2: *All about Evolution*

The word "evolution" is probably one of the most abused words in any argument about science. To some, it is a rallying cry to rationality. To others, it's a term of abuse, the term "evolutionist" hardly less derogatory than "abortionist." There can be few other words that get so much mileage while remaining so poorly understood. "When *I* use a word," said Humpty Dumpty in Lewis Carroll's *Through the Looking-Glass*, "it means just what I choose it to mean—neither more nor less." Matters are made worse by the fact that the meaning of the word has changed over time, and remains ambiguous to this day.

When inventing the wheel, it is best to ensure that it is round before deciding what color to paint it. So, before we can get a handle on the word "evolution" in all its protean and subtle variety, one must first understand how it works, on the most basic nuts-and-bolts level. This is why Darwin started *The Origin of Species* by outlining such a mechanism—and not mentioning the word "evolution" at all. Darwin had very good reasons for not using the word in his masterpiece, as I shall explain a bit further on. Until then one might do a lot worse than follow his example.

Like many people these days, we in the Gee household keep chickens in our backyard. The hens are of several different breeds. We started with bantams, small birds whose function is more ornamental than anything else. They don't lay many eggs, perhaps ninety per bird per year. They are, however, long-lived. At the time of writing, one of our first hens, a Pekin bantam, is four years old and still going strong. Our next two hens, Polish bantams, are almost as old, and in rude and squawking health. We also have several standard-sized hens, which lay more and bigger eggs.

But the prizes for productivity go to those in the flock that started their careers in intensive egg-production facilities. A battery hen can lay as many as three hundred eggs per year, but at a cost—the hens don't live long. When a battery hen stops laying regularly, she dies of old age. Battery hens have been bred that way, to invest as much energy as possible into producing eggs, at a cost to their own bodily maintenance. Our first four battery rescues died of old age within two years, and we are now on our second quartet.

All the battery hens have russet feathers and red combs. They look just like the Rhode Island Reds my mother kept when I was a boy. As every backyard farmer knows, Rhode Islands are just about the best hens to keep if you like lots of eggs. These battery birds plainly have Rhode Island in their heritage, but they've been turbocharged to ramp up egg production at the cost of virtually everything else. In other words, they have been selected. If farmers depend for their livelihood on selling as many eggs as possible, they will breed future stock from the most productive egg-layers, and make the rest of the hens into cat food. They'd continually breed from the best layers in each generation, until, many generations down the line, they'd have created a new breed of hen that routinely lays many more eggs than any hen in the original flock.

This idea—the "artificial" selection by stockmen intent on breeding hens that lay more eggs, sheep with fleecier fleece, bulls with beefier beef, and so on—is intuitive, makes sense to anybody—and was how Darwin started the *Origin*.

What Darwin did next was a master stroke. Once he'd established artificial selection as an obvious and unarguable phenomenon, Darwin used it as an analogy for what goes on in the natural world. In nature the role of farmers is played by the environment. Creatures won't be "artificially" selected by farmers for this trait or that, but "naturally" selected by the ever-changing environmental conditions in which they live. If the climate turns cold, those elephants that happen to have more body hair will be more likely to survive than those that are less hirsute—long enough to breed and pass on their hairiness to their offspring, while the baldies devote their energies to keeping warm rather than reproducing. If the climate continues cold, the bald elephants will eventually be replaced by woolly mammoths.

The beautiful thing about natural selection is its simplicity. All it requires to work are four things, three of which are readily apparent with eyes to see. They are heritable variation, the ever-changing environment, superabundance of offspring, and the passage of long periods of time.

Let's look first at heritable variation. This means that any group of creatures will differ in their appearance or constitutions from one another, and that this variation is inherited from their parents. Unless they are identical siblings, the children in a family will inherit different traits from their parents, to different degrees. Some will be taller, some shorter, some darker, some fairer. For example, if you gathered every adult male (or adult female) in your town and measured them, you'd find that they'd vary greatly in height. You'd have to group men and women separately, as height is in part related to gender—on average, the men in any given population are taller than women from the same population. You'd find that most people would be middling in height, somewhere between 1.5 and 1.9 meters tall. People much shorter or taller than this are relatively rare. Any population is varied, but variation tends to cluster around a "mean" or "average" value. Calculating an average value is easy: add all the heights together, and divide what you get by the number of people you've measured.

The more people you measure, the better, because your result will be a better approximation of reality. If you can't measure everyone in your neighborhood, say, you should still try to measure as large a sample as possible. If you can't do that, you should try to ensure that the people you measure are picked at random. For example, if you measured the heights of the first three people you met, and they happened to be a coven of very small witches, or from a team of very tall basketball players, you shouldn't be surprised that your sample is unrepresentative of people in your neighborhood in general.

When you see reports of preference in the press, such as peoples' voting intentions, or whether their cats prefer ex-battery chicken of one brand over another, you should look out for the small print saying that the evidence comes from a poll of, say, 1,000 people chosen at random. It's important to get lots of people, and to pick them by chance. This chance element is vitally important. There's the probably apocryphal story of a market researcher who found that ninety-nine of a hundred people asked ate porridge for breakfast: it turned out that the people asked all came from the McPherson page of the Inverness telephone directory. This, without meaning any offense to residents of the fine city of Inverness who happen to be called McPherson, is probably not a representative sample of people as a whole.

