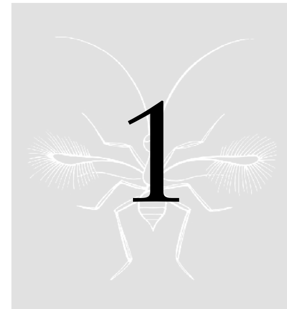
CHAPTER 1



Preambulations

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

WHERE TO START? PERHAPS THE WORLD OF BIOMECHANICS CAN BEST BE introduced by looking at several specific situations, matters part of—or at least close to—your everyday experience. If "mechanics" raises the specter of some formidable physics course, set your mind at rest. No area of contemporary, grown-up science takes as its subject anything closer to home. And no area gives greater explanatory yield with as little investment. So we begin not just with questions posed but with questions answered—at least as part of our open-ended work in progress—questions that might occur to any ordinary person.

How Walking Hits a Speed Limit

Consider an especially literal "preamble." Think for a moment about how you move about on your hindlegs. Ordinarily you walk, swinging your legs alternately back and forth. Pressed a bit, you break into a trot, an easy jog; pressed harder, you run. But note what you've long known but may have never thought about. You don't make a continuous transition between a walking gait and any trotting or running gait. No—the shift is abrupt, and at no point have you the least doubt about which you're doing.

Questions. What's the basic difference between walking and running, and why do you make this abrupt shift? At what speed do you make the shift? Do other legged creatures shift gaits at the same speed or do they at least shift at a speed determined by the same rule we feel compelled to obey?

Walking versus running. Formal recognition of the most obvious distinction between the two goes back to Weber and Weber (1825). When walking, each leg contacts the ground for more than half of each stride, so you always have at least one leg on the ground. When running, each leg stays in contact less than half the time, so you're fully airborne for a time, twice during each full stride. True enough, but it doesn't lead us very far. Less obviously, you go up and down as you move forward. When walking, your body is highest in midstride, when one or the other leg extends almost vertically. By contrast, when running, your body is slightly higher near the extremes of a stride, with one leg extended forward and the other backward. As first recognized by R. McNeill Alexander, this difference in the body's trajectory says more about why we make the transition; his extensive investigations, starting in the late 1970s, have left little doubt about at least the general picture of what's going on.

The underlying problem emerges from a basic feature of animal propulsive systems. Almost all the appendages with which animals push backward on air, water, or the earth's surface reciprocate rather than rotate. Going back and forth (or up and down) means repeatedly starting and stopping legs, fins, wings, and such. And that means accelerating and decelerating masses, which takes force and ultimately energy, force and energy beyond whatever gets usefully invested in propulsion. In short, locomotion with reciprocating appendages suffers a disability that wheeled vehicles never run up against. Consider—you can dramatically reduce the total energy you need to cover a given distance by riding a bicycle, despite the fact that you're now hauling around 20 or 30 percent more mass.

While nature has never achieved a large-scale solution to the problem (as human technology does with rotating propellers and wheels), she has repeatedly come up with at least a partial fix, a way to reduce that accelerative-decelerative cost. The trick consists of storing the braking energy of deceleration for reuse in the subsequent acceleration. Put another way, instead of doing work on the system to stop an appendage's motion, the system does what can be described as "negative work"—it absorbs work for subsequent use.

But how to store the energy? In walking, gravity provides the battery, just as it does when we store energy as a mass of water behind a high dam. You work like a pendulum, which alternately trades off gravitational energy against kinetic energy. In the familiar version of figure 1.1a, gravitational energy is greatest at the high extremes of the swing; kinetic energy is greatest during the fast midswing. A pendulum banks the energy of motion as height and then withdraws it to reaccelerate. But the walking pendulum uses a less

