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the intimacy of strangers

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HOW FUNGI MAKE OUR WORLDS,
CHANGE OUR MINDS &
SHAPE OUR FUTURES

RANDOM HOUSE
NEW YORK

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THE INTIMACY OF STRANGERS

The problem was that we did not know
whom we meant when we said "we."

—ADRIENNE RICH

On June 18, 2016, the descent module of a Soyuz spacecraft landed on a bleak steppe in Kazakhstan. Three people were pulled safely from the scorched capsule following a stint at the International Space Station (ISS). The astronauts weren't alone as they plummeted to Earth. Under their seats were hundreds of living organisms packed tightly in a box.

Among the samples were several species of lichen that had been sent into space for one and a half years as part of the Biology and Mars Experiment. BIOMEX is an international consortium of astrobiologists who use trays mounted on the outside of the ISS—a piece of apparatus known as the EXPOSE facility—to incubate biological specimens in extraterrestrial conditions. "Let's hope they have a safe return," Natuschka Lee, one of the BIOMEX lichen team, remarked to me a few days before the landing was scheduled. I wasn't sure who she meant by "they," but soon afterward Lee got in touch to say that all was well. She had received an e-mail from a lead researcher at the German Aerospace Center in Berlin, and read out the subject line, relieved: "EXPOSE trays back on Earth . . ." "Soon," Lee smiled, "we will have our samples back."

A number of organisms with extreme tolerances have been sent into orbit, from bacterial spores, to free-living algae, to rock-dwelling fungi, to tardigrades—microscopic animals known as "water bears." Some can survive if shielded from the damaging effects of solar radiation. But few, apart from a handful of lichen species, are able to survive in full space conditions, drenched in unfiltered cosmic rays. So remarkable are these lichens' abilities that they have become model life-forms for astrobiological research, ideal organisms "to discern," as one researcher writes, "the limits and limitations of terrestrial life."

It isn't the first time lichens have helped humans to fathom the limits of life as we know it. Lichens are living riddles. Since the nineteenth century, they have provoked fierce debate about what constitutes an autonomous individual. The closer we get to lichens, the stranger they seem. To this day, lichens confuse our concept of identity and force us to question where one organism stops and another begins.

IN HIS LAVISHLY illustrated book *Art Forms in Nature* (1904), the biologist and artist Ernst Haeckel vividly portrays a variety of lichen forms. His lichens sprout and layer deliriously. Veined ridges give way to smooth bubbles; stalks elaborate into prongs and dishes. Rugged coastlines meet unearthly pavilions, their forms lined with nooks and crannies. It was Haeckel who, in 1866, had coined the word *ecology*. Ecology describes the study of the relationships between organisms and their environments: both the places where they live and the thicket of relationships that sustain them. Inspired by the work of Alexander von Humboldt, the study of ecology emerged from the idea that nature is an interconnected whole, "a system of active forces." Organisms could not be understood in isolation.

Three years later, in 1869, the Swiss botanist Simon Schwendener published a paper advancing the "dual hypothesis of lichens." In it, he presented the radical notion that lichens were not a single organism, as had long been assumed. Instead, he argued that they were composed of two quite different entities: a fungus and an alga. Schwendener proposed that the lichen fungus (known today as the "mycobiont") offered physical protection and acquired nutrients for itself and for the algal cells. The algal partner (known today as the "photobiont," a role sometimes played by photosynthetic bacteria) harvested light and carbon dioxide to make sugars that provided energy. In Schwendener's view, the fungal partners were "parasites, although with the wisdom of statesmen." The algal partners were "its slaves . . . which it has sought out . . . and forced into its service." Together they grew into the visible body of the lichen. In their relationship, both partners were able to make a life in places where neither could survive alone.

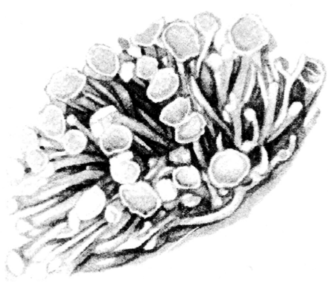
Schwendener's suggestion was vehemently opposed by his fellow lichenologists. The idea that two different species could come together in the building of a new organism with its own separate identity was shocking to many. "A useful and invigorating parasitism?" one contemporary snorted. "Who ever before heard of such a thing?" Others dismissed it as a "sensational romance," an "unnatural union between a captive Algal damsel and a tyrant Fungal master." Some were more moderate. "You see," wrote the English mycologist Beatrix Potter, best known for her children's books, "we do not believe in Schwendener's theory."

Most worrisome for taxonomists—working hard to order life into neat lines of descent—was the prospect that a single organism could contain two separate lineages. Following Charles Darwin's theory of evolution by natural selection, first published in 1859, species were understood to arise by *diverging* from one another. Their evolutionary lineages forked, like the branches of a tree. The trunk of the tree forked into branches, which forked into smaller branches, which forked into twigs. Species were the leaves on the twigs of the tree of life. However, the dual hypothesis suggested that lichens were bodies composed of organisms with quite different origins. Within lichens, branches of the tree of life that had been diverging for hundreds of millions of years were doing something entirely unexpected: *converging*.

Over the following decades a growing number of biologists adopted the dual hypothesis, but many disagreed with Schwendener's portrayal of the relationship. These were not sentimental concerns: Schwendener's choice of metaphor obstructed the larger questions raised by the dual hypothesis. In 1877, the German botanist Albert Frank coined the word *symbiosis* to describe the living together of fungal and algal partners. In his study of lichens, it had become clear to him that a new word was required, one that didn't prejudice the relationship it described. Shortly afterward, the biologist Heinrich Anton de Bary adopted Frank's term and generalized it to refer to the full spectrum of interactions between any type of organism, stretching from parasitism at one pole, to mutually beneficial relationships at the other.

Scientists made a number of major new symbiotic claims in the years that followed, including startling suggestions from Frank that fungi might help plants to obtain nutrients from the soil (1885). All cited the dual hypothesis of lichens in support of their ideas. When algae were found living inside corals, sponges, and green sea slugs, they were described by one researcher as "animal lichens." Several years later, when viruses were first observed within bacteria, their discoverer described them as "microlichens."

Lichens, in other words, quickly grew into a biological principle. They were a gateway organism to the idea of symbiosis, an idea that ran against the prevailing currents in evolutionary thought in the late-nineteenth and early-twentieth centuries, best summed up in Thomas Henry Huxley's portrayal of life as a "gladiator's show . . . whereby the strongest, the swiftest, and the cunningest live to fight another day." In the wake of the dual hypothesis, evolution could no longer be thought of solely in terms of competition and conflict. Lichens had become a type case of inter-kingdom collaboration.



Lichen: *Niebla*

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LICHENS ENCRUST AS much as eight percent of the planet's surface, an area larger than that covered by tropical rainforests. They clad rocks, trees, roofs, fences, cliffs, and the surface of deserts. Some are a drab camouflage. Some are lime green or electric yellow. Some look like stains, others like small shrubs, others like antlers. Some leather and droop like bat wings, others, as the poet Brenda Hillman writes, are "hung in hashtags." Some live on beetles, whose lives depend on the camouflage the lichens provide. Untethered lichens—known as "vagrants" or "erratics"— blow around and don't live their lives *on* anything in particular. Against the "plain story" of their surroundings, observes Kerry Knudsen, the curator of lichens at the herbarium at the University of California, Riverside, lichens "look like fairy tales."

