Prehisporical

[Music begins]

Izzie: Welcome to Morel Dilemma, an exploration of why some fungi are so highly sought, some are so heavily cultivated, and some are so very dangerous. By this time, I hope you've figured out that fungi are everywhere. They're in the air we breathe and the water we drink. They're in the plants we grow and the animals we raise. They are in our food. They are our food. They sustain us, directly and indirectly, and when we die they will help break us down and recycle our matter to keep life going. From the tropics to the poles, fungi are linked to every ecosystem on Earth. Helping people see and appreciate them is literally the reason I made this podcast in the first place. But how far back does the relationship go? How long have fungi been linking all life on Earth? That's easy. The answer is…

[Dramatic pause in music]

Izzie: …Since the start of life itself.

[Music resumes and ends]

Izzie: The Earth has been around for about 4.6 billion years, but the very furthest estimates put life at only (hah, "only") 4.5 billion years old. For at least 100 million years, Earth was just another rock in space, sailing around our sun, nothing too special about it – except for liquid water. You may know that liquid water, or some similar liquid, is considered necessary for life to exist.

[Music starts]

Izzie: One reason is that water is a great insulator, which means temperature changes are gradual. You might recall this from the episode covering the underwater Rogue mushroom. Gradual temperature changes are really helpful because many of the molecular cogs in the machine of life can only operate in a narrow range of temperatures – too cold and they freeze up or break, too hot and they melt. By staying in water, those molecules don't have to deal with major temperature swings.

Water is also a great solvent, which means lots of important materials can dissolve and move around in it. As a basic example, you know you can dissolve sugar, the main energy source for life, in water. As a very advanced example, your brain works because neurons can use freely floating ions to generate electric currents that create signals. From food and waste to neurotransmitters, water keeps everything moving.

[Music ends]

Izzie: Surprisingly, even though 70% of the Earth's surface is water, scientists still aren't sure where it all came from. We also aren't sure how exactly life first arose – was it a simple problem of elements bopping around at random until something coalesced into a proto-cell? Were certain conditions in the primordial ooze conducive to spontaneous life in a way that our modern oceans aren't? These are questions that many scientists have spent their lives exploring, and I don't have an answer. So let's just jump ahead to a time when the first life was already around, about half a billion years into Earth's existence. Let's say hello to bacteria.

[Music begins]

Izzie: Bacteria are single-celled and fairly simple. A lot of people incorrectly equate simplicity with evolutionary failure – the idea that only the organisms that have become more complicated are really "succeeding" at evolution, so multicellular organisms like humans are better adapted than simple organisms like bacteria. But it's important to remember that all the organisms on Earth today have been adapting, changing, and developing since life began. As far as evolution is concerned, they're just as successful as we are.

The best example of successful simplicity is also the most extreme: the oldest known life on Earth, discovered just this year in March 2017, were bacteria that lived in hydrothermal vents 4.2 billion years ago. Hydrothermal vents are places in the deep ocean where hot, iron-rich water boils up out of the crust. They've popped up in various places over Earth's history, and the ancient bacteria are very similar to the bacteria living in hydrothermal vents today. Bacteria might be simple compared with humans, but their simple design has spelled success for billions of years!

[Music ends]

Izzie: We more complicated organisms could not have developed without simple organisms, either. It's not just that one branch of life started down a more complex track, and spontaneously split off from single-celled organisms to form increasingly complicated multicellular organisms like ourselves. The evolution of eukaryotes, the more complicated cells that make up plants, fungi, and animals, arose from cooperation and collaboration between single-celled critters. The theory of *endosymbiosis* states that a large single cell, unable to produce its own food, engulfed a smaller energy-producing cell as if to eat it – only instead of digesting the smaller cell, the larger cell incorporated it as a tiny organ, or "organelle". The engulfing organism received food while the smaller organism received protection from the elements in the world's first symbiosis.

The large cells that would become animals and fungi incorporated organelles that are extremely efficient at generating energy from sugar, which are now called mitochondria. Those destined to be algae and plants incorporated mitochondria as well as photosynthetic organelles that evolved into modern chloroplasts, which give plants their green color. Endosymbiosis was explosively successful, as you can tell from at the amazing diversity of multicellular life on Earth.

Multicellular organisms didn't hit their stride until the colonization of land 425 million years ago. For three billion years before then, the multicellular lifestyle was purely composed of filamentous forms, relatively simple partnerships between cells of the same species that are successful enough to still be present today, and another important stepping stone on the evolutionary trail to land. Photosynthetic cyanobacteria were the first to make the leap to multicellularity about three and a half billion years ago, but fungi and algae were close behind. One billion years later, cells in filamentous organisms began differentiating to perform specific tasks, like how liver and brain cells perform differently in your body. But even the most complex organisms at the time, more than 4 billion years after Earth's birth, had not ventured onto land.