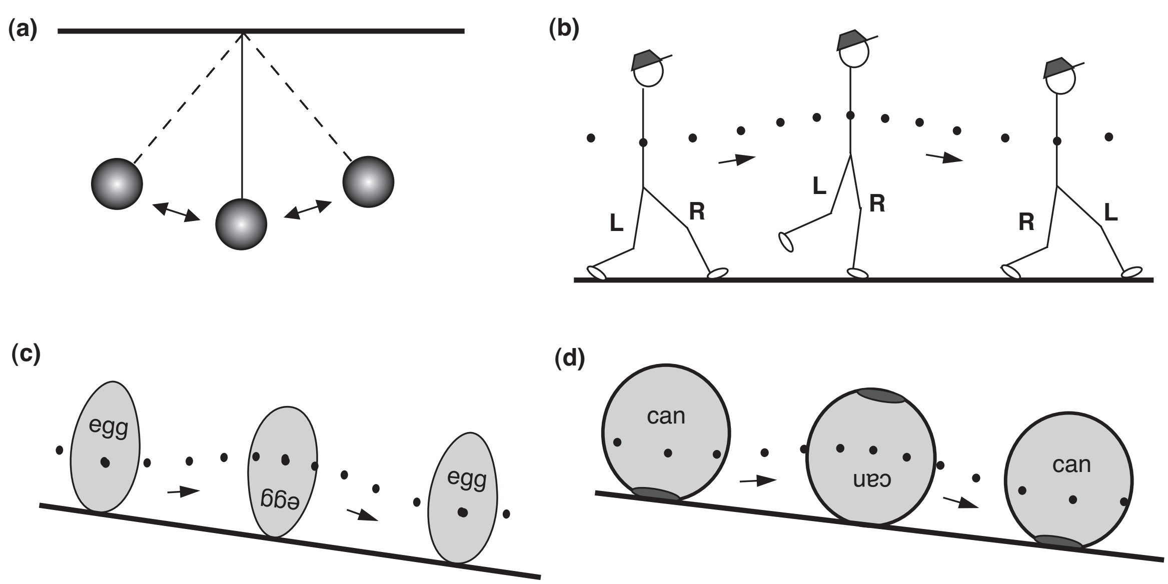


FIGURE 1.1 (a) A conventional pendulum, (b) the inverted pendulum model for walking, (c) an egg rolling down an incline, and (d) a cylindrical can with an off-center weight rolling similarly. In (b), (c), and (d), the centers of gravity are shown as dark spots—their spacings (assume equal time between adjacent spots) give their velocities.

self-evident version. When walking, your body (really your center of gravity) is lowest when your legs are furthest fore and aft, and it's highest in midstride when one or the other leg touches the ground directly beneath your torso. Concomitantly, your center of gravity moves most rapidly at the extremes of the stride and least rapidly at midstride—so gravitational and kinetic energies indeed interchange, pendulum-fashion, as in figure 1.1b.

An egg, rolling end-over-end down an incline (figure 1.1c) provides a partial model. Or, avoiding omelet, tape a weight to the inner side wall of an empty soup can and give it enough of a push so it rolls for a few turns, as in figure 1.1d. It will roll least rapidly when the weight is uppermost—when its center of gravity is highest—and fastest when the weight is at the bottom—when its center of gravity is lowest. So gravitational and kinetic energies rise and fall with opposite time courses, even if these models involve no sharp pendulum-like tuning. In short, we make use of the pendulum principle but, between motion of torso and jointed appendages, not in any simple manner.

Gravity, used pendulum-fashion, has its limits. In particular, it limits the frequency range over which a leg can be swung and a body raised and lowered, much the way a particular pendulum swings at a particular frequency. Try it—to go faster, you swing your legs farther rather than more often. But increasing the amplitude of leg-swinging can't be pushed too far, any more than a practical pendulum can swing through more than a limited arc. What Alexander (see Alexander and Jayes 1983; Alexander 1988) recognized was that this limit sets the maximum speed of a walking gait. To go faster and still store energy from stride to stride, you have to do something different—running gaits store energy elastically, mainly as stretched tendons, rather than gravitationally.

Identifying the nature of the shift leads directly to a prediction about how the shift ought to vary with the size of an animal. One can get a properly quantitative rule in several ways, all more-or-less equivalent in physical terms. All require some assumptions that sound hopelessly crude but are of a type that has been of great value for studies of how animals of different sizes are put together and how they carry out many of their activities. (The parent subject goes by the name of "scaling" and will be taken up in chapter 3). We assume, first, that legs (and bodies) resemble each other in proportions—that they're geometrically similar. Second, we assume that all legs get swung the same way—that strides are dynamically similar. Thus all can achieve about the same maximum swinging angle. Of course we've swept under the rug a staggering amount of biological variability, using the large size range of walking creatures to excuse our sin, and further admitting that we'll get only a crude rule.

