

Kingdom Fungi

The Story of Life, Part 3:

by Robert B. Cates

On our continuing tour of the living universe, it is now time to consider the Kingdom of the Fungi. As with the previous column on Kingdom Bacteria, I shall follow the conventions and outlines developed by Lynn Margulis and Karlene V. Schwartz. Unless otherwise noted, the contents herein are derived from their book, Five Kingdoms: An Illustrated Guide to the Phyla of Life on Earth.¹

Fungi range in size from the single-celled yeasts that make our bread, beer and yogurt, to some of the largest known organisms on Earth.² We eat fungi (mushrooms) and fungi eat us (yeast and athlete foot infections). They provide us with food but are great destroyers of crops. Fungi are the source of penicillin, the world's most widespread and effective general antibiotic. Some fungi are particularly adept at converting sugars to alcohol, the basis of all beers, ciders and hard liquors. Only by partnering with fungi were plants able to colonize the terrestrial environment. In a very real sense we wouldn't be here if it weren't for fungi.

If you go to the supermarket and ask the manager, "Where are your consumable fungi?", he or she will point you to the produce area, where the mushrooms are always surrounded by products of the plant kingdom. Indeed, fungi were long classified as plants, undoubtedly due to the close affiliation of mushrooms and shelf fungi with plants. Phylogenetically, however, fungi are more closely related to animals than to plants. Both plants and fungi produce complex polysaccharide molecules as their basic structural building material (cell walls). In plants this tough molecule is called cellulose. Fungi produce a different polysaccharide, though, resulting in a material called chitin, the same material as the exoskeletons of insects. In fact, it is the closeness of fungi cells to our own animal cells that makes treatment of fungi infections so difficult. It is much easier to find agents that differentiate between bacterial and animal cells, killing the former and leaving the latter unscathed, than is the case with fungi.

Although fungi are fun, from a taxonomic point of view, they are very messy. Many fungi species morph between totally different looking forms, and have formal names assigned to each, even though these different looking organisms have later proven to be one and the same species. Also, lichens, composite organisms of fungi partnered with a photosynthesizing algae or bacteria, are also treated as 'species' under the broad systems of classification adopted by

¹ Readers are reminded that the current state of taxonomic classification systems is in great flux, and that many professional systematists now recognize more than five kingdoms of life. This should come as no surprise, as classification systems have become increasingly sophisticated over the years. Until the late 18th Century, organisms were classified as either plants or animals. With the advent of microscopy, it became quite clear that fungi were quite different from plants or animals. These fundamental differences were articulated by R. Villemet in 1784, from which time a third kingdom of life, Kingdom Fungi, was recognized. The three-kingdom concept worked satisfactorily for almost 200 years, until Cornell University ecologist R.H. Whittaker came out with his five kingdom scheme in 1969, which is based on evolutionary development and relationships between organisms (called 'cladistics'). (See Hudler, Chapter 1—Classification and Naming) The Margulis-Schwartz scheme is a further elucidation on Whittaker, which because of its widespread availability in print I have adopted as a framework to discuss the history of life.

² Samples of the soil-dwelling, wood-eating fungus *Armillaria bulbosa* were analyzed from a Michigan forest in 1992, which revealed that a single fungal organism was occupying an area equivalent to several football fields. Its weight was estimated at 220,000 pounds, the same as a fully-grown blue whale. Scientists estimate the age of this champion fungus at about 1,400 years. (Wolfe, pp. 103-104)

mycologists (those who specialize in the study of fungi). As we did in the previous article on bacteria, we shall follow the simple classification system laid out in Margulis and Schwartz's *Five Kingdoms*, bearing in mind that with the advent of genetic sequencing technology many relationships between individual species and groups of organisms are now in a high state of flux and are likely to be revised.

Margulis and Schwartz define Kingdom Fungi as being "limited to eukaryotes that form chitinous, resistant propagules (fungal spores) and chitinous cell walls and that lack undulipodia (that is, are amastigote, or immotile) at all stages of their life cycle." In plain English, fungi are composed of cells with membrane-bounded nuclei, that reproduce via spores (not embryos), have cell walls made of chitin, and do not possess the flagella or cilia that bacteria use to propel themselves through their environments.

Fungi are classified according to the structure of their reproductive bodies and methods of spore production. Most fungal spores germinate into hyphae—slender thread-like tubes which may or may not be divided into cells by cross-walls (septa). Yeasts are an exception, germinating instead into independent cells. The collective hyphae of a fungal organism is called a mycelium, and is the primary feeding and growing form of most fungi. Mushrooms are the reproductive organs of the largest and most complex fungi—arising from a network of mycelia that may be kilometers in extent.

The reproductive capacity of some of the higher fungi is remarkable. Cornell University plant pathologist George W. Hudler supplies some amazing statistics:

Fungi depending on wind for dispersal produce a lot of spores. In only a few cases has "a lot" actually been counted, but when it has, the results are impressive. For instance, the fungus causing a disease known as "smut" of corn produces about 25 billion spores per average-sized ear of infected corn. The fungus causing stem rust of wheat generates about 10 billion spores from an acre of moderately diseased plants. And the wood decay fungus, *Ganoderma applanatus*, has been estimated to produce spores at the rate of 350,000 per second. It does that for up to six months a year—thus 5.4 trillion spores—and it may continue at that pace for ten years or more.³

Not only are fungi prolific spore producers, but the extremely small size of these propagules means that they stay aloft for very long periods enabling them to be dispersed around the globe. Again from Professor Hudler:

Even in still air, an average-size spore of 20-micrometer diameter is likely to fall at a rate of about 7 feet per minute. But that's in very still air. The fact of the matter is that spores are lifted up by the slightest of drafts and could conceivably stay aloft indefinitely. When they finally do settle out on downdrafts or in falling rain, they are likely to be far from their origin. Professor C.M. Christensen reported once using a marker fungus—one of distinctive color, not normally found in his area—to measure spore dispersal within his office building. Five minutes after the culture dish was opened on the first floor, some spores of the fungus were trapped on the fourth

³ Hudler, p. 26. Another example of the tremendous fecundity of fungi is give by Colin Tudge, who cites the discovery of a giant puffball fungus found growing in Canada that measured 2.6 meters in girth. What is even more remarkable than its size is that the spores contained within puffball, estimated at 10 raised to the power of 18 (1,000,000,000,000,000,000), could easily populate several average size galaxies if they had the means of intergalactic dispersal. (Tudge, p. 160)

floor. Five minutes later, they were falling on the fourth floor in amounts of thousands per square yard.⁴

On even the clearest of days we live in a fungal cloud. It is thus not too surprising that Alexander Fleming's agar gels used to culture bacteria samples were contaminated by various molds in the laboratory he had set up at London's St. Mary's Hospital in 1928. What was extremely serendipitous was that one of those molds happened to be a species of *Penicillium* fungi that produces one of the most powerful antibacterial agents ever discovered (penicillin), and, of course, the fact that Dr. Fleming had the acuity to notice how this invading contaminant affected his specimens.⁵

While most fungi passively release their spores into the environment, a few are more active in dispensing their reproductive bodies. The so-called 'cap-throwers' in the genus *Pilobolus* are one example. Thriving on horse manure, these fungi produce profuse numbers of spore packets on the tips of short stalks that are keyed to tracking the sun. Come mid-morning, when the stalks are oriented at about 45 degrees from the horizon, the trajectory angle which achieves maximum range, hydrostatic pressure causes the tips of the stalks to explode, propelling the spore packets to distances of up to 12 feet. This benefits the fungus, since the spores are shot far from the dung pile onto vegetation likely to be consumed by grazing animals so that the spores can ride through their digestive systems to populate new piles of manure.⁶

⁴ Hudler, p. 27.

⁵ Hudler, as usual, contains an excellent discussion on the discovery and development of penicillin (pp. 113-124). Although Fleming has achieved rightful celebrity for his discovery of the anti-bacterial effects of the *Penicillium* mold, the process of isolating the active penicillin ingredient and proving it effective in humans belongs to Dr. Ernst B. Chain and Dr. Robert Florey, both of Oxford University. Once isolated, it was Florey who supervised the initial tests on lab mice. As Hudler explains, "The choice of mice for this experiment was especially fortuitous. If Florey had chosen guinea pigs instead of mice, penicillin research may have been stopped dead in its tracks. For some still unknown reason, penicillin is toxic to guinea pigs, and a toxic reaction on the test animals would most certainly have squelched the enthusiasm of the Oxford team." In 1945, Fleming, Chain and Florey jointly won the Nobel Prize for medicine. Few people realize the importance of the U.S. Department of Agriculture's Northern Regional Research Laboratory in Peoria, Illinois in its role of developing methods to mass-produce penicillin. Hudler relates an amusing story of the Peoria lab's search for more productive *Penicillium* species, and how one of their young female employees, among her other responsibilities, was to periodically visit local markets and gather up any moldy produce she could find. One day "Moldy Mary," as she came to be known, returned with a rotten cantaloupe containing a culture of *Penicillium chrysogenum*. "It proved to be remarkably productive, and many of the strains used today come from that rotten Peoria melon." We might not elevate "Moldy Mary" to the exalted status of Fleming, Chain and Florey, but all of us who have grown up in the Age of Penicillin certainly owe this dedicated shopper a debt of gratitude.

⁶ Hudler, p. 32. As Professor Hudler so ably puts it, "From the perspective of the mycologist, this is just another piece of evidence that part of the modern military establishment was based on mechanisms used for thousands of years by the microbes coming from the south end of a horse going north." Hudler also relates the story of how the use of wood chips for decorative landscaping can result in a not-so-pleasant side-effect. Wood chips are often contaminated by a common forest inhabitant called the artillery fungus, *Sphaerobolus stellatus*, which can hurl their spore packets, with sticky slime attached, at speeds of up to 27 feet per second and for distances of up to 18 feet. These miniature 'cannons' are actually audible to the human ear when they go off. "Many home and car owners wish that were all there is to the *Sphaerobolus* story, but unfortunately for them there's more. The small bit of slime surrounding each spore packet is a powerful adhesive, and wherever the packets land, that's where they will stay for several days—at least. Efforts to wash them off right away are usually futile, and even later, when the packets do finally flake off, a tenacious brown stain remains. A typical foundation planting bed that is 6 feet wide and 30 feet long, mulched with wood chips, may yield several thousand *Sphaerobolus* spore packets in a good year, and they effectively ruin the appearance of the houses and cars to which they stick. Insurance adjusters in the northeastern United States have received many claims to

All fungi are heterotrophs, i.e., they do not produce their own food from raw materials but must obtain nutrients directly or indirectly from other organisms. Fungi do not typically surround food or bring food into an internal cavity for digestion. Instead they excrete powerful enzymes that act outside the fungal body to break food down into smaller molecules that are absorbed directly across the fungal membrane, a process sometimes called fermentation. Indeed, fungi are among nature's most remarkable chemical factories. As Professor Hudler explains:

Within a few minutes or a few hours of spore germination, growing hyphae begin to exude some of the powerful enzymes needed to digest food for the fungus. Cutinases digest leaf surface waxes, cellulases destroy plant cell walls, and other enzymes dismantle other pieces of the complex organic architecture that was once plant or animal. At the same time, mycotoxins, which are fungal by-products that are poisonous to animals, or antibiotics, which are metabolites that inhibit growth of microbes, may also permeate the substrate. The purpose of these by-products is apparently to discourage potential competitors from getting more than their share of the available food. Even the best of chemists with all the tools that science has to offer looks with envy upon the ease with which the fungi produce chemicals that have long defied laboratory synthesis.⁷

As food supplies become exhausted, the hyphae spread outward and the inner cells of the fungal colony die out, with the colony forming a circumferential ring. 'Fairy rings' of mushrooms in lawns and on forest floors are one example of this growth pattern, as is ringworm on human skin, which is not caused by a worm at all but by a fungus.⁸

Fungi seem to have an uncanny ability to form 'partnerships', or symbioses, with other non-fungal organisms. The early symbiotic fusion of fungi with plants was a necessary step in plant colonization of the terrestrial environment. Almost all land plants are dependent on their symbiotic fungal partners to obtain and enhance the transport of critical soil nutrients, in particular phosphates, nitrates, and trace metals.⁹ This mycorrhizal 'world wide web' not only enables individual plants to survive and flourish, but there is growing evidence that some plants actually share nutrients with each other through the fungal intermediaries that tie them together. In the world of fungi, cooperation through symbiosis may well be as important a factor in evolution as competition among individuals.¹⁰

have spotted houses or cars refinished, and many landscape professionals are rethinking their use of wood-chip mulch." Hudler, pp. 32-33.

⁷ Hudler, p. 17.

⁸ Hudler, p. 18.

⁹ Approximately 90 percent of the 248,000 species of higher land plants on Earth maintain a mutualistic symbiosis with soil fungi. Most plants, in fact, could not survive without the assistance of mycorrhizae, while no mycorrhizae have been found that can survive without a plant associate. (Wolfe, p. 94)

¹⁰ Wakeford, pp. 48-49. The ability of mycorrhizae to transfer nutrients between plants has been demonstrated a number of times, although this was originally thought to be limited to special circumstances and to plants of the same species. But as biologist Tom Wakeford reveals, in the early 1990s a team of researchers led by Oregon State University mycologist Suzanne Simard set the world on end through a series of experiments showing that nutrients were being exchanged even between trees of different species, and between different fungal symbionts through the interconnected mycorrhizal web. "Supplies are shared both within and among species: to those without shall be given, and those with plenty shall have it taken away." Obviously, this Marxian view of forest ecosystems remains controversial, but it is clear that much more is going on in the mycorrhizal world than meets the eye. According to David Perry, a soil ecologist also at Oregon State University, another way to look at this exchange is to consider the groups of trees and their fungal symbionts as a superorganism. The major thrust of Wakeford's book, *Liaison of Life*, is that these higher organizational levels, of which the plant-mycorrhizal exchange is but one example, are ones "in which important new ecological and evolutionary processes can occur." Another source states that in one study "as much as 15 percent of the nitrogen fixed by a species of alder tree

As already stated, fungi are incredible chemical factories, and their ability to produce or transform the molecular world around them has been put to industrial use in the production of many important drugs and chemicals. The citric acid used in most sodas is produced by fungi. Fungal molds are used to manufacture cortisone, hydrocortisone, and prednisone—steroids widely used to control swelling and inflammation. Yeasts and other molds are essential in the production of cheese, beer, wine, and soy sauce. In addition to penicillin, fungi are the sources of other powerful pharmaceuticals such as vitamins, interferons, and steroid hormones.¹¹

The fungi have been around for a long time, with fossil evidence going back to the Ordovician period some 450-500 million years ago, and probably well back into the Precambrian to perhaps 900 million years ago. In the intervening time they have evolved into an estimated 1,500,000 species in three broad phyla: zygomycota, ascomycota, and basidiomycota.

Phylum Zygomycota: Comprising the most primitive grouping, around 1100 species of zygomycotous fungi have been identified living on land around the world. They include many saprophobes that live on decaying vegetation—indeed they are one of the chief recyclers that help keep the world from drowning in dead organic matter. They are also found living on animals, plants and even each other. Taxonomists generally recognize from three to seven groups, of which we shall consider only the four major classes or orders: (1) Mucorales, (2) Entomophthorales, (3) Zoopagales, and (4) Glomales.

(1) Mucorales: The Mucorales are saprobes, i.e., they secrete extracellular digestive enzymes that break down dead organic matter into smaller molecules that are then absorbed into the fungal cells. They reproduce by sending up stalks terminated by globular spore-containing bodies (sporangia) that rupture to release their contents. The common black bread mold, *Rhizopus stolonifer*, is among this group, along with the genera *Phycomyces* and *Pilobolus*. Some species of *Phycomyces* are among the most light sensitive organisms known—sporangia production can be triggered by just a few photons of light.

(2) Entomophthorales: Most of the members of this group parasitize animals, principally insects. Like *Pilobolus*, they forcefully eject their sporangia. The most well known, at least among graduate biology students, is *Basidiobolus*, a consumer of frog dung, which can be easily grown from water that has harbored a frog.

(3) Zoopagales: The Zoopagales, comprised of about 65 species in 10 genera, are another group of parasite specialists, with small animals, nematodes, amoebas and other microbes falling prey to their appetites.