[Music begins]

Izzie: The oceans had water aplenty to support life. In addition to providing a temperature buffer and a medium for all the necessary nutrients and minerals to move around, the constant movement of the water helped weather the rocks under the surface, making the minerals inside the rock available to the living organisms that needed it. On the other hand, early Earth's land was solid stone. Soil literally hadn't been invented yet, which made life on land basically impossible.

Soil as we know it has small pieces of minerals interspersed with a lot of broken down organic matter, which makes it a smorgasbord of the essentials for life. But solid rocks exposed to the air break up into minerals much more slowly than the rocks getting constantly battered by water in the ocean. As for the organic matter, with no available minerals and nothing easy to hold onto, rock doesn't provide an easy living surface for sugar producers like algae. With nothing living on the rock, nothing died and decomposed on the rock, so the organic matter decomposers need wasn't present – and without organic matter, no non-producers could live and no producers could hold on. For four billion years, land was stuck in a lifeless rut.

Fortunately, fungi were on the case.

[Music ends]

Izzie: As you know, fungi digest their food before eating it by releasing chemicals and proteins that break it down. Some of these chemicals are acids, and it turns out that many of them are potent enough to *dissolve rock*. Another set of useful chemicals are chelators, compounds that concentrate the metal atoms released from the rock so they are easier for the fungus to retrieve. So yeah, fungi have been mining minerals from solid stone, without tools, for billions of years. It's pretty metal, by which I mean, there are some metal ions in there. Like iron, aluminum, zinc, magnesium, manganese, calcium, potassium, and copper, which are all necessary for life.

Fungi can also break rocks down physically. Like some futuristic technology, hyphae are just twice the width of spider silk, but strong enough to break through bulletproof Mylar. No, really. The tip of each fungal hypha packs a pressure of more than one thousand pounds per square inch! With that incredible power and their miniscule size, hyphae can easily penetrate tiny cracks and crevices in the stone produced by fungal acid secretions or by natural weathering. By creating and expanding these pockets in the stone, fungi can burrow straight through rock, breaking it down *ten times* faster than natural erosion! With a good microscope, you can actually see tiny, hyphae-sized tunnels curving through rock and mineral particles in soils both ancient and modern.

Now, as you might expect, producing acids powerful enough to dissolve rock is energetically expensive. The fungi that do this need an incredible amount of carbon, both as a food source and as a raw material to craft the acids from. Saprobic fungi, the great recyclers, can use the calories stored in dead organisms for this purpose – although, as we have discussed, there is not a lot of organic carbon hanging out on pure rock. Instead, the best rock colonizers are fungi partnered with photosynthetic organisms. Mycorrhizal fungi, working inside plants, date back about 450 million years, and lichen fungi, working *around* photosynthesizers, have been found as far as 550 million years back. Everywhere these rock-crunching fungi went, they left a trail of the essential elements of life, and when they died, they left organic material that decomposers could break down. About 425 million years ago, land opened up to life for the first time, and rapidly diversifying land organisms took center stage.

[Music begins]

Megan: Hello, hello. This is Megan, from Colorado, and I was wondering about ancient fungi and ancient trees. Do scientists know if they were symbiotic? Is that how things got started for fungi? Anyway, hope to hear the answer, and have fun. Bye.

[Music ends]

Izzie: Perhaps the most important development for the future of life on Earth was the evolution of plants. The Rhynie Chert is a famous fossil deposit in Scotland that dates back 410 million years, at the very start of land colonization. The chert is renowned for its absolutely perfect fossils, which crisply preserve structures, including many fungi, down to the microscopic level. It’s no surprise, then, that the Rhynie Chert is the site of the earliest known arbuscule, the cellular structure that lets plants and mycorrhizal fungi communicate. The first mycorrhizal fungi, the glomeromycetes, are estimated to be about 600 million or even 1 billion years old, though their partnerships with algae likely began contentiously, the algae struggling to defend against a perceived invader looking to steal precious sugar. Once the fungi had evolved arbuscules, though, they could exchange nutrients for algal sugar in a mutually beneficial arrangement, recognized as friends instead of invaders.

Alone, neither algae nor fungi are well suited to life on land. Algae are delicate and rely on an aquatic environment to avoid drying out. On the other hand, aquatic fungi wouldn't have been able to handle dry land either, and since they can't photosynthesize, giving solar radiation something useful to do, the harsh direct rays of the sun would burn them right up. Working together didn't just improve their lot in the ocean; it make it possible to conquer land. The fungi received sugars and specially-crafted molecular sunblock from the algae, while the algae gained structural support, safety from drying out, and minerals from the rock. From the start, the partnership was a hit.

[Musical tone]

Izzie: Although modern arbuscules are exclusively found below the soil, the Rhynie Chert fossils show arbuscules interacting with the plants aboveground as well, with the fungi in some cases reaching all the way to the tips of the aerial parts of the plant – what would eventually become branches and leaves.

