Feeling for the Organism
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Climbing Mount Improbable
Richard Dawkins
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There is a strong urge to begin and end a review of Richard Dawkins's most recent book about evolution at its title: Climbing Mount Improbable. Dawkins's metaphorical mountain provides a handy picture postcard for how he believes evolution by natural selection works, and also locates his gene-centered pulpit (he calls his third chapter "The Message from the Mountain"). Regrettably though, Climbing Mount Improbable does triple duty, characterizing the plausibility of Dawkins's own ultra-Darwinian outlook. Evolution by natural selection is, to be sure, a firmly established part of contemporary science-like continental drift in geology, it's the explanatory bedrock for an entire field. But Dawkins believes, further, that "all questions about life have the same answer-natural selection." Such fundamentalist faith oversimplifies the biological world and obscures important questions about the forces driving evolution.

Adaptationism: The Uphill Climb
Dawkins sets out on seemingly safe ground. We get the stock recipe: one part charmingly-written natural history; one part evolution as the sole explanation for the "goodness of apparent design"; and a dash of selfish genes and "biomorph programs"-computer algorithms simulating the evolution of forms from spider webs to centipede segments-thrown in for spice. At heart, though, Dawkins's book rests on mid-century alpine imagery borrowed from evolutionary theorist Sewall Wright. Wright proposed a now-classic picture of evolution as organisms scrambling uphill in an "adaptive landscape." The terrain's height corresponds to fitness: organisms reach for better vision, fleeter feet, or, from a gene's-eye view, simply increased frequency of that particular gene over time. Dawkins adds to this picture assumptions about the precise lay of the land and how organisms scale slopes-intellectual inheritance from Darwin himself and the evolutionary theorist R. A. Fisher's Genetical Theory of Natural Selection (1930)-to arrive at the "the main lesson" of his book: that "the evolutionary high ground cannot be approached hastily. Even the most difficult problems can be

solved, and even the most precipitous heights can be scaled, if only a slow, gradual, step-by-step pathway can be found." Though the exquisite designs of stems, pistils, eyes, jaws, wings, gills, and tentacles may all seem improbable, we can understand them once we see how they emerged from a long series of tiny improvements. Broken down into three main mountaineering propositions, we have:

1. "[T]here can be no sudden leaps upward–no precipitous increases in ordered complexity" (insect wings can't jump from stubs to full-length flappers overnight).

2. There's no going downhill (species can't get worse as a prelude to getting better).

3. There may be "more than one peak–more than one way of solving the same problem" (eyes, Dawkins explains, or at least eye lens and "camera body," have evolved independently 40 to 60 times).

A world of creatures all driven by selectional pressures, inching upwards to their adaptive peaks–what's wrong with this picture? It's not immediately obvious. Although the metaphor of evolution-as-gradual-mountain-climbing is not fresh, it has endured. The notion of minute, step-by-step improvement descends directly from the famous Linnaean dictum Natura non facit saltum and Darwin's On the Origin of Species: "Extremely slight modifications in the structure or habits of one inhabitant would often give it an advantage over others." Evolutionary gradualism was further bolstered by R. A. Fisher's mathematical marriage of Mendelism to natural selection–the so-called "neo-Darwinian Modern Synthesis." Fisher showed that, under some (strong) assumptions about population size and the underlying mechanism of inheritance, even slight selective advantages could be sifted by natural selection and accumulate over time to weave the "tangled bank" of complex adaptations we see. Ever since, Wright's adaptive landscape has been a staple of evolutionary texts, from Theodosius Dobzhansky's Genetics and the Origin of Species (1937). Local hill-climbing does the trick–or so it seems.

The problem, then, isn't vintage–it is fundamentalism. Perhaps like all fundamentalists, Dawkins over-simplifies: For all his talk of life's

complexity, he makes the biological world out to be much simpler than it actually is. Left unchecked, this ultra-Darwinist faith in natural selection dissolves into a doctrinal irrationality that rivals that of creationism, with a ready answer for all logically possible outcomes.

