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FUNGI IN URBAN AREAS

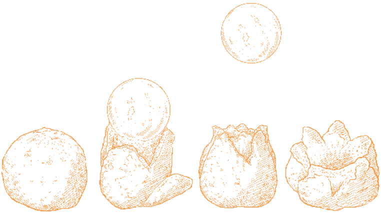
A number of fungi benefit from human practices like transportation, agriculture, and even landscaping. Indeed, many fungi are well suited to life decomposing the ubiquitous wood mulch so popular these days in the urban landscape.

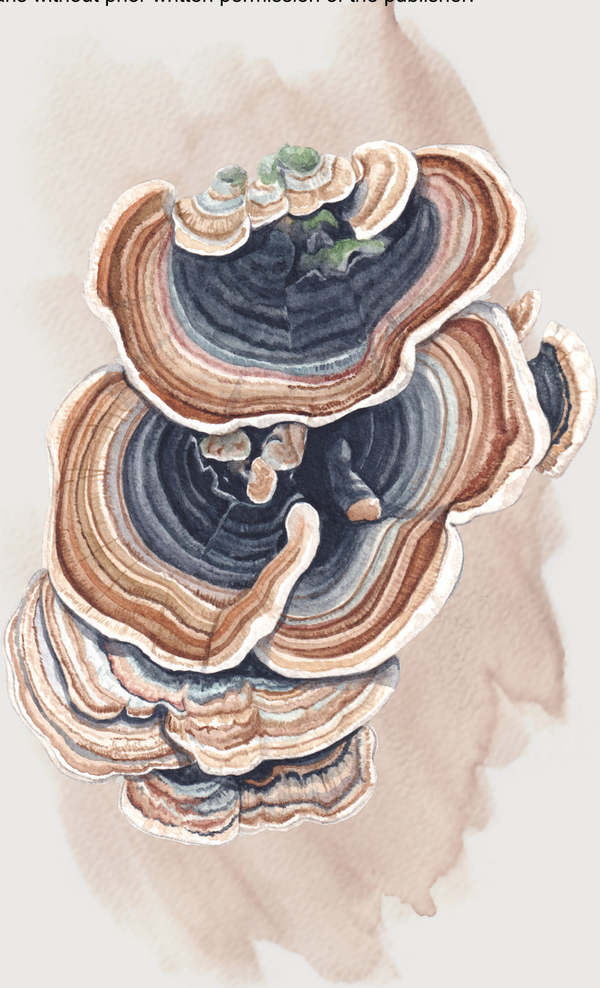
Rarely noticed growing on wood chips and mulch are members of the genus *Sphaerobolus*. These tiny fungi are known as Artillery Fungi for their amazing ability to blast a spore packet (peridiole) great distances. True to their name, the force of the spore ejection even produces an audible sound!

Butt rots, fungal infections at the base of trees, are quite common in forests; probably even more so in urban areas where trees are damaged by vehicles or other machinery. A wound allows all manner of pathogens to enter, weakening the foundation of the tree and making it more susceptible to breakage and wind throw. Trees with these infections are hazards and their timely removal is necessary for public safely.

↓ In recent years, the Artillery Fungi have become a source of distress to homeowners, landscape mulch producers, and insurance companies. Due to the strong adhesion of the discharged peridioles—they stick irreversibly to any smooth surface—they damage anything nearby on a sunny day. The pint-sized popguns have even marred the surfaces of vinyl siding on homes, windows, and automobiles.

→ Commonly seen in urban areas, butt rot fungi include some pretty large and sometimes showy polypores. These include species of *Inonotus*, *Laetiporus*, *Ganoderma* (pictured), and *Meripilus*, as well as *Onnia tomentosa*, *Heterobasidion annosum*, *Grifola frondosa*, and *Phaeolus schweinitzii*.





FUNGI IN OUR HOMES

Our homes, gardens, and lawns are under attack. Despite our best efforts, more than 50 percent of the food produced on Earth is consumed by pests before it reaches our dining tables. Fungi need moisture to thrive, so preservation of food (as well as clothing, homes, and their contents) requires little more than maintaining dry conditions.

FUNGI CAN—AND WILL— CONSUME JUST ABOUT ANYTHING

If moisture is present, just about anything can be turned into a food source by fungi—that includes anything made of cellulose (cotton clothing, books, carpeting), wood, leather, or nearly any natural material. Priceless museum collections, antiques, libraries—virtually anything is at risk of damage. A number of fungi will grow on the materials of which the home is constructed, given the opportunity.

SAVING ANTIQUITIES

Some fungi, curiously, are found almost nowhere in nature but in human dwellings. This is especially troubling when destruction falls upon relics of historical or cultural significance. Mycologist Robert Blanchette is world-famous for researching and helping to preserve artifacts under attack from fungi. He is one of the few ever to be permitted to study the antiquities of the Forbidden City in China; he has studied fungal degradation in Sixth Dynasty Egyptian tombs dating from 4,000 years ago; and more recently he has been called in to investigate fungi at the South Pole. Amazingly, the fungi are not native there, but are of concern because they are causing destruction to wooden buildings abandoned during the "Golden Age of Discovery," when teams led by Robert Scott and Ernest Shackleton were in a race to discover the South Pole over land, a century ago.

