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DARWIN'S DOUBT

THE EXPLOSIVE ORIGIN OF ANIMAL LIFE AND
THE CASE FOR INTELLIGENT DESIGN

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PROLOGUE

When people today hear the term "information revolution," they typically think of silicon chips and software code, cellular phones and supercomputers. They rarely think of tiny one-celled organisms or the rise of animal life. But, while writing these words in the summer of 2012, I am sitting at the end of a narrow medieval street in Cambridge, England, where more than half a century ago a far-reaching information revolution began in biology. This revolution was launched by an unlikely but now immortalized pair of scientists, Francis Crick and James Watson. Since my time as a Ph.D. student at Cambridge during the late 1980s, I have been fascinated by the way their discovery transformed our understanding of the nature of life. Indeed, since the 1950s, when Watson and Crick first illuminated the chemical structure and information-bearing properties of DNA, biologists have come to understand that living things, as much as high-tech devices, depend upon digital information-information that, in the case of life, is stored in a four-character chemical code embedded within the twisting figure of a double helix.

Because of the importance of information to living things, it has now become apparent that many distinct "information revolutions" have occurred in the history of life—not revolutions of human discovery or invention, but revolutions involving dramatic increases in the information present within the living world itself. Scientists now know that building a living organism requires information, and building a fundamentally new form of life from a simpler form of life requires an immense amount of *new* information. Thus, wherever the fossil record testifies to the origin of a completely new form of animal life—a pulse of biological innovation—it also testifies to a significant increase in the information content of the biosphere.

In 2009, I wrote a book called *Signature in the Cell* about the first "information revolution" in the history of life—the one that occurred with the origin of the first life on earth. My book described how discoveries in molecular biology during the 1950s and 1960s established that DNA contains information in digital form, with its four chemical subunits (called nucleotide bases) functioning like letters in a written language or symbols in a computer code. And molecular biology also revealed that cells employ a complex information-processing system to access and express the information stored in DNA as they use that information to build the proteins and protein machines that they need to stay alive. Scientists attempting to explain the origin of life must explain how both information-rich molecules and the cell's information-processing system arose.

The type of information present in living cells—that is, "specified" information in which the sequence of characters matters to the function of the sequence as a whole—has generated an acute mystery. No undirected physical or chemical process has demonstrated the capacity to produce specified information starting "from purely physical or chemical" precursors. For this reason, chemical evolutionary theories have failed to solve the mystery of the origin of first life—a claim that few mainstream evolutionary theorists now dispute.

In Signature in the Cell, I not only reported the well-known impasse in origin-of-life studies; I also made an affirmative case for the theory of intelligent design. Although we don't know of a material cause that generates functioning digital code from physical or chemical precursors, we do know—based upon our uniform and repeated experience—of one type of cause that has demonstrated the power to produce this type of information. That cause is intelligence or mind. As information theorist Henry Quastler observed, "The creation of information is habitually associated with conscious activity."1 Whenever we find functional information-whether embedded in a radio signal, carved in a stone monument, etched on a magnetic disc, or produced by an origin-of-life scientist attempting to engineer a self-replicating molecule—and we trace that information back to its ultimate source, invariably we come to a mind, not merely a material process. For this reason, the discovery of digital information in even the simplest living cells indicates the prior activity of a designing intelligence at work in the origin of the first life.

My book proved controversial, but in an unexpected way. Though I

clearly stated that I was writing about the origin of the first life and about theories of chemical evolution that attempt to explain it from simpler preexisting chemicals, many critics responded as if I had written another book altogether. Indeed, few attempted to refute my book's actual thesis that intelligent design provides the best explanation for the origin of the information necessary to produce the first life. Instead, most criticized the book as if it had presented a critique of the standard neo-Darwinian theories of biological evolution—theories that attempt to account for the origin of new forms of life from simpler preexisting forms of life. Thus, to refute my claim that no chemical evolutionary processes had demonstrated the power to explain the ultimate origin of information in the DNA (or RNA) necessary to produce life from simpler preexisting chemicals in the first place, many critics cited processes at work in already living organisms—in particular, the process of natural selection acting on random mutations in already existing sections of information-rich DNA. In other words, these critics cited an undirected process that acts on preexistent information-rich DNA to refute my argument about the failure of undirected material processes to produce information in DNA in the first place.2

For example, the eminent evolutionary biologist Francisco Ayala attempted to refute *Signature* by arguing that evidence from the DNA of humans and lower primates showed that the genomes of these organisms had arisen as the result of an unguided, rather than intelligently designed, process—even though my book did not address the question of human evolution or attempt to explain the origin of the human genome, and even though the process to which Ayala alluded clearly presupposed the existence of another information-rich genome in some hypothetical lower primate.³

Other discussions of the book cited the mammalian immune system as an example of the power of natural selection and mutation to generate new biological information, even though the mammalian immune system can only perform the marvels it does because its mammalian hosts are already alive, and even though the mammalian immune system depends upon an elaborately *preprogrammed* form of adaptive capacity rich in genetic information—one that arose long after the origin of the first life. Another critic steadfastly maintained that "Meyer's main argument" concerns "the inability of random mutation and selection to *add* information to [preexisting] DNA"⁴ and attempted to refute the book's presumed critique

of the neo-Darwinian mechanism of biological evolution accordingly.

I found this all a bit surreal, as if I had wandered into a lost chapter from a Kafka novel. *Signature in the Cell* simply did not critique the theory of biological evolution, nor did it ask whether mutation and selection can *add* new information to preexisting information-rich DNA. To imply otherwise, as many of my critics did, was simply to erect a straw man.