The Constraining Terrain
One problem with paying exclusive attention to natural selection is a corresponding inattention to physical constraints. If an insect needs to clamber over an adaptive landscape, it's good to know what possible next steps it can take, and what the terrain just ahead looks like-the "physical channel". For example, many biological reactions take place on cell membranes. Why? Because evolution by natural selection made it that way? That sounds like creationist litany, and for good reason. The real explanation probably follows from what Nobel laureate Manfred Eigen dubs the "coffee pot" theorem: Membranes are required for the same reason that people set up coffee pot stations-people cluster more readily around them. Specifically, the limiting probability for two molecules to meet in three dimensions is vanishingly small, but on a flat sheet-a membrane-the probability approaches near certainty. Thus life lingers at a coffee break.

Similarly, why do poliovirus shells resemble geodesic domes? The answer isn't "because evolution by natural selection made them that way." The explanation, as molecular and developmental biologist Sydney Brenner wrote recently, is fundamentally geometric. There are only a handful of physically possible, symmetrical, space-enclosing shapes: pyramids, cubes and octahedrons, the pentagonal- faced dodecahedron (12 pentagons glued together), and the pentagon's dual cousin, the icosahedron (20 equilateral triangles glued together). Plunk down a molecule on the corner of each triangle, and one gets virus shells chunked into three-times-20 or 60-unit multiples. From this inescapable fact of the physical world-its geometry, not the particular environment in which polioviruses evolved-James Watson and Francis Crick long ago predicted (correctly) that most spherical virus shells would come in 60-unit packages.

Of course it may be that natural selection plays some role in shaping spherical virus shells. Icosahedrons approximate spheres more closely than pyramids, so selectional factors like "most nearly

spherical shape" or "optimal packing density" might enter in. Possibly this is the sense in which virus forms are "explained by" natural selection, if in fact they are. But even if so, it's a credit allocation question. Dawkins gives DNA pride of place because it alone stores and passes on the informational know-how to make membranes rather than something else. That's partly true–but only partly. It's also true that evolution, the "blind watchmaker," stumbled onto membranes and icosahedrons because the physical world's regularity constrains the landscape's "search space," and through this regularity the physical world itself contributes to the information encoded in DNA.

Now, it would be a foolish biologist indeed who did not view adaptive evolution by natural selection as the unifying theory lurking behind the contrasting shape and texture of pine needles and oak leaves, as well as the peacock's tail. But it would be equally foolish to deny the constraints of living in the physical world. A decade ago, Dawkins devoted an entire chapter of his book The Extended Phenotype to "constraints on perfection"–engineering design tradeoffs that Climbing Mount Improbable still mentions but largely sets to one side. In fact, all serious biologists, from Darwin to Dawkins, have agreed that factors beyond natural selection play a central role in evolution. Just how central? Turn to the last line of the article "Evolution" in the latest edition of the Encyclopedia Britannica, written by the population geneticist Francisco J. Ayala: "as a point of departure" and for good or for ill, today's working evolutionary biologists start with the "null hypothesis" that natural selection has not occurred.

All Mutations Great and Small
So why the renewed fundamentalism? Perhaps the answer is that Dawkins has now swallowed Darwin's and Fisher's gradualist assumptions whole: add one extra layer of light-sensitive membrane, so the argument goes, and an eye's photon-trapping improves by a fractional percent–a smooth incline with no jumps or "surprises."

Though not literally true, this picture of a smoothly additive world might be a good enough idealization–sufficiently good that evolutionary biologists could dismiss deviations as noise. But is the biological world really so simple? An alternative picture–a nonlinear world–seems to hold considerable promise. Though "nonlinear" is

now a fashionable by-word, popping up in all those books about chaos and the stock market, it also marks out a serious approach to a wide range of natural phenomena. Certainly, when it comes to the electrical engineering side of my own profession, nonlinear circuits have replaced linear ones, and nonlinear dynamics is the framework of choice for describing natural systems of all kinds–from water disappearing down a drain, to cirrus cloud formation, to grouses growing.