→ Pretty but so destructive, the Dry Rot fungus (*Serpula lacrymans*) almost seems to ooze over woody surfaces, where it weakens and ultimately destroys the integrity of the wood.

DRY ROT FUNGUS

Of all the wood decay fungi that cause damage to timber constructions worldwide, the Dry Rot fungus is considered the most destructive. This cosmopolitan fungus wreaks destruction the world over, causing billions of dollars in damage annually. The cause of this destruction, *Serpula lacrymans*, causes brown rot primarily of conifer wood. *Serpula* has the amazing ability to transport water (as well as nitrogen and other nutrients) by way of mycelial cords or rhizomorphs, often over great distances—even through the foundation of homes. Interestingly, the fungus can utilize quite a few inorganic materials for its nutritional needs, including calcium and iron ions extracted from plaster, brick, and stone.

FUNGI IN YOUR JEANS

Scientists have discovered ways to take advantage of some of these destructive fungi. *Trichoderma reesei* is used in industry to produce cellulase (enzymes that degrade cellulose). All strains of this fungus used industrially come from a single isolate collected in the Solomon Islands during the Second World War, where the fungus was the cause of a serious problem for the US Army. This fungus is especially good at making cellulase enzymes and destroyed the canvas tents used by the soldiers stationed in the damp jungles there. Today, the fungus is grown in huge tanks for the cellulases it excretes; much of the cellulase enzyme produced by this fungus goes to denim jean manufacturers. Those fashionable stonewashed jeans? Sometimes pumice is used to lightly abrade and soften the denim material, but much of the time the process involves cellulase enzymes instead to give the same results but at less cost to the manufacturer.

FIRE FUNGI

There is a group of fungi that are poorly known and rarely seen, for they show up almost exclusively following fire. Pyrophilous fungi have recently become the subject of much study, a result of consecutive years of unprecedented fires in many parts of the world, notably in Australia and North America. Where are these enigmatic fungi and what are they doing in the intervening years? And what is it about fires that promotes their growth?

Many of these fungi live as endophytes within lichens, trees, and other plants, in fire-prone areas. The majority of pyrophilous fungi are ascomycetes, as is the case with most of the lichen fungi. A few are basidiomycetes, including some species of *Pholiota*.

Possibly the most beautiful is *Geopyxis carbonaria*, commonly known as the Bonfire Cup and Pixie Cup. These stalked cups appear in spring right after a forest fire and are well known from all over the globe, from Australia to North America. And although the recently burned ground may be carpeted with this fungus, they pretty much only appear during that first year post-fire. After that they go back into hiding—they are not gone but going about their lives as an important symbiont of the forest. And waiting for the next big fire, their signal to spring into action.

STONEMAKER FUNGUS

One of the strangest mushrooms of Australia is also the most reclusive. In fact, the tuberous sclerotium of this fungus is more often encountered than actual fruiting bodies. *Laccocephalum mylittae* occurs in forests of south and eastern Australia. Early written accounts all state that Indigenous Australians regarded the excavated sclerotium as a delicacy, probably sliced and eaten raw, hence the common name for it: "native bread." Possibly the most interesting aspect of this mushroom is when it chooses to fruit. The sclerotia are thought to be perfectly happy growing underground for many years, maybe even decades, and appear to be an adaption to life in fire-prone habitats, for wildfire seems the catalyst for mushroom formation. Following the massive bushfires in 2019, mushrooms of *Laccocephalum* were commonly seen emerging from areas where the fungus was previously unknown.

← Bonfire Cups are often the first life to emerge from the ashes of wildfires. They are common all over the world, but often go unnoticed due to their small size.

FOSSIL RECORD

How old are the oldest fungi? How far back into the geological record do fungi go and how do we know this? Most people would assume that fungi do not fossilize. But it turns out that, although soft, fleshy fungi do not fossilize very well, we do have a fossil record for them. The first fungi undoubtedly originated in water, like much of the earliest life on Earth.

Based on the fossil record, fungi are presumed to have been present in the Late Proterozoic, 900–570 million years ago (Mya), and maybe further back than that. The oldest "fungus" microfossils were found in Victoria Island shale and date to around 850 million to 1.4 billion years old, although scientists are still debating whether these represent truly fungal forms.

MOLECULAR CLOCKS

Scientists use fossils to calculate very old dates. With fungi, most come from amber. Scientists also date organisms using "molecular clocks." This method has become indispensable for revealing the evolutionary pathway of the fungi. Molecular clocks are based on the rate of certain genetic mutations. All organisms are subject to alterations, or mutations, of their DNA. Mutations affect important and indispensable genes—changes to those affect the phenotype and are often lethal, so they alter very little through time. These are said to be highly conserved. Mutations also occur in neutral sequences, which do not affect the phenotype, and are therefore not under selective pressure. These sequences may change more frequently. And the knowledge that the mutation rate of such neutral sequences remains the same through time can be used to estimate the point when two species diverged in the course of evolution.

~ Fungi paved the way for plants ~

The first terrestrial plants date to around 700 Mya and the consensus seems to be that fungi probably arrived on land just ahead of them and paved the way for plants to move from marine to ever drier habitats.