To those unfamiliar with the particular problems faced by scientists trying to explain the origin of life, it might not seem obvious why invoking natural selection does not help to explain the origin of the first life. After all, if natural selection and random mutations can generate new information in living organisms, why can it also not do so in a prebiotic environment? But the distinction between a biological and prebiotic context was crucially important to my argument. Natural selection assumes the existence of living organisms with a capacity to reproduce. Yet selfreplication in all extant cells depends upon information-rich proteins and nucleic acids (DNA and RNA), and the origin of such information-rich molecules is precisely what origin-of-life research needs to explain. That's why Theodosius Dobzhansky, one of the founders of the modern neo-Darwinian synthesis, can state flatly, "Pre-biological natural selection is a contradiction in terms." 5 Or, as Nobel Prize-winning molecular biologist and origin-of-life researcher Christian de Duve explains, theories of prebiotic natural selection fail because they "need information which implies they have to presuppose what is to be explained in the first place." 6 Clearly, it is not sufficient to invoke a process that commences only once life has begun, or once biological information has arisen, to explain the origin of life or the origin of the information necessary to produce it.

All this notwithstanding, I have long been aware of strong reasons for doubting that mutation and selection can add *enough* new information of the right kind to account for large-scale, or "macroevolutionary," innovations—the various information revolutions that have occurred after the origin of life. For this reason, I have found it increasingly tedious to have to concede, if only for the sake of argument, the substance of claims I think likely to be false.

And so the repeated prodding of my critics has paid off. Even though I did not write the book or make the argument that many of my critics critiqued in responding to *Signature in the Cell*, I have decided to write that book. And this is that book.

Of course, it might have seemed a safer course to leave well enough alone. Many evolutionary biologists now grudgingly acknowledge that no chemical evolutionary theory has offered an adequate explanation of the origin of life or the ultimate origin of the information necessary to produce it. Why press a point you never made in the first place?

Because despite the widespread impression to the contrary—conveyed by textbooks, the popular media, and spokespersons for official science—the orthodox neo-Darwinian theory of biological evolution has reached an impasse nearly as acute as the one faced by chemical evolutionary theory. Leading figures in several subdisciplines of biology—cell biology, developmental biology, molecular biology, paleontology, and even evolutionary biology—now openly criticize key tenets of the modern version of Darwinian theory in the peer-reviewed technical literature. Since 1980, when Harvard paleontologist Stephen Jay Gould declared that neo-Darwinism "is effectively dead, despite its persistence as textbook orthodoxy," the weight of critical opinion in biology has grown steadily with each passing year.

A steady stream of technical articles and books have cast new doubt on the creative power of the mutation and selection mechanism.⁸ So well established are these doubts that prominent evolutionary theorists must now periodically assure the public, as biologist Douglas Futuyma has done, that "just because we don't know how evolution occurred, does not justify doubt about whether it occurred." Some leading evolutionary biologists, particularly those associated with a group of scientists known as the "Altenberg 16," are openly calling for a new theory of evolution because they doubt the creative power of the mutation and natural selection mechanism.¹⁰

The fundamental problem confronting neo-Darwinism, as with chemical evolutionary theory, is the problem of the origin of new biological information. Though neo-Darwinists often dismiss the problem of the origin of life as an isolated anomaly, leading theoreticians acknowledge that neo-Darwinism has also failed to explain the source of novel variation without which natural selection can do nothing—a problem equivalent to the problem of the origin of biological information. Indeed, the problem of the origin of information lies at the root of a host of other acknowledged problems in contemporary Darwinian theory—from the origin of new body plans to the origin of complex structures and systems such as wings,

feathers, eyes, echolocation, blood clotting, molecular machines, the amniotic egg, skin, nervous systems, and multicellularity, to name just a few.

At the same time, classical examples illustrating the prowess of natural selection and random mutations do not involve the creation of novel genetic information. Many biology texts tell, for example, about the famous finches in the Galápagos Islands, whose beaks have varied in shape and length over time. They also recall how moth populations in England darkened and then lightened in response to varying levels of industrial pollution. Such episodes are often presented as conclusive evidence for the power of evolution. And indeed they are, depending on how one defines "evolution." That term has many meanings, and few biology textbooks distinguish between them. "Evolution" can refer to anything from trivial cyclical change within the limits of a preexisting gene pool to the creation of entirely novel genetic information and structure as the result of natural selection acting on random mutations. As a host of distinguished biologists technical explained in recent papers, small-scale, "microevolutionary," change cannot be extrapolated to explain large-scale, or "macroevolutionary," innovation. 11 For the most part, microevolutionary changes (such as variation in color or shape) merely utilize or express existing genetic information, while the macroevolutionary change necessary to assemble new organs or whole body plans requires the creation of entirely new information. As an increasing number of evolutionary biologists have noted, natural selection explains "only the survival of the fittest, not the arrival of the fittest."12 The technical literature in biology is now replete with world-class biologists¹³ routinely expressing doubts about various aspects of neo-Darwinian theory, and especially about its central tenet, namely, the alleged creative power of the natural selection and mutation mechanism.

