Nothing in Biology Makes Sense Except in the Light of Evolution: Pattern, Process, and the Evidence

Jonathan B. Losos

Evolutionary biology is unusual: unlike any other science, evolutionary biologists study a phenomenon that some people do not think exists. Consider chemistry, for example; it is unlikely that anyone does not believe in the existence of chemical reactions. Ditto for the laws of physics. Even within biology, no one believes that cells do not exist nor that DNA is a fraud. But public opinion polls consistently show that a majority of the American public is either unsure about or does not believe that life has evolved through time. For example, a Gallup poll taken repeatedly over the past twenty years indicates that as much as 40 percent of the population believes that the Bible is literally correct.

When I teach evolutionary biology, I focus on the ideas about how evolution works, rather than on the empirical record of how species have changed through time. However, for one lecture period I make an exception, and in some respects I consider this the most important lecture of the semester. Sad as I find it to be, most of my students will not go on to become evolutionary biologists. Rather, they will become leaders in many diverse aspects of society: doctors, lawyers, businesspeople, clergy, and artists; people to whom others will look for guidance on matters of knowledge and science. For this reason, although I devote my course to a detailed understanding of the evolutionary process, I consider it vitally important that my students understand why it is that almost all biologists find the evidence that evolution has occurred—and continues to occur—to be overwhelming. If students take nothing else from my course, I want them to understand the evidentiary basis underlying the field of evolutionary biology. And that is what I want you, the reader, to take from this chapter. Of course, that is not to say that each student personally must find the evidence convincing. But, as I tell my students, if they decide not to be convinced by the evidence, not to believe that evolution has occurred, they need to be prepared to address the evidence for evolution and explain why it is not compelling.

The evidence for evolution can be broken into three categories, which I address in separate sections below:

- Demonstrations that natural selection, which is the presumed main mechanism of evolutionary change, operates today.
- Fossil evidence that evolution has occurred.
- Data from fields as disparate as molecular biology, biogeography, and anatomy that make no sense except in an evolutionary context.

Evidence That Natural Selection Leads to Evolutionary Change

So what is "natural selection"? Basically, natural selection occurs when individuals within a population differ in some attribute and, as a result of this attribute, some individuals are more successful at producing more fertile and healthy offspring in the next generation. This enhanced reproductive success can occur in many ways: individuals can live longer and thus have more opportunities to reproduce; they can be more successful in getting to mate more frequently (particularly important for males of many species); they can produce more offspring per reproductive event; or they can produce offspring that are of higher "quality," better adapted to their environment.

For natural selection to produce evolutionary change, one more condition must be met: differences among individuals must be genetically based so that the trait in question tends to be passed on from parent to offspring. If these conditions are met, natural selection will lead to evolutionary change. If the trait is not genetically based, then natural selection will not lead to evolutionary change.

Darwin was not the first to propose that evolution occurs. Indeed, his grandfather, Erasmus Darwin, had proposed a theory of evolution (called "Zoonomia") at the end of the eighteenth century. In the middle of the nineteenth century, ideas about evolution were in the air—Robert Chambers's *Vestiges of the Natural History of Creation* had been a best seller in 1844. Darwin's important advance (independently proposed by the great naturalist Alfred Russel Wallace) was providing a mechanism for evolutionary change to occur. That mechanism was natural selection.

Evolution by natural selection occurs when the genes for traits that cause an organism to produce greater numbers of viable offspring become more common in each succeeding generation (by "viable" we mean "able to reproduce"; it is not enough to produce many offspring if the offspring themselves do not live long enough to reproduce). Natural selection is sometimes referred to as "survival of the fittest," but this is a poor aphorism in two respects: First, the term "fittest" is sometimes misinterpreted to mean "best possible," when, in fact, it just means "better adapted to producing more viable offspring in the current environment than the alternative traits existing in the population." Second, traits that lead to high numbers of viable offspring often have little do with the long-term survival of an individual organism and sometimes can even be detrimental. The long tail of male peacocks, for example, certainly makes these birds more vulnerable to predators. But because females for some reason prefer long tails, males bearing elongated trains tend to father more offspring.*

* Mate choice—technically, a form of sexual selection, which is one type of natural selection—is one of the most controversial topics in evolutionary biology today and could easily be the subject of an essay all its own. In many cases, members of one sex—usually females—choose to mate with members of the other sex that can provide either direct benefits, such as a food-rich territory or help in raising the young, or indirect benefits by providing high-quality genes to the offspring. In other cases, it is not clear why a particular mating preference has evolved. With regard to the peacock, all kinds of outlandish ideas have been proposed. One idea, for example, is that females mate with males that have a handicap, such as a long tail that makes them

I want to emphasize that natural selection and evolution are not the same thing. Natural selection is one mechanism that can cause evolutionary change. Other mechanisms include persistent reoccurrence of a particular mutation, immigration of individuals with different genetic makeup, nonrandom mating, and genetic change resulting randomly as a statistical accident, which usually occurs only in small populations.

Nonetheless, natural selection is in most cases the most powerful mechanism of evolutionary change. Darwin's theory was that natural selection is the cause of evolutionary change, and four lines of evidence around us today indicate the efficacy of natural selection in causing evolutionary change.

Laboratory Experiments

Since the early part of the twentieth century, scientists have conducted experiments in which very strong selection is imposed on a population to see whether evolutionary change results. I present just two of a great number of such studies. The first involves selection on the number of bristles on fruit flies. Fruit flies in the genus *Drosophila* have been the workhorse of genetics research for nearly a century because they can be easily raised in the lab and because they have many traits, such as differences in eye color, that are amenable to genetic study by mating individuals with different traits and seeing what their offspring are like. Fruit flies have hairlike bristles on many parts of their bodies, and in one experiment selection was imposed on the number of bristles on their abdomen. In one condition of this experiment, only the flies with the greatest number of bristles were allowed to breed, whereas in the other condition, only those flies with the fewest bristles were bred. In every generation the

clumsy fliers, because if a male can survive with such an impediment, then the rest of his genetic makeup must be really stellar to compensate for this disadvantage. Hence, because the female mates with such a male, her offspring will get these high-quality genes. Unfortunately, they will also get the gene for the long tail. Although this idea is still debated, most evolutionary biologists are dubious.

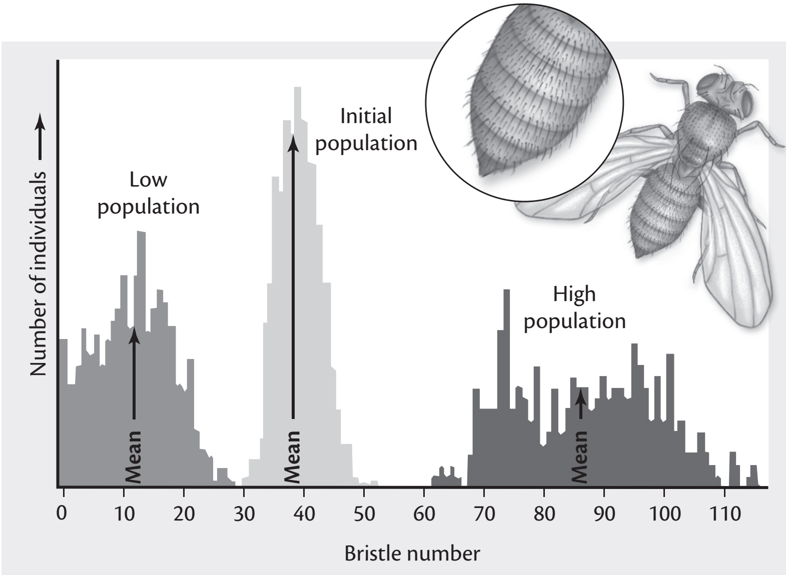

Figure 1. Bristle number in *Drosophila. Drosophila* populations selected for high and low numbers of bristles have evolved large differences. (Image adapted from P. Raven, G. B. Johnson, K. A. Mason, J. B. Losos, and S. S. Singer, *Biology*, 9th ed., © 2011 by The McGraw-Hill Companies, Inc.)

scientists would examine the individuals in the population and segregate out those few flies with the greatest or smallest number of bristles (depending on which experiment). Within fifteen generations, the high-selected and low-selected populations were so different that there was no overlap in the number of bristles—the individual with the smallest number in the high-selected population was more hirsute than the most bristly member of the low population (see Figure 1).