Much of what we know of no-longer-extant fungi comes from specimens found in amber. Amber is one medium that preserves delicate objects, such as fungal bodies, in exquisite detail. This is due to the preservative qualities of the resin when contact is made with entrapped plants and animals. Not only does the resin restrict air from reaching the fossils, it also withdraws moisture from the tissue, resulting in a process known as inert dehydration.

Furthermore, amber not only inhibits the growth of microbes that would decay organic matter, it also has properties that kills microbes. Antimicrobial compounds in the resin destroy microorganisms and "fix" the tissues, naturally embalming anything that becomes trapped there by a process of polymerization and cross-bonding of the resin molecules.

There are a few fossilized mushrooms known from specimens beautifully preserved in amber dating from the Cenozoic Era (starting 66 Mya) and Cretaceous Period (145–66 Mya). The oldest fossilized mushroom is called *Palaeoagaricites antiquus* (100 Mya) and resembles modern-day members of the family Tricholomataceae. Other mushroom species known from amber include *Archaeomarasmius legettii* (90 Mya), *Protomycena electra* (20 Mya), and *Coprinites dominicana* (20 Mya)—all look pretty much the same as mushrooms you would find in your local woods.

→ A rare find: a piece of 25-million-year-old Chiapas red amber, with a fossilized *Marasmius*-like mushroom inside. Only a few mushroom fossils within amber are known.

THE ARRIVAL OF FUNGAL GROUPS

The first "lichen-like" organisms we see date to around 600 Mya. About 550 Mya the chytrids and higher fungi split from a common ancestor. The first taxonomically identifiable fungi are from 460 Mya, and seem similar to modern Glomeromycota. Around 400 Mya the Basidiomycota and Ascomycota split from a common ancestor. The first insects came onto the scene around 400 Mya; the first beetles and flies date to around 245 Mya.

Mycorrhizas are extremely rare in the fossil record. Mycorrhizal relationships are believed to have arisen more than 400 Mya as plants began to colonize terrestrial habitats and are seen as a key innovation in the evolution of vascular plants. Recently, the first fossil ectomycorrhiza associated with flowering plants (angiosperms) was discovered. The fossils were found in a piece of Indian amber from the Lower Eocene (52 Mya), a time only 13 million years after the demise of the dinosaurs.

↓ Ascomycete fungi can form fruiting bodies such as these cups, *Microstoma protractum*. Their spores are then discharged from sac-like asci on the surface of the cup.

↓ Basidiomycete fungi form fruiting bodies like these Hedgehog Mushrooms (*Hydnum repandum*), with spores discharged from basidia on gills, tubes, or in this example, teeth.

→ Taxonomy separates fungi into the phyla Chytridiomycota, Glomeromycota, Basidiomycota, and Ascomycota based on their style of reproduction. Fungi have diverse forms (from the top): from primitive chytrids (e.g., *Chytriomyces hyalinus*) and zygote fungi (e.g., common bread molds like *Rhizopus nigricans*) to more modern mushrooms like the Chanterelle (*Cantharellus* species) and the Violet Coral (*Clavaria zollingeri*).

CONVERGENT EVOLUTION

Similarity of fruiting body forms can be misleading and has even led mycologists to disagree on classification schemes in the past. As a fascinating result of convergent evolution, ascomycete and basidiomycete fungi feature species that produce similar-looking mushrooms—for example, cups, clubs, and truffles.

Convergent evolution (sometimes called parallel evolution) is the evolution of similar traits in unrelated lineages. And it is very common in nature: animals, plants, and fungi all have many examples on display. What causes this? Convergent evolution is driven by the habitat and selective pressures on organisms—similar environments will select for similar traits in any species occupying the same ecological niche.

SIMILAR HABITATS RESULTS IN ANALOGOUS FORMS

Unrelated organisms often develop analogous structures by adapting to similar environments. Readily apparent analogous structures are seen in the animal kingdom: fins and wings. Wings can be found in unrelated groups of organisms like insects, bats, birds, and even extinct reptiles. Likewise, fins can be found in unrelated groups of organisms like fish, whales, penguins, and even extinct reptiles.

Convergent evolution works on the phylum level as well. Readily apparent analogous structures are seen among several orders within the phylum Basidiomycota. Many mushrooms produce shelf-like fruiting bodies on the sides of trees but not all are polypores. The environment and natural selection drives the organism into a form best suited for that niche.

NOT ALL CLUB FUNGI ARE ALIKE

The Purple Fairy Club (*Alloclavaria purpurea*) is a pretty mushroom and demonstrates convergent evolution. It appears to be one of the club fungi—the clavarias—common mushrooms in most temperate forests everywhere. Although it bears a striking resemblance to these fungi, it actually belongs to a larger group of fungi, the Hymenochaetes. Most members of this group are conks and brackets on wood that look and behave like polypores. But even they are masquerading . . . they are not true polypores. It is unknown what has driven these fungi to evolve their convergent forms. All are highly successful, based on their ubiquity in nature. And no one can deny their beauty.

TRUFFLES AND FALSE TRUFFLES

Truffles are another example of convergent evolution, where organisms from quite different evolutionary lines have independently discovered a similar way to make a living. "True" truffles are ascomycetes; they produce spores in elongated sacs and include the morels and cup fungi. "False" truffle is a term reserved for truffles that are not ascomycetes.