This discovery has prompted some scientists to propose that the arbuscular mycorrhizae, or AM fungi, could have helped provide initial structure or even genes to the algae that helped them begin turning into today's plants. The idea of gene swapping was first proposed in 1984 by Dr. W. F. Lamboy, and was expanded in 1988, when Dr. Atsatt proposed that the fungal nucleus itself could have been injected into the plant cell, using a mechanism like the one still used by parasitic oomycetes today. In particular, if the algae incorporated genes that direct the fungus' ability to grow several tips in different directions, then the algae wouldn't have had to evolve roots all on their own, speeding up the evolution of rooted plants. Hyphae are still more efficient at nutrient uptake than roots are, even in ready-made soil, so a little gene stealing here and there wouldn't have spelled an end to the partnership. But it could explain how plant diversity exploded so quickly after life first made landfall.

[Music begins]

Izzie: As the new denizens of land grew, lived, and died, the organic material began building up. Saprobic organisms had access to the nutrient reserves they needed, and soil finally began to make an appearance. Like hydrothermal vent bacteria, modern saprobic fungi are largely unchanged from their ancient ancestors; the earliest known evidence of fungal wood rot comes from the Late Devonian period, about 380 million years ago, and it looks strikingly similar to the wood rot we find today.

The amazing similarities between ancient and modern fungi imply that they must have been as widespread in ancient times as they are now – and yet fungi are fairly hard to find in the fossil record. Some of the reasons are intuitive based on the fungi that exist today: their fruits are ephemeral and often intended to be eaten, as is the case with edible mushrooms, and the hyphae are thin and hairlike, which lets them efficiently gather nutrients but also means they are easily fragmented or destroyed. And fossilization involves millions of years of intense pressures and stresses. Tiny hyphae don't have good odds. As a result, fungi have a much less consistent fossil record than plants or animals.

[Music ends]

Izzie: Though plant and animal fossils have garnered attention for hundreds of years, the first major survey of fossil fungi came in 1921, when Doctors Kidston and Lang published their findings of fungal fossils in the Rhynie Chert. The next study reporting fossilized fungi wouldn't come for another 50 years. Writing in 1969, Doctors Harvey, Lyon and Lewis reported a filamentous fossil, also in the Rhynie Chert, which is similar to the modern fungus *Apodachyla pyrifera*. That's the first time an ancient fungus had been related to an existing one. Perhaps it was this compelling link to the modern day, or perhaps the paper coincided with improved methods of fossil identification; either way, that 1969 paper marked the practical beginning of paleomycology, the study of fossil fungi.

[Music begins]

Jack Mason: Hello, this is Jack Mason in Portland, Oregon. I was wondering about the fossilization of mushrooms. When the mushroom dries, it has a certain smaller size. Is the fossil that same size, or is the fossil smaller than the dried mushroom? Thank you very much. Bye.

Erika: Hi, this is Erika from New York and I was just wondering, because mushrooms are mostly made of water, how do they survive the fossilization process? Thanks!

[Music ends]

Izzie: As we explore the remarkable findings of paleomycology, I'm going to be using terminology used by geologists to separate long periods in Earth's history. The largest chunks of time are called eras, and they are broken into periods. The periods are then broken into epochs. I'm not a geologist, so I don't have the eras and such memorized, and I don't expect you to either. So when I describe the time period a fossil comes from, I'll say both the geologic name of the time period and then when that actually was. Sound good? Let's get started.

After forty years of research and study, paleomycologists have discovered and named fungi from all over the world. Fungal fossils have been found on every continent, including Antarctica. The most common fungal fossils are from the Cretaceous Period, 145 million years ago, or later, though they dot the fossil record all the way back to the beginning of the Paleozoic Era, 540 million years ago.

Chytrids and oomycetes are the earliest known and also the most common fossil fungi, and both unicellular and filamentous forms abound. Chytrids are actually so abundant in the Rhynie Chert that scientists have been able to deduce entire life cycles for extinct species!

In general, though, the fossil record isn't specific or complete enough to support life histories of specific fungi, but it can relate fungal groups to each other and help scientists estimate when certain branches of fungi emerged.

For example, there's a fungus called *Paleosclerotium*, first discovered and named in 1972, that is common in coal fossils from the Pennsylvanian Epoch, 320 million years ago. *Paleosclerotium* has traits considered exclusive to ascomycetes, as well as other traits that are considered exclusive to basidiomycetes. Rather than a mistake, this may mean that *Paleosclerotium* represents an ancestral lineage that predated ascomycetes and basidiomycetes, then continued growing alongside those two groups after their divergence 510 million years ago.

Today, ascomycetes are the largest fungal group. Though possible ascomycetes have been found as early as the late Silurian Period, around 420 million years ago, they are mostly found in fossils from the Mesozoic Era, 250 million years ago, and later. The Silurian ascomycetes are so rare that they are largely discounted, though if later evidence shows that they're the real deal, that might push back estimates for the ascomycete-basidiomycete divergence. Basidiomycetes are currently the second-largest fungal group, and their oldest known member hails from the vascular system of a fern from the middle Pennsylvanian Epoch, about 300 million years ago.