Another experiment involved the ability of rats to run through a maze. In this study, how long rats took to learn the correct path through a maze was recorded, and then selection was imposed, as in the previous experiment; the best performers were bred with other quick studies, while the most error prone were similarly paired with

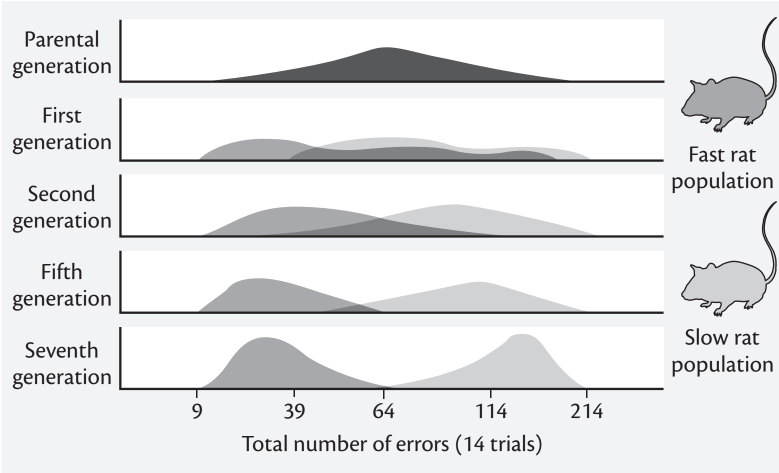

Figure 2. Selection on maze learning in laboratory rats. (Image adapted from P. Raven et al., *Biology*, 9th ed., © 2011 by The McGraw-Hill Companies, Inc.)

each other. This procedure was repeated for seven generations, by which time the population of rodent dummkopfs made, on average, five times more mistakes than the murine Einsteins (see Figure 2).

Artificial Selection outside of the Laboratory

The term "artificial selection" refers to selection imposed intentionally by humans. Besides in the laboratory, such selection has been imposed in a number of ways throughout the history of modern humans. Ranchers, for example, use selection procedures similar to those used by laboratory scientists to increase productivity of livestock. The result is modern livestock, which in many cases bear little resemblance to their wild ancestors, but which are much more productive for the traits for which they have been bred. Consider the milk production of cows, the egg production of chickens, and the amount of fat on the backs of pigs: in all cases, modern breeds are substantially different not only from their wild relatives, but even from the breeds that existed a century ago.

The success of such artificial selection is demonstrated by a long-running selection experiment on oil and protein content in corn, originally begun in 1896 and still being maintained today by scientists at the University of Illinois. At the beginning of the experiment, the average oil content of a corn kernel was approximately 4.5 percent. Throughout the experiment, each year the next high-oil generation was started by choosing the oiliest 20 percent of the corn crop, and the low line was created with the corn in the bottom twentieth percentile of oil content. This experiment has gone on for more than a hundred generations. The results are clear: oil content has increased approximately 450 percent in the high line, and the low-oil line has decreased to about 0.5 percent, a level at which it is difficult to accurately measure corn kernel oil content.

These studies of artificial selection are just a few from a large number. As a gross generalization, we can conclude that artificial selection in domesticated animals and in the laboratory yields essentially the same result. Basically, one can select on just about any trait and increase or decrease its average value; in fact, people have tried to select on an amazing variety of characteristics, almost always successfully. I emphasize that this is a generality and that there are exceptions, but not many; most exceptions occur when variation among individuals in the trait is not the result of genetic differences.

This trend is taken to the extreme in the domestication process. Consider, for example, the vast diversity in breeds of dogs that has resulted from artificial selection. In earlier times, different breeds were produced for particular reasons: greyhounds for their speed, dachshunds for the ability to enter rabbit burrows, and so on. If one looks at various dog breeds, say chihuahuas, dachshunds, and mastiffs, the differences in body size, relative limb length, and face proportions are enormous. By contrast, the differences among wild species of canids—such as foxes, wolves, and coyotes—are substantially less. In

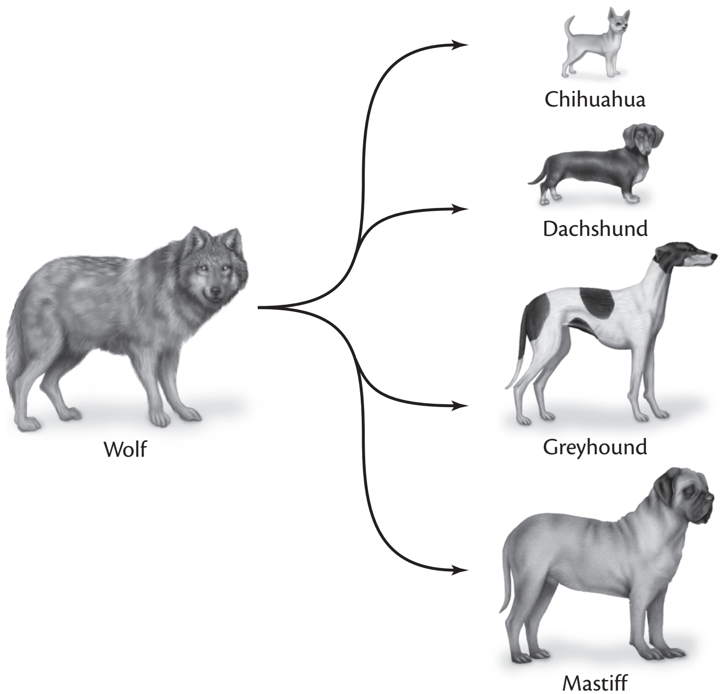

Figure 3. Extreme differences in modern dog breeds. Anatomical differences among these breeds are substantially greater than differences among wild species of canids, such as wolves, jackals, foxes, and coyotes. (Image adapted from P. Raven et al., *Biology*, 9th ed., © 2011 by The McGraw-Hill Companies, Inc.)

other words, in a few hundreds to thousands of years, humans have created substantially greater variation among breeds of dogs than natural selection has created over the greater than 10 million-year span in which modern members of the Canidae have been evolving (see Figure 3).

