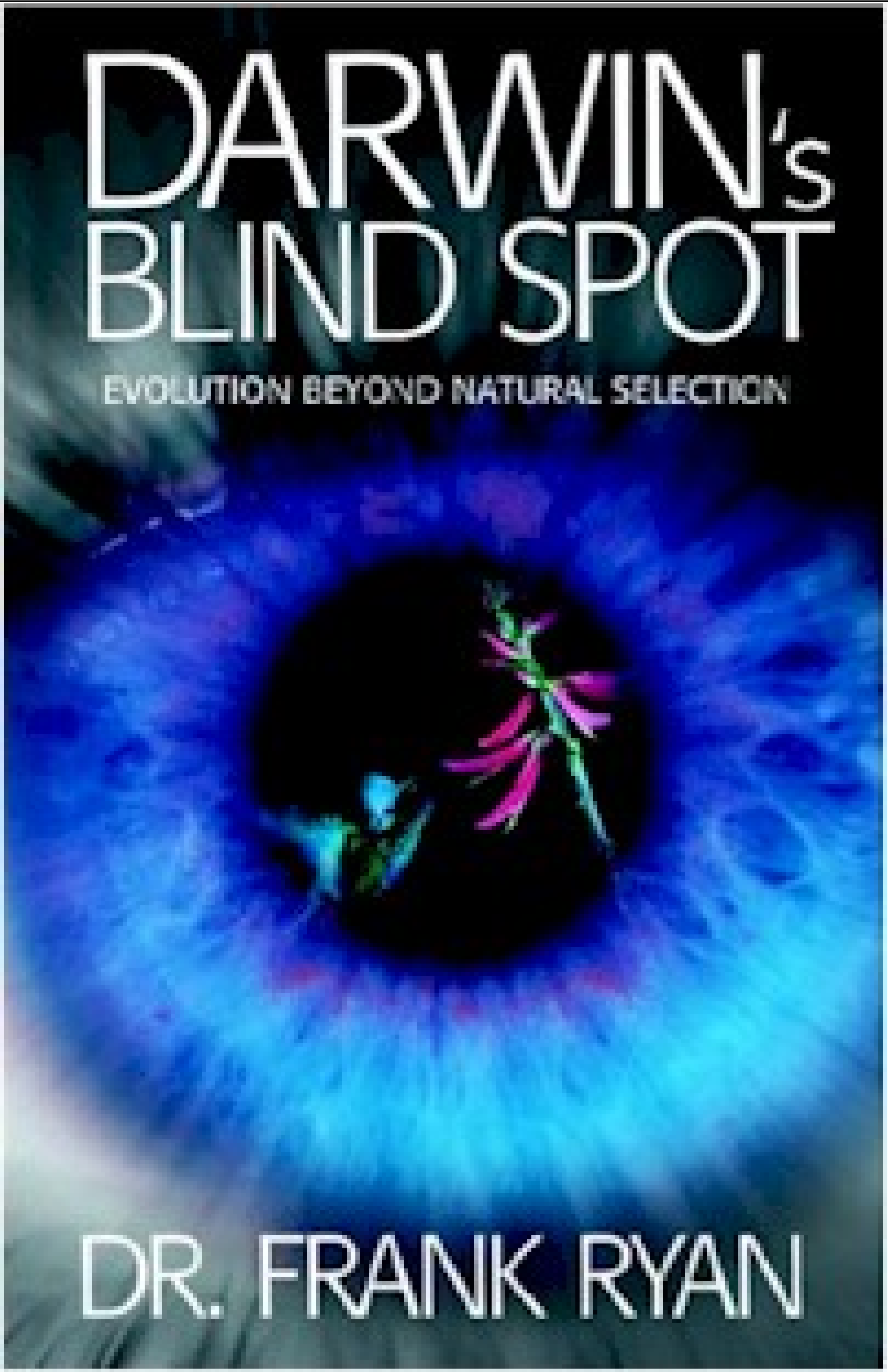

DARWIN's BLIND SPOT

EVOLUTION BEYOND NATURAL SELECTION

DR. FRANK RYAN

Books by Frank Ryan

The Forgotten Plague

Virus X

Taking Care of Harry

Darwin's Blind Spot

DARWIN'S BLIND SPOT

Evolution Beyond Natural Selection

Frank Ryan

For my sister Mary

and my brother Tony

• *Acknowledgments* •

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Why should all the parts and organs of many independent beings, each supposed to have been separately created for its proper place in nature, be so invariably linked together by graduated steps? Why should not Nature have taken a leap from structure to structure? On the theory of natural selection, we can clearly understand why she should not; for natural selection can act only by taking advantage of slight successive variations; she can never take a leap, but must advance by the shortest and slowest steps.

— CHARLES DARWIN,

The Origin of Species by Means of Natural Selection

• *Introduction* •

A MYSTERY OF NATURE

Our universe is a sorry little affair unless it has in
it something for every age to investigate . . . Nature
does not reveal her mysteries once and for all.
— SENECA, *Naturales Questiones,* Book 7

THE FIRST-CENTURY ROMAN philosopher and statesman Lucius Annaeus Seneca had the misfortune of serving as the emperor Nero's adviser. At sixty-nine, he was returning to Rome from retirement in Campania when he learned of the death sentence that Nero had imposed on him. Seneca met his fate calmly, embracing his wife and friends and asking them to moderate their grief through reflection on the lessons of philosophy. His contribution to civilization remains relevant today, especially his insight into the mysteries of nature.

Two millennia later, Kwang Jeon – today a distinguished research scientist in the department of biochemistry at the University of Tennessee at Knoxville – was privileged to investigate such a mystery. His investigation came about indirectly, as so many important discoveries do. Though Jeon would be much too modest to claim so, the mystery he unraveled lies at the very heart of the evolution of life on Earth.

One day in 1966, while studying the humble amoeba at the State University of New York at Buffalo, he experienced an unexpected calamity: his cultures of amoebae had been struck down by a plague. When he investigated, he found that they had been infected with an unknown strain of a bacterium later called the X-bacterium. He had no more idea where the infection had come from than the inhabitants of Europe had of the origins of the Black Death in the Middle Ages. “It just arrived, out of the blue. And suddenly, all of my amoebae began to die.”

To find out if this bacterium was really causing the plague, Jeon tried infecting a few amoebae with the bacteria; the amoebae died. In the everyday world of clinical microbiology, that observation would have been enough: the X-bacterium would have been seen as a parasite to be eliminated. Jeon would have eradicated all the infected amoebae and sterilized his laboratory before starting the weary process of rebuilding his cultures.

The great Louis Pasteur once made a perceptive statement about the role of serendipity in scientific discovery: “Chance,” he declared, “favors only the prepared mind.” In Jeon, a combination of personality and circumstance ensured that chance had favored such a mind.

Korean-born Kwang Jeon never intended to become a biologist. At junior high school he had wanted to become a doctor of medicine: “In my young mind, I felt that I wanted to help others and do research on illnesses.” The Korean War put an end to that ambition. But then he had a stroke of luck. In 1961, having just completed his master’s degree in Seoul, he was adopted by the British Council and sent to London, where he studied zoology at King’s College. After completing his doctorate, he became involved in research for the first time. Once again he ended up on a path he had not originally intended to follow. He was interested in embryology, but several people in the Department of Zoology happened to be studying the amoeba and he rather reluctantly joined their research program. His imagination was quickly captured. “When for the first time I actually saw amoebae moving under the microscope, I was fascinated.” Just so does the thrill of discovery often begin for a scientist.

Most of us are familiar with the amoeba from high school biology, though we soon forget about it, assuming it has no relevance to our lives. This single-celled creature that lives in the mud of freshwater streams and ponds is about a fiftieth of an inch across and consists of a nucleus, which contains the DNA, surrounded by cytoplasm. We might even recall from biology class that the amoeba moves by pushing out blunt, fingerlike processes known as pseudopods. The young and curious Kwang Jeon asked himself how a cell with no limbs or obvious skeletal structures could engage in purposeful locomotion. “I watched, in a perfect stillness, how they put out their pseudopods to move.”

He put amoebae into an environment with another creature, the green hydra. From the human perspective, hydras are minuscule, but they are predatory giants compared with amoebae. They also have a distinctive manner of feeding, pouncing on smaller life forms that come up close, stinging them with poisonous tentacles prior to devouring them. “I was expecting them to make a meal of my amoebae. But what actually happened was the hydra was gobbled up by the amoebae.”

Jeon’s love affair with the amoeba had begun.

One of the commonest amoebae in the world is *Amoeba proteus*. One strain of this species, known as the “D” strain, was discovered in Scotland in the early 1950s and subsequently found its way into research laboratories. Biologists were interested in the D strain because its tissues were known to contain some curious passengers: living particles of unknown origin with a striking resemblance to bacteria. While working in London, Jeon became very interested in the D strain of *Amoeba proteus*.

Like the hydra, the amoeba is a predator of even smaller creatures, such as *Colpidium,* enfolding them, together with a drop of water, within its pseudopodia. This process is known as phagocytosis. But the amoeba is prey to infection by certain bacteria, which it ingests in much the same way. The bacteria are resistant to the amoeba's digestive processes, and they infect it, causing serious ill health and sometimes death.

Some years later, Kwang Jeon moved to Buffalo, taking his beloved amoebae with him, to study under Jim Danielli, a world-renowned theoretical biologist who was interested in the phenomenon of cytoplasmic inheritance. The cytoplasm is the outer zone of the cell, separated from the nucleus by a double membrane. In the 1940s, a small number of scientists, including Danielli, began to doubt that all the hereditary programming was confined to the nucleus. To conventional biologists such doubt was outrageous. Since the close of the nineteenth century, biologists had been convinced that the nucleus was the sole repository of hereditary factors, so that any notion of cytoplasmic heredity seemed almost blasphemous. But those who took the idea seriously were very interested in finding out what actually happened when a microbe, containing its own genetic information, entered the cytoplasm of a cell whose hereditary information was supposedly confined within the nucleus.

Jeon's perspective on the plague that wiped out his amoebae was radically different from what might have been expected of a conventional microbiologist. Examining the lethal epidemic, he discovered that not all of the infected amoebae died. The precious few that survived did so even though their cytoplasm carried tens of thousands of living X-bacteria. It was clear that these few amoebae differed from all the others, possessing some inherited resistance to the plague bacillus. Intrigued, Jeon put aside his populations of uninfected amoebae, making sure they were protected from contamination, and began a new line of experiments, studying the interaction between the infected amoeba and the X-bacterium.

His experiments continued for many years, with some startling observations. After infecting an amoeba, the X-bacteria were resistant to the digestive enzymes that would normally devour them. Infection was followed by multiplication of the bacteria in such massive numbers that the host died, releasing large numbers of bacteria to infect others. This sequence explained both the lethality and means of spread of the plague.

But in the tiny minority of resistant amoebae, the process was very different. The bacteria took up permanent residence in the amoeba's cytoplasm, as if they had found a new home. And then the amoebae began to change. Newly infected ones — called xD amoebae — grew faster than those that had not been infected. They also seemed more fragile, being more vulnerable to starvation, overfeeding, and even minor temperature changes. They were so exquisitely sensitive to overcrowding that in normal colony densities the infected strain simply curled up and died. The hybrid life form might not have survived in nature because of this vulnerability.

Other changes in the xD amoebae were stranger still. The "genome" is the name scientists have given to the sum total of the genes that make up the heredity of any given species. For example, our human genome is made up of about 40,000 genes, parceled out in 46 chromosomes. At the time of Jeon's experiment, biologists thought that all of this genetic material was confined to the nucleus. Jeon wondered if the interaction between the amoeba and the bacteria was confined to the cytoplasm or whether there might be some nuclear component. Knowing that the amoeba's nucleus is remarkably tough, he placed two amoebae side by side and used a blunt probe to transplant the nucleus from one into the other. Normally the recipient amoeba would tolerate this transplantation very well. But when he transplanted a nucleus from an xD amoeba into a normal one, the grafted nucleus killed the recipient amoeba. This told Jeon that the infection was not affecting just the cytoplasm. It had changed the nucleus of the xD amoeba in some way that made it lethal to others.

Interaction with the amoeba also changed the bacterium. While initially up to 160,000 bacteria were found infecting a single amoeba, now, as some kind of equilibrium became established, the numbers of bacteria fell to about 45,000. Stranger still, if he removed the bacteria from the amoeba, they were no longer able to grow and reproduce in a laboratory culture. The bacteria could not survive outside the cytoplasm of their partner. At the same time, the host amoeba had become dependent on the bacterium for its survival. From an evolutionary perspective, something remarkable was taking place. Two utterly different species had melded into one, creating a new life form that was a hybrid of amoeba and bacterium. And the time frame was also interesting: the union was virtually instantaneous, although some further honing of the relationship continued afterward.

Some thirty-five years after it began, Dr. Jeon's experiment is still continuing, but already he has solved a little of the mystery. When I asked him if he had found any evidence for direct genome-to-genome interaction during the evolution of the hybrid, he replied: “We think, now, that we have a handle on some aspects of this question. For example, the bacteria somehow suppress a gene that would normally be essential for the amoeba.”

Many genes work by coding for the manufacture of proteins that play an important role in the body’s inner chemistry. In the hybrid amoebae an important enzyme was no longer being coded by nuclear genes, yet the enzyme was still in place and played a vital role in the hybrid’s chemistry. In Jeon’s words, “The enzyme must be coming from somewhere. Our feeling is that the bacterium is now supplying the gene for the enzyme.”

In evolutionary terms the implications of this experiment are iconoclastic, differing radically from the theory proposed by Charles Darwin. Darwin believed that evolution proceeds by the gradual accumulation of small changes within individuals, governed by natural selection. Competition between individuals within a single species was the driving force. But what Jeon has observed is the union of two dissimilar species in a permanent living interaction. Their genomes, comprising thousands of genes that had evolved over a billennium of separate existence, have, in the evolutionary equivalent of the blink of an eye, melded into one. This is an example of an evolutionary mechanism known as “symbiosis,” which is very different from Darwin’s idea of natural selection. Today the overwhelming evidence suggests that this interactive pattern has played a formative, if largely unacknowledged, role in the origins and subsequent diversification of life on Earth.

Symbiosis complicates the unitary viewpoint taught in biology classes, but it brings a wonderful new perspective on life in general and on human society in particular. From the very beginning, evolutionary theory has been applied to many fields of human affairs, such as sociology, psychology and even politics. Such interpretations, viewed from a Darwinian perspective alone, lead to an excessive emphasis on competition and struggle. Most damaging of all, the social Darwinism of the first half of the twentieth century led directly to the horrors of eugenics. The rise, once more, of social Darwinism is therefore a source of worry to many scientists, philosophers, and sociologists. Recently, some evolutionary psychologists have gone so far as to suggest that rape may be a natural behavior. A broader understanding of evolution, taking into account not only interactions between species but also cooperation within our human species, would introduce some sense of balance into our understanding of these highly controversial aspects of human societal and psychosexual behavior.

PART I

Controversies

The Struggle for Recognition

It is the customary fate of new truths to begin
as heresies and to end as superstitions.
— THOMAS HENRY HUXLEY, *Science and Culture*

• 1 •

THE ORIGINS OF LIFE

We are so obsessed with finding other life forms,
and with how life originated, it's as if life needs to
seek itself out. That is manifest in our thinking.
— PROFESSOR CAROLYN PORCO,
the Lunar and Planetary Laboratory, Arizona

ALL AROUND US, in the most ordinary aspects of our existence, is the weave of life, so familiar we easily ignore its beauty.

Life is the ultimate mystery, from the diversity of species that inhabit the Earth to the labyrinthine complexity of the cells that make it possible. But how did such wonders come to be? This question, perhaps the most fundamental one that humanity has ever asked, is what evolution is all about. It is hardly surprising that many people still believe that life could have been created only by an omniscient and omnipotent God.

On March 31, 1998, I attended an auction at Sotheby's in London of the collected memorabilia of George Cosmatos. I was particularly interested in lot 318, consisting of a faded sheet of paper, once the dedication page of a book, which contained just twenty-two words handwritten in Latin. This piece of paper, the size of a page in a paperback novel, sold for no less than $42,000, which, if you added the buyer's premium, amounted to a staggering $46,000. These are the words written on the paper:

> *Numero pondere et mensura Deus omnia condidit*
> *Hoc symbolum suum honoris et benevolentiae*
> *Gratia Dignissimo Doctissimoque huus Albi*
> *Possessori posuit*

In English it reads, "Number, weight and measure, God created all these things. I have placed this, my motto, for the honor and best wishes of the most worthy and learned possessor of this book."

The clue to the high level of interest in lot 318 lay in the signature below the motto: that of none other than the great English scientist Sir Isaac Newton. To Newton, God had created all life, with humanity at its apogee: we were no less than the image made flesh of our divine maker. In Newton's day, most of his fellow countrymen, including scientists, believed that the Bible was the revealed word of an all-knowing God, who had created the Earth as described in the Book of Genesis. Even today some scientists still believe in the essence of this creationist theory of the origins of life.

The greatest upheaval in the history of biology began very modestly when, on July 1, 1858, a paper on a new theory of evolution was first read aloud to "thirty-odd nonplussed fellows" at a meeting of the Linnaean Society of London. But this no more than lit the fuse for the time bomb that duly exploded a year later when, in *The Origin of Species by Means of Natural Selection,* the

English naturalist Charles Darwin expanded on the paper to propose a scientific basis for the origins of life. Darwin was not alone in proposing this theory; Alfred Russel Wallace shared its discovery with him. Subsequently Wallace came to disagree with Darwin in a number of ways, particularly the application of evolution to humanity. His mind wandered to teleological explanations and dalliances with spiritualism and even phrenology. Consequently, Darwin's interpretation assumed center stage, dominating every branch of evolutionary theory.

More than a century later, we have difficulty imagining the ripples his theory caused in the relatively tranquil pond of accepted belief at the time. Darwin insisted that life had not been created in six days, as stated in the Book of Genesis, but that it had come about through a process of gradual change under the influence of "selection" by nature. Such a revolutionary thought went far beyond the world of biology. Ernst Mayr, the Alexander Agassiz Professor of Zoology Emeritus at Harvard University, did not exaggerate when, in *One Long Argument,* he eulogized *The Origin* as "the book that shook the world." Out went determinism, based on creationist theology; in came concepts such as probability and chance. Almost at once our self-centered conception of our own existence was overthrown. Inevitably, from its inception, Darwin's theory of evolution encountered fierce resistance.

Darwin's ideas ran counter not only to religious faith but also to the prevailing scientific dogmas. His hypothesis was attacked and vilified by representatives of the established churches and, with equal force, by contemporary philosophers and many of his fellow scientists. The great English astronomer Sir John Herschel, regarded as the foremost physicist of his day, dismissed the probabilistic nature of natural selection as "higgledy-piggledy," while at Harvard the zoologist Louis Agassiz dismissed it as “a scientific mistake, untrue in its facts, unscientific in its methods and mischievous in its tendency.”

The problem with much of this counterargument to Darwinism was a flaw that one might call the “Procrustean stance,” after the Greek myth of Procrustes, who invited his victims to sleep on his bed. If they were too short, he stretched their bodies on his rack to make them fit, and if they were too tall, he chopped off their feet. In the 1650s, the archbishop of Ireland, James Ussher, had dated the act of creation to 4004 B.C., based on a meticulous reading of the Bible. For two hundred years this chronology was accepted, and the history of life was made to fit Ussher’s extrapolation — an example of the Procrustean stance. In looking to faith rather than logic, Ussher accepted the literal truth of the Bible without questioning it, assuming his conclusion from the very beginning.

Science, because it is based on logic rather than faith, cannot take such a Procrustean stance. I believe in science because it provides us with a rational system of beliefs based on human logic, backed up by experimental evidence and proof. I am not so arrogant as to claim that science is always right or that it can answer all questions. A sense of humility is as necessary to the scientist as it is to the truly devout. Few scientists today would argue that life was created in the forms we see now; rather, those forms are the result of a long and complex procession of changes we call “evolution.” Scientists and nonscientists alike think they know pretty well what is meant by this term. It is the process by which life first began on Earth and by which that fragile glimmer, over the billions of years that followed, changed and diversified until it gave rise to every form of life, from the simple bacterium to the most complex and colorful plants and animals that have ever lived, including humans.

In time Darwin’s theory became massively influential. Not only did it offer, for the first time, a logical way in which species could diverge from related species, it gave rise to an understanding of “common descent.” Today most educated people assume the truth of natural selection, which has been only a little modified by the century and a half since Darwin first described it. Perhaps understandably, the pendulum has shifted to the opposite extreme: today all too many scientists assume that natural selection is the *only* mechanism of evolution. But Darwin himself was more modest in his conclusion. In the closing sentence of the introduction of *The Origin,* he declared, 'I am convinced that natural selection has been the main but not exclusive means of modification'. Indeed, as Mayr makes clear, for decades after publication of *The Origin,* Darwin kept changing his mind about how species change and diversify. He was aware of inconsistencies difficult to explain on the basis of his original thinking. Where did the vast panoply of variation come from? Was the minor variation that arose from sexual mixing enough to give rise to new species?

From the outset, well-informed people had doubts about this. One of the leading contemporary botanists in America, Asa Gray, supported Darwin, yet he could not accept that natural selection was sufficient in itself to explain the evolution of life. “Natural selection is not the wind which propels the vessel, but the rudder which . . . shapes the course.” For Gray the only logical explanation was that a divine creator supplied the necessary variation, from which natural selection could choose the fittest individuals.

Some other biologists were beginning to think along different lines.

• 2 •

THE OTHER FORCE OF EVOLUTION

In view of this central position of the problem of
species and speciation . . . one would expect to
find in *The Origin* a satisfactory and indeed
authoritative treatment of the subject. This,
curiously, one does not find.

— ERNST MAYR, *One Long Argument*

WHEN BIOLOGISTS look closely at nature they cannot help but notice cooperative partnerships that do not comfortably fit with the competitive struggle that is central to Darwinian evolution.

The hermit crab finds its home in the vacated shell of a whelk or a mollusk. To protect its vulnerable hind parts, it curls backward into the shell, securing the entrance with its armored claws. One species of hermit crab carries a large pink anemone on top of its shell. Fish and octopuses like to feed on hermit crabs, but when they approach this species, the anemone shoots out its brilliantly colored tentacles, with their microscopic batteries of poisoned darts, and sting the potential predator, encouraging it to look elsewhere for its meal. This is a perfect example of living cooperation, since the anemone in turn feeds on the droppings and leftovers from the crab's meals. The crab and the anemone appear to recognize each other as partners by tuning in to individual chemical signals — the equivalent of a bloodhound's fine-tuned sense of smell. The relationship is so firmly established that when the growing crab has to find a bigger shell, it delicately detaches the anemone from the old one and transports it to their new home.

Coral reefs are replete with such partnerships. Off the coast of the Indonesian island of Sulawesi lives a beautiful shrimp, the bright yellow of a buttercup, that lives in partnership with a cream-and-purple-banded fish known as a gobi. The shrimp works hard all day turning over reef debris for food to feed them both, while the gobi watches out for the predatorial approach of scorpion fish that might eat the work-distracted shrimp. Certain anemones play host to clown fish, whose silver-striped bronze heads can be seen peering out of the deadly tentacles. Another crab cleans the surface of a sea cucumber and is rewarded with a sanctuary in the sea cucumber's bottom. Still other crabs live in a mutually supportive relationship with sponges that dissuade predators because of their evil taste. And in the Indian Ocean a type of boxer crab, with a luridly checkered coat of red, white, and black, carries pastel blue anemones in both of its claws. The crab advances on its territorial rivals, holding both claws out and wielding its weapons like living knuckle-dusters.