Consider the textbook formula for the period of a pendulum:

$$t = 2\pi\sqrt{\frac{l}{g}}, \tag{1.1}$$

where t is the period, l is the pendulum's length, and g is the gravitational acceleration of a freely falling object. Assume that the top walking speed of an animal, v_{max}, will be proportional to its leg length divided by the swinging period of a pendulum of that length. Thus,

$$v_{\max} \propto \frac{l}{t} \propto \sqrt{lg}\ , \tag{1.2}$$

where ∝ is the symbol for "is proportional to"—it avoids confusing ourselves with numerical constants of little immediate relevance, and we'll use it often.

Does this work? An answer requires that we specify the length in the formula; the distance from hip joint to ground for a standing animal gets about as close to pendulum length as anything easy to measure and generally applicable. So we're asking whether any single constant of proportionality relates the maximum walking speeds of animals of all sizes to the lengths of their legs. We now have a great deal of data on the speeds at which animals switch from walking to some other gait, initially from the work of R. McNeill Alexander and C. Richard Taylor, each with various collaborators. And examination of the data indicates quite clearly that the formula does work. That body of data, together with the acceleration of gravity on earth (9.8 meters per second squared), produces a practical formula,

$$v_{\max} = 2.2\sqrt{l}, \tag{1.3}$$

with speed given in meters per second and length in meters. The constant can be trusted to about 10 percent each way, not bad when we're talking about animals whose leg lengths span several orders of magnitude. The number of legs per walker—two or four—makes no difference.

As ordinary animals, any one of us can try the formula. For instance, for a leg length of 1 meter (about my datum), maximum speed is 2.2 meters per second, or about 12.1 minutes per mile in the U.S. vernacular. One can walk faster, but the gait gets increasingly awkward and tiring as one does such tricks as rotating the lower back and swinging the hips to increase effective leg length and stride amplitude. The bigger person indeed makes the transition at a higher speed, and an adult walks alongside a trotting child or dog.

Application of the formula isn't limited to mice, elephants, and all extant animals in between. It tells us that a large dinosaur such as a brontosaurus could have walked very fast. Probably no adult brontosaurus did much running. Since walking imposes much lower stresses on the bones of an animal's legs than does running, the brontosaurus's large size might not have caused especially high leg loadings, and we needn't worry whether ordinary bone could support such a large creature. Alexander (1984) also showed that the footprints of some fossil hominids (the Laetoli footprints from Tanzania) were consistent with walking in a fashion similar to the gait of modern humans. But because of their shorter stature, these hominids would have gone more slowly than we do—instead of taking about 20 minutes to stroll a kilometer (the typical speed of a person in a small town), they would have required nearly 30.

We're clearly looking at a constraint that physics imposes on how we move, not at some mere accidental feature of a common vertebrate ancestor. And we have some answers to the questions posed earlier about the difference between walking and running and about the rule for the transition point. The story has a lot more bits and pieces, and we'll return to terrestrial locomotion on legs in chapter 24.

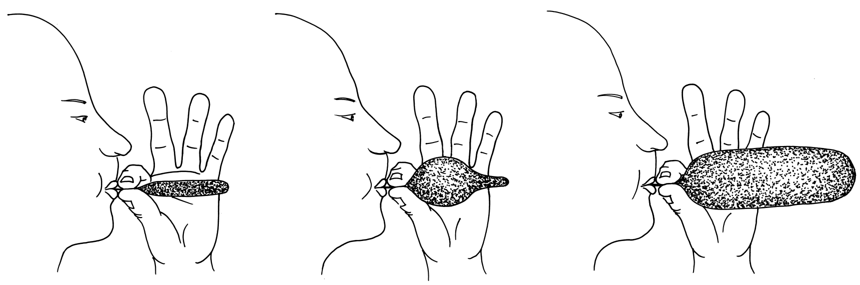


FIGURE 1.2 The way a cylindrical balloon inflates—an initial aneurysm doesn't quite burst but extends with little further expansion toward the balloon's ends.

How Arteries Inflate

Blow up a cylindrical balloon; one of any length will do. Notice the familiar—it doesn't inflate evenly. No, one part expands almost to the point of bursting, as in figure 1.2, and then the expansion extends lengthwise. We put up with this peculiar behavior in balloons, but it's not a nice thing at all when we're concerned with our personal, internal, pressurized cylinders—arteries, especially. Proper arteries need to be stretchy, like rubber balloons, if they're to reduce the pressure fluctuations of our pulsatile hearts. A ventricle, after all, produces no pressure output at all while refilling, and a rigid system of pipes would reflect that directly. But proper arteries need to be stretchy in a way quite distinct from the stretchiness of rubber balloons—physicians have long recognized a dangerous pathology, an aneurysm, when one part expands to near bursting before expansion elsewhere. Simple, rubberlike arteries simply won't do.