I have been most captivated by lichens on the islands off the coast of British Columbia, on the west coast of Canada. Seen from above, the coastline frays into the ocean. There is no hard edge. The land comes undone gradually into inlets and sounds, and then into channels and passages. Hundreds of islands scatter off the coast. Some are no bigger than a whale; the largest, Vancouver Island, is half the length of Britain. Most of the islands are solid granitic rock, the tops of submarine hills and valleys worn smooth by glaciers.

For a few days every year, I and a handful of friends pile onto a twenty-eight-foot sailboat and set off around the islands. The boat, the *Caper*, has a dark green hull, no keel, and one red sail. Making our way from the *Caper* onto land is tricky. We paddle in an unstable dinghy with oars that slip their rowlocks at every other stroke. Pulling up to the shore is an art form. Waves shrug the dinghy onto the rocks and tug it away from our feet as we clamber out. But once on shore, the lichens begin. I've spent hours absorbed in the worlds that they make—islands of life in a sea of rock. The names used to describe lichens sound like afflictions, words that get stuck in your teeth: crustose (crusty), foliose (leafy), squamulose (scaly), leprose (dusty), fruticose (branched). Fruticose lichens drape and tuft; crustose and squamulose lichens creep and seep; foliose lichens layer and flake.

Some prefer to live on east-facing surfaces, some on the west. Some choose to live on exposed ledges, others in damp grooves. Some wage slow wars, repelling or disrupting their neighbors. Some inhabit the surfaces left exposed when other lichens have died and flaked off. They come to resemble the archipelagos and continents of an unfamiliar atlas, which is how *Rhizocarpon geographicum*, or the map lichen, got its name. The oldest surfaces are pitted by centuries of lichenous life and death.

Lichens' fondness for rock has changed the face of the planet and continues to do so, sometimes literally. In 2006, the faces of the presidents carved into Mount Rushmore were pressure hosed, removing more than sixty years of lichenous growth in the hope of extending the lifetime of the memorial. The presidents aren't alone. "Every monument," writes the poet Drew Milne, "has a lichen lining." In 2019, the residents of Easter Island launched a campaign to scrub lichens off hundreds of monumental stone heads, or moai. Described by locals as "leprosy," lichens are deforming the features of the statues and softening the rock to a "clay-like" consistency.

Lichens mine minerals from rock in a twofold process known as "weathering." First, they physically break up surfaces by the force of their growth. Second, they deploy an arsenal of powerful acids and mineral-binding compounds to dissolve and digest the rock. Lichens' ability to weather makes them a geological force, yet they do more than dissolve the physical features of the world. When lichens die and decompose, they give rise to the first soils in new ecosystems. Lichens are how the inanimate mineral mass within rocks is able to cross over into the metabolic cycles of the living. A portion of the minerals in your body is likely to have passed through a lichen at some point. Whether on tombstones in a graveyard or encased within slabs of Antarctic granite, lichens are go-betweens that inhabit the boundary dividing life and nonlife. Looking out from the *Caper* at the rocky Canadian coastline, this becomes clear. Above the tideline, it is only after several meters of lichens and mosses that larger trees start to appear, rooted in crevices well beyond the water's reach where young soils have been able to form.

Lichen: *Ramalina*

THE QUESTION OF what is and isn't an island is fundamental to the study of ecology and evolution. It is no less important for astrobiologists, including those on the BIOMEX team, many of whom wrestle with the question of "panspermia," from the Greek *pan* meaning "all" and *sperma* meaning "seed." Panspermia deals with the question of whether planets, too, are islands, and whether life can travel through space between celestial bodies. It is an idea that has circulated since antiquity, although it didn't take on the form of a scientific hypothesis until the early twentieth century. Some advocates argue that life itself arrived from other planets. Some propose instead that life evolved on Earth *and* elsewhere, and periods of dramatic evolutionary novelty on Earth were triggered by the arrival of fragments of life from space. Others argue instead for a "soft-panspermia," where life itself evolved on Earth but the chemical building blocks required for life arrived from space. There are many hypotheses as to how interplanetary transport might take place. Most are variations on a theme: Organisms get trapped within asteroids or other debris ejected from planets during collisions with meteorites, and hurtle through space before colliding with another planetary body on which they may or may not be able to make a life.

In the late 1950s, as the United States prepared to send rockets into space, the biologist Joshua Lederberg became concerned about the prospect of celestial contamination (it was Lederberg who in 2001 coined the word *microbiome*). Humans were now able to spread earthly organisms to other parts of the solar system. More worrying was the thought that humans could bring back to Earth alien organisms that could cause ecological disruption—or worse, wreak havoc as diseases. Lederberg wrote urgent letters to the National Academy of Sciences to warn them of the possible "cosmic catastrophe." They paid attention and released an official statement of concern. There was still no word to describe the science of extraterrestrial life, so Lederberg coined one: *exobiology.* It was the first version of the field now known as astrobiology.

Lederberg was a prodigy. He enrolled at Columbia University at the age of fifteen and in his early twenties made a discovery that helped transform our understanding of the history of life. He found that bacteria could trade genes with each other. One bacterium could acquire a trait from another bacterium "horizontally." Characteristics acquired horizontally are those that aren't inherited "vertically" from one's parents. One picks them up along the way. We're used to the principle. When we learn or teach something, we're part of a horizontal exchange of information. Much of human culture and behavior is transmitted in this fashion. However, for humans to engage in horizontal gene transfer as bacteria do is a fantastical prospect, even though it has taken place on occasion, deep in our evolutionary history. Horizontal gene transfer means that genes—and the traits they encode—are infectious. It is as if we noticed an unmarked trait lying by the side of the road, tried it on, and found that we had acquired a pair of dimples. Or perhaps we met someone on the street and swapped our straight hair for their curly hair. Or maybe we just picked up their eye color. Or brushed up against a wolfhound quite by accident and developed an urge to run fast for several hours a day.

Lederberg's discovery won him a Nobel Prize at the age of thirty-three. Before horizontal gene transfer was discovered, bacteria, like all other organisms, were understood to be biological islands. Genomes were closed systems. There was no way to take on new DNA midway through a lifetime, to acquire genes that had evolved "off-site." Horizontal gene transfer changes this picture and shows bacterial genomes to be cosmopolitan places, made up of genes that had evolved separately for millions of years. Horizontal gene transfer implied, as lichens had before, that branches of the evolutionary tree that had long since diverged were able to converge within the body of a single organism.

For bacteria, horizontal gene transfer is the norm—most of the genes in any given bacterium do not share an evolutionary history but are acquired piecemeal, just as objects accumulate in a home. In this way, a bacterium can acquire characteristics "ready-made," speeding up evolution many times over. By exchanging DNA, a harmless bacterium can acquire antibiotic resistance and metamorphose into a virulent superbug in a single move. Over the last few decades it has become clear that bacteria aren't alone in this ability, although they remain its most adept practitioners: Genetic material has been exchanged horizontally between all the domains of life.

Lederberg's ideas were tinged with Cold War paranoia. In his hands, panspermia came to resemble horizontal gene transfer on a cosmic scale. For the first time in history, humans were capable—in theory—of infecting Earth and other planets with organisms that had not evolved on-site. Life on Earth could no longer be considered a genetically closed system, a planetary island in an uncrossable sea. Just as bacteria could fast-forward evolution by picking up DNA horizontally, so the arrival of foreign DNA on Earth could "short-circuit" the otherwise "tortuous" process of evolution, with potentially catastrophic consequences.