Many of these relationships are not merely functional but also spectacularly beautiful. Some 319 species of hummingbirds are widely distributed throughout the warmer parts of the Americas, with a variety of dazzling iridescence unmatched by any other birds. They live almost entirely on nectar, a dependence on flowers that has led to an amazing diversity of form and color. Specialized joints in their wings enable them to beat so fast they are practically invisible, their whirring motion producing the characteristic hum; this adaptation enables them to hover with pinpoint accuracy and balance in front of the appropriate flower. Their beaks are exceptionally long and shaped to fit into the flower head, while their tongues, which are even longer, reach down into the well of nectar at the bottom. One of the most beautiful of all hummingbirds is the violet sabrewing, widely distributed from Mexico to Panama, which has a curved bill that fits the columnia flower as accurately as a scimitar fits its scabbard. Every time the sabrewing visits a flower to drink, the columnia's stamens are positioned to dab pollen on exactly the right point of the bird's forehead, so that it fertilizes the next flower it visits. In this way, flower and bird are partners in an exchange of food for assistance with fertilization.

Partnerships like these have been a source of wonder since ancient times. In his *History,* Herodotus described how the plover was known to take leeches out of the mouths of crocodiles, noting that "the crocodile enjoys this and, as a result, takes care not to hurt the bird." Aristotle observed a similar relationship between a bivalve and a crustacean, and Cicero was sufficiently impressed to draw the moral that humans should learn from such friendships in nature. The Roman statesman and scholar was remarkably prescient, for these associations are more than mere colorful scenes in nature. They have important implications for the nutrition, health, and long-term survival of the interacting partners.

These relationships pose an enigma: how can creatures not conventionally attributed with "intelligence" behave in such complex fashion? As far as we know, when the hermit crab puts the anemone onto its back to carry it to their new home, the crab does not "think" about its actions — any more than the anemone pauses to consider whether riding on the back of the crab is in its best interests. Other hermit crabs of that species do the same, as do others of that anemone species. The behavioral patterns of both crab and anemone have been hardwired into the genes of the partners by evolutionary forces over long periods of time.

In my book *Virus X,* I introduced the simple concept of genomic intelligence to help explain this. Genomic intelligence allows us to see that a seemingly rational behavior pattern of any life form, from a virus to a hippopotamus, is really an instinctive mechanism governed by the creature's genetic makeup. Given the anthropomorphic loading of the term "intelligence," it was predictable that this concept would be misunderstood, and it was. Although some might argue that genomic intelligence is no more than genetic programming, the concept is actually more subtle and complex. While an intelligent programmer creates a very specific computer program, genomic intelligence is not quite so fixed: on the contrary, evolution depends on its being able to change through various mechanisms. Genomic intelligence explains how behavior of a limited complexity is written into the genomes of crabs and anemones, enabling them to cooperate with each other in their daily lives and thus improve their chances of survival.

To biologists, such intimate relationships in nature pose an evolutionary dilemma. Darwinian selection is based exclusively on the individual's struggle for survival in competition with others of its own species. Here we find a pattern of evolution based on behavioral interactions between entirely different species.

An alternative approach to evolution began in the late nineteenth century, when the Swiss botanist Simon Schwendener became curious about the nature of lichens, those familiar growths that spread slowly over gravestones and rocks, somewhat floral in outline and often beautifully colored. Nineteenth-century biologists found lichens baffling. Initially they were thought to be primitive plants but when Schwendener examined them under the microscope he saw what appeared to be a combination of two life forms, a captive alga ensnared by fungal threads, or hyphae.

Schwendener could not imagine the two organisms, alga and fungus, living together in a mutually supportive relationship: instead he saw a master–slave relationship in which the fungus imprisoned the hapless alga and drove it mercilessly to work for its benefit. But when Schwendener first reported these findings to his colleagues, in 1868, he was derided and opposed. At this time biologists believed in a very rigid classification of life, based on the system put forward in the mid-eighteenth century by the Swedish botanist Carolus Linnaeus (Carl von Linné). Linnaeus invented the concepts of species and genus, founding the first system of logical classification, or taxonomy, of life. In the Linnaean system each life form was assigned to a single species, and the dual nature of lichens threatened this logic. It is not difficult to see why Schwendener's fellow lichenists were appalled by his claims of a bizarre union between a "captive algal damsel and a tyrannical fungal master."

In 1994 Jan Sapp, professor of the history of biology at York University, in Ontario, published the book *Evolution by Association,* which has become a landmark in the history of the study of symbiosis, which is known as symbiology. In analyzing the formative history of this discipline, Sapp describes how "a neutral term was required for symbiosis that did not prejudge such relationships as parasitic." In 1877 a German botanist, Albert Bernhard Frank, coined the term *Symbiotismus* to cover all relationships in which two different species lived on or in one another. This concept of a living association between species interested Anton de Bary, who had set up the first two institutes of botany in Germany and was the editor of the journal *Botanische Zeitung*. In 1878, just a year after Frank's pioneering definition, de Bary redefined symbiosis as "the living together of differently named organisms," leaving the precise nature of the association vague enough to include parasitism, commensalism, and mutualism. He thereby made the first detailed scientific case for symbiosis as both a biological phenomenon and, implicitly, a major force in evolution. Posterity has forgotten Frank's priority, and de Bary is now acknowledged as having first discovered and extensively investigated symbiosis.

De Bary, Frank, and Schwendener faced formidable opposition from their more conservative colleagues. Nevertheless, news about the Swiss and German discoveries began to spread, and biologists in many countries became interested. In 1873 the zoologist Pierre-Joseph van Beneden had introduced the term "mutualism" during a lecture to the Royal Academy of Belgium. Three years later Beneden brought these interdependent relationships to popular notice in *Animal Parasites and Messmates,* in which he wrote about the intriguing dependency between pilot fish and sharks. He also drew attention to other well-known associations, such as the Egyptian plover that cleans the teeth of crocodiles, the crabs that live inside the shells of mollusks, and the crustaceans, called cirripeds, that hitch a ride on the backs of sharks and whales. Only four years after de Bary defined symbiosis, a Scottish biologist named Patrick Geddes wrote a key article in the British journal *Nature* on the subject of "animals containing chlorophyll."

Forty years earlier the German zoologist Max Schultze had demonstrated that chlorophyll, the green pigment associated with plants, was present in certain species of planarian worms. Other scientists had subsequently found chlorophyll in a range of animals, including the freshwater hydra, freshwater sponges, the common green sea anemone, and even a crustacean. Geddes was particularly interested in a group of marine organisms called radiolarians, most of which contained strange yellow inclusions. Most of his colleagues dismissed the inclusions as glands, but in 1871 a biologist named Cienkowski made what Geddes termed "a very remarkable contribution to our knowledge" in demonstrating that they were independent parasitic algae, capable of living on in amoeboid form after the death of the radiolarian. Other scientists found similar "parasitic" algae in many species of sea anemones. Nevertheless, confusion and controversy continued as to the exact nature of these curious bodies, so Geddes decided he would travel to Naples and investigate the mystery for himself.

Geddes was particularly interested in the so-called yellow anemone, *Anthea cereus,* which in reality was not yellow but green. Indeed, he described it as "a far more beautiful green" than the species of anemone he had worked with before. Proving unequivocally that the green color was derived from algae, Geddes was able to demonstrate that the algae produced oxygen inside the living tissues of the anemone.

"What," he asked, "is the physiological relationship of the plants and animal thus so curiously and intimately associated?" He found it hard to believe that what he was observing was nothing more than parasitism. "Everyone knows that the colorless cells in plants share the starch formed by the green cells; and it seems impossible to doubt that the endodermal cell of the radiolarian, which actually encloses the vegetable cell, must similarly profit by its labors." Geddes observed that when an aquarium of anemones was exposed to sunlight, the hitherto motionless creatures suddenly began to wave their tentacles about, as if stimulated by the oxygen in their tissues. Moreover, he was well aware that just as the algae were producing starch that might be useful for the anemone, the waste products of the anemone were "the first necessities of life for our alga." The parasitic interpretation made no sense. If the alga was merely a parasitic invader, it should weaken its host, yet *Anthea cereus* was one of the most successful of all anemones.

When very different life forms evolve over millennia in close proximity to one another, some will come to influence one another. As Geddes went on to explain in his article and in two subsequent books, such cooperation was commonplace in nature.

Throughout the remaining years of the nineteenth century, this theme was taken up in a number of studies in which the most unlikely partners were found "living together" in mutually dependent relationships. It was the innovative German botanist Albert Bernhard Frank who made the most important of these discoveries, one that would radically alter our understanding of plant evolution.

In the 1880s the government of Prussia was interested in the cultivation of truffles, which were relished as a food delicacy throughout Europe. The Department of Agriculture and Forestry commissioned Frank to conduct scientific studies on the occurrence and development of these fungi. Little was known about truffles other than that they were usually found on or under the forest floor. The few facts that Frank could glean about them were very curious. Biologists tended to think of fungi as living on dead and decaying material, yet truffles seemed to occur only in and around the roots of living trees. Frank was also aware of an observation made by a botanist named Reess, who had noticed a bizarre union between the spreading threads, or mycelia, of a fungus and the roots of pine trees. In Frank's words, "From the outset these facts caused me to question whether true truffles also establish a mycelial connection with the living roots of trees."

At that time biologists regarded fungi in much the same way as they did bacteria: they were parasites. Botanists assumed that any involvement of a living plant with a fungus must therefore be an infection. Frank was far more open-minded than his colleagues in his research on truffles. That these fungi appeared to surround the roots of forest trees suggested an intriguing relationship. In a scientific paper published in 1885, he wrote: "Certain tree species . . . quite regularly do not nourish themselves independently in the soil but establish a symbiosis with a fungal mycelium over their entire root system. This mycelium performs a wet nurse function and takes over the entire nourishment of the tree from the soil."

Frank's astonishing revelations were derided in botanical circles; he had to fight to get his subsequent papers published. His findings, if true, would overturn the cherished beliefs of many senior botanists, notably the highly respected Theodore Hartig, who had, some forty years earlier, been the first to notice the root "mantle" of pine trees. He had assumed that this "Hartig net" was part of the normal root and failed to recognize its fungal nature. He went to his grave refusing to believe in the symbiotic union of trees and fungi.

Frank, meanwhile, conducted many further explorations into this curious, and wonderful, cooperation between fungi and trees. When he examined the roots of such familiar species as oak, beech, hornbeam, hazel, and chestnut, he found that the roots were actually composed of two different elements. The core of the larger roots was derived from the tree, but a mantle of fungal hyphae capped the stunted, club-shaped ends of these true roots. In many cases the mantle completely enclosed the root, forming such a closely woven covering around the growing tip that not even a root hair could escape. In looking at the tree roots, one saw only fungus. What appeared to be fine, filamentous root hairs radiating out into the soil were actually fungal threads growing out of the mantle. Frank did not believe that this was a parasitic infection. How could every tree in the forest be so grotesquely infected when the trees appeared to be perfectly healthy? He was convinced that the two very different elements formed some intimate cooperation, a union of two different beings into a single morphological organ. Frank called this organ a mycorrhiza, from the Greek for "fungus-root."

As realization dawned that he had made a discovery of monumental importance, the excited biologist searched harder, extending his inquiries to every type of tree he could find. The more he looked for this curious partnership, the more he found it. Although the patterns of mycorrhizae varied somewhat from one species to another, all the forest trees he studied had these curious mantles of fungi around their roots.

Frank was aware that swellings called tubercles had been found in the roots of legumes and that some biologists believed the tubercles contained masses of symbiotic soil bacteria. The bacteria were thought to have the ability to fix nitrogen from the atmosphere, which then helped to nourish the plant. Frank had no doubt that the fungi that formed mycorrhizae with the roots of trees were similarly beneficial. Far from being a parasite attacking the trees, the fungus, Frank surmised, was attracted to the roots by a chemical especially secreted for the purpose. Once established, the fungus enlarged the root area of the tree, increasing its absorptive capacity 10,000- or even 100,000-fold. In effect, the fungus was the mouth of the tree, imbibing salts, water, and organic nitrogenous food from the humus, while the tree, in return, supplied the fungus with the carbohydrate it needed for energy.

Controversy raged over Frank's theories. Older botanists opposed him tooth and nail, but more open-minded biologists extended his discoveries, finding mycorrhizae in association with many other plants, including orchids.

Orchids are the most diverse family of all the plants, with more than 17,000 species. In the late nineteenth century orchids were a fashionable topic in botany and subjected to intense investigation. The new thinking about symbiosis provoked a flurry of interest and excitement, and by the 1890s, fungi had been found in symbiotic relationships with no fewer than 500 species of orchids. In time the symbiotic connection between fungus and orchid was found to be even closer and more interdependent than that of trees. The fungal symbiont actually penetrates the orchid roots and enters the living tissues, supplying every nutrient the plant needs, even carbon, which in every other plant is fixed by the photosynthesizing leaves. With delightful aptness, the French botanist Noël Bernard even showed that penetration of the orchid by the fungus was necessary for the seeds to germinate. He compared the action of the fungi on the orchid to that of spermatozoa on eggs.

The intimate cooperation between wholly different life forms — plants and fungi — is not only an amazing biological phenomenon but also a vitally important factor in the diversity of plant life on Earth. It should have been of enormous interest to evolutionary theorists, but few scientists were paying attention. In those formative years at the end of the nineteenth century, as the fundamental principles of biology were being hammered into place in laboratories around the world, Darwinian evolution took center stage. And as Darwinism, with its emphasis on competitive struggle, thrived, symbiosis, its cooperative alter ego, languished in the shadows, derided or dismissed as a novelty.

At this timely moment a Russian anarchist decided to throw his hat into the ring.

• 3 •

FROM ANARCHY TO COOPERATION

Somehow or other, life appeared on Earth. I don't
give a damn if somebody put it here, whether it was
a waste bin cast aside by some visiting spacecraft or
whether God fiddled with the chemicals and started
it. Somehow it started here.
— JAMES LOVELOCK,
BBC2 documentary "Life and Earth"

PETER KROPOTKIN was one of those rare individuals whose contributions to enlightenment are so original and inspiring that they blaze into a social prominence far beyond the confines of their scientific discipline. Though he was a member of the Russian nobility, Kropotkin's anarchist views repeatedly landed him in prison. Yet through every vicissitude he retained his delightful sense of humor. How could one dislike this prince-turned-anarchist who, still feeling himself constrained by courtesy, described how he took a stand against royal patronage: “A month ago I was invited to a banquet of the Royal Geographical Society in London. The chairman proposed, ‘The King!’ Everybody arose and I alone remained seated. It was a painful moment. And I was thunderstruck when immediately afterwards the same chairman cried, ‘Long live Prince Kropotkin.’ And everybody, without exception, rose.”

It is a tribute to this interesting polymath that today he is quoted not only by the symbiotic school of thinking but equally by the Darwinians.

Kropotkin’s interest in biology began when, at the age of eighteen, he first read Darwin’s *Origin of Species*. Abandoning the long-term military career his father had in mind for him, he adopted the short-term strategy of taking a commission in the mounted Cossacks of the Amur. This permitted him to organize an expedition to the unexplored vastness of Siberia, where he could follow his natural interests to his heart’s content. Meanwhile he was beginning to adopt a socialist attitude to political reforms. Although the czar had promised widespread improvements, Russia was turning away from social reform. Kropotkin took it upon himself to write reports on the conditions in the prisons of Siberia. The authorities responded by sending him on a series of exploratory journeys into the mountainous borderlands between Siberia and China, where he relished the opportunity of experience as both a field geographer and a naturalist observer. The young zoologist J. S. Poliakov, who had become his friend, accompanied him in exploring the uncharted territory between the Lena River and the upper reaches of the Amur. Inspired by Darwin’s theory of evolution, the two men were anxious to find evidence of the competition between animals that would help confirm it.

To their surprise, they found little such evidence.

We looked vainly for the keen competition between animals of the same species

. . . We saw plenty of adaptations for struggling, very often in common, against the adverse circumstances of climate, or against various enemies, and Poliakov wrote many a good page on the mutual dependency of carnivores, ruminants and rodents . . . We witnessed numbers of facts of mutual support, especially during the migration of birds and ruminants; but even in the Amur and Usuri regions, where animal life swarms in abundance, facts of real competition and struggle between higher animals of the same species came very seldom to my notice, though I eagerly searched for them.

On his return home the czarist police threw him into prison. He escaped, making his way to Britain, where he kept himself alive by writing notes and columns for the science magazine *Nature,* and for the *Times*. Traveling to France and Switzerland, he carried on with political agitation until he was once more arrested in France in December 1882. Imprisoned in the ancient St. Bernard's monastery at Clairvaux, he received from a sympathetic fellow scientist a copy of a lecture, entitled "On the Law of Mutual Aid," that had been delivered in January 1880 to a congress of naturalists in Russia. The lecture, by Karl Fyodorovich Kessler, a zoologist and dean of the University of St. Petersburg, confirmed Kropotkin's own field observations, posing the theory that "besides the law of mutual struggle there is in Nature the law of mutual aid, which, for the progressive evolution of the species, is far more important than the law of mutual contest." Kropotkin was inspired by this. Keeping faith with Darwin, he perceived in "mutual aid" a development of ideas that Darwin himself had expressed in *The Descent of Man*. "This suggestion seemed to me so correct and of so great an importance, that . . . I began to collect materials for further developing the idea."

Thus, when Thomas Henry Huxley in 1888 published the essay "The

Struggle for Existence" in the magazine *The Nineteenth Century,* Kropotkin had gathered enough evidence to refute it.

Huxley's essay, in retrospect, makes for uncomfortable reading. The tone is one of unrelenting bleakness, laced with his characteristic razor-sharp wit; the subject matter wanders from his views of animal and human evolution to the desperate situation of the poor, including the working classes toiling in the factories of the industrialized world. While statesmen and captains of industry declaimed against the curse of war and extolled the blessedness of peace and the innocent beneficence of industry, yet "so long as natural man increases and multiplies without restraint, so long will peace and industry not only permit, but they will necessitate a struggle for existence as sharp as any that ever went on under the regime of war."

Although the rule of logic is of central importance to science, scientists themselves are humanly prejudiced. Huxley was no exception, any more than Kropotkin was. No doubt the latter saw in evolution the rationale for his anarchist beliefs, in which a true society (each member giving what he or she could give, each receiving whatever he or she needed) lived in perfect cooperation without the need for central government. With this vision of utopia, he was offended by Huxley's bleak extrapolations of Darwinism to human evolution:

> For thousands and thousands of years, before the origin of the oldest known civilizations, men were savages of a very low sort . . . They preyed upon things weaker or less cunning than themselves . . . so, among primitive men, the weakest and stupidest went to the wall, while the toughest and shrewdest, those who were best fitted to cope

> with their circumstances, but not the best in any other sense, survived. Life was a continual free fight . . . The Hobbesian war of each against all was the normal state of existence.

At the time of Huxley's paper, there was very little fossil evidence of early humans. Paleontologists were still searching for the missing link. But Huxley certainly would have known of the fossils of one partial skeleton of an early human, which had caused a sensation when first found, just three years before the publication of *The Origin,* in a cave in the Neander Valley, near Düsseldorf, Germany. An Irish anatomist, William King, had first identified the find as evidence for a new species of humanity, *Homo neanderthalensis,* or Neandertal man. Those fossils were thought to show that early man was brutish in his proportions. The first real scientific appraisal of the fossils was made in 1911 by Marcellin Boule at the Museum of Natural History in Paris, who ignored the Neandertal's large brain and concluded that the creature had but rudimentary intelligence. He stated that the Neandertals were more apelike than human, with slouching posture and awkward gait, a back-sloping brow and prognathous jaw, exceptionally large teeth and no chin.

Even today the epithet "Neandertal" is synonymous with dim-witted brutishness. But subsequent excavations of Neandertal graves have shown plants, perhaps flowers or herbs, placed in a man's grave during burial, indicating that his family and group had almost certainly shown rituals of tenderness or religious belief when they buried him.

Kropotkin countered Huxley's view with a series of influential articles in the same magazine that had published Huxley's paper. These articles were later gathered together in the book *Mutual Aid: A Factor in Evolution,* in which

Kropotkin emphasized the importance of cooperation as opposed to aggression as the formative principle of evolution.

This was not a battle between symbiology and Darwinism. Kropotkin espoused Darwin's theory but believed that others had horribly distorted it. Indeed, Kropotkin quoted the combative Huxley's words to show how Darwin's vision had been twisted into an extreme parody: "From the point of view of the moralist, the animal world is on about the same level as a gladiators' show. The creatures are fairly well treated, and set to fight; whereby the strongest, the swiftest and the cunningest live to fight another day. The spectator has no need to turn his thumb down, as no quarter is given." Dismissing such unrelenting pessimism, Kropotkin described how the "numberless followers of Darwin" had reduced the notion of struggle for existence to its narrowest limits. "They came to conceive the animal world as a world of perpetual struggle among half-starved individuals, thirsting for one another's blood."

Kropotkin argued his case articulately and with much personal observation from his own researches. Referring to the underpopulation of life forms that was the distinctive feature of the immense plains of northern Asia, he explained: "I conceived since then serious doubts — which subsequent study has only confirmed — as to the reality of that fearful competition for food and life within each species, which was an article of faith with most Darwinians, and, consequently, as to the dominant part which this sort of competition was supposed to play in the evolution of new species." Kropotkin amassed a determined case for cooperation at all levels of nature, whether between members of a single species or between very different species. In fact, however much he claimed to be a believer in Darwin's theory, his championing of cooperation ran contrary to the ethos of Darwinism at that time.

In 1798 the English cleric Thomas Robert Malthus had written his *Essay on the Principle of Population,* which argued that society should take a laissez-faire approach to human suffering. Malthus contended that populations had a natural tendency to increase beyond any potential supply of food. He claimed that food supplies could increase only arithmetically while populations burgeoned in a geometric fashion and that an uncontrolled population expansion must lead to disaster unless there were "positive checks" in the form of disease, famine, and war. He included in his "positive checks" the general struggle among individuals and classes by which the weakest go to the wall. If order and balance were to be maintained, he argued, these processes should not be tampered with. Malthus's views had greatly influenced Darwin's thinking, and even more so that of his more extreme followers. Kropotkin's belief in cooperation as a force of life offered a counterbalance to the Malthusian view of the struggle for existence.

In particular, Kropotkin opposed the extrapolation of that view to human affairs, or social Darwinism, which was promoted by such respected figures as Spencer and Huxley. The social Darwinists set out to prove that although humanity, through its higher intelligence and knowledge, might mitigate the harshness of the struggle for survival, nevertheless the pitting of human against human obeyed a relentless law of nature. Kropotkin disagreed. "This view, however, I could not accept, because I was persuaded that to admit a pitiless inner war for life within each species, and to see in that war a condition of progress, was to admit something which not only had not yet been proved, but also lacked confirmation from direct observation."

In this perception Kropotkin was not entirely alone. In 1844, some fifteen years before the publication of *The Origin,* the German socialist philosopher

Friedrich Engels had published a treatise on economics in which he dismissed Malthus's theory on the grounds that it offered no convincing proof for the assumption of an imbalance between human population increase and food supply. Later on Alfred Russel Wallace, the codiscoverer of natural selection, also pointed out that Malthus had ignored the effects of political structure and social relationships. A member of the "established church," Malthus spoke from the same background of privilege as Darwin.

In *Mutual Aid,* Kropotkin's became the clearest voice raised in considered rebuttal of Malthus, Huxley, and Herbert Spencer. Beginning with evidence for cooperation among animals, he expanded this view to cooperation as an alternative strategy to competition in human society, declaring: "The mutual-aid tendency in man has so remote an origin, and is so deeply interwoven with all the past evolution of the human race, that it has been maintained by mankind up to the present time, notwithstanding all vicissitudes of history."

Tireless in his advocacy of such views, Kropotkin traveled widely, with two trips to North America in 1897 and 1901, lecturing on the importance of mutual aid in any interpretation of social biology. He believed that his was the true interpretation of Darwin's vision, for he accepted the importance of natural selection, and even the role of competition within and between species, questioning only its extreme Malthusian interpretation. But was Kropotkin's interpretation really closer to Darwin's than that of his bitter adversary Huxley?

