

Second Edition

Comparative Biomechanics

Life's Physical World

Steven Vogel



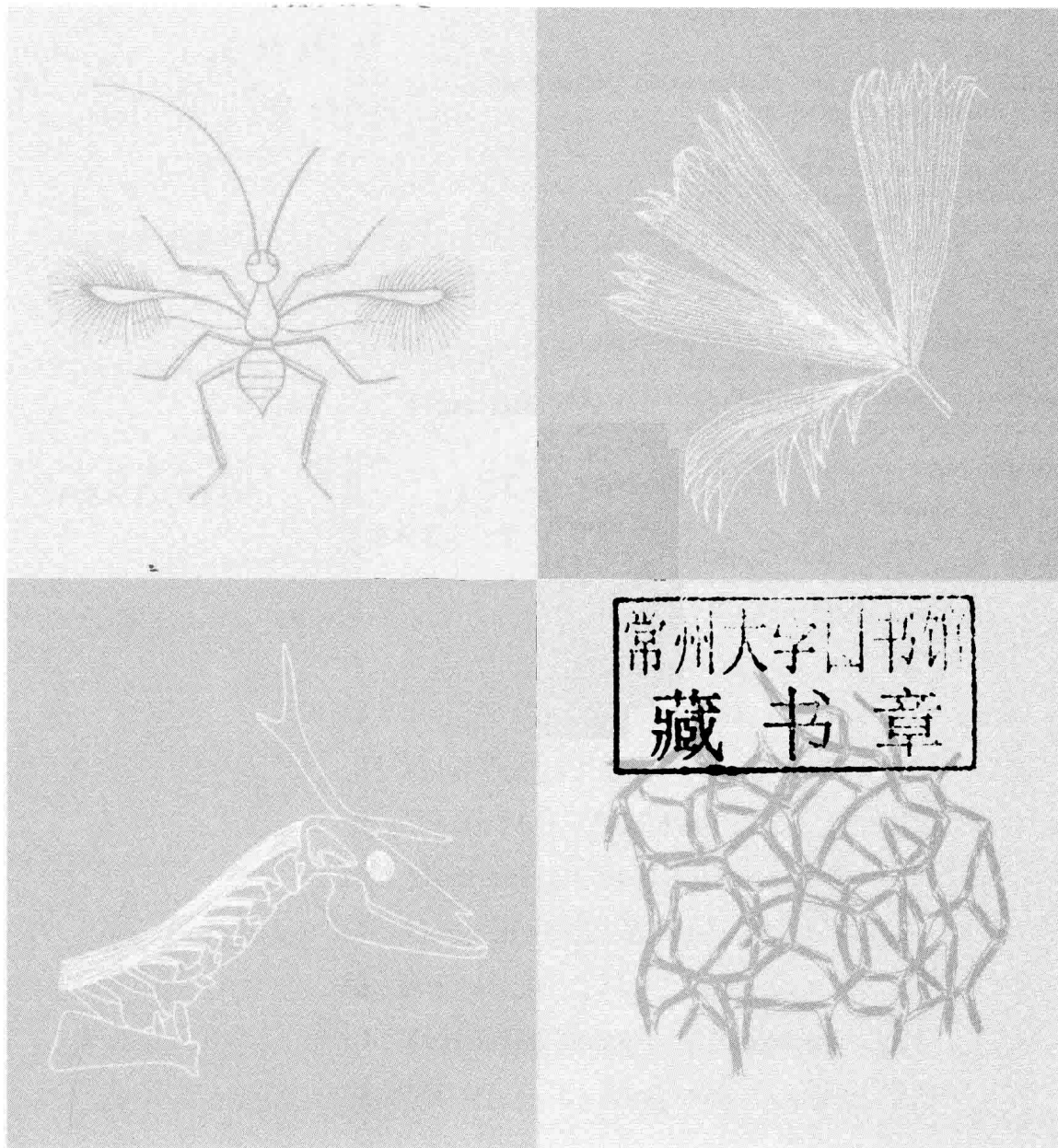
Illustrated by Annette deFerrari

STEVEN VOGEL

Comparative Biomechanics

LIFE'S PHYSICAL WORLD

Second Edition



PRINCETON UNIVERSITY PRESS

Princeton and Oxford

Copyright © 2013 by Princeton University Press
Published by Princeton University Press, 41 William Street, Princeton,
New Jersey 08540