From this it is clear that variation acts at different levels. As people vary in height even in your neighborhood, so do people from different places. Different populations have different average heights. The average American man is 1.76 meters tall, whereas the average American woman is 1.62 meters tall.[1] Dutch men and women tend to be taller, on average—1.87 and 1.69 meters respectively,[2] whereas urban men and women of the east African nation of Malawi tend to be shorter, 1.67 and 1.55 meters.[3] This means that although men tend to be taller than women in general, the average Dutch woman will be taller than the average Malawian man. Because people tend to marry within their locality or ethnic group, the figures for average height differ from place to place.

Although people vary in all sorts of ways, and even though traits might be influenced by other things, such as nutrition and the environment, it's plain that height tends to run in families—that is, variation is inherited. Tall parents tend to have tall children. My own daughters are among the tallest in their year groups—but I am relatively tall for an Englishman (1.83 meters, against the average of 1.75), and my wife is very much taller than the average Englishwoman (1.8 against 1.6 meters).[4] She also comes from a family of tall women, who tended to marry guardsmen—not just tall, but proverbially tall. Hmm. The tallness strong within them it is.

From all this it's clear that people (and other animals) vary, and that this variation can be passed on through the generations. If this weren't true, then farmers wouldn't be able to breed prime egg-laying hens by selecting the best layers in each generation as brood stock. Such variation is entirely obvious to anybody, yet in Darwin's day nobody knew how variation was maintained. In his time it was generally assumed that the traits of parents got merged among the offspring—but if this were the case, all the variation would quickly get mixed together (like mixing paint of lots of different colors to get brown), and everyone would tend to look the same. But this doesn't happen. Offspring are always varied. Even if the human population were well mixed, such that every person on Earth were obliged to choose their partner through a worldwide dating service, and did so for generations, their children would still vary in height, skin tone, eye color, and a host of other traits. The answer came long after Darwin, with the discovery of genetics, in which it is shown that traits are the expressions of atoms of inheritance called genes, which combine and recombine with one another to create variation, but remain individual and distinct. Some traits are influenced by single genes. Others, such as height, are influenced by many thousands.

The second factor that contributes to natural selection is the variability of the environment in which organisms live. I mentioned the case of mammoths above. If the climate turns cold, hairier elephants will have a better chance of surviving to reproductive age than elephants that are less hairy. Because hairiness will be to some extent inherited, the tendency toward hairiness will spread, so that, over time, the population of elephants will become hairier, on average.

You'll of course have appreciated that the environment is very much more complicated than this cartoon explanation implies. The term "environment" means any circumstance, however small, that affects the chances of a creature surviving long enough to pass its traits on to the next generation. The environment doesn't just mean the climate, or even the weather, but also the relationships that a creature has with other creatures, whether of different species or its own. The environment is therefore not one single thing, but uncountably many, each one changing minute by minute. A creature will have to be able to gather enough resources to grow, all the while trying not to be eaten by other creatures. Once mature, a creature will have to find a mate, and produce offspring, whose interests might differ from its own. All such factors constitute the environment.

Not surprisingly, some parts of the environment actually act in opposition to one another. Perhaps the best-known example is the case of sickle-cell anemia. This is an inherited disorder in which a person's red blood cells fold up like squashed footballs and become very stiff. This makes them poor at carrying oxygen round the body. The malformed cells are also prone to clogging up blood vessels, causing all kinds of potentially life-threatening complications, including increased incidence of infection, damage to internal organs, thrombosis, and stroke. Sickle-cell anemia is a very serious disease indeed, and children with the disease stand much less chance of living long enough to reproduce than children without it. As a result, sickle-cell anemia is rare in most populations—people die of it before they can grow up to have children themselves.

The inheritance of sickling is well understood: it results from a defect in a single gene that codes for part of the molecule of hemoglobin, the protein in red blood cells that carries oxygen in the blood. Most genes are carried in two versions or "alleles," one inherited from the father, the other from the mother. A child can carry two normal alleles, one normal allele alongside one sickling allele, or two sickling alleles. Only that child whose unhappy lot it is to carry two sickling alleles will suffer full-blown anemia. People with two normal alleles will, of course, not get the disease. People with one normal and one sickling allele will be normal, because the normal allele will produce more than enough normal hemoglobin to get by, and they are likely to suffer only if they happen to find themselves up a mountain where oxygen is scarce and hemoglobin has to work overtime.

Now, you'd think that because of the sickling allele's effects on the chances of a young person's reaching adulthood, natural selection would have expunged it pretty smartly from the population. But there's a catch. It so happens that people with the sickle-cell trait are more resistant to malaria than those without. Malaria is debilitating enough in adults, but in children it can be lethal. It is caused by a microscopic parasite that hides out in red blood cells for part of its life cycle. Fewer red blood cells mean a less friendly place for malaria. People with sickle-cell anemia will be very ill anyway, but in the lottery of life, serious illness is often preferable to immediate death. People who have one sickling allele and one normal allele will be very much less ill, but much more resistant to malaria than those with normal alleles.

