Darwin's Blind Spot

The Role of Living Interactions in Evolution

Frank Ryan

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The beautiful cover photograph of the "purple throated Carib

hummingbird feeding" was kindly provided by Charles J. Sharp – see

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For my sister Mary and my brother Tony

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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*

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PRAISE FOR FRANK RYAN'S PREVIOUS BOOKS

Tuberculosis: The Greatest Story Never Told

'Dr Ryan is superlatively good at explaining matters with which the reader may have no previous acquaintance. … he makes the story as exciting as a good detective novel. His book should be compulsory reading for those who ignorantly or dishonestly deny the power of science to contribute to human welfare.' – *The Sunday Telegraph*

'[Frank Ryan] tells the story of the discovery of the first antituberculosis drugs, and he tells it well, making a potentially dry subject fascinating with an upbeat, fast-moving detective story approach. Will the book appeal to the readership of *New Scientist*? Yes, it is clearly a popularist book, meant to appeal to a wider circle than scientific literati alone. All power to Ryan.' – *New Scientist*

'… a superbly documented, dramatic and alarming history of the ancient plague.' – *Publishers' Weekly*

'This is a story of heroic science performed by all-too-human scientists. Dr Ryan has done an admirable job of tracking down survivors, reconstructing a very complicated theory with newly available material and even-handedly assessing the versions already on record. [This] is an important book.' – *The New York Times Book Review*

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– *Wall Street Journal*

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– *The Washington Post*

'Ryan's book makes excellent reading because he combines accounts of his characters' achievements with their personal histories, gleaned from diaries, documents, and interviews with their contemporaries.'
– *The New York Review of Books*

Virus X: Understanding the Real Threat of the New Pandemic Plagues

'Extremely well written … Frank Ryan has the page-turning and spine-chilling ability of a good novelist.'

– Matt Ridley, author of *Genome: The Autobiography of a Species in 23 Chapters*, writing in *The Sunday Telegraph*

'Spellbinding … intellectually adventurous. Difficult to put down.'

– Valerius Geist, writing in *Nature*

'Ryan takes us through the drama of discovery and challenges the notion that certain questions are too appalling to contemplate.'

– New Scientist

'Compelling and frightening … the plot could not be bettered.'

– The Scotsman

'Ryan is very good at making technical matters comprehensible to the lay reader but more impressive still is the way he conveys the intellectual excitement and elation of scientific discovery.' *– Literary Review*

'Dr Ryan writes well in a difficult technical field, weaving the technicalities of scientific history, medicine, molecular biology and evolution into the human narratives of a sequence of epidemics, with victims, heroes (the medical teams) and villains (the politicians, more or less). Very readable and disturbing.' *– New York Times*

'Meticulously researched … with bracing ideas about coevolution, symbiosis and life's global web. … *Virus X* comes alive when Ryan delves into the science.' *– Washington Post Book World*

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 to serve 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 civilisation 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 it, the mystery he unravelled 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.'[1]

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 sterilised 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, 'favours only the prepared mind.'[2] In Jeon, a combination of personality and circumstance ensured that chance had favoured 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 programme. 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 and 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.

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. 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, parcelled 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. 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 behaviour. A broader understanding of evolution, taking into account not only interactions between species but also co-operation within our human species, would introduce some sense of balance into our understanding of these highly controversial aspects of human societal and psychosexual behaviour.

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 £28,000, which, if you added the buyer's premium, amounted to a staggering £31,000. 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 honour 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 of 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 centre 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 eulogised *The Origin* as 'the book that shook the world'.[1] Out went determinism, based on creationist theology; in came concepts such as probability and chance. Almost at once our self-centred 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 4004BC, 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

* Throughout this text I take billions in the American sense to mean 1000 million.

form of life, from the simple bacterium to the most complex and colourful 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[2] 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.'[3] 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 co-operative 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 mollusc. To protect its vulnerable hind parts, it curls backwards into the shell, securing the entrance with its armoured 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 coloured 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 co-operation, since the anemone in turn feeds on the droppings and leftovers from the crab's meals. The crab and the anemone appear to recognise each other[1] 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 colour. Specialised 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 fertilises the next flower it visits. In this way, flower and bird are partners in an exchange of food for assistance with fertilisation.

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 colourful 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 a 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 behavioural 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[2] to help explain this. Genomic intelligence allows us to see that a seemingly rational behaviour 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. 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 behaviour of a limited complexity is written into the genomes of crabs and anemones, enabling them to co-operate 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 behavioural 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 coloured. 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. 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 analysing the formative history of this discipline, Sapp describes how 'a neutral term was required for symbiosis that did not prejudge such relationships as parasitic'.[3] 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[4] as having first discovered and extensively investigated symbiosis.

De Bary, Frank, and Schwendener faced formidable opposition from their more conservative colleagues. Nevertheless, news of 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 molluscs, 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'.[5]

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 colour 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?'[6] He found it hard to believe that what he was observing was nothing more than parasitism. 'Everyone knows that the colourless 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 labours.' 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 co-operation was commonplace in nature.[7]

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.'[8]

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 recognise its fungal nature. Hartig went to his grave refusing to believe in the symbiotic union of trees and fungi.

Frank, meanwhile, conducted many further explorations into this strange, and wonderful, co-operation 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 co-operation, a union of two different beings into a single morphological organ. Frank called this organ a mycorrhiza, from the Greek for 'fungus-root'.

As realisation 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 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 photosynthesising 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 orchids to that of spermatozoa on eggs.

The intimate co-operation 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 centre stage. And as Darwinism, with its emphasis on competitive struggle, thrived, symbiosis, its co-operative *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.