Now feel the surface of the balloon when partially inflated. Curiously, it feels as if it has a high-pressure region beneath the expansion and a lower pressure everywhere else. With no internal barriers, though, it's hard to imagine how the internal pressure can be anything but uniform throughout. So what you feel can't be place-to-place variation in the pressure difference across the balloon's walls. No, it's the degree to which the walls have been stretched by that constant pressure difference. Perhaps counterintuitively, the stretch ("tension") caused by a given pressure depends on the curvature of the cylinder's walls.

The rule turns out to be straightforward, dependent on simple geometry rather than on any arcane behavior of materials. Biologists usually refer to it as Laplace's law; we'll say more about it in chapters 3 and 20. Put explicitly, wall tension, T, equals transmural pressure, Δp, times radius of curvature, r:

$$T = \Delta p r. \tag{1.4}$$

Thus, a given transmural pressure difference generates more tension in the wall of a part of the balloon that has already begun to expand (greater radius of curvature) than in a part that has not. In ordinary rubber, extension is roughly proportional to stress applied, and so a given pressure extends the already expanded part more than the more flaccid unexpanded part. Only a slight extra resistance to stretch just before breaking makes cylindrical balloons practical at all.

In effect, Laplace's law rules out the use of ordinary elastic materials for arterial walls, requiring that an appropriate material fight back against stretch, not in direct proportion to how much it's stretched, but disproportionately as stretch increases. Which, again in obedience to the dictates of the real world, our arterial walls do—aneurysms, fortunately, remain rare and pathological. We accomplish the trick first, by incorporating fibers of a nonstretchy material, collagen, in those walls, and second, by arranging those fibers in a particular way. In an unstretched wall, the fibers are folded into kinks. Thus, as the wall expands outward, more and more of these inextensible fibers are stretched out to their full lengths and add their resistance to stretch to that of the wall as a whole—figure 1.3 gives the relevant histology in simplified form.

Arterial walls that resist stretch disproportionately as they extend characterize circulatory systems that have evolved within lineages quite distinct from our own—in cephalopods and arthropods, for instance. Recruitable collagen fibers don't represent the only possible solution to the basic problem, and they're not nature's inevitable choice. Laplace trumps Mendel—both microstructure and molecular composition differ far too much to support the idea of a common artery-endowed ancestor underlying the similarity in mechanical behavior. Yet the force-extension curves (technically stress-strain curves, as will be explained in chapter 4) match remarkably. At least they match when adjusted for the transmural pressure differences—blood pressures—that occur in the arteries of the different animals. And that permits an odd but useful prediction. If one has the force-extension curve for a sample of arterial wall, one can guess the arterial blood pressure of an animal. So from fresh samples of arterial wall, Shadwick (1994) estimated the blood pressure—about the same as our own, incidentally—of a giant squid, an animal that inevitably dies in the process of capture.

We'll return to circulatory systems in chapter 10.

How Weak Leaves Deal with Strong Winds

Next time a storm blows up, watch one or a few leaves on nearby trees; a pair of binoculars will help focus your attention and minimize the distraction of other storm-related activities. Where I live, maple, sweet gum, and tulip poplar leaves flutter and show their undersides with only modest wind; as the wind rises further the various oaks get into motion. Amid the swaying of branches one can easily miss noticing that few leaves flutter much when the wind rises to substantial intensity—any initial excitability dies down as if they're then taking the storm more seriously.

Leaves—trees, really—have a problem, the same one as our solar panels. Their function, trapping solar energy photosynthetically, demands exposure

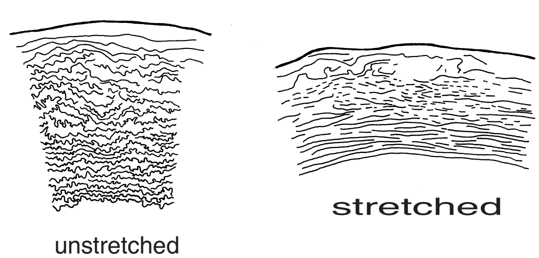


FIGURE 1.3 A bit of arterial wall, showing kinky fibers and the way they stretch out and take an ever-increasing fraction of the load.

of lots of area skyward. But biology compounds the problem. With adequate water and soil, more trees would like to expose more leaves to sunlight than their acreage allows. So trees compete, synthesizing great wooden columns that elevate their leaves above, ideally, those of neighboring trees. Few naturally isolated trees grow tall—competition drives trunks rather than any advantage from getting closer to the sun. Result? Large areas of surface well above ground level. Surface translates into drag; height translates into leverage; high wind then means real trouble, possibly breaking trunks or wrenching roots out of the ground. Figure 1.4 puts the matter diagrammatically.