In the United Kingdom: Princeton University Press, 6 Oxford Street, Woodstock,
Oxfordshire OX20 1TW
press.princeton.edu

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Library of Congress Cataloging-in-Publication Data

Vogel, Steven, 1940–

Comparative biomechanics : life's physical world / Steven Vogel ; illustrated
by Annette de Ferrari. — Second edition.

pages cm

Includes bibliographical references and indexes.

ISBN 978-0-691-15566-1 (hardcover : alk. paper)

1. Biomechanics. 2. Physiology, Comparative. I. Title.

QH513.V643 2013

571.4'3—dc23

2012037463

British Library Cataloging-in-Publication Data is available

This book has been composed in Sabon with Myriad Pro display
by Princeton Editorial Associates Inc., Scottsdale, Arizona.

Printed on acid-free paper. ∞

Printed in the United States of America

10 9 8 7 6 5 4 3 2 1

Comparative Biomechanics

Also by Steven Vogel

Cats' Paws and Catapults: Mechanical Worlds of Nature and People

Glimpses of Creatures in Their Physical Worlds

Life in Moving Fluids: The Physical Biology of Flow

The Life of a Leaf

Life's Devices: The Physical World of Animals and Plants

Prime Mover: A Natural History of Muscle

Vital Circuits: On Pumps, Pipes, and the Workings of Circulatory Systems

PREFACE

COMPARATIVE BIOMECHANICS, MEANING A BROADLY BIOLOGICAL RATHER THAN a narrowly human subject, deals with the cheap, physical stuff—to rehabilitate a phrase from my youth. It worries about why trees so rarely fall over, why legged creatures switch from walking to running at particular speeds, how slugs slither, how flies fly, how samaras spin. In short, it starts with the ordinary activities of ordinary organisms, posing the questions a person might ask while exploring a coastline or tramping through a forest.

What draws its particular questions together is the kind of explanations to which they yield. Initially, at least, they draw on a physical and macroscopic world, a world closer to the purview of mechanical engineers than that of most contemporary biologists. The bad news is this unfamiliarity of its context. But that's a minor snag next to the good news—its wonderfully commonplace character. Comparative biomechanics invokes notions closer to one's everyday experience and intuitive sense of reality than does any other area of contemporary science. Gravity and elasticity have an immediacy that cells and molecules, let alone galaxies and subatomic particles, do not.

Although that physical world may be immediate and attractive, we have to face the fact that neither explaining nor quantifying it draws on well-used items in the biologist's intellectual toolbox. The present book tries to lead the reader into that world as gently as the author knows how; it tries both to make the case that biomechanics matters and that the subject need not be approached with fear, trepidation, and dark memories of first-year physics. It tries to demystify biomechanics, making it something to bear in mind, something to pursue more specifically when it proves relevant to a particular question, whatever the origin or context of the question. The field shouldn't be the private domain of initiates, isolated and insulated within its jargon and journals.

The primary purpose of the book is to provide a basic textbook for undergraduates and graduate students who may have taken an introductory biology course but who've had minimal exposure to physics and mathematics and none to engineering. It reflects about 25 years of offering—or co-teaching—such a course. My perception of the needs of students and investigators in the field has defined the level and scope of the book.