The same is true in the domestication of agricultural crops. For example, a remarkably diverse group of dinner table vegetables—including cabbage, cauliflower, broccoli, brussel sprouts, kale, and others—were all derived in the last few thousand years from the same ancestral species of cauliflower, which still occurs in the Mediterra-

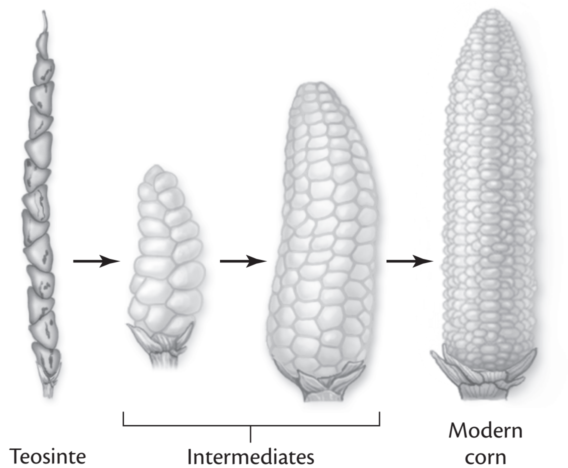

Figure 4. Modern corn compared with its ancestor, teosinte. (Image adapted from P. Raven et al., *Biology*, 9th ed., © 2011 by The McGraw-Hill Companies, Inc.)

nean region of Europe and northern Africa. Similarly, the ancestral species from which corn was developed still occurs in Central America (although it is endangered). Diminutive and bearing only five to ten irregularly shaped kernel-like seeds, teosinte bears little resemblance to our familiar source of niblets and corn on the cob (Figure 4).

Artificial selection is not a perfect analogy to natural selection—it is usually substantially stronger than natural selection, as well as unidirectional (always favoring the same variants, such as the largest or most long-legged individuals) and usually focused on only one or a few traits, whereas natural selection may simultaneously operate on many different traits and may change directionally over short periods of time, sometimes favoring one trait in one year and the exact opposite in the next. Nonetheless, the biological diversity we see around us is the result of hundreds of millions of years of evolutionary diversification. Surely, if selection caused by humans can lead to such substantial evolutionary change in relatively short periods of time, it would seem reasonable to conclude that natural selection, operating over considerably longer intervals, is capable of producing the variety of species extant today.

Natural Selection in Modern Society

Humans have changed the environment in many ways; these changes could be expected to lead to natural selection for new traits. For example, disease-causing organisms have evolved resistance to drugs such as malarial prophylactics and many antibiotics. The way the resistant strains of these microbes evolve is easy to envision. A new drug, such as chloroquine, which is used to protect against malaria, kills almost all of the target microorganisms. However, if a few are, just by chance, less susceptible, or if a mutation causes resistance, then individuals with resistant genes will be able to survive and reproduce. Relatively quickly, such genes will sweep through the microbe population and before long, the drug will be rendered useless.*

The cost in human lives of the evolution of drug resistance is staggering. The Centers for Disease Control and Prevention (CDC) esti-

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* One of the earliest criticisms of the theory of evolution by natural selection was that it could not create new traits but could only favor one variant already present in a population—such as a gene for antibiotic resistance in a population of bacteria—over another (e.g., the previously common gene that did not provide resistance). To these critics, mutation was the key to understanding evolution; when and how mutations occurred was seen as the crucial factor that determined how evolution occurred, and natural selection was just the arbiter that caused a new mutation to replace a previously widespread one. However, it turns out that for many traits, mutations occur at a high enough rate that new genetic variation is constantly being replenished, and thus variation is often available upon which natural selection can work. For example, when bristle number is selected in fruit flies, within relatively few generations the range of variation exhibited in the experimental population is completely outside that seen at the beginning of the experiment (see Figure 4). This phenomenon is particularly true for traits affected by many genes, which includes all complex traits, such as eyes, as well as continuously distributed traits, such as body height, leg length, and bristle number, which are affected by many genes, with each having only a small effect.

One other important consideration to keep in mind about mutations is that favorable mutations do not arise when they are needed. Rather, mutations occur randomly with respect to the environment and natural selection; indeed, the vast majority of mutations are detrimental. Nonetheless, this does not mean that mutations occur randomly throughout the genome. Rather, modern molecular genetic studies have revealed that mutations occur much more commonly in some parts of the genome than in others. So mutations themselves do not occur randomly; however, their occurrence with respect to whether or not they are beneficial is random.

mates that more than 45,000 deaths annually in the United States are caused by infections by bacteria resistant to at least one commonly used antibiotic. The most recent problem is with a strain of bacteria known as methicillin-resistant *Staphylococcus aureus* (MRSA). Methicillin is the drug that was developed when penicillin resistance evolved. In 2007 the CDC reported that 100,000 serious infections a year in the United States are caused by MRSA, including 19,000 fatalities. Particularly worrisome is that this problem is no longer found only among people confined to hospitals, where risks of staph infection from *S. aureus* are particularly high. Now MRSA infections are increasingly being reported from people without any hospital exposure; for instance, there have been reports of infections spread through skin contact in high school football players who developed infections in skin abrasions received while playing on Astroturf.

An even bigger concern is that we are running out of antibiotics to use. For example, the drug that is now considered to be the last resort for treating staph infections is vancomycin, but recently some strains of MRSA were found to have evolved vancomycin resistance. Fortunately, these bacterial strains have not yet become widespread.

Resistance has evolved repeatedly to other products, such as pesticides and herbicides. It is a continually escalating evolutionary war, and, for all intents and purposes, it seems that we are losing. For example, resistance has evolved in more than 500 pest species, and one recent study put the economic cost in the United States, in terms of lost agricultural crops, at $3–$8 billion per year.

Natural Selection in Wild Populations

Darwin built his theory entirely by thought exercises and analogy to artificial selection. The reason is simple: there were no data from wild populations; no one at that time was studying whether natural selection actually occurred in nature. In recent years, however, many researchers have gone to the field to measure natural selection, and they have found that its action can frequently be detected. We now know that natural selection is a very powerful force. Nonetheless, it is not ubiquitous and it is not all-powerful, and the way it operates on particular traits varies; for example, in some circumstances, natural selection does not favor larger individuals, whereas in other cases, it does. In fact, sometimes this changes from one year to the next.

In addition, natural selection sometimes is not strong enough to outbalance other evolutionary processes, such as the immigration of individuals importing genetic variation from genetically different populations. For example, on isolated lava flows in the American Southwest, black mice blend in better than normal, light-colored mice, and thus are less vulnerable to predators. However, because small lava flows are surrounded by light-colored sand, where light-colored mice are favored, the continual influx of genes for light color, brought in by mice that wander in and live long enough to reproduce, prevents the population on the lava flows from becoming composed of only black individuals. Nonetheless, on the whole, natural selection is surely the most powerful force driving evolutionary change, and it is often detected when researchers look for it.

Evolutionary biology is an unusual science in that we still look to Darwin's writings for inspiration and ideas. In other fields of science, foundational works are usually of little more than historical interest, but Darwin's writings still contain much of substance, in part because he was an excellent naturalist, adept at observing and interpreting the world around him, and in part because he was remarkably correct in many of his ideas about how evolution proceeds.

Nonetheless, Darwin was wrong in two major respects. The first is that his ideas about inheritance were muddled and completely mistaken. Of course, that is not surprising. Mendel's famous studies on peas, though conducted just after *On the Origin of Species* was published, received little attention and were not rediscovered until 1900; DNA itself was not discovered for a further half century.