ONE OF THE main objectives of BIOMEX is to find out whether lifeforms can indeed survive a journey through space. Conditions outside the protective skin of the Earth's atmosphere are hostile. Among the many hazards are massive levels of radiation from the sun and other stars; a vacuum that causes biological material, lichens included, to dry out almost immediately; and rapid cycles of freezing, thawing, and heating, with temperatures that swing from −120 to +120 degrees Centigrade and back again within twenty-four hours.

The first attempt to send lichens into space didn't end well. In 2002, an unmanned Soyuz rocket carrying the samples exploded and crashed seconds after liftoff from a Russian spaceport. Months after the accident, when the snow had melted, the remains of the cargo were recovered. "Curiously enough," the lead researchers reported, "the LICHENS experiment was one of the few identifiable pieces of wreckage, and we discovered that despite the circumstances, the lichen[s] . . . still showed some degree of biological activity."

The capacity of lichens to survive in space has since been demonstrated in a number of studies, and the findings are broadly the same. The hardiest lichen species can recover their metabolic activity in full within twenty-four hours of being rehydrated and are able to repair much of the "space-induced" damage they may have sustained. In fact, the toughest species—*Circinaria gyrosa*—has such high survival rates that three recent studies decided to expose samples to even higher levels of radiation than they receive in space, to test them to their "uttermost limits of survival." Sure enough, a dose of radiation could kill the lichens, but the amount required to disrupt their cells was enormous. Lichen samples exposed to six kilograys of gamma irradiation—six times the standard dose for food sterilization in the United States and twelve thousand times the lethal dose for humans—were entirely untroubled. When the dose was doubled to twelve kilograys—two and a half times the lethal dose for tardigrades—the lichens' ability to reproduce was impaired, although they survived and continued to photosynthesize with no apparent problems.

For Trevor Goward, the curator of the lichen collection at the University of British Columbia, the extreme tolerances of lichens are an example of what he calls the "lichening rod effect." Lichens invite flashes of insight, or "supercharged understanding" in Goward's words. The lichening rod effect describes what happens when lichens strike familiar concepts, splintering them into new forms. The idea of symbiosis is one such example. Survival in space is another, as is the threat that lichens pose to systems of biological classification. "Lichens tell us things about *life*," Goward exclaimed to me. "*They inform us.*"

Goward is foremost a lichen obsessive (he has contributed around thirty thousand lichen specimens to the university collection) and is no less a lichen taxonomist (he has named three genera and described thirty-six new lichen species). But he has the feel of a mystic about him. "I like to say that lichens colonized the surface of my mind many years ago," he told me with a chuckle. He lives on the edge of a large wilderness in British Columbia and runs a website called Ways of Enlichenment. For Goward, thinking deeply about lichens changes the way we apprehend life; they are organisms that can lure us toward new questions and into new answers. "What is our relationship to the world? What are we *about*?" Astrobiology pitches these questions at a cosmic scale. No wonder that lichens loom—if not large, then certainly vivid—at the front and center of the panspermia debate.

However, it is closer to home that lichens and the concept of symbiosis they embody have triggered the most profound existential questions. Over the twentieth century, the concept of inter-kingdom collaboration transformed scientific understanding of how complex life-forms evolved. Goward's questions may sound theatrical, but it is precisely our relationship to the world that lichens and their symbiotic way of life have led us to reexamine.

Life is divided into three domains. Bacteria make up one. Archaea—single-celled microbes that resemble bacteria but which build their membranes differently—make up another. Eukarya make up the third. We're eukaryotes (pronounced *you-KA-ree-otes*), as are all other multicellular organisms, whether animal, plant, alga, or fungus. The cells of eukaryotes are larger than bacterial and archaeal cells, and organize themselves around a number of specialized structures. One such structure is the nucleus, which contains most of the DNA in a cell. Mitochondria—the places where energy is produced—are another. Plants and algae have a further structure: chloroplasts, where photosynthesis happens.

In 1967, the visionary American biologist Lynn Margulis became a vocal proponent of a controversial theory that gave symbiosis a central role in the evolution of early life. Margulis argued that some of the most significant moments in evolution had resulted from the coming together—and staying together—of different organisms. Eukaryotes arose when a single-celled organism engulfed a bacterium, which continued to live symbiotically inside it. Mitochondria were the descendants of these bacteria. Chloroplasts were the descendants of photosynthetic bacteria that had been engulfed by an early eukaryotic cell. All complex life that followed, human life included, was a story of the long-lasting "intimacy of strangers."

The idea that eukaryotes had arisen "by fusion and merger" had drifted in and out of biological thought since the start of the twentieth century, but it had remained at the margins of "polite biological society." By 1967, little had changed, and Margulis's manuscript was rejected fifteen times before it was finally accepted. After publication, her ideas were vigorously opposed, as similar suggestions had been before. (In 1970, the microbiologist Roger Stanier waspishly remarked that Margulis's "evolutionary speculation . . . can be considered a relatively harmless habit, like eating peanuts, unless it assumes the form of an obsession; then it becomes a vice.") However, in the 1970s Margulis was proved correct. New genetic tools revealed that mitochondria and chloroplasts had indeed started off as free-living bacteria. Since then, other examples of endosymbiosis have been found. The cells of some insects, for example, are inhabited by bacteria that themselves contain bacteria.

Margulis's proposition amounted to a dual hypothesis of early eukaryotic life. No surprise, then, that she mobilized lichens to fight her cause—so too had the earliest proponents of her view at the turn of the twentieth century. The earliest eukaryotic cells could be thought of as "quite analogous" to lichens, she argued. Lichens continued to figure prominently in her work over the following decades. "Lichens are remarkable examples of innovation emerging from partnership," she later wrote. "The association is far more than the sum of its parts."

The endosymbiotic theory, as it came to be known, rewrote the history of life. It was one of the twentieth century's most dramatic shifts in biological consensus. The evolutionary biologist Richard Dawkins went on to congratulate Margulis on "sticking by" the theory, "from unorthodoxy to orthodoxy." "It is one of the great achievements of twentieth-century evolutionary biology," Dawkins continued, "and I greatly admire Lynn Margulis's sheer courage and stamina." The philosopher Daniel Dennett described Margulis's theory as "one of the most beautiful ideas [he'd] ever encountered," and Margulis as "one of the heroes of twentieth-century biology."

Among the biggest implications of the endosymbiotic theory is that whole suites of abilities have been acquired in a flash, in evolutionary terms, ready-evolved, from organisms that are not one's parents, nor one's species, kingdom, or even domain. Lederberg demonstrated that bacteria can horizontally acquire genes. The endosymbiotic theory proposed that single-celled organisms had horizontally acquired entire bacteria. Horizontal gene transfer transformed bacterial genomes into cosmopolitan places; endosymbiosis transformed cells into cosmopolitan places. The ancestors of all modern eukaryotes horizontally acquired a bacterium with a preexisting ability to release energy using oxygen. Likewise, the ancestors of today's plants horizontally acquired bacteria with the ability to photosynthesize, ready-evolved.

In fact, this wording doesn't get it quite right. The ancestors of today's plants didn't acquire a bacterium with the ability to photosynthesize; they emerged from the combination of organisms that could photosynthesize with organisms that couldn't. In the two billion years that they have lived together, both have become increasingly dependent on each other to the point we find ourselves in today, where neither can live without the other. Within eukaryotic cells, distant branches of the tree of life entwine and melt into an inseparable new lineage; they fuse, or anastomose, as fungal hyphae do.