Nevertheless, popular defenses of the theory continue apace, rarely if ever acknowledging the growing body of critical scientific opinion about the standing of the theory. Rarely has there been such a great disparity between the popular perception of a theory and its actual standing in the relevant peer-reviewed scientific literature. Today modern neo-Darwinism seems to enjoy almost universal acclaim among science journalists and bloggers, biology textbook writers, and other popular spokespersons for science as the great unifying theory of all biology. High-school and college textbooks

present its tenets without qualification and do not acknowledge the existence of any significant scientific criticism of it. At the same time, official scientific organizations—such as the National Academy of Sciences (NAS), the American Association for the Advancement of Sciences (AAAS), and the National Association of Biology Teachers (NABT)—routinely assure the public that the contemporary version of Darwinian theory enjoys unequivocal support among qualified scientists and that the evidence of biology overwhelmingly supports the theory. For example, in 2006 the AAAS declared, "There is no significant controversy within the scientific community about the validity of the theory of evolution." The media dutifully echo these pronouncements. As *New York Times* science writer Cornelia Dean asserted in 2007, "There is no credible scientific challenge to the theory of evolution as an explanation for the complexity and diversity of life on earth." 15

The extent of the disparity between popular representations of the status of the theory and its actual status, as indicated in the peer-reviewed technical journals, came home to me with particular poignancy as I was preparing to testify before the Texas State Board of Education in 2009. At the time the board was considering the adoption of a provision in its science education standards that would encourage teachers to inform students of both the strengths and weaknesses of scientific theories. This provision had become a political hot potato after several groups asserted that "teaching strengths and weaknesses" were code words for biblical creationism or for removing the teaching of the theory of evolution from the curriculum. Nevertheless, after defenders of the provision insisted that it neither sanctioned teaching creationism nor censored evolutionary theory, opponents of the provision shifted their ground. They attacked the provision by insisting that there was no need to consider weaknesses in modern evolutionary theory because, as Eugenie Scott, spokeswoman for the National Center for Science Education, insisted in The Dallas Morning News, "There are no weaknesses in the theory of evolution."16

At the same time, I was preparing a binder of one hundred peer-reviewed scientific articles in which biologists described significant problems with the theory—a binder later presented to the board during my testimony. So I knew—unequivocally—that Dr. Scott was misrepresenting the status of scientific opinion about the theory in the relevant scientific literature. I also knew that her attempts to prevent students from hearing

about significant problems with evolutionary theory would have likely made Charles Darwin himself uncomfortable. In *On the Origin of Species*, Darwin openly acknowledged important weaknesses in his theory and professed his own doubts about key aspects of it. Yet today's public defenders of a Darwin-only science curriculum apparently do not want these, or any other scientific doubts about contemporary Darwinian theory, reported to students.

This book addresses Darwin's most significant doubt and what has become of it. It examines an event during a remote period of geological history in which numerous animal forms appear to have arisen suddenly and without evolutionary precursors in the fossil record, a mysterious event commonly referred to as the "Cambrian explosion." As he acknowledged in the *Origin*, Darwin viewed this event as a troubling anomaly—one that he hoped future fossil discoveries would eventually eliminate.

The book is divided into three main parts. Part One, "The Mystery of the Missing Fossils," describes the problem that first generated Darwin's doubt—the missing ancestors of the Cambrian animals in the earlier Precambrian fossil record—and then tells the story of the successive, but unsuccessful, attempts that biologists and paleontologists have made to resolve that mystery.

Part Two, "How to Build an Animal," explains why the discovery of the importance of information to living systems has made the mystery of the Cambrian explosion more acute. Biologists now know that the Cambrian explosion not only represents an explosion of new animal form and structure but also an explosion of information—that it was, indeed, one of the most significant "information revolutions" in the history of life. Part Two examines the problem of explaining how the unguided mechanism of natural selection and random mutations could have produced the biological information necessary to build the Cambrian animal forms. This group of chapters explains why so many leading biologists now doubt the creative power of the neo-Darwinian mechanism and it presents four rigorous critiques of the mechanism based on recent biological research.

Part Three, "After Darwin, What?" evaluates more current evolutionary theories to see if any of them explain the origin of form and information more satisfactorily than standard neo-Darwinism does. Part Three also presents and assesses the theory of intelligent design as a possible solution to the Cambrian mystery. A concluding chapter discusses the implications

of the debate about design in biology for the larger philosophical questions that animate human existence. As the story of the book unfolds, it will become apparent that a seemingly isolated anomaly that Darwin acknowledged almost in passing has grown to become illustrative of a fundamental problem for all of evolutionary biology: the problem of the origin of biological form and information.

To see where that problem came from and why it has generated a crisis in evolutionary biology, we need to begin at the beginning: with Darwin's own doubt, with the fossil evidence that elicited it, and with a clash between a pair of celebrated Victorian naturalists—the famed Harvard paleontologist Louis Agassiz and Charles Darwin himself.

PART ONE

THE MYSTERY OF THE MISSING FOSSILS

1

DARWIN'S NEMESIS

When Charles Darwin finished his famous book, he thought that he had explained every clue but one.

By anyone's measure, *On the Origin of Species* was a singular achievement. Like a great Gothic cathedral, the ambitious work integrated many disparate elements into a grand synthesis, explaining phenomena in fields as diverse as comparative anatomy, paleontology, embryology, and biogeography. At the same time, it was impressive for its simplicity. Darwin's *Origin* explained many classes of biological evidence with just two central organizing ideas. The twin pillars of his theory were the ideas of *universal common ancestry* and *natural selection*.

The first of these pillars, universal common ancestry, represented Darwin's theory of the history of life. It asserted that all forms of life have ultimately descended from a *single common ancestor* somewhere in the distant past. In a famous passage at the end of the *Origin*, Darwin argued that "all the organic beings which have ever lived on this earth have descended from some one primordial form." Darwin thought that this primordial form gradually developed into new forms of life, which in turn gradually developed into other forms of life, eventually producing, after many millions of generations, all the complex life we see in the present.