[Music begins]

Izzie: When paleomycology began, it was lumped in with paleobotanical studies, just as early mycology had been considered part of plant biology. Identification of fungal fossils was based almost exclusively on morphology of the fossilized parts, which is not very helpful for identification. Consider the most diagnostic characteristics we use in modern mycology. We look at habitat – is it growing on grass? In a swamp? On a tree trunk? We consider colors of the cap, the stipe, the mycelia and the spores. And, in many cases, we rely heavily on the shape of the fruiting body.

Well, it's hard to tell what kind of substrate a fungus was growing on before fossilization turned the substrate to rock. It's also impossible to know if there were any plants nearby if they didn't get fossilized alongside the fungus. Color is completely lost after a few hundred million years, and of course, mushrooms, with their captivating diagnostic shapes, were probably just as fleeting then as they are now. Many of the traits that don't get fossilized have probably changed considerably – it's hard to imagine that the first terrestrial fungi had fruits as complicated as morels, for example, or that fruits well suited to the Devonian world are just as well equipped to today's very different environmental conditions.

But in terms of what scientists can see in fossils, the similarities between ancient and modern fungi are incredible. In 400 million years, it seems that the structure of hyphae hasn't really changed. Remember the 410 million year old arbuscules from the Rhynie Chert? Paleomycologists can recognize that they are sites of plant-fungus nutrient exchange because they look *just like* the arbuscules we see today. Similarly, aquatic fungi in Precambrian fossils, dating back more than 540 million years, are almost identical to their modern counterparts. Even the mechanisms fungi use to digest food are apparently unchanged – Permian and Triassic wood fossils from Antarctica show clear signs of white wood rot. That means white rot fungi have been eating in almost exactly the same way for 300 million years!

[Music ends]

Izzie: The incredible consistency of fungi in history – at least, of the fungi that get fossilized – demonstrates just how successful the structure of hyphae is. With their ability to release and absorb materials all along their length and infiltrate tiny particles or holes, hyphae are a very low-cost, high-efficiency growing style. That also helps explain why very different modern fungi, from molds to morels, all hold to the same hyphal method. And despite all the information we're missing for specimens in the fossil record, paleomycology can still tell us quite a bit about how these mysterious ancient fungi interacted with other organisms.

Interactions between fungi and animals are extremely rare in the fossil record, but they do exist. Generally, the denser a deposit is in animal fossils, the more likely it is that a fungus will be found too. The most common type of fungal fossil is actually indirect - the bore holes of aquatic fungi, probably chytrids, frequently appear on the skeletons of marine animals that lived as far back as the Ordovician Period, 485 million years ago. Insects and arachnids also joined in the fungal fun, though they might not have been alive to appreciate it. Oligocene-Miocene amber, about 23 millions of years old and discovered in the Dominican Republic, encases a fungus growing on the surface of an arachnid (the branch of life that includes spiders). The arachnid's tissues had not been penetrated by the fungus, so the fungus was probably a decomposer rather than a symbiont. Another collection of amber, dating to 25 million years ago, shows two more insect decomposing fungi, one trapped in the act of digesting a termite and the other working on an ant. But fungi weren't the only ones chowing down.

[Music begins]

Erika: Hi, this is Erika from New York, and I was just wondering, do we know if any ancient fungi were edible? Thanks!

[Music ends]

Izzie: Although the fruits probably looked nothing like modern chanterelles, fungi might still have been haute cuisine millions of years ago. Coprolite is the fancy word for fossilized poop, and it's another great source of fungal fossils. It's not always clear just what these fossils represent – are they evidence of a rodent's tasty snack, millions of years before cooking would make the chitin digestible? Or, are these decomposer fungi that colonized the poop once the animals were, uh, finished with it? As a matter of fact, there might have been a bit of both. Some coprolites have a mix of materials, including plant fragments, and then fungal spores. They are more likely to have come from animals that incorporated fungi as part of a balanced breakfast. Other coprolites can be almost entirely made up of hyphae, and may represent fungi colonizing and utilizing ancient fertilizer.

[Music begins]

Izzie: Possibly more compelling evidence of ancient fungal cuisine came to light in 2016, when a 50 million year old piece of amber containing a mushroom was found in the Dominican Republic. Amber is fossilized tree sap, which can flow quickly enough to entrap critters as fast as insects (think Jurassic Park). That's why amber can be so good at preserving artifacts, such as fungi, that would ordinarily rot away or be eaten long before fossilization could occur. This fossil is doubly interesting, though, because it doesn't just include a prehistoric mushroom, it *just* includes a prehistoric mushroom. That is, the mushroom had been separated from its mycelia, as though picked for lunch – presumably by the rodent whose hair is also trapped inside. The authors of the paper suggest that the rodent picked the mushroom and took it to a suitable dining location, when along came a sap flow. Fearing entrapment, the rodent made a run for it, leaving the delicious mushroom – and one compelling hair – behind.