What to do? Natural selection doesn't lend itself to any mutual trunk-reduction treaty. Streamlining (chapter 7) fits poorly with an area-maximization imperative. Building photosynthetic structures of sufficient rigidity that they stay parallel to the wind and don't flutter, the latter concomitant with high drag, takes lots of material and generates lots of weight. Nature does something relatively uncommon in human technology. She (by which pronoun we assume natural selection) arranges leaves and their attachments so they adjust their configurations and thus reduce their exposure and flutter as the wind increases. Motive force presents no problem, even for these nonmuscular structures, because the wind itself provides more than enough. Photosynthesis? Intermittently strong winds come mostly with reduced sunlight, so temporary reduction in exposure to sky can't entail a great long-term cost.

Here I refer to my own work (a privilege of writing the textbook oneself), in particular to a brief project (Vogel 1989) that took an initial (and thus far unpursued) look at what leaves do in winds that might put trees in (to use the political euphemism) harm's way. Figure 1.5a shows what one kind of leaf, that of a tulip poplar, does at a series of increasing wind speeds. This curling into a tightening cone characterizes quite a few kinds of leaves—

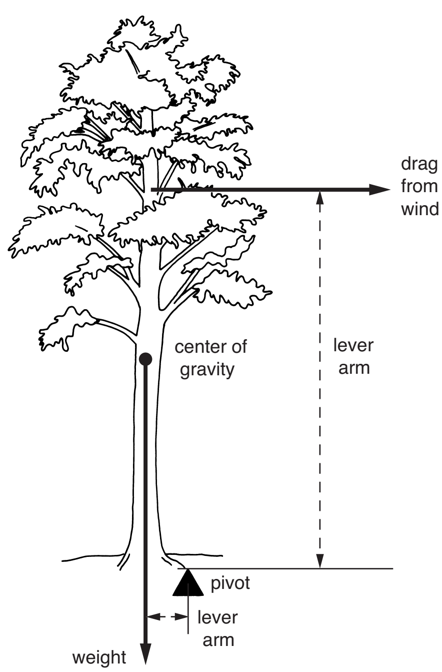


FIGURE 1.4 The problem of a tree in a wind—the sideways force from drag acts far above the tree's base, so its drag causes a large turning force. That must be resisted by the tree's weight, with the small lever arm given by the radius of its base. (Attachment to the ground also helps a little.) The advantage of minimizing drag should be obvious.

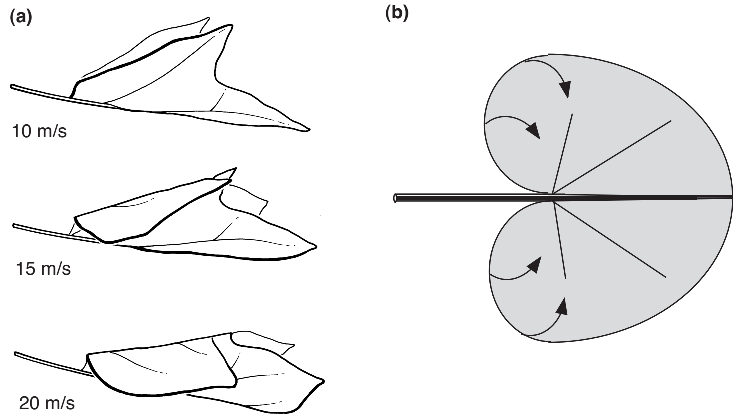


FIGURE 1.5 (a) The reconfiguration of a leaf of the tulip poplar tree (*Liriodendron tulipifera*) in an increasing wind. (b) The way the leaf's basal—hence upwind—lobes catch the wind and facilitate the process.

including maples, sweet gums, sycamores (plane trees), and redbuds among the ones abundant where I live. All are characterized by relatively long petioles (leaf stems) and lobes on their blades that protrude back toward their parent branches from the point of attachment of their petioles. What appears to happen (based on observation and crude models) is that the lobes, upwind because leaves always extend downwind like kites on strings, bend upward (abaxially, technically) and get the curling started, as in figure 1.5b.