Based both on my aspirations and experience with the first edition, I intend a wider role for the present edition, in fact several of them. Even the course served a wider group, as about a third of the students came from engineering, and it usually attracted a small but diverse scattering of other people. But my correspondence made clear that “textbook” in the present sense didn't fully

describe the first edition's readership. Biologists outside the biomechanical community seemed to have found it a useful reference. People involved in human biomechanics—kinesiologists, exercise scientists, orthopedists—took notice of it. Engineers appeared to use it as a window on what we biologists of a biomechanical persuasion spend our time doing. An institute focused on biomimetics mined it for portentous ore. And the hands-on, macroscopic character of the material drew attention from science museums. For that matter, the book grew out of (by way of *Life's Devices*, a predecessor) a course for adult nonscientists that used the very commonplace character of biomechanical questions as a way to get them thinking in scientific terms rather than simply seeing science as a body of someone else's knowledge.

When I decided to have a go at a proper textbook, I sent e-mailings (e-missions or e-missives or e-missiles?) to all the people I knew who might be teaching comparative biomechanics to undergraduates. The overwhelmingly positive response came as no surprise—what had anyone to lose? What mattered more were all the useful suggestions, lists of references, and offers to test-run any preliminary version. A little worrisome, though, were the course outlines. With no standard book or long tradition, courses were divergent and eclectic; I envisioned a bunch of people waiting for the book, each with the expectation that it would follow a specific course description sent in a couple of years earlier.

And that brings up a problem that remains. Breaking with some canon is one thing, inadvertently creating a canon in a field blessedly unconstrained by one is quite another. So I must admit at the start, if more as warning than apology, its unavoidably idiosyncratic content. More deliberate is its equally idiosyncratic style. No generally accessible area of science better illustrates the way science is a process and a perpetual work-in-progress, and I've tried to give a sense of that reality with anecdotes, examples, and suggestions—but as best I could distinguishing the accepted from the opinionated. Similarly, I've included a fair dose of experimental particulars to connect the book to the reality of doing biomechanics, whether retrospectively or prospectively.

Content. Biomechanics covers an awesome diversity of things. The sheer mass of the book (and its 260,000 words) may strike the reader as some assurance of comprehensiveness (never mind comprehensibility). Do not be misled—major areas of perhaps equivalent relevance have been left out. Indeed, I've been driven nearly nuts deciding what to put in and what to leave out. My first rule has been to begin at the beginning, focusing on material that forms the background needed to go further into the subject. My second has been to pick material that tells useful stories, cases with general explanatory value. And my third has been to focus on topics that could be presented without presuming much background in the particulars of other areas of biology—and the various fields of biology have no end of particulars. And, good intentions aside, one tends to use material with which one is familiar, biasing coverage toward one's own work and that of associates.

As a result, the relative emphasis on different subjects doesn't reflect the relative attention they've received by investigators or my full judgment about relative importance. In particular, it has led to an underrepresentation of "hard" subjects, such as unsteady flows, computational approaches, and the work of some of the most impressive current investigators. As a further consequence, subjects whose understanding depends on a lot of morphological information have been given short shrift—however impressed I remain with what functional morphologists have done in recent years. Locomotion gets the

lion's share of current effort; it's not an equivalent presence in number of pages here. Concomitantly, animals get more attention than plants; I've no brief for equal time, but sap and wood matter at least as much as blood and bone. Paleobiomechanics gets ever more interesting, but I felt myself too far from the subject to have any decent perspective. And so on.

Organization. We're dealing with a subject lacking an obviously sequential character. So I've mostly made up the sequence of presentation myself, and I present it with no great conviction of its superiority, with a sense of fairly arbitrary decisions forced by the linearity of pagination. But I have tried to facilitate the use of the book by courses with different sequences, at least as far as I could with naturally interdependent topics. Part one serves a role that's both necessary and initiatory—although engineers may find most of it laughably primitive. In contrast, parts two and three can be done with either coming first or, for short courses, omitting one or the other. Part four forms a coda that can be used in its entirety, or in part, or augmented, or else ignored altogether. On a finer level, certain chapters can be omitted without laying traps that will catch the reader further along—in particular, chapters 10, 13, 14, 18, 22, 25, and, of course, 26. Gaining versatility, though, has cost some redundancy. Once again, I'm painfully conscious of the possibility that I may be *de facto* defining a canonical course in comparative biomechanics, and I want to impose as few constraints as possible.