Given his close friendship and long-standing relationship with Darwin, Huxley was far better placed to interpret Darwin than Kropotkin could ever be. Almost a century later, Lee Dugatkin, professor of biology at the University of Louisville, explained that Kropotkin was unable to see that Darwinians have difficulty in believing that individuals behave altruistically for the good of the larger group. Kropotkin believed that humans were naturally cooperative and that crime and violence were the results of governments that entrenched inequality; but as Dugatkin stated, “The literature on every sort of noncooperative act imaginable suggests that this view is naive — nice in principle, wrong in fact.”

However naive he may have been in his political views, in his grasp of the universal principle of cooperation Kropotkin was not mistaken. The failure of his contemporaries to take into account the balancing ethos of cooperation in relation to competitive struggle was to have terrible human consequences.

• 4 •

THE PRICE OF FAILURE

But it is quite certain that no existing democratic government would go as far as we eugenicists think right in the direction of limiting the liberty of the subject for the sake of the racial qualities of future generations.

— LEONARD DARWIN,
Cambridge University Eugenics Society lecture, 1912

TO UNDERSTAND the reasons for the failure of Kropotkin's views to be accepted, one needs to look at the nature of society and the prevailing climate of belief in the nineteenth century and earlier years of the twentieth century.

Malthusian laissez-faire attitudes that would seem brutal today were accepted in nineteenth-century British society. Class divisions were much more clearcut than they are today, and at the bottom of the social structure was a teeming underclass, largely but not exclusively urban, uneducated, and teetering on destitution. For men, voting rights depended on a certain level of wealth and property; women, regardless of class or education, had no right to vote. The great centers of learning, Oxford and Cambridge, were the exclusive fiefdoms of the established church. A professor of geology had either to be a clergyman, or, as in the case of Charles Lyell, whose geological theories had influenced Darwin, had to be vetted for religious orthodoxy by the archbishop of Canterbury and the bishops of London and Llandaff.

In many ways Britain was probably the most enlightened of the "civilized" Western countries. When Darwin published *The Origin* in 1859, slavery was still legal in the United States and it would take a civil war to bring it to a close. In this zeitgeist the more sympathetic and cooperative ethos of symbiosis struggled for critical recognition against the competitive theory of Darwinism. Although Darwinism challenged the creationist viewpoint of Christianity, it posed no threat to societal mores. On the contrary, it espoused and validated the status quo. Class divisions, like wars of conquest between countries, were seen as natural consequences of the evolutionary struggle. To understand how evolutionary theory interacted with social belief, it is necessary to consider how ideas spread.

In his pioneering book *The Selfish Gene,* Richard Dawkins, the Charles Simonyi Professor of Public Understanding of Science at Oxford, invented the highly relevant concept of the meme, arguing that most of what is unusual about man can be summed up in one word: "culture." Dawkins saw cultural transmission as analogous to genetic transmission and thus a mechanism of evolution in its own right. Language in particular can evolve much faster than organisms do, and nowhere is cultural transmission more important than in the form of "communicable" ideas. To describe the phenomenon of contagious ideas, he took the Greek word *mimeme,* for imitation, and reduced it to "meme," simply because it sounded like "gene." Memes govern people's behavior and the evolution of social belief. Once "infected," people will incorporate the meme into their lives, as a central doctrine of truth.

Scientists are not immune to memes, which also play an enormous part in the communication of scientific messages and, ultimately, in their acceptance into popular consciousness. And for scientist and nonscientist alike, no meme is more easily accepted than one that confirms existing prejudices.

At the time *The Origin* was published, imperialism was the dominant political and social ethos in Europe. A nation was defined as "one that could defend its own boundaries," and the Britain in which Darwin lived as a comfortable country squire was the greatest imperial power since the Roman Empire. Contemporary Darwinism was in perfect harmony with imperialism, which was seen as the national expression of the evolutionary paradigm, the fittest nation dominating all others through the quality of its culture and the struggle of its armed forces. What was the empire but the just reward for quality and struggle! One of the most important arenas in which evolutionary memes gain power is, of course, political philosophy. And while Darwin eschewed any extension of his views to politics, his successors had no hesitation in carrying his ideas into more controversial arenas. By the late nineteenth and early twentieth century, Darwinian evolutionary theory was being applied to the fields of education, law, philosophy, behavioral psychology (including the sexual aspects), and politics. Translated into sociology, it became the social Darwinism that so offended Kropotkin.

As early as January 1860, Darwin's English contemporary Herbert Spencer published the essay "The Social Organism," in which he drew parallels between living organisms and societies at various levels of complexity. Spencer, who was privately educated rather than university trained, was more a philosopher than a biologist; and it was only after Darwin published his much more rigorously formulated hypothesis that Spencer was able to tie biological evolution to society, challenging Darwin's metaphor of "natural selection" with his harsher expression, "the survival of the fittest." That succinct phrase would change the history of the world.

For evolutionary biologists, terms such as "struggle," "competition," and "fitness" have precise biological meanings that differ from their everyday uses. The core Darwinian concept of fitness is not brute physical strength or stamina but reproductive success. Darwin made this abundantly clear in *The Origin:* "I use the term Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny." This means that socially deprived parents who produce bigger surviving families are "fitter," in the evolutionary sense, than the most cultivated and brilliant members of society, if the latter produce few or no children. The eugenicists who turned this idea on its head, to favor the rich, cultivated, and brilliant, thus perverted biological theory for their own agenda.

Even Alfred Russel Wallace made the mistake of embracing Spencer's concept of "survival of the fittest" as a more objective conceptualization of natural selection, as indeed did the general public, for whom it seemed custom-made to fit all manner of prejudices and crackpot notions of ethnic and racial primacy.

Spencer himself stated explicitly that the rapid elimination of "unfit" individuals would benefit the human race, and thus the state should do nothing to relieve the conditions of the poor and needy. Quite apart from the cruelty implicit in this policy was the monumental arrogance of assuming that the only value of individual human beings was to further some culturally laden evolutionary purpose. For example, although his friendship with Mary Ann Evans, better known as the novelist George Eliot, might have persuaded Spencer that women had intelligence, he was convinced that their role was essentially reproductive; any attempt to educate them on a mass scale would overtax their brains and thus prove damaging to progress. A far more ruthless exponent of Malthusian thinking than Darwin himself, Spencer provided the defenders of laissez-faire capitalism with the intellectual justification to oppose state interference in market forces.

Spencer's world view was treated with suspicion by the more socially minded politicians in Britain, but it took a firm hold on the imagination of pioneering Americans. Peter Singer, DeCamp Professor of Bioethics at Princeton University, describes how the capitalist magnates used it to argue their case for the deregulation of industry in the Supreme Court. Andrew Carnegie used Spencerian thinking to justify the rat race of competition, "because it insures the survival of the fittest in every department." And John D. Rockefeller Jr. went so far as to use the analogy of the American Beauty rose, which could be brought to its full splendor and fragrance only by sacrificing the lesser buds. This wasn't an evil tendency in business but the working out of a law of nature and a law of God.

As Singer relates in his tiny jewel of a book, *A Darwinian Left,* "So often did the opponents of regulation appeal to Spencer, that Mr. Justice Holmes felt compelled . . . to point out that 'the Fourteenth Amendment does not enact Mr. Herbert Spencer's *Social Statics.*'"

Of course competition and struggle are normal elements of business, and Carnegie and Rockefeller were more than merely paradigms of capitalist selfish exploitation: both were liberal in temperament and generous philanthropists in practice. What their example reveals is the power of the Spencerian meme and the ease with which it so captured the public imagination. Spencer's editor Robert L. Carneiro openly admits that such Spencerian concepts have no basis in science. "Since they proclaim what ought (or ought not) to be done, they are tenets of political philosophy rather than scientific statements. As such one may freely reject them." But that is not how memes work. And while scientists today might object to this abuse of evolutionary theory, it was in fact scientists themselves, including some misguided representatives of the medical profession, who paved the way.

The notion that heredity can be controlled through breeding is ancient. Farmers and breeders have used breeding techniques for thousands of years to improve the yield of domesticated animals and plants for human use and consumption. The question inevitably arose whether humans could direct the evolution of their own species toward goals that might be defined as "good" or "desirable." References to such improvement of the human stock by deliberate selection appear in the Old Testament and Plato's *Republic*. For many members of the British middle class, the question acquired new urgency as well as a respectable scientific validity when, in *The Descent of Man,* Darwin explained how his evolutionary theories applied to humanity. As in all of Darwin's writings, animals were described with perception and sympathy, but he was somewhat less discerning about people. It is difficult for a twenty-first-century reader not to take offense at many of Darwin's assumptions about the superiority of

Western, especially Anglo-Saxon, culture, and his patronizing references to so-called "inferior" peoples, which riddle the text. Equally objectionable are his views that medical and humanitarian programs were preserving the "unfit":

> We civilized men, on the other hand, do our utmost to check the process of elimination; we build asylums for the imbecile, the maimed, and the sick; we institute poor-laws; and our medical men exert their utmost skill to save the life of every one to the last moment. There is reason to believe that vaccination [of children] has preserved thousands, who from a weak constitution would formerly have succumbed to smallpox. Thus the weak members of civilized societies propagate their kind. No one who has attended the breeding of domestic animals will doubt that this must be highly injurious to the race of man. It is surprising how soon a want of care, or care wrongly directed, leads to the degeneration of a domestic race; but excepting in the case of man himself, hardly any one is so ignorant as to allow his worst animals to breed.

It seems incongruous to find such views being championed by a man who was described by his contemporaries as extremely modest and gentle, somebody who would go out of his way to avoid hurting the feelings of others. In mitigation, he added a paragraph explaining why we nevertheless feel we must give aid to the helpless. "Nor could we check our sympathy, even at the urging of hard reason, without deterioration in the noblest part of our nature." Unfortunately, urgings of "hard reason" would prove altogether more compelling to the eugenicists who followed Darwin than any appeal to the nobility in their nature.

The Descent of Man portrayed men as physically stronger and more intelligent than women, who are described as kinder and more sensitive. Thus, "Man is more courageous, pugnacious and energetic than woman, and has a more inventive genius.” Such prejudicial views of women were far from abstract considerations. They were employed, ruthlessly and systematically, to keep women in their place. Darwin himself supported the view that women should be excluded from meetings of the Geological Society.

The effects of such bigoted thinking are illustrated by the example of Beatrix Potter, who had devoted years of her life to the classification of fungi, in particular to the dual nature of lichens. When, in 1890, she attempted to speak about her observations at the Linnaean Society of London, she was barred from doing so. She suffered the further humiliation of having her uncle, the distinguished chemist Sir Henry Roscoe, present her findings at a meeting from which she was excluded. When similar obstacles were placed before her research in the British Museum and the Royal Botanical Gardens, she abandoned any hopes of a career in science, taking up instead the writing of her famous series of children’s books.

Indeed, it seems at times that every prejudice of Victorian Britain finds expression in Darwin’s book. Under the heading “Civilized Nations,” Darwin included the opinions of his friend William R. Greg, a fervent phrenologist and brash apologist for the labor practices of the Lancashire mill owners. Greg was thus afforded a respectable platform for his prejudiced opinions of the entire Irish nation. Thus Darwin quoted Greg, word for word:

> The careless, squalid, unaspiring Irishman multiplies like rabbits: the frugal, foreseeing, self-respecting, ambitious Scot, stern in his morality, spiritual in his faith, sagacious and disciplined in his intelligence, passes his best years in struggle and celibacy, marries late, and leaves few behind him. Given a land originally peopled by a thousand Saxons and a thousand Celts — and in a dozen generations five-sixths of the population would be

> Celts, but five-sixths of the property, of the power, of the intellect, would belong to the one-sixth Saxons that remained.

For Greg, who understood the implications of fitness, the evolutionary outcome made no sense. "In the eternal 'struggle for existence,' it would be the inferior and *less* favored race that had prevailed — and prevailed by virtue not of its good qualities but of its faults."

But Darwin's readers could console themselves with the Malthusian argument that a provident nature had evolved checks to "this downward tendency." Darwin duly listed the checks that nature had placed in the path of too high a birthrate among the poor, in particular the high death rate of young mothers and of their children during the first five years of life in their crowded urban hovels. And so, in a painful progression throughout *The Descent,* the prejudices of upper-middle-class English pomposity, in the guise of established knowledge, condemn to inferiority an extensive list of groups, including all women, the Irish, the physically and mentally afflicted, the poor, and indigenous people in all corners of the globe. Blacks were stupid, inferior, and lazy, as evidenced by the numerous references to "savages" and discussions as to whether or not the races of man constituted distinct and separate species, in which the "inferior vitality of mulattoes" might be seen as possible evidence of the "specific distinctness of the parent races." Summarizing the "various checks" on undesirable breeding, Darwin went on to state that if these "do not prevent the reckless, the vicious and otherwise inferior members of society from increasing at a quicker rate than the better class of men, the nation will retrograde, as has too often occurred in the history of the world." "Progress," he cautioned, "is no invariable rule."

Huxley, though so often portrayed as Darwin's bulldog, expressed it differently:

> It needs no argument to prove that when the price of labor sinks below a certain point, the worker infallibly falls into that condition which the French emphatically call *la misère* — a word for which I do not think there is any exact English equivalent. It is a condition in which the food, warmth, and clothing which are necessary for the mere maintenance of the functions of the body in their normal state cannot be obtained; in which men, women, and children are forced to crowd into dens wherein decency is abolished and the most ordinary conditions of healthful existence are impossible of attainment; in which the pleasures within reach are reduced to bestiality and drunkenness; in which the pains accumulate at compound interest, in the shape of starvation, disease, stunted development, and moral degradation; in which the prospect of steady and honest industry is a life of unsuccessful battling with hunger, rounded by a pauper's grave.

It is curious to reflect that the passage above, so radically different in tone from *The Descent,* was part of the essay that Kropotkin, the anarchist, so strongly condemned. Concealed under the gruff affectations of misanthropy and antisentimentalism, Huxley is making a case for working-class improvement through technical education. "There is, perhaps, no more hopeful sign of progress amongst us, in the last half-century, than the steadily increasing devotion which has been and is directed to measures for promoting physical and moral welfare amongst the poorer classes." Although he may have overstated the bestial nature of the struggle for existence, he did not present such behavior as a desirable norm in human society. On the contrary, he stood, in his own words, "like a man" and implored enlightened humanity to do everything in its power to oppose such natural tendencies. "The ethical progress of society depends, not on imitating the cosmic process, still less in running away from it, but in combating it."

It is not altogether surprising that when Darwin's book on human evolution was first published, it elicited little of the fierce opposition he had encountered twelve years earlier with *The Origin*. Indeed, it was readily accepted by a society in perfect tune with its message, quickly selling a second edition that netted its author £1,500 — "a fine big sum," he boasted to Henrietta, his daughter, offering her £30 for her labors in helping him.

Sadly, though acknowledged both a genius and a genial man, Charles Darwin did not altogether rise above the prejudices of an English gentleman of his day.

Some years prior to publication of *The Descent,* Darwin's cousin Francis Galton became so convinced by the type of argument put forward by Greg that he decided humans must control their own evolutionary future. Galton pioneered the application of statistical methods to the study of heredity and founded the scientific discipline now known as genetics, a laudable achievement. Unfortunately, he is better remembered for having extrapolated Darwinism into a much more controversial arena.

In 1869 Galton published *Hereditary Genius,* in which he purported to show that "it would be quite practical to produce a highly gifted race by judicious marriages during several consecutive generations." In 1883 he took these theories a major step further when he published *Inquiries into Human Faculty,* coining there the term "eugenics," which he defined as the theory and practice of improving the human condition from a genetic point of view. There are some beneficial applications of eugenic thinking, for example our modern genetic counseling services, which allow informed decision making about various inherited risks without societal or professional pressure. However, the prevailing class misconceptions and racial and ethnic prejudices were extremely influential to eugenicist thinking. Poverty and criminality, for example, were linked, and the essential underlying cause was considered to be bad heredity.

In 1907 a twenty-one-year-old widowed Englishwoman, Sybil Gotto, with Galton's help, founded the Eugenics Education Society (later the Eugenics Society) in Britain, with the purpose of "promoting those agencies under social control which might improve the human race." As the historian Pauline M. H. Mazumdar makes clear, its interests were more social than biological. Galton defined the practical applications of eugenics as "the science of improving stock, which is by no means confined to questions of judicious mating, but which, especially in the case of man, takes cognizance of all influences that tend in however remote a degree to give the more suitable races or strains of blood a better chance of prevailing speedily over the less suitable than they otherwise would have." To promote these aims, he endowed a research fellowship and chair in eugenics at University College, London, both of which were, in the early years of the twentieth century, held by Karl Pearson, a brilliant mathematician who helped pioneer statistical methods in biology. Pearson never actually joined the Eugenics Education Society, preferring to keep his academic distance. Nevertheless, he took Galton's ideas to new extremes, believing that environment played little or no part in human mental or emotional qualities. Negative eugenics now had an evangelist.

Pearson accepted the earlier prejudices toward the poor as constitutionally inferior — they were “a breeding isolate on the margins of the human race” — and their negative morals and degenerate physical qualities made their high birthrate a threat to future civilization. Assuming that such moral and physical qualities were hereditary, the members of the Eugenics Education Society concluded “that if the prolific breeding of this class were not controlled, pauperism and its associated undesirable qualities must necessarily keep on increasing until the direction of evolution of the human race was reversed.”

Although the Eugenics Society membership was not large, it included some of the most influential people in society. The Australian historian Lyndsay Farrall showed that 80 percent of the early members were listed in the *Dictionary of National Biography,* including the Reverend William R. Inge, future dean of St. Paul’s Cathedral, many prominent biological and social scientists, and a small but significant number of doctors. Even the contribution of the mathematician Ronald A. Fisher, who would play a leading role in the “synthesis” revival of Darwinism in the 1930s, was tainted by his ardent commitment to wholesale eugenic practices, which he somehow reconciled with his equally ardent Christianity. Eugenics was not, however, supported by the British medical establishment as a whole and was never accepted into any British university medical curriculum.

Nonetheless, the committed members of the Eugenics Society found it possible to demonstrate, “in chilling manner,” how pauperism was passed on from generation to generation. In lectures this process was illustrated with lengthy family pedigrees. Poverty was hereditary because the sons and daughters of the poor were themselves more likely to be poor. Included as evidence of degeneracy were medical conditions such as tuberculosis and epilepsy, which could be shown to run in families. Today we know that tuberculosis is not a hereditary disease but an infectious one, caused by the most lethal germ in history, *Mycobacterium tuberculosis*. Any child growing up in overcrowded, impoverished conditions in which a close relative was coughing up sputum containing the germ from morning to night was more likely than the rest of the population to contract the disease. Epilepsy, or a tendency to fits, affects 1 percent of the population, but its causative influences, often an otherwise minuscule scar in the brain, are hereditary only in a minority of sufferers. No serious person would consider Julius Caesar, Vincent van Gogh, Napoleon Bonaparte, Ludwig van Beethoven, or Charles Dickens as degenerates, although they are all believed to have suffered from epilepsy. Of course, for the eugenicists, there was a greater purpose in linking poverty, disease, and criminality to degenerative genetic causes: it meant that the "higher races" had a duty to make sure that future generations were not ruined by a progressive dilution with the more fecund "lower races."

In 1909, when Ronald Fisher went up to Cambridge to read mathematics, he came across Pearson's line of thinking. Two years later, Fisher helped found the Cambridge University branch of the Eugenics Society, one of many based in the British universities, including Oxford, Liverpool, Manchester, Belfast, and Glasgow, and extending to Australia and New Zealand. The meetings of the Cambridge branch, which were reported in detail in the *Cambridge Daily News,* capture the prevailing paranoia. At the inaugural launch, the Reverend Professor Inge expressed his fears that the "degenerates" of the urban proletariat "may cripple our civilization," as they had that of ancient Rome. The second public meeting was a "lantern" lecture by R. C. Punnett, professor of genetics at the university, who issued a call for action in words that are hard to reconcile with this otherwise avuncular historian of the early days of genetics: “We may object to the way in which God made some people; we may decide the world would be better without them. But it must be done calmly and without prejudice, in the clear light of reason, and not under the cloak of righteousness or of doing a thing that is pleasing to any but ourselves.” Punnett was not calling for these degenerates to be put down like unwanted dogs but for the elimination of their kind by the enforced control of their future breeding.

The third public lecture to the Cambridge branch was delivered by none other than Darwin’s son, Major Leonard Darwin, who later, as president of the Eugenics Education Society, strongly supported Fisher in his eugenics aims and his mathematical career. (So central was Fisher to the Cambridge branch that the eugenics meetings came to an end soon after he left the university.)

While many members of the British Eugenics Society supported charitable causes, promoting the education of the poor and fighting the scourge of alcoholism, it was inevitable that Pearson, as a respectable academic and a man of high intellectual ability, would give credibility to the many others who were committed to half-baked notions of the “hereditary taint” of inferior classes and races. It is disturbing to consider the impact of memes based on extremist application of Darwinian principles on the minds of doctors, teachers, employers, judges, and those on the control boards of the workhouses.

In 1912 the British Eugenics Society hosted the first International Congress of Eugenics, open to the public. A series of charts explained genetic inheritance alongside Galton’s “Standard Scheme of Descent,” and as a paradigm of the “inheritance of ability,” one chart showed the family trees of the interrelated Darwins, Galtons, and Wedgwoods. The congress was attended by the faithful from many nations, including the American Breeder’s

Association, which put forward evidence that mental deficiency was hereditary. The largest section of the exhibition was taken up by the German contingent, which included such notables as Eugen Fisher, Max von Gruber, Ludwig Plate, and General von Bardeleben, the official genealogist to the German nobility.

By now the eugenicists in each nation had evolved their own notions of "ideal type." In Britain, for example, the pauper class was perceived as the greatest threat to civilization. In the United States, where social Darwinism became even more firmly entrenched than in Britain, wealth was equated with fitness and the poor were not to be assisted. Any attempt to change the domination of society by what came to be known much later as the WASP — or white Anglo-Saxon Protestant — would undermine the natural evolution of the human species. Theodore Roosevelt and Stephen B. Luce are judged to have supported a militaristic foreign policy on social Darwinian grounds, and the eugenicist Charles B. Davenport urged selective breeding to eliminate the physically and mentally infirm. When the American Eugenics Society was founded in 1926, its members claimed scientific corroboration for the idea that the white race was superior to all other races. Races, in this sense, were assumed to be "pure" lineages that had evolved in isolation from one another. Even within the white category, American eugenicists considered the Nordic white superior, naturally including themselves. And the undesirables with high birthrates were the feeble-minded and criminal classes, who were filling prisons and long-stay hospitals at such cost to the nation. In Germany the "undesirables" were identified as the psychotics and psychopaths filling up the mental asylums. In all such prejudicial assumptions, the one commonality was that the existing ruling classes had already proved their superiority.

Darwin would have been horrified to observe how his biological theory had been misused to support negative eugenic policies being put into place in many countries, with the aim of improving the species by identifying individuals and couples carrying "inferior" genes.

Those judged undesirable were to be prevented from reproducing, while people carrying "good" or "beneficial" genes were encouraged to have children. Inevitably, such decisions, put forward by some self-serving and socially powerful group determined to impose its opinion on more vulnerable groups, were subjective and controversial. In the United States, as in Britain and elsewhere, studies purported to show that entire families were degenerate, having inherited "bad genes." It was claimed that immigrants to the United States from southern and eastern Europe were innately inferior and given to criminality. Laws, such as the Immigration Act of 1924, sought to restrict immigrants from areas with suspect gene pools.

