LICHENS: FUNGAL FARMERS

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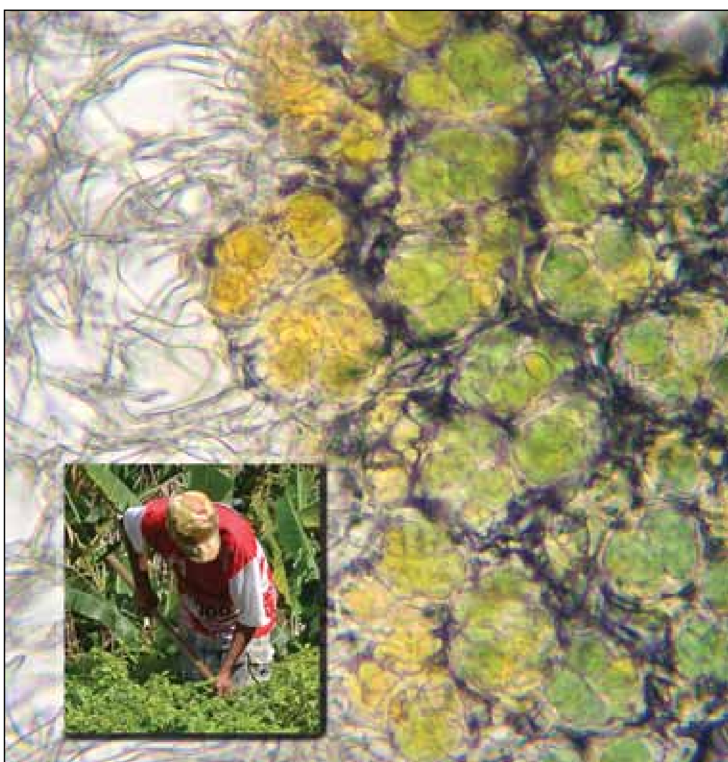
Imagine yourself as a farmer cultivating a field of wheat. You select a variety of seeds, prepare the soil, water the plants, and eventually harvest. It's called agriculture. Now replace those crops by tiny plants called algae, while you are a fungus. Yeah, that's right. Instead of arms and legs and machines tending your crops, you grow hyphae around those tiny algal cells. That's called a lichen. Indeed, the renowned Canadian lichenologist, Trevor Goward, used this analogy in describing lichens as "fungi that discovered agriculture." So, what's the deal with those lichen fungi?

Fungi include an enormous variety of life forms, ranging from edible and poisonous mushrooms, to bread and beer producing yeasts, to formidable stinkhorns, to nasty molds, to rusts and smuts feared by those very farmers. But they all have two things in common: unlike plants, they lack chlorophyll to perform photosynthesis, and unlike most animals, they are basically sessile organisms. As a result, obtaining carbohydrates is a challenge for fungi, and they stepped up to this challenge by evolving such different lifestyles as saprotrophism (decaying dead organic matter), parasitism (attacking and stealing "food" from plants, animals, and even other fungi), and mutualism (forming mutually benefitting relationships with photosynthetic organisms), including mycorrhizae and lichens. Albeit mostly hidden, these fungi are all around us, playing indispensable roles in ecosystem function and impacting our daily lives in multiple ways. Just think of that delicious beef-mushroom stroganoff! But even if you are just OK with wine and cheese, those were made with yeasts and molds. The plants you grow in your garden? Without mycorrhizae they would look pretty shabby. Clean air for healthy breathing? Rest assured when lush lichens grow on trees in your neighborhood. And of course, those antibiotics that help you get rid of a nasty infection? Some of the best natural engineers of antibiotics are fungi.



Like a farmer tending his crop, in a lichen, the fungus tends his algae or, in this case (the basidiolichen *Cora sublactuca*), cyanobacteria. Photos R. Lücking.