In parts of the world where malaria is endemic, such as sub-Saharan Africa, a child with sickle-cell anemia, or even a "carrier" with one copy of the sickling allele covered by a normal copy, will be better able to resist malaria and survive than a child with two copies of the normal allele, who is more likely to die from malaria than from sickle-cell anemia. This difference is crucial, for it alters the balance of survival in favor of the child who has sickle-cell anemia over the child who has not—and has allowed the otherwise entirely unwelcome sickle-cell trait to persist. In places haunted by the specter of malaria, carrying a gene for a debilitating disease is actually an advantage—it is the lesser of two evils.

Sickle-cell anemia demonstrates that natural selection is not some agent that drives creatures ever closer to the perfection imagined by advertising copywriters. Far from striving for bigger, better, more complex, or more enlightened, it does *precisely* and *only* what it needs to do to get a creature from egg to adulthood—*and no more*. This can mean carrying a trait for a dreadful disease that happens to offer protection from something worse. And because the environment is complicated, subtle, and ever changing, it is always a mistake to reduce natural selection to a simple mechanism that creates trends or tendencies that can be easily identified as such, and whose causes can easily be worked out.

The third factor that contributes to natural selection is superabundance of offspring. This means that creatures tend to produce many more offspring than can possibly survive. And by "many more," I mean *vastly* more. Anyone who thinks evolution is all about elegance and orderly perfection in nature would be shocked by its profligacy and waste.[5] Next to our chicken run is a pond, which I dug specifically to encourage the arrival of frogs, which would feast on garden pests such as slugs. Each spring the pond bubbles with hot frog-on-frog action, after which the water seethes with thousands of tadpoles—only one or two of which will survive long enough to reach sexual maturity. In the fall, our apple tree is groaning under the weight of fruit, but few or none of its seeds will ever germinate. Every woman produces hundreds of eggs throughout her lifetime, but only a few will be fertilized and come to term; every man produces millions of sperm, but relatively few children.

In ages past, people used to have large families, expecting that many (or most) of their offspring would die of something or another before they reached adulthood. Demons hovered around every crib and outside every nursery. I mentioned malaria, but even today millions of people, most of them children, die from dysentery, diarrhea, tuberculosis, cholera, or the effects of malnutrition. Darwin's daughter Annie died from scarlet fever, which is now relatively rare. When I was a child, less than half a century ago, children even in Britain were severely disabled by or even died from diseases such as measles, mumps, rubella, pertussis (whooping cough), diphtheria, and poliomyelitis. Smallpox was a vanishing threat, but had not at that time been entirely eradicated. There is a reason that many of these dread diseases are associated with childhood—people who contract them as children might not survive to adulthood.

Thanks to improvements in public health and, notably, the success of vaccination, most of these diseases now figure only in period dramas, despite the best efforts of a deluded few anti-vaccination campaigners to turn fiction back into documentary. In the developed world nowadays, mortality among children is less likely to result from infectious disease than from accidents or relatively rare birth defects.

Inherited diseases (as opposed to infectious ones) result from the fact that in a process as complicated and delicate as the development of a creature from an egg, mistakes are often made. The process is so complicated that it's a wonder any of us actually gets born, and it could be that genetic variation itself exists as a hedge against error. By this, I meant that a certain amount of sloppiness is tolerated in the system, creating variation, and those variations that cause lethal or severe inherited disease are the price we all pay for being born at all.[6]

In the meantime—and it sounds desperately cruel—natural selection is likely to favor an earlier death (rather than a later one) from a debilitating disease so that harmful traits are less likely to be passed on (unless they provide an advantage, as in the case of sickle-cell anemia) and, more immediately, so that parents can get on with devoting limited resources to producing healthier offspring instead. In a world in which the threat of disease or mishap is always present, superabundance is a way of beating the odds, of maximizing your chances of your progeny surviving long enough to reproduce. The gambler at the roulette table who places all his chips on a single outcome will almost certainly lose. The gambler who puts a chip on every possible outcome is bound to win something. The second gambler will have lost an awful lot of chips but can stay in the game, whereas the first will have lost all of them and has no choice but to leave the casino.

These three things—heritable variation, the changing environment, and superabundance of offspring—are neither particularly special nor inherently mysterious. The fourth factor is time, and that's a little more tricky.

Darwin saw natural selection not as an agency in itself, but the ongoing result of the interaction of several factors. Creatures tend to produce offspring that vary, and this variation is heritable. They also tend to produce more of them than can possibly survive. Nature will select those few offspring that are most suited to living in the prevailing environment, in much the same way that a stockman will select those animals most suited to his ends. Given enough time, the creatures will change, their adaptations tracking changes in the environment.

But how much time is "enough"? Darwin envisaged that change would be slow, perhaps even imperceptible on the scale of human lifetimes, and reasoned that many millions of years would be required for natural selection to transform a blob of primordial protoplasm into the diversity of animals and plants we see all around us. The problem was that, in Darwin's youth, such time didn't exist. So no matter how obvious heritable variation, superabundance, and environmental change are to every child and countryman, without time, natural selection wouldn't be able to do very much.