Lichens don't reenact the origin of the eukaryotic cell exactly, but as Goward remarks, they certainly "rhyme" with it. Lichens are cosmopolitan bodies, a place where lives meet. A fungus can't photosynthesize by itself, but by partnering with an alga or photosynthetic bacterium it can acquire this ability horizontally. Similarly, an alga or photosynthetic bacterium can't grow tough layers of protective tissue or digest rock, but by partnering with a fungus it gains access to these capabilities—suddenly. Together, these taxonomically remote organisms build composite life-forms capable of entirely new possibilities. By comparison with plant cells that can't be parted from their chloroplasts, lichens' relationships are open. This gives them flexibility. In some situations, lichens reproduce without breaking up their relationship—fragments of a lichen containing all the symbiotic partners can travel as one to a new location and grow into a new lichen. In other situations, lichen fungi produce spores that travel alone. Upon arrival in a new place, the fungus must meet a compatible photobiont and form their relationship afresh.

In joining forces, the fungal partners became part photobiont and the photobionts part fungus. Yet lichens resemble neither. Just as the chemical elements of hydrogen and oxygen combine to make water, a compound entirely unlike either of its constituent elements, so lichens are emergent phenomena, entirely more than the sum of their parts. As Goward emphasizes, it is a point so simple that it is hard to grasp. "I often say that the only people who *can't* see a lichen are lichenologists. It's because they look at the parts, as scientists are trained to do. The trouble is that if you look at the parts of the lichen, *you don't see the lichen itself*."

IT IS EXACTLY the emergent forms of lichens that are interesting from an astrobiological point of view. In the words of one study, "it is hard to imagine a biological system that better summarizes the characteristics of life on Earth." Lichens are small biospheres that include both photosynthetic and non-photosynthetic organisms, thus combining the Earth's main metabolic processes. Lichens are, in some sense, micro-planets—worlds writ small.

But what, exactly, do lichens do while in orbit around the Earth? To get around the problem of monitoring biological samples while they're in space, members of the BIOMEX team harvested specimens of the hardy species *Circinaria gyrosa* from the arid highlands of central Spain and took them to a Mars simulation facility. By exposing the lichens to space-like conditions on Earth, they hoped to be able to measure the lichens' activity in real time. It turned out there wasn't much to measure. Within an hour of "turning on" Mars, the lichens had reduced their photosynthetic activity to near zero. They remained dormant for the rest of their time in the simulator and resumed their normal activity when rehydrated thirty days later.

It is well-known that the ability of lichens to survive extreme conditions depends on them entering a state of suspended animation—some studies have found that they can be successfully resuscitated after ten years of dehydration. If their tissues are dehydrated then freezing, thawing, and heating don't cause much damage. Dehydration also protects them from the most hazardous consequence of cosmic rays: highly reactive free radicals, produced when radiation cleaves water molecules in two, that damage the structure of DNA.

Dormancy appears to be the most important survival strategy for lichens, but they have others. The hardiest lichen species have thick layers of tissue that block damaging rays. Lichens also produce more than a thousand chemicals that are not found in any other life-form, some of which act as sunscreens. A product of their innovative metabolisms, these chemicals have led lichens into all sorts of relationships with humans over the years: from medicines (antibiotics), to perfumes (oak moss), to dyes (tweeds, tartan, the pH indicator litmus), to foods—a lichen is one of the principal ingredients in the spice mix garam masala. Many fungi that produce compounds of importance to humans—including penicillin molds—lived as lichens earlier in their evolutionary history but have since ceased to do so. Some researchers suggest that a number of these compounds, penicillin included, may have originally evolved as defensive strategies in ancestral lichens and persist today as metabolic legacies of the relationship.

Lichens are "extremophiles," organisms able to live, from our point of view, in other worlds. The tolerances of extremophiles are inconceivable. Collect samples in volcanic springs, superheated hydrothermal vents, a kilometer under the ice in Antarctica, and you'll find extremophilic microbes living, apparently unfazed. Recent findings from the Deep Carbon Observatory report that more than half of all Earth's bacteria and archaea—so called "infra-terrestrials"—exist kilometers below the planet's surface, where they live under intense pressure and extreme heat. These subsurface worlds are as diverse as the Amazon rainforest and contain billions of tons of microbes, hundreds of times the collective weight of all the humans on the planet. Some specimens are thousands of years old.

Lichens are no less impressive. Indeed, their ability to survive many different types of extreme qualify them as "polyextremophiles." In the hottest, driest parts of the world's deserts, you'll find lichens prospering as crusts on the scorched ground. Lichens play a critical ecological role in these environments, stabilizing the sandy surface of deserts, reducing dust storms, and preventing further desertification. Some lichens grow inside cracks or pores within solid rock. The authors of one study, reporting the presence of lichens within chunks of granite, confess that they have no idea how these lichens got there in the first place. Several species of lichen are able to make a runaway success of life in the Antarctic Dry Valleys—an ecosystem so fierce it is used to approximate conditions on Mars. Long periods of freezing temperatures, irradiation with high levels of UV, and near absence of water don't seem to trouble them. Even after immersion in liquid nitrogen at −195 degrees Centigrade, lichens revive rapidly. And they live far longer than most organisms. The record-holding lichen lives in Swedish Lapland and is more than nine thousand years old.

In the already curious world of extremophiles, lichens are unusual for two reasons. First, they are complex multicellular organisms. Second, they arise from a symbiosis. Most extremophiles don't develop such sophisticated forms and enduring relationships. This is part of what makes lichens so interesting for astrobiologists. A lichen moving through space is a neat bundle of life—a whole ecosystem traveling as one. What better organisms to make interplanetary journeys?

Although a number of studies have shown that lichens are capable of surviving in outer space, to be transported between planets, they would have to survive two additional challenges. First, the shock of their ejection from a planet by a meteorite. Second, the reentry into a planetary atmosphere. Both present considerable hazards. Nonetheless, the shock of ejection is unlikely to be too much for them. In 2007, researchers demonstrated that lichens could withstand shock waves with a pressure of 10 to 50 gigapascals, 100 to 500 times greater than the pressure at the bottom of the Mariana Trench, the deepest place on Earth. This is well within the range of shock pressures experienced by rocks catapulted by meteorites into escape velocity from the surface of Mars. Reentry into a planetary atmosphere might present more of a problem. In 2007, samples of bacteria and a rock-dwelling lichen were attached to the heat shield of a reentry capsule. As the capsule scorched through the Earth's atmosphere, the samples were exposed to temperatures of more than two thousand degrees Centigrade for thirty seconds. In the process, the rocks partially melted and crystallized into new forms. When the remains were examined, there was no sign of any living cell whatsoever.

This finding hasn't disheartened astrobiologists. Some argue that life-forms encased deep within large meteorites would be protected from these extremes. Others point out that most of the material that arrives on Earth from space does so in the form of micro-meteorites, a type of cosmic dust. These small particles experience less friction and lower temperatures as they enter the atmosphere, and may be more likely to carry life-forms safely to Earth than rocket capsules. As a number of researchers cheerily announce, the question remains open.

NO ONE KNOWS when lichens first evolved. The earliest fossils date from just over four hundred million years ago, but it's possible that lichen-like organisms occurred before this. Lichens have evolved independently between nine and twelve times since. Today, one in five of all known fungal species form lichens, or "lichenize." Some fungi (such as *Penicillium* molds) used to lichenize but don't anymore; they have de-lichenized. Some fungi have switched to different types of photosynthetic partner—or re-lichenized—over the course of their evolutionary histories. For some fungi, lichenization remains a lifestyle choice; they can live as lichens or not depending on their circumstances.

