Circus Fungorum: The Aesthetics of Fungal Movement

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Abstract: Fungi reproduce by spore formation and the subsequent dispersal of these seed-like structures is stimulated by an array of discharge mechanisms that employ pressurized squirt guns, controlled gas explosions, and catapults powered by surface tension. The bird's nest fungi form elaborate tiny nests that cradle "eggs" filled with millions of spores. The eggs, called peridioles, are splashed from the nests by raindrops, eaten by herbivores, and dispersed via the animals' guts. There is surprising aesthetic appeal to these processes when viewed using high-speed video. This innovative technology transforms an esoteric feat of evolutionary engineering into a flight of unanticipated beauty. This essay celebrates the science and the art of microbial movements that are invisible to the unaided eye.

By any measure, fungi are among the commonest eukaryotes on the planet. They grow on the surface of every plant and animal, they populate grassland soils, support forest trees and shrubs, decompose wood, and mist the air with microscopic spores. Filamentous fungi and yeasts multiply in lakes and rivers, grow in the mud of estuaries, and colonize sunken galleons in the sea. As agents of disease, fungi are unmatched as killers of plants, and fungal pathogens of animals are viewed as indicators of impending planetary doom. They remain, however, the least studied and most misunderstood kingdom of organisms.

In popular western culture fungi are treated as intangible, slimy, smelly, and generally disagreeable entities that hide in damp basements, spoil our food, and make us itch and sneeze. In *Great Expectations*, fungi garnished Miss Havisham's derelict wedding banquet, and Poe described "minute fungi... hanging in a fine tangled web-work from the eaves" of Usher's mansion. The association of fungi with inactivity is a slanderous accusation that misreads their biology and behavior. Contrary to this common misimpression, the mobility of these organisms was evident from the first microscopic studies on fungi in the 17th plant sciences century. Investigators were captivated by streams of fluid trickling through the tubular cells of molds growing on food scraps and they treated these microbes as curiosities allied to the animal kingdom. The subsequent adoption of fungi by botanists accorded with the unwritten policy of assigning anything rejected by the zoologists to the plant sciences. By default, botanists also assumed responsibility for all manner of photosynthetic protists (algae) and cyanobacteria, as well as the non-photosynthetic slime molds and plant-killing water molds.

I have invested a good deal of energy celebrating the wonders of fungal biology. In presentations to diverse audiences—groups of elderly people in libraries more often than bookstores filled with youthful enthusiasts—video clips of spores blasting across the screen have proven the best way to keep people engaged. Rhetorical skills are a boon for selling a subject as ostensibly tedious as the biology of the fungi, but the visual demonstration of fungal movements is the only way guaranteed to stimulate a more nuanced inquiry into this slice of life. This effect is related, presumably,

Crucibulum laeve. Photo courtesy of J. Hammond.

