Rhizomorphs above and belowground: finally we see the humongous fungus

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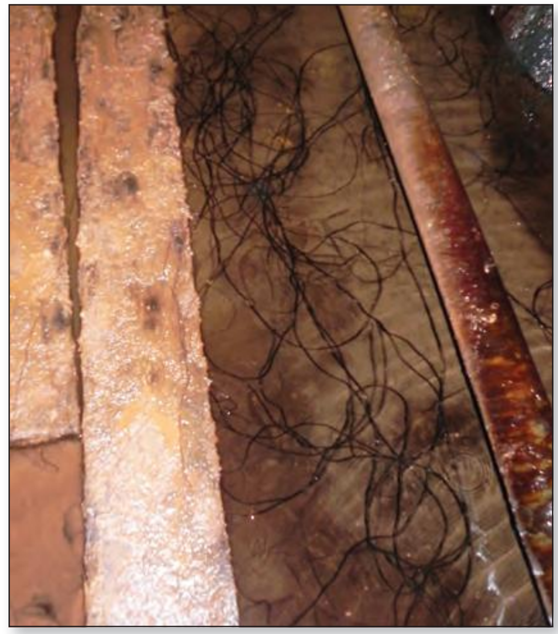
Rhizomorphs are thick strands of mycelium that are fused together and often protected by melanin. They can be found belowground or above—where they are produced aerially along the forest floor, in the understory, or up in the canopy of some forests. In temperate regions, they remain unseen and you have to dig into the ground or remove the bark of infected trees to see small segments of them. *Armillaria*, commonly called the Honey Mushroom, is one fungus that produces rhizomorphs as it moves from one substrate to another. The rhizomorphs seek out new hosts, attach to them, and cause infection that may kill woody plants. Round, black, shoestring-like subterranean rhizomorphs or flat subcortical rhizomorphs under the bark are produced.

When a tree is killed by the fungus, new rhizomorphs extend out through the soil as they search for new substrates to colonize. Trees are killed, new rhizomorphs develop, and the fungal colony gets bigger. If you can imagine this process taking place year after year in a large forested area with unlimited access to trees, the colony can be huge and very old. In fact, the fungus may never die. *Armillaria* has often been referred to as the "humongous fungus." Studies in Michigan have found colonies of the same *Armillaria* clone to cover 37 acres and in Oregon one root rot center has been determined to inhabit 2,384 acres and estimated to be 1,900 to 8,600 years old. The rhizomorphs are well adapted to this unusual mode of growth through the soil with their thick layer of melanin coating the mycelial strands. This provides a physical and chemical protective barrier for the fungus as it ramifies through the ground in search of new hosts. In addition, our past research has shown that fungal melanin absorbs high concentrations of metal ions from surrounding soil producing an armor-like protective covering for the fungus (this work completed when Professor David Rizzo, mycologist at UC Davis, was a PhD student at the University of Minnesota; https://doi.org/10.1139/b92-190). All this is happening underground and out of sight.

It is impossible to see the complete

***Armillaria* is a root rot pathogen producing rhizomorphs that attach to roots, penetrate them and kill the root and stem (left photo, courtesey of Martin MacKenzie, US Forest Service). *Armillaria* produces a white mycelial fan under the bark that is bioluminescent at night and shoestring-like subterranean rhizomorphs. One of these is pointed out by the knife blade. In larger trees such as this dead oak (right photo), flat subcortical rhizomorphs are produced under the bark .**