By 1931 enforced sterilization of undesirables had been introduced by law into twenty-seven states in America, and by 1935 similar laws had been passed in Denmark, Switzerland, Germany, Norway, and Sweden — all countries with substantial "Nordic" populations. Enforcement of these laws led to the involuntary sterilization of people judged to be "insane, mentally retarded or epileptic," as exemplified by William Faulkner's great novel *The Sound and the Fury*. Other groups that were similarly violated included "habitual criminals" and "sexual deviants." As a medical student in Britain in the late 1960s, I came across a poignant example of such eugenic madness: a woman who was condemned to roam the grounds of a large mental hospital after her frontal lobes had been severed from the rest of her brain as a treatment for "moral insanity." Her moral insanity consisted of having had two illegitimate children.

Social Darwinism took on a far greater potential for evil when it was adopted as policy by a ruthless dictatorship. In Germany, which was impoverished and demoralized following World War I, the eugenics meme found its most receptive audience. Adopted as gospel by the National Socialist party, the idea was seeded into the population through a combination of unrelenting propaganda and utter ruthlessness, culminating in the barbarities of programmed genocide. Again and again, in the writings of those advocating such inhumane policies, the reader is left in no doubt where the moral authority for such actions originated. Thus, citing Adolf Hitler, “It is the struggle for existence that produces the selection of the fittest.” Regimes elsewhere were every bit as ruthless as Hitler’s National Socialist Party, including the Communist party in the Soviet Union, Pol Pot’s murderous policies in Cambodia, and the more recent genocidal tragedy in Rwanda. But these brutal killings were motivated more by political expediency and ethnic hatred than by eugenics. Even William H. Schneider, whose authoritative book on the French eugenicist movement tends to downplay the horrific implications, draws attention to the French eugenicist Georges Vacher de Lapouge, whose proposals “beginning in the 1880s, also contained an appreciation of the *possible far-reaching consequences* of Darwin’s and Galton’s ideas on heredity and human selection.” Altogether revealing is the title of the book by the French science historian André Pichot: *La Société Pure: De Darwin à Hitler*.

• 5 •

A CONFUSION OF TERMS

Biologists ridiculed the idea that groups of organisms might gain a survival advantage over other groups because they shared some beneficial trait. Now that is changing. We are starting to understand that evolution happens on a variety of levels.

— ecologist LYNN DICKS

EVEN AS THE EUGENICS SOCIETY was meeting in London, summer visitors to the coastal resort of Roscoff, in Brittany, might have observed a certain English gentleman behaving rather oddly. Walking at low tide across the golden beach, he passed scattered granite rocks before approaching the main brown belt of seaweed. Here he trod softly as he approached some dark green patches that glistened on the sand. Kneeling down carefully, he scooped up some of the green just before, astonishingly, the rest of it appeared to evaporate like magic from the warm surface of the sand. When, in response to the visitors' curiosity, he showed them his catch, they must have been exceedingly surprised.

The gentleman, Frederick Keeble, was a professor of botany at University College, Reading, and he was actually collecting not seaweed but minuscule worms of two species of the genus *Convoluta*. His listeners' dismay surely deepened as he explained that these two very lowly worms, no more than an eighth of an inch long, were not even segmented, as any decent high-class worm should be. But dismay invariably turned to interest as he explained why he was studying these creatures. The clue lay in their color, which he invited his listeners to examine with the aid of a magnifying glass. *Convoluta roscoffensis* was dark spinach green; *C.* paradoxa a brownish yellow. Indeed, these little "plant-animals," as Professor Keeble called them, were an odd composite of worm and plant. The otherwise transparent worms were packed with a brilliantly colored alga called *Platymonas,* which lived symbiotically within the tissues of the worms. The algae passed on the products of photosynthesis to the worms, which in turn donated their waste products to the algae.

Keeble might also have explained that nature abounded in such examples of symbiosis. Life was not merely an individual struggle for existence. The evidence for living interactions could be found everywhere if people cared to look.

Some ten years before Keeble began his studies at Roscoff, Patrick Geddes and J. Arthur Thompson had urged the world to take a more balanced view of biological reality. In the case of animals, hunger was only one of the driving forces of life. For all of life, procreation was of paramount importance, and it often involved mutual support between members of a species, with complex interactions between parents and offspring. Mutual support, they argued, was an important driving force of life. Recognition of symbiosis, the interspecies equivalent of mutual support, had been quietly growing. But obdurate Darwinians, if forced to acknowledge the existence of symbiosis, were determined to limit its importance.

In 1892 an American botanist, Roscoe Pound, speaking at a botanical seminar at the University of Nebraska, summarized the current status of symbiosis in the botanical world. His presentation so impressed his peers that it was subsequently published as a paper. After mentioning examples such as the relationship between humanity and wheat, the yucca moth and *Yucca,* and the familiar relationship in lichens between fungi and their algal hosts, he systematically downgraded the importance of symbiosis while advocating a Darwinian interpretation of all such phenomena. Pound, only twenty-three years old, no doubt represented the views of those who had taught him botany. But he was already director of the Nebraska state botanical survey and had recently discovered a rare fungus that was later named after him, *Roscopoundia.* Indeed, as Jan Sapp makes clear, Pound's opinions were important in a manner that went far beyond his youth.

"Who," he asked his seminar audience, "would not sympathize with those who derided de Bary's symbiotic descriptions of lichens!" Pound grudgingly accepted the reality of symbiosis in the plant kingdom, but he dismissed many purported examples of cooperation as "sheer exaggerations." Even if mutualism, for all "its seeming unreasonableness," could be shown to exist, it "does not exist in all lichens."

He reserved his utmost scorn for Albert Frank, the German botanist who had discovered mycorrhiza. "Frank asserts that certain species of algae have become so adapted to life in the lichens and so accustomed to it, that they have partially or wholly lost the power of independent growth. No examples of this, however, are certainly known." Again, referring to another of Frank's claims about lichens, Pound added, "It seems, like some other theories of Frank, which I shall have occasion to mention presently, if I may say so, decidedly 'fishy.'"

Microbes, Pound declared, were nothing more than parasites. Any perceived cooperation was a delusion resulting from superficial examination. The "*Rhizobia,* as Frank calls them," were another example of parasitic bacteria. As for Frank's mycorrhizal fungi, the notion that they cooperated with the trees or the orchids they infected was nothing more than "Frank's statements calculated to try our patience and credulity." Step by step, Pound undermined the extent and importance of Frank's discoveries, going so far as to side with Frank's colleague and most vehement detractor, Hartig — "a more sober and trustworthy writer than Frank" who "said the last word so far on Mycorrhiza in 1891." Although Hartig had admitted that some fungi were found around the roots of certain trees, "his conclusion is that they are of no use to the tree, and are probably injurious by taking nourishment properly belonging to the tree." Pound then gave a clue to his underlying thinking: "It would seem that they must do this, even were there mutualism between them and the roots — else why are they there?"

As we now know, Pound, like Hartig, was — one is tempted to say "Frankly" — mistaken.

The downgrading of symbiosis became a recurring pattern in the decades ahead. But in a single respect, Pound proved astute. As the aggressive-competitive ethos of Darwinism came to dominate evolutionary thinking, the semantic difference between symbiosis and mutualism became increasingly confused. Mutualism is a form of symbiosis in which benefit is conferred on all of the contributing partners. But symbiosis, in de Bary's original definition, is much wider in scope, including parasitic, commensal (that is, doing neither good nor harm to each other), and mutualistic relationships.

In the highly volatile politics of the second half of the nineteenth century, politicians and social reformers opposed to the aggressive-competitive ethos of Darwinism looked to mutualism in nature for an alternative philosophy. Inevitably, the concept became even more confused, as biologists and nonbiologists alike used the term to denote any loose kind of cooperation, not only between dissimilar species but also between members of the same species. Mutualistic ideas led to the growth of working-class organizations, such as trade unions and "friendly societies," which pooled resources to help one another. Such socialistic developments, in particular their links to trade unions, provoked increasing anxiety in the ruling classes. In time this trend would change the political spectrum in Britain, leading to the formation of the Labour Party. It will come as no surprise that it was also the left, and Marxist groups in particular, that put up the most effective challenge to the dominance of eugenics in the study of human genetics.

Mutualism, in the eyes of some people, became identified with notions of anticapitalism. It is little wonder that a biological phenomenon tinged with such social implications was no longer discussed in polite capitalistic society. Pound, perhaps, was a creature of his place and time.

Fortunately, not all Americans adopted a negative view of symbiosis. Albert Schneider, a lichenologist in Illinois, had a vision of symbiosis that went far beyond its shackling by Pound. In a seminal paper published in the first edition of *Minnesota Botanical Studies* in 1897, he opened with a challenging declaration: “All living organisms manifest a more or less intimate biological interdependence and relationship.” Schneider saw symbiosis not as a rare event in an otherwise Darwinian world but as a commonplace biological situation; it was the very abundance and variety of examples that confused the issue. Acknowledging that even among the experts opinions varied as to what symbiosis meant, he redefined and classified its various manifestations.

For Schneider the only “true symbiosis” was an interaction between species at the physiological level. The intimacy and intensity of such a relationship would inevitably change the chemistry and even the physical makeup of one or both symbionts. Moreover, he saw that such a change must be controlled and passed on in a hereditary manner. Suddenly a new clarity of vision appeared. Schneider realized that symbiosis was far more than a curiosity in nature: it could create important evolutionary change.

In attempting to prove his theory, he faced the fact that symbiosis was more complex, and therefore harder to grasp, than Darwinism, a difficulty that would repeatedly hinder the understanding of this phenomenon. There was a wide range of symbioses. Although parasitism was an extreme form, it had to be included within the overall definition, even if this type of living interaction might lead to the destruction of one partner, the host. Mutualistic symbiosis, in which each symbiont possessed some property the other benefited from, was one of the most interesting forms, for it suggested that the survival potential of the interacting partnership might amount to more than the sum of the individual partners living alone. Take the lichens: the coming together of fungus and alga led to the creation of a composite life form that was better able to adapt and survive in a variety of environments than were the individual symbionts separately. Lichens are widespread in distribution from the tropics to the polar regions and are found in the lowest valleys as well as on the highest mountain peaks. In Schneider's view, symbiosis was best understood in the terms de Bary had first defined it: a living together of dissimilar life forms.

Schneider was certain that symbiosis could sometimes lead to changes in the structure and chemistry of the symbionts' bodies. Did such changes make possible the appearance of new tissues, new organs — even new forms of life? This question would be proposed, over the first two decades of the twentieth century, by a number of biologists, such as the Russians Andrei S. Famintsyn and Konstantine Merezhkovskii.

Famintsyn, the founder of Russia's first laboratory of plant physiology and a professor of botany at St. Petersburg University, became convinced, while investigating mutualistic symbioses between algae and other life forms, that he was observing major evolutionary change. What if the cells of every plant and animal on Earth had evolved from the symbiotic merging of smaller living organisms?

Over many years, Famintsyn struggled to investigate this question by extracting and attempting to grow chloroplasts, the organelles within plant cells that enable the leaves to capture the energy of sunlight. In a paper published in 1906 he claimed that although he had failed to grow chloroplasts, he had managed to extract and grow other organelles from the living cells of "lower animals." These, he thought, must have derived from free-living microorganisms that had made their homes inside the cells. He was now convinced that all of life had begun as "consortia" of simpler life forms.

Only a year earlier, Famintsyn's colleague and bitter rival, Merezhkovskii, working at the University of Kazan, had declared the symbiotic nature of chloroplasts. In 1910 Merezhkovskii coined the term "symbiogenesis" to signify evolutionary change as a result of symbiosis. Both Russians went on to perform a great many experiments, looking for hard evidence that the cell, and therefore all "higher" forms of life, derived from the symbiotic union of smaller life forms. Their experiments led to some limited successes, but these Russian symbiologists were no more successful in convincing their Darwinian-minded colleagues of their theories than were symbiologists elsewhere.

A few enlightened biologists scattered over the world plowed their obstinate furrows in this lonely field. For these few there was a truly inspiring consolation: growing evidence that symbiosis really did constitute an evolutionary force, quite different from that proposed by Darwin, even if the world at large ignored their findings. Indeed, after decades of resistance to all challenges, the world was also looking at Darwinism with a growing skepticism. There had always been doubts and criticisms within the mainstream of biology; and, after Darwin's death, in 1882, those questioning voices slowly gathered momentum.

As science moved into the opening years of the twentieth century, Darwinism was in crisis.

• 6 •

DUELS AND GENES

Nothing could be happier than this invention
[survival of the fittest — Herbert Spencer's coinage]
for . . . giving vogue to whatever it might be
supposed to mean . . . It is the fittest of all phrases to
survive.
— GEORGE JOHN DOUGLAS CAMPBELL,
"Organic Evolution Cross-examined" (1898)

IN AUGUST 1904, the biologist William Bateson arrived in London to attend a meeting of the British Association for the Advancement of Science. Bateson was to be nominated president at the meeting, but he had not arrived in a state of contentment. On the contrary, he strode in prepared for battle, with a six-foot-long chart full of controversy rolled up and slung, riflelike, over his shoulder. Among the more distinguished members of the audience were two colleagues with whom he shared an intense mutual loathing. One was Karl Pearson, the patrician mathematician, one of the founders of modern statistics and a supporter of Galton's radical eugenics. The other was Bateson's former friend and senior colleague at Cambridge University, Walter F. R. Weldon. The hall teemed with eager undergraduates, whispering among themselves in anticipation of a battle. The stage was set for the climax of what Michael R. Rose, professor of evolutionary biology at the University of California, Irvine, has called "one of the most destructive episodes in the history of biology."

People assume that great discoveries arise fully formed in the mind of genius, but in fact most evolve over time, with the discoverers having to wrestle with and modify their ideas long after they first put them forward. Darwin was no exception to this. Throughout his life, he struggled with various aspects of his evolutionary hypothesis, often changing his views on certain aspects and extensively rewriting his books to accommodate the changes. Moreover, although his theory is often portrayed as the single idea of natural selection, in fact it is a composite of related theories.

Ernst Mayr, regarded as the foremost living authority on Darwin, has subdivided Darwin's overall concept into five related theories: the general concept of evolution; the common descent of all life on Earth from a single ancestral life form; the diversity arising from the multiplication of species; gradual as opposed to sudden change; and the action of natural selection acting upon genetic variation. Those theories had differing fates when it came to acceptance by biologists.

Although Darwin himself considered all of these theories integral to one common theme, most evolutionists picked and chose among them. Even among those who believed in Darwin's evolutionary hypothesis, the term "Darwinism" took on a range of different meanings.

A major difficulty lay in explaining the differences between offspring of the same parents and between offspring and their parents. These differences, or “variations,” were essential, according to Darwin’s theory, if nature was to have enough variety to select from. And “variations” had to be inherited by future generations if they were to lead, over time, to new species. In Darwin’s day nobody understood genetics, so he could only speculate that variation arose from a kind of “blending” of the pedigrees of the two parents. The first two chapters of *The Origin* are devoted to explaining how blending worked, both in animals and crops domesticated and bred by humans and in nature through the influence of natural selection. But over time, even Darwin became less convinced that blending was a sufficient explanation. In fact, in Mayr’s words, “The origin of this variation puzzled him all of his life.”

Another obstacle to general acceptance of his theory was Darwin’s insistence on gradual change. As he explained it in *The Origin:*

> Why should all the parts and organs of many independent beings, each supposed to have been separately created for its proper place in nature, be so invariably linked together by graduated steps? Why should not Nature have taken a leap from structure to structure? On the theory of natural selection, we can clearly understand why she should not; for natural selection can act only by taking advantage of slight successive variations; she can never take a leap, but must advance by the shortest and slowest steps.

Before publication of *The Origin,* some of Darwin’s stoutest defenders opposed his notions of gradualism. With what would appear great prescience to modern-day symbiologists, T. H. Huxley wrote to Darwin the day before the book was published: “You have loaded yourself with an unnecessary difficulty in adopting *Natura non fecit saltum* [Nature does not jump] so unreservedly." After *The Origin* was published, other supporters, including Francis Galton and the great Swiss embryologist Rudolf A. von Kölliker, urged him to modify his insistence on gradualism. In the words of Michael Ruse, "The appeal to large variations was certainly made more plausible because artificial selection working on small variations failed to produce specific changes, not to mention that no one had any direct evidence that natural selection in the wild changes one species into another."

Darwin, however, refused to budge. Like his critics, he believed that natural selection was only one of several forces driving evolution. But, impressed by the uniformitarian theories of the geologist Charles Lyell as much as by his own researches into human selection, he remained convinced that evolution depended on an incremental progression of small variations between individuals of the same species.

The diversity of life on Earth is staggering. More than 2 million species of plants have been named, and many more remain to be discovered. The total number of living species may be as high as 30 million, from the resilient chemosynthetic bacteria that take what they need for life from volcanoes miles under the ocean surface to the leviathans that for millions of years have swum over them. How could such diversity possibly have arisen from the relatively small amount of variation that might come from parental mixing? By the end of the nineteenth century, many scientists were openly skeptical of Darwin's theory.

Since the 1850s, biology had advanced a great distance, in terms of microscopic structure (histology), physiology, and biochemistry. Biologists were increasingly awed by the layer within layer of complexity in highly developed organs such as the eye and the brain. Even the simplest of creatures, such as the amoeba, turned out to be amazingly complex when they were studied at the level of microscopic and biochemical detail.

As knowledge of these fields grew, a number of eminent scientists were so awed by life's complexity that they doubted that any evolutionary theory was capable of explaining it. Skeptical creationists moved in for the kill.

One of these was the Swiss-American naturalist and geologist Jean Louis Rodolphe Agassiz, who had performed landmark work on glaciers and extinct fishes. Credited by some as the greatest teacher of biology of his day, Agassiz made no secret of the fact that he had little sympathy with Darwin's theory of evolution by slow and gradual changes selected by nature. Instead he taught his pupils that Darwin's theory was "a scientific mistake, untrue in its facts, unscientific in its methods, and mischievous in its tendency." Life, he claimed, came about through repeated acts of divine intervention.

Yet another attack came from studies of the fetus. Thomas Hunt Morgan was an American zoologist with a particular interest in embryology. From 1893 to 1910, he analyzed the patterns of the developing fetus with a view to understanding the governing mechanisms. He was a very knowledgeable scientist but, like most embryologists of his day, he found it difficult to explain how the remarkable embryonic adaptations could have evolved by the incremental addition of minute variations. At that time some evolutionists believed that the human fetus passed through all the stages of its previous evolution, a theory known as the "biogenetic law" and popularized by Darwin's German supporter Ernst Haeckel with the slogan "Ontogeny recapitulates phylogeny."

Scientists no longer believed that parental blending was the true mechanism of heredity. As an example, they pointed out that even if the blending of parental stocks gave rise to some kind of advantage in one offspring, the advantage would be diluted by half in every subsequent generation. Even more damning was the realization that blending could take place only through sexual reproduction. The earliest and longest period of evolution had involved simpler forms of life, such as the bacteria, which reproduce only by nonsexual means. The hereditary apparatus of bacteria did not undergo blending, so each offspring cell could only be identical to its mother. Yet bacteria also evolved. Nobody could offer a convincing alternative to blending, however, since genes and chromosomes were unknown and the central role of DNA was half a century into the future.

While heated debate was taking place in biological circles, August Weismann — a German biologist who would play a major role in the early understanding of genetics, in particular chromosome theory — became a passionate supporter of Darwin. He conducted a famous series of experiments on the markings of caterpillars, the shapes and colors of flowers, and the aquatic adaptations of marine mammals, using his findings to clarify and develop Darwin's theory. For twenty years he insisted that natural selection was sufficient to explain all of evolution. But leading evolutionists, including Huxley in England and von Kölliker in Germany, remained unconvinced, seeing Darwin's insistence on gradualism as an ideational blind spot. They believed that major jumps, resulting in changes all at once, must take place in evolution, a theory now referred to as "saltationism," from the Latin word *saltus,* which means a "jump."

That was exactly the argument that led to the confrontation in London in August 1904.

At the end of the nineteenth century, Francis Galton was the leading figure in the study of variation and a supporter of gradualism. His "Law of Ancestral Heredity" purported to show that an infinite potential for variety could arise from the blending of parental stock. Galton's thinking was taken up by Weldon, a close friend of Bateson's. After working happily together for years, however, Weldon and Bateson had a falling out. Half a century later, Bateson's assistant, R. C. Punnett (the geneticist who had lectured to the Cambridge branch of the Eugenics Society), recounted their story in a centenary address to the Genetical Society in Cambridge, outlining how it had all begun: "Both were convinced . . . that an attack must be made on the problem of [the origin of] species."

The problem between the two men was that Weldon, now a professor at Oxford, continued, like his friend Pearson, to accept Galton's theory of blending, while Bateson, more a naturalist than a statistician, became convinced that the variation necessary for evolution to work came from saltations. Pearson went on to develop statistical support for Weldon's gradualistic thinking, while Bateson took steps to confirm the saltationist perspective. Both were ambitious, combative men, and confrontation was inevitable.

With the gloves now off, Bateson gathered information from stockbreeders, bird fanciers, and horticulturists, and by 1894 he had accumulated enough material for a book, *Materials for the Study of Variation,* which was openly critical of Darwinian gradualism. Pearson and Weldon were incensed. Gradualism, based on the continuous variation afforded by blending, was so fundamental to their notion of Darwinism that they saw any criticism as a rejection of the whole concept of evolution. They fought Bateson with tongue and pen as viciously as Tennyson's bloody tooth and claw.

Four years earlier, while traveling by train to give a botanical lecture titled "Problems of Heredity," Bateson had happened to read some papers written thirty years before by an obscure Moravian monk named Gregor Mendel. Convinced by Mendel's reasoning, Bateson had rewritten his entire lecture.

Mendel's story is now well known. The abbot of an Augustinian monastery in Brünn, Moravia (now Czechoslovakia), he had a brilliantly logical mind, which led him, a farmer's son, to undertake highly original studies of the peas he cross-bred in the monastery vegetable garden. From these studies Mendel discovered the basis of what we now know as the laws of heredity. He found that certain characteristics of the peas were transmitted to the offspring in a predictable manner. These characteristics included tallness or dwarfishness, presence or absence of color in the blossoms or axils of the leaves, yellow or green color, and wrinkled or smooth skin in the peas. A single example will explain his line of reasoning.

When Mendel took the pollen from yellow peas and used it to fertilize the female parts of the flowers of green peas, the offspring peas were not a yellowish green, as one might have expected if parental characteristics blended. Instead they were all yellow. Even more intriguingly, when Mendel used the pollen from this new generation to fertilize the flowers of this same generation, the next generation of peas was no longer all yellow but a mixture of yellow and green, like the original parents. The ratio of yellow to green in that generation was not equal: there were three times as many yellow as green peas. By analyzing his results, Mendel showed that the inheritance of pea color could not be based on blending, as Darwin had believed; some *discrete* factors must be responsible for the two different colors. He had discovered what we now call genes.

Genes code for proteins, which become a part of the body's structure or play a part in its internal chemistry. They are the basic building blocks of heredity in much the same way that atoms are the basic physical units of everything in the world. We now know that some genes are "dominant," as was the gene that coded for the yellow color of Mendel's peas; some are "recessive," like the gene that coded for green color; and in some cases, both genes may express themselves, so the offspring exhibits an intermediary trait.

Mendel's findings, made as early as 1860, were of such fundamental importance that they still form the basis of our understanding of genetics today: we recognize that the genome, the genetic makeup, of any creature is composed of a discrete number of these building blocks. All that makes us human, as we have recently discovered, is a mere 40,000 or so genes, gathered together on 46 chromosomes.

Mendel reported his studies to the Brünn Society for the Study of Natural Science in February and March 1865, and his talks were published in the transactions of the society in 1866, just seven years after Darwin published *The Origin*. Although Mendel had read Darwin's book and had jotted down notes in the margins, Darwin was completely unaware of Mendel's experimental conclusions published in this obscure journal. Sadly, the truth is even more perverse than mere irony. Mendel corresponded with the distinguished Swiss botanist Karl Wilhelm von Nägeli and sent him his findings. But Nägeli, who shared with Pearson, Weldon, and Weismann an unshakeable faith in blended inheritance, did nothing to encourage the isolated Moravian monk, even misleading him by downplaying the importance of his work. Nägeli's prestige as a leading botanist guaranteed that nobody took much notice of Mendel's findings.