(4) Glomales: Here we have one of the most important and widespread groups of organisms on Earth. The Glomales contain many of the 100 or so zygomycote species that form symbiotic relationships with plants. These are endomycorrhizal specialists, i.e., the thread-like hyphae of the fungi actually penetrate the root cells of the host plant (as opposed to fungi with hyphae that insert themselves

between the root cells (called ectomycorrhizal). As Margulis and Schwartz explain:

The roots of nearly all healthy tracheophytes (vascular plants) have symbiotic relations with fungi. Fungi inhabiting (endomycorrhizal) and coating (ectomycorrhizal) the roots of grasses and trees are especially critical to plants growing in nutrient-poor soils; the fungi function as root extensions. Such mycorrhizal associations enhance the transport of soil nutrients, such as phosphates, nitrates, copper, zinc, and manganese. Fungi inhabiting the roots of trees are responsible for transporting nutrients from the soil to the roots. Most orchid seeds, for example, require specific fungal partners to germinate. . . . The fungi that transport nutrients through soil may have helped prevent the earliest plants from succumbing to desiccation and direct sunlight as plants made the transition from water onto land. Plant-fungus relations became truly terrestrial. In any case, a strong association between most plants and some fungi has persisted for at least 400 million years.¹²

About 90 percent of all plants have roots surrounded by an active 'rhizosphere', where fungi are busy absorbing and transporting critical soil nutrients to their host plants. In return, the fungi may tap between a tenth and a third of the photosynthate produced by the plant. There is much more to this symbiotic relationship than first meets the eye, and scientists are just beginning to unravel how sophisticated and pervasive the fungi-plant partnership has become.¹³

Phylum Basidiomycota: The Basidiomycetes include many of the fungi we are most familiar with—the smuts, rusts, jelly fungi, mushrooms, and stinkhorns. The phylum takes its name from the microscopic truncheon-like reproductive structures common to all members in this group (*basidion* is Greek for 'small base'). In mushrooms, the gills on the underside of the cap house thousands of basidia, usually with each bearing four spores, called basidiospores. There are about 22,000 recorded species of basidiomycetes. Many form important symbioses with plants (most forest trees and shrubs), called 'ectomycorrhizae', by encapsulating the plant root with a sheath of hyphae. In pine, beech, willow, and perhaps other trees, fungus-secreted hormones stimulate roots to branch. Plants with basidiomycote partners may actually cease producing root hairs in favor of the much more extensive surface area being exploited by the fungal mycelia. Mushrooms are just the reproductive organs of a much larger organism silently working beneath the ground in concert with surrounding plants. Recent findings indicate that different basidiomycetes can actually 'trade' or 'share' nutrients with each other, in effect creating a 'world-wide web' (a food-web, as opposed to our new-fangled electronic information web).

The Basidiomycota are divided into two classes: Heterobasidiomycetae and Homobasidiomycetae.

Heterobasidiomycetae: These include the rusts and smuts that parasitize many plants, especially the cereal crops upon which much of the world's food supply is based. Some have complex life cycles intimately linked with the seasons, local climate conditions, and the developmental biology of their host plants. Corn smut, *Ustilago maydis*, can occasionally devastate a heavily infested crop, and in this country, at least, has been brought under control through the breeding of resistant strains of corn. However, in Mexico corn smut, called *cuitlacoche*, is harvested and fried as a delicacy. Now breeders are

was transferred to nearby pine trees through a fungal connection." (Wolfe, pp. 102-103) One could counter Wakeford's view with a Capitalistic spin in which the mycorrhizal fungi are operating out of pure self interest in 'assisting' all the plants within their purview in order to maximize the total root growth environment upon which the fungi depend.

¹¹ One wonders how the popularity of sodas would be affected if the list of contents was changed to read 'fungus-derived citric acid' in place of plain citric acid. Fungi might even produce rocket fuel one day. Monomethyl hydrazine, the same chemical used to propel many rockets is found in some of the fruiting bodies of false morels, in which it can cause poisoning of unwary fungi eaters. (Hudler, pp. 151-152)

¹² Margulis, p. 351.

¹³ A good portion of Wakeford's *Liaisons of Life* is dedicated to the interaction between mycorrhizal fungi and plants. See particularly Chapter 3, *The Wood Wide Web*. The statistics on nutrient transfer from plants to mycorrhizae is taken from page 43 of this work.

trying to develop varieties that are susceptible as a host for this gourmet food.¹⁴

Homobasidiomycetae: This group includes most of the common mushrooms that we have all encountered growing in our lawns and on forest walks. Among their numbers are the cultivated *Agaricus* button mushroom found in every market, many other delicious wild species that are harvested around the world, plus many that are highly toxic. The homobasidiomycetae form the core group around which most mycological societies are based and about which every 'mushroom picker' develops at least a rudimentary understanding.¹⁵

Phylum Ascomycota: Along with the Basidiomycota, the Ascomycota form the other huge phylum of fungi. Among its 30,000 known species are the true yeasts, blue-green molds, morels, truffles, and lichens. Common to all is the microscopic sack-like reproductive structure called an ascus (plural: asci) (from the Greek *askos* = bladder). Most ascomycotes are 'absorptive heterotrophs', i.e., they release digestive enzymes into their immediate surroundings and then absorb the resultant dissolved nutrients. Some act on living tissues and are therefore pathogenic, or disease-causing agents. Many more work as the great recyclers of the world, being the chief organisms involved in the breakdown of highly resistant plant and animal molecules such as cellulose, lignin, and collagen. As such, they are essential to maintaining a healthy ecosystem. Lichens, which we will discuss later, are an exception in that they are photosynthesizers.