Biology textbooks today usually depict this idea just as Darwin did, with a great branching tree. The trunk of Darwin's tree of life represents the first primordial organism. The limbs and branches of the tree represent the many new forms of life that developed from it (see Fig. 1.1). The vertical axis on which the tree is plotted represents the arrow of time. The horizontal axis represents changes in biological form, or what biologists call "morphological distance."



FIGURE 1.1

Darwin's evolutionary tree of life, as depicted by the nineteenth-century German evolutionary biologist Ernst Haeckel.

Biologists often call Darwin's theory of the history of life "universal common descent" to indicate that *every* organism on earth arose from a single common ancestor by a process of "descent with modification." Darwin argued that this idea best explained a variety of biological evidences: the succession of fossil forms, the geographical distribution of various species (such as Galápagos finches), and the anatomical and embryological similarities among otherwise highly distinct organisms.

The second pillar of Darwin's theory affirmed the creative power of a process he called *natural selection*, a process that acted on random variations in the traits or features of organisms and their offspring.² Whereas the theory of universal common descent postulated *a pattern* (the branching tree) to represent the history of life, Darwin's idea of natural selection referred to a *process* that he said could generate the change implied by his branching tree of life.

Darwin formulated the idea of natural selection by analogy to a well-known process, that of "artificial selection" or "selective breeding." Anyone in the nineteenth century familiar with the breeding of domestic animals—dogs, horses, sheep, or pigeons, for example—knew that human breeders could alter the features of domestic stock by allowing only animals with certain traits to breed. A sheepherder from the north of Scotland might breed for a woollier sheep to enhance its chances of survival in a cold northern climate (or to harvest more wool). To do so, he would choose only the woolliest males and woolliest ewes to breed. If generation after generation he continued to select and breed only the woolliest sheep among the resulting offspring, he would eventually produce a woollier breed of sheep. In such cases, "the key is man's power of accumulative selection," wrote Darwin. "Nature gives successive variations; man adds them up in certain directions useful to him."

Darwin noted that pigeons have been coaxed into a dizzying variety of breeds: the carrier, with its elongated eyelids and a "wide gape of mouth"; the "short-faced tumbler," with its "beak in outline almost like that of a finch"; the common tumbler, with its penchant for flying in close formation and "tumbling in the air head over heels"; and, perhaps strangest of all, the

pouter, with its elongated legs, wings, and body overshadowed by its "enormously developed crop, which it glories in inflating" for its astonished patrons.⁴

Of course, pigeon breeders achieved these startling metamorphoses by carefully sifting and selecting. But, as Darwin pointed out, nature also has a means of sifting: defective creatures are less likely to survive and reproduce, while those offspring with beneficial variations are more likely to survive, reproduce, and pass on their advantages to future generations. In the *Origin*, Darwin argued that this process, natural selection acting on random variations, could alter the features of organisms just as intelligent selection by human breeders can. Nature itself could play the role of the breeder.

Consider once more our flock of sheep. Imagine that instead of a human selecting the woolliest males and ewes to breed, a series of very cold winters ensures that all but the very woolliest sheep in a population die. Now again only very woolly sheep will remain to breed. If the cold winters continue over several generations, will the result not be the same as before? Won't the population of sheep eventually become discernibly woollier?

This was Darwin's great insight. Nature—in the form of environmental changes or other factors—could have the same effect on a population of organisms as the intentional decisions of an intelligent agent. Nature would favor the preservation of certain features over others—specifically, those that conferred a functional or survival advantage upon the organisms possessing them—causing the features of the population to change. And the resulting change will have been produced not by an intelligent breeder choosing a desirable trait or variation—not by "artificial selection"—but by a wholly natural process. What's more, Darwin concluded that this process of natural selection acting on randomly arising variations had been "the chief agent of change" in generating the great branching tree of life in all its variety.

On the Origin of Species seized the attention of the scientific community like a thunderclap. Darwin's analogy to artificial selection was powerful, his proposed mechanism of natural selection and random variation easily grasped, and his skill in dispensing with potential objections unrivalled. Moreover, the explanatory scope of his argument for universal common descent constituted something of a tour de force. By the close of the Origin, it seemed to many that Darwin had dispensed with every conceivable

objection to his theory but one.

THE ANOMALY: DARWIN'S DOUBT

Despite the scope of his synthesis, there was one set of facts that troubled Darwin—something he conceded his theory couldn't adequately explain, at least at present. Darwin was puzzled by a pattern in the fossil record that seemed to document the geologically sudden appearance of animal life in a remote period of geologic history, a period that at first was commonly called the Silurian, but later came to be known as the Cambrian.

During this geological period, many new and anatomically sophisticated creatures appeared suddenly in the sedimentary layers of the geologic column without any evidence of simpler ancestral forms in the earlier layers below, in an event that paleontologists today call the Cambrian explosion. Darwin frankly described his concerns about this conundrum in the *Origin:* "The difficulty of understanding the absence of vast piles of fossiliferous strata, which on my theory were no doubt somewhere accumulated before the Silurian [i.e., Cambrian] epoch, is very great," he wrote. "I allude to the manner in which numbers of species of the same group suddenly appear in the lowest known fossiliferous rocks." The sudden appearance of animals so early in the fossil record did not easily accord with Darwin's new theory of gradual evolutionary change, and there was one scientist who would not let him forget it.

THE ANTAGONIST

Swiss-born paleontologist Louis Agassiz, of Harvard University, was one of the best-trained scientists of his age, and he knew the fossil record better than any man alive. Hoping to enlist Agassiz as an ally, Darwin sent him a copy of *On the Origin of Species* and asked him to consider the argument with an open mind (see Fig. 1.2). One can almost see the great, aging naturalist receiving the unremarkable package from the postman, unwrapping the small green volume that had stirred such a tempest on both sides of the Atlantic. Perhaps he retired to his study the better to concentrate, scrutinizing the book's prepossessing title, recalling what he had already heard about the work. He read the book with deep interest, making notes in the margin as he moved through it, but in the end his verdict would disappoint its author. Agassiz concluded that the fossil record, particularly

the record of the explosion of Cambrian animal life, posed an insuperable difficulty for Darwin's theory.