The unassuming monk was not alone in being cheated. In dismissing Mendel, Nägeli also cheated his hero Charles Darwin, who, had he but known of Mendel's experiments, would have found in them a much better basis for the hereditary aspects of his evolutionary theory.

On the train to his botanical lecture, William Bateson had realized the enormous importance of Mendel's experiments. Now, four years later, he felt ready to do battle in front of the crowded lecture hall at the meeting of the British Association for the Advancement of Science. Unfolding his six-foot chart, he talked about the evidence he had amassed in support of Mendel's discrete units of inheritance. He had repeated every one of Mendel's experiments with peas, confirming his results. He had found similar support for Mendel in experiments with mice. Where, he demanded to know, was the evidence of Pearson's Law of Ancestral Heredity?

The rest of the morning was given over to more experimental presentations.

Discussion moved on to inheritance in chickens. Bateson had slit open their unhatched eggs with his big, blunt-bladed knife, calling out to his wife, "Have you got that, Beatrice?" Loyal Beatrice would duly enter the details of down and comb, whether there was an extra toe or feathering on the leg, in the "Dead Book." Sweet peas were another hot topic of debate. Bateson grew thousands in his own garden, until his vegetable garden could no longer accommodate them, in spite of his wife's protestations that she needed her vegetables to keep the household alive. On then to the University Farm, where the experiments continued, flowers emasculated, their discrete hereditary characters crossed and recrossed. The results, read from the microscope perched on an old box from the farm, were entered in the book by Beatrice. All such experiments had further confirmed Mendel’s concept of particulate inheritance.

At the meeting Bateson pressed home his advantage until everyone adjourned for lunch. When they returned, the room was packed full; even the windowsills had been requisitioned. The battle between Bateson and his opponents resumed, as Weldon, with sweat dripping from his face, stood up and addressed the audience in a loud voice.

Then, near the end, Pearson proposed a three-year truce between the two sides in the heated debate. The chairman, Reverend T. R. Stebbing, a mild and benevolent looking figure, stood to speak, deploring the ill feelings that had been aroused. The audience started to fidget, anticipating a tame conclusion to so spirited a meeting. But then he remarked, “You have all heard what Professor Pearson has suggested,” adding, with a sudden swell of animation, “but what I say is let them fight it out.”

The battle, which would rope in those most English of passions, the breeding of racehorses and even the gentlemanly art of cricket, was indeed far from over. Nine years later, in *Problems of Genetics,* Bateson, with extraordinary insight, examined how saltations might give rise to new species: “If we could conceive of an [infectious] organism . . . which may become actually incorporated with the system of its host, so as to form a constituent of its germ cell . . . we should have something analogous to the case of a species which acquired a new factor.” (Insert in Refs: Bateson W, 1913. Problems of Genetics. Yale Univ Press, New Haven; 88. Quoted from Sapp; 126) Nowadays we regard Bateson as one of the founding fathers of genetics. It is ironic, therefore, to acknowledge that this was a proposal for symbiosis as a potential mechanism for evolutionary saltation.

As so often with symbiotic explanations, nobody appeared to notice. By the first decade of the twentieth century, uncertainties about the mechanism of hereditary change had had such a negative effect that belief in Darwinism was at its nadir. By 1900 even Weismann was forced to agree with his long-time opponents that Darwinian natural selection based on the variation that arose from sexual mixing was not enough to explain all of evolution. In the words of Ernst Mayr, “The voices of Haeckel, Weismann, F. Müller, and Darwin’s naturalist friends were merely cries in the wilderness, for the opposition to the mechanistic process of natural selection was almost universal.”

What was needed, and needed urgently, to settle the argument in favor of a Darwinian explanation, was a new understanding of genetically based variation.

In 1900, the same year that Bateson had read Mendel’s papers on the train, a Dutch biologist, Hugo de Vries, also had discovered Mendel’s work. But de Vries thought of a remarkable application that Bateson had never considered. What if the discrete hereditary factors (what we call genes) could change? De Vries put forward a new mechanism of variation: the concept of random change in a unit of inheritance. Opportunity for change exists when genes are copied during reproduction, when a random change in the coding of a gene might arise from an error in copying, which de Vries called a “mutation.” Logic would suggest that mutation was the natural ally of natural selection, providing Darwinian theory with the much-needed source of variation. But de Vries rejected natural selection and espoused an entirely different force of evolution. A convinced saltationist, he argued that mutations could produce a new species in a single leap, making natural selection redundant.

In time geneticists would confirm de Vries's theory of mutations, which occur at a low but fairly predictable rate. But today we know that a mutation affecting a single gene may have no effect at all, or it may decrease or increase the fitness of the individual in some way, usually to a very small degree. In time geneticists realized that most mutations are immaterial or even harmful. But occasionally one is "beneficial" in the evolutionary sense, and even though the benefit may be slight, a steady accumulation of such variations can cause significant change to a species. This realization took several decades to dawn; it wasn't until the 1930s, when a new mathematics of natural selection was put forward by R. A. Fisher and J.B.S. Haldane in Britain, by Sewall Wright and Theodosius Dobzhansky in the United States, and by S. S. Chetverikov in the Soviet Union, that the importance of de Vries's breakthrough was fully appreciated by mainstream biologists.

These scientists demonstrated that all that was required for selection of a mutated strain was that the mutation gave the offspring a 1 percent advantage for survival over others that did not possess it. Natural selection acting cumulatively on a steady series of these small variations could, over a long period of time, give rise to major evolutionary changes.

With this "synthesis" of Darwinism and Mendelism, Darwinian evolution reestablished its credibility. Today the majority of Darwinians perceive evolution as arising exclusively from the gradual accumulation of mutations and from sexual recombination, under the controlling influence of natural selection. This viewpoint, commonly known as the synthesis viewpoint or simply as "neo-Darwinism," has had an enormous impact on naturalists and experimental biologists, stimulating a new wave of evolutionary studies around the world. Indeed, for more than half a century, reductionist elaborations became the sole preoccupation of evolutionary biology, and the core philosophy of Darwinian competition was extrapolated to human behavior and psychology.

In symbiosis the mechanism of change is radically different from this Darwinian model. When two or more life forms interact, they bring together genomic and metabolic abilities that have already been honed by evolution. This interaction can involve a major evolutionary jump or saltation. Moreover, for Darwinians the mechanism of change (mutation) is essentially random and hence noncreative, while for a symbiologist, the mechanism of change is not random but a creative force in itself.

• 7 •

THE INNER LANDSCAPE

In October 1838 . . . I happened to read for amusement "Malthus on Population," and being well prepared to appreciate the struggle for existence which everywhere goes on from long-continued observation of the habits of animals and plants, it at once struck me that under these circumstances favorable variations would tend to be preserved, and unfavorable ones to be destroyed. The result of this would be the formation of a new species. Here then I had at last got a theory by which to work.

— CHARLES DARWIN, *Autobiography* (1876)

IN THE LATE 1990S Jochen Brocks and Roger Buick, of the School of Geosciences at the University of Sydney, teamed up with Graham Logan and Roger Summons of the Australian Geological Survey Organization in Canberra, to search for fossils in the sun-scorched wastes of the remote Pilbara Craton in northwestern Australia. They were not searching for conventional fossils. Instead they were looking for "molecular fossils" that could be used to date the earliest evolution of complex life from preexisting bacteria.

If you examine the structure of a human cell, you find that it has the same basic plan as all complex life forms on Earth, including plants, animals, fungi, and even the unicellular organisms formerly known as protozoans: it has a nucleus, enclosed within a double membrane that contains the hereditary material — the genes packed together in chromosomes — surrounded by the fluid-filled "cytoplasm," where most of the routine chemistry of life takes place. This elemental organization is called a eukaryotic cell. In the opinion of Ernst Mayr, the evolutionary transition from the humble bacterium to the complex eukaryotic cell — a quasi-miracle of integration and coordination — was the single most important step in the history of life.

Evolutionists wanting to understand how this process happened posed many questions, two in particular. How early in the history of the planet did the first eukaryotic cells appear? And how, from such simple beginnings, was it possible for such exquisite complexity to arise?

The Australian scientists addressed the first of these questions. Taking great care to avoid contamination, they used a diamond drill to cut through 700 meters of rock until they found what they were looking for in shales that had been deposited during the Archaean period, an extremely ancient epoch of the Earth's evolution. They made an important discovery. In layers dating back an astonishing 2,700 billion years, they found molecular markers of membranes found only in eukaryotic cells. In the words of their report in the journal *Science,* "The biomarkers we report are the oldest known . . . They are more than a billion years older than those from the Barney Creek Formation, previously the oldest well-characterized molecular fossils."

These findings, if confirmed, would have great evolutionary significance. The appearance of the eukaryotic cell, even in primitive form, some 2.7 billion years ago implies far too rapid an evolution than would be possible through

Darwinian gradualism alone.

In 1918, just five years after Bateson had imagined the evolutionary consequences of an infectious organism becoming incorporated into the germ cell of its host, a fifty-two-year-old French bacteriologist, Paul Portier, issued the most provocative challenge to evolutionary thinking since Darwin. In a book titled *Les Symbiotes,* he declared: "All living creatures, all animals from Amoeba to Man, all plants from Cryptogams to Dicotyledons, come about through the union of two different beings." He added: "Each living cell contains, within its protoplasm, formations which histologists call 'mitochondria.' To me these organelles are nothing other than symbiotic bacteria, which I call 'symbiotes.'"

Like the incredulous colleagues who first read these statements, we should take a mental step backward and consider the implications of Portier's claims.

He began with an observation made some thirty years earlier by the German physiologist W. Pfeffer. Only one life form on Earth, the bacterium, is capable of feeding independently: that is, it extracts life-giving energy from food that has not been processed by any other life form. Pfeffer called this independent nutrition "autotrophic." Portier saw in this fact an astonishing implication: since every other form of life is dependent in some way on food that has been processed by other life forms, then all of life must ultimately depend on the prior existence and continuing presence of these autotrophic bacteria.

In Portier's day, people took a very negative view of bacteria, which were known to cause tuberculosis, rheumatic fever, scarlet fever, puerperal fever, diphtheria, and bubonic plague. Publication of his book coincided with the end of World War I, when the war-torn populations of eastern Europe were ravaged by an epidemic of typhus, caused by a bacterium known as *Rickettsia* and spread by the body louse. This would eventually infect 30 million people and kill at least 3 million, while the pandemic of influenza, known as Spanish flu, carried off at least 20 million.

It was not altogether surprising that for the majority of scientists, as for the public, bacteria had only one role in life: a grim and evil role, as carriers of sickness and death. Any counterargument, that bacteria were often benign or even beneficial — let alone that they might be absolutely vital to life on Earth — seemed impossible.

Portier's book was received with incredulity and scorn. A year after its publication, his French colleague Auguste Lumière dismissed it derisively in *Le Mythe des Symbiotes*. Some of the criticism was warranted. For example, Portier claimed that mitochondria were the "ultimate units" of living matter. He set up experiments aimed at removing them from cells and he attempted to culture them in media, like any other bacteria. But Jan Sapp is convinced that Portier never went so far as to claim he could culture mitochondria outside the living cell, believing they had been adapted for life within the cell over eons of time. In Sapp's opinion, much of the subsequent criticism was misplaced, in part because Ivan Wallin, who could not read French, reconstructed some of Portier's statements as claiming that he had cultured mitochondria. Such was the unrelenting fury of microbiological orthodoxy that even thirty-seven years later, Paul Buchner, professor emeritus at the University of Munich and the greatest living German biologist, still felt the need to ridicule such notions, denigrating as "far-fetched" the hypothesis of those who believed the eukaryotic cell had evolved from the union of microbial forms: "Portier . . . began the controversy with his book *Les Symbiotes* (1918) . . . The wild flights of fancy he embarked on knew no bounds.” Buchner was no scoffing Darwinian. The world leader in symbiology in his day, he pioneered studies of symbiosis in the lives of insects.

In spite of setbacks, new evolutionary theories continued to emerge. The German biologists Andreas Schimper and Richard Altmann had also proposed that chloroplasts and mitochondria were symbiotic lodgers inside living cells. A fellow German, Friedrich Meves, attributed all cellular differentiation to these structures. From Buchner’s perspective, all “such ‘errors’ only served to retard our progress towards general understanding of symbiosis.” Buchner went on to make abundantly clear what his own more modest understanding of symbiosis implied: “Independently of such extravagant concepts, in clear-headed unassuming work, the science of endosymbiosis has been laid stone upon stone . . . For us who have remained aloof from such speculations, endosymbiosis . . . represents a widespread, though always supplementary, device.”

To shake the world, Portier and his German colleagues would have needed incontrovertible proof of the role of symbiosis in the origin of the eukaryotic cell. They just did not have it. And so the broad movement of science took no notice of such quaint notions as whole organisms physically merging.

In Portier’s day there were serious conceptual obstacles to the acceptance of symbiosis as a major evolutionary force. One of the most formidable was that symbiosis extended into so many kinds of relationships, from the interdependence of different types of bacteria to the great cycles of life, such as the circulation of oxygen in the atmosphere. And the symbiologists were scattered throughout many disciplines, working in isolation in different countries and even continents, with little or no contact. Above all, they lacked a coherent voice. But slowly, over the decades leading to the 1950s, progress in other branches of science would make biologists stop and think afresh about the prejudices against bacteria.

By the 1930s, in agricultural colleges such as Rutgers in New Jersey, microbiologists were taking a different view. They knew that vast numbers of bacteria inhabit the soil, where they play a vital part in the carbon, sulfur, and nitrogen cycles. Ecologists realized that if the bacteria on Earth were to be wiped out tomorrow, all of life, including humanity, would quickly follow. Even disease-causing bacteria, such as staphylococci, live, for the most part, in a benign relationship on the skin or in the nostrils of their human hosts. The most lethal plague in history, tuberculosis, kills only a tiny fraction of the people it infects. Even today, in the opening years of the twenty-first century, tuberculosis exists as a latent infection in 1.7 billion people worldwide, yet it causes clinical disease in only 8 to 10 million and death in 3 million. It is necessary to remind ourselves that all such infections imply an interaction between parasite and prey: in other words, they are symbioses.

In 1974 the pathologist Lewis Thomas published his award-winning *The Lives of a Cell,* in which he supported the radical idea that infectious disease might be included within the umbrella of symbiosis. Thomas disagreed with the notion, still prevalent even then, that symbiotic organisms were merely enslaved. Symbiosis, to Thomas, was not the predatorial relationship predicted by the Darwinism of the nineteenth century, but something else entirely: a relationship that “seems especially equable.”

In the popular series *The Science of Life,* the distinguished writers H. G. Wells, Julian Huxley (the grandson of T. H. Huxley), and G. P. Wells — all three convinced Darwinians — declared that many of the known symbiotic associations were actually driven by hostility. They examined a number of such symbiotic associations to show how they broke down under stress. As the situation changed, the nature of the interaction changed.

There was a good deal of truth in this statement. Mutualistic symbioses often evolve from parasitisms. Peter W. Price, professor of biology at Northern Arizona University, has even investigated and explained the selective mechanisms by which parasitism evolves into mutualistic symbiosis. Even after symbiosis is established, the interaction between the partners may sometimes involve a delicate balance to suit a certain environment, so that the balance changes if the ecological circumstances change. An example of this is found in the green hydra that lives in ponds and slow-moving rivers.

The hydra is green because of the presence of *Chlorella* algae within its cells. Angela Douglas, an evolutionary biologist at the University of York, in England, has made a careful study of this relationship, drawing attention to the fact that the hydra will survive even if the algae are bleached out by intense light. Comparing populations of green and bleached hydras under conditions of starvation shows that the symbiotic hydras survive in conditions where they have a good supply of light, whereas the bleached hydras die. But if there is a plentiful supply of food, the bleached hydras grow better. The explanation is that under starvation the algae provide the hydra with a sugar called maltose, which they manufacture using photosynthesis. But when the hydra has plenty of alternative food the maltose becomes unimportant, although the hydra still has to feed its algal partner. In other words, symbiosis may be useful much of the time, but under certain circumstances it can be a burden.

Even if this is true in certain cases, the overall concept remains. The modifications to an organism arising from natural selection are also derived from interaction with the environment: the modifications may fail or lead to further adaptation if the environment changes. For example, a lizard living in a desert climate will have adapted to a life of dry heat and scanty nourishment. If its desert ecology is subjected to a flood, this adaptation may no longer suffice, and those lizards that can swim best will be most likely to survive and to produce a new generation.

Any scientist who performs research in the field soon realizes that relationships are often messy and governed by multiple variables. Douglas sees the common denominator of symbiosis not as mutual benefit but as a novel metabolic capability acquired by one organism from its partner.

John Maynard Smith, emeritus professor of biology at the University of Sussex, and Eörs Szathmáry, of the Institute for Advanced Study in Budapest, both Darwinians, have noted, “It is a curious fact that one can kill aphids with antibiotics.” They explain that aphids live by sucking plant sap, which lacks certain vitamins. The aphids obtain the needed vitamins from symbiotic bacteria that are transmitted from generation to generation of aphids by penetrating the eggs immediately after fertilization. This symbiosis, which has existed for at least 50 million years, is an example of mutualism: neither aphid nor bacterium can live without the help of the other.

For many life forms, symbioses with microbes help guarantee the supply of essential amino acids and vitamins. For example, legumes, such as peas and clover, form symbiotic unions with nitrogen-fixing bacteria, known as rhizobia, around their roots. This symbiosis plays a crucial role in one of the great cycles of life, that of nitrogen.

Nitrogen accounts for 80 percent of the Earth’s atmosphere, but in this gaseous form it is not available for the myriad of metabolic processes that must incorporate elemental nitrogen. Nitrogen fixation is the essential step that makes the element available, yet this ability, widely distributed among the bacteria, is absent from all other organisms. Symbiosis between nitrogen-fixing bacteria and other forms of life offers an ideal solution. The bacterium gets the high energy it needs from its symbiotic host while the host gets nitrogen in a suitable form for its internal chemistry from the bacterium.

In 1927, nine years after Portier's contribution to symbiology, an American biologist took up the baton. Ivan E. Wallin, professor of anatomy at the University of Colorado School of Medicine, showed the crucial role of symbiosis in the biological structure and lives of many creatures, including corals, turbellarian worms, cockroaches, and even the Portuguese man-of-war. He also put forward new evidence, based on seven years of original research, that mitochondria really are symbiotic bacteria. Moreover, he asserted that bacteria are the true building blocks of life, "the primordial stuff" from which all higher organisms have evolved.

His arguments extended far beyond mitochondria. He proposed that symbiotic union between different organisms had led to the incorporation of chloroplasts into plants and that incorporation of motile bacteria had led to the locomotion of small organisms, such as *Euglena,* by means of the whiplike appendages known as cilia. He also suggested that the nucleus of the eukaryotic cell might have arisen from such a symbiotic union. Wallin went on to propose that the symbiotic inclusion of bacteria within cells might be a means by which new genes were added to the genome and that such genes might be transferred directly into the nucleus. This process would be a remarkable force for evolutionary change, radically different in nature from Darwinian theory. Indeed, Wallin believed that symbiosis and not Darwinian mutation was the explanation for the origin of species.

But it was difficult to explain certain aspects of how this type of evolution might work. For example, once the mitochondria or chloroplasts had been symbiotically incorporated into the cell, how were they transmitted to future offspring? This question — I shall call it "the enigma of heredity" — was a major hurdle to understanding and therefore credibility.

Wallin was well aware of the importance of such questions, but science in his day could not answer them convincingly. Like Portier before him, he encountered nothing but ridicule. Two of his colleagues declared that if mitochondria were in fact true living entities, it would "force a complete readjustment in our ideas of the organization of living matter and the applications to it of the laws of physics and chemistry." Wallin never wrote another paper on his evolutionary ideas.

In the same year that Wallin published his book on symbiosis, Hermann J. Muller published his first report on how the mutation frequency of certain genes in the fruit fly, *Drosophila,* could be increased 1,500 times, using heavy x-ray bombardment. Mutation became the fashionable research tool of genetics.

As we have seen, mutation was an extremely useful concept, giving Darwinians all they needed to revive their beleaguered theory. It provided a sound basis for the small increments of change necessary for nature to have a range of diversity to select from. In Muller's own words, the principle was reductively simple: "mutation, reproduction and the reproduction of mutation." And the finding that mutation itself could, in certain circumstances, be greatly accelerated gave an even firmer basis to natural selection.

Once again symbiosis was consigned to limbo.

• 8 •

THE ENIGMA OF HEREDITY

We are survival machines — robot vehicles blindly
programmed to preserve the selfish molecules
known as genes. This is a truth that still fills me with
astonishment. Though I have known it for years, I
never seem to get fully used to it.
— RICHARD DAWKINS,
preface to *The Selfish Gene* (1976)

THE PARAMECIUM is a single-celled life form almost as familiar to biology students as the humble amoeba. Familiarly known as the "slipper animalcule" because of its engaging shape, it can be seen as a grayish white speck moving slowly about in the water of ponds, where it feeds on the bacteria that digest dead leaves. It moves by means of rows of fine protoplasmic threads known as cilia, which lash at the water and enable it to swim and gather its food. In the 1940s this creature became a focus of great interest as a result of research conducted by Tracy Sonneborn, professor of genetics at Indiana University.

By that time it was becoming obvious that symbiosis existed in two broad forms: exosymbiosis (some call this ectosymbiosis), in which two or more species interact but remain separate, as in the partnerships of hermit crabs and anemones or the pollination of flowering plants by insects; and endosymbiosis, in which the interacting species actually combine physically, one, usually microscopic in size, entering the body of a second, usually much larger and referred to as the host. From the point of view of genetics, endosymbiosis posed the greatest challenge and thus became the focus of a great deal of research into what came to be known as cytoplasmic inheritance.

Sonneborn realized that the cytoplasm must play an important part in heredity and the physical makeup of the individual organism. As Sapp says, "We have genes that make proteins, but how do the proteins organize themselves into supermolecular structures? Are we supposed to believe that genes make whole cells? Or to put it another way: if I give you all the genes and you shake them up in a test tube with all the other cellular components, do you think you are going to make a cell?" He is perfectly correct in pointing out that if all we have is genes, no matter how much we shake them up with all the other cellular components, we are not going to manufacture a living cell.

In fertilizing the ovum, the sperm inserts its DNA into an existing cell, the ovum, which includes not only the DNA of the maternal line but also the maternal cytoplasmic structures. When the fertilized egg begins to divide, the cytoplasm, with all of its component organelles and organization, faithfully reproduces with it. This cytoplasmic reproduction is a distinct event from what goes on in the nucleus. The cytoplasm of the ovum can be viewed as providing a living template of cellular structure in which the nucleus, with its DNA, resides.

From the early days of theorizing about cytoplasmic inheritance, some evolutionists have wondered what this inheritance might really mean. In providing future offspring with a preexisting cytoplasm, with all of its component organelles, the ovum is contributing far more than its nuclear DNA. This cytoplasmic contribution was what interested Sonneborn. In his investigations of the genetics of the paramecium, he was setting out to contradict the most strongly held dogma of the world of biology: that the nucleus is the sole carrier of the genetic inheritance of the cell.

In one experiment, Sonneborn cut out a few rows of cilia and reimplanted them with the cilia facing in the wrong direction. Offspring paramecia, whether they arose through sexual or nonsexual reproduction, inherited this change of direction, and the change persisted through 200 generations. This kind of inheritance could not be attributed to nuclear genes. As Sapp explains, a "cortical" hereditary factor had been affected by outside influence, through mechanisms of cytoplasmic inheritance that are still largely unknown.

