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CHAPTER 1

Constraints and opportunities

“Throw physic to the dogs: I’ll none of it.”

Shakespeare, *Macbeth*

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 menage 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 experience the same acceleration due to gravity at the surface of the earth. Some, but not many, can walk on water, but all face the same value of that liquid’s surface tension if they attempt the trick. No amount of practice will enable you to stand 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 before. 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 impose powerful constraints on the range of designs available for living systems. The case for the pervasive operation of such constraints has been pointedly put forth in a recent essay by Alexander (1986).¹

Were these restrictions the physical world’s sole impact on life, we

¹ Allusions to a person and a year refer to entries in the bibliography at the end of the book. This practice, used in most scientific journals, not only gives some idea of the antiquity of the source, but emphasizes the fact that we who do science and write about it are real people.

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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 are far from self-evident, and the materials on earth are themselves complex and diverse. Tiny cells with thin walls can withstand far greater pressures than would produce a blowout in any vertebrate artery, yet the materials of cellular and arterial walls have similar properties. The slime a snail crawls on may be alternately 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 large enough to prevent an ant from coming 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, with consequences deriving from both constraints and opportunities. In one sense it is a long essay defending that single argument against a vague opponent—the traditional disdain for or disregard of physics 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 relevant items of physics, but a limited set of mostly mechanical and largely macroscopic matters. I mean to work through various bits of physics relevant to the design and operation of organisms and to illustrate their pervasive influence wherever I have appropriate examples.

The macroscopic bias should be emphasized. This book in places deals with some rather bizarre phenomena but never gets far from a kind of everyday reality. Explanations, where possible, deliberately ignore the existence of atoms and molecules, waves and rays, and similar bits of *deus ex machina*. Not that these aren't as real as our grosser selves (or so implies some very strong evidence); rather, in explanations for the general reader, they have an unavoidable air of ecclesiastical revealed truth. More importantly, to incorporate particle physics in a more rigorous view of the immediate world would take far more space and complexity than a single book. 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 Democritus, commonly credited with the “invention” of atoms, just made a lucky guess as an accident of his inability to imagine anything infinitesimally small! Only when we consider the phenomenon of diffusion (Chapter 8) do we need to recognize atoms and a real world in which matter cannot be subdivided ad infinitum.

ABOUT SIZE

The largeness of people was implicit in our blithe disposal of molecules. The general topic of size receives undivided attention in Chapter 3, but, in fact, the widespread role of size is one of several secondary themes throughout the book.

The ease with which we can avoid worrying about atoms reflects the vast gap in scale between them and us, between the size of atoms or small molecules and even small organisms. Cells (or unicellular creatures) may be small, but inhabitants of the atomic realm are *much* smaller. There are, roughly, as many molecules in a cell as there are cells in the cat observing me write. (The point is crucial in Schrödinger’s 1944 classic essay, “What is Life.” One of his arguments is that well-ordered structures can be built of individually ill-behaved atoms only if enough atoms are used so that their actions are statistically dependable.)

But from smallest to largest, we organisms ourselves occupy an extensive size range—from the tiniest bacterium about 0.3 micrometers long (about a hundred-thousandth of an inch) to a whale about 30 meters long (100 feet). (Some trees are 100 meters high but are no more massive than the whale.) The range is about 100,000,000-fold; eight orders of magnitude we call it, counting the zeroes, or factors of ten. An excellent introduction to the truly cosmic subject of size is *Powers of Ten* by Morrison and Morrison (1982).

Among organisms, humans are near an extreme—we’re relatively big creatures a meter or two long. Only a little over an order of magnitude separates us from the largest living things, but six to seven orders lie between us and the smallest. On a scale of orders of magnitude, a “typical” organism would be between a millimeter and a centimeter in length—roughly an eighth of an inch. The point about size isn’t trivial—the appearance of the physical environment to an organism and the phenomena of immediate relevance to its life depend most strongly on how big the organism is. You may not need to imagine the world of an atom, but you’ll find challenge enough in trying to get some intuitive sense of the physical world of small creatures. Incidentally, for all of our fixation

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on microscopes, biologists have not usually had much of that intuitive sense to which we'll aspire here.

The relationship between size and reality can be best put with a half-serious example. Consider all animals that live in air, that is, neither in water nor in some solid material. These creatures are much denser than the medium around them and therefore can fall if released from a height. But size enters into any examination of this business of falling. We can divide organisms according to the consequences of a fall into four categories that depend mainly on size.

In the first category, made up of creatures above roughly 100 kilograms (220 pounds) in mass, injury is possible if the animal falls a distance as short as its own height—tripping is a potential danger to cows, horses, and the like. The fall of an elephant is a matter of the utmost gravity. (We, especially as we get older, run a similar risk even at a lower mass; the upright posture of a human gives us an unusually great height relative to our mass.)