What do I mean by time "not existing"? I'm being deliberately arch here. Nowadays we are accustomed to thinking of the earth as very old—around 4,500,000,000 years old, in fact—plenty of time for natural selection to have done its work. We are inclined to take such things for granted, so it's very hard for us to put ourselves into the minds of the average Victorian who had no reason to doubt that the earth was any more than the 5,500 years or so required by the Bible. It took quite a long time for even those interested in the subject to realize that the earth is very much older than this, and even then, only when they were confronted by an otherwise insupportable weight of evidence. (The many people who to this day cling to the old biblical timescale have no such excuse.)

And that's it. Take heritable variation, the changeable environment, superabundance, and time. All these things can be seen—or, at least, understood—by anyone.

So much for natural selection. What, then, about evolution? How is one related to the other? The terms are not equivalent, and that's part of the problem. Here I hope to disentangle the word from some of its ancient baggage, look into its history as a word as well as a concept, and show what (I think) Darwin meant it to mean—which is (I think) rather different from what most people think when they use the term. In fact, I'd go as far as saying that it would be hard to find a worse choice of word than "evolution" to describe what Darwin, very sensibly, called "descent with modification." To Darwin, the word "evolution" did not mean what we think it means today.

As you might expect, the word has Latin roots. According to the online *Oxford English Dictionary*, henceforth *OED*,[7] the Roman writer Cicero used *evolutio* to mean the action of unrolling a scroll. Thus was born the concept of evolution as a process of development, elaboration, and, with it, revelation—that is, the deliberate transformation, by the action of unrolling, of a closed scroll to an open one whose information might be read: an orderly dance from simplicity into complexity. Medieval Latin texts use the term to refer to the passage of time during which any metaphorical unrolling might take place.

The first recorded use of the word "evolution" in English was in 1616, in a translation of the *Tactics* by the second-century Greek military historian Aelian (Aelianus Tacticus), where it means, quite specifically, the movement of forces from one position to another:

> The nature of this Euolution is clearely to leaue the File-leaders in front, and Bringers-vp in reare.

This nuanced view of evolution, as a series of maneuvers along a studied course from known beginning to desired conclusion, broadened to describe the occult movements of the wands of wizards, the gyrations of gymnasts, and, eventually, the choreography of dancers. The many examples given by the *OED* have one thing in common—that the term "evolution" in this sense came to encapsulate an exact, directed and predetermined series of events, as predetermined as a choreographed dance routine. More generally, the word "evolution" came to mean the opening out or unfolding of a series of events in an orderly succession, or the action of elaborating a simple idea into something more rounded, very much by analogy with Cicero's unfurling scroll. As an aside, almost, consider this notable example from Erasmus Darwin's *Zoonomia* (1801):

> The world . . . might have been gradually produced from very small beginnings . . . rather than by a sudden evolution of the whole by the Almighty fiat.

Given what we think we know of evolution—as a gradual process—it is startling to come across Charles Darwin's grandfather Erasmus using the term in precisely the opposite sense.

Those admen I lampooned in chapter 1 would find in the *OED* plenty of precedents for their use of the term "evolution" to refer to the refinement of consumer products (the first recorded such usage being in 1882). But in biology, as in life more generally, the term began to be used very much by way of analogy with Cicero's original meaning—the elaboration of something simple into something more complex, such as a plant from a germinating seed, or the development of a butterfly from a caterpillar—like so many scrolls unrolling, each in its own precise, preprogrammed manner. Here is an entry from the earliest days of the *Philosophical Transactions of the Royal Society*, in 1670:

> By the word Change is nothing else to be understood but a gradual and natural Evolution and Growth of the parts.

And once again from Erasmus Darwin:

> The gradual evolution of the young animal or plant from its egg or seed.

As a term, evolution gets around. I haven't mentioned the several different usages of "evolution" in mathematics, astronomy, and chemistry. All of the above, of course, is by way of a curtain-raiser to what the *OED* lists as sense 8 of evolution (out of eleven), namely "the transformation of animals, plants and other living organisms into different forms by the accumulation of changes over successive generations." The first recorded use of "evolution" in this sense is in 1832, in Charles Lyell's *Principles of Geology*, a work with which Charles Darwin was very familiar.

> The testacea of the ocean existed first, until some of them by gradual evolution, were improved into those inhabiting the land.

As I noted, Darwin did not use the word "evolution" in the *Origin* (and continued not to do so until the sixth edition of 1873). He did, however, use the word "evolved." It appears once, as the very last word in the book, the final word of a justifiably famous paragraph.

> There is grandeur in this view of life, with its several powers, having been originally breathed by the Creator into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.

It is important to remember that Darwin was no Darwinist. He could hardly have used the words "evolution" or "evolved" in the sense we generally understand them today, given that it was his own work that was largely responsible for altering the balance of their usage—from Cicero's unrolling scroll, to the transformation of organisms over geological time. We, however, are in a different position. To us, the shade of Darwin looms large. His insights have colored the way we think of ourselves and our place in nature.