[Music ends]

Izzie: Much more abundant in the fossil record are examples of fungi coexisting with photosynthetic organisms. The first lichens date back to the Paleozoic Era, which began 540 million years ago. Possibly the most convincing lichen from this era comes from the good old Rhynie Chert again. *Winfrenatia reticulate* is a thin mat of mycelia with regular, shallow depressions on the upper surface. Each depression contains small cells, probably cyanobacteria, intertwined in the hyphae.

But the crowning glory of fossil fungal interactions is their extensively documented relationship with ancient plants, beginning with liverworts. Liverworts are the oldest group of land plants that survive today, and are fairly basic as far as plants go. They don't have a vascular system, so they are extremely short, and morphologically they look pretty similar to mosses or lichens: low to their substrate, with a leafy texture. Because they are as close to the original land plants as we currently have, liverworts have been extensively studied as models of ancient life. In lab studies, liverworts that have been colonized with root mycorrhizal fungi are given a major boost – they're significantly more photosynthetically active, are significantly bigger, and engage in significantly more sexual reproduction than liverworts that are grown without mycorrhizal fungi. The benefits of mycorrhizae on liverworts actually increase in high-CO2 conditions that mimic a Paleozoic atmosphere, another piece of evidence supporting the theory that fungi helped plants colonize land.

[Musical tone]

Izzie: While liverworts dominated the scene, there wasn't a lot of aboveground area for fungi to colonize. Leaves or leaf-like structures wouldn't evolve until the Middle Devonian, about 390 million years ago. But as plant diversity increased and their floor plans got more complex, the diversity of the fungi living with and on them also increased. Plant fossils from the early Mesozoic Era, 250 million years ago, and onward commonly show fungi living inside the leaves of vascular and pre-vascular plants. The intervening time between land colonization and the Mesozoic show a conspicuous absence of fungal endophytes, making it difficult to estimate when fungi developed the ability to live inside a leaf. It's generally assumed that leaf endophytes evolved in the Cretaceous period, 145 to 70 million years ago. However, highly complex fungi, fossilized on their own, are known from the Silurian period, as late as 440 million years ago, so leaf endophytes or their precursors may go way back.

[Musical tone]

Izzie: There are even fossils showing fungi growing on other fungi! Well, it's only natural that the world's greatest decomposers would figure out how to recycle each other too. The first fossil fungal spores with smaller, parasitic spores inside were described in 1921. Early Devonian chytrid parasites have been found on fungal hosts, with different chytrids on different parts of the parasitized fungi. That means host specificity, adaptation of a parasite to a specific host location, has been around for more than 420 million years! My favorite example of fossil myco-cannibalism is a 100 million year old mushroom encased in Dominican amber, which has threads of a mycoparasite on the cap... and threads of a hyperparasite on that parasite! It's a tower of fungal colonization.

[Musical tone]

Izzie: So now you know the vital role fungi have played in the development of life on Earth, and throughout its history. Present from the early primordial ooze, ancient fungi made land livable and helped plants conquer the aerial environment, all the while adapting to help or break down plants, animals, and each other. In a way, fungi laid the foundation for all terrestrial life, even humans, by sculpting the ground we walk on and giving us access to the nutrients we need. I find it truly humbling to think about all the remarkable fungi that have contributed to modern ecosystems and modern life – and to consider all the enormous gaps in our understanding and classification of these amazing prehistoric critters.

[Theme Music Intermission]

Izzie: Despite a few pieces of compelling evidence that fungi have been around and interacting with other organisms for ages, there are still major gaps in their fossil record – spans of millions of years for which we don't have anything to show. In my 50 pages of notes summarizing all my research for this episode, there are fewer than 60 examples of fossil fungi that are clearly detailed and fairly widely accepted in the paleomycological community. To be sure, people spend their lives working on this topic and I definitely wasn't able to cover the entire body of literature. But all the same, we're missing a lot of fungi! Where have they gone?

[Music begins]

Izzie: Paleomycology still faces a lot of problems, the biggest of which is that fossil fungi are just hard to find in the first place. Hyphae are small and delicate, fossilized hyphae even more so. That’s why known fungal fossils are mostly found in association with larger fossils under study for other reasons - for example, endophytes that appear in the leaves of early vascular plants under study by a botanist. That means we're much more likely to know about fungi that lived in close association with other organisms than to know about fungi that lived independently – like, for example, ancient decomposers, which are mostly known from coprolites. That might, in part, be because decomposers fossilized in the act of decomposing would be surrounded by decomposing plants or animals, and incomplete fossils are considered less interesting or valuable than complete specimens. The effective decomposers of the past are much less likely to come under scrutiny than the effective endosymbionts.