In the second category, comprising animals with masses between about 100 kilograms and 100 grams (4 ounces), falling may be injurious, but the fall must involve a distance greater than the height of the animal. Dogs should avoid cliffs, and cats must climb down trees with deliberation, but squirrels, near the lower limit, can take riskier-looking leaps of faith. Hedgehogs (about 500 to 1000 grams in mass) are also just above the lower limit but, according to Vincent and Owers (1986), cope with falls using a special device—spines that can act as shock absorbers.

In the third category, from 100 grams down to perhaps 100 milligrams (give or take an order of magnitude), no height is great enough to cause substantial injury from a fall—the hazard, if any, is the predator at ground level. Falls may all too often befall nestling birds, but do we ever notice one injured by impact? A few years ago, at the instigation of my skeptical colleague, Knut Schmidt-Nielsen, I dropped two adult mice from the roof of a five-story building onto pavement. Not only were they uninjured (briefly stunned, though), but they adopted a spread-eagle, parachutelike posture and fell stably. It certainly looked as if the neural circuitry of these small rodents was arranged to deal with the circumstance. (The extent to which this posture reduces falling speed might bear looking into.)

The fourth category includes the smallest airborne organisms, for whom falling itself takes on a peculiar meaning. Upon release, the creature (by which I mean either plant or animal—the word “organism” is awkwardly deficient in commonplace synonyms) goes downward only in an uncertain, statistical sense. Air is never still, and if falling speed is comparable or less than the speeds of upward and downward movement

of air, then the direction of a fall is no longer dependably earthward. In fact, air is host to quite a diversity of seeds, pollen, spores, and tiny animals, to the great discomfort of those of us with allergies.

On the surface of the earth, gravity (gravitational acceleration, strictly) is everywhere the same. Yet its practical effects are widely divergent, depending mainly upon the size of the organism in question. As Haldane (1928) put what took me far more words, “you can drop a mouse down a thousand-yard mine shaft and, on arriving at the bottom, it gets a slight shock and walks away. A rat is killed, a man is broken, a horse splashes.”

PHYSICAL VERSUS BIOLOGICAL SCIENCE

“Interdisciplinary” is a contemporary buzzword. By the usual divisions among fields, the present topic is, if it matters, thoroughly interdisciplinary. The mix does generate a few practical peculiarities, mainly a jumbled lot of antecedents with some resulting oddness in presentation.

Ordinarily we probably 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 reach about the same maximum height irrespective of their body sizes (Haldane, 1928). (More will be said about jumping in Chapter 14.) 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, and the basic law for laminar flow of fluids in pipes was determined about the same time by a French physician, Poiseuille.

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 sea urchin whose roe is accounted a delicacy by some) to anterior zygapophysis (a minor protuberance on a vertebra). Each word has been defined more precisely than your workaday household noun in order to reduce misunderstanding and terminological controversy. That the jargon tends to exclude the uninitiated and those without youthfully spongelike memories is not (for better or worse) given much consideration.

By contrast, physics (and engineering) eschews Greco-Latin obfuscation and pretension; in doing so, it creates an equally serious difficulty. The most ordinary, garden-variety words are given 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

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are entirely distinct, the former commonly causing the latter. Mass is not the same as weight, even if they are 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 an ordinary word with a special definition for scientific use easily passes unnoticed.

The next chapter will be largely given to the task of establishing a necessary physical base, with a fair dose of the associated terminology. Biological terminology will enter piecemeal—for present purposes physics does a better job of providing a logical framework.

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 it *does* have a precise meaning in the physical sciences, the trouble is that the meaning doesn't lend itself to expression in mere words. Basic dictionaries and textbooks are little help—they define energy as the capacity for doing work, unblushingly evading the issue! Feynman (et al. 1963), comes right out with the unusually candid admission (no company man was he, whether teaching physics or serving on the commission probing the shuttle explosion), “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 is sometimes considered the greatest generalization of 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 ready definition and thereby to avoid some crucial explanations. So the word and the concept will be only a parenthetical presence until the final chapter.

EVOLUTION AND NATURAL DESIGN

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, one that ought to be resolved before we go further. If the process of evolution is incapable of anticipation, that is, if it is blindly purposeless, the term “design” is seriously misleading—in common usage, design implies anticipation and purpose. The problem is not just terminological. Why do organisms appear to be well designed if they are not designed at all? Perhaps it's best to begin by reviewing the logical scheme for which “evolution by natural selection” is the quick encapsulation.

