evolve—over time. Indeed, although now largely unjustifiably ridiculed or ignored in biology texts and classes, Lamarck was the intellectual father of a field he called *biology*.

The idea that fossils of animals were arranged in layers of rocks along an arrow of time got Darwin thinking about life on time scales he could barely imagine and could not easily quantify. If the oldest fossils were many meters beneath other fossils, how long had it taken for the layers of rock to build up?

Darwin was extremely puzzled by the early fossils that Murchison and Sedgwick had found. He knew that beneath the layers of rocks with fossil animals were layers that contained no fossils, but he could not understand why. The record of animals appeared to come out of nowhere, and their evolution appeared to be relatively rapid. But how rapid? And why, all of a sudden, were there fossils of fish, but in the rocks below there were only organisms that looked like invertebrates? And even further below, why were there no fossils of animals at all? It was the geological equivalent of unrolling a Turkish rug depicting the story of the ark, but half or more of the rug had no animals. Darwin needed to explain these issues first to himself and then to his colleagues. To answer these questions, he needed to try to date the rocks, and for that he needed a clock.

On September 7, 1859, the bells in the clock tower housing Big Ben rang for the first time. The clock was meticulously designed and is extraordinarily accurate; indeed, it is an iconic symbol of English engineering and craftsmanship at the dawn of the Industrial Revolution. Two months after that historic event, on November 24 to be precise, John Murray, III, the venerable London publisher on Albemarle Street, sent Charles Darwin's new book, *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, to market.

In Chapter 9 of *The Origin of Species* (the title was later shortened), Darwin attempted to account for the time required for extinct fossil animals to have changed, or evolved, to become the modern forms. The problem was not straightforward. Lyell and his predecessor, the Scottish physician James Hutton, had proposed that the Earth was infinitely old. Darwin did not know whether that concept was true, but he certainly believed that it had to be more than 6000 years old. To obtain a more realistic age, he developed a rather interesting, if not downright ingenious, approach to measuring geological time.

Darwin's clock was based on a geological phenomenon: the rate of erosion of sedimentary rocks, the kind that contain fossils. He specifically chose the Weald, a well-studied chalk and sandstone cliff abutting the sea in Kent, England. Darwin calculated that this formation eroded about one inch per century, and based on the size of the formation at the time, he calculated that the "denudation of the Weald must have required 306,662,400 years; or say three hundred million years."

Darwin didn't account for the time required for the formation of the cliff itself, but that was a detail. Moreover, he didn't account for the rocks below the Weald, which would have only made the age of the cliff even older, and possibly infinitely old, as thought by Lyell. Darwin's estimate of the age of the cliff certainly was a bold speculation, and without a better constraint, it was apparently based on a rational, physically verifiable idea. The implication was obvious. The Earth was very old. It was much, much older than Ussher had calculated, and it was a lot older than most people could possibly have imagined at the time. And while the date of the origin of life on Earth had not been determined (and remains unclear to this day), that there were rocks that had no fossils beneath those above implied that Darwin's estimate of the age of the Earth was conservative.

Regardless, millions of years are not the history in the Bible, and they certainly didn't fit what everyone had been taught at school. Darwin clearly knew his estimate was going to be met with skepticism, but he had no way of knowing what was to come. Besides assaulting the Biblically held, seventeenth-century calculations of the Archbishop of Armagh, Darwin's estimated age of the Earth was assailed by a fellow scientist, the Einstein of the day, the physicist William Thomson, later to become Lord Kelvin. Thomson set out to put the record straight, based on first principles of physics.