Lichens are one of the three principal mutualistic lifestyles in fungi, including also ecto- and endomycorrhiza. In many ways, lichen-forming or lichenization is the most intriguing of these. In contrast to mycorrhizal fungi, which maintain their hyphal and mushroomy appearance, lichens do not immediately look like fungi. They rather resemble small plants, and in fact were mistaken for plants until the second half of the nineteenth century, when the Swiss Botanist Simon Schwendener, the German biologist Albert Bernhard Frank, and the German microbiologist Heinrich Anton de Bary discovered independently around

Unlike other fungi, lichen fungi (in this picture *Lobariella sipmanii* from Colombia) produce an often complex vegetative thallus adapted towards optimizing photosynthesis under different conditions. Photo R. Lücking.

the same time their symbiotic nature, being composed of a fungus and what at that time was known as algae. That fungi are involved in lichens becomes obvious when considering their sexual reproductive structures, which look very much like those of their non-lichenized cousins, mostly like cup-fungi but sometimes also resembling mushrooms. The intriguing part of lichens, however, is their vegetative body, or thallus, which is very different from that of non-lichenized fungi: instead of a mycelium of hyphae overgrowing or penetrating the substrate, the lichen thallus is an often highly structured and complex makeup optimized to acquire nutrients and for the photobiont to perform photosynthesis and produce carbohydrates under different, often extreme environmental conditions.

The farmers and their crops

The fungal component (often termed mycobiont) is virtually the farmer in the lichen symbiosis, whereas the photobiont represents the crops. The geographical and cultural diversity of farmers all around the globe is reflected in the diversity of fungi involved in lichens. Right now, we count about 18,000 species, but in many groups we are just seeing the tip of the iceberg, and estimates of more than twice this number are not unrealistic. Traditionally, almost all lichen fungi were ascribed to the sac fungi or Ascomycota, a large phylum that includes yeasts, witch's brooms, molds, dead man's fingers, morels, and truffles. Almost one third of the currently known Ascomycota form lichens. The other large phylum, the Basidiomycota, which comprise rusts and smuts, jelly fungi, puffballs, stinkhorns, bracket fungi, and almost all mushrooms, were believed to contain very few lichen-formers. This picture has changed recently and some lichenized basidiomycetes groups are as diverse as lichen-forming ascomycetes. One group in particular, the genus *Cora*, which until recently contained a single species, is now thought to comprise more than 400 species.

In contrast, much fewer types of algae and cyanobacteria are involved in lichens,

Some lichens contain two different kinds of photobionts, a green alga and a cyanobacterium, either in the same thallus (*Placopsis roivainenii*) or in separate thalli or lobes (*Sticta subscrobiculata*). Photos R. Lücking.

the "breeding" of optimized photobiont strains. This is another aspect where lichen fungi virtually behave like farmers, with the difference that farmers sell and buy seeds for money.

Quite a number of lichen fungi are capable of something that is, to say the least, cool. Rather than associating with a single type of photobiont, they can form lichens with either green algae or cyanobacteria. In many cases this happens in one and the same lichen, the primary photobiont then being a green alga and the secondary photobiont a cyanobacterium, found in portions of the thallus called cephalodia, since they may look like small heads (Greek: *kephalos* = head). The reason for this is that green algae and cyanobacteria have different virtues, being able to photosynthesize under different conditions and provide different types of carbohydrates. Most importantly, cyanobacteria are able to fix atmospheric nitrogen and hence can provide the lichen with an important nutrient, since nitrogen is a crucial element in amino acids and other organic molecules. This allows lichens to grow in nutrient-poor environments. And even cooler: some lichen fungi can form lichens with either green algae or cyanobacteria separately. These lichens then often look very different from each other and were long believed to represent different species, until it was discovered that they sometimes grow on each other and the same lichen fungus is involved. Such lichens are called photosymbiodemes and they lead us to another issue: naming lichens.

just as farmers around the globe mostly grow the same kinds of crops: corn, wheat, rice, potatoes, and soybeans, to name the five most important ones. Yet, there are many varieties of these crops, and just the same, lichen fungi cultivate many varieties of the same basic types of photobionts, with DNA studies unraveling the enormous genetic diversity found in lichen photobionts. The most common lichen photobionts include the cyanobacterial genus *Nostoc* and the green algal genera *Trebouxia* and *Trentepohlia*. However, other cyanobacteria and green algae and even some brown algae are also found in lichens, and ongoing research continuously discovers new photobiont lineages. One of the most diverse groups in terms of photobionts is the lichenized fungal family Verrucariaceae; its members are mostly inconspicuous and even cryptic but it is a goldmine for anybody studying photobiont diversity.