Level. The course I gave preredquired basic college physics and calculus, which I could afford to do, because we required no less for our biology majors. But I've never been particularly taken with the choice of material of basic physics courses, and the book has had to cover for the way those courses avoided fluids, dimensionless numbers, nonrigid materials, and structures (beams and columns). Chapters 2 and 3 provide some extra background; more will be found in the appendices—enough, I hope, so even someone who has not taken a physics course can manage.

What's different in this second edition? The first chapter has been shortened, and quite a bit of the material in what were chapters 2–4 has been moved to appendices—both changes were made to move more quickly into the subject proper. Surface tension, shells, specific solid materials, viscoelasticity, and friction receive more attention. What had been chapter 5 is now chapters 4 and 5; what had been 16 is now 16 and 17. Most chapters now end with problems for students—or compulsive readers. And the references are considerably greater in number as well as more recent, the last recognizing that the 10 years between editions have seen a host of rich additions to our field.

A few other prefatory notes:

- The choice of symbols may strike the nonbiomechanic as inefficient or worse. I've tried to follow the conventions used in more specialized books, especially the ones by engineers. The awkward consequence is a marriage of various fields, traditions, and histories, in particular because solid and fluid mechanics have been pursued by different people.
- The extensive references to the primary literature in the text may be a bit unusual for books intended for undergraduates, but much of the biomechanical literature ought to be accessible to them. In addition, I want to encourage use of this book as an entry point into the field for anyone who wants one. I strongly recommend that the rapidly superannuating references be

popped into one or another forward-searching (“cited by”) engine, such as Google Scholar or Web of Science.

- Nonbiologists might find it useful to buy some old (thus cheap) edition of an introductory biology textbook—all have copious indices and, even for terminological matters, will be more useful than a biological dictionary. Alternatively, instructors can accumulate a pile of loaners from the recipients of publisher’s samples. My experience indicates that returns hit 100 percent when you suggest that return of the loaner is prerequisite for getting a grade.
- A collection of teaching resources may be obtained for the asking; for more information, please visit <http://press.princeton.edu/titles/10046.html>. These include suggestions for classroom demonstrations, small out-of-class projects, useful web sites, and so forth—plus an ongoing list of errors that have turned up in the text. Contributions to the collection will be welcomed. Most of that material can also be found under “biomechanics” on the web site of the Society for Integrative and Comparative Biology, <http://www.sicb.org/dl/>.
- Physicians take an oath by which they promise at least to do no harm; textbook writers should take an equivalent oath at least to tell no lies. For some subjects, that’s no simple matter.



The number of people who have helped me in this endeavor goes beyond what I can conveniently list here. Students, other faculty members, other writers, and friends began contributing long before the book became a specific task and continued to respond to queries right up to submission time. And I kept no proper list. I note, with appreciation and good memories, that the first edition was sketched out while I was a guest at the Raman Research Institute in Bangalore, India—I’m grateful in particular to my host, V. Radhakrishnan (“Rad”). Several chapters were written at the Friday Harbor Laboratories, San Juan Island, of the University of Washington, where I enjoyed residence at the Whiteley Center—I must especially thank Arthur Whiteley and Dennis Willows. I wrote in a room called “Arthurs’ Study”—the position of the apostrophe alludes to Arthurs Martin and Whiteley, both of whom, as it happens, appear in the present references. Gestation of the present edition took place at Croasdaile Village, in Durham, North Carolina, distracting me from proper participation in the community.

Most of the drawings here are the products of Annette deFerrari, although I’ve reused ones done by Susan Tanner Beety, Rosemary Calvert, Kate Davis, and Sally Schrohenloher. All the illustrations have been drawn specifically for this or my previous books, although a few represent only slight modifications of specific originals. Where single published sources have been used, acknowledgment of permission has been made in the legends.

