

Now is a time of very rapid change with mushrooms springing up like...well, like mushrooms. From one day to the next there are fungal fruiting bodies where there were none, and vice versa, and new species of fungi make their appearance. People who know what they are doing are collecting food in the woods while Frederick the mouse is collecting shapes and colours. The fungi can now produce spores because the air at ground level is close to saturation humidity and because their primary source of food is at a maximum with fallen leaves and dead wood constantly saturated. However, they must access this food...

Trees require structurally strong cell walls that allow them to support their own weight as they grow tall to escape shading from the surrounding trees, and to stop their cells from being eaten alive. They achieve this via the exceptionally strong lignin in their cell walls but this brings the problem of not being eaten when dead and so having nutrients forever trapped within their cells. Coal was formed at a very high rate from trees that fell into swamps up until 300 million years ago when the rate of coal formation dramatically decreased due to the appearance of white-rot fungi with enzymes that could digest lignin. Lignin produces the colour of wood so it has a bleach white appearance and is fibrous following attack from white-rot fungi, seen here as white crust and threads (01). Only white-rot fungi have species that bioluminesce, possibly for detoxification of peroxides formed during ligninolysis, with Lilac Bonnet (*Mycena pura*) (02) as one example from Weiherfeld (the mycelia glows green underground). Without the activity of white-rot fungi we would soon be buried under carbon.



After the white-rot fungi has digested the lignin of the plant cell walls, then other elements inside the plant cells that have less structural strength become accessible for white-rot fungi and other decomposers. Plant cellulose is the most abundant element that is decomposed; the most abundant enzyme on earth is ribulose 1,5-bisphosphate which captures the atmospheric carbon that is used to produce cellulose, and the second most abundant enzyme is cellulase which breaks down cellulose. Fungi digest large compounds such as lignin by excreting the necessary enzyme(s) and then they ingest this solution and further process the resultant smaller and less structurally strong compounds. Brown-rot fungi digest cellulose and leave the lignin which makes the brown darker and causes the wood to shrink and break into cubical pieces, appropriately displayed here within a surrounding of white-rot (03). The third kind of rot is done by soft rot fungi which can decompose wood with high levels of compounds such as pectins that resist biological attack. They can remain active under conditions too extreme for white- or brown-rot fungi, so it is soft rot fungi that is digesting the early explorer huts in Antarctica. Soft rot fungi secrete cellulase from their hyphae, and the Turquoise Elfcup (*Chlorociboria aeruginosa*) also secretes the pigment xylindein which stains the wood blue-green (04). Mostly the fungi is identified via the stain as the very small fruiting bodies appear only rarely.



The reason why fungi do not digest themselves with these excreted enzymes is because the cell walls of fungi are made of chitin rather than cellulose. The exoskeletons of insects are also made of chitin, and chitin is one of many factors telling us that fungi are far more closely related to animals than to plants. Plants require light whereas fungi make pigments to protect themselves against ultraviolet radiation, so Lumpy Bracket (*Trametes gibbosa*) may possibly benefit from the algae that typically grows on the top of its cap but not on the spores in the shade underneath (05).



The part of the fungi that we see is the above ground reproductive structure, whereas the energy- and resource-obtaining vegetative part of fungi is the mycelia – an extensive mass of branching thread-like filaments under the ground or in dead wood. These mycelia are structures that decompose and take up nutrients and water across their massive surface area; if the mycelia only does this then the fungi is saprobic, whereas if the mycelia also connects with the roots of a plant then the fungi is mycorrhizal. If the mycelia enter into the cells of a plant's root then the fungi is arbuscular mycorrhizal and it has no above ground fruiting bodies so I will not discuss these any further. If the mycelia form a bundle around the plant's root then the fungi is ectomycorrhizal and it transfers nutrients and water to the plant in exchange for carbon compounds. Most plants form mycorrhizal associations with fungi with substantial mutual benefit to both parties (similar to lichen where algae is housed in fungi). For mycorrhizal fungi the above ground fruiting bodies show approximately where the mycelia has joined to the plant root, sometimes producing a fairy ring (Hexenringe). Fairy rings are more common for saprobic fungi, with the above ground fruiting bodies showing the edge of the mycelial disc; the most prominent fairy rings for Weiherfeld are of the Trooping Funnel (*Clitocybe geotropa*) (06a) with this ring having a diameter of 4 meters (06b). *Clitocybe nebularis* from the same genus expands very rapidly because the mycelia assimilate only the most readily available nutrients while growing outward at 0.9 meters / year. The Trooping

Funnel fungi is probably 2-3 years old whereas a slow growing species may take 10 years to form a fairy ring of this size, however a slow growing species will win the war when they encounter the fast growing Trooping Funnel.