So, when Darwin used the word "evolved," it was in the earlier sense, of something unfolding. Creatures would appear, perhaps in successively more elaborate forms, from simple beginnings—perhaps as an analogy with the production of a shoot from a seed, or a frog tadpole from a mass of spawn. Darwin was a great believer in the power of analogy. After all, his entire argument about natural selection was based on just such a comparison with the "artificial" selection that stockbreeders use to enhance the desirable traits in their charges.

Darwin, therefore, used the word "evolved" to mean growth and development of a complex form from a simpler one, and used it to draw an analogy with the altogether grander process in which life itself would from simple beginnings become more diverse, elaborate, and complex. Darwin had a term for this process to which evolution was a mere analogy: he called it "descent with modification," a much less loaded term than "evolution."

In general, though, when scientists in Darwin's time and earlier referred to the gradual change of species—what we today call "evolution"—they used the word "transformation." If evolution meant the unfolding of individual organisms, from seed to shoot, from egg to adult, then transformation meant the change in form of entire species, usually (though not necessarily) from simpler forms to more complex ones.

The two processes—evolution and transformation—were analogous, but distinct. Today, though, they have become conflated. When most people today talk of "evolution," what they mean is "transformation." This conflation has had the consequence of conferring a sense of direction and choreography onto the idea of Darwinian evolution. This is why people, when they think of "evolution," imagine (for example) a series of individuals, each one an improvement on the one before, and if there are gaps in the series, they are "missing links"—pieces in a metaphorical chain whose beginning, end, and intermediate progress are already known.

There are deeper roots to this conflation, however, but before I get to that, I must tempt you into a little digression about the nature of and evidence for Darwin's descent with modification.

Earlier I mentioned that the "community of descent" provides much evidence for descent with modification. By this I mean that all forms of life are organized in fundamentally the same way, down to the minutest detail, supporting the view that all life shares a common heritage.

It's worth considering this in a little more detail. As far as we know, all organisms owe their structure to the peculiar chemistry of the element carbon. Carbon atoms readily bind with one another and with atoms of other elements (notably oxygen, hydrogen, nitrogen, phosphorus, and sulfur) to produce highly elaborate molecules, sometimes disposed in long chains of smaller, similar units strung together. So it is that all organisms so far discovered carry genetic information in the form of long, carbon-based, chain-like molecules called nucleic acids, either DNA (deoxyribose nucleic acid) or the related form RNA (ribose nucleic acid). This information specifies the structure of a different set of chain-like, carbon-based molecules called proteins, and does so using a code that's the same (albeit with minor variations), irrespective of the organism concerned. All organisms more complicated than viruses have cells, bounded by a membrane constructed of two layers of carbon-based, chain-like molecules called lipids, sometimes bound in an extracellular matrix made of chain-like carbon-based molecules such as cellulose or collagen. The contents of the cells are pretty much the same, irrespective of the organism in which they occur.

The similarities between creatures at this most detailed level are so great that it's a wonder that organisms as a whole come to look so different—from the worms burrowing beneath Darwin's tangled bank to the birds and insects flitting above it. This underlying sameness is such compelling evidence for descent with modification that it would, according to Richard Dawkins (in his book *The Greatest Show on Earth*), stand alone, even had no fossils ever been discovered.

Why is the evidence so strong? Because life needn't have been arranged like that. It is possible to imagine systems that have some of the properties of life that use only some of the above features, or none. It is also possible to imagine a situation in which different living organisms sharing the same planet have fundamentally different constitutions. The fact that all life, no matter how various in form, is specified so minutely according to the same recipe suggests that all living creatures descend, ultimately, from a creature that had all these same fundamental features of inheritance and construction.

So much for descent: what of modification? Darwin supposed that the pattern of inheritance might vary, the offspring of parents becoming sorted by natural selection, so that the offspring would come to look different from their parents. These differences would accumulate, and the offspring would spread and diversify. As with offspring and parents, so, eventually, with new species arising from existing ones. It is a testament to Darwin's perspicacity that even though Darwin had no clue about the mechanisms of genetic variation, his suppositions have been borne out, innumerable times, and in exquisite detail.

Darwin imagined that life, governed by such a process, would be connected in a treelike pattern, rather like a family tree, with one ancestor at the bottom—the root and trunk—and progressively more (and more diverse) descendants as the branches and twigs. Darwin's conception of the treelike pattern of evolution formed the only illustration in the *Origin*. Darwin's innovation was his invocation of a process, natural selection, acting in the here and now, which, when summed over history, produced this pattern.

In geometrical terms, a tree is a box of boxes, a set of sets: one trunk gives off a number of branches, each of which gives off a bunch of twigs, each of which bears several leaves, and so on. The idea that life can be catalogued as a system of nested sets goes back to Aristotle, but it was formalized in the eighteenth century by the Swedish botanist Linnaeus, who originally devised the hierarchical means of classification we use today, in which species (*erectus*, *sapiens*) are grouped into more inclusive genera (*Homo*), which in turn are grouped with other genera into orders (Primates) and with other orders into classes (Mammalia). Linnaeus's conception of life was profoundly and inevitably pre-evolutionary: he was organizing life simply as he (and everyone else) saw it.