With regard to natural selection, however, Darwin was wrong in a second respect, as field studies have now made clear. Darwin predicted that natural selection would not be very strong and that, as a result, evolutionary change would occur only slowly, taking many thousands, if not millions, of years to produce detectable change ("We see nothing of these slow changes in progress, until the hand of time has marked the long lapse of ages" [Darwin 1859]). He had, of course, no actual data to inform this prediction; rather, it sprang from Victorian sensibilities about the pace of change in general, in accord with the prevailing wisdom of the time about the slow and gradual manner in which change occurs in both geology and human civilization. Darwin's views in this matter influenced evolutionary biologists for more than a century—well into the 1970s, most thought that evolution usually occurred at a snail's pace. Spurred by data from long-term studies of natural selection that began in earnest around that time, as well as by ideas promulgated by Harvard evolutionary biologist Stephen Jay Gould and others, we now know that Darwin was far off the mark. Many studies now clearly indicate that selection in nature is often quite strong and that, as a result, evolutionary change can occur quite rapidly. I provide two examples.

Darwin's finches. Among the most renowned organisms in all of evolutionary biology are the finches that occur on the Galápagos Islands. They are famous because Darwin saw them and realized that they were a perfect example of an ancestral species evolving into a variety of species adapted to different parts of the environment. The common version of this story gives Darwin a bit too much credit, invoking a Eureka-like moment when Darwin was making his observations during the voyage of the *Beagle.* Actually, during his visit to the Galápagos, Darwin misinterpreted what he was seeing, believing that the various species of finches were actually members of a number of different bird families. It was only when Darwin returned with his specimens to

London that the noted ornithologist John Gould set him straight, explaining that the birds were all members of a single, newly discovered family. It was at this point that Darwin (1845) realized what they represented, remarking in *The Voyage of the Beagle:* "Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species has been taken and modified for different ends."

In recent years, researchers from Princeton University have carefully studied a population of one species, the medium ground finch. What they found is that variation exists in the size of the beak. Moreover, this variation has important consequences: birds with bigger beaks can crack larger seeds, but birds with smaller beaks are more adept at manipulating small seeds. Following this population for over thirty-five years, the researchers found that in times of heavy rains, plants grew luxuriantly and seeds, most of them small, were abundant. As a result, birds with small bills were particularly successful at exploiting this cornucopia, and the population evolved to have a smaller beak size. However, when droughts occurred, all of the small seeds were quickly eaten, leaving only the larger, tougher-to-crack seeds. In these times, only the birds with the largest beaks survived, and as a result of this episode of natural selection, average beak size increased. These results clearly indicate that natural selection can be a powerful force and that it can produce rapid evolutionary change. They also demonstrate, however, that natural selection can be inconsistent and can actually counter itself over the course of many years, producing no net change, even if changes from one year to the next can be quite large.

Guppies. Everyone is probably familiar with the guppy, an extremely colorful fish popular in the pet trade. Guppies are native to northern South America and nearby islands. A few years ago, researchers studying guppies on the island of Trinidad discovered that populations varied along the length of streams that cascaded down from the mountains. At high elevations, the fish were extremely colorful, but lower down, they were much blander. Why might this be? It turns out that a major predator of these fish, the pike cichlid, is limited to lower stretches of these streams. Where it is present, the guppies need to be able to blend into their background as much as possible to avoid standing out and being preyed upon by the larger predators. By contrast, high in the mountains, the pike cichlid is absent. In these circumstances, males are extremely colorful. Why? Laboratory studies indicate the females greatly prefer more colorful males for reasons that are still obscure. In the absence of predators, there is no penalty to being colorful, and so selection has favored those males that are the most vibrant, whereas in lower parts of the stream, the more colorful males might have an advantage with the ladies, but this does them little good, as they are not likely to survive long enough for it to matter.

A nice story, but how could it be tested? The first test of this hypothesis was conducted in large pools set up in greenhouses at Princeton University. Ten pools emulating mountain guppy habitats were established, and a group of guppies was randomly split up and placed in the pools. The fish were allowed to breed for several generations to reach a large population size, at which point pike cichlids were introduced into some of the pools, while the other pools remained as predator-free controls. After fourteen generations, scientists examined all the guppies and discovered that populations in the two types of pools had diverged. Guppies in the pools without the pike cichlids were all brightly colored. In contrast, the surviving guppies in the pike cichlid pools were drab in coloration. These results support the hypothesis that it is selection resulting from the presence of the predator that leads to evolutionary differences in color in guppies. But these experiments were still artificial, in the laboratory.

To further test the hypothesis, several experimenters went into the field in Trinidad and transferred guppies from pools containing pike cichlids to nearby pools above a waterfall that contained neither guppies nor their predators. Coming from pools originally inhabited by cichlids, the guppy populations were initially drab. However, two years (about fifteen guppy generations) after the transfer into a predator-free environment, the bland color patterns of the guppy population had shifted toward the more complex and colorful pattern typical of guppy populations living where there are no predators. This study not only clinched the predator selection hypothesis for the evolution of guppy color but also demonstrated that, at least in some cases, the study of evolution can be conducted in an experimental fashion in natural conditions.

Note that one limitation on the ability to conduct evolutionary experiments in the wild is that scientists do not want to move species to localities where they do not occur naturally. In this particular study, the fish were only moved a few yards upstream to the immediately adjacent pool, so little disruption of natural ecosystems occurred, but more substantial introductions are frowned upon. However, evolutionary biologists are increasingly focusing on what happens to species unintentionally introduced to areas in which they are not native, studying how these introduced species adapt to their new circumstances and, in turn, how the native fauna and flora respond evolutionarily. Although such invasive species can be a huge ecological and economic problem, they do provide quasi-experimental studies in which evolutionary change can be studied.

These lines of evidence make clear that selection, whether natural or artificial, can quickly lead to substantial evolutionary change. Some people who do not believe in evolution do not dispute these findings but claim that the observed evolutionary changes are relatively minor fine-tuning, rather than the substantial changes that would be required to understand the evolution of the vast biological diversity in the world around us. That is, these are changes that allow a species to adapt to different conditions. What these people contend, however, is that one species cannot evolve into another. A guppy is still a guppy, they say, or a dog still a dog.

This argument is not compelling for several reasons. First, the amount of evolutionary divergence produced by human-caused selection can be substantial. If paleontologists discovered fossils of the various breeds of dogs, they would be classified not only as different species but even as different genera—dog breeds are that different in comparison to extant species and genera of canids. The differences between many other domesticated species of plants and animals and their ancestors are also greater than the differences between different closely related species in nature. Second, many scientists contend that what makes one species distinct from another is the inability to interbreed—two individuals are members of the same species if they would mate and produce fertile offspring, whereas they are members of different species if they are unable or unwilling to do so. By this criterion, too, scientists have been able to document the evolutionary process, both observing the evolution of new species in nature, as members of two populations evolved to no longer interbreed, and conducting selection experiments in the laboratory that have produced populations of fruit flies and other organisms that do not interbreed, usually because their mating behavior has changed so that members of the two nascent species will no longer mate, even if given the opportunity. In sum, the critics' claims are without foundation. Selection clearly has the power to produce substantial evolutionary change, rather than just fine-tuning, and it can lead to the production of new, noninterbreeding species.

Evidence from the Fossil Record

Darwin noted the imperfections in the fossil record. Although many more fossil species have been discovered in the 150 years following the publication of *Origin,* it is still correct to say that for most types of organisms, we have only a sketchy fossil record. Opponents of evolution make much of these missing fossils. They claim that there is no evidence of "missing links" and hence no evidence for evolution. Although it is true that we cannot show how every extant species has evolved from its primordial ancestors, many very well-documented fossil sequences show the evolution of modern forms. I briefly provide a few examples.