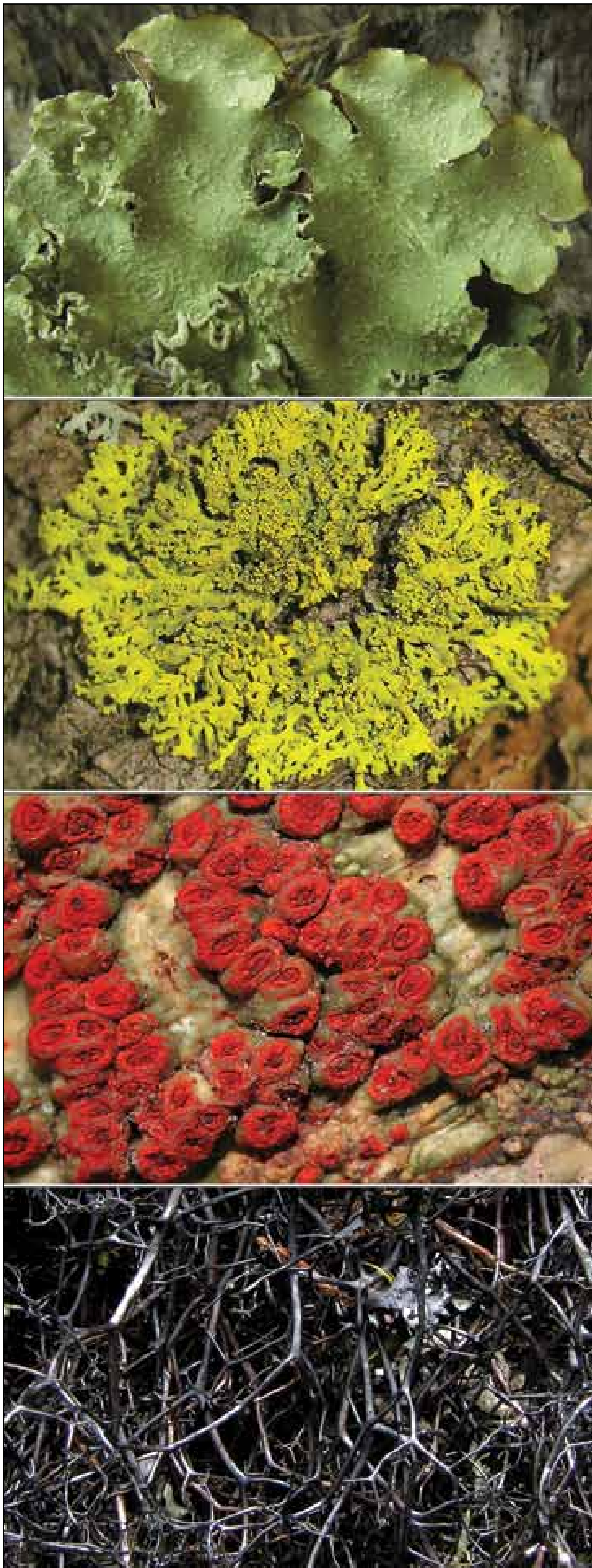
In most cases, the relationship between fungi and their photobionts in the lichen symbiosis is rather specific. A particular fungus will always associate with a particular type of photobiont. However, the genetic strain and sometimes even the species of photobiont may vary and often depends on environmental conditions. This allows the lichen fungus to associate with different types of photobionts to optimize its fitness in a particular ecological niche. It also increases the likelihood that a fungal spore dispersed from the lichen finds a suitable partner to form a new thallus. Recent studies suggest that the variation found in lichen photobionts is not random but evolved as an interaction between the partners over millions of years. Simply speaking, lichen fungi indirectly select the best-performing photobiont strains because these optimize the growth of the lichen and its reproduction, increasing the abundance and availability of these photobionts. Lichen photobionts of a given thallus become accidentally available to other lichen fungi through mechanical and biological processes such as fragmentation, and since unrelated fungi might partner with the same photobiont type, all these fungi participate in

What is the name of that lichen?

