CHAPTER

Preambulations

> Physics-envy is the curse of biology.
>
> **JOEL COHEN, biologist**

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 make 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?

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 takes 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 though 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 sanctified 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 droehbachiensis* (a species of sea urchin, whose roe some consider a delicacy) to anterior zygopophysis (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 organisms are built and operate. In combination they represent a subtle contradiction. If the process of evolution is incapable of anticipation, that is, if it's blindly purposeless, the term "design" misleads—design ordinarily implies anticipation and purpose. The problem isn't just terminological. Why do organisms appear to be well designed if they're not designed at all? Perhaps we should to begin by reviewing the logical scheme for which "evolution by natural selection" is our facile encapsulation.

First, some observations (in logic, these would be axioms). Every organism of which we have any knowledge can produce more than one offspring, so populations of organisms are always capable of increasing. But it takes some minimum quantity of resources for an organism to survive and reproduce; and in the long run, the resources available to a population are never unlimited. Next, three consequences of the observations. A population in an area ought to increase to some maximum. Once that maximum is reached, more individuals will be produced than can find adequate resources. So some individuals will not survive and reproduce. Then two further observations. Individuals in any population vary in ways that affect their success in reproduction, and at least some of that individual variation passes on to their offspring. And then the final consequence. Characteristics that confer increased relative success in reproduction will appear more often among the individuals of the next generation. We say, in short, that these features will have been "naturally selected." By that we mean selection among preexisting variations, not design in our usual intentional sense.

Figure 1.1a casts the model as a feedback loop—a positive feedback system that feeds on its own success. The indirect character of natural selection as an agent becomes evident when the system is contrasted with the more direct one of figure 1.1b. Darwin could not exclude this second one; we now can—acquired characteristics are not ordinarily inherited, Lamarck and Lysenko notwithstanding. At this level, the model is about the least controversial item of modern biology—every aspect has been observed and tested, and competing models for the generation of biological diversity (even if without logical flaw) uniformly fail to correspond to reality. Indeed, given geological time and the variation generated by an imperfect hereditary mechanism, how could evolution have been avoided? Where argument remains, it devolves about details—whether the process is usually steady or episodic, the roles of specific genetic mechanisms (such as sexual recombination), the relative importance of selection and pure accident, and so forth. The model leaves no place for anticipatory design, and it doesn't require (and no evidence supports the notion) that environmental challenges determine the character of the variation on which natural selection acts. But, as a moment's consideration should persuade you, most results of such selection look as if deliberately designed. How come?

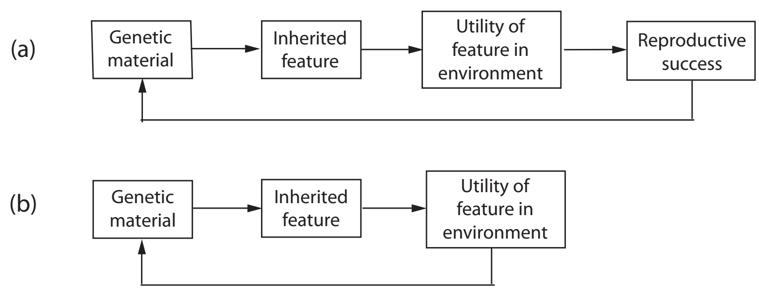

FIGURE 1.1 Logical schemes for self-improving systems. (a) The indirect mechanism of evolution by natural selection, the dominant evolutionary device of life on earth. (b) A more direct mechanism involving perpetuation of advantageous acquired features.

Quite clearly selection operates most directly on organisms, not on cells or communities. An organism is the reproductive unit, and its success in engendering progeny defines its "fitness." (Some adjustment has to be made for indirect contributions by way of aiding the reproduction of one's kinfolk or perhaps other associates, but that's of little present concern.) The selective process knows next to nothing about species; despite casual statements to the contrary, it does little if anything "for the good of the species." Nor does the process care directly about parts of an organism. Legions of cells die on schedule in the development of an individual; in no way can we speak of such cells as more or less "fit" than any others. A tree commonly sheds leaves; those leaves were not less fit than its others—the term "fitness" is inapplicable to the leaves, referring only to the reproductive potential of a potentially reproductive individual, here the whole tree.