In another experiment Sonneborn studied the species *Paramecium aurelia*. Several strains of *P. aurelia* produce a poison that leaks out into the culture fluid, where it kills other sensitive species of paramecia. Sonneborn went on to mate killers with sensitives, a process that was possible only because the sensitives became temporarily immune to the poison during the act of mating. Mating and reproduction are often confused. In fact, they are not the same. Paramecia mate to blend nuclear genes, but they reproduce by the simpler process of binary fission. During mating, the parent generation shares its nuclear DNA, so each individual emerges with identical new nuclei while keeping its cytoplasmic structures exactly the same as before mating. If the killer and sensitive types were determined by nuclear genes, the parents should now be identical, as should all future generations. Sonneborn showed that not only did the parents maintain their traits of killer and sensitive after mating, but all subsequent generations inherited this difference: one mate still passed on its killer cells and the other its sensitive cells.

Another observation was even more revealing. Now and then two paramecia came together in a very different kind of mating, during which cytoplasm could be seen to cross from mate to mate across a connecting bridge. No nuclear material was involved in this. Yet after such conjugation, sensitive strains were changed into killers.

Clearly the hereditary factor that determined whether a paramecium was a killer or a sensitive was based not in the nucleus but in the cytoplasm. Sonneborn labeled this killer predisposition “kappa.” Whereas nuclear genes would express themselves regardless of the environmental conditions in which the organism lived, variation in the environmental conditions seemed to influence the behavior of this kappa entity. Even stranger still, although kappa appeared to be determined by cytoplasmic inheritance, it influenced the whole organism. For example, it caused the paramecium’s growth rate and even cellular divisions to be responsive to temperature and the available sources of nutrition. If the temperature was right and nutrition plentiful, killer paramecia ceased (temporarily) to be killers.

Another puzzling aspect was that the kappa entities appeared to reproduce independently of the reproduction of the organism as a whole — rather like mitochondria. Similar results were found in experiments with chloroplasts in *Euglena mesnili*.

It seemed that within the cytoplasm, and cohabiting with the organism, there were living entities that could be increased, decreased, or even eliminated entirely. Their elimination appeared to radically change the organism. To the Indiana geneticists, the conclusion was inescapable: some of the inheritance of the paramecium was stored and passed down to future generations through the cytoplasm. Sonneborn's experiments became the exemplars for others to follow.

At the base of every eukaryotic cilium and flagellum, the whiplike appendages associated with cellular locomotion, is a structure known as a "kinetosome." André Lwoff, at the Pasteur Institute in Paris, found evidence in single-celled creatures other than paramecia that the kinetosome could reproduce independently of any division by the cell as a whole. As with kappa in the paramecium, the environment influenced the kinetosome. In England, C. D. Darlington found the same capacity for self-duplication in centrioles, which play a vital role in mitosis. Self-replication was also found in mitochondria, chloroplasts, and many cytoplasmic bodies found in insects and plants.

But for Darwinians, convinced that the nucleus alone was the cradle of heredity, any such concept of cytoplasmic inheritance remained anathema. Sapp quotes the leading American biologist of the early twentieth century, Thomas Hunt Morgan, who aptly captured the prevailing view: "In a word the cytoplasm may be ignored genetically."

All such claims for cytoplasmic inheritance threatened evolutionary geneticists with the resurrection of what had once been the most formidable challenge to Darwinism, a rival they hoped was dead and buried.

In Paris, on December 18, 1829, an eighty-five-year-old naturalist died, blind and in penury, believing his work had been dismissed and forgotten by the uncaring world of science. Born of aristocratic parents, he had survived the terrors of the French Revolution to usher in the modern systematic approach to the study of nature. He had coined the term “biology” and, at the very least, had set in motion the conceptual revolution that was to follow. His name was Jean-Baptiste de Monet Lamarck and, for many French biologists even today, he, rather than Charles Darwin, was the true founder of evolutionary theory.

Darwin did not, of course, *invent* the concept of evolution. Varying notions of it had been around since the time of the ancient Greeks. But Lamarck popularized the concept some fifty years before Darwin.

Born in 1744, a time when belief in biblical creationism dominated Western culture, Lamarck intuitively grasped what we now call geological time. “Time,” he wrote, “is insignificant and never a difficulty for Nature. It is always at her disposal and represents an unlimited power with which she accomplishes her greatest and smallest tasks.” After years of studying plants and invertebrates, he put forward a theory of evolution in which life could be visualized as a series of staircases, from the simplest to the most complex. Humanity, in such a sublime and perhaps theologically inspired vision, was at the top of the uppermost staircase.

This same progression imbued his view of evolutionary mechanisms. Impelled by what he called “excitations” and “subtle and ever-moving fluids,” Lamarck thought that the organs of animals became more complex. Perhaps there was a first glimmer of “adaptation” as a result of natural selection in his belief that organs became progressively strengthened and more complex with repeated use or weakened by disuse. Certainly he was mistaken in imagining that such changes were then inherited to become the basis of evolution. Lamarck believed that offspring could inherit a parental character developed through environmental interaction during the parent's own lifetime. The notion of hereditary change arising from repeated use was, for example, Lamarck's explanation for the long necks of giraffes, which derived from straining to reach high branches. In the same way, a blacksmith's son might inherit stronger muscles from the occupational exercise of his father.

Lamarck suffered for the revolutionary nature of his theories and was reduced to the humiliating status of scientific outcast long before he died. But interest in his theories grew after his death, and many leading biologists came to accept his thinking. Darwin, for example, advanced Lamarckian arguments in parts of *The Origin,* and Spencer was a firm believer in Lamarckian inheritance for most of his life.

But Lamarck had no more understanding of the mechanisms of genetics than Darwin, and his outmoded concept of the "inheritance of acquired characteristics" was abandoned by science when the synthesis of Darwinism and Mendelism placed the evolutionary emphasis on nuclear genes. From the orthodox perspective, it did not support the symbiologists' case that evolutionary change arising from the coming together of two different species during their lifetimes sometimes depended on the inheritance of acquired characteristics.

Throughout the 1950s and 1960s, the enigma of heredity became the center of a great deal of controversy. Meanwhile, for proponents of cytoplasmic inheritance it became increasingly clear that proving their theory would provide new information on how, perhaps as long ago as 2.7 billion years, symbiotic mechanisms might have played an important role in the greatest evolutionary transition of all, the origins of the nucleated cell.

As the inheritance controversy moved closer to the boil, it was caught up in a tsunami of change that was rushing through the world of genetics. The discipline was expanding to include leading-edge microbiology and, particularly, biochemistry. In England the discovery by Francis Crick and James Watson of the structure of DNA stimulated a new wave of nucleus-dominated genetic research, confirming and extending the gene-centered laws of Mendelian inheritance.

During this same period, fascinating information was coming from the relatively new science of virology. An earlier generation of microbiologists had regarded the viruses that infect bacteria as nothing more than parasites, taking over the bacterial genome to produce new viruses by infecting and then rupturing the cell. But as knowledge advanced, it became clear that while many viruses behaved in this way, others did not kill the bacterium they infected but entered into a long-term union of genomes, thus offering an extraordinary potential for evolutionary change.

For example, some viruses transform the bacterium's ability to survive certain stressful conditions, such as the arrival of an antibiotic in its neighborhood. Because viruses and other gene-swapping mechanisms could readily alter bacterial heredity, it was becoming difficult to rigidly classify bacteria according to their hitherto accepted taxonomies. Yet infection and heredity were still being viewed as disparate processes. Infection was merely a destructive force, the antithesis to life.

It was hardly surprising that the world of genetics was becoming confused. In 1952, in an effort to rationalize this confusion, the future Nobel laureate Joshua Lederberg published an overview explaining why the nucleus could no longer be regarded as sacrosanct and why geneticists should consider a new idea of “infective heredity,” which included the potential of viruses to change the genetic pool of infected bacteria. In this paper Lederberg proposed the term “plasmid” to embrace all extrachromosomal genetic elements. A plasmid might be a virus or any of a number of other genetic packages comprising whole genes or parts of genes. Lederberg went on to show how such genetic elements could move from cell to cell — or from one organism to another. When plasmids entered the cytoplasm, their actions and subsequent evolution were symbiotic. At that time the great population geneticist Theodosius Dobzhansky was also considering the possibility that all of the hereditary components found in the cytoplasm were symbionts.

The evolutionary origins of mitochondria now moved center stage. Cytoplasmic inheritance had an obvious appeal to those promoting the idea that mitochondria had evolved through symbiotic incorporation of bacteria. For example, in endosymbiosis, in which one symbiont lives in the cytoplasm of its partner, the cytoplasmic symbiont could reproduce by binary fission, providing an independent mechanism of inheritance that could exist side by side with nuclear reproduction. Indeed, confirmatory evidence of this scenario was rapidly accumulating, with new research suggesting that mitochondria had retained at least part of their former bacterial genomes.

Genes in the cytoplasm! The Darwinian reaction was to dismiss this idea as nonsense, but the evidence in favor of it continued to grow. The Darwinians then argued that if genes were associated with these cytoplasmic inclusions, the only plausible explanation was that they had been borrowed from the nucleus. In 1950, when the Genetics Society of America held its golden jubilee at Ohio State University, the *Drosophila* expert Hermann Muller took the view, then prevalent among Darwinians, that if mitochondria and chloroplasts had genes, these were just genetic debris from some early evolutionary stages of the organism, before the primitive cell had sequestrated its genetic material in the nucleus.

Like most biologists of his day, Muller wanted to keep things simple: an autocratic nucleus, sacrosanct within its membrane, governed all of the genetic apparatus of the cell and controlled all the biological processes taking place in the cytoplasm.

But the truth was not so simple and elegant. The interdependence of organisms in symbiotic associations was so vague and wide-ranging that it blurred the boundaries of taxonomic definition: where did the individual organism begin and end if genetic material could arrive from beyond the cell walls and change an organism's heredity? But now Lederberg was reinterpreting Portier, declaring that all heterotrophs — in other words, all of life other than certain bacteria and green plants that could extract their nutrients from the non-organic environment — were "genetically insufficient." It was possible to construct a graded series of symbioses as genetic interactions, from the genes inhabiting a single chromosome, to plasmids, and even to extracellular (and extraorganismic) ecological associations with varying degrees of stability and specificity. Biological science would have to reappraise every great transition along the march of evolution, from the earliest beginnings of self-replicating entities to that most remarkable of sentient primates, humanity itself.

When Lederberg raised such possibilities, the scientific world was forced to take some notice. A formidable figure in microbiology and genetic thinking, he could not be dismissed in the way so many earlier symbiotic thinkers had been. But even Lederberg did not wish to proclaim this as anything beyond a possibility; as yet, nothing was certain.

As late as 1972, two biologists at the University of Indiana, R. A. Raff and H. R. Mahler, refuted all evidence for cytoplasmic inheritance in a paper titled “The Non-Symbiotic Origin of Mitochondria.” These authors claimed that mitochondria had never been bacteria. Rather, they had evolved from specialized invaginations of the cell membrane in the distant past, acquiring some genes from the nucleus through the mediation of a plasmid. Three years later, in a manner reminiscent of the dismissal of Portier by Lumière, they poked fun at the concept of mitochondria arising from bacteria in a book chapter entitled “The Symbiont That Never Was: An Enquiry into the Evolutionary Origin of Mitochondria.”

Even at this stage, in the words of Jan Sapp, “To call a particle a symbiont amounted to name calling.” What was now needed was a new, clear perception of the role of symbiosis that made sense in an expanding era of molecular biology. And the person who provided this leadership was Lynn Margulis, who would later become professor in the department of geosciences at the University of Massachusetts at Amherst. Although at this time she was no more than a graduate student, she was also a symbiotic thinker of great innovation. Equally important, she was a woman of courage and tenacity, prepared to stand up and fight from her corner against a skeptical and, from a symbiotic perspective, largely ignorant neo-Darwinian world.

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SYMBIOSIS COMES OF AGE

The writings of contemporary symbiosis researchers
are replete with episodes and anecdotes about how
their intellectual ancestors were ignored and
ridiculed by an unappreciative scientific community.
— JAN SAPP,
"Evolution by Association: A History of Symbiosis"

ONE DAY in 1991 Lynn Margulis presented a lecture to the American Association for the Advancement of Science. Her audience ranged from students struggling to come to grips with life's taxonomy to combative fellow leaders in the world of biology. Most biologists illustrated their lectures with attractive animals, birds, or mollusks, but the slides Margulis projected onto the screen were of the microscopic creatures called protoctists — a vast kingdom of nucleated microorganisms, including those formerly known as protozoans. These organisms had been the focus of her research for decades. She had long bemoaned the fact that the scientific world had so ignored this entire kingdom that only a few had names (amoeba, euglena, paramecium, spirogyra). In the words of John Maynard Smith, “She knows an incredible amount about strange beasts most of us don’t know anything about.”

Margulis began by warning her audience that the conventional systems of biological classification concentrated too much on the larger animals, creatures that rightfully should be classified as only a small branch of the subdomain of the eukaryotes. In part this incorrect emphasis was the reason evolutionary biology had become bogged down in dependency on neo-Darwinism. She went on to illustrate her point by explaining the diversity of microbial life, including predation, photosynthesis, communication, social organization, and motion. Suddenly, in discussing the evolutionary origins of eukaryotic life from bacterial precursors, she became openly combative.

“Neo-Darwinism,” she declared, “is misleading. I see no evidence whatsoever that these changes can occur through the accumulation of gradual mutations.”

Of course, many in her audience were neo-Darwinians. Exasperated by their silent skepticism, she issued a challenge: Would anyone care to name an unambiguous example of a species that had been shown to evolve by the building up of chance mutations? One man stood up to name a species of corn, only to be contradicted by another. Where, then, she asked, almost a century and a half after Darwin first put forward his theory, was the overwhelming evidence that gradual change brought about by the accumulation of chance mutations is responsible for the origin of species?

“See for yourself!” she proclaimed, projecting a slide of a “red tide” microorganism that lives on the surface of Finnish lakes. Visible in the cytoplasm of each translucent body were tiny bodies, the vestigial remains of a smaller microorganism called a cryptomonad. “Long ago,” she explained, “one of these guys ate but did not digest the other. Now they require each other to reproduce.”

She added, “I can give you a dozen of these examples — and you give me a type of corn . . . maybe. You give me maybe — I give you the evidence. So why do you think that you are right and I am wrong?”

In science, just as any other field of human endeavor, personalities become important.

Lynn Margulis first met the late astronomer Carl Sagan when she was fourteen and attending an undergraduate course at the University of Chicago. He was a graduate student with a physics degree and she was studying for her A.B. in liberal arts. She was charmed by Sagan’s single-mindedness. “He just taught us that we chickens could contribute to the scientific world, the scientific enterprise.” They married and later divorced. By the time she was pregnant with their son Dorion, Margulis had switched to biology, in particular evolutionary genetics. Unimpressed by the “overly abstract neo-Darwinian concepts” then promulgated almost as religious dogma in population genetics, she turned to genetic systems that other scientists were inclined to ignore: “The data on cytoplasmic genes fascinated me from the time I first learned about them.” Inevitably this interest carried her toward symbiosis and the controversy that surrounded it.

At college her instructors adopted a revolutionary attitude to teaching. Eschewing textbooks, they insisted that the pupils read scientists’ original papers, so they could discover for themselves the actual thinking of Newton, Galton, and Mendel. This single-minded approach would become important in Margulis's future career. In 1957 she moved to the University of Wisconsin, where she studied genetics with James Crow, "the best teacher in the world." Joshua Lederberg, who taught in the genetics department, later asked her why she fell asleep in morning lectures. She replied, "When I go home, I am nursing children."

At Wisconsin Margulis became aware of the inconsistencies in the prevailing ideas about heredity. Green female plants crossed with white males of the same species sometimes gave rise only to green offspring. Yet if green males were crossed with white females, the plants that grew from the fertilized seeds were all white. If inheritance arose solely from nuclear genes, with random mixing during sexual fertilization, it would not matter which parent contributed which color trait. It was becoming ever more obvious that cytoplasmic factors, presumably genes, must play an important role in the germ cells of animals and plants.

Mitochondria are vital components of nucleated cells, where they enable the use of oxygen in respiration. And it was now known that the mitochondria of animal cells contained genes. Genes had also been found in the chloroplasts of plant cells. Without question, both mitochondria and chloroplasts were passed down through generations as part of reproduction. Yet they came from only a single parent, usually the female, and the inheritance was not through the nucleus.

For her master's degree, Margulis cut up amoebae to determine if any DNA or RNA activity remained in isolated portions of cytoplasm. She soon had her answer: RNA played an active part in the cytoplasm, and DNA was also present. Later this DNA would turn out to mark the presence of bacterial bodies without walls. During an interview she remarked to me, “That was my first experience of cytoplasmic inheritance.” In 1960, after completing her master’s degree at Wisconsin, aged twenty-two and already the mother of two young boys, Margulis enrolled as a graduate student in the genetics department of the University of California at Berkeley.

By now she was intrigued by the abundance of symbiotic interactions in nature, particularly those involving bacteria living with — sometimes inside the cells of — insects and worms. Like others before her, she suspected that the mitochondria and chloroplasts were remnants of what had once been free-living bacteria. “It seemed obvious to me that there were double inheritance systems with cells inside cells.” She became fascinated by Tracy Sonneborn’s work on cytoplasmic inheritance in paramecia, grasping at once that his experiments had confirmed that characteristics acquired by the organism in its lifetime could be passed on: “They confirmed a kind of neo-Lamarckian inheritance.”

Margulis searched for and found many other examples of cytoplasmic inheritance in which the agents of inheritance were not “naked genes” left over from some past evolutionary accident but elements within the vestigial bodies of once free-living bacteria, now incorporated as organelles within the cells. Living survivors of a more ancient eukaryotic cell, one of the archaeprotists, had a nucleus containing rod-shaped chromosomes, but with cytoplasm that contained no mitochondria. It was not far-fetched to wonder if some archezoan had once swallowed up a bacterium, which then entered a symbiotic partnership with the cell, remaining forevermore within its cytoplasm as the mitochondrion.

The familiar mitochondria and chloroplasts still resembled bacteria in their behavior and metabolism. In fact there seemed little difference between a bacterium newly trapped within a cell and a mitochondrion inherited as part of cellular evolution. What everybody called a chloroplast was simply a blue-green bacterium, known as a cyanobacterium, that had shed its cell wall to reside inside the cytoplasm of a plant cell.

Emboldened by her survey of the literature, Margulis predicted that if mitochondria and chloroplasts had once been free-living bacteria, they might still retain some of their bacterial DNA.

Bacterial DNA is identifiable in its structure and genetic coding. If her prediction proved to be correct, then the origin of these cytoplasmic bodies could be absolutely confirmed. Her deduction was subsequently proven by geneticists around the world. Mitochondria not only reproduce independently of the nucleus, by binary fission, they also have their own DNA, which, as in bacteria, takes the form of a single circular molecule. They also have their own messenger RNA and transfer RNA, which form part of the protein-manufacturing factories called ribosomes. Today scientists accept the evidence that mitochondria and chloroplasts were once free-living bacteria, related to surviving forms on Earth. Some chloroplasts can be distinguished from existing cyanobacteria only with such difficulty that the distinction between them is biologically meaningless.

With this new understanding, the concept of symbiosis came of age. Mutualistic symbiosis, for example, no longer implied some cuddly living together but a metabolic interaction or dependency between different kinds of organisms, on which their survival depends and from which great evolutionary changes may arise.

If current estimates are correct, the hard bargain that resulted in the evolution of mitochondria took place somewhere around 2 billion years ago. That original endosymbiotic union was similar to what Kwang Jeon witnessed in his study of the amoeba and the X-bacterium. The particular bacterium involved is still uncertain, but recent gene mapping of bacteria has suggested an extraordinary candidate.

Epidemic typhus fever is one of the most notorious plagues of history. Commonly associated with famine and civil unrest in the wake of war, it caused the major epidemic already referred to in the wake of World War I in Europe. The causative germ, one of the rickettsias, is passed from person to person through the bite of the human body louse. This rickettsia is extremely unusual. Halfway between a bacterium and virus in size, it resembles a virus in that its life history takes place inside the infected host cell, a so-called obligate intracellular parasite. In evolving its endosymbiotic lifestyle, the germ has lost a good deal of its metabolism, along with the coding genes.

Michael W. Gray, professor of biochemistry and cellular biology at Dalhousie University in Halifax, Nova Scotia, and one of the foremost experts on the evolution of cytoplasmic organelles, believes that the typhus-causing germ is the closest living relative that we know of to our human mitochondria. This does not necessarily mean that our mitochondrial ancestor was the typhus-causing rickettsia; in time, even closer relatives may be found.

Some important deductions about the story of evolution can now be drawn. One of the most intriguing is that all eukaryotic life, including many of the 250,000 species of protoctists, the fungi, and every plant and animal species on Earth, must have evolved from that singular endosymbiotic merger of two types of bacteria. If leading authorities on bacterial evolution are correct, other commonalities of origin may go back to the very beginnings of life. Scientists have found similarities in the genetic sequences of a highly conserved form of RNA in hundreds of early life forms, suggesting that the most ancient bacteria, the modern bacteria, and the eukaryotic cell all have a common origin.

In 1961 the evolution of the nucleated cell was one of the greatest enigmas in biology. So, only one year into her Ph.D. studies, Margulis became very interested in the possibility that symbioses of this nature might provide the answer.

At Berkeley, she was surprised to find that the geneticists, with a single exception, had no interest in evolution. But Curt Stern assigned her to read up on the genetics of the alga *Chlamydomonas,* which contained mitochondria and chloroplasts within its cytoplasm. “It was a gorgeous organism from the point of view of evolutionary logic. All I wanted to do for my doctorate was get the DNA from the chloroplast to prove the basis of cytoplasmic inheritance. But when I took this idea to various people, they told me, ‘You’re looking for Father Christmas!’” At this stage she became very interested in Sonneborn’s studies of the paramecium.

By the early 1960s, evidence for the symbiotic origins of mitochondria and chloroplasts was steadily accumulating. Mitochondria were killed off by streptomycin, a drug used to treat bacterial diseases such as tuberculosis. Chloroplasts very closely resembled the common photosynthetic cyanobacteria. The nucleus was being intensively explored in every major genetic laboratory. But the “cortical” inheritance discovered by Sonneborn remained a mystery. One day Margulis had her “Eureka” moment. As she would recall later, “I remember, as a graduate student, I was standing in the library at Berkeley, poring over the Sonneborn papers and the literature on chloroplasts, when I came across a review of a book by Herbert F. Copeland.” Copeland, a botanist, taught biology in Sacramento. In his book *Classification of the Lower Organisms,* published in 1956, he suggested a new way of looking at the tree of life. One reviewer wrote, “This classification is so idiosyncratic that this reviewer has great difficulty in evaluating it.” In time this would encourage Margulis to consider that a classification system, or taxonomy, might be useful in her attempts to solve the evolutionary enigma.

Margulis had to go to the Library of Congress in Washington to read Copeland’s book. As big as a telephone directory and dense with detail, the book was based on Copeland’s studies over thirty years. One organism he discussed was a protist (a single-celled protoctist) symbiont that lives in the guts of termites. The symbiont surface was so covered with wriggly, corkscrew-like bacteria, called spirochetes, that the bacteria had been mistaken for cilia and the protist mistakenly classed with the ciliates. As Margulis recalled to me, “When I first saw that, I said to myself, ‘That’s the last symbiont I need. That’s the ciliate symbiont.’” She was now sure she had the information needed to advance a theory of how a series of bacterial mergers gave rise to the first nucleated cells.

Many of the single-celled life forms known as protists still live in an atmosphere without oxygen, for example in the intestines of plant-eating insects and herbivores. This anaerobic existence suggested to Margulis that anaerobic protists represented the first stage in cellular evolution, the stage before the incorporation of mitochondria. To explain how the first anaerobic protist came into being, Margulis proposes an initial union between a freely mobile modern bacterium (known as a eubacterium) and an ancient bacterium (an archaebacterium) that could breathe sulfur rather than oxygen and also tolerate extreme heat.