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FIGURE 1.2

Figure 1.2a (left): Louis Agassiz. Figure 1.2b (right): Charles Darwin.

THE TWO-PRONGED CHALLENGE

To see why, consider brachiopods and trilobites, two of the best-documented creatures in the Cambrian fossil record by 1859. The brachiopod (see Fig. 1.3), with its two shells, looks like a clam or an oyster, but is very different inside. As shown in the accompanying figure, it possesses a gonad, mantle, mantle cavity, anterior body wall, body cavity, gut, and lophophore, the last of which is a feeding organ like a ring of tentacles, usually in the shape of a coil or horseshoe, with a mouth inside the ring of tentacles, and an anus outside. The brachiopod exhibits a highly complex overall body plan, with many individually complex and functionally integrated anatomical systems and parts. Its tentacles, for instance, are covered by cilia precisely arranged to generate and direct a current of water toward the mouth.



FIGURE 1.3

Figure 1.3a (top): Brachiopod internal anatomy. Figure 1.3b (bottom, left): Brachiopod fossil showing remains of internal structure. Courtesy Paul Chien. Figure 1.3c (bottom, right): Fossil showing exterior structure of brachiopod shell. Courtesy Corbis.

MIDDLE OR AXIAL LOBE

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FIGURE 1.4

Figure 1.4a (top): Trilobite anatomy. Figure 1.4b (bottom): Trilobite fossil of the species Kuanyangia pustulosa. Courtesy Illustra Media.

Even more sophisticated was the trilobite (see Fig. 1.4), with its three longitudinal lobes across its head (a raised middle lobe and a flatter pleural lobe to either side) and a body divided into three parts—head, chest, and tail, the former two consisting of as many as thirty segments. It had a pair of legs for every pleural groove and another three pairs for the head. Most dramatic of all were the compound eyes found on even some of the very early trilobites—eyes that afforded these not so primitive animals a 360-degree field of vision.⁷

The abrupt appearance of such complex anatomical designs presented a challenge to each of the two main parts of Darwin's theory of evolution.

THE CAMBRIAN EXPLOSION AND THE ACTION OF NATURAL SELECTION

The Cambrian fossil evidence represented a significant challenge to Darwin's claim that natural selection had the capacity to produce novel forms of life. As Darwin described it, the ability of natural selection to produce significant biological change depends upon the presence of three distinct elements: (1) randomly arising variations, (2) the heritability of those variations, and (3) a competition for survival, resulting in differences in reproductive success among competing organisms.

According to Darwin, variations in traits arise *randomly*. Some variations (such as thicker fleece) might confer advantages in the *competition for survival* in particular environmental conditions. Those variations that are heritable and that impart functional or survival advantage will be preserved in the next generation. As nature "selects" these successful variations, the features of a population change.

Darwin conceded that the beneficial variations responsible for permanent change in species are both rare and necessarily modest. Major variations in forms, what later evolutionary biologists would term "macromutations," inevitably produce deformity and death. Only minor variations meet the test of viability and heritability.

It followed that, over human timescales, the benefits of this evolutionary mechanism would be difficult or impossible to spot. But given enough time, favorable variations would *gradually* accumulate and give rise to new species

and, given more time, even fundamentally new groups of organisms and body designs. If artificial selection could conjure so many strange breeds from a wild strain in a few centuries, Darwin argued, imagine what natural selection could achieve over many millions of years. Even the origin of complex structures such as the mammalian eye—which seemed at first to present a significant challenge to his theory—could be explained if one postulated the existence of an initially simpler structure (such as a light sensitive spot) that could be gradually modified over long periods of time.

And that was the rub. Darwin's mechanism of natural selection and random variation necessarily required a lot of time to generate wholly novel organisms, creating a dilemma that Agassiz was keen to expose.

In an 1874 Atlantic Monthly essay titled "Evolution and the Permanence of Type," Agassiz explained his reasons for doubting the creative power of natural selection. Small-scale variations, he argued, had never produced a "specific difference" (i.e., a difference in species). Meanwhile, large-scale variations, whether achieved gradually or suddenly, inevitably resulted in sterility or death. As he put it, "It is a matter of fact that extreme variations finally degenerate or become sterile; like monstrosities they die out." 8

Darwin himself insisted that the process of evolutionary change he envisioned must occur very gradually for the same reason. Thus, Darwin realized that building, for instance, a trilobite from single-celled organisms by natural selection operating on small, step-by-step variations would require countless transitional forms and failed biological experiments over vast stretches of geologic time. As University of Washington paleontologist Peter Ward would later explain, Darwin had very specific expectations for what paleontologists would find below the lowest known strata of animal fossils—in particular, "intervening strata showing fossils of increasing complexity until finally trilobites appeared." As Darwin noted, "If my theory be true, it is indisputable that before the lowest Silurian [Cambrian] stratum was deposited, long periods elapsed, as long as, or probably far longer than, the whole interval from the Silurian age to the present day; and that during these vast, yet quite unknown, periods of time, the world swarmed with living creatures." 10

The mechanism of natural selection necessarily had to work gradually on small incremental variations. And, indeed, the kinds of variations that Darwin actually observed and described in developing his analogy between natural and artificial selection were in every case minor. Only by selecting and accumulating minor variations over many generations were breeders able to produce the striking changes in the features of a breed, changes that were, nevertheless, extraordinarily modest compared to the radical differences in form between, say, Precambrian and Cambrian forms of life. At the end of the day, as Agassiz hastened to note, the pigeons Darwin cited in support of the creative power of artificial and, by analogy, natural selection were still pigeons. More significant changes to the form and anatomical structure of organisms would, by the logic of Darwin's mechanism, require untold millions of years, precisely what seemed unavailable in the case of the Cambrian explosion.