Horses

The ancestor of all horses was a fox-sized animal looking somewhat like a deer, named *Hyracotherium*. Although modern horses only have one toe, the hoof, *Hyracotherium* had four toes on the forefeet and three on the hindfeet. How did these evolutionary reductions in toe number occur? Horses are actually quite common in the fossil record, and we can clearly trace the evolutionary reduction in toe number from four to one through a series of intermediate forms. At the same time, horses were also evolving larger molars and overall body size, and again, the fossil record documents in exquisite detail these increases in size through time.* These changes were coincident with the widespread occurrence of open grasslands in North America approximately 20–25 million years ago. *Hyracotherium* was likely a forest dweller, adapted to move nimbly through dense underbrush and nibble on tender ferns and shoots. By contrast, the changes documented in horse evolution likely represent adaptations to living in wide-open expanses. In such a setting, concealment from predators would be difficult, and speed—enhanced by long limbs capped by a single supporting toe—would be at a premium. Moreover, the food of choice in grasslands is, not surprisingly, grasses, which contain large quantities of grit, requiring sturdy teeth to withstand the continual abrasion.

* Horse evolution used to be portrayed as a linear progression from a small, many-toed, small-toothed ancestor to the modern equids of today. However, detailed examination of the fossil record reveals that horse history is much more complex, with many side branches in the horse evolutionary tree. Moreover, although the general trend in horse evolution has been as described, not all evolutionary change has occurred in the same direction. For example, at some points, some species evolved to be smaller than their ancestors.

Birds

From what did birds evolve? At first glance, this would seem to be a difficult question, because birds appear to be so distinct from all other animals alive today. The oldest known fossil bird is a famous species named *Archaeopteryx* from the Jurassic Period in the middle of the age of dinosaurs, 165 million years ago. Fossils of this species come from particularly fine geological deposits in Germany in which details of the specimen are unusually well preserved, including soft parts that usually do not fossilize. Some fossil specimens of *Archaeopteryx* include structures that very clearly are feathers, indicating without a doubt that this species was a bird. Nonetheless, examination of *Archaeopteryx* reveals a number of reptilian traits, including teeth, clawed fingers, abdominal ribs, and a long, bony tail. Based on these characteristics, scientists believe that *Archaeopteryx* evolved from a particular type of dinosaur, which was fairly closely related to *Velociraptor,* the star of *Jurassic Park.* In fact, a few years ago, a paleontologist discovered a fossil specimen of *Archaeopteryx* in a museum cabinet. In this specimen, the feathers had not been preserved, and it was misclassified as a dinosaur. Thus, in many respects, *Archaeopteryx* was no more than a feathered dinosaur—take away the feathers, and it would be mistaken for a dinosaur. Many of the other skeletal features characteristic of birds must have evolved later.

Whales

Scientists have long suspected that whales evolved from four-legged mammals related to today's ungulates (hoofed mammals such as cows). However, this idea was based on similarities in certain features of the skeleton and in DNA; no direct fossil links were known. In recent years, however, a series of transitional fossils has been discovered, documenting the evolutionary move from land to sea. Most impressive was the finding of a four-legged animal whose skeletal anatomy revealed that it was the earliest ancestor of the lineage that gave rise to whales.

Snakes

In a similar fashion, scientists long had recognized the many similarities between snakes and certain types of lizards and had hypothesized that snakes evolved from lizards. As with whales, however, until recently the early stages in snake evolution were not documented in the fossil record. However, several recent discoveries in Israel revealed fossils that, while clearly snake ancestors due to the structure of the skull and elongate body form, nevertheless possess small, but well-developed, limbs.

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In summary, the fossil record provides many well-documented cases in which we can trace, step by step, the evolution of modern species from their very different ancestors. Paleontology currently is experiencing a golden age, with expeditions occurring throughout the world and important discoveries occurring routinely. Recent years, for example, have seen the discovery of *Ardipithecus,* the common ancestor of humans and chimps, as well as *Tiktaalik,* a primitive fish exhibiting the first hints of the transition from fins to legs (Figure 5).

More generally, the combination of studies of natural selection in present-day populations with the fossil record makes a compelling case for the theory of evolution by natural selection. Natural selection clearly has the ability to produce large-scale change, and the fossil record indicates that such change, has, indeed, occurred.

Data That Make No Sense, Except in an Evolutionary Context

Evolutionary biologists are fond of quoting a statement by the noted evolutionary biologist Theodosius Dobzhansky, who said that nothing makes sense in biology, except in the light of evolution. Although

Figure 5. *Tiktaalik*, a fossil fish that lived nearly 400 million years ago and was a transitional form between fish and land-dwelling amphibians, was discovered on an expedition led by Harvard paleontologist Farish Jenkins, curator of vertebrate paleontology at Harvard's Museum of Comparative Zoology, and Neil Shubin, a Harvard-trained PhD now at the University of Chicago. (Photo: The Shubin Lab/University of Chicago.)

perhaps a slight overstatement, this comment has a lot of truth to it. Consider the following sorts of evidence.

Homologous Structures

Homologous structures are features in different species built from the same elements. For example, the forelimbs of all mammals are made from the same skeletal elements: one long element, two paired elements (sometimes fused), a bunch of little bones (the wrist), and a set of long bones arranged in lines (fingers). Vertebrates use their forelimbs for many different purposes: birds and bats, for example, use their forelimbs to fly, whales and seals to swim, primates to grasp, and horses to run. Nonetheless, the structure of the forelimb of all of these species is fundamentally the same (see Figure 6). This makes perfect sense if they are all descended from a common ancestor and their limbs have been modified by natural selection for different ends; in the absence of evolution, however, such similarity, with no functional explanation, would not be expected.

Vestigial Structures

Related to the concept of homology are vestigial structures (i.e., structures that have no current use and are presumably holdovers from useful structures in ancestors). These are my favorite examples of evidence of evolution and I will quickly provide a number of examples of vestigial structures:

* Each year, I ask my students how many of them can wiggle their ears, and invariably one or two can do so. Many mammals move their ears around as social signals or to facilitate hearing. This ability is retained in some humans, although it aids neither hearing nor social communication.
* Similarly, humans retain some of the muscles used to move tails, even though the most recent ancestor of humans that bore a tail lived more than 20 million years ago.
* Whales have no hind limbs, yet they have skeletal remains of a pelvis (see Plates 2 and 3). Some snakes also have slight remnants of their hind limbs. As already discussed, both whales and snakes evolved from four-legged ancestors, and their rudimentary pelvises are vestiges of their quadrupedal past.
* Many animals that spend their entire lives in lightless caves still have eyes, although they often are not functional because some elements are missing. Why a troglodyte would have eyes would be a mystery, were it not known that they have evolved from surface-dwelling ancestors.
* Most beetles (such as fireflies) can fly, but beetles on many islands have lost this ability. Beetles have a hard outer shell, called a