Many groups of basidiomycete fungi (mushrooms with a cap and stem) have lost their "normal" shape and gone underground (become hypogeous). Both feature a layered or convoluted hymenium (where the asci and basidia produce asco- and basidiospores, respectively) that is sequestered inside and not exposed. Clearly the truffle form is adaptive, but how; and how did it come about?

FORM FOLLOWS FUNCTION: THE CONVOLUTED HYMENIUM

Although not obvious, true truffles (*Tuber* species) are most closely related to members of the order Pezizales, which includes *Peziza*— very large, brown cups, commonly seen on woody debris. How did one branch of ascomycete fungi go from a flattened morphology and epigeous (above ground) growth habit to highly convoluted and hypogeous (subterranean)? Taking the reproductive surface layer, or hymenium, and convoluting it allows for more surface area (and more spore production) per unit area of mushroom. Morels are another group of ascomycete fungi that do this (but they are epigeous).

Truffle-like forms have evolved several different times within the Basidiomycota. In fact, for just about any common genus of mushrooms, we could follow an evolutionary progression from "typical" mushroom morphology to ever more truffle-like. As one example, milk mushrooms (*Lactarius* species) have a sequestrate form, *Arcangeliella*, and a very truffle-like form, *Zelleromyces*; and just like their milk mushroom relatives, both exude a milky latex. In fact, no fewer than 14 families of mushrooms have separately given rise to sequestrate or false truffle forms.

There are several possible reasons why truffle forms adopted an hypogeous existence. Various groups of hypogeous fungi may have been driven underground by some biotic factor like mycophagy; maybe mushroom-grazing animals were consuming too many fruiting bodies for that style of reproduction to be successful within the group. More likely it was due to environmental, or abiotic, factors. Most fungi are very sensitive to dry conditions, especially when forming the fruiting body. It is probable that development of a sequestrate and hypogeous fruiting body gives those fungi an advantage in drier areas. Drier habitats of Earth seem to favor truffle forms; Australia is thought to have far and away the most species of truffles and false truffles.

~ Spore dispersal ~

Producing spores in a subterranean fruiting body presents new challenges: namely, how to disperse those spores. Truffles entice other animals to help. Several mammals like deer and squirrels dig up and consume truffles. Many invertebrates are truffle feeders, including slugs and insects; many fly species are probably strict truffle feeders.

TRUFFLES DRIVE MAMMALS WILD

Tuber species attract mammalian vectors by producing a smelly compound called alpha-androstenol. This chemical is also found in the saliva of rutting boars and acts as a pheromone to attract sows. Many other mammals probably also produce this pheromone, which explains why numerous digging mammals are attracted to these fungi.

↙ Truffles are simply underground mushrooms. The spores are produced on the convoluted surface within.

CO-EVOLUTION AND MIGRATION

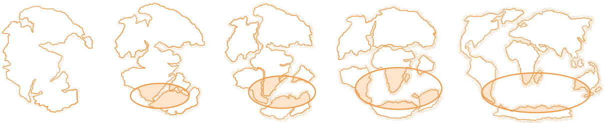
During his voyage on HMS *Beagle* in 1839, Charles Darwin (1809–1882) collected a peculiar fungus from large cankers on trees during a stop at the southern tip of South America. Resembling alien life-forms, those brightly colored *Cyttaria* fruiting bodies are relatives of morels. Indeed, both are apothecia, a sort of cup-shaped ascocarp, with sterile ridges separating the fertile areas.

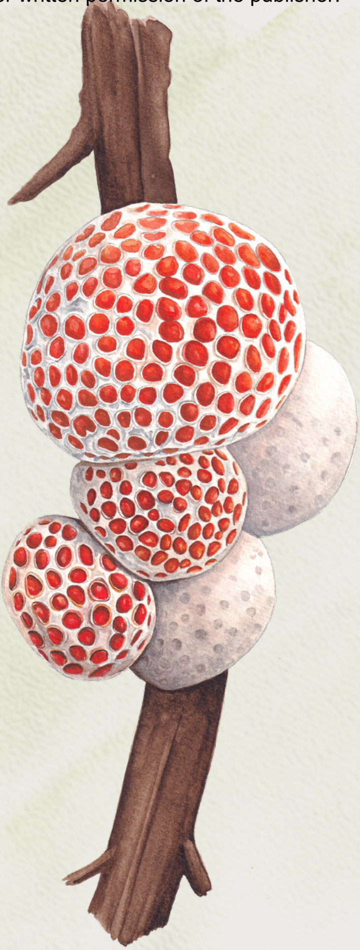
Cyttaria are obligate biotrophs of Southern Beech (*Nothofagus*) and are restricted to the Southern Hemisphere, inhabiting southern South America and southeastern Australasia. The relationship of this fungus with its host tree remains unclear. And it's hardly the only strange aspect of this fungus.

How has *Cyttaria* spread all across the vast oceans of the Southern Hemisphere? *Cyttaria* had co-evolved—and been geographically isolated on landmasses—with their respective host species of *Nothofagus*. Thus, species of *Cyttaria* and *Nothofagus* have not actually moved anywhere at all—they've been stuck with each other since the breakup of Gondwanaland, more than 200 million years ago.