This curling into cones dramatically decreases drag—at least if we pick the right item for a comparative baseline. Relative to surface area, the drag of a tulip poplar leaf at 20 meters per second (45 miles per hour) is only a third of that of a square flag that's free to flutter. Still, the drag remains several times higher than that of the gold standard, a rigid, flat plate oriented parallel to the wind. Another wind-dependent reconfiguration, one in which the leaflets of a pinnately compound leaf such as black walnut or black locust roll up around their axial rachis, does a bit better. Nor do these two exhaust the reconfigurational possibilities. The very stiff leaves on a branch of a holly (*Ilex americana*) swing inward toward the branch and lie, one against another, in a common sandwichlike pile. Pine needles cluster instead of being splayed outward. Yet other modes surely occur as well.

A common problem has called forth variations on a common mode of solution. Some, but not all, members of at least fifteen families of broad-leafed trees use the tulip poplar's conical reconfiguration, so it must have arisen on quite a number of separate occasions in the evolutionary history of these trees. The solution, again, is one we don't ordinarily encounter in the devices of our own nonbiological technology. It involves two aspects as common in nature's technology as they are rare in our own. First, shape isn't held constant, but rather shape and the forces of flow interact complexly, each dependent on the other. The local wind forces on a leaf depend (in part) on its shape; its shape, in turn, depends (in part) on the local wind forces. Second, variable circumstances are dealt with by altering functional priorities. Photosynthesis, overall, matters far more than drag minimization; in storms, though, such priorities must reverse.

But that distinction between what we do and what nature does pervades each of the three examples we've discussed. We usually put wheels on our vehicles and so needn't worry about pendulum-based cycle-to-cycle energy storage. We most often use rigid pipes (or at least ones of fixed maximum diameter) and do any buffering of pump pressure fluctuations elsewhere in our systems of plumbing. And we build stiff structures whose shapes vary little with the vagaries of environmental insults. Such comparison of human and natural technologies consumed an entire book I wrote a few years ago (Vogel 1998a). We'll return to the subject in chapter 25; until then human technology need be only a parenthetical presence. Still, it will be our constant companion. To be painfully honest, biomechanics has mainly been the study of how nature does what engineers have shown to be possible. Nature may have gotten there first, but human engineers, not biologists, have provided us with both analytical tools and practical examples.

Joining Physical and Biological Worlds

These stories about gait transitions, inflated arteries, and draggy leaves represent a concert of contexts—the properties of biological materials such as arterial walls, the fluid mechanics of laminar liquid flow through pipes and turbulent atmospheric wind, the evolutionary preference of organisms for doing things with minimal expenditure of energy, and the peculiar dependence of biological design and performance on the size of the organism. These matters, and most of what follows, address a single general issue, that of the ways organisms deal with their immediate physical world. Before going further, we ought to place that issue within biology. Biology, I mean to emphasize, is a particular and exceedingly peculiar domain.

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. On the other hand, 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 innovative 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 due to gravity at the surface of the earth. Some, but not many, can walk on the surface of a body of water; but all face the same value of that liquid's surface tension if they attempt the trick. 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 sawhorse, 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, there is an underlying world with which life must contend. 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 R. McNeill 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. There is, however, 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 vertebrate artery. Yet the materials of cellular and arterial walls have similar properties. The slime upon 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 no Prometheus could exist among ants—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 appears to our unending fascination as a designer of the greatest subtlety and ingenuity.

This book is about such phenomena—the ways in which the world of organisms bumps up against a nonbiological 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 it will be a long essay defending that single argument against a vague opponent—the traditional disdain or disregard of physical science by biologists. In fact, 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, matters 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 a kind of everyday reality—like shifting from a walk to a run. Explanations, where possible, 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 some very strong evidence); rather, as the bases for explanations, they have an unavoidable air of ecclesiastical revelation. More importantly, it would take far more space and complexity than a single book for them to help a person take a more ordered view of the immediate world. After all, can you think of any part 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 "invention" of atoms by Democritus was just a lucky guess, an accident of his inability to imagine anything infinitesimally small! Only when we consider diffusion and a few other phenomena 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. Galileo, whom we regard as a physical scientist, figured out that jumping animals, from fleas on up, should jump to about the same maximum height irrespective of their body sizes (Haldane 1928). A key element in developing the idea of conservation of energy was established by a German physician, Mayer, in 1841, from observations on the oxidation of blood. The basic law for laminar flow of fluids in pipes was established about the same time by a French physician, Poiseuille, who was concerned with circulatory systems (Pappenheimer 1984).