Because this book focuses on organisms, it considers a level of biological organization on which the invisible hand of the selective process should have fairly immediate consequences. That immediacy makes organisms appear well designed—as a colleague of mine put it, "The good designs literally eat the bad designs." But note again the unusual sense in which we use "design," implying only a functionally competent arrangement of parts resulting from natural selection. In its more common sense, implying anticipation, it's a misnomer—it connotes the teleological heresy of goal or purpose. Still, talking teleologically provides verbal simplicity—teeth are for biting and ears for hearing. And the attribution of purpose isn't a bad guide for investigations—biting is more than an amusing activity incidental to the possession of teeth. If some arrangement in some organism seems functionally inappropriate, the most likely explanation (by the test of experience) is a faulty view of its functioning. As a late-nineteenth-century physiologist Ernst von Brücke supposedly said, "Teleology is a great mistress, but no one with whom you'd like to be seen in public" (Gray 1893, quoted by Swanson 1973).

We functional, organismic biologists are sometimes accused of assuming perfect design in the living world, largely because we find the presumption of a decent fit between organism and habitat a useful working hypothesis. For some, "adaptationism" has become a pejorative term (see, for instance, Gould and Lewontin 1979) for the practice. Admittedly, taking literally a mere verbal convenience or baseline presumption is all too easy. Showing that a particular structure both serves some particular function and evolved under selection for just that function isn't trivial. No direct functional test in the laboratory can prove such a point. One must turn to comparisons among organisms whose evolutionary ("phylogenetic") relationships have been determined. Harvey and Pagel (1990) face the issue directly; we'll return to it in chapter 26.

Furthermore, nature's designs must be imperfect. At the very least, perfection would require an infinite number of generations in an unchanging world, and "unchanging" implies not just a stable physical environment but also a preposterous scenario in which no competing species underwent evolutionary change. Beyond that, we're dealing with an incremental process of trial and error. In such a scheme, major innovation is no simple matter—features that might ultimately prove useful will rarely persist through stages in which they do no good. So-called hopeful monsters are not in good odor. So many good designs must not be available on the evolutionary landscape because they involve unbridgeable functional discontinuities. Because they entail milder transitions, jury-rigged arrangements occur instead. This ad hoc character of many features of organisms provide evidence of the absence of a rational designer. They're recounted with grace and wit in some of the essays of the late Stephen Jay Gould; his collection titled *The Panda's Thumb* (1980) is particularly good. Finally, a fundamentally poorer but established and thus well-tuned design may win in competition with one that's basically better but still flawed—paleontologists call this the "privilege of incumbency."

I make these admittedly abstract points with some sense of urgency, because this book is adaptationist in its outlook and teleological in its verbiage. The limitations of the viewpoint won't get much attention, so the requisite grain of salt should be kept in the mind of the reader—as well as the author.

In the end, this book is about organisms rather than physical science—the latter simply contributes tools to disentangle aspects of the organization of life. But, beyond using physics to organize the sequence of things, we'll take an approach more common (historically, at least) in the physical sciences. Biologists love their organisms, whether singly, collectively, sliced, macerated, or homogenized. Abstractions and models are vaguely suspect or reprehensible. As D'Arcy Thompson (1942a,b)—the godfather of our subject—put it, biologists are "deeply reluctant to compare the living with the dead, or to explain by geometry or by mechanics the things which have their part in the mystery of life." But we will repeatedly use the dead to explain the living. Explanation requires simplification, and nothing is so unsimple as an organism. And the most immediate way to simplify capitalizes on nonliving models, whether physical or (even) mathematical.

The Two Fields of Biomechanics

We come back down to earth with a few words to show how our subject nestles in its niche among the various areas of biology. At present, biomechanics consists of two distinguishable fields. Current usage, at least in North America, considers "biomechanics" without further qualification as a branch of human functional biology. Its concerns include the efficient design of devices to be used by humans, mechanical prostheses, locomotion as related to rehabilitation or athletics, and similar matters. It has several specific journals and active national and international organizations; its practitioners mostly inhabit departments of physical education and schools of engineering and medicine.

The other field looks at biological systems in their full diversity of size, structure, ancestry, and habitat. It considers biological materials, structural mechanics, and every kind of locomotion. It looks at fluid mechanical matters from how organisms, both plants and animals, resist the forces of flow to the operation of circulatory and other internal fluid transport systems. It asks questions about both living and extinct organisms and about how environmental factors impinge on biological design. As implied earlier, it looks at how the design and operation of organisms reflect the values of physical variables, such as gravity, viscosity, elastic moduli, and surface tension.