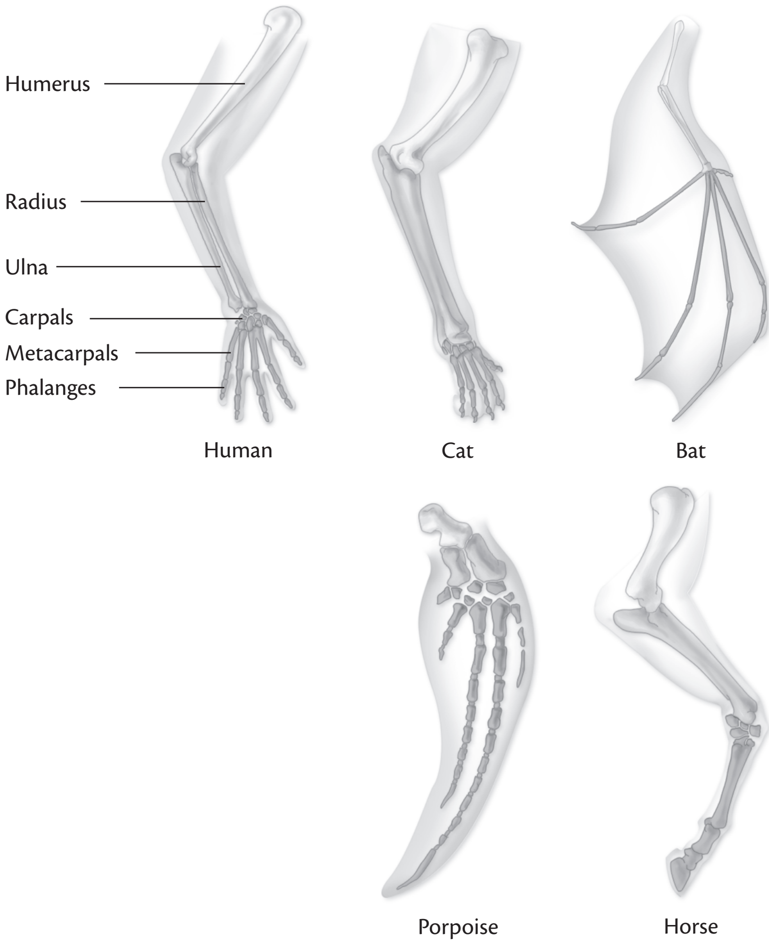

Figure 6. Homologous vertebrate forelimbs. Note that the limbs of these animals, though very different in structure, are composed of the same series of bones. (Image adapted from P. Raven et al., *Biology*, 9th ed., © 2011 by The McGraw-Hill Companies, Inc.)

carapace. When a flying beetle takes off, it elevates the carapace, exposing the wings that lie underneath. In flightless beetles, the carapace has fused shut and cannot be opened. Nonetheless, if you dissect away the carapace in such species, underneath it you find the structures of the wing.

Vestigial traits can also be seen in the genomes of many organisms. For example, the icefish is a bizarre-looking, nearly see-through fish that occurs in the frigid waters of the Antarctic. The icefish's transparency results not only from a lack of pigment in its body structures but also from the near invisibility of its blood. What makes our blood red is the presence of red blood cells, which contain hemoglobin, the molecule that transports oxygen from the lungs to the tissues. However, oxygen concentration in water increases as temperature decreases. In the waters of the Antarctic, which are about 0° Centigrade (32° Fahrenheit), there is so much oxygen that the fish do not need special molecules to carry oxygen. The result is that these fish do not have hemoglobin, and consequently their blood is colorless. Nonetheless, when the DNA of icefish was examined, scientists discovered that they have the same gene that produces hemoglobin in other vertebrates. However, the icefish hemoglobin gene has a variety of mutations that render it nonfunctional, and thus the icefish does not produce hemoglobin. The presence of this inoperative version of the hemoglobin gene in icefish means that its ancestors had hemoglobin; however, once the icefish's progenitors occupied the cold waters of the Antarctic and lost the need for hemoglobin, mutations that would be harmful and thus would be filtered out by natural selection in other species were able to persist in the population. Just by chance, some of these mutations increased in frequency in the population through time, eventually becoming established in all individuals and knocking out the fish's ability to produce hemoglobin.*

* This process, by which a mutation may randomly increase or decrease in frequency in a population through time in the absence of natural selection, is termed "genetic drift." A new mutation will initially begin

"Fossil genes" or "pseudogenes," such as the hemoglobin gene in the icefish, are actually quite common in the genomes of most organisms: when a trait disappears, the gene does not just vanish from the genome; rather, some mutation renders it inactive, and once that occurs, other mutations can accumulate.

I could provide many more examples of vestigial structures; modern genome sequencing is a particularly rich vein that continually discovers new, vestigial pseudogenes. These examples only make sense when one considers that these structures were probably of use in ancestral forms and have not yet been entirely lost.

Geographical Differences

One of the observations that most struck Darwin was that many of the species in the Galápagos are endemic and are found nowhere else in the world. Yet these species are almost always similar to species in South America. Darwin wondered: Why was this? If each species was created independently, there would be no reason that they should be particularly like species in nearby regions. Moreover, the climate and structure of these islands is not like that of South America, so there is no reason that species in the two localities should be similar. Indeed, Darwin pointed out, the Cape Verde Islands off the western coast of Africa are similar to the Galápagos in topography and climate. Nonetheless, species on the two island archipelagoes are not notably similar to each other. Rather, the Galápagos species have affinities to South America and the Cape Verde species to Africa. Darwin ultimately realized that this is evidence of evolution—islands tend to be colonized by plants and animals from the most proximate continent, thus explaining the similarities of island inhabitants to those of nearby landmasses.

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with a very low frequency in the population because it is found in only one individual. Most such mutations, which start at very low frequency, would eventually disappear just by random fluctuations through time; some, however, may become widespread in the population and replace the formerly common genetic form.

Geographical evidence of a different sort comes from Down Under. In Australia, almost all of the mammals are marsupials (i.e., they have pouches, like kangaroos, where their offspring—born in an embryonic state—spend most of their developmental period attached to a teat). Many Australian mammals exhibit great similarities to their placental counterparts in the rest of the world (most mammals are "placentals," so named because the embryo develops for an extensive period within the mother's body, nourished through the placenta). There are, or were until recently, marsupial "cats," "wolves," "moles," "mice," "gliding squirrels," "badgers," and "anteaters." Why should such "duplicate" forms exist in Australia, but as marsupials, whereas everywhere else they are placental mammals? In evolutionary terms, it makes perfect sense. When Australia broke off from the rest of the ancient landmass of Gondwanaland more than 70 million years ago, placental mammals did not occur in that part of the world. After the dinosaurs disappeared, mammals everywhere experienced an evolutionary flowering, diversifying to occupy many of the ecological niches previously inhabited by dinosaurs. However, this adaptive radiation—as it is called—was undertaken by marsupials in Australia, and primarily by placental mammals elsewhere. In many cases, similar ecological niches were occupied evolutionarily in similar ways, a phenomenon termed "convergent evolution," resulting in marsupial and placental counterparts in different parts of the world.

Embryology

Some of the strongest anatomical evidence supporting evolution comes from comparisons of how organisms develop. Embryos of different types of vertebrates, for example, often are similar early on, but become more different as development proceeds. Early in their development, human and fish embryos both possess pharyngeal pouches, which in humans develop into various glands and ducts and in fish turn into gill slits. At a later stage, every human embryo has a long bony tail, the vestige of which we carry to adulthood as the coccyx at the end of our spine. Human fetuses even possess a fine fur (called lanugo) during the fifth month of development. Similar evolutionary holdovers are seen in other animals: baleen whale embryos have teeth; horse embryos have three toes; embryos of frogs that have lost the tadpole stage still produce—and then lose—a tail. These vestigial developmental forms suggest strongly that our development has evolved, with new genetic instructions modifying ancestral developmental patterns.

Conclusion

I would like to conclude with one thought of a more philosophical nature. What I want to discuss is what we mean by the term "fact." In common terms, people think of things as facts if they can be directly demonstrated: apples are red, water is liquid at room temperature, and so on. But these statements are completely mundane. What about atoms? We cannot see them. How do we know they exist? Or gravity? We know that something keeps us from floating off into space, but how can we know that it is the mass of our planet that is responsible?