Thompson argued that the age of the Earth could be accurately determined by assuming that the planet began as a molten rock and subsequently cooled. Using measurements of the change in temperature with depth through the Earth's crust and experiments he performed about the conduction of heat by rocks, he developed an equation for how fast the Earth had cooled to its present state. In 1862, Thomson proclaimed that the Earth was about 100 million years old. He admitted a huge uncertainty of between 20 and 400 million years, but as time went on, he became increasingly dogmatic and convinced that the actual age was closer to 20 million years. This estimated age appeared to be too short to allow evolution, as Darwin envisaged it, to proceed. Thomson became one of the harshest critics of Darwin's new ideas regarding evolution, not because he did not believe in evolution per se, but rather, because as a physicist, he did not believe the calculations of the age of the Earth based on geological processes such as rates of erosion. Ultimately, the contrarian views of Thomson forced geologists to develop better models for the age of the Earth, but doing so would take almost another century.

If Darwin was even remotely correct, then life evolved on Earth over a very, very long time—much, much longer than anyone imagined. But how did it evolve? In a doodle on page 36 in Notebook B from 1837, Darwin sketched a tree of life in which he had the radical idea that organisms were related to each other from a common ancestor and that their relationship could be discerned from similarities in physical appearance. That basic notion was similar to Lamarck's concepts that had been developed more than fifty years earlier; however, Darwin had a different idea as to how the process occurred.

The changes in the animal forms were subtle and, based on the distance between fossils in the rock record, appeared to be slow. In addition, for the proposal to work, some organisms that appeared earlier in the fossil record had to go extinct and be replaced by new species, or the Earth would have an ever-increasing number of animal and plant species. In other words, once an organism becomes extinct, it should never reappear later in the fossil record.

Darwin realized that this remarkable, revolutionary idea would be challenged; and so it was. The fossils were clearly relics of animals and plants, but there were no bones of humans in the rocks. If that were true, then Darwin clearly understood the implications of the "missing" humans; like animals in the fossil record, we must also have arisen by some process that allows one organism to evolve into another over some undefined, but prolonged, time.

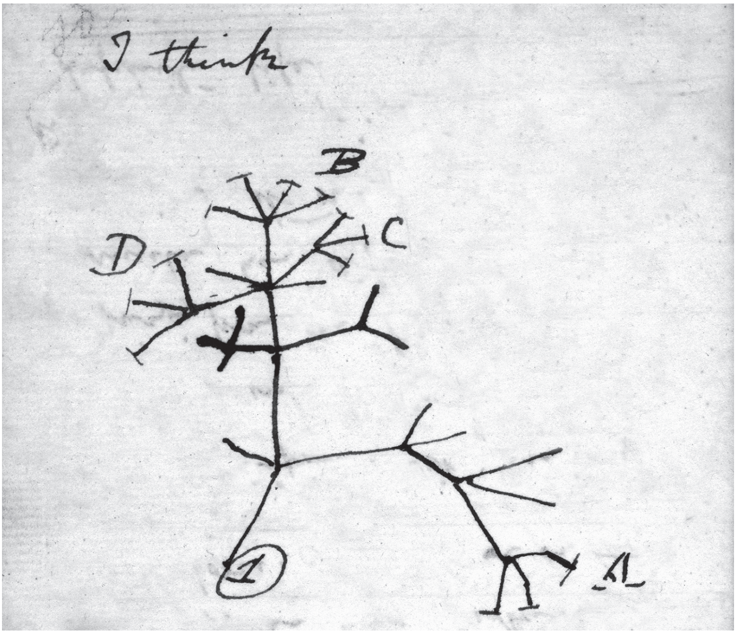

FIGURE 2. A reproduction of the doodle that Darwin sketched in Notebook B between 1837 and 1838. The basic idea is that extant species are descended from extinct species but are also related to other extant species to form a historical tree of life. This doodle was the kernel for the theory of descent with modification followed by selection—the core of Darwinian evolution. (With permission from Cambridge University Press and thanks to Peter and Rosemary Grant. Copyright © 2008 The Committee for the Publication of Charles Darwin's Notebooks.)