And let's not forget that some of the most diagnostic features of fungi don't survive even the most delicate fossilization processes - traits like color of the mycelia, type of substrate, or anything at all relating to the fruit. That’s rough because fungal fruits contain the reproductive structures, some of the most diagnostic features for fungal identification! For that reason, paleomycologists are exceedingly careful when they suggest that fossil fungi might have belonged to, or been related to, a group of currently existing fungi. Even modern fungi that are closely related can look very different, and similar-looking fungi can be far apart on the evolutionary tree. With so many features missing, it's often impossible to identify fossil fungi down to even the genus level. As a result, fossil fungi are usually not identified or named using modern taxonomic groups, as fossil plants and animals are, but are described only as being similar to existing groups.

[Music ends]

Izzie: The absence of diagnostic features isn't just hard for determining which type of fungus a fossil represents; it can also make it hard to determine whether a fossil is fungal at all. Fungi have both single-celled and filamentous life stages, as do algae, and bacteria are single-celled as well. They would have lived in similar environments, especially when land was just getting colonized and there weren't many localities to choose from. Frequently the history of paleomycology has been reinterpreting algal fossils as fungi, or going back over so-called fungal fossils and discovering that they are actually algae. There are a few ways of getting around this issue. One is to look at the host, if there's another organism nearby; a fungus is much more likely than an alga to grow inside a plant or on a termite. Another is to look at fossils from a different angle, or from more angles; taking a three-dimensional cast of a fossil bore hole in marine animal skeletons can reveal hallmarks of fungi that aren't apparent in the more traditional two-dimensional sections. But in general, the similarities of algae and fungi, or fungi and bacteria, probably keep a lot of fungi from getting noted in the fossil record.

[Background music starts]

Izzie: On the topic of host specificity, though, it’s very difficult to determine whether a fungus grew at the same time as a potential host organism, or colonized its body after it died. It's also nearly impossible to figure out the relationship between the two without live evidence. Many modern fungi are facultatively saprobic, which means they can live in harmony with a host plant, and then switch to a decomposing lifestyle to digest it once it dies. This blurred line in the modern day means a headache for anyone trying to puzzle out that relationship millions of years after the fact. To make matters worse, proximity of two organisms in a fossil doesn't imply that they were living symbiotically – imagine if a Frisbee got fossilized inside a tree.

[Music ends]

Izzie: Sometimes it's possible to clarify things somewhat by looking for evidence of a host response. While they are alive, plants like to stay planty, and they don't let pests or diseases in easily. Even early in their evolution, plants would have needed some type of defense against infection or they wouldn't have lived to reproduce and ensure survival of the species. By that logic, some of the same mechanisms that successfully protected early plants would survive today, and scientists can look for fossil structures that are similar to modern plant responses to figure out if a fungus was a welcome guest, an invader, or a decomposer.

One modern response plants have to infection is an extra cell wall called an apposition. The apposition goes up around a fungus' break-in point, sort of like using caulk to seal up a hole in your house. If a fungus is surrounded by sap – which is basically tree blood – that can be another sign that it’s not a welcome guest.

[Musical tone]

Izzie: Of course, drawing parallels between living and ancient organisms assumes that the fossils are related enough to modern organisms that we can be confident that we're seeing something similar in both time periods, and plant defenses have come quite a long way in hundreds of millions of years. Just as the classification of some fossils has swung wildly between algae and fungi, classification of lifestyle for many fungal fossils has swung between mutualist, saprobe and parasite. Many saprobes and parasites have probably been misinterpreted as plant symbionts, or ignored completely, due to their location in incomplete plant or animal fossils.

If there's all this confusion about what the fungi are, and their supposedly diagnostic features are missing or misleading in the fossil record, why can't we just reach into the fossils' DNA to determine what they are? Well, DNA is an extremely fragile molecule. While a cell is alive and protecting it, its DNA is going to be very reliable and useful for both the organism and for scientists hoping to identify the organism. But unfortunately, as soon as the cell dies and dries up, that DNA is just another fragile molecule exposed to the elements. And the process of fossilization does not tend to be gentle.

Even amber fossilization doesn't really spare DNA – sorry, I know I brought up Jurassic Park before like you could trust it completely, but you actually can't. In 2013, researchers at the University of Manchester tried extracting DNA from insects caught in tree sap between 60 years and 10,600 years old, in the process of becoming amber. From the youngest specimens, researchers were able to extract some DNA – strands just about long enough to code a single gene. In the older samples, they found no evidence that DNA was present – and those were 10,000 years old, nowhere near the hundreds of millions of years we've been discussing. Plus, specimens in amber are very delicate, and DNA extraction, which involves grinding, dissolving, or spinning, could damage them. When the specimen you're talking about is one of the only complete mushroom fossils known on Earth, you don't want to take that risk. So paleomycologists, whether working with amber or chert or coal, rely mostly on morphology and context, and ID's are ambiguous, and mistakes are made.