Living organisms usually have two names: a scientific name and a common or vernacular name. Vernacular names may be very old, in some cases going back many hundreds or even thousands of years if the organism had importance in daily life, traditional medicine, or religious culture. Scientific names, on the other hand, have "birth dates," which are different for each group of organisms. Scientific names of plants and most fungi go back to the Swedish botanist Carl Linneaus's seminal work *Species Plantarum*, published in 1753, but some fungal names have their "birth dates" based on works published by the Swedish mycologists Christiaan Hendrik Persoon and Elias Fries in the early nineteenth century. As you can see, the Swedish were very influential in science back then and continue to be, not only in the production of furniture. So, what does this mean for how we name lichens? Scientific names are in Latin and follow very strict rules and one of them is that a scientific name can only apply to a single organism. Now, a lichen is a symbiosis of at least two different organisms, and so at some point, those wise people who make the rules for scientific names decided that the scientific name of a lichen is the name of its fungal component. That means, if you use the scientific name *Lobaria pulmonaria*, that name is the name of the fungus that forms the lichen. It does not cover the photobiont, which gets its own name, in this case the green alga *Dictyochloropsis*. The vernacular name, on the other hand, is usually meant to address the entire lichen. Hence, the name lungwort refers to the lichen as such, including its symbiotic components. This might seem confusing but actually has a very practical aspect, in that we can name both the lichen as a whole (vernacularly) and its individual components (scientifically). This comes in very handy in the aforementioned case of these peculiar photosymbiodemes, which may look like completely different lichens but are formed by the same fungus. In such a case, the scientific name is the same for the fungus in both lichens, but different vernacular names can be used for each lichen.

A firework of colors

There are many things that make lichens special, but one thing is certainly the variety of colors. While lichens in many aspects behave like plants, their diversity in colors reveals their true relationships with fungi, which certainly display a similar firework of coloration. The difference lies in the detail. Fungi produce their colors almost invariably in their fruiting bodies, whereas the vegetative mycelium is mostly uncolored or brown-black. In contrast, lichens feature their colorful display also and especially in their vegetative thallus, although their fruiting bodies are often colorful as well. These colors are mostly caused by pigments deposited in the upper portions of the lichen thallus, and since these pigments are chemical substances, this raised curiosity in lichen chemistry early on and already in 1866 the Finnish lichenologist William Nylander used chemical characters to distinguish morphologically similar species. Today, lichens are among the best studied organisms in terms of chemistry, because it provides a valuable tool for their identification. Of course, chemistry is found in all living organisms, but while organisms share chemical aspects of their primary metabolism, such as respiration and photosynthesis or the formation of carbohydrates, protein and fats, each organism also has a specific secondary metabolism that is often unique to a particular lineage or found scattered in different groups. In lichens, the chemical substances produced by this secondary metabolism—the secondary substances—play important roles in the biology of these symbiotic systems. For instance, those pigments that produce the variety of colors characteristic of lichens serve as sunscreens, protecting the photobiont from damage through high UV radiation and enabling the lichen to grow under conditions where the photobiont alone could not exist. Other substances, usually found in the inner portion of the lichen or medulla, have functions in the internal water and gas exchange of the thallus and also may prevent lichens from being eaten. That's very important because there are certain critters such as snails, mites, and bark lice that specialize in feeding on lichens. The study of lichen substances is today a field of its own, with simple to very sophisticated methods to detect even the rarest compound, and over 1,000 different substances have so far been identified.



[Above] Two examples of the diversity of lichens: lichens growing on living leaves of the tropical cycad *Zamia fairchildiana* in Costa Rica, and the shoehorn lichen, *Glossodium aversum*, in Colombia. Photos R. Lücking.

[Left] Common lichen colors and pigments: *Flavopunctelia flaventior* (light green: usnic acid), *Candelaria concolor* (yellow: calycin), *Marcelaria purpurina* (red: xanthorin), *Oropogon bicolor* (black: melanins). Photos R. Lücking.

Lichen diversity

It is obvious from what we have seen so far that lichens are quite a diverse bunch. Lichen diversity can be measured in many ways, including morphological diversity and colors, but also ecological diversity and numbers of species that exist globally or co-occur locally. Lichens can be found in all terrestrial ecosystems and a few even grow submersed in fresh or salt water. Some ecosystems such as the tundra, Antarctica, and coastal fog deserts are dominated by specific lichen communities and few other organisms can exist under these conditions. Yet, what lichens have in common with many other groups, and what is not immediately obvious, is that their highest species richness is found in tropical rain forests. We still don't know exactly how many lichens coexist in tropical rainforest, but 600 or more within a hectare is not rare. No ecosystem on earth harbors more lichen species in a comparable area. Lichens even surpass tropical trees in that respect! Lichens can also grow on almost any substrate one can imagine. Bark, rocks and soil are no-brainers, but in tropical rainforests they also amply colonize living leaves to form tiny, colorful communities. Lichens growing on animals? You bet. Some longer-lived mantids support tiny lichen colonies that make their leaf mimicry perfect. From rock-dwelling lichens to those growing on gravestones and buildings is not far to go, but can you imagine lichens growing on plastic signs, glass windows, old cars, and laundry lines? As long as it is humid enough, that seems to be no problem for these highly adaptable critters. The only disadvantage that lichens have is that they grow very slowly compared to other fungi and plants, so for them to grow on unusual surfaces, those surfaces have to be exposed for quite a while. The fact that some lichens easily grow on artificial substrata can be brought to good use in experimental science. Thus, growing lichens on small, transparent microscope slides allowed researchers for the first time to document lichenization between a germinating spore and an alga in nature.