Most of the saprobic and ectomycorrhizal fungi that we see are within two major groups of fungi, the cup-fungi (Ascomycota) or the club-fungi (Basidiomycota). The surface area for the production of spores is increased within the concave depressions on the surface of cup-fungi, and on the projected gills of the club-fungi. The Tinder Hoof fungi (*Fomes fomentarius*) has 2-3 pores / mm in which it can produce 887 million spores / hour in spring (07). The single-cell spores are very small (1-8 micrometer diameter – smaller than the particles we see in a beam of light in still air) so they are suspended in air at an average density of 10,000 – 20,000 spores / cubic meter by microbreezes that we do not realize. In still air the spores fall at less than 10 mm / second onto the fungal caps below them to form a creamy white spore deposit for Honey fungus (*Armillaria mellea*) (08).



The primary purpose of the stem of the fungi fruiting body is to raise the spores above the ground zone of laminar airflow up into the turbulent zone where they are suspended in the air for long distance dispersal. Some spores are dispersed worldwide, hence fungi high up on the single dead branch of a tree is not so surprising (09).



Here are three different species of fungi that are in close proximity to each other and that have each raised their spores above the zone of laminar airflow, however, even though they may be decomposing the same dead plant material the three have contrasting life-history strategies (10). The saprobic Rosy Earthstar (*Geastrum rufescens*) in front of the green leaf is a club-fungi that produces all its spores at one time within a flexible sack (peridium) that then develops an opening through which air is rapidly expelled while carrying suspended spores. When I squeeze the sack I am replicating a large animal stepping on it (11), whereas the usual case is for raindrops to impact the sack, reduce its volume and so expel puffs of spore laden air in a bellows-like effect.



In contrast, the Strict-branch Coral fungi (*Romaria stricta*) in front of the red leaf is mycorrhizic and a tough rubbery cup-fungi that continuously produces and releases its spores over summer and autumn (10). The related Grey Coral fungi (*Clavulina cinerea*) sends out a cloud of spores when wind blows by it or when it is moved (12). The Dead Man's Fingers (*Xylaria polymorpha*) in front of the yellow leaf is saprobic and a hard brittle cup-fungi that produces and releases asexual spores from spring through to summer and sexual spores in autumn (10). Candlesnuff (*Xylaria hypoxylon*) from the same genus is now growing the black layer that will produce sexual spores over the top of the white structure that has been producing asexual spores (13).



The primary function of the sexual spores is to remain dormant despite adequate resources for their growth until they receive another signal (eg heat or cold or animal digestion) and so they maximize the likelihood that they will start to grow under conditions optimal for that species. In contrast, asexual spores disperse and germinate when they sense nutrients which signals a low level of competition (for saprobic spores) or the close proximity of roots (for mycorrhizic spores). Spores of some mycorrhizal fungi only germinate in response to the cues from their exclusive host, such as our Birch Knight (*Tricoloma fulvum*) (14). Likewise, some saprobic species have specific requirements, such as our Porcelain fungus (*Oudemansiella mucida*) (15) which is exclusively on Beech wood – and has the Beech wood exclusively for itself as it produces the powerful fungicides Strobilurin A and X and Oudemansin A which annihilate competitors; replicated since 1996 for protection of cereal and soybeans and currently the second most important fungicide.



