

## Solid Biomechanics

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on the lectern and holding forth, with anecdotes.) What was needed to make this a textbook, or at least a more accessible and usable reference, was an editor's attention to enforce consistency, focus, and coherence.

The final chapter ("Living the good life in a lower EROI future") is a quick overview of the potential issues and the distinct possibility of a lower-energy but more fulfilling life, to which I personally subscribe. It is a soft landing after the hard delivery in much of the book but leaves us short on details. The final thought that I carry, however, is from chapter 15, which shows the EROI diagrams mentioned above. In making the diagrams, the authors assumed that the world energy system had an EROI of 20 in 2005, which, they say, will sink to 5 by 2050. (An EROI of 1 means a zero net energy yield.) They admit to an arbitrary value, but by putting it out, they reinforce the question of what minimum EROI is needed to run a modern society—not the society we have now, but the one we want. We do not know now what that minimum value is, but we will have to know by, say, 2050.

If you are ready to embrace this bedrock problem, reading *Energy and the Wealth of Nations* is a place to start. You will either hate it or (maybe) love it, but you will not sleep through it.

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## THE MECHANICAL PROPERTIES OF BIOLOGICAL MATERIALS

**Solid Biomechanics.** Roland Ennos. Princeton University Press, 2011. 264 pp., illus. \$65.00 (ISBN 9780691135502 cloth).

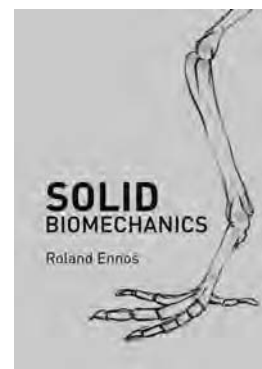
**M**y interest in biomechanics really took off with the 1975 publication of R. McNeill Alexander's *Animal*

*Biomechanics*, a volume that, for the first time, provided readers with an accessible coverage of mechanical principles as applied to animal biology: materials, structures, fluid dynamics, and energetics. The focus of the field then was essentially on the application of these principles to animals. In the recent book *Solid Biomechanics* by Roland Ennos, the scope is both narrower, insofar as the author largely ignores dynamic systems, and far broader. His work encompasses both plant and animal materials—the structures they create, the problems they encounter, and the interactions among the components of a structure, among the structures themselves, and, finally, between structures and their environments. These are topics in which Ennos is well versed; for many years, he has conducted pioneering research on the mechanics of such diverse subjects as the designs permitting controlled bending of insect wings and the ways in which plants either resist or facilitate deformation and how they anchor themselves to the ground.

Too often, biologists enter the field of biomechanics with an inadequate foundation in the most basic properties of materials; I certainly did when I fumbled my way into the field over 50 years ago and then gradually acquired related knowledge in a haphazard fashion. Now it is easier: Ennos gives us a first-rate introduction to how material properties can be examined; how they are affected by the way in which forces are applied to them; how they deform then recover from stress; how they break; and how, in certain configurations, their fracture can be avoided. All this is basic to the author's subsequent treatment of biological materials.

In *Solid Biomechanics*, Ennos very sensibly does not distract us with discussions of conventional solids such as crystals or metals; these, after all, are rarely found in biological systems. Instead, he considers the properties of what we have inside us—and what may be found in insects or trees: the real materials of living organisms. One of the most remarkable biological

materials to exist is *resilin*, the rubbery protein found in arthropods that acts as a restoring force in insects' wings or as a versatile energy store. The book's treatment of this protein is as clear as any I have read, revealing just why rubbers show long-range soft elasticity, thus differing from more familiar, stiffer though nonetheless springy materials. Of course, nature has access to the gamut of organic polymers, from the ever-versatile cellulose with its varied everyday uses to the (biologically) more expensive structural proteins and carbohydrate-protein or protein-mineral composites, in which the mechanical properties can be fine-tuned by adjusting the relative proportions or the degree of cross-linking between the components. One example of this is the exoskeleton of insects, in which different regions form tough rigid plates and tubes or flexible joints or strong fibers.



At their simplest, material structures can be fibers, plates, tubes, or sacs. In general, fibers may be pulled, twisted, or pushed; they resist the first action but not the other two. More complex structures may be subjected to a greater range of stresses, and their reactive behavior, in turn, becomes more complex. Some biological structures, such as worms or blood vessels, can be modeled as internally pressurized tubes; bones or grass stems may be more usefully modeled as beams having load-bearing behaviors, such as bending, breaking, or buckling. These

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various cases are handled lucidly in the book, and Ennos moves on to consider how some of the potentially disastrous failings of these ubiquitous structures are, instead, successfully modified in living organisms—in their innate design, as the creature grows, or in response to stress.