Lichens and dinosaurs

Lichens have one advantage over humans. While we can only dream of dinosaurs and have to rely on computer animation to make them come alive, lichens were around long before the first dinosaurs appeared on earth. While we have very few lichen fossils, we can use DNA data to figure out when lichens,

We don't know for certain what prehistoric lichens looked like, but rock tripes of the genus *Umbilicaria* might have been around for over 200 million years. Photo R. Lücking.

as we know them today, first appeared on Earth, and these studies suggest that this was some 250 to 300 million years ago in the Permian. Dinosaurs came slightly later, during the Triassic, some 230 million years ago. And while dinosaurs came and went, lichens are still around and what we can reconstruct about ancient lichens suggests that they did not change much in general appearance. Notably, early diverging lineages of lichen-forming fungi are even today mostly found growing on bare rocks, often in dry conditions, probably resembling what lichens had to face when they first appeared hundreds of millions of years ago. Some of these lichens, such as the enigmatic rock tripes of the genera *Umbilicaria* and *Lasallia*, really make the impression of ancient life forms, virtually "living fossils." So it might well be that dinosaurs saw such lichens hanging around on rocks, wondering whether this stuff might be edible. Humans apparently are not so picky, since *Umbilicaria* lichens are a delicacy in East Asia. Some ideas about the evolution of lichens put them even further back in time. So-called protolichens might have existed as far back as 400 million years or more and some researchers think that they were the ancestors to most of that we today recognize as the phylum Ascomycota. An even more spectacular idea suggests that some Ediacarans, critters that were around in the Precambrian, some 630 to 540 million years ago, were lichens. Or at least lichen-like. Whatever the truth, fact is that lichens have been around for quite a while.

Why should we care about lichens?

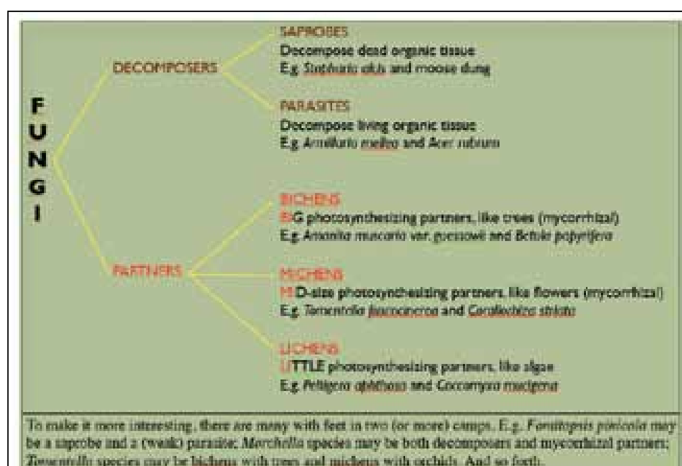
For a researcher, this question is difficult to answer. Not because we wouldn't know about the importance of lichens. But when appreciating the diversity of life on our planet, it is difficult to understand why we have to look for obvious reasons to protect and conserve this diversity. Humans are capable of destroying in the blink of an eye what evolution took millions of years to create. Somehow, we are unable to appreciate something unless it has an economic value or some other level of importance attached to it. But make no mistake, lichens are important. Lichens have many different roles in ecosystem function, ranging from being pioneers in soil formation, to regulating the water cycle and atmospheric humidity, to serving as biological fertilizers by fixing atmospheric nitrogen. Lichens are homes to a diversity of microorganisms and small animals, functioning as miniature ecosystems themselves. Some animals have lichens on their menu as principal food. Secondary compounds of lichens bear the potential of being the base for pharmaceutical drugs, and drug screening projects have lichens on their radar. Lichens have long been used in traditional medicine, to produce dyes, and as food. However, most of their use is in applications as biological indicators of environmental health, such as atmospheric pollution and conservation status of native ecosystems. In a famous paper published in *Nature*, it was shown that a decline of lichen diversity in an urban area correlated with increased lung cancer mortality rates, not because lichens prevent lung cancer, but because they respond in similar ways to pollution as humans. Thus, even if we just appreciate lichens just for what they are, a unique component of nature's diversity, it is obvious that lichens play an important role in ecosystem function and are useful to humans in many ways.