Scholars before Darwin thus had two distinct phenomena to explain. First was evolution—sometimes called generation—in which a small and simple germ was elaborated ("evolved") into a large and complex adult. The second was the apparent arrangement of life in a hierarchical or treelike fashion.

The analogy Darwin drew between evolution and transformation was not his own invention. Editions of William Harvey's *Exercitationes de generatione animalium* (1651), one of the earliest works in the modern era to address the question of generation, bore engravings illustrating Zeus holding an egg from which all manner of creatures poured forth, with the legend "Ex Ovo, Omnia"—everything comes from the egg—a slogan that could be applied to generation and transformation with equal facility.

A more explicit connection between the two processes was drawn by the adherents of "nature philosophy," a tendency popular in the late eighteenth and early nineteenth centuries, and particularly associated with the poet, protoscientist, playwright, and all-around egghead Johann Wolfgang von Goethe. The nature philosophers were inclined to be somewhat romantic, which doesn't always go down well among scientists, and it's easy to make fun of them nowadays. However, they made two vital contributions to biological thought—one somewhat mystical, as one might expect; the other highly practical.

Although people saw life arranged as a tree, they also noticed that trees grow upward, from the ground; that you need a ladder to climb a tree if it is tall; and that it takes more effort getting to the upper branches than sitting on the ground. The treelike arrangement was therefore in accord with the ancient idea of the "great chain of being," in which living creatures occupied a station in life according to their structure, the simpler ones (worms, insects, and so on) toward the bottom, the more complex ones (fishes, birds, mammals) toward the top. Human beings would—noblesse oblige—occupy the topmost rung, above the apes, but below the angels.

At first, this arrangement was simply a statement of the order of creation. There was no sense in which creatures on a lower rung could be transformed into creatures on a higher one. Some thinkers, however, began to question why the tree should be ordered in the way it was, rather than in any other way, and began to imagine processes whereby creatures might be transformed.

Perhaps the most famous exponent of transformation before Darwin was Jean Baptiste de Lamarck, who outlined a scheme in his book *Philosophie zoologique* (1809) in which creatures would be driven to transform by an inner force or *besoin* (need) in response to their environmental circumstances, and such transformations would be inherited by any offspring. Thus the canonical picture of giraffes extending their necks ever longer to reach the highest leaves, and passing the results of their exertions onto baby giraffes, which would tend to have longer necks than their parents. This idea sounds quaint today, but Lamarckism was a theory with legs.

Today we are inclined to think that after the publication of the *Origin*, Darwin's ideas just went from strength to strength (such is our view of history as forever progressive), but this is not the case. Natural selection required that creatures provide a constant source of variation on which this selection could act. In Darwin's time, though, no such mechanism was known. The discovery of genetics around the turn of the twentieth century was to answer the question and so rehabilitate Darwin, but for half a century—between Darwin's death in 1882 and the reconciliation of evolution and genetics in the late 1930s—evolution by natural selection was in eclipse: influential scientists turned away from Darwinism for want of an explanation of variation, leaving evolution as not much more than a set of just-so stories. William Bateson—the scientist who would later coin the term "genetics"—was typically scathing.[8] "In these discussions [of evolution] we are continually stopped by such phrases as 'if such and such a variation then took place and was favourable,' or, 'we may easily suppose circumstances in which such and such a variation if it occurred might be beneficial,' and the like . . . 'If,' say we with much circumlocution, 'the course of Nature followed the lines we have suggested, then, in short, it did.'" As a result of this Darwinian vacuum, many mainstream thinkers continued to favor Lamarckism, so much so that it formed the grounding of university-level textbooks such as E. S. Russell's classic *Form and Function* (1916).

The nature philosophers looked at the pattern of life, but rather than Lamarckian *besoin*, a mechanism that was actually meant to cause transformation in the real world, they saw in each successively more elaborate form a more concrete manifestation of some ideal, cosmic striving toward perfection that would reach its acme in Man (with a capital *M*). Creatures in the real world were imperfect expressions of a transcendental ideal. No actual transformation was meant to have happened.

The practical aspect of nature philosophy came with nature philosophers' approach to the problem of generation. The problem of generation was working out how a seemingly unformed germ (such as a seed or egg) evolved into a complex, adult creature. Where did all that complexity come from?

Some scholars thought that it appeared out of nothing, whereas others, the so-called preformationists, thought that the adult form was there all the time, just in some occult, condensed form, waiting for the right cue to unravel. The problem was that investigating the subject directly proved impossible, and by the end of the eighteenth century the subject had reached an impasse. The problem couldn't be solved until the adoption of the cell theory, in the 1840s, and with that, the invention (one is tempted to say "evolution") of staining techniques whereby translucent, filmy cells could be made visible under a microscope. Only then was it realized that new organisms arise from the fusion of male and female sex cells (sperm and eggs) followed by a complex series of elaborations ("evolutions").