What does nonlinearity imply for hill climbing? The linear alpine metaphor suggests that an insect scaling Mount Improbable can attain optimal insecthood by independently pondering each factor that makes it a functioning, adaptive whole, even if the insect does this by sending out multiple "search teams" across hill and down dale in parallel. But the success of this piece-wise strategy of self-improvement depends on a particularly simple connection between changes in individual traits and improvements in fitness–essentially a noninteractive, nonecological world.

Dawkins assumes just such a topography. His evolutionary hills have gentle slopes, so that inching uphill always works. That follows Fisher chapter and verse: picture each gene that contributes to better eyesight as if it were one of millions upon millions of fine sand grains. Piling up all that sand automatically produces a neatly conical sand pile with just one peak, a smooth mound to climb. In this way, complex adaptations such as the eye can always come about via a sequence of extremely small, additive changes to their individual parts, each change selectively advantageous and so seized on by natural selection.

The key question is whether the biological world really works that way, or rather, how often it works that way. And that question divides into two parts. Theoretically speaking: what works better as the raw material or "step size" for adaptation–countless genes each contributing a tiny effect, or a handful of genes of intermediate or large effect? Empirically speaking: how does adaptation really play out in the biological world? Are large mutations really always harmful, as Fisher argued? Do organisms usually tiptoe in the adaptive landscape or take larger strides? Are adaptive landscapes usually smooth sand piles, jagged alpine ranges, or something in between?

Fisher addressed the theoretical question via a mathematical version of the "monkey wrench" argument: A large mutation would be much more likely than a small one to gum up the works of a complex, finely-constructed instrument like a microscope. It's not hard to see why. Once one is at a mountain top, a large step is much more likely to lead to free-fall disaster. But the microscope analogy can easily mislead. Fisher's example considers a mutation's potential benefits in a particularly simple setting-precisely where there is just one mountain top, and in an infinite population. But if I'm astride K90 with Mt. Everest just off to the left, then a large step might do better to carry me towards the higher peak than a small one. The more an adaptive landscape resembles the Himalayas, with peaks crowded together-a likely consequence of developmental interactions, which crumple the adaptive landscape, as we'll see-the worse for Fisher's analogy. Small wonder then that Dawkins's topographic maps and the gradual evolutionary computer simulations he invokes constantly alter how mountain heights get measured, resorting to a single factor-first for eyes, it's visual resolution; next, for spider webs, it's insect-trapping effectiveness; then, for insect wings, it's aerodynamic lift or temperature-regulating ability. An appropriate move, since hill-climbing is guaranteed to work only if there's exactly one peak and one proxy for fitness that can be optimized, one dimension at a time.

Even assuming a single adaptive peak, Fisher's microscope analogy focuses on only half the evolutionary equation-variation in individuals, essentially the jet fuel that evolution burns-and not the other half-the selective engine that sifts variations and determines which remain written in the book of life. Some 50 years after Fisher, the population biologist Motoo Kimura noted that most mutations of small effect do not last: Because small changes are only slightly selectively advantageous, they tend to peter out within a few generations (ten or so). Indeed, most mutations, great or small, advantageous or not, go extinct-a fact often brushed aside by selectional enthusiasts. Kimura calculated that the rate at which a mutation gains a foothold and then sweeps through a population is directly proportional to the joint effect of the probability that the mutation is advantageous and the mutation's size.2 The upshot is that medium-scale mutations are much more likely to take hold than minuscule Fisherian sand grains. Moreover, even if medium-scale changes were less likely to fix in a population than "micromutations," by definition a larger change will contribute

correspondingly more to an organism's overall response to natural selection than a small one and, as we will see, there's real evidence from fruitflies that this happens.3