One of the most infamous of the Ascomycota is the ergot fungus, caused by species of *Claviceps* (typically *Claviceps purpurea*), that appears as an infestation on the flowers of many of our cereal crops (wheat, barley, oats, and especially rye), and whose toxic substances (mycotoxins) can be passed right on through the milling and baking process to the final bread product. Probably no other fungus has had as great an effect on humans as ergot.¹⁶ The symptoms of ergot poisoning are manifold, but besides possibly resulting in death, can cause severe psychological aberrations and a decrease in fertility. Interestingly, episodes of decreased fertility throughout the Middle Ages have been statistically linked to climatic conditions favorable to outbreaks of ergot in the rye fields that provided the basic sustenance throughout northern Europe during this period. Even more intriguing is the high correlation of witchcraft persecutions to the same ergot-favoring seasons. It is thought now that the strange behaviors experienced by the 'victims' of witchcraft and of the accused 'witches' themselves was due to the consumption of ergoty bread and the associated intake of psychoactive mycotoxins. A strong case has even been made for ergotism as the cause of the 17th Century Salem, Massachusetts witchcraft affairs.¹⁷

¹⁴ While corn smut has its devotees, we may owe one of our standard dessert cookies to one of the wheat smuts, *Tilletia foetida*. This fungus can infest flowering wheat, resulting in harvested grain purported to smell like rotting fish. The story goes that in an effort to cover up the fetid aroma, an enterprising miller added molasses to darken the flour, as well as the new ginger spice from India, to produce the original ginger snaps. (Hudler, p. 51)

¹⁵ There are so many guides to mushrooms that it seems superfluous to walk through the various families and key species in our limited space. Two excellent texts that are also highly entertaining in their treatment of these organisms are Elio Schaechter's *In the Company of Mushrooms* and David Arora's *Mushrooms Demystified*. See the bibliography at the end of this article.

¹⁶ Ergot derives its name from the fact that its reproductive sac protrudes from the grain head of its host and in shape resembles a rooster's spur, or *ergot* in French. Hudler, p. 71.

¹⁷ The role of ergot poisoning in history is the primary subject of Mary Kilbourne Matossian's book *Poisons of the Past: Molds, Epidemics, and History*. She summarizes the different mycotoxins produced by ergot on p. 9. Among them are several powerful alkaloids, most prominent of which are ergotamine, ergonovine, ergine, and lysergic acid hydroxyethylamide. From the last, it is quite simple to

Aspergillus fumigatus is another ascomycote fungus capable of great mischief. This mold is commonly found in stored cereals, and is known to cause tremors and convulsions in humans and animals. According to researcher Mary Kilbourne Matossian, some of the metabolites of this fungus are the same as ergot alkaloids, and hence may also have been responsible for outbreaks of ergot-like epidemics.¹⁸ Its cousin, *Aspergillus flavus*, is even more notorious as the source of aflatoxins, currently the most potent natural carcinogenic agent yet found. *A. flavus* is a common fungus capable of growing on many different crops.¹⁹

Residents of Southern California are routinely exposed to a pathogenic ascomycote fungus in the very air they breathe. The fungus, *Coccidiomyces immitis*, is found in arid regions throughout the Western Hemisphere, and the disease it causes,

extract the more famous lysergic acid diethylamide (LSD), which is exactly how LSD was first isolated for pharmaceutical evaluation. This was first achieved by a chemist named Albert Hoffmann working for the Swiss firm, Sandoz Pharmaceuticals, in 1943. The fascinating story of LSD's discovery and subsequent history is recounted in Hudler, pp. 77-81.

The ergot alkaloids are quite stable; some retaining significant toxicity for up to 18 months. Nor do they break down during low temperature baking or even by boiling in water for three hours. Thus ergot mycotoxins were most often consumed in baked products. In Russia, home brewers were poisoned through the use of ergot-contaminated grains, although distilled products were purged of all alkaloids and were thus safe to drink. (Matossian, p. 14). It thus appears that rye is most safely consumed in the form of rye whiskey, at least from the standpoint of ergot poisoning. Home brews may be another matter, though.

Ergotamine is an exceptionally strong vasoconstrictor, so powerful as to completely block the flow of blood to parts of the body, creating the condition known as gangrenous ergotism. Limbs are of course particularly susceptible and in its initial stages the extremities can feel as though they are on fire. This 'plague of fire' or 'holy fire' as it was sometimes called, could set off whole afflicted communities in involuntary dancing movements—the infamous "St. Vitus's Dance" or "St. Anthony's Fire" of the Middle Ages. Hudler relates the interesting story of how after the staff of a Viennese hospital dedicated to Saint Anthony specialized in treating the sufferers of ergotism, the disease became known as St. Anthony's Fire. To this day paintings of the ministry of St. Anthony in churches throughout western Europe depict his followers with missing or burning limbs. (Matossian, p. xiii, Hudler, p. 72).