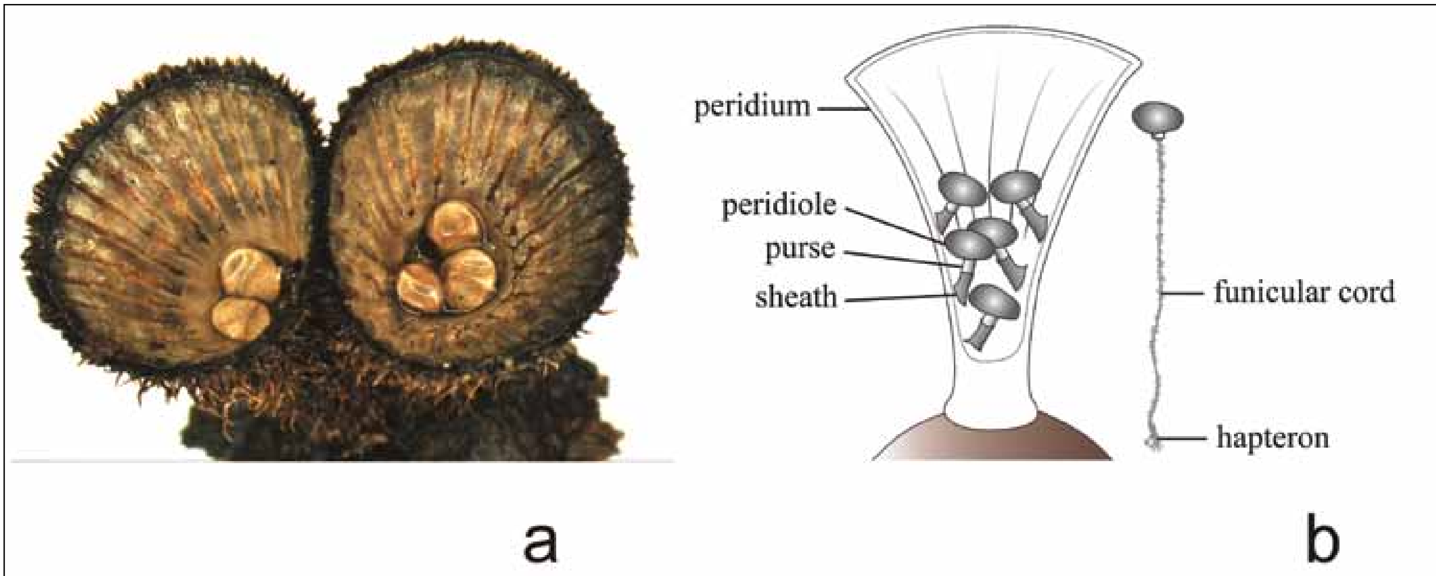


Figure 1. The fruit body, or basidiome, of the bird's nest fungus; (a) Photograph of a pair of fruit bodies of *Cyathus striatus* showing peridioles glistening with surrounding fluid at the bottom of the fruit body; (b) Diagram of sectioned fruit body showing structure of peridioles before discharge and single peridiole following splash discharge.

to the fact that humans are mobile primates programmed to be wary of moving objects. This is a place where the PowerPoint presentation can shine.

Beautiful flights have evolved in Circus Fungorum. Scientists had a pretty good idea how these mechanisms worked before they were captured with high-speed cameras, but we had little preparation for how beautiful they would appear. Microscopic molds poke above the surface of decaying leaves and propel their spores into the air by choreographing the explosion of gas bubbles in their supporting cells; mushrooms use a motor energized by surface tension to catapult 30,000 spores per second from their gills; morels, cup fungi, lichens, and tens of thousands of related species have mastered the ballistic device of a pressure-gun to squirt their spores into the air at fantastic speeds; and, strangest of all, the artillery fungus forms a tiny rubbery plunger that blasts a capsule containing 10 million spores over a distance of 6 meters. If your hearing is acute—mine was destroyed by *Motorhead* concerts in the 1970s—I am told that you can hear a popping when the plungers of the artillery fungus evert and a pinging of the capsules hitting the lids of culture dishes. My description suggests something of the Flea Circus to all this activity, or the "Mouse Trap Game"—where the succession of seemingly incongruous movements climaxes with the skinny guy jumping into a tub. The difference is that the fungi, unlike the fictional circus fleas (I was fooled as a boy), are doing this for real and perform with unrivaled grace.

One of the most elegant mechanisms of spore discharge omitted from this list is the use of splash cups by the bird's nest fungi (Figure 1). Thanks to high-speed video this is better understood today than ever before. Bird's nest fungi grow on a variety of materials, ranging from the dung of herbivores, to fallen twigs, and wood chips used for landscaping and spread under trees and shrubs. The food common to all of these materials is the elaborate composite of lignin and cellulose manufactured by plants. Colonies of the filamentous cells, or hyphae, of the bird's nest fungi secrete enzymes that digest these resilient materials and absorb sugars and other small molecules released by this biochemistry. The formation of the characteristic cup-shaped sex organs begins when the food begins to run out. Sexual reproduction in these fungi involves the fusion of pairs of compatible colonies and successful unions allow the resulting chimeras to generate spores inside cups. The fruit bodies range in size from a few millimeters in diameter to about one centimeter and serve as ejection devices for the spore-filled packets, called peridioles, which develop in the center (Figure 1). Each peridiole weighs one milligram (0.001 gram) and contains 100 million spores. When the fruit body is mature it opens and looks like a tiny nest cradling a clutch of minuscule eggs. I wonder if a child has ever discovered these exquisite goblets and wondered what bird could be so small?