What then of the empirical issue? Four years ago, the evolutionary biologists Allen Orr and Jerry Coyne found that the genetic evidence for the role of micromutations as the source of adaptive differences between species, such as color differences in fruitflies in desert environments, was surprisingly thin–in the handful of verifiable examples (eight) drawn from the 1940s on, which easily fit into a single half-page table in their original paper, four were due to essentially one gene.4 More recently, biologists have gathered evidence that mutations with medium- to large-scale effects occur and, far from always being harmful as Fisher asserted, can even play an important, beneficial role. For instance, fruitfly resistance to certain insecticides seems to be caused by the alteration of a single "letter" in the DNA sequence of a single gene. Even for more quantitative or countable traits that have often been taken as the natural province of Fisher's additive-type model–lots of genes with small effects piling up–recent evidence suggests the contrary. Consider the bristle hairs on a fruitfly's abdomen–a fairly sophisticated part of the fly's sensory system, and often taken as a "classic" example of a quantitative trait. In 1995, Anthony Long, Susan Mulaney, Trudy Mackay, and their colleagues showed that the number of abdominal hairs is largely determined by just one to three genes, not dozens or hundreds.5 Moreover, the effects don't simply add up: if one factor contributes an average of 2 bristle hairs by itself, and another pitches in two more, an additive model would predict four hairs on average, but the two factors together produce roughly six.

Interactions
All this is not to say that such intricate and highly functional organs as eyes could emerge in one giant mutational leap, like Athena springing forth from Zeus's forehead on the slopes of Mount Olympus. That seems exceedingly unlikely. But the troubles for small mutations indicate one major stumbling block for Dawkins's hill-climbing metaphor. So, too, do interactions among traits.

We all know how hard it can be to solve a problem that depends on lots of interacting parts: Imagine trying to tune a television picture by simultaneously twiddling a million knobs at once. Evolution's in

the same boat. A trait may appear to have an intermediate optimum because it's correlated with other traits that affect fitness in opposite directions, as in the classic example of body size: A bigger body yields more offspring, but makes it harder to escape predators. Tradeoffs again–but how to "solve" them?

Worse for aspiring alpinists, the biological world might not be pleasantly additive. Suppose ecological interaction rules: more anteaters mean fewer ants. Then trying to improve the whole organism by improving one trait at a time can grind to a halt and the organism's fitness may not be maximized. Stumbles become inevitable, as Dawkins rightly stresses: "ideal outcomes are not the only possibility." But the situation is worse than that. Fitness can even be minimized by natural selection–as our crumbling spines attest. Evolution by natural selection in a finite population can result in a decreased growth rate, and in some ecological settings lead to a higher probability of extinction–about as nonadaptive as one could imagine.

History and Evolutionary Tides
Bad backs are not, then, simply some quirky evolutionary offshoot. Rather, in the real world–with natural selection and physical constraints, in which large mutations sometimes dominate small, and improvements depend on lots of interacting factors–nonadaptation itself is a central ingredient in the evolution's ebb and flow.

It is all too easy to fall under the sway of natural selection as Supreme Engineer, because it is a retrospective tautology that "the mechanisms of evolution have, indeed, produced every result that has appeared in evolution."6 Evidently, even Darwin was susceptible. As many others have observed, far from purging the last vestige of the anthropocentric Great Chain of Being, Darwin can be read as retaining (a perhaps Victorian) "progressive," perfectionist" residue, as he reveals in his autobiography: "Believing as I do that man in the distant future will be a more perfect creature than he is now."7 So the perfectionist pyramid lives on–not only in those who perpetually appeal to natural selection as Supreme Engineer, but also in those who believe that, yes, if we rewound the evolutionary tape and played it all over again, we would end up about where we are now, with intelligent creatures like us to boot. Such unwavering faith reveals a misunderstanding about the