Another ergot alkaloid, ergonovine, causes spontaneous abortions in human females as well as other animals. Both ergine and lysergic acid hydroxyethylamide can cause convulsive ergotism, "with symptoms ranging from vomiting, diarrhea, and general lethargy, to a sensation of ants crawling over the body (formication), vivid hallucinations, twitching, grotesque distortion of limbs, and seizures similar to those associated with epilepsy. Some of the awesome if terrifying capabilities of ergot have at times been tamed and put to beneficial use. Since at least the mid 1700s and right on through the 1800s, ergot decoctions were administered to induce labor in pregnant women. In addition, the vasoconstricting effect that could cause the 'holy fire', under proper dosage, was useful in preventing or treating postdelivery hemorrhaging in new mothers. Ergotamine is still used today in an array of drugs for treating migraine headaches. Most of this discussion on medical facets of ergot is taken from Hudler, Chapter 5, *Ergot of Grain Crops*. He also discusses the probable use of ergot-laced potions in the ancient Greek ceremonies called the Eleusian Mysteries, particularly by those inducted into the Greater Mysteries, which required the consumption of a drink called *kykeon*. The fact that the sacred liquid was described as containing meal and being purple in color is highly suggestive of ergot. Ergot flour, when roasted, turns red or purple.

I apologize for the length of this footnote, but I include it to give some indication of the extraordinary nature of the fungal world. This is just a short example of a few key facts that are known about one kind of fungus. Presumably, similar stories could be told about the million-and-a-half others that are out there. Truly the words of Leonardo da Vinci are as apt today as they were five hundred years ago: "We know more about the movement of celestial bodies than about the soil underfoot." (quotation from Wolfe, p. 2)

¹⁸ Matossian, p. 13.

¹⁹ On *Aspergillus flavus*, see Hudler, pp. 86-89. Aflatoxins are actually a suite of at least four separate toxic chemicals. Per Hudler, these chemicals "remain, today, some of the most potent toxins produced by any life form." *A. flavus* is responsible for the deaths of thousands of people each year (Tudge, p. 161).

coccidioidomycosis, has been reported from Argentina to California. In our own state, the prevalence of the disease in the San Joaquin Valley has given the pestilence its common name of 'Valley fever.' The spores are inhaled and can establish a fungal community in the lungs. Most healthy individuals who become infected develop little more than a mild cough and a barely discernible lesion in the lung once their immune systems swing into action. However, for individuals whose immune systems have been compromised, the battle with *C. immitis* can be for their very lives. Symptoms can then range from fever, chest pains, shortness of breath, coughing and fatigue, to episodes of anorexia resulting in weight loss of 20-30 pounds over short periods, and finally to widespread lesions throughout the body. The epidemiology of this disease is explained by Professor Hudler:

Under natural conditions, spores are lifted into the air by wind and dust. However, human activities such as farming and construction, which tend to loosen soil and accelerate wind erosion, also encourage liberation of *C. immitis* spores. Following the Northridge, California, earthquake of 1994, 208 cases of coccidioidomycosis were attributed to the enormous amount of dust (and spores) raised by the quake. Three people died from the disease after contracting it during the upheaval.²⁰

Other pathogenic ascomycetes are responsible for the near eradication of the American chestnut and American elm. Yet for every disease-causing ascomycote, there seem to be several others that are of great benefit. Cyclosporins, extracted from several different molds, such as *Cylindrocarpum lucidum* and *Tolypocladium inflatum*, provides the basis of Cyclosporin A (Sandimmune®), used to depress the human immune system to enable organ transplants. Cyclosporin has also been highly effective in the treatment of diabetes, enabling many patients to discontinue insulin injection regimens altogether. The anti-cholesterol drugs, compactin and lovastatin, the basis of Mevacor® and Pravachol®, are derived from *Penicillium*, as well as from ascomycote species in the genera *Paecilomyces* and *Trichoderma*. Lovastatin is produced commercially by culturing of a strain of *Aspergillus terreus*, cousin of the feared *A. fumigatus* and *A. flavus*.²¹ Another *Aspergillus*, *A.*

²⁰ Being one of the 208 cases of coccidioidomycosis referenced above, I can attest to its insidious attack on the human body. I live in Chatsworth in the far northwest corner of the San Fernando Valley only a few miles from Northridge. Throughout the summer of 1994, I began to develop a dull ache deep in my chest. By fall, it had become so noticeable that I sought medical attention. The X-rays showed a small lesion on my right lung, and since I have never smoked, the pulmonologist interpreted it as most likely due to 'Valley fever' as opposed to a cancer. The prescription: lots of rest, as the 'cure' would consist of a week of hospitalization under an intense regimen of intravenously-administered cocktails of powerful antibiotics. In short, at my level of infection, the cure was much worse than the disease. Over the next six months, my immune system finally overcame the fungus; but I'll always carry its mark on my lung. The information on *C. immitis* is taken from Hudler, pp. 108-110. In those same pages Hudler also relates the story of how Ernest Dickson, a researcher who did much of the early work on coccidioidomycosis, was a bit of a poet. Instead of giving the disease the more logical name of 'coccidiomycosis', he threw in an extra 'ido' to make the name more 'pleasing to the ear when spoken or sang.' In that spirit, a classic piece of doggerel is passed around in mycological circles:

Some fungi produce a mycosis
Like blasto- or histoplasmosis
But for musical sake
The one I will take
Is coccidioidomycosis

²¹ On cyclosporins and anti-cholesterol drugs, see Hudler, pp. 123-124. We cannot leave the *Aspergillus* tribe without acknowledging the important contribution of the common mold, *A. niger*. Like *A. flavus*, it can pose a danger through the production of mycotoxins, including the highly carcinogenic aflatoxins. However, it also produces an enzyme named alpha-D-galactosidase, which has the unique ability to suppress methane production in the human

oryzae, is used in the making of sake, or rice wine. Finally, it should be noted that many of the Ascomycota also form healthy mycorrhizal symbioses with plants, and thus are critical to the health and well-being of many of the 90 percent of vascular plants that benefit from such relationships.