Finally I want to thank the people at Princeton University Press, a publisher with whom I have had a long and productive association. This book would not have happened without the timely and effective urging of Alison Kalett. And Natalie Baan, Quinn Fusting, and Dimitri Karetnikov have pushed the project along with remarkable—and again effective—expeditiousness.

CONTENTS

Preface vii

PART ONE *Life's Physical Context* 1

- 1 Preambulations 3
- 2 Setting the Stage 11
- 3 More Tools 29

PART TWO *Fluids* 51

- 4 Gases and Liquids: Fluids at Rest 53
- 5 Gases Meet Liquids: The Interface 71
- 6 Viscosity and the Patterns of Flow 87
- 7 The Forces of Flow 111
- 8 Fluid Events Near Surfaces 141
- 9 Where Flows Are Inside 163
- 10 More about Circulatory Systems 183
- 11 Flows in Small Worlds 207
- 12 About Lift 225
- 13 Thrust for Flying and Swimming 251
- 14 Motion at the Air-Water Interface 271

PART THREE *Solids and Structures* 285

- 15 A Matter of Materials 287

16	Biological Materials: Tuning Properties Properly	313
17	Biological Materials: Cracks and Composites	329
18	More about Complex Materials: Viscoelasticity	347
19	Simple Structures: Beams, Columns, Shells	363
20	Less Simple Structural Matters	389
21	Hydrostatic Structures, Hydraulic Devices	407
22	Structural Systems	425
23	Motility and Mobility	449
24	Using Muscle: Tuning and Transmissions	473
25	Getting Around on Land	491

PART FOUR

The Contexts of Biomechanics 513

26	Loose Ends and Perspectives	515
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APPENDICES

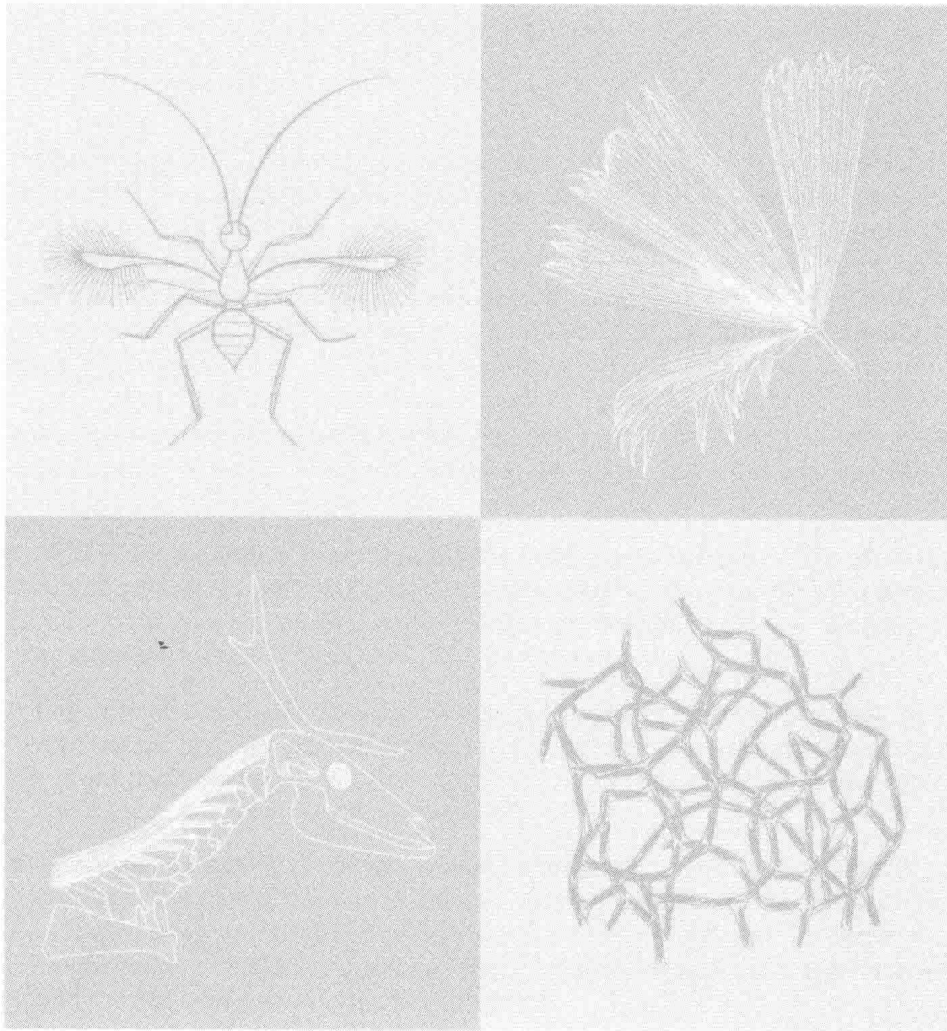
1	Quantification: Rules of the Road	537
2	Motion and Direction	547
3	Size and Scaling	553