If Jochen Brocks and his colleagues were right in their interpretation of the molecular fossils they found, this union, forming the primal substance of all nucleated cells, must have taken place more than 2.7 billion years ago. Then the two bacterial genomes became incorporated in some way within a separate entity from the rest of the cell, enclosed within a membrane, perhaps even forming, or helping to form, the first nucleus. The "modern" bacterium was able to swim and was probably one of the corkscrew-shaped spirochetes mentioned in Copeland's book, a eubacterium that could move through water by wriggling its body. Its ancient partner would have been similar to one called *Thermoplasma,* an archaebacterium that is found today in the hot springs of Yellowstone Park, which may well have breathed sulfur rather than oxygen. *Thermoplasma* supplied the spirochete with its hydrogen sulfide wastes, and the spirochete supplied the consortium with the capability of rapid movement. If Margulis is right, the spirochete's attachment sites later evolved into cellular structures known as centrioles. These play a vital role in one of the most beautiful mechanisms in biology, the complex ballets of cellular reproduction known as mitosis and meiosis, in which the centrioles help orchestrate the "dance of the chromosomes."

Initially, the sulfur-loving, heat-resistant, freely mobile life form could not breathe oxygen. With the evolution and global spread of the cyanobacteria, which generate oxygen, that element became a significant component of the Earth's atmosphere, encouraging the evolution of oxygen-breathing bacteria. One of these oxygen-breathers became the mitochondrion, through an endosymbiotic union with the previously anaerobic protist. This larger, more complex protist acquired the ability to take in particulate food, much as an amoeba does today. So, as Margulis explained, a new "complex and startling being" began to spread over the shorelines of the Earth about 2 billion years ago. Some of these protists entered into an endosymbiotic union with cyanobacteria, resulting in the first aquatic green algae, the forerunners of all the plants.

Natural selection acting on gene mutations cannot create new genes; it can only modify those that already exist. These formative symbiotic unions, on the other hand, involved the merging of thousands of genes, every one of which had already evolved over an eon or more, into a new hybrid organism. Although that scenario is not quite what Lamarck had in mind, Margulis sees it as an example of neo-Lamarckian evolution that is orders of magnitude greater in its potential for change than Darwinian gradualism. This process of change is so sudden and spectacular that she has compared it to an evolutionary lightning strike.

There is another implication of Margulis's theory for evolutionary biology. Neo-Darwinians believe that evolution takes no definite path toward increasing complexity. Symbiologists take a very different perspective: with each of these endosymbiotic steps, the resulting hybrid involved a huge increase in genetic and biological complexity.

After years of orthodox rejection, Margulis's first paper describing this series of endosymbiont unions was published in 1966, and it became the basis for her now famous "serial endosymbiosis theory," or SET. Hailed by Sapp as the most daring and serious effort in pursuit of the symbiont hypothesis during the 1960s, SET proposes that the nucleated cells of plants and animals, as well as those of fungi and the protoctists, originated through mergers of different types of bacteria and that the hybrid forms evolved in a specific sequence of symbiotic steps. Given the broadly hostile reaction to symbiosis over the previous century, it will come as no surprise that Margulis encountered a wall of skepticism. But in time, as she refined and extended the concept, even the most doubting Darwinians not only accepted her theory, they marveled at the beauty of it. As Richard Dawkins generously remarked, in *River Out of Eden,* the serial endosymbiosis theory of the origin of the eukaryotic cell is "incomparably more inspiring, exciting and uplifting than the story of the Garden of Eden . . . Like most biologists, I now assume the truth of the Margulis theory."

But we should not get too carried away by this story of the triumph of symbiosis. The eukaryotic cells in the fingers that hold open these pages, or in the cells in the retinas that scan them, are more exquisitely wonderful than mere unions of bacteria: they are labyrinthinely complex miniature worlds, and like worlds they incorporate all manner of evolutionary mechanisms. In their influential book *The Origins of Life,* Smith and Szathmáry put forward a composite of Darwinian and symbiotic mechanisms that enlarge on SET; they advance reasonable theories of how the nucleus, and even the physical construct and concept of the cell itself, could have arisen through essentially Darwinian mechanisms.

Common sense would suggest that evolution has embraced both neo-Lamarckian saltations in the form of symbiosis and neo-Darwinian gradualism through the accretion of useful mutations.

Certain aspects of SET remain controversial. For example, Hyman Hartman, working at the NASA Ames Research Center at Moffett Field, California, has suggested that the nucleus began as a free-living organism. And there are extraordinary new discoveries that suggest that the role of viruses in many aspects of cellular evolution has been greatly underestimated. Such is the nature of science that hypotheses are put forward to be proved or disproved, often resulting in further honing and modification of the theory. As a scientist, Lynn Margulis does not pretend to be above criticism or even refutation: "I am prepared to be incorrect."

But if she is correct in her spirochete hypothesis, there may be implications for the evolution of the human brain. Our nerve cells, like those of all animals, have threadlike extensions called axons and dendrites, which are based on a microtubular infrastructure that has similarities to the spirochetes that fused with the Archaebacteria in SET. If these did originate with the incorporation of a spirochete a billion or more years ago, then we might even owe the evolution of our human brains to that ancient symbiosis.

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THE WONDER OF SYMBIOSIS

To look still more broadly, we discovered that terrestrial
life is a dense web of genetic interactions.
— JOSHUA LEDERBERg

CORAL REEFS have been called the rain forests of the sea. In these precious domains, swimmers equipped with no more than masks and snorkels can watch creatures with the luminescent colors of gems engage in behavior rituals as enchanting as the mating of the most splendid birds.

The builders of these reefs are small marine animals that secrete their own external skeletons; the slow accumulation of these skeletons over millions of years forms the framework of the reefs. Members of the phylum Cnidaria, which also includes the jellyfishes and anemones, corals exist in a multitude of forms. All are colonial animals equipped with stinging tentacles (*cnida* is the Greek word for stinging nettle) that emerge like opening flowers to catch tiny prey and drag it into the saclike stomach for digestion. On the 2,000 square kilometers of the Great Barrier Reef of Australia, there are about 350 coral species, including both hard and soft varieties. These reef-building corals grow in clusters, extending in a confluent surface layer over the graveyards of past generations. Each species has a different shape or color or blend of colors; in association with other related cnidarians, they create all manner of sculptural forms. Some fashion huge rounded domes elaborated with sulci, like the human brain; others form twigs, bifurcating into staghorns or wide fan-shaped arborescent branches or the most exquisitely floral forms, all decorated with every subtlety of tone and hue.

Of course, coral reefs are much more than just a beautiful curiosity. They are the homes and nurseries for almost a million species of fish and other marine creatures and algae, many of which we rely on for food.

Nature films about the coral reef ecology used to focus on the predatory activities of its many residents, and certainly a reef can be a dangerous territory to inhabit. But lately the focus has become more balanced as filmmakers cater to a public delighted by the many symbiotic relationships among its life forms. Reef-building corals are exclusively symbiotic with the unicellular yellow-brown photosynthetic organism known as dinomastigotes, which live their entire lives inside the cells lining the coral's gut. The coral's stinging tentacles are predators by night and the dinomastigotes capture sunlight by day, storing its energy in the form of carbohydrates. The ecosystem depends on this symbiosis, for the dinomastigotes supply half or more of the coral's energy needs, vastly increasing its ability to lay down calcification. This symbiotic union is believed to have evolved in the late Triassic period, some 210 million years ago.

Another group of tiny aquatic life forms is known collectively as the Foraminifera. With over 35,000 described species, "forams" are the most widespread of the organisms in the oceans. The individual shells are no bigger than grains of sand, yet in their billions they form an important component of plankton, the basic food source of all marine life. They also incorporate intracellular symbioses with a wide variety of photosynthetic microbes, which make the foram bigger and strengthen its shell, thereby improving its ability to survive. The symbiotic union is so self-sufficient it needs only a few additional vitamins to survive and reproduce. Mutualistic symbioses like coral and forams are important components of life in the sea.

On land, one of the five kingdoms of life, the fungi, comprise some of the most ancient terrestrial life forms. Like bacteria, fungi are essential to the cycles of life. Underneath the soil certain fungi form immense labyrinths of filamentous mycelia, which can extend for miles and which play vital roles in plant nutrition. Aboveground these fungi emerge as the fruiting bodies we recognize as mushrooms, which cast vast quantities of spores into the air. So enormous are the numbers of fungal spores and so efficient is their distribution they are found at every level and within every crevice of the biosphere. Fungi cannot live without carbon, which must be obtained from other creatures, whether bacteria, plants, or animals. This is why fungi are found growing in and around other forms of life, on their secretions, excretions, dead flesh, and — in saprophytic, parasitic, or mutualistic symbioses — in intimate relationships with a vast array of life forms.

As we have seen, fungi are an integral part of lichens. Even more important, most land plants have evolved from a joint venture between fungi and green algae, a relationship that evolved over hundreds of millions of years to become the mycorrhizae that nourish the roots of most species of plants today. Only recently have scientists realized that a single pine tree may have several different fungi in a mutualistic symbiosis with its roots. Peter Atsatt, emeritus professor in the department of ecology and evolutionary biology at the University of California, has proposed an even more radical concept: that land plants may have arisen from the very early incorporation of a fungal genome into that of a green alga and that this hybrid organism went on to play a central role in the evolution of embryos, then of pollen and seeds.

Many fungi enter into complex symbiotic relationships with insects, in which the fungus helps break down the tough cell walls of plants so that the insect can digest them, while in return the fungus has a seat at the insect's dining table. Among the many species of insects that have mutualistic symbioses with fungi are scale insects, gall midges, wood wasps, and anobiid beetles.

One delightful example of such a relationship concerns the *Atta* ants of Central and South America, which harvest leaves and carry them back into their subterranean nests. After the ants masticate the leaves, they are further digested by a domesticated fungus growing in the nest's inner garden. The fungus breaks down the leaves' cellulose walls, liberating their hidden stores of nourishment for the ants, while the ants give the fungus protection and shelter and a constant supply of leaves to feed on.

Almost a third of all known species of fungi are involved in mutualistic symbiosis of one form or another, which clearly has evolutionary implications. In the words of Bryce Kendrick, "Several of these relationships have given rise to major evolutionary innovations, which have conferred on the interdependent organisms the ability to colonize habitats previously unavailable to them." In this way, symbioses of many different types made possible the expansion of life into hitherto barren and hostile ecologies in the water and on the land surfaces of the primal Earth.

Phyla are the major divisions, below kingdoms, in the hierarchical classification of life. All members of a phylum share a fundamental physical or physiological characteristic, whose evolution gave rise to that phylum. In 1987 Lynn Margulis and her colleague David Bermudes suggested that many, perhaps all, of the fundamental characteristics that define each phylum came about through the creativity of endosymbiosis.

They showed how twenty-eight of the seventy-five phyla, excluding bacteria, depended on the incorporation of organelles that had once been free-living microbes. These include thorny-headed worms, the Cnidaria, and the exotic creatures known as Ventimentifera, which live around the deep sea vents; they also include all mycorrhizal plants, such as_conifers, angiosperms, cycads, and ginkgos, as well as fifteen protoctist and two fungal phyla. Lower down the taxonomic system, symbiotic mergers have given rise to legumes with their nitrogen-fixing rhizobial bacteria, many wood-eating cockroaches and termites, as well as all ruminant mammals and the luminous fish that inhabit the ocean deeps.

In all these cases the enigma of heredity demanded an explanation that was far more varied and complex than Darwinian mutation alone. Each case of symbiosis had to be examined in its own light, a daunting prospect for evolutionary geneticists. In some cases it was clear that the symbiont was passed down through bacterial-style binary fission within the cytoplasm. Richard Law, a lecturer in the biology department at the University of York, described the hydroid *Myrionemia amboinense,* whose eggs carry algal cells within them. Giant clams have a more complex relationship with the dinoflagellate *Symbiodinium microadriaticum,* for the symbiosis has to be reassembled in each new generation after the host reproduces. Mechanisms for transmission of exosymbioses rely on one partner's ability to locate the other even if they do not live closely together, as in the symbioses between flowering plants and bees, butterflies, and hummingbirds.

But the diversity of solutions to the enigma of heredity could be a strength of symbiotic evolution rather than a weakness. Simplicity in science has a compelling elegance, but as Ernan McMullin, a philosopher and historian of science, admits, simplicity appeals more to our human aesthetic instinct than to any real objective logic.

We need, moreover, to put these symbiotic "flashes of lightning" into perspective. The evolutionary landscape they illuminate is not steeped in darkness but bathed in a pale, shimmering phosphorescent glow, the result of steady, unrelenting Darwinian change. The glow is cut through and altered by these lightning flashes and, quite occasionally, severely shaken and disturbed by the brilliant thunderbolt of a major endosymbiotic event.

The two different evolutionary mechanisms we see in this wonderful landscape are not separate from one another; they are tightly interwoven not only with one another but, in the most astonishing fashion, with the landscape itself.

• 11 •

PLANETARY EVOLUTION

The tree of life is a twisted, tangled, pulsating
entity with roots and branches meeting
underground and in mid-air to form eccentric
new fruits and hybrids.
— LYNN MARGULIS, *The Symbiotic Planet*

IN 1962 THE SCIENCE HISTORIAN and philosopher Thomas S. Kuhn introduced the concept of "paradigm" to describe how an important new scientific discovery or understanding causes a revolutionary shift in the way scientists think. Examples include Aristotle's *Physica,* Newton's *Principia,* and Einstein's theories of relativity. With the synthesis of Darwin's theory of evolution and Mendelian genetics, neo-Darwinism became such a paradigm. The paradigm concept has important repercussions, for once a paradigm is accepted, it is regarded as beyond challenge.

After the discovery of the chemical structure of DNA in the 1950s, the main thrust of neo-Darwinian argument was closely bound to molecular biology. As genomic mechanisms became clearer — in particular, as they applied to replication, change, and inheritance — evolutionary scientists turned away from nature as a whole and took an increasingly reductionist perspective. In 1976 this view culminated in the publication of Richard Dawkins's *The Selfish Gene,* which advocated that the struggle for existence occurred not at the level of the individual organism but in the most basic unit of inheritance, the gene. This idea, which originated with Dawkins's mentor at Oxford, William Hamilton, coincided with the proliferation of knowledge in genetics. The "selfish gene concept" explained much that had hitherto baffled evolutionists, from the behavior of "jumping genes," which duplicate themselves with a selfish disregard for the genome as a whole, to seemingly altruistic human behavior. No idea could have more neatly encapsulated the modern Darwinian zeitgeist. Dawkins's book achieved such massive popularity that it and Stephen Hawking's *A Brief History of Time* were the only two science books mentioned in a poll of middlebrow British readers asked to list their personal choices of the one hundred most important books of the twentieth century.

The notion of the selfish gene was accepted by the great majority of evolutionary biologists, and it became the central tenet of population genetics and evolutionary ecology. The concept was readily amenable to mathematical extrapolation, and biology teachers treated it as gospel; the next generation of scientists came to maturity assuming that reductionist neo-Darwinism and evolution were one and the same. By the 1970s the mimetic influence of the selfish gene extended into the highly controversial spheres of evolutionary psychology and sociology, where it was applied to individual and social patterns of human behavior.

Nevertheless, an important question remained: was Darwinian gradualism, even with all the panoply of selfish genes, mutation, and selection by nature, sufficient to explain the diversity of life on Earth?

As Kuhn made clear, when a paradigm is accepted not only do scientists stop inventing new theories, “they are often intolerant of those invented by others.” It took a rare single-mindedness and courage to dare to contradict the paradigm. However, just three years after *The Selfish Gene* was published, its reductionist focus was challenged by a novel vision, one that looked not to the submicroscopic wonder of the gene but to the Earth in its entirety and, beyond it, to the cosmos.

In September 1965 three people were sitting in a small office in the Space Science Building of NASA’s Jet Propulsion Laboratory in Pasadena, California. They were the astronomer Carl Sagan; Dian Hitchcock, a philosopher employed by NASA to assess the logic of their experiments; and the English polymath scientist James Lovelock, who, four and a half years earlier, had been thrilled to work with NASA on plans to explore the moon. In the interim NASA had become more ambitious and had turned some of its attention to Earth’s planetary neighbor, Mars. But the Mars program was not going according to plan and Lovelock was convinced that it was based on a very shaky premise. Thirty-six years later, when I asked him about that fateful meeting in Pasadena, he invited me to visit him and his charming wife, Sandy, in their wood-girdled home in southwestern England.

Lovelock had a vivid recollection of that meeting in an office overlooking the San Gabriel Mountains. And he also recalled what he described as a sudden flash of inspiration. A fourth person had joined their gathering, an astronomer named Lou Kaplan, who brought a large sheet of paper with the latest infrared sightings of Mars and Venus that provided a detailed analysis of the planetary atmospheres. Everybody present was looking forward to examining the chemical compositions.

As Lovelock remembered it, “I was even more fascinated because it was already my theory that Mars and Venus were dead planets. Here, suddenly, my predictions were proved bang on. We saw that the atmospheres were full of carbon dioxide and very little else. All the indications were that they were at a chemical equilibrium state. I knew now that there could be no life on either of the planets; if life had been present, the atmospheres would have been changed by it. And so it was at that moment I thought: ‘My goodness! How different is our Earth!’”

In time that flash of insight would cause Lovelock to suggest that all of life, from the plankton underlying the marine food webs to the great canopy trees of the rain forest, “could be regarded as constituting a single living entity, capable of manipulating the atmosphere to suit its needs and endowed with faculties and powers far beyond those of its constituent parts.”

For a growing number of scientists from many disciplines, this hypothesis, named Gaia, would become the most provocative challenge to the existing perception of our world. Inevitably, from the moment of its birth, Gaia was enmeshed in controversy.

James Lovelock has been variously described as an unorthodox chemist and inventor, space scientist, marine biologist, the Earth Father, and so on. Many such descriptions seem to imply a rebellious nature, but he denies that this is the case. “Not at all. I’m a fairly tribal person who likes to belong. It’s just that I was cursed, or blessed as the case might be, with a mind independent enough to see things differently, and so I always found myself in a rebel position."

When he was just four years old, his father gave him a Christmas present of a wooden box full of odd electrical bits and pieces. In retrospect, Lovelock considers this an inspired gift because it encouraged him to think. "Why," the boy demanded, "do you need two wires to send the electricity along when you only need one pipe for water?" Nobody seemed able to give him an answer. "Finally I realized that if I wanted to find out the answers to such questions, I would have to become a scientist and find out for myself."

Eventually he obtained a chemistry degree at Manchester University, then completed his Ph.D. while working at the Medical Research Council in London. Beginning in 1941, he spent twenty years at the council on various investigations, mostly of infection. While studying the common cold at a hospital in Salisbury, he had the opportunity to indulge an innate skill at scientific instrument building. His colleagues, believing that drafts of cold air might play a part in spreading cold viruses, asked him to make an instrument that would measure air currents. Lovelock constructed two anemometers, one incorporating ionization and the other ultrasonics. The ionization version met the need. Ten years later he invented the electron-capture device, a brilliantly simple instrument that can detect trace amounts of pesticides in animal blood and tissues and of chlorofluorocarbons in the atmosphere, which allowed scientists to measure levels of environmental pollution. This device helped vindicate Rachel Carson's timely warning in *Silent Spring,* which alerted the world to the dangers of an environmental disaster.

In typical Lovelockian fashion, he made no attempt to claim the patent on the instrument, which was claimed by the U.S. government in 1964. Money was never the primary motive for this man, who, however eccentric he appeared to his colleagues, was essentially a scientific purist.

It was his inventiveness that first brought him to the attention of NASA. In March 1961 Lovelock was invited to assist them in their plans to explore the solar system. At the Jet Propulsion Laboratory he became a consultant to a team led by Norman Horowitz, a space biologist, whose objective was to devise ways of detecting life on other planets. The team's plan was to dispatch an automated sampling device coupled to a microbiological laboratory to sample the Martian soil and judge if it would support microbes. Other experiments would test for chemicals that normally accompany microbial life.

After a year or so, Lovelock's independent thinking began to show. Disenchanted with the prevailing assumptions, he began to ask himself some questions. Would Martian life, if it existed, reveal itself in tests based entirely on the patterns of life we observe on Earth? Increasingly interested, he probed even more deeply, asking, "What is life, and how should it be recognized?"

When he challenged his colleagues on their current strategies, they asked him what alternatives he was proposing. Lovelock, who had been approaching the problem from the perspective of physical science rather than biology, replied that he would look for a reduction in entropy, based on the second law of thermodynamics, as a cardinal sign of life.

For physical scientists the second law is one of the fundamental planks in understanding the universe. Put simply, it states that when two bodies are brought into contact, heat (energy) flows from the hotter body (higher energy state) to the colder body (low energy state). This may sound like simple common sense, but it has cosmic implications. For example, if the energy of the universe tends to dissipate in the form of heat, then the universe must be winding down from an initial state of enormously concentrated energy: the big bang, as some scientists conceive the start of everything. Life, which gathers and organizes energy — for example, through photosynthesis — appears to reverse this process. But when Lovelock suggested that his colleagues should search for evidence of this, they seemed less than impressed. Nevertheless, the idea took root in his mind. Back home in the quiet of the Wiltshire countryside, he spent some time thinking about the true nature of life.

It wasn't an easy subject to conceptualize. "Like a lot of terms we employ in everyday life, we haven't the slightest idea of what it means."

Lovelock trawled the scientific literature for workable definitions of life, not in conventional biological terms but in physical terms that a chemist could use as the basis for life-detection experiments. His search was unsuccessful. He found a vast repertoire of information on the anatomy, physiology, classification, and evolution of life, but nothing that satisfied his question about its essential nature. With the philosopher Dian Hitchcock, he attempted to probe it further. They asked themselves a much simpler and more specific question: How might a planet be altered by the presence of life?

The only planet they had to go by was Earth, with its variety of living species, its peculiar atmosphere, and its oceans. It was obvious that life on Earth interacts with its environment. For example, some of the raw materials and all of the waste products come from and are returned to the land, atmosphere, or oceans. It seemed likely that the changes they were looking for might show up in these domains.

Applying this new line of reasoning, Lovelock and Hitchcock soon confirmed that Earth's atmosphere, in particular, is dramatically changed by the presence of life. Atmospheric gases are in a permanent state of disequilibrium, which is the opposite of what one would expect from the second law of thermodynamics. A good example is the simultaneous presence of methane and oxygen. In sunlight these two gases should react to form carbon dioxide and water, removing the gases from the atmosphere. Yet the methane level in the atmosphere is relatively stable. To keep it so, vast amounts of methane must be constantly added. The same is true of oxygen, which, though it is being used up in a great many chemical reactions, including combustion and the respiration of animals and plants, stays at a steady level in the atmosphere. Recycled oxygen must be added regularly to the atmosphere to keep its level constant. Lovelock was convinced that the main source of both these gases was life.

Here was simple and yet convincing evidence for his line of thinking that the presence of life alters what one would expect according to the second law of thermodynamics. Moreover, the evidence of this change should be apparent to somebody observing our Earth from a distant source in space. The conclusion was inevitable: "The atmosphere of a life-bearing planet would thus become recognizably different from that of a dead planet."

Lovelock then applied this test to Mars, which, of course, has no surviving oceans but has an atmosphere that can be analyzed from Earth. Even at that time, ten years before the 1976 *Viking* landings, Lovelock was convinced that any life on Mars would have left its signature in the atmosphere. At the meeting in Pasadena in 1965 he learned that the Martian atmosphere consists largely of carbon dioxide. To Lovelock this ruled out the presence of life, a conclusion that was not altogether popular among his colleagues on the NASA project. But Lovelock's mind was already entranced by an extension of his new idea, a grander notion running at a tangent to the Mars deliberations. In his own words, as he reminisced later: "I found, in looking at Earth's wonderful atmosphere, with all of those gases out of equilibrium, yet somehow keeping constant, that something must be regulating this. It was natural for me to think that it was life that was regulating it — and regulating it in such a way as to keep it comfortable for itself."