essentially stochastic and historical nature of evolutionary change. For evolution, small and medium-size numbers matter–because of the slings and arrows of outrageous sampling. By Mendel's "laws," the genes for, say, completely dominant brown (B) and recessive blue eyes (b) should segregate out into exactly four offspring as three brown (1 BB, 2 Bb) and one blue (bb). But as all parents know, it's a pure stroke of luck for that to happen with just four children. (Even Mendel's 929 pea plants had 705 purple and 224 white flowers, a 3.15:1 ratio, not the exact 3:1 ratio predicted by theory.) Because organisms often have this kind of detailed structure, with differing groups of grouses at different ages, fluctuations in age-specific birth and death rates lead to enough variation in population numbers so that the likelihood of new mutations taking over varies in a probabilistic way. The bottom line is that if we run the evolutionary tape again, we aren't going to get the same "perfection" we see now–that is, not unless one adopts very strong constraints on the space of possible animals that, as far as we know from this book, Dawkins explicitly disavows.

So historical contingency matters–we've got four limbs because we're descended from four-lobed Crossopterygiian fish and evolution can select only the better of possible alternatives–no silk purses from sow's ears. Evolution is much like a chess game where the next move depends on the possible legal next moves–the biological and physical constraints like icosahedron–as well as the position one is at right now, summarizing the moves made up to the present. But evolution is in worse shape than a chess player, because the "search strategy" for the best next move is local hill climbing without a goal–we don't have a teleological target like checkmate. Because gradual hill-climbing evolution by natural selection can ascend only to local peaks, and since evolution can't see ahead, and according to Dawkins, evolution can't ever climb down again, our ant might climb up on a foothill and stay stuck. Indeed, if evolution were really just one smooth, additive hike to a single fitness peak, we might expect, echoing the Cole Porter song "You're the Top," to see just one organism stand supreme as the Tower of Pisa. We do not. Rather, evolution's more like an ant trundling over a crumpled piece of paper, with the nooks and crannies revealing where the possible animals can be.

The bottom line is that mathematical evolutionary biologists as yet don't have any good general solutions to such nonlinear problems–

and they unabashedly say so. According to Alan Hastings and Gordon Fox, "the equations of population genetics are complicated nonlinear equations, and therefore general solutions, particularly of dynamic behavior [of evolution] have not been found." Dawkins provides no such cautionary road signs. We are treated to much less catholicism and certainly much less of the "controversy and uncertainty" that ought to figure, as Dawkins's mentor John Maynard Smith has written, in the best science writing. Instead Dawkins's faith in simple hill-climbing seems boundless–as it must if one embraces adaptation-as-problem solving and incremental hill-climbing as the only means to tackle evolutionary design questions.

Genes or Organisms?
The same lack of sophistication–ultimately fundamentalism–infects Dawkins's (in)famous selfish-gene conceit: that genes "manipulate the world for their replication." For Dawkins, genes drive the explanatory show. He even calls organisms "vehicles"–an old conceit that leads us straight back to origins of 20th century genetics. By 1926, the geneticist H. J. Muller could write that the rest of the cell was simply a "by-product" of gene action: "its 'function' (its survival value) lies only in fostering the genes."8 This conceit also simplifies the evolutionary climb. The more direct the connection between gene and organism, the easier for the gene to "drive" the vehicle–the organism.

Here again Dawkins oversimplifies. Not that his view is completely off. Usually, one can think about evolution "one gene at a time," as John Maynard Smith, following R. A. Fisher, has written. A gene only has to worry about how it contributes to "average fitness"–its own frequency–and can ignore its neighbors'. And averages are additive. But it doesn't follow that we can talk as if organisms weren't there, and as if all genes were individually selfish. Genes' causal fingers touch the world only indirectly through organisms' walls. The further we move out into the world of interacting organisms, the more our adaptive explanations get couched as differences among organisms, not genes. True, genes benefit and get implicated in organisms' success, but genes don't necessarily figure in our explanation of why things are they way they are.