I would argue that something should be considered a fact when the available evidence compellingly supports that conclusion. With regard to evolution, I would argue that the evidence is so overwhelming that it should be considered a fact, rather than a theory. In this context, there are many theories about how evolution occurs, one of which is that it is driven by natural selection.

Not everyone takes this perspective. Some people—both scientists and nonscientists—draw a distinction between the terms "theory" and "hypothesis," at least as used in a scientific context. They use "hypothesis" for speculative ideas, and theory only for those ideas that are strongly supported by many lines of evidence, like the theories of gravity and evolution. In this sense, it is important to recognize that evolution is not just "another theory"—the term "theory" is not the equivalent of a hunch or a notion, or even an idea spouted by a scientist. Rather, it is a well-tested phenomenon, so well supported by data that it is hard to envision what sort of data might be found to disprove it.

So this has been a quick survey of the types of evidence that persuade most scientists that evolution is a very well-established scientific idea. Data from so many disparate fields of biology all are explicable in an evolutionary framework that it is hard to envision any other plausible explanation amenable to scientific investigation. Moreover, the power of the evolutionary perspective is continually demonstrating itself. For example, an important new approach to computer software writing was invented a few years ago. Called "genetic algorithms," this approach uses a process modeled after natural selection to devise solutions to programming problems that otherwise were not evident. Essentially, from a simple starting program, random changes in computer code are introduced, and those programs which perform best are selected, followed by more random changes. This procedure is repeated many times until a program is produced that solves the problem at hand.

Scarcely a decade ago, most molecular biologists had little use for evolutionary biology, as it generally was of little practical importance in their investigations about the workings of the molecular machinery underlying life. However, when the human genome was first sequenced in 2001, molecular biologists realized that to understand the structure and functioning of the human genome, it was critical to understand how it was constructed. And to do that required sequencing the genome of other species, allowing comparisons that helped identify which parts of the genome are uniquely human and which we have inherited from our ancestors, both recent and distant. For example, comparison with the genome of the platypus has shed light on the evolution of milk production and the origin of the mammalian sex chromosomes, whereas comparison to the genome of the chimpanzee has identified many genes potentially involved in the evolution of the human brain and the development of speech. Today, one of the most vibrant areas in evolutionary biology is the study of genome evolution, a subdiscipline that has united molecular and evolutionary biologists and proven that, indeed, nothing in biology does make sense except in the light of evolution.

Appendix

As I mentioned at the outset of my essay, evolutionary biology is unusual, if not unique, among the sciences in that many people (at least in the United States) do not believe in its basic tenet, that evolution has occurred. Of course, one of the great virtues of American society is that people are free to believe whatever they want, especially for topics that may have religious implications. However, this freedom runs into other cherished principles when we consider whether alternatives to evolution should be taught in our public schools. The key question concerns whether there are scientific alternative theories that should be taught in science classes, or, to put it in recent parlance, should we "teach the controversy"?

The history of what has—or has not—been taught in the public schools spans most of a century and goes back to the famous Scopes Monkey Trial (*State v. Scopes*, 152 Tenn. 424, 278 S.W. 57 1925). I will only briefly review this history here, but a number of books and Web sites are available that treat the subject in great detail.

In the 1960s opponents of evolution, "creationists," invented what they called "scientific creationism," which began with the claim that geological formations were the result of the Great Flood that inundated the world for forty days and forty nights. Proponents of this view argued that the reason that we see different fossils in different rock strata is that animals were trying to escape the rising water, and some were able to get higher than others. Thus, rocks, and the fossils they contained, were said to be several thousands of years old, rather than millions.

When the U.S. Sixth Circuit Court of Appeals struck down the teaching of creationism in *Daniel v. Waters* (515 F.2d 485 6th Cir. 1975), creationists retooled their approach by removing all reference to biblical quotations. Several states subsequently passed laws mandating the teaching of this new "creation science" alongside evolution. However, there was not much science in this creation science. There were no testable hypotheses; rather, the approach was to try to find evidence supporting the literal wording in the Bible. In addition, a primary point was to poke holes in evolutionary science—"Where are the missing fossils?" and so on—and then conclude that if evolution could not explain diversity, creationism must be the answer. In other words, instead of laying out testable hypotheses that supported creation science, the approach was to argue that perceived inadequacies in evolutionary science were the same as positive evidence in favor of creationism. The Supreme Court was not fooled by this and recognized in *Edwards v. Aguillard* (482 U.S. 578 1987) that this "science" was just religion masquerading in a pseudo-scientific coat, striking down laws mandating the teaching of creationism. Harvard's Stephen Jay Gould was one of the key experts for the plaintiffs in this case.

When creation science was ruled to be nothing more than religion, the creationists took a new tack. They eliminated the word "creationism" and instead came up with the term "intelligent design." The idea is that the complexity in life is too well designed to have arisen by a process like natural selection. Hence, some designer must be responsible. The proponents of ID, as it is called, are very careful not to say who or what this designer is: "Sure, it could be God, but maybe it's some extraterrestrials or who knows what else? But certainly, this is a scientific idea, with no religious overtones."

This is actually an old idea, going back to William Paley in 1804. Paley stated that the existence of a watch implies the existence of a watchmaker. Darwin, of course, knew of this argument and made great efforts to oppose it, concluding late in life: "We can no longer argue that, for instance, the beautiful hinge of a bivalve shell must have been made by an intelligent being, like the hinge of a door by man. There seems to be no more design in the variability of organic beings and in the action of natural selection, than in the course which the wind blows. Everything in nature is the result of fixed laws" (Barlow 1958, 87).

In considering ID, there are three key considerations:

1. Are organisms too well designed to have resulted from the process of natural selection?
2. Are organisms, in fact, so well designed? (What about the eye of backboned animals such as ourselves, with the visual nerve exiting in front of the photoreceptors and causing a blind spot? What about the human back, which seems more like a disaster waiting to happen than an optimally, intelligently designed structure?)
3. Is ID a scientific theory? If so, how is it tested? In theory, ID is a theory. But in reality, to make it a testable theory—that is, an idea that potentially could be refuted—we would have to be able to specify what constitutes a design too good to result from natural selection (point 1 above). No one has come up with a successful means of doing this.

In response to this point, ID proponents have a reasonable response. Is evolutionary biology truly a testable theory? What sort of evidence could disprove that evolution has occurred? In fact, they argue that whenever evolutionary biologists disprove a hypothesis, they erect explanations that can account for the discrepancy, rather than simply concluding that evolution does not occur. For example, suppose you did an experiment in which you selected on a trait in fruit flies, say, bristle number, and you did not get an evolutionary response. Would you conclude that, in fact, the theory of evolution was incorrect? Probably not. Rather, you would ask why the trait had not evolved. In this case, my first inclination would be to suggest that in fact the variation upon which selection occurred was not genetically based, and thus evolution could not occur. IDers say that this is what goes on all the time, and that as a result evolution is no more a scientific theory than ID.

Evolutionary biologists have two rejoinders. First, they argue that evolution has passed so many tests so many times that any single failure to find evidence for evolution is more parsimoniously explained by looking at the circumstances of that particular instance rather than rejecting evolution wholesale. Certainly, if we never got a response to selection, we would have real doubts about the theory of evolution by natural selection. But, in fact, most of the time tests such as this—as well as many other types of evidence—support the theory that evolution has occurred.