The concept of genes and the basis of the physical inheritance of traits were totally unknown to Darwin, or anyone else at the time. (Gregor Mendel would not present his work on inheritance of traits in peas until more than six years after the publication of the first edition of *The Origin of Species*, in 1866). Indeed, despite the confusion in most biology texts, Darwin would not have had a major problem accepting Lamarck's basic concept that organisms can inherit traits from their environments; however, Darwin's major contribution was the idea that within all species there is natural variation that can be selected. Breeders of dogs and pigeons did this all the time. However, in nature, Darwin proposed that the traits are selected by the environment in which the species lives. Selection either enhances the ability of the organism to reproduce, or not. If it does, then the traits most suitable for the particular environment are passed on to subsequent generations. The concept of descent with variation followed by selection occupies six chapters in the *Origin*. It was one of the most remarkable scientific ideas ever put forth, and to this day, it remains a core, unifying principle of biology.

There is a single illustration in the *Origin*, at the end of the book, of a hypothetical origin of taxa, which is loosely based on the doodle from Notebook B. Curiously, the figure does not show a single origin for all taxa but, rather, many origins giving rise to new species. The concept of origin, as in the origin of life, was in the back of Darwin's mind but not explicitly discussed in the book.

More than a decade after the publication of the *Origin*, in a letter to Joseph Hooker dated 1871, Darwin mused that life arose in a "little warm pond with some sorts of ammonia and phosphoric salts,—light, heat, electricity, etc. present, that a protein compound was chemically formed, ready to undergo still more complex changes, at the present day such matter would be instantly devoured, or absorbed, which would not have been the case before living creatures were formed."

Eighty years after that notion was put forth, a young chemist, Stanley Miller, and his Nobel Laureate advisor, Harold Urey, actually did make amino acids (the building blocks of proteins) in a laboratory at the University of Chicago. They used ammonia gas, methane, hydrogen, and water and a spark to simulate lightning. That experiment, which was published in 1953, gave great hope that an understanding of the origin of life was imminent. However, there is a huge gap between making the chemical constituents of organisms and making the organisms themselves. In even the simplest organisms, the chemical constituents are organized into microscopic machines that give rise to metabolic processes and allow the cell to replicate. No one has yet created a living organism from scratch, but that is not to say it is impossible.

The simplest organisms are microbes, organisms of which Darwin was surely aware but not certain how to accommodate in his theory. Indeed, Darwin took a microscope with him on the *Beagle*. (Along with his Bible and natural history books, he also took two pistols, twelve shirts, two books to help him learn Spanish, and a coin purse.) But because microbes do not leave a fossil record that is clearly visible to the naked eye, Darwin could not have known that the rocks beneath the visible fossils were not from a period in Earth's history that was before the origin of life—but rather a period before animals or plants. Even if Darwin had observed fossil microbes, he would almost certainly not have understood what their relationship to plants or animals was. Darwin, and virtually every other scientist in the nineteenth century, would have been profoundly surprised to learn that plants and animals had all descended from microbes over a period of time that was completely unimaginable in the nineteenth century—far longer than 300 million years. Indeed, microbes are not mentioned in the Bible, except indirectly in reference to diseases like the plague. They certainly weren't deliberately taken by Noah on the ark, nor are they woven into the Turkish tapestries depicting the story of the Great Flood.

While we have made great progress in the 150 years since the publication of the *Origin*, scientists are still struggling to understand whether life began in a small warm pond, at a deep-sea hydrothermal vent, or somewhere else. How might it have started? How did it get going? How did microbes lead to the evolution of plants and animals? How were these organisms missed for so long in our search for the origins and evolution of life?

The answers to these questions are complex, and many aspects are still far from fully understood, but we have learned a lot because of the tools developed during the last century. If Darwin had been on an oceanographic research voyage in the Black Sea early in the nineteenth century, he might have observed that there were no animals below the upper hundred meters and concluded that the deep water was lifeless. But had he been a microbiologist, our understanding of the origins of species would have been very different. Although microbes were well known in the nineteenth century, it took another century before they were included in our understanding of the evolution of life on Earth. Microbes were missed because of our observational biases. They had been on this planet for billions of years before the first animal arose.

Let's meet the missing microbes and see how they played an outsized role in making this planet function. Without microbes, we would not be here.

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