Take one of Dawkins's own Mount Improbable success stories: insect wing evolution. Do we need mention "gene" to explain why

stubby-winged insects produced more offspring than wingless varieties? No. Only the ecological description of organism and environment is required. The wing stubs were adaptations for the good of the insect, the genes benefited indirectly. Of course DNA is necessary for evolution by natural selection; it's just not always an equal partner in explanation. Dawkins recounts how Joel Kingsolver and Mimi Koehl built hypothetical insect models to test whether and when wing stubs could develop enough lift to get off the ground, but genes were not part of this picture and not part of their counterfactual predictions about the improvements in flight that would result from 1 millimeter changes in wing size. You can apply the test yourself when you read Dawkins's book: he opens and closes with the ever-fascinating story of the co-evolution of figs and fig wasps, adapted from evolutionary biologist W. D. Hamilton's 1975-76 field work in Ribeirao Preto, Brazil. The figs "yearn" for pollination; the fig wasps oblige, and themselves go through an elaborate competition to see which male wasps will get there "fastest with the mostest" to mate inside the fig-killing already-arrived males and mated females if they can and pollinating the fig as a side-effect. To be sure, the end result promotes both a fig and fig wasp's genome. But, if the explanations and predictions about how figs and wasps have adapted rely on features of whole figs and wasps, then the organisms are the players; if, on the other hand, the story is told in terms of genes that happen to coexist alongside other genes in figs and wasps, then we don't need the organisms for the explanation and the explanatory game goes the other way.

Of course in some environments DNA does get directly selected without an intervening body getting in the way-most obviously in the environments of other genes. Not surprisingly, that's precisely where we do see evidence of "selfish DNA" that, like a virus, says only "copy me," and does not benefit the organism itself.

As to whether DNA drives the biological show-as opposed to the entire cell with its internal "skeleton" that serves as scaffolding and meeting place, organelles, and detailed exterior "cortex"-history again has some lessons for us. Dawkins's position belongs to a long tradition, extending from the 1920s-era enthusiasm for genes as ultimate choreographers and active "agents," to physicist Erin Schröedinger's famous 1944 "What Is Life?" proclamation that the chromosome contains "architect's plan and builder's craft in one," to molecular biology's cybernetic lingo and triumph in the 1960s, to

the 1980s view of the gene as "computer program" (or, as David Baltimore put it in 1984, the "cell's brain"). But much has changed over the past ten years. The deeper the biologists plumb DNA and replace the tell-tale words "gene action" with "gene activity," the further the image of DNA-as-agent seems to recede-so much so that by 1991, even Scientific American announced the "news" that "organisms control most of their genes."9

Thus "vulgar biology" appears to be turned on its head: DNA is not self-replicating; only cells are properly self-replicating. As Richard Lewontin has pointed out, newly-minted DNA is "a copy of the old . . . but we do not describe the Eastman Kodak factory as a place of self-reproduction [of photographs]."10 DNA doesn't produce proteins; proteins produce DNA. And the complete DNA in the nucleus of a cell, its genome, isn't a program for "computing the organism." Some now dub DNA simply the "data" that the cell uses. For even a computer program needs a computer to run it, but unlike a computer program, a genome doesn't contain all the information about the required sequence and timing of steps. Moreover, even a computer program requires particular hardware and software to interpret what the program code means, and that means supplying extra information. And what might that interpreter be? The most recent edition of the popular Alberts-Watson textbook Molecular Biology of the Cell names-you guessed it-the heroine of its title, the cell, as the computer.

If you still believe that DNA carries all the requisite instructions to build organisms, consider Gunter Stent's gedanken experiment: Ship a cat's DNA to the planet supposedly circling Pegasi 51 and see whether the creatures on the other end can grind out a Felix. Not a chance. Or, to take a real example, consider biologist Frank Solomon's discovery of "mitotic sisters": Take two "mother" developing neural cells sitting next to each other, each looking very much the same. Both cells obviously have identical genes, and are sitting in virtually the identical external soup. The first cell divides, yielding two sisters with a particular shape-a long extension fiber down and then a short twist to the right. The second mother cell divides and its offspring look very different from the first two, with short nerve fibers. Each pair of sisters is shaped completely differently from its genetically identical neighbors. Genes don't fix the "surface" traits of organisms-except in conjunction with a complex, nonlinear waltz of external and internal cellular positions,