A predictable consequence of living in real environments is that organisms may be subjected to unpredictable stresses, either from winds or currents or from their own weight; they may also be stressed differentially in the to-and-fro movements of locomotion. Ennos discusses recent work that was focused on mechanical systems in both animals and plants that respond to such stresses in a way that improves their performance or helps them avoid damage. Natural selection, in fact, has exploited mechanics in structures where, for example, insect wings emulate umbrellas and tree trunks act as vertical cantilevers.

In such systems, mechanical interactions occur either between different organisms or between an organism and its substrate. How does one hold onto mud? How does one plant hold onto another as it grows toward better light? Many of these curiosities have been studied, and the observations of these organismal adaptations have led to inventions such as Velcro hook-and-loop fasteners and paste. *Solid Biomechanics* offers clear discussions of how such attachments—and their detachment—work; however, I feel that the area of hinges and articulations is treated somewhat cursorily. In human engineering, a great deal of effort and ingenuity is devoted to the design of movable joints and to minimizing the attendant frictional losses. I do not think that this is entirely the fault of the author; rather, it is a field that has been sadly neglected.

Early research on biomechanics relied on the classic methodology and instruments of engineering of the nineteenth and twentieth centuries, but, in a forward-looking final chapter, Ennos highlights the potential of submicroscopic techniques that have emerged in the present century.

Biological systems are, let one not forget, constructed at the molecular level, making an examination at that level likely to be instructive.

As a whole, *Solid Biomechanics* is very well constructed, and its themes are readily accessible. The book is well illustrated with clear and effective line drawings and graphs, and its lucid text is supplemented by a useful eight-page glossary of terms used in engineering, physics, and biology. The extensive bibliography extends to 2010, with the majority of the references dating from after 1970, but I was delighted to note that it also includes Robert Hooke's *Micrographia* (1665)! It is noteworthy that Ennos has effectively confined himself to the mechanics of solids in biological systems, although it is clear that he is familiar with fluid dynamics, the mechanics of locomotion, and energetics. Others have written in this area, but his is the most comprehensive monograph so far. For me, the book works.

HENRY BENNET-CLARK

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## EVOLUTION REPLAYED

**Convergent Evolution: Limited Forms Most Beautiful.** George McGhee. MIT Press, 2011. 336 pp., illus. \$35.00 (ISBN 9780262016421 cloth).

**H**ow predictable is evolution? If the evolution of plants and animals were to be replayed, would the Earth have similar creatures? Would wings and eyes be formed? Would consciousness arise, and would the universe become aware of itself again? If carbon-based life forms were found on an Earth-like planet elsewhere in the universe, would their shapes look similar to our own? Or would

there be a cast of wholly unrecognizable characters? Most evolutionists, I suspect, believe the last scenario to be the case: Evolution is not predictable any more than it is progressive. It is stochastic.

This perception seemed to belong to a whole generation of evolutionists of the last century, but author George McGhee stands apart. In his new book, *Convergent Evolution: Limited Forms Most Beautiful*, the question of directed evolution is not merely a matter of speculation and just-so stories. As a professor of paleontology at Rutgers University, McGhee has combed through and organized a rich body of published data regarding convergent evolution. In this compelling and thoughtful discussion, he includes the views of other evolutionary biologists who have pointed to convergent evolution to argue against a directionless and infinite diversity. *Convergent Evolution* complements McGhee's other landmark books, *Theoretical Morphology: The Concept and Its Applications* (1999) and *The Geometry of Evolution: Adaptive Landscapes and Theoretical Morphoscapes* (2007).

Much of Darwinian evolutionary biology has been focused on how species diverged gradually from common ancestors to illustrate a great branching tree of plant and animal diversity—species within genus, niche within niche. Darwin concluded in *On the Origin of Species* that “whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning, endless forms most beautiful and most wonderful have been, and are being, evolved” (1964, Harvard University Press, p. 490). But Darwin may have gotten carried away.

As the book's subtitle suggests, evolution does not produce unlimited forms. Constraints exist that limit possibilities. Some are functional; others are developmental. Certainly, there is great divergence from common ancestry, but characteristics in those

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