We shall now consider five groupings or classes of ascomycetes: Hemiascomycetae, Euascomycetae, Loculoascomycetae, Laboulbeniomycetae, and the Deuteromycetes.

Class Hemiascomycetae: The most well-known of the hemiascomycetae have the simplest structures of all fungi, the yeasts. Most do not develop hyphae and hence have no mycelium. However, yeasts do form asci, and their methods of reproduction put them firmly in the fungi camp. Humans have utilized yeasts, in particular those of the genus *Saccharomyces* in two important ways since the dawn of civilization: to make bread and to make alcoholic beverages. *Saccharomyces* means literally "sugar fungus", and it is the action of these yeasts upon their primary food source, sugar, that is of interest. In proper concentrations, and in environments lacking oxygen, the yeast secretes enzymes that break sugars apart leaving two main byproducts—carbon dioxide and ethyl alcohol. In making leavened bread, bakers add sugar to the dough—sometimes as honey or molasses, along, of course with Baker's Yeast, which is usually one of many strains of *S. cerevisiae* bred for this purpose. As carbon dioxide bubbles are released through the process of fermentation, the dough 'rises', increasing in volume three times that of the original mass, at which time the baker punches it down to repeat the process. The CO₂ lightens and flavors the dough. The alcohol is driven off by kneading the dough and by baking the bread.

A similar process is used by vintners and brewers. Sugar fed to *Saccharomyces* in the form of grape juice results in wine. If the sugar is provided as partially rotted rice (another fungus does this job), then the end product is sake.²² When the sugar comes from partially germinated barley seeds, or 'malt', the resulting liquid is beer. Wild yeasts that start the fermenting process cease functioning and die when they have polluted their environment with only about 4 percent alcohol. Wine vintners, however, have developed strains of a special wine yeast, *Saccharomyces ellipsoideus*, that can thrive in alcoholic concentrations up to around 12 percent. The various strains developed by master vintners over the centuries are carefully guarded, for they can impart their own unique flavors to the final kegged or bottled product.²³

Because of their simple structure and ease of cultivation, yeasts are at the center of genetic engineering, being particularly useful in the creation of artificial chromosomes.

Class Euascomycetae: This large group includes morels and truffles, but also provides most of the fungal partners in lichens (of which more will be said further on).

Class Loculoascomycetae: Many of the members of this class feed on decaying soil organics, thus being of great importance in the recycling of nutrients through the biosphere. One genus, *Elsinoe*,

digestive tract. Now grown and harvested in commercial quantities, *A. niger* yields up this enzyme in the form of Beano®, much favored by the more flatulent members of the human race and appreciated by those who must stand downwind of them. "This unique product made from a fungal metabolite and now found on drugstore shelves throughout North America is yet another testimony to the immense potential for the fungi to improve the quality of our lives." (Hudler, pp. 130-131)

²² The starch in rice is completely resistant to conversion to sugar by yeast enzymes. The organism that performs this service is *Aspergillus oryzae*. See Hudler, pp. 140-141.

²³ See Hudler, pp. 135-146, for a thorough discussion of baking and brewing with yeasts.

includes many pathogenic species that prey on plants, causing serious diseases of citrus, raspberry, and avocados.

Class Laboulbeniomycetae: These are all highly host-specific parasites of insects. They are a picky crowd, often not content just to prey upon a given species of insect, but limiting their target to just one sex or to particular body part.

The Deuteromycetes. About 15,000 species of ascomycota are termed deuteromycetes, and are all characterized by a lack of organs for sexual reproduction. Yet these organisms do practice a form of 'parasexual' reproduction that is still poorly understood. Some species change from a non-sexual form to a sexual form, and were given two distinct and valid names before it was realized they were one and the same species. Thus the well-known deuteromycote (non-sexual) *Penicillium* can morph itself into a sexual ascomycotous stage which is named *Talaromyces*. Athlete's foot fungus is one of several infamous members of this tribe.

Another famous deuteromycote is *Botrytis cinerea*, or the 'noble rot' that infests late harvest grapes on the vine, causing them to lose water and increase their relative sugar content. When combined with special wine yeasts in the vat, the noble rot is said to impart a distinctive but 'not moldy' flavor to the resulting product. Wine connoisseurs pay a premium to have their grapes get this special rotten treatment.²⁴

The deuteromycetes are further subdivided into four 'sub-classes': spaeoropsids, melanconias, monilias, and Mycelia Sterilia. By far the most important group are the 10,000 species lumped under the monilias. *Penicillium* falls under this grouping. So too, do many yeasts that form neither asci nor basidia, but reproduce by the budding of new individuals from a parent cell. Moniliasis is a common vaginal infection caused by the growth of the monilia yeast *Candida albicans*. The disease is called 'thrush' when other mucous membranes are affected. Another important monilia is *Pneumocystis carini*, the agent of fatal pneumonia that attacks those with compromised immunological systems such as people with AIDS or those who have their immune systems deliberately suppressed for cancer treatments or organ transplants.

Lichens: About 20,000 species of fungi are known to associate with photosynthesizing partners from at least 40 genera of algae and bacteria to form mutualistic symbioses called lichens. Lichens have been called 'pioneer plants' due to their hardiness and capability to colonize extreme environments. But since they are really composite organisms (one in which the fungal partner usually dominates) they are not really 'plants' at all.

While lichen fungi may be found growing as stand-alone colonies in nature, lichen algae are rarely, if ever, found on their own. Thus for the algal partners the relationship appears to be not merely beneficial but absolutely necessary to their survival. For lichens the whole is indeed more than the sum of the parts, since the combined organism can create compounds such as lichenic acids and pigments (many have been used as natural dyes) that neither partnering organism can produce on its own. The huge variety of partnerships implies that the fungus-algae-bacterial symbiosis has evolved independently on numerous occasions.