Physics and biology, with separate histories for the past few centuries, 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). Each has been defined in a manner more precise than your workaday household noun in order to reduce misunderstanding and terminological controversy. That the jargon tends to exclude the uninitiates and those without youthfully spongelike memories gets (for better or worse) little consideration.

By contrast, physics and engineering eschew Greco-Latin obfuscation and pretension; in 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. It takes *work* to pull something upward but not to hold it suspended. *Stress* and *strain* are entirely distinct, with the former commonly causing the latter. *Mass* is not *weight*, even if they're functionally equivalent on terra firma. Both physical and biological practices will plague the reader, but the former tends to be more subtly subversive—a bit of biological jargon is jarring when you don't know its meaning, but the special definition of an ordinary word put to technical use easily passes unnoticed.

One term from physics needs special attention at the start—*energy*, which gets the most cavalier treatment by press and politicians. We ought to be able simply to define it with care and proceed from there. While energy 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 (Feynman, Leighton, and Sands 1963), 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."

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

The next chapters will be largely given 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 does a better job of providing a logical framework.

Adaptation and Evolution—The Biological Context

Nonetheless, biology as well as physics needs a bit of introduction. The words "evolution" and "design" have already surfaced; I find it hard to avoid either in any general discussion. Used together, 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 seriously—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 always are capable of increasing. It takes, though, some minimum quantity of resources for an organism to survive and reproduce; and, in the long run, the resources available to no population are 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 this individual variation is passed 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 imply only selection among preexisting variations, not design in our usual intentional sense.

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, indeed, no evidence supports the notion) that environmental challenges determine the character of the variation upon which natural selection acts. But, as a moment's consideration should persuade you, most results of such selection will look as if deliberately designed. How come?

Selection, quite clearly, operates most directly on organisms. An organism's 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 kinfolks, but that's a matter of little present concern.) The selective process knows next to nothing about species; there's little evidence that any organism ever does 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 here since it refers only to the reproductive potential of a potentially reproductive individual, here the whole tree.

Since this book focuses on organisms, it considers a level of biological organization upon which the invisible hand of the selective process should have fairly immediate consequences. That immediacy of the operation of that unseen hand 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, verbal simplicity is obtained by talking teleologically—teeth are for biting and ears for hearing. And the attribution of purpose isn't a bad guide to investigation—biting isn't just an amusing activity incidental to the possession of teeth. If the arrangement of an organism seems functionally inappropriate, the most likely explanation (by the test of experience) is a faulty view of its functioning. As the 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. To some "adaptationism" has become the perjorative term (see, for instance, Gould and Lewontin 1979) for the practice. And, indeed, it's all too easy to take literally what often amounts to no more than verbal convenience or baseline presumption. It's not trivial to show that a particular structure not only serves some particular and biologically useful function but that it evolved under selection for that particular function. 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 (1991) faced the issue directly; we'll return to it in chapter 25.

Furthermore, the designs of nature must be imperfect. At the very least, perfection would require an infinite number of generations in an unchanging world, and a fixed world requires not only a stable physical environment but a preposterous scenario in which no competing species underwent evolutionary change. Furthermore, we're dealing with an incremental process of trial and error. In such a scheme, major innovation is no simple matter—features that will ultimately prove useful will rarely persist through stages in which they do no good. So-called hopeful monsters are not in good odor. Many good designs must not be available on the evolutionary landscape because they involve unbridgeable functional discontinuities. Obviously jury-rigged arrangements occur instead because they entail milder transitions. The ad hoc character of many features of organisms are recounted with grace and wit in some of the essays of the late Stephen Jay Gould; his collection entitled *The Panda's Thumb* (1980) is particularly good. The more multifunctional the structure, the greater must be the constraints on what evolution can come up with. Finally, a fundamentally poorer but established and thus well-tuned design may win in competition with one that is basically better but still flawed.

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

In the final analysis, this book is about organisms rather than physical science—the latter simply provides tools to disentangle some 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 (1942)—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. Look how far a few simple models took us toward explaining the upper speed limit for walking and the requisite design of arterial walls.