In the meantime, though, the nature philosophers took the view, possibly informed by their somewhat mystical outlook, that the earliest stages of generation might be forever hidden from view, impossible to discover even in principle. If this sounds familiar, it should—astrophysicists have adopted the same view about the birth and very earliest moments of the universe, ruled by physics beyond current theory to explain, and probably beyond any capacity of experiment or observation to penetrate. But that doesn't stop astrophysicists observing and theorizing about the history of the universe after that mystical instant of birth, and nature philosophers took the same view of generation. If the earliest moments of generation could not be seen, there was still a wealth of information to be gained about embryos, and how they grew and developed.

When German-speaking embryologists such as Karl Ernst von Baer and especially Ernst Haeckel, who had been drenched in the culture of nature philosophy, came to look at the embryology of various creatures, they found that the stages through which a developing organism "evolves" reflects its station in the grand ordering of Creation. Creatures start from single cells, much like blobs of protoplasm. They then form into balls of cells, similar to lowly algae or sponges, which fold into cup shapes, blind sacs with an opening at one end—much like simple polyps. They then elongate, coming to look like lowly worms, with yet further evolutions demarcating successively higher states. The necks of human embryos, for example, show rudiments of the gill slits that perforate the throats of fishes. They have tails, which are reabsorbed, and just before birth, some babies are quite furry. The elision, therefore, became obvious. The great tree of life, the great chain of being—whatever one wants to call it—maps the evolution of every individual creature as it develops. To put it another way, the evolution of any creature goes through a number of stages, the last one of which determines its place on the tree of life. The canonical summary of this idea is "ontogeny recapitulates phylogeny." This concept was meat and drink to the nature philosophers, who could now see the archetypal ideas of creatures on the grandest scales played out everywhere in the dramas of individual development. As one nature philosopher put it: "What is the animal kingdom other than an anatomized man, the macrocosm of the microcosm?"[9] It was the nature philosophers then, who, when they became embryologists, made the explicit connection between what might otherwise have been seen as two quite distinct processes—evolution and transformation. Partly for this reason, one can lay the blame for today's muddled thinking about evolution at the door of the nature philosophers and their inheritors, especially Haeckel.

The nature philosophers did not see the natural world in terms of actual transformation, only as the expression of cosmic or divine ideals. Haeckel, though, became a firm adherent of Darwin's evolution, doing much to popularize it. Haeckel missed the essential metaphor of Darwin's tangled bank, however, and saw natural selection instead as a kind of motor that would drive transformation from one preordained station on the ladder of life to the next. This is the view of natural selection—as another word for the cosmic urges of nature philosophers—that some scientists[10] found exceptionable toward the end of the nineteenth century, leading to Darwinism's eclipse, yet is the view that has become ingrained in the public mind whenever the word "evolution" is mentioned. It is this Haeckelian bastardization of natural selection that's responsible for the arrows in figure 2, the engine that drives evolution forward, from simplicity to complexity, in a series of Ciceronian maneuvers with a definite beginning and a culmination in Man—as far from the undirected, contingent, and moment-by-moment actions of natural selection on the tangled bank as might be imagined.

And if we think that this piebald view of evolution, as forever progressive and improving, striving ever toward the transcendent light, is something espoused only by misinformed journalists and newspaper readers who know no better, we must think again. When I was an undergraduate, back in the mists of time (okay, it was 1981), my zoology textbook was the very latest edition of *The Life of Vertebrates*, by the influential, immensely respected, and very sensible zoologist, the late John Zachary Young. Here is Young summarizing the evolution of mammals, the group of creatures to which we ourselves belong.

> We shall expect to find in the mammals even more devices for correcting the possible effects of external change than are found in other groups. Besides means for regulating such features as those mentioned above we shall find that the receptors are especially sensitive and the motor mechanisms able to produce remarkable adjustments of the environment to suit the organism, culminating in man with his

> astonishing perception of the "World" around him and his powers of altering the whole fabric of the surface of large parts of the earth to suit his needs.[11]

Yes, you read that correctly—Young really does use the phrase "culminating in man." And if that's in a modern undergraduate textbook, written by an acknowledged authority, it is little wonder that people more generally find it hard to grasp what evolution (in the sense of descent with modification) is all about.

We can't put all the blame at Haeckel's door, however. When the *Origin* first erupted (there is no other word) into the public consciousness, commentators were less worried about the niceties of natural selection, still less that Darwin could not explain the mechanism of inheritance on which his theory depended, but about the challenge that Darwin's ideas made to established social orthodoxy. In place of a static social order, a possibility of change—of liberation, progression, advancement, improvement. What we would now call a left-wing thinker such as Harriet Martineau (who knew Darwin personally) and particularly Herbert Spencer (who coined the phrase "survival of the fittest") co-opted Darwinian evolution in support of a general theory of social evolution that had all the hallmarks of the directed, progressive strivings that one would see turning up everywhere from manifest destiny and Marxism to fascism and advertising.

The *OED* defines sense 10 of "evolution" as "progression from simple to complex forms, conceived as a universal principle of development, either in the natural world or in human societies and cultures" and cites Martineau.