[Musical tone]

Izzie: Possibly the greatest story of identity confusion ever is that of *Prototaxites*. This group of fossils dates back to the era of first land colonization, 420 million years ago – that's 40 million years after simple vascular plants like liverworts arose and 50 million years before large trees appeared. By the end of *Prototaxites*' reign 350 million years ago, plants had evolved important traits like seeds, leaves and roots, and tall trees were present. But for 70 million years, a mostly ground-level landscape was punctuated by 26-foot-tall, three-foot-wide columns of … something. This was *Prototaxites.*

[Music begins]

Izzie: The massive fossils were first discovered and described in 1859 by John William Dawson on the shores of Gaspé Bay in Quebec, Canada. Gaspé is known as "a jewel of the Devonian" thanks to its rich deposits of fossils from the Devonian period, 420 to 360 million years ago. Since that first discovery, examples of Prototaxites have been found all over the world, from the UK, continental Europe, Saudi Arabia, Australia, and Africa. They appear both in marine sediments and landlocked fossil beds – anywhere that was wet and marshy in the days when life first made landfall. Most are smaller than the famous 26-footer – but, by the way, 26 feet is more than two stories tall, so smaller than that can still be pretty dang big.

[Music ends]

Izzie: All *Prototaxites* are unbranched and composed of densely interwoven tubes going in different directions, none smaller than spider silk and the largest just half the width of a dust particle. As remarkable as it may seem for a time when the tallest plants were ground cover, scientists do believe that *Prototaxites* stood upright, dominant over a world of liverworts, algae, lichens, worms, and millipedes. Even when woody vascular plants developed, by the time of *Prototaxites*' extinction, trees would have been seven feet tall at the most.

The weird intertwining interior and massive size of *Prototaxites* have made them the target of scientific fascination – and debate – for 150 years. In that time, more than 13 species of *Prototaxites* have been identified, despite the fact that higher classification has remained elusive. Since I'm spending so much time on it, you've probably figured out that yes, our current understanding is that *Prototaxites* were fungi.

[Music begins]

Izzie: Dr. Church, an evolutionary biologist writing in 1919, is credited as being the first to suggest that *Prototaxites* was a fungus… though to be honest with you, I have read the source material everyone cites for that, and Church doesn't actually say *what* he thinks *Prototaxites* is. This is the book I live tweeted, and it's got some real turn-of-the-last-century gems, like when he called fungi the "decadent survivors" of marine algae. But while he goes into a lot of detail in his theories of how fungi and plants might have helped each other colonize land, he never explicitly says he believes *Prototaxites* is a fungus. I'm not sure why everyone cites that book for that idea.

[Music ends]

Izzie: At various points in the last 150 years, *Prototaxites* has been described as a lichen, one of several types of algae, or even a vascular plant – in fact, when Dawson first described it, he thought it was an ancient tree related to yew, the genus *Taxus*, hence the name. In 1988, a study headed by a Dr. Stubblefield suggested that Prototaxites might have been an intermediate organism between algae and fungi that has since gone extinct. At any rate, putting aside Church's potential suggestion in 1919, the first claim of *Prototaxites'* fungal nature that was backed by solid evidence came fairly recently.

[Music begins]

Izzie: In 2001, Dr. Francis Hueber of the National Museum of Natural History performed an intense survey of the internal physical structures of *Prototaxites* specimens from Canada, Australia, and Saudi Arabia. A 2010 paper called Dr. Hueber's work "the most authoritative report" on Prototaxites anatomy and structure ever written. Based on that work, Dr. Hueber and his team brought back, or maybe formally proposed for the first time, the idea that *Prototaxites* is a fungus. Specifically, the fruiting part of a fungus – that's right, a mushroom.

[Music ends]

Izzie: The idea seems absurd at first. Most of the fungi known from the Devonian period are small and live in or on a host plant – not even macroscopic, let alone the tallest thing in the world by several meters. And Dr. Hueber's team proposed the mushroom idea without ever having found any reproductive structures of any kind, which you'd expect to see in a mushroom. The strongest evidence actually comes not from the fossils' morphology – we all know how treacherous *that* can be – but from isotope studies.

[Music begins]

Izzie: This episode is about fossils, not chemistry, so for our purposes isotopes are just atoms of the same element that have slightly different weights. Carbon-12 is the most common type of carbon atom, and there are slightly heavier and less common versions called Carbon-13 and Carbon-14. The proportion of these isotopes in the air is distinct and matches the isotope ratio in organisms that make their own sugar from the CO2 in the air. However, the isotope ratio is different for organisms that can't make their own sugar. This is super important because it means that autotrophs, which make their own food, look different on an atomic level from heterotrophs. This was just as true in the ancient past as it is today, and this is the relationship Dr. Hueber's team looked at.