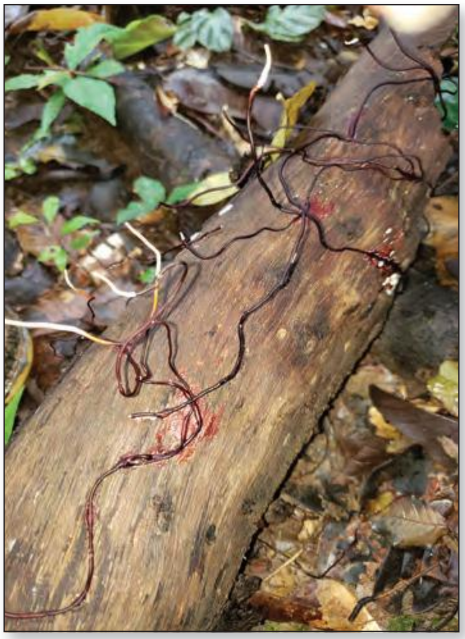


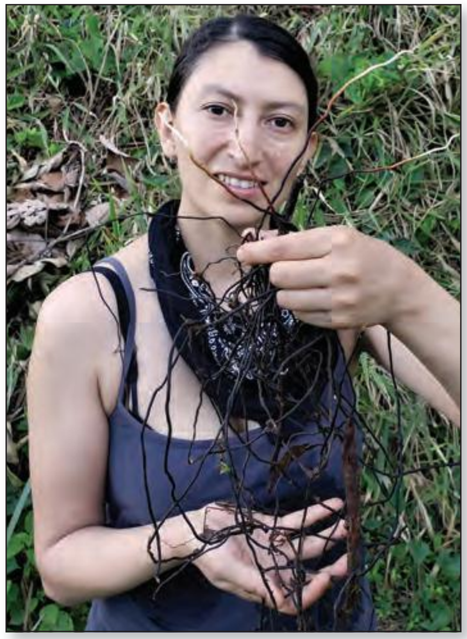
The mine provides a view of rhizomorph biology that usually remains unseen. Massive *Armillaria sinapina* rhizomorphs grow from colonized wood (top photo) and extend many meters in their search for new food sources (bottom photo). The mine has exceedingly high concentrations of heavy metals but *Armillaria* growth is unaffected by them.

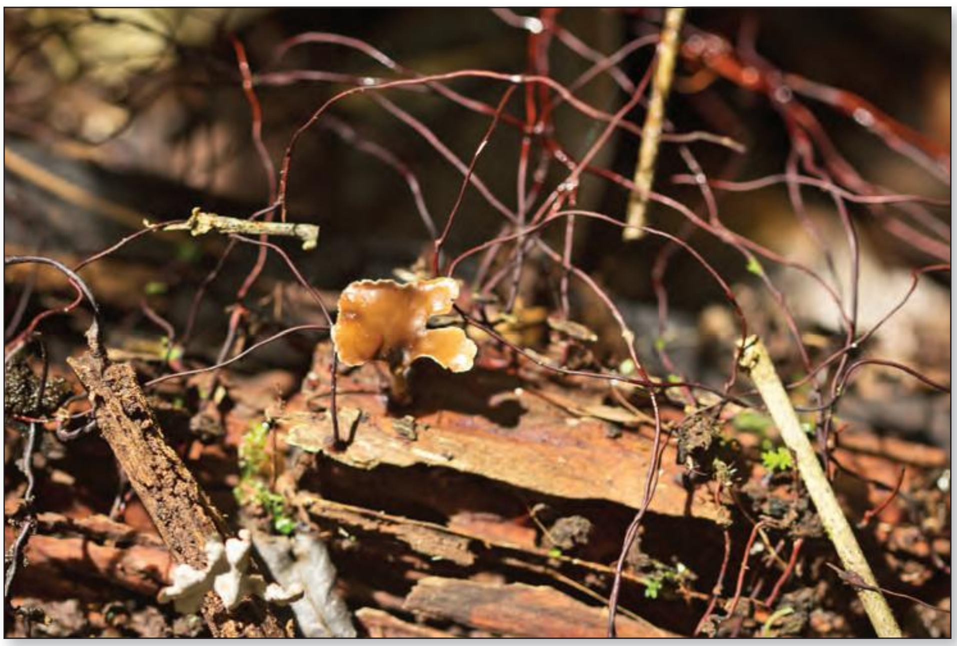
***Armillaria sinapina* rhizomorphs growing in the Soudan Iron Ore Mine in northern Minnesota. Rhizomorphs grow in the wet mine environment (top photo) colonizing wood timbers (bottom photo) and move from timber to timber throughout the mine.**

extensive underground network of rhizomorphs produced by *Armillaria* but recently we have had the opportunity to view this fungus in an unusual subterranean environment. The Soudan Iron Ore Mine located in northern Minnesota (now a State Park) has a main shaft that is 2,341 feet deep and 18 different levels extending out laterally long distances. Large numbers of wooden timbers were used throughout the mine as rail ties for carts to remove the ore and for other structural uses. Our team from the University of Minnesota which included Benjamin Held and Christine Salomon, investigated the fungi in this mine to better understand their association with very high levels of iron, copper, and other heavy metals that occur there (https://doi.org/10.1371/journal.pone.0234208). We were surprised to find *Armillaria sinapina* rhizomorphs in huge numbers as they colonized the timbers. In wet areas, the rhizomorphs were many meters long and they could be seen extending long distances as they searched the mine passageways for more wood substrates. It is likely that the many miles of rhizomorphs in the mine are all from one introduced fungus and compose one big clone. The heavy metals in the Soudan Mine are at concentrations high enough to inhibit many microorganisms—but not *Armillaria*. This fungus has the capacity to tolerate metal ions and use them as a protective coating on the melanized rhizomorphs. Our studies at the Soudan Mine help illustrate what is taking place with *Armillaria* rhizomorphs underground and how spectacular their network must be as it grows through forest soils.