↓ *Nothofagus* trees have been well-studied (more so than their fungal partners). Their geographic range is directly linked to the movement of Earth's landmasses. This time-lapse series shows the movement of landmasses over a period of 200 million years, until the final image of modern Earth.

→ Young fruiting bodies of *Cyttaria darwinii* are smooth and firm, but later develop numerous fertile pits once the membrane bursts. These ascomycete mushrooms produce spores like morels and other cup fungi.





ONE PATHOGEN, DIFFERENT HOSTS

Rust fungi (order Pucciniales) are fascinating and numerous (about 7,000 species in 168 genera worldwide). And enigmatic: rusts have up to five spore stages (spermagonia, aecia, uredinia, telia, and basidia in successive stages of reproduction). They are all obligate parasites, requiring a living host. Most rust fungi that infect trees have spore stages on two completely unrelated hosts.

RUST OF LUMBER TREES

White Pine Blister Rust (*Cronartium ribicola*) is among the most famous of forest tree diseases. Native to Asia and introduced to North America in the early 20th century, it arrived on pine seedlings from France. The fungus causes elongate perennial cankers on stems and branches; its complex life cycle requires two hosts: a white pine and a bush (*Ribes* species, currant or gooseberry).

This disease is very important economically, and to stop outbreaks the disease cycle must be broken. The US government launched a program to eradicate wild currant and gooseberry plants in the East, lasting from the 1920s to the 1950s, significantly reducing the population of *Ribes*. The federal ban on *Ribes* cultivation and sale was lifted in the 1960s, but state quarantine laws still exist today in many eastern states, where white pine is an important plantation tree.

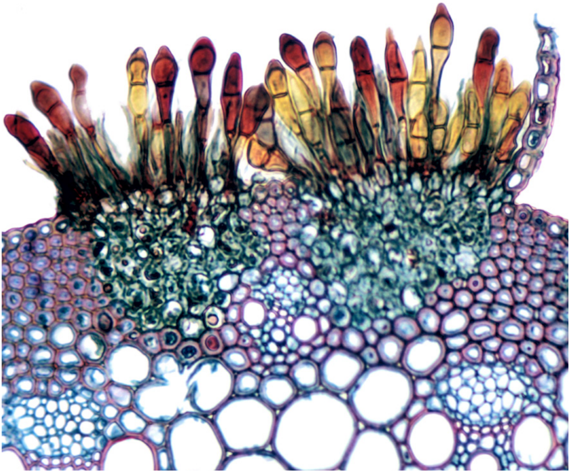
→ Wheat Stem Rust (*Puccinia graminis*) requires two very different host plants to complete its life cycle. Light microscopy reveals spore production from wheat tissues.

RUST OF CEREAL GRAINS

Rusts are responsible for the most important diseases of many of our cereal grains, including Wheat Stem Rust and Crown Rust of oats. Rusts of wheat plants, caused by the fungus *Puccinia graminis*, could be the most economically important disease of plants, globally. This disease has annually caused losses in excess of 1 million tons in North America, but in severe epidemic years losses reach tens or hundreds of millions of tons. As the world becomes more crowded, and hungry, this fungus will certainly be the cause of mass famines and even wars.

ROBIGALIAS

Human civilizations have struggled with Wheat Stem Rust for centuries; the Romans tried to appease the fungal gods with "robigalias"—elaborate ceremonies in which dogs were sacrificed in an effort to stave off the rust-colored "red fire" that annually descended upon and consumed their fields of wheat.



OUR ROTTEN WORLD

Next time you encounter a fallen tree in the forest, examine it. You will find a tiny ecosystem. Ultimately, sunlight was the original input of energy into that system; the tree captured it autotrophically. Now in death, all that organic matter—likely tons of carbohydrates and proteins and other building blocks of life—are sitting there for the taking, for any organism with the ability to break down wood. Simple single-celled bacteria can ingest sugars sitting on the surfaces of the wood; slime molds ooze over and engulf them.

Fungi are well adapted to break down wood using cellulase enzymes; wood-boring beetles, wood wasps, and other arthropods can feed on degraded wood inhabited by fungi—much of the time, the fungi were inoculated into the wood by their insect partners. Woodpeckers, other birds, and mammals tear through the wood in search of arthropods to dine on. Other members of the forest make homes out of cavities in the wood. The circle of life for the ecosystem that was a single tree is complete when the log serves as a nurse tree for seedlings or is decomposed entirely back into soil.

↙ Fungi are good at decomposing wood, but it can take a long time. The Dyer's Polypore (*Phaeolus schweinitzii*) is commonly found on conifer wood.

WOOD DECOMPOSITION

Decomposition of carbohydrates and other organic matter is pretty much the same chemical process as photosynthesis, but in reverse. During photosynthesis, plant chlorophyll captures the energy of red and blue wavelengths of sunlight (green is not much used and is reflected, with the result that plants appear green), and converts that into energy to "fix" single carbon molecules (the very plentiful carbon dioxide of the atmosphere) into growing chains of carbons and hydrogens—literally the carbohydrates of plant matter. One by one, carbons are fixed into six-carbon sugars; these are linked together to form cellulose and other carbohydrates, and plants grow.