It was Spencer, not Haeckel, who championed evolution among what we might now call the "chattering classes," in opposition to the nobility and the established church, and who wrote, just before the *Origin* was published, that "those who cavalierly reject the Theory of Evolution, as not adequately supported by the facts, seem quite to forget that their own theory is supported by no facts at all." The battle lines were drawn between the agents of political progress, marching forward with evolution as a kind of justification for social improvement, and the established orthodoxy to which evolution was seen as a threat. One sees the same lines drawn to this day, especially in the United States. It's a pity that somewhere along the line, the exquisite beauty and infinite subtlety of natural selection as a mechanism has been lost, trampled into the dust by the simplistic slogans of those who'd use evolution as a device to further their own ends.

The accretion of all this social, political, and philosophical baggage over the past century and a half has tended to dull any appreciation of the disarming simplicity and beauty of natural selection as a mechanism. All other schemes of transformation current in Darwin's day required strange and mysterious ingredients, such as Lamarck's *besoin*, or cosmic strivings for betterment favored by the nature philosophers—none of which could be seen or touched, and whose existence had to be taken on trust. Natural selection required nothing that couldn't be seen, touched, and appreciated by anyone.

Natural selection is unique in another way, too, for unlike all other theories of transformation, it has no inherent direction. Darwin's contemporaries and antecedents looked at the tree of life and invented processes to "explain" it that were directional and improving. Darwin turned this idea on its head. He came up with a simple process in which no particular direction was implied, but whose result would be the treelike pattern we see. The tree is just natural selection summed over history.

Natural selection, therefore, does not demand what we from our human perspective think of as "improvement." To go further, natural selection cannot be seen as evolution's guiding hand. It has no personality, no memory, no foresight, and no end in view. To be sure, it's easy to see that natural selection, if left to operate for long enough, will create the branching patterns of the tree of life in much the way that Darwin suspected it did. However, there is nothing in natural selection that allows you to predict any *particular* pattern that it might generate. This marks a crucial distinction between natural selection and earlier ideas of transformation that presupposed a ladderlike scheme with *Homo sapiens* at the top. In natural selection, the pattern we see was not preordained, manifest, or inevitable in any way. Stephen Jay Gould expressed this idea very well in his book *Wonderful Life*—if we could rerun the tape of life, we shouldn't necessarily expect the same result every time.

I'd like to go much further than Gould did. In a famous scientific paper, Gould and his colleague Niles Eldredge proposed that evolution would not always proceed gradually, according to the "insensible gradations" proposed by Darwin, but might in some circumstances proceed very rapidly, and in other circumstances not move at all.[12] This was the "punctuated equilibrium" model of evolution, much debated ever since. But the arguments about evolution's speed—and these arguments have been fierce and acrimonious—all rest on the assumption that there is a narrative to be uncovered, a story that might be read from analysis of the fossil record.

However, any patterns that we see in the fossil record are reconstructed by us, after the fact. Because the fossil record is so fragmentary and imperfect (a point that Darwin grasped with his usual percipience), it is easy for us to read into it any narrative we like and assume that this narrative must be the right one. It is only natural for us to compose a story that suits our own prejudices of evolution (driven by natural selection) leading to ever greater refinement. This is, however, a profound misreading of Darwin's ideas and reflects a failure to understand the uniqueness of natural selection as a mechanism of transformation. With natural selection, no fate is ever inevitable, unless reinforced as such by hindsight.

The blob of protoplasm in Darwin's proverbial "warm little pond" could have evolved into anything—or nothing. The fact that evolution took the course it did was a result of natural selection acting on it and its descendants, moment by moment, according to the environmental circumstances prevalent at each given instant. Looking back at the course of evolution from our privileged height, we naturally assume that the only course of evolution possible was the one that led to ourselves.

This idea seems to have made insufficient impact among science communicators, members of the public, and even some scientists. In the world at large, many evolutionary transformations and adaptations are assumed to have been imbued with purpose. For example, feathers are seen as adaptations that allow birds to fly, as if flight were somehow the manifest destiny of birds. That this idea is wrong is shown by the evidence, which suggests that feathers evolved many millions of years before birds took to the air, among dinosaurs that patently would not have been able to fly. It is even possible that some dinosaurs, having evolved feathers, lost them again. This kind of backward-reasoning, in which adaptations are seen as having a purpose in some great transcendental game that lasts for millions of years, is also widely seen in schemes of human evolution that suppose, for example, that humans stood on two legs in order to free up the hands for making tools, to nurse babies, and so on.

This style of reasoning, in which evolution is assumed to have a purpose or a goal, is naturally accompanied by an assumption of progress, very much in the pre-Darwinian style. The assumption of progression is not only a misrepresentation of evolution, but ignores most of what is actually going on.

When we strip away the assumption that evolution is progressive, we find a different picture, both richer and stranger. Most of what seems to be going on in evolution is not the acquisition of new, improved ways of living, but their wholesale loss. This is quite at variance with the picture of evolution most people have, of a march of greater complexity and improvement—a picture that, as I hope is becoming clear, is sometimes misinformed. The concept of loss is explored in the next chapter.