The bird's nest fruit body taps the kinetic energy in falling raindrops to propel its peridioles into the air. Raindrops offer a free and readily available energy source for dispersal and many fungi and plants make use of them. The largest raindrops are 10 to 100 times heavier than the peridioles, stimulating me to propose the upsetting thought experiment of being clobbered by a shower of free-falling bull elephants while you read this essay. Far from being damaged by raindrops, the bird's nest fungus employs a tiny sliver of this power—just two percent of the energy in a raindrop—to eject its eggs. This may seem inefficient, but it has enabled these fungi to transmit their bird's nest genes down the great river of time for tens of millions of years. The beauty of the mechanism is revealed with a high-speed camera running at the relatively sedate speed of 6,000 frames per second. (Camera speeds of up to one million frames per second are needed to capture the squirt gun mechanisms of spore discharge.) At the replay speeds best suited for general viewing, drops of water descend from the top of the video frame and hit the cup after a second or two of free-fall (watch a video at http://www.youtube.com/watch?v=EGlaQhDi5ts or go to the FUNGI homepage and click on the link). Drops that impact the center of the cup deepen the tiny pool of water surrounding the eggs and fluid is shed off the rim without jettisoning a peridiole. Drops that hit the rim are carved into a portion that is shed from the perimeter of the cup and a portion that flows into the cup. The latter merges with the water in the pool and propels fluid from the cup that fragments into droplets. One of these droplets carries a peridiole in a parabolic arc away through the air (Figure 2, first two frames).

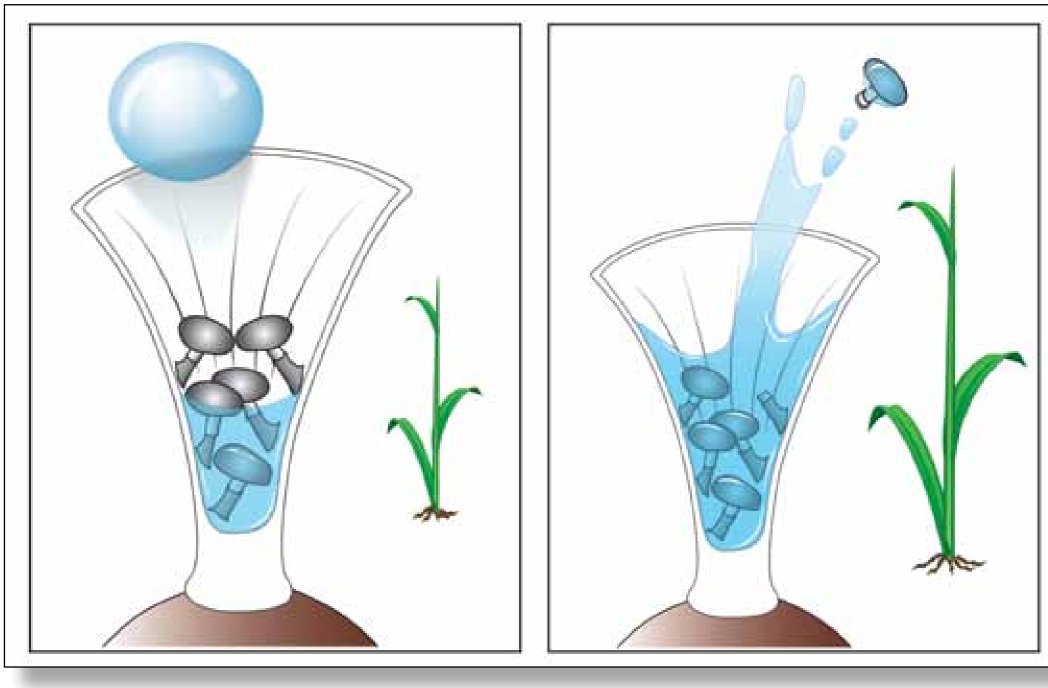
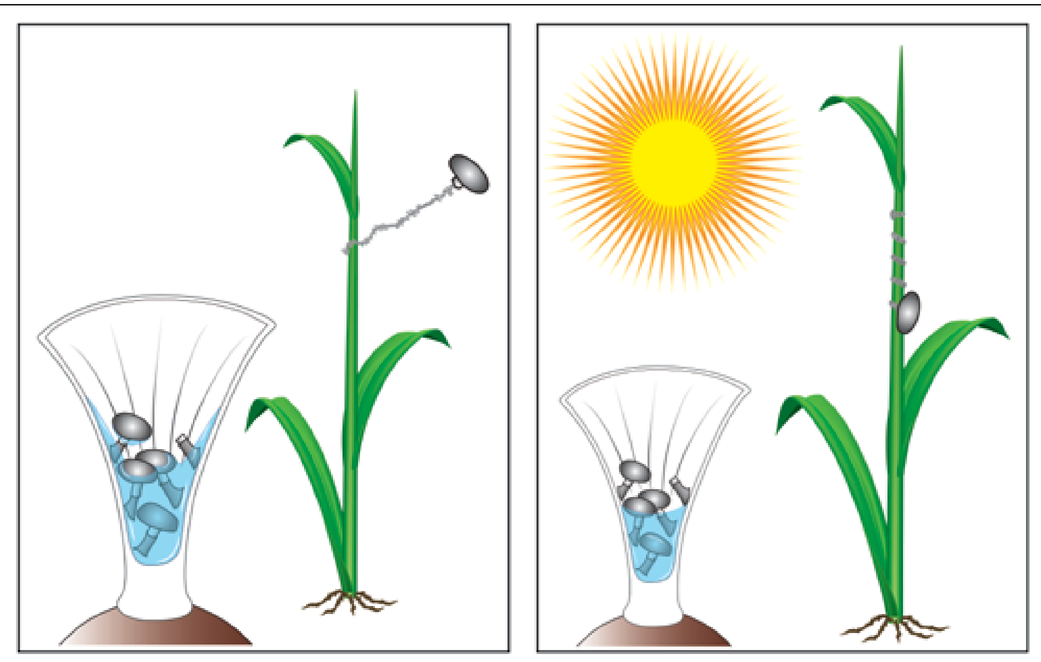