Plants are mostly composed of cellulose and water. Woody plants or those with a rigid structure also contain a great deal of lignin. Lignin is a polymer of very tough ring molecules crosslinked in a random fashion that strengthens wood. Both cellulose and lignin are difficult to break down and require arsenals of enzymes and other machinery. For the most part, wood-degrading fungi are good at breaking down one or the other, but they're largely after the same thing: cellulose.

FOSSIL FUELS: A THING OF THE PAST

We are truly fortunate that fungi came along. Without them, we would surely be buried under miles of dead organic matter. Fungi do the planet a great service by breaking down and recycling the dead organic matter that accumulates all over Earth, most of which is cellulose and lignin from dead trees and other plants. That we can dig up vast pockets of buried coal and petroleum is evidence that, at one time, there were no wood rot fungi.

Scientists have determined that fungi capable of rotting woody plants didn't come onto the scene until the end of the Carboniferous Period (360–290 Mya)—quite a bit after the evolution of woody plants. So instead of decomposing, all that organic matter piled up and changed by a process of chemical reduction (the opposite of oxidation), and thus fossilized—into fossil fuels like coal. With the proliferation of wood rot fungi, the buildup of coal deposits dramatically decreased during the Permian Period (299–251 Mya).

BROWN ROT AND WHITE ROT

Plants are mostly made up of cellulose and lignin. Both compounds are made of carbohydrates but are very tough to break down. Armed with wood-degrading enzymes, fungi are just about the only organisms that can do this.

BROWN ROT FUNGI

Fungi that directly break down cellulose, leaving the brown lignin behind, are called “brown rot” fungi. The removal of the cellulose destroys the structural integrity of the wood and it cracks and falls apart as cubes. Examples found worldwide are the polypores *Laetiporus*, *Phaeolus schweinitzii,* and *Fomitopsis*.

WHITE ROT FUNGI

In contrast, the “white rot” fungi decompose lignin, bleaching the wood and initially leaving stringy, white cellulose behind. These fungi have powerful peroxidase and laccase enzymes that break down the lignin. While there is evidence that they can decompose lignin completely to carbon dioxide, many researchers suggest the fungi are mostly removing it from the woody pulp to better get at the cellulose. White rot fungi found worldwide include polypores like *Inonotus*, *Ganoderma*, and *Trametes*, as well as *Pleurotus* and *Armillaria*. The popular cultivated Shiitake mushroom (*Lentinula edodes*) is also a white rot fungus. The power to bleach wood pulp of lignin makes the white rot fungus *Phanerochaete chrysosporium* important to the paper industry as an environmentally benign replacement for harsh synthetic chemicals.

→ The white, stringy debris resulting from the peroxidase and laccase enzymatic action of white rot fungi. Decomposition of lignin leaves the white cellulose behind.

WOOD ROT ATTACKS LIVING TREES

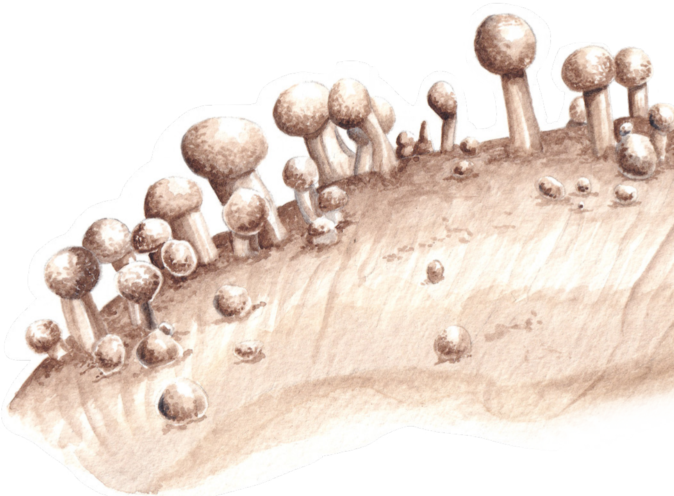
Many of the wood rot fungi familiar to us (for example, the big polypores) don't wait for trees to die before launching their assault. Living trees often sport big fruiting bodies of shelf fungi. This is because most of the tree is heartwood—the dead inner wood. (Only the outer layers, just under the bark, are living tissue.) All it takes is a wound to disrupt the integrity of the bark and heart rot can ensue. Similarly, butt rot happens at the base of the tree.

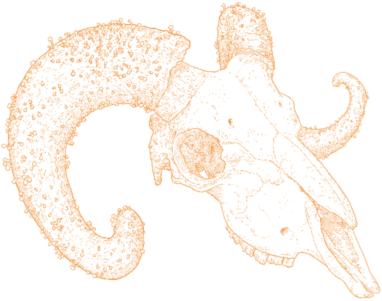
Heart rot can proceed for many years without really having much negative effect on the tree. Upon seeing large polypore shelves hanging off the side of a tree, most people assume the fungus is a parasite of the tree. In reality, few polypores are truly parasites of living tissue. An otherwise healthy tree takes measures to contain these heart rot fungi, preventing them from invading living tissues in most cases.

FUNGI WITH A UNIQUE LIFESTYLE

No matter the source of nutrition, there is a group of microbes to utilize it. Some components of animals persist long after death, including those constructed of keratin like fur, feathers, and horns. Keratinized material is so tough that only a single group of fungi can decompose it: the order Onygenales.