It turns out that fungi and algae come together at the slightest provocation. Grow many types of free-living fungus and algae together, and they'll develop into a mutually beneficial symbiosis in a matter of days. Different species of fungus, different species of algae—it doesn't seem to matter. Completely new symbiotic relationships emerge in less time than it takes for a scab to heal. These remarkable findings, rare glimpses of the "birth" of new symbiotic relationships, were published in 2014 by researchers at Harvard University. When fungi were grown with algae, they coalesced into visible forms that looked like soft green balls. They weren't the elaborate lichen forms depicted by Ernst Haeckel and Beatrix Potter. But then, they hadn't spent millions of years in each other's company.

Not just any fungus could partner with any alga, however. One critical condition had to be fulfilled for a symbiotic relationship to arise: Each partner had to be able to do something that the other couldn't achieve on its own. The identity of the partners didn't matter so much as their ecological fit. In the words of the evolutionary theorist W. Ford Doolittle, it was "the song, not the singer" that appeared to be important. This finding sheds light on lichens' ability to survive in extreme conditions. As Goward points out, lichens by their nature are a kind of "shotgun marriage" that arises in conditions too severe for either partner to survive alone. Whenever it was that lichens occurred for the first time, their very existence implies that life outside the lichen was less bearable, that together they were able to sing a metabolic "song" that neither can sing in isolation. Viewed in this way, lichens' extremophilia, their ability to live life on the edge, is as old as lichens themselves and a direct consequence of their symbiotic way of life.

There is no need to go to the Antarctic Dry Valleys or a Mars simulation facility to see lichen extremophilia in action. Most shorelines will do just fine. It is on the rocky coast of British Columbia that I've found lichens' tenacity most eye-catching. A foot or so above the barnacles, just beyond the farthest reach of the water, is a black smear that stretches across the rock in a band about two feet high. Close up, it looks like cracked tar on a dock. It forms a ribbon that traces the line of the shore, which becomes important when we're sailing around the islands. We use it when we anchor, to help us bet against the tide; it is a sure indicator of the limits of the water's reach. The dry-land mark.

The black streak is a type of lichen, though one might never guess it was a living organism. It certainly doesn't grow into elaborate structures. Nonetheless, along much of the upper West Coast of North America this species, *Hydropunctaria maura* (water speckled midnight), is the first organism to live beyond the reach of the waves. Look at high-tide lines around the world and you'll see something similar. Most rocky shorelines are rimmed with lichen. Lichens start where the seaweeds stop, and some extend down into the water. When a volcano creates a new island in the middle of the Pacific Ocean, the first things to grow on the bare rock are lichens, which arrive as spores or fragments carried by the wind or birds. Likewise when a glacier retreats. The growth of lichens on freshly exposed rock is a variation on the theme of panspermia. These bare surfaces are inhospitable islands, remote possibilities for most organisms. Barren, seared by intense radiation, and exposed to wild storms and temperature fluctuations, they may as well be other planets.

LICHENS ARE PLACES where an organism unravels into an ecosystem and where an ecosystem congeals into an organism. They flicker between "wholes" and "collections of parts." Shuttling between the two perspectives is a confusing experience. The word *individual* comes from the Latin meaning "undividable." Is the whole lichen the individual? Or are its constituent members, the parts, the individuals? Is this even the right question to ask? Lichens are a product less of their parts than of the exchanges between those parts. Lichens are stabilized networks of relationships; they never stop lichenizing; they are verbs as well as nouns.

One of the people worrying these categories is a lichenologist from Montana called Toby Spribille. In 2016, Spribille and his colleagues published a paper in the journal *Science* that pulled the rug from underneath the dual hypothesis. Spribille described a new fungal participant in one of the major evolutionary lineages of lichens, a partner that had gone entirely undetected despite one and a half centuries of painstaking scrutiny.

Spribille's discovery was an accident. A friend challenged him to grind up a lichen and sequence the DNA of all its participant organisms. He expected the results to be straightforward. "The textbooks were clear," he told me. "There could only be two partners." However, the more Spribille looked, the less this appeared to be the case.

Each time he analyzed a lichen of this type, he found additional organisms besides the expected fungus and alga. "I dealt with these 'contaminant' organisms for a long time," he recalled, "until I convinced myself that there was no such thing as lichens without 'contamination,' and we found that the 'contaminants' were remarkably consistent. The more we dug in, the more they seemed to be the rule not the exception."

Researchers have long hypothesized that lichens might involve additional symbiotic partners. After all, lichens don't contain microbiomes. They *are* microbiomes, packed with fungi and bacteria besides the two established players. Nonetheless, until 2016, no new stable partnerships had been described. One of the "contaminants" Spribille discovered—a single-celled yeast—turned out to be more than a temporary resident. It is found in lichens across six continents and can make such a substantial contribution to lichens' physiology as to give them the appearance of an entirely different species. This yeast was a crucial third partner in the symbiosis. Spribille's bombshell finding was only the beginning. Two years later, he and his team found that wolf lichens—some of the best-studied species—contain yet another fungal species, a *fourth* fungal partner. Lichens' identity splintered into even smaller shards. Yet this is still an oversimplification, Spribille told me. "The situation is infinitely more complex than anything we've published. The 'basic set' of partners is different for every lichen group. Some have more bacteria, some fewer; some have one yeast species, some have two, or none. Interestingly, we have yet to find any lichen that matches the traditional definition of one fungus and one alga."

What do the new fungal partners actually *do* in the lichen, I asked. "We're not yet sure," Spribille replied. "Every time we go in and try to find out who's doing what, we get confounded. Instead of finding out the roles of the players, we bump into yet more players. The deeper we dig, the more we find."

Spribille's findings are troubling for some researchers because they suggest that the lichen symbiosis is not as "locked in" as it has been thought to be. "Some people think about symbiosis as being like a package from IKEA," Spribille explained, "with clearly identified parts, and functions, and order in which it's assembled." His findings suggest instead that a broad range of different players might be able to form a lichen, and that they just need to "tickle each other in the right way." It's less about the identity of the "singers" in the lichen, and more about what they do—the metabolic "song" that each of them sings. In this view, lichens are dynamic *systems* rather than a catalogue of interacting components.

It's a very different picture from the dual hypothesis. Since Schwendener's portrayal of the fungus and alga as master and slave, biologists have argued about which of the two partners is in control of the other. But now a duet has become a trio, the trio has become quartet, and the quartet sounds more like a choir. Spribille seems unperturbed by the fact that it isn't possible to provide a single, stable definition of what a lichen actually is. It is a point Goward often returns to, relishing the absurdity: "There is an entire discipline that can't define what it is that they study?" "It doesn't matter what you call it," writes Hillman on lichens. "Anything so radical & ordinary stands for something." For more than a hundred years, lichens have stood for many things and will probably continue to challenge our understanding of what living organisms are.

Meanwhile, Spribille is pursuing a number of promising new leads. "Lichens are completely jam-packed full of bacteria," he told me. In fact, lichens contain so many bacteria that some researchers hypothesize—in another twist on the panspermia theme—that they act as microbial reservoirs that seed barren habitats with crucial bacterial strains. Within lichens, some bacteria provide defense; others make vitamins and hormones. Spribille suspects that they might be doing more. "I think a few of these bacteria might be necessary to tie the lichen system together and get it to form something other than a blob on a dish."