chemical gradients, and signaling environments. These nonlinearities in moving from DNA sequences to organisms wrinkle the evolutionary landscape even more. As Howard Patee memorably remarked, "life loiters over two . . . spaces, the first alphabetic [DNA, the genetic code], the second, zoological." We don't know—yet—what this mapping from genes to bodies looks like. We are just beginning to tease apart the cascaded genetic control sequences and feedback loops needed to assemble a fruitfly's eye. Yet it is absolutely crucial for evolutionary theory to understand the possible range of organisms that can spring from the platform of a developing egg. If turning the genetic steering wheel one degree left can jerk the vehicle into a new pothole, the evolutionary process becomes even more nonadditive.

To appreciate the complexity of moving from genes to organisms, consider first the space of possible genes. Genes are DNA sequences, and DNA uses a finite coding "alphabet" of just four letters (amino acids) with the tags A, T, G, C, and a small number of words with exactly 3 letters each (for example, ATG or AGC). DNA sequences are just strings of such words. This space is effectively infinite, then, because one could simply go on forever, building longer and longer "sentences"—bigger and bigger genes—though physical limits intervene to bar indefinitely long sequences. Still, the set of possible DNA sequences is countable: We can pair each sequence with a unique integer: 1, 2, 3, etc.

We know far less about the space of possible organisms—what Dawkins calls "Animal Space." But if we take literally Darwin's claim that variation "extends continuously [my emphasis] in all directions," then this space is infinite too, but bigger than the merely countable infinity of possible genes. For every inch long worm, there can be one half as long, another half again as long, and so on, with gradations as fine as we wish. But that means the space of possible organisms may not be computable—that is, a computer program might not be able to calculate it. A fortiori, the function from genes to organisms that represents developmental transformation—what biologists call "epigenesis"—may not be computable. There may be no algorithm to characterize epigenesis. Statements trumpeting the self-evidence of computability—Dawkins says "we are von Neumann machines"—are sheer bluff. We might be. We might not. It is an open question.

Dawkins does take a step in the right (nonlinear) direction in this respect. In the chapter "Kaleidoscopic Embryos," he opts for a gene-to-organism mapping that multiplies "gene" values together—reaching, as he says, for a model that works like a kaleidoscope. Gene effects can twist about like bits of glass and then suddenly jump together into a novel pattern, like an eye cup bending in instead of out. This is probably closer to the real picture than the "additive" model. But once we allow for such "jumps," we leave smooth hill climbing behind. Indeed, we know that kaleidoscopic jumps must happen, because very small differences between organisms' genes can get amplified into very large differences in what comes out of the embryological oven. Chimps, for example, differ from people by a very tiny amount of DNA, say 1 percent, and in surprising direction: chimps have forty-eight chromosomes and we have forty-six. But only you and I can read this issue of Boston Review.11 Having embraced the kaleidoscope, does Dawkins now agree with Richard Lewontin that "context and interaction are of the essence"?

Yes, But . . .
In the end, it is hard to tell where Dawkins comes out. Once all the complications are at hand, Dawkins begins to resemble Captain Corcoran in H.M.S. Pinafore, singing, "What never, well œ hardly ever." One by one he backs off from his original alpinist assumptions.

Can there be only infinitesimally graded intermediates? Perhaps not. We also have kaleidoscopic" embryos. But especially not if physical possibilities are discontinuous, like the geometric shapes available to spherical virus shells.

Does evolution never step downhill? Well, hardly ever. Dawkins tinkers with another of Sewall Wright's innovations, the famous "shifting balance" model, which one might caricature as clumping uphill with one's weight first on the left foot and then rocking back onto the right foot. The two feet correspond to two local, but distinct, populations, what Wright called "demes." If one gets stuck on a local foothill with the right foot, then it might be possible to rock back onto the left foot and continue uphill.