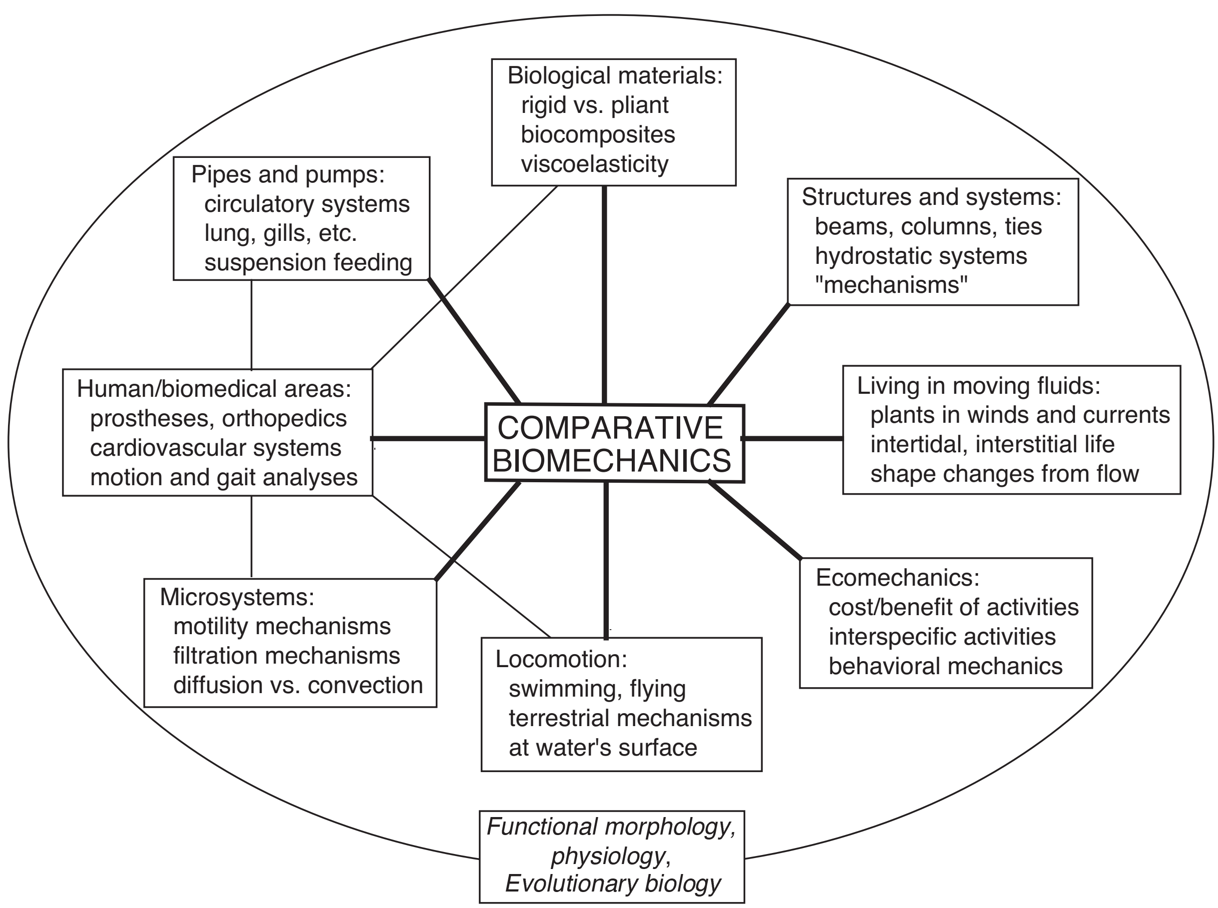


FIGURE 1.6 An opinionated view of the place of comparative biomechanics in the larger world of biology, medical science, engineering, and so forth.

The Two Fields of Biomechanics

Back down to earth, with a few words to show how our subject nestles within its niche among the various areas of biology. Biomechanics at present consists of two distinguishable fields. Current usage, at least in North America, considers "biomechanics" without verbal qualification to be 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 schools of engineering and medicine.

The other field takes for its concerns 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. Put another way, it looks at how the design and operation of organisms, including of course ourselves, reflect the values of physical variables such as gravity, viscosity, elastic moduli, and surface tension.

Some of us have begun calling this 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, their human or medical analogs. It's 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 1.6 shows where it sits among its academic parents, sisters, and cousins. Comparative biomechanics can claim no historical novelty—it traces its ancestry at least to Borelli's *De Motu Animalium* of 1680. But it appears to be enjoying something of a renaissance by at least one measure. 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 percent to 12 percent between 1985 and 1995; by the 2001 meeting the fraction had increased to 27 percent. A similar picture emerges from the tables of contents of issues of the *Journal of Experimental Biology*.