[Music ends]

Izzie: If the isotopic ratio of carbon atoms in *Prototaxites* is the same as it was in the Earth's atmosphere from 400 million years ago, that would mean *Prototaxites* was either making its own carbon or eating a vegetarian diet. But if the isotopic ratio of the fossils doesn't match ancient air or plants, then *Prototaxites* was heterotrophic, getting at least some of its sugar from non-plants. The data strongly support this second option

– the isotopic carbon in *Prototaxites* had to come from something besides pure photosynthesis, which means it couldn't have been a plant. Based on this study, *Prototaxites* were probably decomposers with access to both plants and some other food source, probably bacteria that grew in flooded areas and then died when the marshy waters receded.

Isotopic evidence of the fossil's diet is pretty darn convincing, but this still doesn't solve the problem of how a mushroom could become so massive, while still not containing any reproductive structures. Dr. Hueber proposed that unlike a button mushroom or morel, which grows rapidly and then dies each reproductive season, *Prototaxites* would have been more like a modern bracket fungus. His idea is that the fruiting body would add new layers every year, covering up the old layers with a new spore-bearing surfaces that would get buried the year after as the mushroom slowly grew to an extraordinary size.

[Musical tone]

Izzie: I had a lot of fun researching *Prototaxites* and seeing the evidence everyone gives for their various theories. The most fun was a paper called [deep breath] "Structural, physiological, and stable carbon isotopic evidence that the enigmatic Paleozoic fossil *Prototaxites* formed from rolled liverwort mats." Long title. This paper basically proposes that *Prototaxites* were no different from the liverworts living on the ground beneath them, and that in fact there was no "beneath" because *Prototaxites* were rolled up logs, not freestanding structures. The idea is that wind or rain tugged up the edge of the liverworts, causing them to roll downhill and into river beds, all the while swirling up into a massive spiraled log shape. They think this makes more sense than Dr. Hueber's theory, which they don't think adequately explains the lack of reproductive structures on the fossils. They also don't believe that a saprobic lifestyle could have supported something two stories tall when both life and soil were so new to land.

There were a few problems with their methods, though, as I read through their paper. For example, they worked with mats only a few millimeters wide and rolled them by hand, using neither a size comparable to *Prototaxites* nor the natural mechanisms they were proposing. Also, to mimic hundreds of millions of years of fossilization processes, they dried out their tiny mats with fans and then dipped them in acid, but didn't explain whether their process could be expected to be at all similar to the real forces applied to the fossils.

I wanted to make sure it wasn't just me being like "what no, these incredible fossils are definitely fungi because that's what I want them to be." Fortunately my suspicions were confirmed when I read a rebuttal, submitted just one week after the first paper's publication, literally titled "The Enigmatic Devonian Fossil Prototaxites is Not a Rolled-Up Liverwort Mat." There is a lot of compelling evidence against the liverwort mat idea and the paper that proposed it. My issues didn't all come up, though the rebuttal still had a lot of material to work with. The number one flaw the rebuttal emphasized? *Prototaxites* has rings. It's literally just *not a spiral*.

The liverwort roll idea would have one edge tugged up and rolled into another, which means the internal structure would need to show a spiral. But in cross section the fossils have concentric rings, suggesting that, like a tree, *Prototatixes* must have grown steadily outwards. It's impossible that something that rolled down a hill would have concentric rings. I'm flabbergasted by how much trouble everyone could have been spared if the authors of the first paper literally took a colored pen and traced one of the rings on a picture of *Prototaxites*' cross section – which the rebuttal literally does. In bright colors. Sassy scientists, man, I'm telling you.

[Musical tone]

Izzie: There are a lot of other things I could say about the liverwort paper, but I'm not trying to science-shame anybody. I'm just here to talk about a cool fossil fungus that dominated the landscape of the Silurian and has been mysterious for a long time. The bottom line of this story is to read science reports critically and, if you're doing the writing, rule out opposing theories starting with the most obvious. If you base a theory on a fossil being a spiral, you should *probably* make sure that it's actually a spiral.

[Musical tone]

Izzie: Well, there you have it: the fossilized history of fungi, as we know it. Fungal fossils are so evocative of ancient struggle and cooperation, the balance of survival with the sacrifice and benefits of working with others. The history of life on Earth is one of seeking out untapped resources, and in that aspect, fungi are the pioneers and the ones who paved the way for all the beautifully diverse life on land. It really chokes me up…

[Music begins]

Izzie: Now if you'll excuse me, I need to go encase a lot of mushrooms in tree sap so their diversity can be preserved for another few hundred million years. Where to begin…?

Morel Dilemma is written and produced by me, Izzie Gall. Our theme song is Fungi Among I, written and performed by John Bradley, and additional music is by Mihai Sorohan. You can find more of Mihai's music at mihaisorohan.bandcamp.com. Special thanks to everyone who called in. Your questions were so fun to research!

Morel Dilemma is on Patreon, where you can receive cool rewards for donating to the podcast, and donations start at just $1 a month. You can also post a review on iTunes, or wherever you listen. Next episode is about the fungi of the final frontier! Call 347-416-6735 if that tickles your interest or your imagination, and leave a mushroomy message to have your voice in the next episode. However you show it, thank you for your support! Mycelia later!

[Music ends]

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