First, some observations. Every organism of which we have any knowl-

edge is capable of producing more than one offspring; thus, populations of organisms are always 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 any population are limited. Next, three consequences. One is that a population in a particular area ought to increase to some maximum. A second is that once the maximum is reached, more individuals will be produced than can find adequate resources. The third is that some individuals will not survive to reproduce. Pause here to consider 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. Now a final consequence. Features that confer increased relative success in reproduction will appear more often or in exaggerated form in the individuals of the next generation. We say, in short, that these features will have been “naturally selected,” that is, by selection only from preexisting, even if latent, variations.

The model, at this level, is one of the least controversial items of modern science—every aspect has been observed and tested, and competing models for the generation of biological diversity (even if logically without flaw) uniformly fail to correspond to reality. Indeed, given geological time and the variation generated by an imperfect hereditary mechanism, it is difficult to see how evolution could be avoided. Remaining argument devolves about details—whether the process is usually steady or episodic, the roles of specific genetic mechanisms (such as sexual recombination), and so forth. The model has no place for anticipatory design, and there is no need (indeed, no evidence) that an environmental challenge can determine the character of the variation upon which natural selection can act.

Selection, quite clearly, operates most directly on individual organisms. The main test, defining its “fitness,” is an organism’s success in engendering progeny. (Some adjustment has to be made for indirect contributions that aid the reproduction of one’s kinfolk, but this is of little present concern.) The selective process knows nothing about species; no clear evidence indicates 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. Trees commonly shed leaves; the shed leaves were not therefore less fit—the term fitness is inapplicable here since it refers only to the reproductive potential of potentially reproductive individuals, that is, the whole trees.

This book is mainly about organisms, so we will be concerned with a

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level of biological organization upon which the invisible hand of the selective process should incur fairly immediate consequences. It is the immediacy of operation of that unseen hand that makes organisms appear well designed—as a colleague of mine put it, “The good designs literally eat the bad designs.” But it must be emphasized that we mean “design” in a somewhat unusual sense, implying only a functionally competent arrangement of parts resulting from natural selection. In its more common sense, implying anticipation, “design” is 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 an organism is arranged in a way that seems functionally inappropriate, the most likely explanation (by the test of experience) is that one’s view of its functioning is faulty. As the late Frits Went said, “Teleology is a great mistress, but no one you’d like to be seen with in public.”

We functional, organismic biologists are sometimes accused of assuming a kind of perfection in the living world—“adaptationism” has become the pejorative term—largely because we find the presumption of a decent fit between organism and habitat a useful working hypothesis. But the designs of nature are certainly imperfect. At the very least, perfection would require an infinite number of generations in an unchanging world, and a fixed world entails not only a stable physical environment but the preposterous notion that no competing species undergoes evolutionary change. Furthermore, we’re dealing with an incremental process of trial and error. In such a scheme, major innovation is not a simple matter—features that will ultimately prove useful are most unlikely to persist through stages in which they are deleterious or neutral. So-called hopeful monsters are not in good odor. Many good designs are simply not available on the evolutionary landscape because they involve unbridgeable functional discontinuities. Instead, obviously jury-rigged arrangements occur because they entail milder transitions. In addition, the constraints on what evolution can come up with must be greater in more multifunctional structures. 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 incorrigibly adaptationist in its outlook and teleological in its verbiage. The limitations of this viewpoint will not insistently be repeated, so the requisite grain of salt should be in the mind of reader as well as author. Incidentally, the ad hoc character of many features of organisms are recounted with grace and wit in some of the essays of Stephen Jay Gould,

not just as an argument against extreme adaptationism but as evidence for the blindly mechanical and thus somewhat blundering process of evolution. His collection entitled *The Panda's Thumb* (1980) is particularly appropriate here.

SIMPLIFYING REALITY—MODELS

This book is, in the final analysis, about organisms rather than physical science—the latter merely 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, collectively, singly, sliced, macerated, or homogenized. Abstractions and models are vaguely suspect or reprehensible. As D'Arcy Thompson (1942) 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 un-simple as an organism. And the most immediate sort of simplification is the use of nonliving models, whether physical or (even) mathematical.

Science is, in fact, utterly addicted to models for simplification and generalization. Even a tiny aspect of the world is just too complex to yield to simultaneous and systematic analysis of all of its diverse characteristics. Consider, for a moment, your left thumb—how many facets of this minor appendage might be measured, recorded, and subjected to statistical treatment? Simplification and abstraction have marked all progress in science; one begins very simply and then adds elements of complication as necessary and possible. We'll do just that, introducing some topic and asking very simple questions about it, then repeatedly returning to the same topic with questions that require more sophisticated analyses. Acceleration, for instance, will be discussed with reference to simple jumps, to jumps with air resistance and the trajectories of projectiles, and to the mechanics of the supply and storage of the work of propulsion.