List of Symbols 565

References and Index of Citations 567

Subject Index 601

Life's Physical Context



Here we take a quick look at the contexts of biomechanics—physical, mathematical, and biological. After setting the stage with a sampling of the kinds of questions of interest in biomechanics, we introduce the relevant physical variables and talk about how they can be manipulated. And we look at the basic issues raised by the extreme variability of both the sizes and shapes of organisms.

Preambulations

WHERE TO START? DOING SCIENCE INVARIABLY STARTS WITH A QUESTION ABOUT the world around us, sometimes a qualitative one, sometimes a quantitative one. As much as their histories and techniques, what separates one field from another is the questions each poses—what each is trying to figure out. So we begin with a scattershot sampling of biomechanical questions. The only criteria for choice are their ease of description and their discussion in later chapters of this book.

- As you increase the speed at which you move, at some point you shift from walking to running. What distinguishes the gaits, and what sets the transition point?
- Almost all mammals devote about the same fraction of their blood to red blood cells. But marine ones typically concentrate their red blood cells further. What sets the normal concentration, and what might marine animals accomplish by going higher?
- One often hears claims that the silks made by spiders have spectacularly good mechanical properties. Putting aside that judgmental assertion, their properties are certainly unusual. Why might the task of, say, an orb-weaving spider call for a particularly peculiar material?
- Almost all mammals (including ourselves) have about the same resting blood pressure. But those taller than humans generate higher pressures, with the tallest animals (giraffes) holding the record. Why this shift (at about our height) from constant and size-independent pressures to those that increase with height—and what sets the shift point?
- A diverse but limited fauna moves about on the surface of ponds, lakes, and streams—water striders, a few running lizards, and some swimming waterfowl. Far more creatures swim fully submerged. What special problem does surface swimming pose—or are there multiple problems, dealt with in separate ways by these three groups?
- For the past 300 million years, tree-like plants have topped out at about the same maximum height. Trees face strong winds with leaves of large surface areas borne high above the ground—and thus risk breaking or uprooting. What sets that maximum tree height, and what special tricks might decrease their chances of failure?

Physics-envy is the curse
of biology.

JOEL COHEN,
biologist

Questions such as these could not be closer to everyday experience. That's not just because I've selected them for easy description, but also because this field of comparative biomechanics addresses just such mundane matters, ones that might well have been raised at the beginning of that mode of inquiry we call "science." Yes, they're all mechanical, but if "mechanics" raises the specter of some formidable physics course, set your mind at rest. Not only does no area of contemporary, grown-up science take as its subject anything closer to home, but also no area gives greater explanatory yield for such small investment. Although our educational systems take little advantage of it, the subject provides a first-rate place to start thinking as thinking is done by a scientist starting some investigation—making "science" into a verb. After all, addressing the unnoun is the mission of science.