THE CAMBRIAN EXPLOSION AND THE TREE OF LIFE

The abrupt appearance of the Cambrian fauna also posed a separate but related difficulty for Darwin's picture of a continuously branching tree of life. To produce truly novel animal forms, the Darwinian mechanism would —by its own internal logic—require not only millions of years, but untold generations of ancestors. Thus, even the discovery of a handful of plausible intermediates allegedly linking a Precambrian ancestor to a Cambrian descendant wouldn't come close to fully documenting Darwin's picture of the history of life. If Darwin is right, Agassiz argued, then we should find not just one or a few missing links, but innumerable links shading almost imperceptibly from alleged ancestors to presumed descendants. Geologists, however, had found no such myriad of transitional forms leading to the Cambrian fauna. Instead, the stratigraphic column seemed to document the abrupt appearance of the earliest animals.

Agassiz thought the evidence of abrupt appearance, and the absence of ancestral forms in the Precambrian, refuted Darwin's theory. Of these earlier forms, Agassiz asked, "Where are their fossilized remains?" He insisted that Darwin's picture of the history of life "contradict[ed] what the animal forms buried in the rocky strata of our earth tell us of their own introduction and succession upon the surface of the globe. Let us therefore hear them;—for, after all, their testimony is that of the eye-witness and the actor in the scene." 12

MURCHISON, SEDGWICK, AND THE CAMBRIAN FOSSILS OF WALES

Darwin, for his part, responded with more than civility. Far from dismissing

Agassiz, he conceded that his objection carried considerable force. Nor was Agassiz alone in pressing these concerns. Other leading naturalists thought the fossil evidence presented a significant obstacle to Darwin's theory. At the time, perhaps the best place to investigate the lowest known strata of fossils was Wales, and one of its leading experts was Roderick Impey Murchison, who named the earliest geologic period the Silurian after an ancient Welsh tribe. Five years before *On the Origin of Species*, he called attention to the sudden appearance of complex designs like the compound eyes of the first trilobites, creatures already thriving at the apparent dawn of animal life. For him, this discovery ruled out the idea that these creatures had evolved gradually from some primitive and relatively simple form: "The earliest signs of living things, announcing as they do a high complexity of organization, entirely exclude the hypothesis of a transmutation from lower to higher grades of being." 13

The other pioneering explorer of Wales's rich fossil record, Adam Sedgwick, also thought that Darwin had leaped beyond the evidence, as he told him in a letter in the fall of 1859: "You have deserted—after a start in that tram-road of all solid physical truth—the true method of induction." Sedgwick might have had in mind the same evidence the two men had studied together some twenty-eight years before when the Cambridge professor had brought Darwin along as his field assistant to explore, in the Upper Swansea Valley in northwestern Wales, the very strata that seemed to testify so powerfully to the sudden appearance of animal life. It was these strata that Sedgwick named after a Latinized English term for the country of Wales—"Cambria," a designation that eventually replaced "Silurian" as the name for the earliest strata of animal fossils.

Sedgwick emphasized that these Cambrian animal fossils appeared to pop out of nowhere into the geological column. But he also stressed what he viewed as a broader reason to doubt Darwin's evolutionary model: the sudden appearance of the Cambrian animals was merely the most outstanding instance of a pattern of discontinuity that extends throughout the geologic column. Where in the Ordovician strata, for instance, are many of the families of the trilobites and brachiopods present in the Cambrian just below it?¹⁵ These creatures along with numerous other types suddenly disappear. But just as suddenly one finds newcomers in the Ordovician strata like the eurypterans (sea scorpions), starfish, and tetracorals (see Fig. 1.5).¹⁶ In a later Paleozoic period called the Devonian, the first amphibians (e.g.,

Ichthyostega) arise. Much later, many staples of the Paleozoic era (which encompasses the Cambrian, Ordovician, and four subsequent periods) suddenly go extinct in a period called the Permian.¹⁷ Then, in the Triassic period that follows, completely novel animals such as turtles and dinosaurs emerge.¹⁸ Such discontinuity, Sedgwick argued, is not the exception, but the rule.

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EURYPTERANS

TETRACORAL

FIGURE 1.5

Three organisms that first appear in the Ordivician period: eurypterans (sea scorpions), starfish, and tetracoral.

DATING BY DISCONTINUITY

Already by Sedgwick's time, the various strata of fossils had proved so distinct one from another that geologists had come to use the sharp discontinuities between them as a key means for dating rocks. Originally, the best tool for determining the relative age of various strata was based on the notion of superposition. Put simply, unless there is a reason to believe otherwise, a geologist provisionally assumes that lower rocks were put down before the rocks above them. Now, contrary to a widespread caricature, no respected geologist, then or now, adopts this method

uncritically. The most basic training in geology teaches that rock formations can be twisted, upended, even mixed pell-mell by a variety of phenomena. This is why geologists have always looked for other means to estimate the relative age of different strata.