CONTRASTING TWO TECHNOLOGIES

Much of the popularity of science fiction, I think, comes from its common focus on technologies alternative to the one developed on earth through human activity in the late twentieth century. A similar attraction must underly popular support for the search for extraterrestrial intelligence—the possibility of comparing what we've made here with alternative scenarios holds a strong intellectual appeal. But extraterrestrial life,

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much less intelligence, is elusive and its discovery is only a very remote prospect (the recent recognition of its remoteness was described by Horowitz, 1986). And the stuff of science fiction is both pretty anthropocentric and ultimately fictional.

Such a comparison between our technology and an alternative can nonetheless be made and turns out to be an unavoidable, if perhaps adventitious, aspect of the present book. The alternative technology available for our examination is the one generated here on earth through the operation of natural selection, which has resulted (in the most corporeal sense) in ourselves. The comparison is particularly interesting in that, first, the generating mechanisms are as different as can be—natural selection, strictly, implies no anticipation or calculation, unlike human design. Second, both sorts of technology use the substances available on the surface of the same planet. The contrast between them is another secondary theme, best introduced through a set of comparisons between “natural” (but not entirely unhuman) and “human” (not completely unnatural) technologies.

(1) Surfaces of and within organisms are curved, most commonly cylindrical, but sometimes with spherical or elliptical elements. (The major theme of Wainwright 1988 is the ubiquity of such shapes.) Flat surfaces are less common. By contrast, people make load-bearing flat surfaces in profusion—floors, roofs, walls, even the surfaces of beams. Cylindrical elements—pipes, cans, bicycle frames—are certainly not scarce but don’t dominate.

(2) Our technology is rife with right angles—never mind pyramids, it’s the 90° angle to which we seem addicted. It appears in almost every door, window, floor tile, box, book pages, many letters of our alphabet, the pockets of my shirt, and on and on. Yet right angles are surprisingly rare among organisms. Tree trunks are generally at right angles to the ground or horizon, but other examples are not easy to find.

(3) We use a few pliant materials—plastic hinges, elastic bands, rubber pads, and so forth; but relative to the abundance of our stiff stuff, soft and stretchy substances are unusual. We manage to live with the awkward tendency of stiff materials to fracture. We even fabricate them in curious geometries to take advantage of their limited deformability—coiled springs of steel spring to mind. Nature is typically pliant—skin, muscle, viscera, even fresh wood (dry timber is several times stiffer). Stiff material does occur—teeth, clam shells, big bones—but less commonly.

(4) Our preferred structural materials are most often made of single components above the molecular level, and the values of their properties are the same (isotropic) whatever the direction of measurement—we mostly use metals and ceramics. Nature’s materials are composites, com-

binations of two or more components, almost always arranged so that the materials' mechanical behavior depends on the direction in which they're loaded. We do make such anisotropic composites—we combine oriented glass fibers and glue to make fiberglass—but their use is limited. (And “composite material” seems always to be preceded in the popular press by “advanced”!)

(5) Substantial pieces of metal, either pure or alloyed, never occur in nature, even though metallic atoms are crucial to the biochemistry of all organisms, and tiny chunks are basic in magnetic sense organs. Ours is an overwhelmingly metallic technology, and we capitalize on the impressive mechanical advantages and diversity of properties available in metals.

(6) Both gases and liquids resist being squeezed and thus can be used as structural materials; air and water are the cheapest and most available of substances. Occasionally we use air as a compression-resisting material—in blimps, inflatable buildings, door closers, and so forth—but I can't think of a clear case where nature employs air in such a manner. Conversely, nature makes elaborate and extensive use of water as such a compression-resisting material in sea anemones, penises, squid tentacles, worms, sharks, and elsewhere; but we use it in only a few devices such as fire hoses that collapse when not being used.

(7) Life may tolerate a reasonable range of ambient temperatures, but organisms are basically isothermal machines rather than heat engines and do their business without depending on large internal differences in temperature. Heat conduction, therefore, is not a major issue in organisms—handy, since we aren't built of the wonderfully conductive metals. But our functional parts (cells and so forth) are often very small, and a formally analogous process, “molecular diffusion” (Chapter 8), is always crucial. Human technology makes impressively elaborate use of heat conduction but less of diffusion.

One can continue such a list, although the items get more obscure and complex. You'll notice that I haven't given more than a hint of an explanation of the differences between the two technologies for any of these examples. The notion of evolution can provide some basis for the distinctions. Beyond that, explanations and rationalizations will come later, at least for those items about which something reasonable can be said.

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