Joining Physical and Biological Worlds

These questions may be mundane, but they fit awkwardly within science as we've divided the enterprise over the past few centuries. They may address a general issue—the ways organisms deal with their immediate physical worlds—but their explanations draw on an odd combination of fields. Sometimes it helps to ask just who lives where, using habitat differences to explain why a structure in one kind of creature probably helps with a function that arises in its particular location. Sometimes we get hints about how organisms operate from their evolutionary histories—the stories of their lineages, ancestries, and, especially, convergences. Sometimes we draw on what might be learned in a physics or engineering course. And sometimes we look at how our measurements on organisms fit computational or mathematical models. Occasionally, chemistry or geology can help us, but they're of less help than in other areas of biology. So, although our field may be nothing if not ordinary in content, its context is a little unusual and needs a few words right up front.

We might begin by stepping back a little. Biology conveys two curiously contrasting messages. In a strictly genetic sense, all organisms are unarguably of one family. Our numerous common features, especially at the molecular level, indicate at least a close cousinhood, a common descent from one or a few very similar ancestors. But what a gloriously diverse family we are, so rich and varied in size and form! The extreme heterogeneity of life impresses us all—trained biologists or amateur naturalists—with the creative potency of the evolutionary process. The squirrel cannot be mistaken for the tree it climbs, and neither much resembles its personal ménage of microorganisms. The apposition of this overwhelming diversity with the clear case for universal kinship tempts us to assume that nature can truly make anything—that, given sufficient time, all is possible through evolutionary innovation.

Some factors, though, are beyond adjustment by natural selection. Some organisms fly, others do not, but all face the same acceleration stemming from gravity at the surface of the earth. Some, but not many, can walk on the surface of a body of water; but any creature that attempts the trick faces the same value of that liquid's surface tension. No amount of practice will permit you to stand for long in any posture other than one in which your "center of gravity," an abstract consequence of your form, is above your feet. If an object, whether sea horse or saw horse, is enlarged but not changed in shape, the larger version will have less surface area relative to its volume than did the original. In short,

life must contend with an underlying extrabiological world. Put perhaps more pretentiously, the rules of the physical sciences and the basic properties of practical materials provide powerful constraints on the range of designs available for living systems—a point put persuasively by Alexander (1986).

Were these restrictions the extent of the physical world's impact on life, we might be content to work out a set of limits—quantitative fences that mark the extent of the permissible perambulations of natural design. However, they have a more positive side, at least from our point of view as observers, investigators, and rummagers for rules. The physics and mathematics relevant to the world of organisms are rich in phenomena and interrelationships that we find far from self-evident, and the materials on earth are themselves complex and diverse. Tiny cells with thin walls can withstand pressures that would produce a blowout in any of our arteries. Yet the materials of cellular and arterial walls have similar properties. The slime on which a snail crawls may alternately be solid enough to push against and sufficiently liquid for a localized slide. An ant can lift many times its own weight with muscles not substantially different from our own. (But ants can produce no Prometheus—as Went, 1968, remarked, the minimum sustainable flame in our atmosphere is too large for an ant to come close enough to add fuel.) By capitalizing on such possibilities, the evolutionary process provides unending fascination as a designer of the greatest subtlety and ingenuity.

This book looks at the ways in which the world of organisms bumps up against an extrabiological reality. Its theme is that much of the design of organisms reflects the inescapable properties of the physical world in which life has evolved, a world that at once imposes constraints and affords opportunities. In one sense, the book is a long essay defending that single argument against a vague opponent—the traditional disdain for or disregard of physical science by biologists. In practice, the theme will function mainly as a compass in a walk through a miscellany of ideas, rules, and phenomena of both physical and biological origin. We'll consider, though, not the entire range of biologically relevant parts of physics, but a limited set of mostly mechanical and largely macroscopic matters, a domain more commonly claimed by mechanical engineers than by physicists.