In 1815, Englishman William Smith had hit upon just such an alternative means.¹⁹ While studying the distinct fossil strata exposed during canal construction, Smith noted that so dissimilar are the fossil types among different major periods and so sharp and sudden the break between them, that geologists could use this as one method for determining the relative age of strata. Even when layers of geological strata are twisted and turned, the clear discontinuities between the various strata often allow geologists to discern the order in which they were deposited, particularly when there is a broad enough sampling of rich geological sites from the period under investigation to study and cross-reference. Although not without its pitfalls, this approach has become a standard dating technique, used in conjunction with superposition and other more recent radiometric dating methods.²⁰

Indeed, it's difficult to overemphasize how central the approach is to modern historical geology. As Harvard paleontologist Stephen Jay Gould explains, it is the phenomenon of fossil succession that dictates the names of the major periods in the geological column (see Fig. 1.6). "We might take the history of modern multi-cellular life, about 600 million years, and divide this time into even and arbitrary units easily remembered as 1-12 or A-L, at 50 million years per unit," Gould writes. "But the earth scorns our simplifications, and becomes much more interesting in its derision. The history of life is not a continuum of development, but a record punctuated by brief, sometimes geologically instantaneous, episodes of mass extinction and subsequent diversification."21 The question that Darwin's early critics posed was this: How could he reconcile his theory of gradual evolution with a fossil record so discontinuous that it had given rise to the names of the major distinct periods of geological time, particularly when the first animal forms seemed to spring into existence during the Cambrian as if from nowhere?

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FIGURE 1.6

The geological timescale.

A SOLUTION UNSEEN

Of course, Darwin was well aware of these problems. As he noted in the Origin, "The abrupt manner in which whole groups of species suddenly appear in certain formations has been urged by several paleontologists—for instance, by Agassiz, Pictet, and Sedgwick—as a fatal objection to the belief in the transmutation of species. If numerous species, belonging to the same genera or families, have really started into life all at once, the fact would be fatal to the theory of descent with slow modification through natural selection."22 Darwin, however, proposed a possible solution. He suggested that the fossil record may be significantly incomplete: either the ancestral forms of the Cambrian animals were not fossilized or they hadn't been found yet. "I look at the natural geological record, as a history of the world imperfectly kept, and written in a changing dialect," Darwin wrote. "Of this history we possess the last volume alone, relating only to two or three countries. Of this volume, only here and there a short chapter has been preserved; and of each page, only here and there a few lines. . . . On this view, the difficulties above discussed are greatly diminished, or even disappear."23

Darwin himself was less than satisfied with this explanation.²⁴ Agassiz, for his part, would have none of it. "Both with Darwin and his followers, a great part of the argument is purely negative," he wrote. They "thus throw off the responsibility of proof. . . . However broken the geological record may be, there is a complete sequence in many parts of it, from which the character of the succession may be ascertained." On what basis did he make this claim? "Since the most exquisitely delicate structures, as well as embryonic phases of growth of the most perishable nature, have been preserved from very early deposits, we have no right to infer the disappearance of types because their absence disproves some favorite [i.e., Darwinian] theory."²⁵

Though Darwin himself was less than enthusiastic about his response to Agassiz's objection, it seemed adequate to satisfy the needs of the moment. The overwhelming preponderance of evidence that Darwin had marshaled seemed to support his theory. In any case, many leading naturalists—Joseph Hooker, Thomas Huxley, Ernst Haeckel, and Asa Gray—all younger than Agassiz, quickly aligned themselves with his evolutionary line of thinking. True, some scientists, notably the Scottish engineering professor Fleeming

Jenkin and (later) the English geneticist William Bateson, expressed persistent doubts about the efficacy of natural selection. But despite the views of some weighty scientific critics, Darwin's revolutionary theory won increasingly wide support and soon defined the terms of the debate about the history of life. Those who rejected it wholesale, as Agassiz did, consigned themselves to increasing irrelevance.

AGASSIZ UNDER THE MICROSCOPE

So did Agassiz identify a genuine problem for Darwin's theory, a mystery, at least, waiting to be solved? If so, whatever became of this problem? And if not, how could such a brilliant and knowledgeable scientist, someone so steeped in the evidence, fall so far outside the mainstream of scientific opinion?

Historians of science in the post-Darwinian era have typically attempted to answer this later question by portraying Agassiz as a brilliant and respected scientist who nevertheless was too ossified to catch the new wave, a figure past his prime and mired in philosophical prejudice. Biographer Edward Lurie describes the Harvard naturalist as a "giant of the nineteenth century . . . a person deeply involved in his surroundings, a man who understood the possibilities of life with an uncommon awareness." Similarly, historian Mabel Robinson says that she long awaited a biography of Agassiz that "would re-create this man of genius and his headlong splendid race through life." He was, she said, "a man to remember because genius is rare," "an immortal Pied Piper." These scholars are merely echoing what Agassiz's contemporaries, even Darwin himself, said. "What a set of men you have at Harvard!" Darwin told the American poet Henry Wadsworth Longfellow. "Both our universities put together cannot furnish the like. Why, there is Agassiz—he counts for three." 29

Even so, many historians argue that Agassiz was too infected by German idealism to properly assess the factual basis of Darwin's case. According to idealist philosophers of biology, living forms exemplified transcendent ideas and in their organization provided evidence of purposive design in nature. Comments historian A. Hunter Dupree, "Agassiz's idealism was of course the basis of his concepts of species and their distribution," of his insistence that a divine or intellectual cause must stand behind the origin of each type.³⁰ The ship of science was transitioning from idealism to modern

empiricism. Agassiz had fallen overboard, since he had imbibed too deeply an outmoded idealism from his teacher, the French anatomist Georges Cuvier, and from philosophers like Friedrich Schelling, who "ran wild in trying to put all nature into a unified and absolute system of ideas." Agassiz wasn't merely wrong, Dupree explains, but an annoying obscurantist, actively fighting "against the extension of empiricism into natural history." 32

Edward Lurie offers a similar if somewhat more nuanced assessment: although "quite capable of making the most admirable scientific discoveries reflecting complete devotion to scientific method," Agassiz "would then interpret the data through the medium of what seemed to be the most absurd metaphysics." The very man who made "the most careful, exact, and precise descriptions" of the natural world would, in his generalizations from those observations, "indulge in flights of idealistic fancy." In short, Lurie thought that "Agassiz's cosmic philosophy shaped his entire reaction to the evolution idea."