Can evolution of traits stall at the top of local foothills? Sometimes. So Dawkins adopts "preadaptation." The insect wing models

suggest that the first insect wing stubs probably served as body temperature regulators, rather than flying wings, given the insects' smaller size; only later, after a burst in overall body size, could the wings develop enough lift. Dawkins concludes this "teaches us a subtle new way, a kind of sideways diversion, by which paths up Mount Improbable may be found." In other words, the familiar story that an organ developed for one purpose may later serve another.

Were eyes independently invented more than 40 times? Possibly only once. The larger number tallies distinct lens-and-retina shapes, not the basic light-processing machinery–a big difference, like counting the camera lens and body but not the film. For as Dawkins himself writes, Walter Gerhing has shown that eye photoprocessing apparently evolved just once and stayed that way, right down to the finest molecular detail–the "film" biochemistry, the structural and regulatory genes, even the molecular "chaperones" that escort other proteins to erect the right "external scaffolding" to build the photoreceptive machinery. From owls to the single-celled Euglena gracillis with a carrot-colored eye spot: All this has been conserved, seemingly back to the very first single-celled organisms that could see the light. If so, then eye evolution seems more like a automotive redesign that changes the chrome on the body, while leaving the engine untouched.

Indeed, it has become increasingly apparent that all organisms also come equipped with roughly the same developmental tool kit that literally builds us from stem to stern and front to back. This control system, a sequence of genes that activates in a precise linear order, fixes the head-to-tail orientation of growing embryos, and (like the eye developmental system) probably evolved exactly once, prior to the last common ancestor of flies and vertebrates, a half-billion years ago or more, and then stayed that way. Same for front to back: When the 19th-century biologist Etienne Geoffrey-Saint Hillaire flipped over a crayfish and dissected it, he discovered that its nerve cord, muscle, digestive system, and heart were in the same top-to-bottom order as a human being's. Thus we have the same body plan as a crayfish, but inverted: one vertebrate's ceiling is another invertebrate's floor, and the reason why is a common genetic developmental system. A great puzzle of modern biology is how to reconcile the remarkable diversity of organisms we see with the equally astonishing conservatism of the genetic developmental toolbox: as if there really were only one organism, as if little kids

were really made of snakes and snails and puppy dog tails. The oft-castigated Bäuplane theorists of the past century perhaps guessed rightly–but in a far more sophisticated way, within the context of modern molecular biology.

With all these qualifications in mind, ponder Dawkins's central evolutionary pledge and judge whether it reduces to a truism: "[I]f an engineer looks at an animal or organ and sees that it is well designed to perform some task, then I will stand up and assert that natural selection is responsible for the goodness of apparent design. 'Magnets' or 'attractors' in Animal Space cannot, unaided by selection [my emphasis], achieve good functional design."

Even if we put to one side the tangles we've seen with "responsible for" and "good functional design," with "unaided by selection" as an escape clause, it is hard to see what this pledge amounts to. Along with any other rational person, I assume that no living thing has come into the world "unaided by selection." I can't understand a word that you say "unaided by" my inner ear bones, which evolved from a fish gill arch to a reptilian jaw residue. But that doesn't mean my inner ear bones are "responsible for" sentence understanding.

What, then, of Dawkins and his metaphorical mountain? The scope and operation of evolution by natural selection remains a matter of controversy. And when controversy emerges, Dawkins frustrates. As Dawkins himself notes in his earlier work The Extended Phenotype, "I myself admit to being irritated by a book that provokes me into muttering 'Yes but . . . ' on every page, when the author could easily have forestalled my worry by a little considerate explanation early on." In Climbing Mount Improbable Dawkins seems to have abandoned his own advice. The "yes-buttery" that he had so artfully condemned slips in at every page.

So read Climbing Mount Improbable for charming natural history, and an introduction to evolutionary landscapes. But beware the slippery slopes. "Charm," as Anthony Blanche in Brideshead Revisited reminds us, "is the great English blight." The question is whether Dawkins, like the narrator Charles Ryder in Brideshead, will forever remain repainting pictures of English village architecture and South American birds, or will go on to do something much more–feeling for the organism.