Our understanding about rhizomorphs expanded greatly after a trip deep within the Amazon rainforest. Most previous research has focused on forest fungi in temperate areas and seminal publications have been written on these fungi. We did not







Unlike temperate areas of the world, the tropical Amazon rainforest has fungi that produce rhizomorphs that grow aboveground. These move along logs (top left photo) and over forest vegetation from tree to tree producing large numbers of aerial rhizomorphs (top right photo, with author Cristina Toapanta holding a large mass of rhizomorphs). We recently described several new species of Polyporaceae producing these rhizomorphs (bottom photo).

expect the Amazon forest to be filled with massive networks of rhizomorphs above ground. To our amazement, we saw black and reddish brown fungal rhizomorphs on logs, tree trunks, branches, and small plants extending in every direction, including up, in the wet forest. One area we studied was the rainforest in Yasuni National Park in Ecuador. These investigations were done with Ecuadorian collaborators Maria Ordoñez, Charles Barnes, and the Pontificia Universidad Católica del Ecuador. The park is well known for being one of the most biodiverse places on earth. As an example, there are more tree species in one hectare than are native to the United States and Canada combined. With this type of diversity, you can only speculate how many fungi may be found in the forest.

One major group of fungi are the *Polyporus*-like species with aboveground rhizomorphs. These species produce rhizomorphs as exploratory structures to find new substrates for the fungus. Although it is not currently known if they are pathogenic, our studies suggest they may be similar to some *Armillaria* species acting as opportunistic pathogens on compromised and unhealthy trees. However, they differ from *Armillaria* in their aboveground growth and tendency to grow upward toward light. In Yasuni National Park, the various species produce rhizomorphs with different morphological characteristics in terms of their surface texture, branching characteristics, and growth patterns. Little is known about these fungi, and our studies showed they are genetically different from known species. We recently described four new species and a new variety from our research site: *Atroporus yasuniensis*, *Atroporus tagaeri*, *Neodictyopus sylvaticus*, *Polyporus taromenane* and *Polyporus leprieurii* var. *yasuniensis* (https://doi.org/10.1371/journal.pone.0254567). The most common species is *Polyporus leprieurii* var. *yasuniensis* which is found in different habitats from temporary flooded valleys to high forested ridges allowing the fungus to prevail for long periods of time in a competitive ecosystem where hundreds of species are fighting for a niche to grow in.

Other aerial rhizomorph producing fungi in subtropical and tropical forests are *Marasmius* and *Gymnopus*, often referred to as the Horsehair fungi. These species produce rhizomorphs that are thin thread-like structures. With rhizomorphs abundant above ground, some bird species selectively use them for nests in the Brazilian Amazon and the Yanomami Indigenous People collect rhizomorphs to incorporate into baskets they weave. This provides a black fiber for making interesting patterns to decorate their baskets. Professor Noemia Kazue Ishikawa, one of Brazil's leading ethnomycologists from the Instituto Nacional de Pesquisas da Amazônia in Manaus, has documented the use of rhizomorphs for decorative work in basketry in a new book, *Përisi: the Fungus that Yanomami Women Use in Their Basketry* (a pdf is available from the authors).

Rhizomorphs are versatile structures that provide advantages to the species producing them. These vegetative

A bird's nest in the tropical rainforest of Brazil made up of *Marasmius* rhizomorphs. Photo courtesy of Neomia Kazue Ishikawa.

exploratory structures are used to find new substrates for nutrient exploitation and provide protection from environmental stress, combative antagonistic fungi, insects, toxic substances, and even provide protection from UV light. Species developing rhizomorphs tend to be abundant in their ecosystems; *Armillaria* in temperate forests, *Polyporus*-like species and the Horsehair fungi in subtropical and tropical ecosystems. We know a lot about the biology and ecology of *Armillaria* from decades of studies but little to no information on the rhizomorphic tropical fungi. We are continuing our investigations to learn more about these intriguing fungi and their significance in tropical ecosystems.

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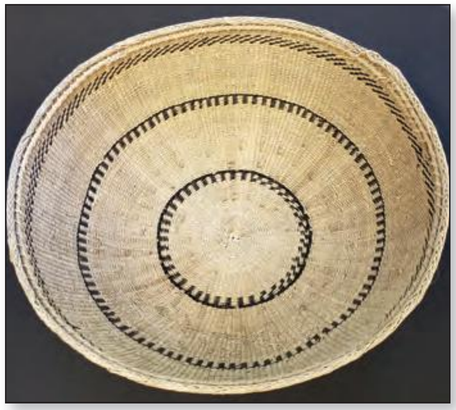

Baskets (top photos) made by Yanomami Indigenous women from the Maturacá community in the tropical rainforest of Brazil using black rhizomorphs in different weaving patterns for decoration. An enlargement photo of a basket (bottom) showing the shiny black rhizomorphs used to weave the basket.