Spribille told me about a paper called "Queer theory for lichens." ("It comes up as the first thing in Google when you enter 'queer' and 'lichen.'") Its author argues that lichens are queer beings that present ways for humans to think beyond a rigid binary framework: The identity of lichens is a question rather than an answer known in advance. In turn, Spribille has found queer theory a helpful framework to apply to lichens. "The human binary view has made it difficult to ask questions that aren't binary," he explained. "Our strictures about sexuality make it difficult to ask questions about sexuality, and so on. We ask questions from the perspective of our cultural context. And this makes it extremely difficult to ask questions about complex symbioses like lichens because we think of ourselves as autonomous individuals and so find it hard to relate."

Spribille describes lichens as the most "extroverted" of all symbioses. Yet it is no longer possible to conceive of any organism—humans included—as distinct from the microbial communities they share a body with. The biological identity of most organisms can't be pried apart from the life of their microbial symbionts. The word *ecology* has its roots in the Greek word *oikos,* meaning "house," "household," or "dwelling place." Our bodies, like those of all other organisms, are dwelling places. Life is nested biomes all the way down.

We can't be defined on anatomical grounds because our bodies are shared with microbes and consist of more microbial cells than our "own"—cows can't eat grass, for example, but their microbial populations can, and cows' bodies have evolved to house the microbes that sustain them. Neither can we be defined developmentally, as the organism that proceeds from the fertilization of an animal egg, because we depend, like all mammals, on our symbiotic partners to direct parts of our developmental programs. Nor is it possible to define us genetically, as bodies made up of cells that share an identical genome—many of our symbiotic microbial partners are inherited from our mothers alongside our "own" DNA, and at points in our evolutionary history, microbial associates have permanently insinuated themselves into the cells of their hosts: Our mitochondria have their own genome as do plants' chloroplasts, and at least eight percent of the human genome originated in viruses (we can even swap cells with other humans when we grow into "chimeras," formed when mothers and fetuses exchange cells or genetic material in utero). Nor can our immune systems be taken as a measure of individuality, although our immune cells are often thought of as answering this question for us by distinguishing "self" from "nonself." Immune systems are as concerned with managing our relationships with our resident microbes as fighting off external attackers and appear to have evolved to enable colonization by microbes rather than prevent it. Where does this leave you? Or perhaps y'all?

Some researchers use the term "holobiont" to refer to an assemblage of different organisms that behaves as a unit. The word *holobiont* derives from the Greek word *holos,* which means "whole." Holobionts are the lichens of this world, more than the sums of their parts. Like symbiosis and ecology, holobiont is a word that does useful work. If we only have words that describe neatly bounded autonomous individuals, it is easy to think that they actually exist.

The holobiont is not a utopian concept. Collaboration is always a blend of competition and cooperation. There are many instances where the interests of all the symbionts don't align. A bacterial species in our gut can make up a key part of our digestive system but cause a deadly infection if it gets into our blood. We're used to this idea. A family can function as a family, a touring jazz group can give a captivating performance, and both still be fraught with tension.

Perhaps it isn't so hard for us to relate to lichens after all. This sort of relationship-building enacts one of the oldest evolutionary maxims. If the word *cyborg*—short for "cybernetic organism"—describes the fusion between a living organism and a piece of technology, then we, like all other life-forms are symborgs, or symbiotic organisms. The authors of a seminal paper on the symbiotic view of life take a clear stance on this point. "There have never been individuals," they declare. "We are all lichens."

DRIFTING AROUND ON the *Caper*, we spend a lot of time looking at sea charts. On these maps, the familiar role of sea and land are reversed. The landmasses are blank, beige expanses. The water is busy with contours and indications, which pucker around the rocks. Faceless flakes of land are laced with branching, joining seaways. The ocean moves through the network of waterways unpredictably. Some passages can only be navigated at certain times of the day. When the tide rushes through one perilous, narrow channel, its currents course together into a five-foot-high wave that stands still, a self-supporting wall of water. In a particularly treacherous corridor between two islands, fifty-foot tidal whirlpools appear and suck down floating logs.

Many of these seaways are edged with rock. Granitic bluffs tumble down to the sea. Trees lean, toppling in slow motion. Along the shore, trees, moss, and lichens are rinsed off by the tides, revealing boulders and ledges, many wearing glacial scratch marks. It is hard to forget that much of the land is solid rock, slowly falling to pieces. Uneven shelves slope their way into sheer drops. My brother and I often sleep on these ledges overnight. Lichens are everywhere and I wake up with a face full of them. For days afterward I find fragments lining my trouser pockets. I turn them out, feeling like a human meteorite, and wonder how many will make a life in the unexpected places where they now find themselves.

lecular clock"—suggest that the earliest fungi diverged around a billion years ago. In 2019, researchers reported fossilized mycelium found in Arctic shale that dates from around a billion years ago (Loron et al. [2019] and Ledford [2019]). Prior to this finding, the earliest undisputed fungal fossils date from around 450 million years ago (Taylor et al. [2007]). The earliest fossilized gilled mushroom dates from around 120 million years ago (Heads et al. [2017]).

68 *ceaselessly remodel themselves:* For Barbara McClintock see Keller (1984).

68 *to make sense of:* Ibid.

69 *oldest of life's labyrinths:* Humboldt (1849), vol. 1, p. 20.

3. THE INTIMACY OF STRANGERS

70 *when we said "we":* Rich (1994).

71 *"have our samples back":* BIOMEX is one of several astrobiological projects. For BIOMEX see de Vera et al. (2019); for the EXPOSE facility see Rabbow et al. (2009).

71 *"limitations of terrestrial life":* For "limits and limitations" quote see Sancho et al. (2008); for a review of organisms sent into space, including lichens, see Cottin et al. (2017); for lichens as models for astrobiological research see Meeßen et al. (2017) and de la Torre Noetzel et al. (2018).

71 *be understood in isolation:* Wulf (2015), ch. 22.

72 *neither could survive alone:* For a discussion of Schwendener and the dual hypothesis see Sapp (1994), ch. 1.

72 *"believe in Schwendener's theory":* For "A useful and invigorating" see Sapp (1994), ch. 1; for "sensational romance" see Ainsworth (1976), ch. 4. Some of Beatrix Potter's biographers have suggested that she was a proponent of Schwendener's dual hypothesis, and it is possible she changed her mind over the course of her life. Nonetheless, in 1897, in a letter to Charles MacIntosh, a rural postman and amateur naturalist, she appeared to take a clear stance on the question: "You see we do not believe in Schwendener's theory, and the older books say that the lichens pass gradually into hepaticas, through the foliaceous species. I should like very much to grow the spore of one of those large flat lichens, and also the spore of a real hepatica in order to compare the two ways of sprouting. The names do not matter as I can dry them. If you could get me any more spores of the lichen and the hepatica when the weather changes I should be very much obliged" (Kroken [2007]).

72 *entirely unexpected:* converging: The tree is one of the founding images in modern theories of evolution, and famously the only illustration in Darwin's *On the Origin of Species*. Darwin was by no means the first to deploy the image. For centuries, the branching form of trees has provided a framework for human thought in fields from theology to mathematics. Perhaps most familiar are genealogical trees, which have their roots in the Old Testament (the Tree of Jesse).

73 *relationships at the other:* For a debate about Schwendener's portrayal of lichens see Sapp (1994), ch. 1, and Honegger (2000); for Albert Frank and "symbiosis" see Sapp (1994), ch. 1, Honegger (2000), and Sapp (2004). Frank first used the word "symbiotismus" (which translates literally as "symbiotism").