The macroscopic bias should be emphasized. In places, this book deals with some rather bizarre phenomena, but it never gets far from the kind of everyday reality involved in shifting from a walk to a run. Where possible, explanations will deliberately ignore the existence of atoms and molecules, waves and rays, and similar bits of *deus ex machina*. Not that the latter aren't as real as our grosser selves (or so implies overwhelming evidence); rather, as bases for explanations, they have an unavoidable air of ecclesiastical revelation. More importantly, bringing an understanding of these concepts to the point of helping a person take a more ordered view of our particular domain would take far more than a single book. For instance, can you think of any element of your perceptual reality that demands the odd assumption that matter is ultimately particulate—that if you could slice cheese sufficiently thin, it would no longer be cheese? Maybe the invocation of atoms by Democritus was just a lucky guess, an accident of his inability to imagine anything infinitesimally small. Only for a few phenomena, such as diffusion, will we need to recognize atoms and a real world in which matter cannot be subdivided *ad infinitum*.

We may make too much of the distinction between biological and physical science, between living and nonliving devices. It certainly isn't a practice sancti-

fied by antiquity. A key element in developing the idea of conservation of energy was established by the German physician Julius Robert von Mayer in 1841 from observations on the oxidation of blood. The basic law for laminar flow of fluids in pipes was established at about the same time by the French physician Jean Louis Marie Poiseuille, who was concerned with circulatory systems (Pappenheimer 1984).

With separate histories for the past few centuries, physics and biology have developed their necessarily specialized terminologies in different and virtually opposite ways. Biology goes in for horrendous words of classical derivation, from *Strongylocentrotus droehbachensis* (a species of sea urchin, whose roe some consider a delicacy) to anterior zygapophysis (a particular protuberance on a vertebra). To reduce misunderstanding and terminological controversy, each term has been defined in a manner more precise than your workaday household noun. That the jargon tends to exclude the uninitiated and those without youthfully sponge-like memories receives (for better or worse) little consideration.

In contrast, physics and engineering eschew Greco-Latin obfuscation and pretension; by doing so, they create an equivalent difficulty. They take the most ordinary, garden-variety words and give them precise definitions that unavoidably differ from their commonplace meanings. Pulling something upward takes *work* but holding it suspended doesn't. *Stress* and *strain* are entirely distinct, the former commonly causing the latter. *Mass* is not *weight*, even if they're functionally equivalent on terra firma. The higher its *elastic modulus*, the less stretchy the material. Both physical and biological practices will plague the reader, but the first tends to be more subtly subversive—a bit of biological jargon may be jarring when you don't know its meaning, but the special technical definition of an ordinary word easily passes unnoticed.

One term from physics needs special attention at the start. Press and politicians presume that everyone (including themselves, of course) know what *energy* is. In reality, although it has a precise meaning in the physical sciences, the meaning doesn't lend itself to expression in mere words. Basic dictionaries and textbooks help little—they define energy as the capacity for doing work, unblushingly evading or offloading the issue. Feynman comes right out with an unusually candid admission (no company man was he, whether teaching or serving on the commission probing the space shuttle explosion of 1986). “It is important to realize that in physics today, we have no knowledge of what energy *is*. We do not have a picture that energy comes in little blobs of a definite amount” (Feynman et al. 1963).

In practice, the idea of energy explains so much—conservation of energy may be the greatest generalization in physics. Ultimately that's the advantage of energy. For us, this ubiquity can be a trap—it's all too tempting to hide behind a word with no easy definition and thereby avoid some crucial explanations. So word and concept will play only a minor role throughout most of this book.

The next chapters (and the appendices) are largely devoted to the task of establishing a necessary physical base, with a fair dose of the associated terminology. Biological terminology (and biology itself) will enter piecemeal—for present purposes, the physical material provides a better logical framework.

Adaptation and Evolution—The Biological Context

Nonetheless, the relevant biology also needs some introduction. I find it hard to avoid either “evolution” or “design” in any general discussion of how organ-