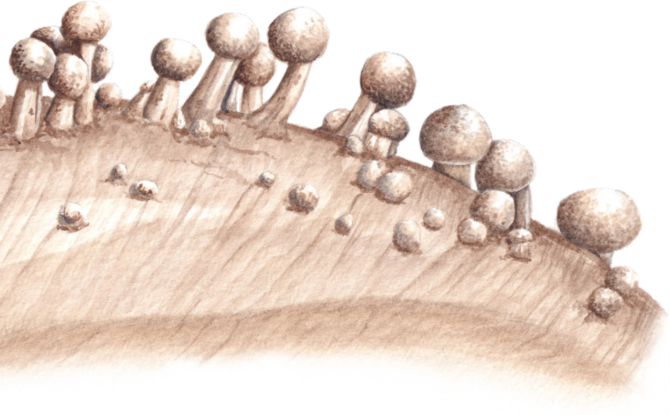
Undoubtedly the most unusual but least understood genus of the group is *Onygena*. If on the odd chance you happen to find an animal's horns lying in the forest, examine them. They may be covered with tiny, stalked, mushroom-like fruiting bodies, a sure sign of *Onygena*. (Antlers are bones and not made of keratin.) Owls and other birds will regurgitate a pellet of bones, fur, feathers, toenails, and other undigestible material. These are good places to find *Onygena*, as well as to see what's on the menu of predators in your area.





↙ The genus *Onygena* consists of just two species: *Onygena corvina* is associated with animal feathers and fur, while *O. equina* is a decomposer of the hooves and horns of herbivorous mammals.

↙ Close examination of *Onygena equina* sporophores will reveal that what appear to be tiny, stalked mushrooms are, in fact, masses of spores at the tips of aggregations of hyphae.



ANIMAL PARASITES

Fungi are now routinely making the headlines and the news is not often good. We are currently facing two major animal crises: a massive decline in amphibian species and an explosive disease outbreak among bats in North America. What a terrible loss to the future planet it would be if there were no amphibians to sing in our wetlands and no bats in our evening skies.

GLOBAL AMPHIBIAN DIE-OFFS

For many years, herpetologists around the world had noticed that amphibian populations were in decline, but the evidence remained largely anecdotal. In the 1990s, an unknown fungal disease was identified—chytridiomycosis—which was causing widespread amphibian mortality in Australia, as well as North, South, and Central America.

The causative agent is *Batrachochytrium dendrobatidis* (Bd). The lifecycle of Bd involves a motile, swimming spore that finds a host animal and sticks to its skin. In a matter of days, new zoospores are released, which swim about and further infect the same host; if they find another amphibian, a new infection begins. When covered in fungal zoospores, the host is unable to breathe and dies. Bd is responsible for what is perhaps the largest panzootic in history and infects many frog, salamander, newt, and other amphibian species. Undoubtedly, some amphibians will be wiped out, but immunity is cropping up in various places and some amphibians are beginning to bounce back.

← In the United Kingdom, most populations of the native Natterjack Toad (*Epidalea calamita*) have tested positive for the fungal disease chytridiomycosis, but are apparently unaffected.

WHERE DO THESE PANDEMICS COME FROM?

Both pandemics are not fully understood. Chytrid fungi may have long been associated with amphibians. Increasing UV sunlight levels and global climate change may stress amphibians, allowing these fungi to become pathogenic. However, *Batrachochytrium dendrobatidis* (Bd) could be new: examination of preserved amphibians in museum collections found no Bd prior to 1938, which corresponds to the inception of trade in African Clawed Frogs (*Xenopus laevis*) used in research labs and pet aquaria.

White-nose Syndrome (WNS) seems to be a newly emerging disease from Europe—it is found in caves throughout Europe, although doesn't seem to cause problems for bats there. It's likely that European bats have been around the fungus for millions of years and have had time to develop resistance to it.

EPIDEMIC BAT DIE-OFFS

In late winter 2007, researchers found thousands of dead Little Brown Bats (*Myotis lucifugus*) with a white growth on their muzzles and ears in five caves in upstate New York. Bat White-nose Syndrome (WNS), caused by *Pseudogymnoascus destructans* (Pd), has since spread throughout eastern North America. The fungal pathogen is known to infect at least 13 species and millions of bats have been killed. Since bats pollinate some plants and eat pest insects, their value to US agriculture has been estimated at least $3.7 billion a year.

Pseudogymnoascus destructans is a saprobe living on organic matter found in caves. Its growth on living bats is still somewhat of a mystery, and seems to be opportunistic. Growth on the skin of bats seems to irritate them out of hibernation, causing them to fly about. This activity consumes winter reserves bats can ill afford. If they leave the cave before spring, they waste further energy in a vain search for food. Thus, bats that succumb to WNS often die of starvation.

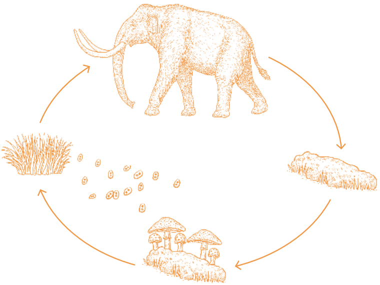
COPROPHILOUS FUNGI

Spores of coprophilous (dung-loving) fungi are tough and resistant, with thick walls adapted to survive passage through the intestinal tracts of herbivores. This makes them conducive to fossilization and they are often found deep in soil layers, lake deposits, and permafrost. Scientists use these fungi as a tool to study mammals long gone.