One useful way to classify lichens is by the type of fungi partner—an ascomycote (the most common), a basidiomycote, or a deuteromycote (classed under the ascomycotes in the Margulis-Schwartz scheme). This turns out to be very difficult in practice because of the extreme morphological variations between the free-living form of the fungus and its lichenized form. Most naturalists

therefore group lichens by their more general physical appearance—either crustose (low, crusty), foliose (leafy), or fruticose (bushy).

Many lichens propagate through the release of soredia, tiny fragments carried by wind or water and consisting of at least one algal cell surrounded by fungal hyphae. Landing on bare rocks, the soredia can establish a foothold and prosper, if only at growth rates that sometimes approach zero in the harshest of environments.²⁵

Through the release of acids and organic compounds lichens accelerate weathering of rock and initiate the formation of soils.

Lichens are a dominant life form in the arctic regions. *Cladonia* species are eaten by many animals, and people have survived on them in emergencies. Being widespread and able to thrive on air and rocks, they form the base of the arctic food web that includes caribou (grazers of lichen) and native peoples.

Besides the Arctic tundra, lichens are also abundant in Antarctica (growing on rocks in the Dry Valleys), on high mountains, in the tropics, and in northern old-growth forests. A lichen named *Lobaria*, growing as an epiphyte in the canopy of old-growth forests, fixes as much as 75 percent of the nitrogen required by Douglas firs. Either rains wash the soluble nitrogenous compounds produced by *Lobaria* directly down to the soil, or fragments of the lichen, or even whole limbs carrying substantial *Lobaria* colonies, fall to the forest floor. There, mycorrhizal fungi in the soil and roots complete the recycling of these needed nutrients. Some trees short-circuit this process by sending rootlets directly into canopy lichens to absorb fixed nitrogen directly.²⁶

The common appearance of lichens in the deserts of the world attests to the drought-tolerance of these organisms. However, continuous drought will kill lichens, just as will continuous wetness. The only exception are a few species of marine lichens, such as *Verrucaria serpuloides*, which requires complete submersion.

Despite their abilities to survive and even thrive in some of the harshest environments on Earth, lichens are very sensitive to airborne pollutants such as sulfur dioxide and volatile metal compounds released from burning coal. The humble lichens, hardly noticed by those of us who wander the hills, deserts and forests of the world, turn out to be critical indicators of the health of the planet.²⁷

²⁵ Studies of lichens growing on dated monuments, such as tombstones, reveal average lichen growth rates of 0.1 millimeter to 10.0 mm per year. Margulis, p. 366.

²⁶ On the crucial role of *Lobaria* in northern old-growth forests, see Luoma's *The Hidden Forest: The Biography of an Ecosystem*.

²⁷ The remarkable ability of lichens to reflect and amplify changes in the atmospheric environment around them was first demonstrated in 1965, "when a study was launched to learn more about the effects of radioactive fallout from nuclear bomb tests. The plan was to sample people from all over the world, with Lapps serving as the control group. After all, it was assumed, where else but in the frozen tundra could one find people whose innards were so unspoiled by the poisons of progress." Unfortunately for the study, and even more so for the poor Lapps, analysis showed that their tissues contained 55 times the radioactivity of Finns living just to the south. As it turns out, the lichens consumed by reindeer that were eaten by the Lapp population are efficient concentrators of radioactive cesium and strontium, the byproducts of above-ground nuclear testing. The Chernobyl disaster of 1986 was even more dramatic. "Within eight months of the accident, meat from reindeer in Norway and Sweden that had fed primarily on lichens had over ten times the legal limit of measurable radiation. In some areas, it exceeded the limit by twenty times. The reindeer were slaughtered and the carcasses were sold to mink and fox farms. Be forewarned if you are offered a 'hot' deal on a fur coat from Russia." (Hudler, pp. 227-228)

²⁴ The information on *Botrytis cinerea* is from Hudler, pp. 140-141.

STORY OF LIFE BIBLIOGRAPHY—KINGDOM FUNGI:

- Arora, David, *Mushrooms Demystified*. Ten Speed Press. Berkeley, California; 2nd edition; 1986
- Hudler, George W., *Magical Mushrooms, Mischievous Molds*. Princeton University Press; Princeton, New Jersey; 1998
- Luoma, Jon R., *The Hidden Forest: The Biography of an Ecosystem*. Henry Holt and Company; New York; 1999.
- Margulis, Lynn, and Karlene V. Schwartz, *Five Kingdoms: An Illustrated guide to the Phyla of Life on Earth*. Third edition. W.H. Freeman and Co.; New York; 1997
- Matossian, Mary Kilbourne, *Poisons of the Past: Molds, Epidemics, and History*. Yale University Press; Newhaven, Connecticut; 1989
- Tudge, Colin, *The Variety of Life: A Survey and a Celebration of All the Creatures that Have Ever Lived*. Oxford University Press; New York; 2000
- Schaechter, Elio, *In the Company of Mushrooms: A Biologist's Tale*. Harvard University Press; Cambridge, Massachusetts; 1997
- Wakeford, Tom, *Liaisons of Life: From Hornworts to Hippos, How the Unassuming Microbe Has Driven Evolution*. John Wiley & Sons; New York; 2001
- Wolfe, David W., *Tales From the Underground: A Natural History of Subterranean Life*. Perseus Publishing; Cambridge, Massachusetts, 2001