The tree lungwort (*Lobaria pulmonaria*) is symbolic of the sensitivity of lichens to environmental changes and pollution, as it is nowadays extinct from many places. According to the "Doctrine of Signatures," extracts of this lichen were used to cure pulmonary diseases and are still found in homeopathic drugs. It is also the signature lichen of the International Association for Lichenology (IAL). Photo R. Lücking.

Putting lichens in their place.

Andrus Voitk

Sometimes it helps us to understand a new thing if we can relate it to other things that we already know. In that spirit, perhaps it will be easier to understand what lichens are if we relate them to the mushrooms that form the main fare for readers of FUNGI. Simply put, lichens are mushrooms. The majority are ascomycetes, with a few basidiomycetes among them. The ascomycete-basidiomycete classification is not helpful here. More helpful is to classify mushrooms



by their lifestyle, according to behavior. This democratic system cares not a whit for their looks (morphological or Friesian classification) or family connections (phylogenetic classification), only what they do on their own. The image is an attempt at such classification. Not heard of bichens or michens? Relax, neither have I. But the terms help to make a point: from a functional point of view, there is no difference between mushrooms that we call lichens and other mushrooms using a photobiont for a partner.

Although you may smile and scan that image for evidence of tongue in cheek, please consider it a little closer. It does not help you identify the mushrooms that you encounter. It does not help you understand where mushrooms came from or how different lineages are genetically linked to each other. But this *Pilzanschauung* sure does explain what mushrooms do, how they fit into the system, how they glean their energy.

Mushrooms do only one of two things for a living: they either decompose organic material, or they enter a partnership with an organism capable of making sugars, trading water and minerals for some of these sugars. The decomposers break down either dead or living organic material. The former are saprobes and the latter parasites: as food, organic material is organic material, unaltered by its life or death.

Considering the mushrooms that have chosen partnership routes, it becomes immediately clear that the important principle is to have an organism with chlorophyll, able to photosynthesize—a photobiont. The size of the organism—pine or alga—is unimportant, and varies with the paths of coevolution these organisms took to their mutualistic ends. The partner's size only dictates the mechanics that must be worked out by the fungus to make it work: wrap around roots, penetrate roots, encapsule tissue, etc. there are always two organisms, the mushroom and its partner. That is why no lichen ever made it to the Tree of Life. But both partners did, be they *Boletus edulis* and *Quercus alba*, or *Peltigera aphthosa* and *Coccomyxa mucigena*.

But lichens have different shapes when together versus when both organisms are alone, I hear you protest. Hence, they must be different organisms. Well, The mushroom-tree combination is also different. There are many experiments showing what stunted shrubs trees are, if grown in sterile, fungus-free soil. And, of course, mycorrhizal fungi grown without trees differ even more: they would be non-existent.

Lichens are mushrooms. Period. Well, OK, with little photobionts.

Springtime in the Rockies, Lichen

By Lew Welch

All these years I overlooked them in the
racket of the rest, this symbiotic splash of
plant and fungus feeding on rock, on sun,
a little moisture, air - tiny acid-factories
dissolving salt from living rocks and
eating them.

Here they are, blooming!
Trail rock, talus and scree, all dusted with it:
rust, ivory, brilliant yellow-green, and cliffs
like murals!

Huge panels streaked and patched, quietly
with shooting-stars and lupine at the base.

Closer, with the glass, a city of cups!

Clumps of mushrooms and where do the
plants begin? Why are they doing this?
In this big sky and all around me peaks &
the melting glaciers, why am I made to
kneel and peer at Tiny?

These are the stamps of the final envelope.

How can the poisons reach them?
In such thin air, how can they care for the
loss of a million breaths?

What, possibly, could make their
ground more bare?

Let it all die.

The hushed globe will wait and wait for
what is now so small and slow to
open it again.

As now, indeed, it opens it again,
this scentless velvet,
crumbler-of-the-rocks,
this Lichen!

Lew Welch who was born in 1926 and "disappeared into the Sierra Nevada in 1971." "Springtime in the Rockies, Lichen" copyright © 2012 by the Estate of Lew Welch. Reprinted by permission of City Lights Books.