Spores of *Sporormiella* are unmistakable in soil sediments—even from thousands of years ago. Archaeologically, these spores are an indicator of vegetation changes throughout history. Accumulations of *Sporormiella* spores are correlated to an abundance or absence of herbivores today, as well as in the past.

Scientists can determine when the mammalian megafauna dominated North America, and when they began their decline due to factors like a changing climate and Paleo-Indian hunting pressures at the end of the Pleistocene Epoch (2.6 million to 11,700 years ago). Following the last Ice Age, the numbers of these dung fungi remained low until 17th-century European settlers brought livestock to North America.

↓ The spores of dung fungi are inadvertently consumed along with grass and pass through the herbivore's gut; the spores are then discharged with feces. These germinate in the new substrate and the life cycle continues.



→ The undigested plant matter that passes through grazing animals is mostly cellulose, and therefore it is highly nutritional for dung-loving fungi, including *Deconica coprophila*, shown here. Since the animal did much of the mechanical work by grinding and partially breaking down this material, being the first to colonize dung before competition arrives has led to some interesting specialization, e.g. *Pilobolus* lifecycle.

BIOLUMINESCENCE

Glowing mushrooms are amazing to see . . . and mysterious. Bioluminescence has been documented since the time of Aristotle (384–322 BCE) and Pliny the Elder (23–79 CE). The four lineages of bioluminescent fungi contain around 80 different species. Mushrooms familiar to us that glow include *Armillaria*, *Mycena*, *Omphalotus*, and *Panellus*. "Foxfire" is glowing deadwood, a sure sign of wood decay by hyphae of *Armillaria*.

WIDESPREAD IN NATURE

Bioluminescence is common in the natural world; in addition to fungi, some animals, plants, and bacteria can do it. Two things to keep in mind about bioluminescence are that it is ongoing, even in the light of day, although not visible. Likewise, bioluminescence generates no heat and is thus very different from incandescence, which is a thermal glow. Today it is known that the light originates from a metabolic reaction of the fungus where electrons are transferred to an acceptor molecule (luciferin), which is cleaved by an enzyme (luciferase) in the presence of oxygen. This results in the formation of an electronically excited state of the luciferin and the subsequent emission of light with a maximum wavelength of approximately 525 nanometers (nm) during return to the ground state. This process is much the same for all organisms that bioluminesce, although the luciferins and luciferases are not exactly the same.

→ *Omphalotus* species are wood rot fungi that seem to produce large, but pretty drab mushrooms when seen in the light of day. But after dark, their eerie green glow can be properly seen.

FUNGAL BIOLUMINESCENCE REMAINS AN ENIGMA

What is the purpose of bioluminescence? Might it serve as an attractor of invertebrates for the purposes of spore dispersal? Although the subject of much research over many years, we still don't know. Bioluminescence may simply be a way for fungi to dissipate energy as a by-product of oxidative metabolism (most organisms, including us, give off heat as a by-product). Moreover, this chemical reaction may be tied to detoxification of the peroxides formed during lignolysis. Many bioluminescent fungi rot wood and leaf litter—for example, *Armillaria mellea* and *Panellus stipticus* are white rot fungi. There are genera with glowing and non-glowing species that all seem to be equally successful in nature; thus, many argue it serves no selective advantage. Within the genus *Mycena* there are at least 33 species, from 16 sections, known to bioluminesce.

THE SEX LIVES OF FUNGI

Fungi reproduce very differently from other life-forms. Most, if not all, fungi can reproduce asexually. A benefit of sexual reproduction comes from genetic recombination (which is undoubtedly why it is so common among eukaryotes). Also termed "crossing over," offspring receive a combination of DNA from both parents of that individual. Sexual reproduction in all organisms involves three events: the fusion of two haploid (*n*) cells (plasmogamy); fusion of nuclei (karyogamy) to form a diploid (2*n*); and meiosis that results in recombinant haploid nuclei that will be offspring.

Animal cells are diploid dominant, and during sexual reproduction haploid gametes of two parents fuse to restore the diploid state. Most fungi exhibit a life cycle with both a haploid and a diploid phase; for many, each cell contains two haploid nuclei (one from each parent) as a dikaryon.

BASIDIOMYCETES DO IT

Basidiomycetes can live as a dikaryon for a long time; only at the time of sexual reproduction does karyogamy take place (in the basidium) of the fruiting body and results in haploid spores (basidiospores). These germinate and fuse with an opposite mating type hypha pretty quickly in order to restore the dikaryon state and a full complement of necessary genes.

ASCOMYCETES DO IT

With ascomycetes, the timing of these steps depends on the group. Many common ascomycetes are anamorphs (asexual forms), and seem to do just fine as monokaryons. In teleomorphic (sexual) ascomycetes, the fungus can undergo plasmogamy and live as a dikaryon. At the time of sexual reproduction, karyogamy takes place in the ascus of the fruiting body. Karyogamy and the diploid state is quickly followed by meiosis and haploid spore production.

(continued...)

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