Another species on Beech wood in Weiherfeld and useful for humans for a very long time is Tinder Hoof fungi (*Fomes fomentarius*) (07) – also known as Iceman fungus because Ötzi had four pieces with him to use as tinder for lighting and transporting fires because it burns very slowly. It is made into Amadou by soaking, beating and stretching it to produce a felt cloth that serves as tinder or for making clothes. It was used between the years 770 and 1066 in the Hedeby (Haithabu) Viking town of Schleswig-Holstein, and remained in common usage in 1800 in Scandinavia. Ötzi also had pieces of the Birch Bracket fungi (*Piptoporus betulinus*) strung on two goatskin leather thongs, and this species is currently bursting out of the bark of dead Birch in Weiherfeld (16). Both of Ötzi's fungi contain compounds which are active against bacteria and tumours but *Piptoporus betulinus* may have had solely a spiritual purpose as only *Fomes fomentarius* has a history of medical use; it

was used by Hippocrates for cauterization and it is still used for this purpose in Lapland, China and Japan, where it is also used against illness in smoking rituals to banish bad spirits or demons.



There are important interactions between the rate of development of a fungal fruiting body and its susceptibility to predation and desiccation. The Iceman's Fungus can develop over a period of 30 years as a new layer of active spore producing cells is produced each year over the previous growth which has become woody. For such growth to occur, the primary mechanism is through cellular division which is a relatively slow process. As a consequence of growth via cellular division, bracket fungi may grow around obstacles during their initial first year of establishment (17), or during any subsequent year (07). In contrast, a soft fungal fruiting body grows rapidly via cellular expansion so their form is altered when a barrier prevents further expansion and a margin is then formed there (18)



or by differential expansion, for example when the cells on the underside of the cap expand more than those above which causes the cap to flair up for better release of spores of Crimson Waxcap (*Hygrocybe punicea*) (19). The Scarlet Waxcap (*Hygrocybe conica*) is also present at this site and as these species look almost identical it is good for distinguishing between them that the Scarlet Waxcap is also called Witches Hat because it becomes black and pointed after shedding its spores (20)



The slower growing fungi reproduce more slowly but lose less to predation due to their hardness; the gastropods on the surface of the Dead Man's Fingers (21) will expend more energy for less return than the gastropods eating through Porcelain fungus (22) (NB it is recommended that when getting a spore print you cover the cap with a tumbler to slow the loss of moisture, but you will greatly appreciate the tumbler when you see the insects and grubs that also come out of the cap; (22) is 5 days after (15)).



Thus there is a trade-off in the fast or slow development strategies for predation, but the more important factor for fungal fruiting bodies is desiccation. A slow strategy increases the risk that the exposed spores will dry out before they develop; hence it is postulated that the slow strategy Earthstar / Puffball evolved an enclosing sack as protection against desiccation for their developing spores. An alternative strategy may be the rapid development and dispersal of spores, with Ink Caps as the most extreme example (23).

The full process for a *Coprinus cinereus* Ink Cap to develop its fruiting body requires 4-5 days with alternating darkness and then light, as the development processes are dark- and light-dependent. The first process is a concentration of hyphae to form a knot of 0.2mm diameter in darkness. With light there is then the formation of an 'initial' of less than 2mm diameter which is committed to forming the fruiting body. The next dark-light signal causes cell differentiation (cells are assigned to their future functions and signals for development come from the cap cells) and proto-spore development. During the next period of light the gills are produced and the first process for spore formation occurs – all of the division of cells has now happened and they are ready to take in water and rapidly expand. In the following darkness there is stem elongation, cap expansion and final spore formation – Ink Caps are unique in forming all their spores more or less simultaneously rather

than over an extended time. The stem elongation has enough force to push the Ink Cap through bitumen, so the cell walls must have rigidity to withstand this pressure (70,000 N / m<sup>2</sup>) but also the plasticity for rapid elongation (80 mm in less than 12 hours). Vertical lengths of chitin provide the cell wall rigidity while bonds between the vertical lengths are repeatedly broken and formed to provide plasticity, and chitin is added to the cell wall as the cell elongates. The cap opens in the early morning hours, and within a few hours the spores are shed, the enzyme chitinase is released and the cells of the cap dissolve into a black liquid (23). So the Ink Cap fruiting body makes an appearance and is soon gone without a trace, with the exception of the Firerug Ink Cap (*Coprinellus domesticus*) which may produce an external orange fuzzy mat of hyphae (ozonium) that remains for a long time (24). The purpose of the ozonium is unknown.