73 *described them as "microlichens":* Ancestors of green sea slugs—*Elysia viridis*—ingested algae that continued to live within their tissues. Green sea slugs obtain their energy from sunlight, as a plant would. For new symbiotic discoveries see Honegger (2000); for "animal lichens" see Sapp (1994), ch. 1; for "microlichens" see Sapp (2016).

73 *of inter-kingdom collaboration:* For Huxley quote see Sapp (1994), p. 21.

74 *"look like fairy tales":* For the eight percent estimate see Ahmadjian (1995); for a greater area than tropical forests see Moore (2013a), ch. 1; for "hung in hashtags" see Hillman (2018); for the diversity of lichen habitats, including erratics and lichens that live on insects, see Seaward (2008); for the interview with Knudsen see aeon.co/videos/how-lsd-helped-a-scientist-find-beauty-in-a-peculiar-and-overlooked-form-of-life [accessed October 29, 2019].

75 *a "clay-like" consistency:* For "every monument" quote see twitter.com/GlamFuzz [accessed October 29, 2019]; for Mount Rushmore see Perrottet (2006); for Easter Island heads see www.theguardian.com/world/2019/mar/01/easter-island-statues-leprosy [accessed October 29, 2019].

75 *been able to form:* For lichens' approach to weathering see Chen et al. (2000), Seaward (2008), and Porada et al. (2014); for lichens and soil formation see Burford et al. (2003).

76 *to make a life:* For the history of panspermia and related ideas see Temple (2007) and Steele et al. (2018).

77 *now known as astrobiology:* In response to Lederberg's concerns about interplanetary infection, NASA developed ways to sterilize spacecraft before departure from Earth. These have not been entirely successful: There is a thriving volunteer population of bacteria and fungi aboard the International Space Station (Novikova et al. [2006]). When the Apollo 11 mission returned from the first trip to the moon in 1969, the astronauts were isolated in stringent quarantine in a converted Airstream trailer for three weeks (Scharf [2016]).

77 *several hours a day:* It had been known that bacteria are capable of acquiring DNA from their surroundings since the work of Frederick Griffith in the 1920s, later confirmed by Oswald Avery and his colleagues in the early 1940s. What Lederberg showed was that bacteria could actively exchange genetic material with each other—a process known as "conjugation." For a discussion of Lederberg's findings see Lederberg (1952), Sapp (2009), ch. 10, and Gontier (2015b). Viral DNA has had a profound influence on the history of animal life: It is thought that viral genes played key roles in the evolution of placental mammals from their egg-laying ancestors (Gontier [2015b] and Sapp [2016]).

78 *the domains of life:* Bacterial DNA is found in the genomes of animals (for a general discussion see Yong [2016], ch. 8). Bacterial and fungal DNA is found in plant and algal genomes (Pennisi [2019a]). Fungal DNA is found in lichen-forming algae (Beck et al. [2015]). Horizontal gene transfer is pervasive in fungi

(Gluck-Thaler and Slot [2015], Richards et al. [2011], and Milner et al. [2019]). At least eight percent of the human genome started off in viruses (Horie et al. [2010]).

78 *potentially catastrophic consequences:* For foreign DNA "short-circuiting" evolution on Earth see Lederberg and Cowie (1958).

78 *within twenty-four hours:* For hostile conditions in space see de la Torre Noetzel et al. (2018).

79 *"degree of biological activity":* Sancho et al. (2008).

79 *with no apparent problems:* Even at 18 kilograys of gamma irradiation, samples of *Circinaria gyrosa* only suffered a seventy percent reduction in photosynthetic activity. At 24 kilograys, photosynthetic activity was reduced by ninety-five percent but wasn't eliminated entirely (Meeßen et al. [2017]). To put these results in context, one of the most radiotolerant organisms ever documented, an archaea isolated from deep-sea hydrothermal vents (appropriately named *Thermococcus gammatolerans*), can withstand levels of gamma irradiation up to 30 kilograys (Jolivet et al. [2003]). For a summary of lichen space studies see Cottin et al. (2017), Sancho et al. (2008), and Brandt et al. (2015); for effects of high-dose irradiation on lichens see Meeßen et al. (2017), Brandt et al. (2017), and de la Torre et al. (2017); for tardigrades in space see Jönsson et al. (2008).

79 "They inform us": Some disciplines are routinely "informed" by lichens. Lichens are so sensitive to some forms of industrial pollution that they are used as reliable indicators of air quality—"lichen deserts" extend downwind of urban areas and can be used to map the zone affected by industrial pollution. In some cases, lichens serve as indicators in a more literal sense. They are used by geologists to determine the age of rock formations (a discipline known as lichenometry). And litmus, the pH-sensitive dye used to make the indicator paper found in all school science departments, comes from a lichen.

80 *where photosynthesis happens:* Recent work by Thijs Ettema and his group at Uppsala University suggest that eukaryotes arose within archaea. The exact sequence of events remains much debated (Eme et al. [2017]). Bacteria have long been thought of as having no internal cellular structures, known as "organelles." This view is changing. Many bacteria appear to have organelle-like structures that perform specialized functions. For a discussion see Cepelewicz (2019).

81 *"intimacy of strangers":* Margulis (1999); Mazur (2009), "Intimacy of Strangers and Natural Selection."

81 *that themselves contain bacteria:* For "fusion and merger" see Margulis (1996); for origins of endosymbiosis see Sapp (1994), chs. 4 and 11; for Stanier quote see Sapp (1994), p. 179; for "serial endosymbiosis theory" see Sapp (1994), p. 174; for bacteria within bacteria within insects see Bublitz et al. (2019); for Margulis's original paper (under the name Sagan) see Sagan (1967).

81 *"sum of its parts":* For "quite analogous" quote see Sagan (1967); for "remarkable examples" quote see Margulis (1981), p. 167. For de Bary, in 1879, the most significant implication of symbiosis was that it could result in evolutionary novelty (Sapp [1994], p. 9). "Symbiogenesis" ("becoming by living together") was the term given to the process by which symbiosis could give rise to new species by its earliest Russian proponents, Konstantin Mereschkowsky (1855–1921) and Boris Mikhaylovich Kozo-Polyansky (1890–1957) (Sapp [1994], pp. 47–48). Kozo-Polyansky included several references to lichens in his work. "One should not think that lichens are just a simple sum of certain algae and fungi. Rather, they have many specific features found neither in algae nor in fungi . . . everywhere—in its chemistry, its shape, its structure, its life, its distribution—the composite lichen exhibits new features not characteristic of its separated components" (Kozo-Polyansky trans. [2010], pp. 55–56).

82 *"twentieth-century biology":* For Dawkins and Dennett quotes, among others, see Margulis (1996).

