN 9780801884450 cloth).

Ants have a long history as the foci for research in a variety of disciplines. Because of their diversity and ecological dominance in many ecosystems, they are model organisms for ecological studies, and their advanced sociality makes them ideal for studies of behavior and cooperation. There are many scientific books about ants, ranging from treatises on individual species or closely related groups to Pulitzer Prize–winning reviews of their biology. Charlotte Sleigh has taken a novel approach in *Six Legs Better: A Cultural History of Myrmecology* by taking a historical perspective on the study of ants. Her previous book, *Ant,* focused on popular culture, whereas *Six Legs Better* examines the history of ants as study organisms from the perspective of a scientific historian. She concentrates on a period (the late 19th century to the mid-20th century) when biology was undergoing a renaissance with the growth of evolutionary thinking, the modern synthesis, and the birth of quantitative population biology.

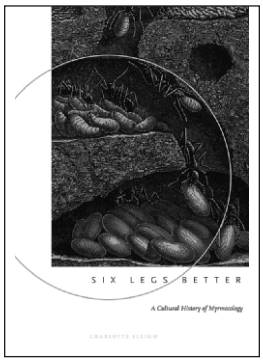
The book has three sections, each of which highlights a prominent scientist who used ants as model organisms: Auguste Forel (1848–1931), William Morton Wheeler (1865–1937), and Edward O. Wilson (1929–). These researchers came to the study of myrmecology with different perspectives—Forel as a psychiatrist, Wheeler as a natural historian, and Wilson as a sociobiologist with an interest in communication. *Six Legs Better* explores how these scientists have looked to ant biology and communities for parallels with social behavior in human societies. These views changed over the time period covered in the book from rather utopian to anarchistic without central control to self-organized and mathematical. The differences in scientific approach and in each scientist's perspective on social organization stemmed from both their backgrounds and the social and scientific context in which they worked.

Sleigh provides great insight into the social and cultural contexts that motivated the approaches each scientist took and the type of research questions each one asked. She does so in part through her examination of correspondences and interactions among the focal scientists and their colleagues and other scientists. This unique perspective on the mindset of each researcher is a highlight of the book, with specific attention given to how cultural and scientific attitudes have changed over time. A

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recurring theme is that many interactions among these scientists and their respective colleagues were fueled by conflict rather than cooperation—surprising, perhaps, given the taxa of interest.

Although the book was rich with information about these three scientists, I did at times find Sleigh's prose unnecessarily esoteric, and the lay reader with an interest in ants might find the book inaccessible. I also found that an appreciation of how much these pioneers loved their study organisms was lacking from the chapters. One thing that all three myrmecologists held in common was a genuine passion for ants, studying ants for ants' sake. This is evidenced in part by the taxonomic work each did. Their scientific descriptions of species and keys are still used today.



Six Legs Better serves as a novel companion to previous publications on ants by taking a look at the ant researchers themselves (much more than their study organisms) and examining the motivation for their scientific inquiry. The book's strong point is placing each of these people in the context of the science and culture of their day. I recommend this book to anyone who is interested in the history of science or who wants to learn more about some of the founding fathers of modern myrmecology.

ANDREW V. SUAREZ
Andrew V. Suarez (e-mail: avsuarez @life.uiuc.edu) is an assistant professor in the Department of Entomology and the Department of Animal Biology at the University of Illinois in Urbana.

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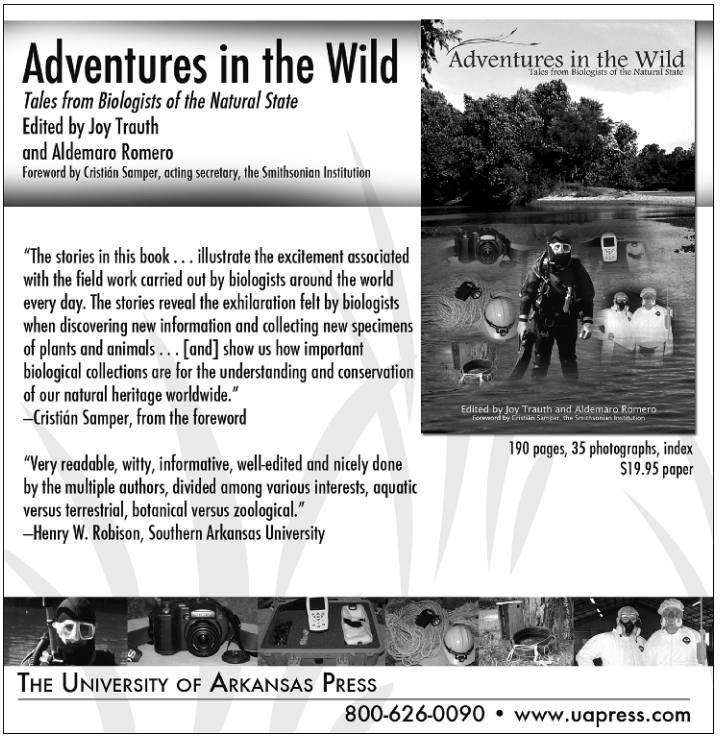
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