He went on to examine other gases in the Earth's atmosphere, such as nitrous oxide and ammonia. And when he looked deeper still, through experiments on air pollution, his conclusions differed in spectacular fashion from those of his geochemical colleagues. Lovelock now had evidence that the atmosphere was not some chance mixture of gases resulting from nonbiological processes, as the geochemists assumed. The atmosphere might actually be an extension of the biosphere, intimately interactive with, and regulated by, life.

He needed a name for the concept, and this, famously, was provided by a man who lived in his village: William Golding, a Nobel laureate and the author of many novels, including *Lord of the Flies*. Without hesitation, Golding recommended that this "living Earth" should be called Gaia, after the Greek Earth goddess. It was almost too wonderful a name, for it derived from a second great mind more connected with humanism and the arts and was a conceptual metaphor of huge historical resonance and metaphorical impact.

Now Lovelock needed to convince his colleagues.

In 1969, he was given the opportunity to put forward his Gaia hypothesis at a scientific meeting in Princeton, New Jersey, whose focus was the origins of life. His presentation was not well received. It appealed to nobody except a Swedish chemist, Gunnar Sillen, and a biologist he had never met before who had been given the job of editing the papers presented at the meeting — Lynn Margulis. Lovelock encountered even more resistance when he attempted to have his theory published. Mainstream scientific journals rejected all his submissions. When his paper was sent out for peer review, biologists, in particular evolutionary biologists, treated his ideas with outright scorn.

Even Carl Sagan disagreed with him and, in Lovelock's opinion, not just on scientific merit. "He disagreed with me emotionally. He was so tied up with the American dream of finding life on Mars: it must be there, hiding in some oasis somewhere." When Lovelock addressed a congress of geophysicists at Mainz, Germany, the Europeans among his audience were enthusiastic, one offering to publish his lecture in the journal *Tellus,* while the Americans in the audience were openly hostile.

The more Lovelock promoted his hypothesis, the more this skepticism continued to grow. The geologists in particular were flatly dismissive. As the eminent geochemist H. D. (Dick) Holland of Harvard University exclaimed, "We don't need Gaia. We can explain all the facts about the Earth through straightforward geology and geochemistry." The microbiologist W. Ford Doolittle of Halifax, Nova Scotia, made the comment: "If Gaia were to be real, it would require trade unions of all the species of organisms to meet annually on Mount Ararat and negotiate next year's climate." Richard Dawkins was more focused in his criticism: life forms could not regulate anything other than their own kind. Evolution, viewed from a reductionist neo-Darwinian perspective, could not lead to cooperation on a global scale. Dawkins considered Gaia's webs of mutual dependency mere pop ecology. Natural selection meant that nature had to be presented with choices to select from.

Lovelock later conceded that the neo-Darwinian criticisms were the greatest challenges for his theory. Yet he believed that Gaia and natural selection were perfectly compatible.

In the early 1990s John Maynard Smith went so far as to refer to Gaia as an "evil religion." Such attitudes, as much as the refusal of prestigious scientific journals to publish any papers related to Gaia, wounded Lovelock. "I was puzzled," he confessed, "by the response of some of my scientific colleagues who took me to task for presenting science this way . . . It is the scientific establishment that now forbids heresy." Frustrated by years of academic resistance, he published his hypothesis as a book for a general audience, *Gaia: A New Look at Life on Earth,* in 1979. In it he wrote: "I see the Earth as more than just a mixture of living things and inanimate matter. I see it as a tightly coupled entity, where the evolution of the living things and the evolution of the inorganic matter constitute a single and totally inseparable process. It's a whole system."

It is ironic that even as his planetary vision was under ferocious attack, the Gaia theory, unbeknownst to Lovelock, was in actuality a step further along an older road of scientific exploration.

Belief in the balance of nature goes back to the Greeks and has been incorporated into many of the great systems of religious belief. But all such holistic thinking had been attacked by Darwinian-minded evolutionists and ecologists since the early decades of the twentieth century. Despite the opposition, belief in the essential interdependence of life had never entirely gone away. Unfortunately, the concept did not become any easier to define, given the labyrinthine complexity of life, and any "natural balance" was difficult to conceptualize and even more difficult to subject to rigorous scientific testing. An apparently insoluble drawback, in the words of Frank N. Egerton of the University of Wisconsin at Parkside, was that "a synthetic balance-of-nature theory would necessarily have included knowledge from earth and atmospheric sciences as well as from botany and zoology."

In the nineteenth century, many scientists adhered to the older scientific philosophy that knowledge could be advanced only by the systematic accumulation of facts. Theoretical deduction — first constructing a hypothesis or theory that could subsequently be challenged — was not their way of doing things. But Darwin, for example, took a different approach, examining the world through a preformed conceptual framework. In a letter to a friend, dated September 18, 1861, he reflected on the advances in geology since his voyage on the *Beagle*. "About thirty years ago there was much talk that geologists ought only to observe and not theorize; and I well remember some one saying that at this rate a man might as well go into a gravel-pit and count the pebbles and describe the colors. How odd it is that anyone should not see that all observation must be for or against some view if it is to be of any service."

In 1926 a Russian mineralogist and biogeologist, Vladimir I. Vernadsky, asked himself whether the landscape evolves in an intimate partnership with life. Eschewing any prior hypothesis, Vernadsky set out to advance knowledge through a series of objective observations that, once pointed out, become self-evident to any thoughtful observer.

At this time the evolution of life was seen as a serendipitous phenomenon that had no relationship to the inanimate world. Unconvinced by such Darwinian reductionism, Vernadsky believed that a critical evolutionary relationship existed between life and its geophysical environment, a relationship he later encapsulated in the concept of "biosphere," a name that had earlier been proposed by Professor Eduard Suess, of Vienna University, for the geological zone in which life dwells. Vernadsky's vision was dramatically grander, redefining "Biosphere" (spelled with a capital B) to encompass the "envelope of life where the planet meets the cosmic milieu." For Vernadsky, Biosphere included both life and its environment: the Earth's surface, oceans, and atmosphere. In its interaction with the landscape, life was not merely a geological force, it was *the* geological force that had shaped the surface of our planet over the eons of evolution. And since it derived its energy from the sun, Biosphere, and the diversity of life within it, was a cosmic phenomenon that could be understood by the same laws that applied to such constants as gravity and the speed of light.

Of prime importance to Vernadsky's thinking was the exchange of gases involved in respiration, which on the one hand was vital for the evolution of all forms of life and on the other determined the composition of the atmosphere. Perhaps his greatest contribution to our understanding of life and its interaction with the inanimate Earth was his recognition of the central importance of the steady and essentially eternal supply of solar energy, which life converted and reutilized through photosynthesis. This primal transfer of energy from cosmic source to planetary recipient makes possible many of the great cycles of life.

For example, the oxygen in the atmosphere is produced by photosynthesis, notably by microbes and planktonic life forms in the oceans. But as Vernadsky perceived, these photosynthesizers do not actually "create" this oxygen; they liberate it from oxides "as stable and as universal as water and carbon dioxide." Thus does life interact with inanimate nature, in the process radically altering the chemical composition of the Earth's crust and further changing it through the highly reactive nature of the released oxygen. Today we are well aware that carbon dioxide, produced as a byproduct of the respiration of oxygen, has an important greenhouse effect on Earth's surface temperature. Vernadsky popularized the need to take measurements, however colossal, to quantify these vital processes.

He estimated that the total mass of “green” life responsible for the trapping of sunlight and the production of atmospheric oxygen was $738 \square 10^{15}$ grams of organic carbon, which is nearly a hundred times the mass of the life forms dependent on that oxygen. The global mass of rock-dwelling lichens amounts to a staggering $13 \square 10^{13}$ tons, a biomass greater than that of all life in the oceans. These colorful symbiotic life forms, which are photosynthetic through their algal partners, wear the rock face away to soil, which in its turn is enriched by the humus of dead organic life, to become the root habitat of plants. Similarly for every environment, and every life form, Vernadsky dissected out and measured chains of interactions. In the oceans alone, he estimated the organic carbon content (mainly photosynthetic life forms) to be about $1.9 \square 10^{12}$ tons.

Vernadsky observed many other interactions that form part of what we now regard as the cycles of life. He examined the biological processes involved in the formation of limestone and the numerous interactions that make up the cycles of food and waste disposal, including the organic cycling that is an essential part of death and decay. From the planetary perspective, all such cycles consist of a transfer of solid and liquid matter between life and the environment. Water itself erodes rock and alters the landscape. It dissolves minerals washing in from the land and ferries these to the seas. And water has its own natural cycle, evaporating from the oceans, carried in clouds, then returning to the land as rain. Even in the form of rain, water cycles minerals, another facet of the great interactions of Biosphere.

In this way, Vernadsky measured and confirmed not only the great cycles of interactions, in which life forms depend on or cooperate with other life forms, but also a colossal series of interactions between all of life and the inorganic environment. Life, he explained, generates biomass, biological reproduction, and physical movement, radically changing the composition of the Earth's crust, whether soil or rock or water, and, most vital, the atmosphere. Life directly controls all crustal geological processes. In a clear echo of earlier beliefs in the balance of nature, Vernadsky concluded that the biosphere as a whole should be viewed as a single orderly mechanism, its formation influenced by life at every step, and subject to fixed laws.

This vision was revelatory, but for more than half a century after publication of his book in Russian, and its translation into French three years later, Vernadsky was ignored by the Western world. As Lovelock admitted, "When I first formulated the Gaia hypothesis, I was entirely ignorant of the related ideas of scientists such as Vernadsky." Lovelock made a great intuitive leap beyond Vernadsky's observationally based deductions in deciding that the biosphere evolved its own systems of self-regulation. But if he was to convince the world, he desperately needed the help of an evolutionary biologist courageous enough to do battle with paradigms. This he gained with the growing support of the redoubtable Lynn Margulis. Gaia and symbiosis, two quite different and distinct paradigms, acquired a curious symbiosis of their own.

Lovelock and Margulis developed one of those interactive relationships that happen now and then in science, in which innovative minds from disparate disciplines come together. In Lovelock's words, "Lynn's deep knowledge and insight . . . was to go far in adding substance to the wraith of Gaia." She began by helping him redefine Gaia as "the series of interacting ecosystems that compose a single huge ecosystem at the Earth's surface, incorporating all of life, the atmosphere, oceans and soil." The totality could be viewed as a physiological system, including temperature, alkalinity, acidity, and reactive gases, equipped with feedbacks that keep the physical and chemical environment constant and in a state comfortable for life.

Years earlier, in ending his employment with the British Medical Research Council, Lovelock had abandoned any notion of permanent employment, whether in academia or industry. "It gave me a feeling there were tramlines going all the way to retirement and the grave . . . I thought, 'To hell with it! I'm going to break free.'" It was a tough decision for a married man with a wife and four children to support, but he was able to fund his own researches through a much extended scientific career in which he made a living from his inventive dexterity and an extraordinary capacity for innovative thought.

Confounding his unrelenting neo-Darwinian critics, Lovelock declared that his original definition of Gaia, as put forward in his first book, was wrong. He had come to accept the Darwinian dictum that organisms cannot regulate anything but themselves. Where earlier he had claimed that life adjusted its environment to suit itself, the newer Gaia theory proposed an intrinsic coupling of life with its inanimate environment that in the totality was self-regulating.

Lovelock now put forward a model analogy in the form of a world similar to Earth in which the only plants were black daisies and white daisies. The model is more complex than I explain it here, but essentially, if the temperature is too cold, dark daisies dominate, because they absorb more heat and thrive, and if the temperature is too hot, the dark daisies suffer from overheating while the white daisies thrive, by reflecting the excess heat back into space. Using this "Daisyworld" model, Lovelock demonstrated, with elegant simplicity, how the planetary temperature could be regulated by the competitive growth of dark- or light-colored plants. Lovelock did not pretend that Earth was this simple: the purpose of Daisyworld was to answer the criticisms of Ford Doolittle and Richard Dawkins, who claimed that Gaia was not objective but teleological. In a more complex argument based on Daisyworld modeling, Lovelock confirmed that it was not life alone but the whole system of life tightly coupled with the physics and chemistry of the Earth's environment that does the regulating, the process of regulation being an emergent property of this tightly coupled system. To satisfy the neo-Darwinians, he even introduced a capacity for cheating, with gray daisies given a slight advantage over the others. However, the gray daisies did not proliferate and conquer. Computer extrapolation of his Daisyworld model confirmed that it allowed autoregulation of climatic temperature. But if Lovelock thought these steps would satisfy his critics, he was mistaken. As recently as 1998 Gaia was dismissed in contemptuous terms by the Darwinians D. Robertson and J. Robinson in the *Journal of Theoretical Biology*.

In a sense such antagonism was predictable, for Gaia theory has been the greatest challenge to the prevailing reductionist thinking. In his autobiography, *Homage to Gaia,* Lovelock concedes, "If Daisyworld is valid, seventy-five years of neo-Darwinian science will need to be rewritten."

To the late Stephen Jay Gould, professor of geology and zoology at Harvard University and a leading American evolutionist, Gaia was "warm and fuzzy and it strikes a chord . . . a pretty metaphor, and not much more." John Maynard Smith disagreed with Margulis's support for Lovelock. "I believe she's wrong about Gaia . . . But I must say, she was crashingly right once, and many of us thought she was wrong then, too." Even Ernst Mayr declared, "It's startling to find a reputable scientist arguing such fantasies."

But were these scientists right in their opposition? Surely there is something very curious about the long-term stability of the Earth's environment. Geologists and astronomers have questioned why Earth has kept its oceans while Mars and Venus are dry. When ecologists, basing their calculations on Darwinian assumptions, predict that with increasing complexity, ecosystems become more fragile, why, we might ask, are such complex ecosystems as the rain forests wonderfully stable? Such observations suggest a resilient and sustained homeostatic stability.

In spite of the rancorous opposition, Gaia theory is now moving from the shadows of unorthodoxy into the light of contemporary consideration. For the science journalist Fred Pearce, writing in *New Scientist,* Lovelock is to science what Gandhi was to politics. "His central notion, that the planet behaves as a living organism, is as radical, profound and far-reaching in its impact as any of Gandhi's ideas." Indeed, in the opinion of the Swiss historian of science Jacques Grinevald, Gaia "is the major cultural and scientific revolution of our time."

There will continue to be debate and differences of opinion between believers in Gaia theory and Darwinian-oriented evolutionists, but few would disagree with Lovelock's emphasis on the importance of a holistic view. "It is little use having climatologists, earth scientists, ocean scientists, community ecologists and atmospheric chemists all working in separate subjects, separate buildings, and worse, with no common language between them." We have seen how the lack of common ground has dogged evolutionary science, leading to misunderstandings between Darwinians, symbiologists, and the proponents of Gaia theory. At the same time, if we are to examine the contributions of Darwinism, symbiosis, and Gaia theory to the wonder of life's evolution on Earth — indeed if we are to consider how these forces interact with each other —

we need to dispel any residual confusion about symbiosis and its evolutionary role. Since the concept of symbiosis was first mooted by de Bary, enormous advances have been made in our understanding of biology and genetics. It would seem both appropriate and reasonable to reexamine symbiosis from this modern perspective.

• 12 •

REDEFINING CONCEPTS

If you analyze the evolution of a viral lineage, you discover that 80 percent of the genes have no counterpart in the genetic database. What this means is that viruses are capable of creating complex genes all by themselves. The oceans are filled with viruses like these, so what you have is genetic creativity on a very large scale, a kind of biological big bang.

— LUIS VILLARREAl

WHEN CHARLES DARWIN put forward his theory of evolution, he compared deliberate selection by humans — in the breeding of animals or crossing of grains for better yield — to what must also happen in "nature." To conceptualize this, he used the metaphor "natural selection." Darwin made no attempt to consider evolutionary change arising from interactions between species: he limited his theory to nature selecting the "fittest" individuals within a species. His theory also demanded a mechanism of inherited change, since nature required some degree of choice for selection to operate.

As we have seen, neo-Darwinism assumes that the mechanisms of genetic change — gene mutation and recombination of genes as part of sexual reproduction — are random and that the creative force is natural selection. A literary analogy makes the implications clear. Let us say that a writer merely jots down random thoughts as they come into his head, leaving it to the editor to make sense of the script. The editing, which is the essential role of natural selection for Darwinians, is more creative than the act of writing.

Symbiogenesis, the evolutionary force that derives from the interaction of different species, reverses this situation: the creative force is not natural selection but the act of symbiotic union.

The genome is, of course, the sum total of all the genetic material that makes up the heredity of any given life form. We have seen that this heredity is not confined to the nucleus but is shared between the nucleus and certain organelles within the cytoplasm. The study of genes is called genetics, and the study of how genomes work within themselves and how they compare with one another is called genomics. Both genetics and genomics have advanced at astonishing speed, opening up a new world that is of profound importance to the understanding of evolution. It is also a world in which symbiogenesis can be seen as a major evolutionary force, deriving from the essential nature of the genome, with its pluripotent capacity for change.

I propose to show that the genome has an additional capability above and beyond those of self-replication and template function. Implicit in its chemical structure — or "chemical behavior" — is the innate capacity for change.

In every example of evolution, genomic change always precedes natural selection. Smith and Szathmáry are in no doubt about this: “The crucial step [in evolution] is to understand the mechanism of heredity, because the whole process of evolution by natural selection depends on it.” In his metaphor of the selfish gene, Dawkins also directs attention to the genetic level. The genome is the ultimate determinant of life. The physical bodies we recognize — in plants, animals, fungi, protoctists, even bacteria — are all constructed around the template of their genomes. What natural selection does is select the consequences of genomic change that has already taken place when, for one reason or another, the physical expression of that change gives the organism some advantage for survival and, implicitly, better reproductive fitness. Any alternative theory of evolution, such as symbiosis, must, by implication, also govern and be governed by the genome.

In de Bary’s original definition of symbiosis as “the living together of differently named species,” he embraced parasitism and predation but excluded short-term associations. This definition has proved important and enduring, but its vagueness has given rise to what David Lewis, emeritus professor of botany at Sheffield University and a leading British authority on symbiosis, has described as “soggy semantics.” Some interpret de Bary’s insistence on long-term associations as excluding such mutualisms as the pollination of flowering plants by insects and hummingbirds. Such exclusions make no conceptual sense, since these involve interactions between different species with obvious evolutionary significance. Lewis has suggested that the concept of symbiosis merely requires that two organisms interact with each other. In his words, “It requires neither close nor prolonged association.”

Lynn Margulis subdivides the evolutionary force of symbiosis (symbiogenesis) into four categories of increasing intimacy: “ecological,” in which the interaction involves behavioral sharing; “metabolic,” in which a chemical product or metabolite is shared; “gene-product transfer,” in which a protein or RNA molecule is donated to a partner; and complete “gene transfer” between partners. I will adopt both Lewis’s and Margulis’s views and add in a third: the genomic perspective.

Werner Reisser, emeritus professor at the Botanical Institute at the University of Leipzig and a lifelong symbiologist, has long been interested in symbiotic green algae. In 1992, with the role of viruses in mind, he suggested a change to de Bary’s definition, from the “living together as different species” to the “interaction of dissimilar genomes.” With some slight redefinition to include the thinking of Lewis and Margulis, I propose the following genomically based defi-nition:

> Symbiogenesis is evolutionary change arising from the interaction of different species. It takes two major forms: endosymbiosis, in which the interaction is at the level of the genomes, and exosymbiosis, in which the interaction may be behavioral or involve the sharing of metabolites, including gene-coded products.

This definition will provide the basis for my discussion of the evolutionary role of symbiosis throughout the remainder of this book. Because symbiogenesis is rather a mouthful, I will revert to the simpler term “symbiosis” as an understood abbreviation for it. By genome I mean all of the hereditary material, that is, the DNA and RNA in the cytoplasm as well as the nucleus. The symbionts do not need to live together over the long term since this makes no difference from an evolutionary perspective. Moreover, from this genomic viewpoint, the definitions of endosymbiosis and exosymbiosis are somewhat different from their usual counterparts. The powerfully creative force of endosymbiosis is now given full emphasis: it is a mechanism for sudden evolutionary change arising from the fusion of genomes, whether this involves the transfer of a single gene or the blending of the genomes of different life forms. In this sense endosymbiosis equates with the fourth and most intimate of Margulis's categories.

The shared behavior of the hermit crab and the anemone is a typical example of exosymbiosis, which also includes the gut-living microbiota of ruminants and the root-living fungi of mycorrhizae. While endosymbiosis may be less common than exosymbiosis, it is much commoner than Darwinians assume.

In this definition of symbiogenesis I have avoided the term "fitness," which would be inappropriate since, as Kwang Jeon discovered, endosymbiosis does not necessarily improve survival or reproductive capacity. It could, indeed, be deleterious to the survival of one or more of the interacting partners, or to the resulting hybrid organism, the "holobiont." What symbiogenesis does is to create genetic change. Some fine-tuning of the symbiotic partnership will still be necessary, but if we attribute this role to natural selection we are employing a very different, indeed rather emasculated, concept compared to Darwin's. In symbiosis, the decisive evolutionary event is the interaction between life forms and not the subsequent honing of the organism.

My definition will help resolve some dilemmas. For example, the pollination associations involving insects, hummingbirds, and flowering plants are now readily accommodated as exosymbioses. It also clarifies the distinction between endosymbiosis and exosymbiosis in cases that might otherwise cause confusion. For example, a bacterium that lives within the tissues of its host is no longer endosymbiotic, as some would currently classify it, but exosymbiotic, unless we can demonstrate a direct interaction between the two genomes. It will also help resolve a dilemma that I consider to be the most important of all: the symbiotic evolutionary potential of viruses.

Biologists differ on whether or not viruses constitute living entities. It all comes down to one's definition of life, and, as Lovelock discovered, this is not as simple as it seems. Margulis, for example, takes the view that they are not, because they lack the chemical metabolism necessary for their own living processes. Having personally worked with viruses, both in the laboratory and in treating infected patients, and having sounded out the opinions of many other experts, I take a different view. For me, viruses are every bit as alive as a butterfly or a great blue whale.

Like all other life forms, viruses are coded by genes, made up of DNA or RNA. They are classified by strains (the equivalent of species), grouped within lineages called families. They replicate using genomic mechanisms similar to those of all other life forms. Viruses even have their own complex behaviors, for example, in penetrating the host's immune defenses, in locating the target organ and cell within the host while evading the fierce attack of antibodies and cellular immunity and, in the case of pandemic influenza viruses, in spreading throughout the world without any means of locomotion. I have taken this argument further in *Virus X,* but here it might be useful to summarize my views in the form of a thought experiment.

Let us suppose that our purpose is to create an organism that will survive and prosper in the strangest, most wonderful ecology on Earth: the living genome. Consider the characteristics this organism will need to possess. Physically, to inhabit what is essentially a molecular world, our hypothetical organism must be ultramicroscopic — as indeed viruses are, being on average about one one-thousandth the size of a bacterium. To accommodate the physiological and biochemical requirements of life on such a minuscule scale, the organism can take advantage of its environment, which is nothing other than a factory of genomic programming and manufacturing capability. In Darwinian terms, the organism adapts to its ecology.

Viruses are wonderfully adapted for survival within the genomes of their hosts. Indeed, if we do not regard them as alive, how do we deal with the awkward fact that all the laws of evolution apply to entities that are not living? Every viral infection involves a meeting of genomes. When the host is a single-celled life form, such as a bacterium or protist, or a germ cell in an animal, plant, or fungus, all biologists, whatever their views on viruses, agree that this interaction has evolutionary potential.

We are now ready to examine the mechanisms that underlie the broad sweep of evolution. In doing so we shall consider where and when the great evolutionary paradigms interact not only with each other but also with the inanimate world, as proposed by Lovelock's Gaia.

And where better to start than the very beginning, the first glimmer of life on Earth.