82 *as fungal hyphae do:* "The evolutionary 'tree of life' seems like the wrong metaphor," the geneticist Richard Lewontin remarked. "Perhaps we should think of it as an elaborate bit of macramé" (Lewontin [2001]). It's not entirely fair on trees. The branches of some species can fuse with each other. It is a process known as "inosculation," from the Latin *osculare,* which means "to kiss." But look at the tree nearest to you. The chances are that it forks more than it fuses. The branches of most trees are not like fungal hyphae, which meld with each other as part of their daily practice. Whether the tree is an appropriate metaphor for evolution has been debated for decades. Darwin himself worried about whether the "coral of life" would make a better image, though he decided in the end that it would make things "excessively complicated" (Gontier [2015a]). In 2009, in one of the most acrimonious upwellings of the tree question, *New Scientist* published an issue that proclaimed on its cover that "Darwin was wrong." "Uprooting Darwin's tree," shrieked the editorial. Predictably, it inflamed a furious response (Gontier [2015a]). Amid the storm of reaction a letter sent by Daniel Dennett stands out: "What on earth were you thinking when you produced a garish cover proclaiming that 'Darwin was wrong' . . . ?" You can understand why Dennett was cross. Darwin wasn't wrong. It is just that he came up with his theory of evolution before DNA, genes, symbiotic mergers, and horizontal gene transfer were known to exist. Our understanding of the history of life has been transformed by these discoveries. But Darwin's central thesis that evolution proceeds by natural selection is not contested—though the extent to which it is the primary driving force in evolution is debated (O'Malley [2015]). Symbiosis and horizontal gene transfer provide new ways that novelty can be generated; they are new *coauthors* of evolution. But natural selection remains the editor. Nonetheless, in the light of symbiotic mergers and horizontal gene transfer, many biologists have begun to reimagine the tree of life as a reticulate meshwork formed as lineages branch, fuse, and entangle one another: a "network," or a "web," a "net," a "rhizome," or a "cobweb" (Gontier [2015a] and Sapp [2009], ch. 21). The lines on these diagrams knot and melt into each other, connecting different species, kingdoms, and even domains of life. Links loop in and out of the world of viruses, genetic entities not even considered to be alive. If anyone wanted a new poster organism for evolution they needn't look far. This is a vision of life that resembles fungal mycelium more than anything else.

83 *form their relationship afresh:* In some lichens, specialized dispersal structures called "soredia" form, which consist of fungal and algal cells. In some cases, a newly germinated lichen fungus might team up with a photobiont that doesn't quite satisfy its needs and survive as a small "photosynthetic smudge" known as a "prethallus" until the real thing comes along (Goward [2009c]). Some lichens can disassemble and reassemble without producing spores. If certain lichens are placed in a petri dish with the right kind of nutrients, the partners disentangle and creep apart. Once separated, they can re-form their relationship (though usually imperfectly). In this sense, lichens are reversible. At least in some cases, the honey can be stirred out of the porridge. However, to date only in the case of a single lichen—*Endocarpon pusillum*—have the partners been separated from each other, grown apart, and then recombined to form all the stages of the lichen, including functional spores—known as a "spore-to-spore" resynthesis (Ahmadjian and Heikkilä [1970]).

83 *"see the lichen itself":* The symbiotic nature of lichens presents some interesting technical problems. Lichens have long been small nightmares for taxonomists. As the situation stands, lichens are referred to by the name of the fungal partner. For example, the lichen that arises through the interaction of the fungus *Xanthoria parietina* and the alga *Trebouxia irregularis* is known as *Xanthoria parietina*. Similarly, the combination of the fungus *Xanthoria parietina* and the alga *Trebouxia arboricola* is known as *Xanthoria parietina*. Lichen names are a synecdoche, in that they refer to a whole by reference to a part (Spribille [2018]). The current system implies that the fungal component of the lichen *is* the lichen. But this isn't true. Lichens emerge out of a negotiation between several partners. "To see lichens as fungi," Goward bemoans, "is to miss seeing lichens altogether" (Goward [2009c]). It is as if chemists called any compound that contained carbon—from diamond to methane to methamphetamine—*carbon*. You'd be forced to admit that they might be missing something. This is more than semantic grumbling. To name something is to acknowledge that it exists. When any new species is found, it is "described" and given a name. And lichens do have names, plenty of them. Lichenologists aren't taxonomically ascetic. It's just that the only names they can give glance off the phenomenon they aim to describe. It is a structural issue. Biology is built around a taxonomic system that has no way to recognize the symbiotic status of lichens. They are literally unnameable.

83 *worlds writ small:* Sancho et al. (2008).

83 *rehydrated thirty days later:* de la Torre Noetzel et al. (2018).

84 *legacies of the relationship:* For unique lichen compounds and human uses see Shukla et al. (2010) and State of the World's Fungi (2018); for metabolic legacies of lichen relationships see Lutzoni et al. (2001).

84 *thousands of years old:* For a report from the Deep Carbon Observatory see Watts (2018).

85 *nine thousand years old:* For lichens in deserts see Lalley and Viles (2005) and State of the World's Fungi (2018); for lichens within rocks see de los Ríos et al. (2005) and Burford et al. (2003); for Antarctic Dry Valleys see Sancho et al. (2008); for liquid nitrogen see Oukarroum et al. (2017); for lichen longevity see Goward (1995).

85 *to make interplanetary journeys:* Sancho et al. (2008).

86 *any living cell whatsoever:* For the shock of ejection see Sancho et al. (2008) and Cockell (2008). In a number of studies, bacteria have proved to be more resistant to high temperatures and shock pressures than lichens. For reentry see Sancho et al. (2008).

86 *the question remains open:* Sancho et al. (2008) and Lee et al. (2017).

86 *depending on their circumstances:* For origins of lichens see Lutzoni et al. (2018) and Honegger et al. (2012). There is a lot of debate about the identity of ancient lichen-like fossils and their relationship to extant lineages. Marine lichen-like organisms have been found dating from 600 million years ago (Yuan et al. [2005]) and some argue that these marine lichens played a role in the movement of lichens' ancestors onto the land (Lipnicki [2015]). For multiple evolution of lichens and re-lichenization see Goward (2009c); for de-lichenization see Goward (2010); for optional lichenization see Selosse et al. (2018).

87 *in each other's company:* Hom and Murray (2014).

87 *symbiotic way of life:* For "the song, not the singer" see Doolittle and Booth (2017).

88 *well be other planets: Hydropunctaria maura* used to be known as *Verrucaria maura* (or "warty midnight"). For a long-term study of the arrival of lichens on a newly born island see the case of Surtsey at www.anbg.gov.au/lichen/case-studies/surtsey.html [accessed October 29, 2019].

88 *as well as nouns:* For "wholes" and "collections of parts" see Goward (2009a).

88 *centuries of painstaking scrutiny:* Spribille et al. (2016).

89 *"one fungus and one alga":* For a discussion of diversity of fungi within lichens see Arnold et al. (2009); for additional partners in wolf lichens see Tuovinen et al. (2019) and Jenkins and Richards (2019).

90 *what living organisms are:* For "It doesn't matter what you call it" see Hillman (2018). Goward has formulated a definition of lichens that takes account of these recent findings: "The enduring physical byproduct of lichenization defined as a process whereby a nonlinear system comprising an unspecified number of fungal, algal and bacterial taxa give rise to a thallus [the shared body of the lichen] viewed as an emergent property of its constituent parts" (Goward 2009b).

90 *"blob on a dish":* For lichens as microbial reservoirs see Grube et al. (2015), Aschenbrenner et al. (2016), and Cernava et al. (2019).

91 *"it hard to relate":* For queer theory for lichens see Griffiths (2015).

92 *Or perhaps y'all:* See Gilbert et al. (2012) for a more detailed breakdown of how microbes confuse different definitions of biological individuality. For more on microbes and immunity see McFall-Ngai (2007) and Lee and Mazmanian (2010). Some propose alternative definitions of biological individuals based on the "common fate" of the living system. For instance, Frédéric Bouchard proposes that "A biological individual is a functionally integrated entity whose integration is

linked to the common fate of the system when faced with selective pressures from the environment" (Bouchard 2018).

92 *that they actually exist:* Gordon et al. (2013) and Bordenstein and Theis (2015).

92 *be fraught with tension:* For infections caused by gut bacteria see Van Tyne et al. (2019).

92 *"We are all lichens":* Gilbert et al. (2012).

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