Figure 2. Diagram showing splash discharge of peridiole and its mechanism of attachment to vegetation. The funicular cord is packed within the purse before discharge. The force of the raindrop fractures the purse leaving the sticky end of the cord exposed during the flight of the peridiole. Deployment of the funicular cord occurs when the hapteron contacts an obstacle. The process is completed in less than 200 milliseconds.

Cyathus striatus. Photo courtesy of J. Hammond.

The vital statistics are interesting, beautiful even, when viewed beside the familiarities of our macroscopic world. Peridioles are splashed from their nests at speeds of 1 to 5 meters per second, or up to 18 kilometers per hour, and can cover a distance of 1 meter in 200 milliseconds. An eye blink lasts from 40 to 200 milliseconds. The splash cup is a relatively sedate launch pad compared with other fungal devices. Some of the squirt guns of ascomycete fungi shoot single spores at 115 kilometers per hour. The bird's nest fungi pursue a different reproductive strategy, discharging 100 million spores inside a peridiole with each shot. Single squirt-gun spores weigh 1 nanogram; peridoles are one million times heavier. The ballistic mismatch is comparable to throwing a pea versus a pickup truck, and the truck would be shot over Manhattan if its flight were comparable with the peridiole!

The splash discharge controlled by the bird's nest fungus is an impressive feat of natural engineering, but there is much



Really cool!

Hey kids… want to see more high-speed videos of mushroom spore discharge?

Go to the *FUNGI* homepage (fungimag.com) and click on the links. Each has a great soundtrack, too, so turn up the volume on your speakers!

more to the fate of the peridioles that, at least at first, boggles the mind. Each peridiole is equipped with a harness that operates like the tailhook and arresting cables that brake naval aircraft landing on the deck of a carrier (Figure 2, second pair of frames). The harness is packed within a purse attached to the peridiole: one end is fixed to the peridole, the other is exposed at the bottom of the purse and is sticky. If the peridiole grazes a plant stem after discharge, the sticky end fastens to the vegetation and the harness unravels as the peridole continues its flight. The harness can stretch to a length of 12 centimeters before it halts the peridole in mid-air; the momentum of the tethered peridiole carries it in a wide arc, then a gyre, wrapping the harness around the stem. The whole process is completed in less than one second and the spores of the bird's nest fungus are in the perfect location for grazing by herbivores. After consumption, the peridioles pass through the herbivore gut and are re-exposed to air in manure deposited some distance from the parent colonies. The job of dispersal is complete. Spores that germinate in the manure find a convenient volume of plant carbohydrates to sustain them. The resulting fungal colonies digest plant debris in the dung to the point of exhaustion before embarking upon the next round of mating and splash-cup development. And so on.

Theirs is a supremely beautiful reproductive mechanism. The genetics of bird's nest fungi proves their relationship to fungi that produce conventional gilled mushrooms. This is a bit puzzling. Colonies of both kinds of organism operate in the same fashion, but their differences in spore discharge mechanism are profound. There is no fossil record that can help here, which leaves the biologist in the position of contemplating the evolutionary past with little guidance from objective data. All of the components of the bird's nest fungus are found in gilled mushrooms, but they are arranged in radically different ways to create the different kinds of fruit body. At this point, based on the available evidence, we can do little but make educated guesses about the evolutionary pathways that link these fungi.

Anyone who claims that their art offers more opportunities for creativity than the work of a scientist does not understand the potential for awe and meditation in the face of nature. The biologist works with facts and employs great sweeps of imagination to arrive at ideas that may be tested by experimentation. There is no greater art than the grand pursuit of the workings of life.