As science advanced in the late nineteenth century, it increasingly excluded appeals to divine action or divine ideas as a way of explaining phenomena in the natural world. This practice came to be codified in a principle known as methodological naturalism. According to this principle, scientists should accept as a working assumption that all features of the natural world can be explained by material causes without recourse to purposive intelligence, mind, or conscious agency.

Proponents of methodological naturalism argue that science has been so successful precisely because it has assiduously avoided invoking creative intelligence and, instead, searched out strictly material causes for previously mysterious features of the natural world. In the 1840s, the French philosopher August Comte argued that science progresses through three distinct phases. In its theological phase, it invokes the mysterious action of the gods to explain natural phenomena, whether thunderbolts or the spread of disease. In a second, more advanced metaphysical stage, scientific explanations refer to abstract concepts like Plato's forms or Aristotle's final causes. Comte taught that science only reaches maturity when it casts aside such abstractions and explains natural phenomena by reference to natural laws or strictly material causes or processes. Only in this third and final stage, he argued, can science achieve "positive" knowledge.

During the late nineteenth century, scientists increasingly embraced this "positivistic" vision.³⁶ Agassiz, by insisting that the Cambrian fossils pointed to "acts of mind"³⁷ and an "intervention of an intellectual power," stood firmly against this new vision. For many, his reference to the work of a transcendent mind merely demonstrated that he was unable to abandon an outmoded idealistic approach. The train of scientific progress had left Agassiz behind.

AN OLD FOSSIL RECOVERED

Though clearly Agassiz did reject the principle of methodological naturalism, as it is now named, there are problems with portraying him as a fossil of another age. First, Agassiz was unsurpassed in his commitment to the empirical method. It is Agassiz about whom the story is told of the professor instructing one of his students to observe a fish for three arduous days, a story iconic enough that it is reprinted in freshman composition textbooks. In the story, the student, Samuel Scudder, pulls out his hair trying to see anything new about the slimy creature, wondering why Professor Agassiz is torturing him with this "hideous fish." But in the end Scudder breaks through to new levels of observational depth and precision. Mabel Robinson notes that if such teaching methods seem less revolutionary to contemporary readers than they did to Scudder, that's because Agassiz trained an army of able young naturalists who took his method to other universities, and they in turn passed them on to their students, themselves future professors.³⁸

William James, the founder of American pragmatism, extolled Agassiz's commitment to empirical rigor in a letter he wrote to his father while on an expedition with Agassiz in 1865 to South America. In the letter the young man commented that he felt a "greater feeling of weight and solidity about the presence of this great background of special facts than about the mind of any other man I know,"³⁹ a storehouse of precise data made possible by "a rapidity of observation, and a capacity to recognize them again and remember everything about them."⁴⁰ James would eventually enter the field of psychology, but he took with him the empirical approach to problem solving that Agassiz had modeled so impressively.⁴¹

As Lurie concedes, Agassiz's stature among American scientists grew out of his unrivaled knowledge of geology, paleontology, ichthyology,

comparative anatomy, and taxonomy. So passionate was Agassiz for the particulars of the natural world that he began organizing a system of information-sharing among naturalists, sailors, and missionaries around the world. He collected more than 435 barrels of specimens, among them an extremely rare group of fossil plants.⁴² In a single year, Agassiz amassed more than 91,000 specimens and identified close to 11,000 new species,⁴³ making Harvard's natural history museum preeminent among such museums in the world.

He also appears to have gone to great lengths, literally and figuratively, to assess *On the Origin of Species* empirically, going so far as to make a research voyage retracing Darwin's trip to the Galápagos Islands. As he explained to German zoologist Carl Gegenbauer, he "wanted to study the Darwin theory free from all external influences and former prejudices." ⁴⁴

The idea that religious or philosophical prejudice compromised Agassiz's scientific judgment raises other questions. As historian Neal Gillespie explains, Agassiz was "second to no man in his opposition to sectarian religious interference with science."45 Moreover, Agassiz showed himself perfectly willing to accept natural mechanisms where before supernatural intervention had been the preferred explanation. Since he regarded material forces, and the laws of nature that described them, as the products of an underlying design plan, he saw any creative work they did as deriving ultimately from a creator. For instance, he assumed this was the case with the development of embryos: he attributed their natural evolution from zygote to adult as a natural phenomenon and considered this no threat to his belief in a creator. 46 He also readily accepted the notion of a naturally evolving solar system.47 He thought a skillful cosmic architect could work through secondary natural causes every bit as effectively as through direct acts of agency. The marginalia in his copy of On the Origin of Species suggest that he had this same attitude concerning biological evolution. "What is the great difference," he wrote, "between supposing that God makes variable species or that he makes laws by which species vary?"

A third problem with the official portrait of Darwin's chief rival concerns Lurie's suggestion that Agassiz was a master of particulars, but not of generalizing from those particulars. The historical record suggests otherwise. For example, Agassiz was the man who ably generalized from a wide array of particular clues in his work on the ice age, winning over the geological establishment by demonstrating how a range of facts were best

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