The Ink Cap is the most thoroughly studied macro-fungi due to its rapid and highly synchronized development, however the reason for its autodigestion is unknown. Nevertheless, autodigestion has evolved at least four times and always co-evolved with multiple other changes necessary for rapid development so it is assumed to be adaptive. Likewise, it is assumed that each species of fungi has adapted to its own specialised needs and this has produced an enormous diversity of fruiting bodies. There is a 100-fold difference in spore producing surface areas between our large Trooping Funnel (06) and Birch Bracket (16) and their miniature versions Collared Parachute (*Marasmius rotula*) (25) and Grass Oysterling (*Crepidotus epibryus*) (26) respectively, yet they all persist together in Weiherfeld. One advantage that the small fruit body species may have is that they can both revive after being dehydrated (marasmius is Latin for drying out).



Jelly fungi such as Jelly Ear (*Auricularia auricula-judae*) and Warlock's Butter (*Exidia nigricans*) (27 right, left) and Yellow Staghorn (*Calocera viscosa*) (28) can survive months of dehydration as the walls of their structural hyphae are not rigid like other fungi but instead are expanded out to a diffuse and indefinite extent. The hyphae collapse down during dry periods and expand back out to their original gelatinous texture when wet. (The Dutch of the Middle Ages believed that the Devil churned butter within fairy rings, which is perfectly understandable if it looks like Warlock's Butter).



The spores of terrestrial species are hydrophobic so that they do not become wet and heavy, or bound, or sunk. The dry spores within the cup of the Cup fungi (*Tarzetta cupularis*) are thus dispersed by wind or by raindrops that splash the floating spores out (29). The Fluted Bird's Nest (*Cyathus striatus*) common name obviously comes from its fantastic resemblance to a nest containing eggs, and its spore dispersal mechanism is every bit as fascinating as its appearance (30a). The spores of the Fluted Bird's Nest are contained within its eggs (peridioles) and due to the angle of the cup the eggs are washed out at between 50 and 87 degrees and travel in a parabolic arc of up to half a meter high and one meter wide at 13 km / hr by raindrops that impact the bottom of the nest, dislodge the egg and launch it out of the nest. The eggs are attached to the nest by a hollow tube (funiculus) which contains a coiled up hyphal cord a few centimetres long with a mass of sticky hyphal threads at the end (hapteron). As the raindrop impacts on the egg the tube breaks and the hyphal cord is exposed. When the egg flies through the air the hapteron may stick to an object and then the cord unravels and the momentum of the egg causes it to circle the object and wrap the cord around it. If the object is vegetation then the egg may be eaten and the coat softened in the animal's stomach, and then the spores can grow on the dung, or the egg will break down and spores will either germinate on the object or be further dispersed by wind or rain. The egg glued to the blade of grass next to the nest has the hyphal cord twice wrapped around it (30a), and there are at least three other eggs on the tussock of grass. The nests from which these eggs came are unknown and the eggs may have flown a meter, but for one of the eggs the nearest nest is more than 20 cm away. More important for dispersal is that all eggs were above 5 cm height and so are more likely to be ingested by a grazing animal. Video shows the ejection of eggs by raindrops and a flying egg sticking to and wrapping around an object at up to 6000 frames per second:

<https://www.sciencedirect.com/science/article/pii/S1878614613001165>



For a nest with 5 eggs where I replicated the experiment (drops of water through a tea-strainer from 1.2 meters above the nest in a clamp), the eggs flew an average horizontal distance of 35 cm and stuck to the cardboard (a pin at each egg) which corresponds to an average modelled maximum height of 60 cm (30b). I then did what the fungi wants the dumb animal to do and dispersed the eggs to another patch of woody debris, although without doing the eating and dung part of it.



The general case is that we only know what fungi are present when we see their fruiting bodies, but the Hairy Curtain Crust (*Stereum hirsutum*) (31; note the hirsute upper surface) is an exception; the food source for Leafy Brain (*Tremella foliacea*) comes only from parasitizing Hairy Curtain Crust therefore I know that mycelia of the Hairy Curtain Crust are within the dead wood even though it has not produced a fruiting body there (32).