Some of us have begun calling the latter field "comparative biomechanics" to draw a distinction analogous to that between, on the one hand, "comparative anatomy" and "comparative physiology," and, on the other, the human or medical analogs, usually just "anatomy" and "physiology." The field is part of a larger subject most succinctly described as the study of function at the level of the organism, or more formally as physiology and functional morphology.

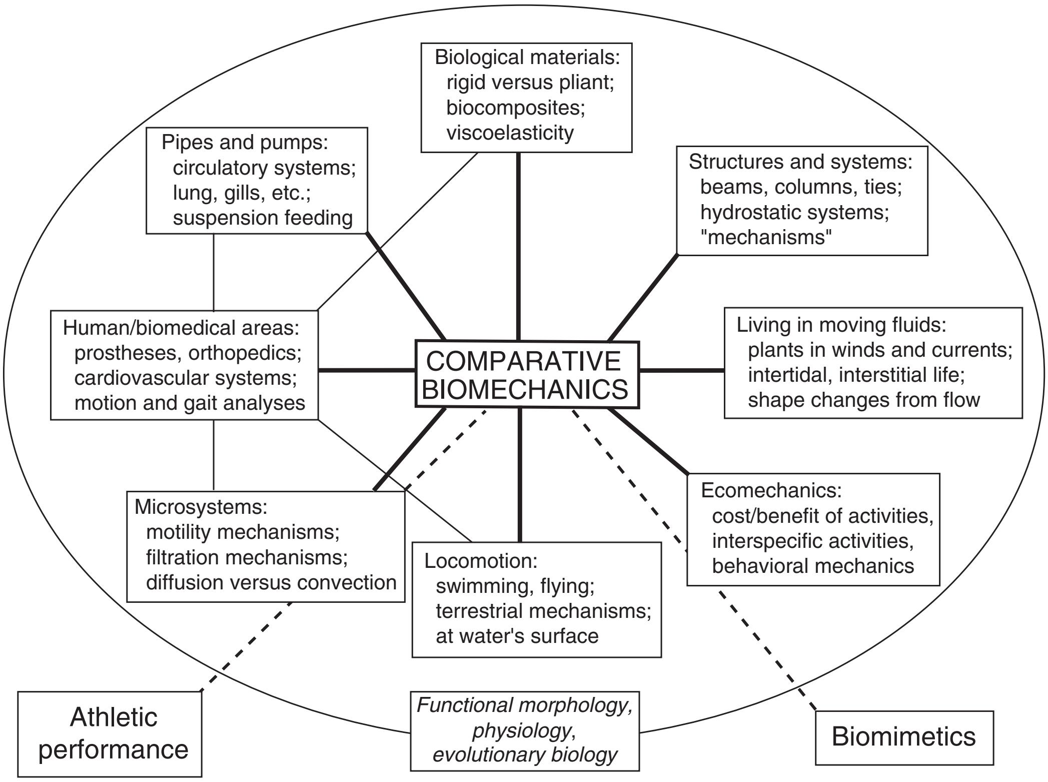

FIGURE 1.2 An opinionated view of the place of comparative biomechanics in the larger world of biology, medical science, engineering, and so forth. I put athletics and biomimetics outside as being only indirectly biomechanical.

Figure 1.2 shows where it sits among its academic sisters, and its cousins, and its aunts.

Comparative biomechanics can claim no historical novelty—it traces its ancestry at least to Borelli's *De Motu Animalium* of 1680 and perhaps to Aristotle's work of the same name. But by at least one measure, it appears to be enjoying a renaissance. I've done some (admittedly subjective) counts of the abstracts for the annual meetings of the Society for Integrative and Comparative Biology (formerly the American Society of Zoologists). Identifiably biomechanical contributions increased from about 5 to 12 percent between 1985 and 1995; by the 2001 meeting, the fraction had increased to 27 percent, and it's now running at about 33 percent. A similar picture emerges from the tables of contents of issues of the *Journal of Experimental Biology.* But by contemporary standards, it remains a relatively unpopulated field—lots of good problems relative to the number of investigators. So even a newcomer can stake a claim to a decently extensive chunk of the world it explores.