Second, one evolutionary biologist suggested that evolution could be falsified in this way: if we found a fossil rabbit in rocks that were a billion years old. Because everything we know about evolution says that mammals evolved through a process that began with unicellular organisms and did not produce mammals until about 125 million years ago, a billion-year-old rabbit would be utterly incompatible with our theories of evolution. So, in some sense, the fossil record is a potential means of disproving evolution. Discovery of fossils completely discordant with our understanding of how life has diversified through time could cast serious doubt on our conclusion that the history of life documents the existence of "descent with modification" (Darwin's original term for what we now call evolution).

The intelligent design argument has led to the development of one new idea, the theory of irreducible complexity. The idea here is that natural selection cannot build up a structure part by part unless each added part is favored by natural selection. Thus, if you have an object with, say, ten parts, and all ten are necessary for the object to function, then it is not possible for natural selection to have built that structure, because it could not have put together the first nine parts, given that at that point, lacking the tenth part, the structure would have had no functional advantage, and thus would not have provided any increased fitness. Such structures are termed "irreducibly complex," and their existence is said to be evidence of the existence of a designer. One purported example of an irreducibly complex structure is the rotary motor of a bacterial flagellum (the little tail-like structure that some bacteria use to propel themselves), which is said to be nonfunctional if any of the parts are not present, although this is disputed.

The basis of this argument is that natural selection can only operate by building an adaptation for the same function throughout the structure's existence. If this were so, then, of course, every incremental improvement would have to be advantageous and lead to increased fitness (eyes may have evolved in just this way, as every increase in the ability to detect and focus light provides an advantage over the previous condition). But this is not always the case. Rather, many traits initially evolved for one purpose and then were subsequently modified for another. In this way, it is possible to see how a so-called irreducibly complex trait could evolve. It might not be able to function at all for its current task if one component were removed, but it still might be useful for some other purpose. It has been argued that this can explain the rotary motor of the flagellum, as well as many other structures. For example, the first feathers that evolved in dinosaurs did not have the aerodynamic properties that allow modern birds to fly. Rather, they probably evolved to provide insulation—like a goose's down—or as ornaments used in courtship behavior. Only after the initial protofeather evolved did subsequent changes occur that permitted feathers to provide flying capability.

There is another way in which irreducibly complex structures are compatible with the action of natural selection. It may well be that a perfectly functioning structure adds a component that, though not essential, makes it function even better. At this point, the structure is not irreducibly complex, because that last part can be removed without rendering the structure functionless. However, subsequent adaptive evolution may build on this new part, so that at a later date, it does become integral to function, and thus the structure becomes irreducibly complex, but as a result of natural selection–driven evolution. Here's an analogy. Consider the GPS unit, now standard in many cars. Certainly a nice addition, but by no means essential—if the GPS unit breaks, the car still is fine. But it is not difficult to imagine that fifty years from now, cars may be driven by their GPS units: just type in (or shout out) the address and the car does the rest. At that point, the car would be irreducibly complex with respect to the GPS.

In summary, there really are no tenable, alternative scientific theories to explain the diversity of life we see around us, and hence no other ideas are appropriate to be taught in science classes, a view once again affirmed in 2005 by a U.S. federal court when it considered and rejected the teaching of ID in *Kitzmiller v. Dover Area School District* (400 F. Supp. 2d 707 M.D. Pa. 2005). In other words, there is no scientific controversy to teach.

Further Reading

Darwin, C. 1845. *The Voyage of the Beagle*, 2nd ed. London: John Murray.
This travelogue, a best seller in its time, tells of the natural history wonders Darwin recorded in his epic, five-year circumnavigation of the world. Fascinating today as it was to his contemporaries, in it the reader can see the early stages of Darwin's formulation of the theory of evolution by natural selection, as well as many fascinating tidbits of the biology, natural history, and sociology of far-flung corners of the world. This book is a particular must-read for anyone traveling to the Galápagos, as one can see today the exact geological formations and life forms that Darwin detailed in his journey.

———. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray.
Although a bit dense, it is all here, the overwhelming mass of evidence from so many different areas of scientific inquiry that convinced the educated world that evolution had occurred, even if support for his proposed mechanism for evolutionary change, natural selection, did not solidify for another fifty years.

Barlow, Nora, ed. 1958. *The Autobiography of Charles Darwin 1809–1882: With the Original Omissions Restored. Edited and with Appendix and Notes by His Grand-daughter Nora Barlow*. London: Collins.
This and the other Darwin publications can be found online at http://darwin-online.org.uk/.

Weiner, J. 1994. *Beak of the Finch*. New York: Vintage Press.
Weiner follows the work of Princeton biologists Peter and Rosemary Grant as they conduct their pathbreaking studies on Darwin's finches in the Galápagos. Although now a bit out of date (the Grants have made many important new discoveries in the past seventeen years), the book is still an exceptionally well-written discourse on how biologists study evolution, branching out from its focus on the Grants to cover the field as a whole. I continue to assign this book to my class, and the students still love it. For a more up-to-date account of the finch work, written for a slightly more advanced audience, try the Grants' *How and Why Species Multiply: The Radiation of Darwin's Finches* (Princeton, NJ: Princeton University Press, 2007).

Quammen, D. 1996. *Song of the Dodo: Island Biogeography in the Age of Extinction*. New York: Scribner.
Possibly the best book on the evolution of biological diversity written for a popular audience. Quammen seamlessly intertwines three themes: the diversity of life on islands, the development of scientific theories to understand how such diversity arose and how it is maintained in modern environments, and how diversity is studied, starting with the parallel stories of Darwin and Alfred Russel Wallace up to the present-day research of Harvard's Edward O. Wilson and other scientists. This book is about my area of research, so I already knew much of what he wrote, yet I could not put it down and still enjoy rereading it. Quammen understands the science at a very deep level and portrays it in completely accurate, yet lyrical, terms.

Carroll, S. 2006. *The Making of the Fittest: DNA and the Ultimate Forensic Record of Evolution*. New York: Norton.
Carroll, a leader in the field of evolutionary biology, reviews the evidence for evolution by natural selection with special emphasis on recent findings from studies of DNA.

Shubin, N. 2007. *Your Inner Fish: A Journey into the 3.5-Billion-Year History of the Human Body*. New York: Pantheon Books.
Shubin, a remarkable scientist who conducts paleontological research in remote parts of the Arctic and DNA studies in the laboratory, illustrates how the oddities of the human body make sense when understood in an evolutionary context. Along the way, he describes the rigors of fieldwork and the excitement of discovery of a truly remarkable fossil, *Tiktaalik,* a fish caught, in an evolutionary sense, halfway along the road to the conquest of land.

Coyne, J. 2009. *Why Evolution Is True*. New York: Viking Press.
Dawkins, R. 2009. *The Greatest Show on Earth: The Evidence for Evolution*. New York: Free Press.
Reznick, D. 2009. *The* Origin *Then and Now: An Interpretive Guide to the* Origin of Species. Princeton, NJ: Princeton University Press.

These are three of the best books written to capitalize on the celebrations of 2009, the 200th anniversary of the birth of Charles Darwin (born on the exact same day as Abraham Lincoln) and the 150th anniversary of the publication of the *Origin*. Coyne and Dawkins cover similar ground, making the same case, in much extended form, that is the subject of this essay. Reznick reviews the *Origin* and explains it in light of modern ideas about evolution and biological diversity.