Hairy Curtain Crust is probably also being parasitized by Golden Ear (*Tremella aurantia*) (33), or the Golden Ear is actually Yellow Brain fungus (*Tremella mesenterien*) in which case it is parasitizing *Peniophora* eg *P. quercina* (34). It is possible that these *Tremella* are in turn being parasitized by the fungi *Ophiostoma epigloeum*, and perhaps the chain goes further \*.



There is no hiding the parasite relationship in this case, but I do not know either the species of fungi that is the parasite or the fungi that is being parasitized (35). Feel free to ask around or have a guess and let me know.



Purple Jellydisc (*Ascocoryne sarcoides*) is in the asexual stage when it has the brain form (36a), and in the sexual phase when it has the cup form (36b).



Living plants protect themselves against fungal attack with a variety of chemical compounds, and the faster growing, softer trees are less well protected. Consequently, the willows around the Weiherfeld ponds that are declining in condition but still alive are parasitized by various fungi. Few fungi can parasitize living hardwood trees, with Honey fungus (*Armillaria mellea*) (08) as a notorious example. Honey fungus can parasitize a wide variety of plants and it forms rhizomorphs, long black root cords that have developed under the bark to spread the fungus throughout the tree, and have grown through the soil to new host plants (37). Rhizomorphs are typically 2mm diameter but can bunch up to 5cm diameter and travel up to 9m underground. The Honey fungus here is within a patch of large dead standing and fallen trees in Weiherfeld.



The leaf litter rapidly decays in Weiherfeld which lies in the southern part of the zone of Temperate climate, whereas the litter forms a layer of organic soil in the boreal forests of the more northern Temperate zone. The decay of litter is limited by temperature in the north, however a comparison within Temperate climate across the globe reveals that history and nutrients are equally as important as temperature for the rate of decay of litter. Earthworms are ecosystem engineers, with Charles Darwin calculating that they raise the level of soil in Europe by 0.2 inches per year for our climate zone. The history of northern North America included an intense iceage that removed the earthworms, and now that European earthworms have inadvertently been transported to North America they are rapidly consuming the otherwise thick layer of organic soil. In contrast, European earthworms were purposely transported to Australia, but they have a negligible effect on the level of eucalyptus leaf litter. The wet sclerophyll forests of temperate Australia accumulate 100 tonnes of litter per hectare, but because the soil is nutrient poor the leaves are also nutrient poor and hard and covered with wax. When drought is severe enough to dry the litter then it can burn with an intensity of 88,000 kW / m (very fast cycling of carbon). Earthworms are unique because they make molecules (drilodefensins) that counteract the defensive chemicals made by leaves to hinder their digestion. White-rot fungi is essential for the cycling of carbon in wood, but it is the earthworms that determine the rate of decomposition for leaves.

Caveat 1: the reproductive system of fungi is extraordinarily complex and variable and unlike all other forms of life so my account is massively simplified.

Caveat 2: I am reasonably confident of my identification of Dappled Webcap (*Cortinarius bolaris*) from matching its picture, description, habitat (mycorrhizal on Beech), and its spore print (38). The guide recommends that I do not eat it, and tells me that it resembles Fool's Webcap (*Cortinarius*

*orellanus*) which is also mycorrhizal on hardwood (especially Oak). However the guide also says that Fool's Webcap contains orellanine and states in bold caps; **DO NOT TASTE EVEN A SMALL PIECE OF THIS MUSHROOM** it is deadly poisonous and even a small piece can cause fatal kidney and liver failure. The author of *Horse Whisperer* and his family mistook it for the similar very popular edible *Cantharellus cibarius* and almost died from eating it. I am not so much a Fool as to trust any of my identifications when it comes to eating them.



\* "Siphonaptera"

Great fleas have little fleas upon their backs to bite 'em,  
And little fleas have lesser fleas, and so ad infinitum.

And the great fleas themselves, in turn, have greater fleas to go on;  
While these again have greater still, and greater still, and so on

- from Augustus De Morgan's *A Budget of Paradoxes* (1872), which is in turn derived from Johnathan Swift's satirical poem "On Poetry: A Rapsody" (1733).