Slime Moulds

An exquisite obsession

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Few naturalists are fortunate enough to live in a place where they can immerse themselves in the study of their lifelong passion, which in my case is birds.

In 1988 my partner and I established our home in the middle of a eucalypt forest in central north Tasmania. The forest had been logged by the previous owner, but its recovery was remarkable. Our move coincided with the start of the Australian Bird Count, a project run by Birds Australia (now Birdlife Australia[2]) that called on volunteers to survey the birds in their area. This was my first experience of a "citizen science" activity. As well as contributing data to a project I considered worthwhile, counting birds every two weeks for five years was a great way to learn more about birds, their habits, ecological niches and extensive vocal repertoires. Further information that could influence the occurrence of birds during each survey including the names of flowering plants or prevalence of invertebrates was also requested and I began to learn their names assisted by field guides and my field naturalist colleagues.

Following the bird count I attempted to document all the species around home. Some of my early photographs indicate that I had not completely overlooked the fungi but I did not start seriously to list them until I embarked on another foray into a citizen science project, this time by contributing to Fungimap, Australia's fungi mapping scheme.[3]

The dearth of popular field guides when I began my exploration left me completely bewildered by the bucket loads of fungi I collected every season. Gradually more resources became available and their identification, although still tricky, became a little easier. However, it was researching their ecological roles that changed my view of the world.

In the forgotten zone beneath the soil's surface, fungi have a crucial ecological role. They exchange nutrients with plants via their microscopic hyphae, and their cocktail of powerful enzymes helps to break down organic material and convert it to forms that can be used by other organisms. The services of fungi help to ensure that vegetation communities are more resilient and better able to withstand weed invasion and drought.

Several slime mould species are Fungimap "targets" (i.e. particular species being mapped) and one, *Fuligo septica,* the evocatively named "dog's vomit" or "scrambled egg" slime mould (Figure 1) appears regularly near home.

The sight of three fruiting bodies one morning on logs 50 metres apart got me wondering about the stimulus for their sudden appearance. If learning about fungi changed my view of the world, it was intriguing to learn that a slime mould spends some of its life as an animal-like organism, and some as a fungus-like structure.

Figure 1. "Dog's vomit" or "scrambled egg" slime mould *Fuligo septica*

Neither slimy nor mouldy

Except at a certain stage of their lives slime moulds are neither slimy nor mouldy – or even smelly. Rather, they have qualities of both animals and fungi. During their two trophic (feeding) stages the organisms live in the soil and dead organic matter where they move about to feed in a manner akin to animals; then they transform into spore-bearing fruiting bodies more akin to fungi. This duality has befuddled classifiers for centuries. Slime moulds have at different times been placed alongside plants, animals and fungi, but they now reside with amoebae and other single-celled organisms in the kingdom Protista.[4]

If their dual life modes are not remarkable enough, consider their often very beautiful fruiting bodies. These range in size from large amorphous blobs such as those of the aforementioned *Fuligo septica* that may contain billions of spores, to tiny spheres less than 0.5 millimetre tall with as few as one or two spores. Some of the miniscule spheres are sessile (stalkless), but most sit atop stalks that vary from thread-like to chunky granular. The outer coverings that encase the spores called peridia (single: peridium) take exquisitely different forms: some are white and crystalline; some have nets of fine threads; others are wrapped in iridescent membranes that shine like Christmas baubles (Figure 2); some are fine like porcelain; some are fluffy brown tufts. Within these fruiting bodies are spores and threads (called capillitia) intricately decorated with spines, ridges, cogs, rings, warts or spiral bands.

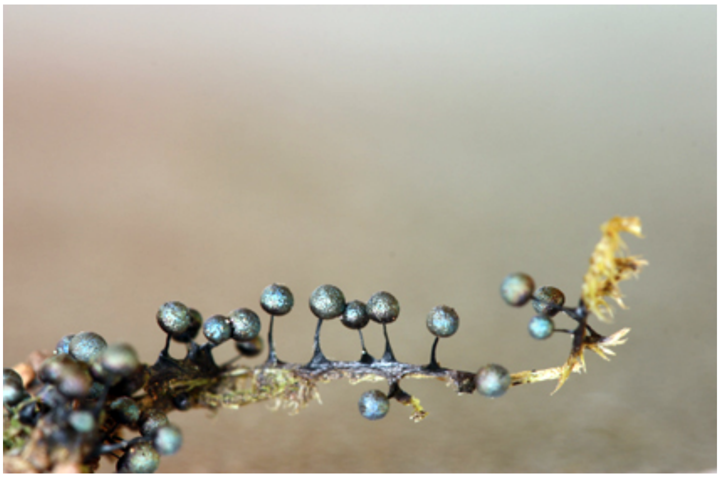

Figure 2. *Lamproderma* species have iridescent peridia.

Slime mould groups

To avoid confusion it is important to keep in mind that modern classification recognises three groups of slime moulds. There are the microscopic Dictyostelids, also known as cellular slime moulds; the very obscure and little-studied Protostelids and the acellular slime moulds. It is this last group, the acellular slime moulds also known as plasmodial – or true – slime moulds or myxomycetes, that are the subject of this essay.

Myxomycetes start life when microscopic spores released from their fruiting bodies germinate into one or several amoebae. The amoebae take one of two different forms: myxamoebae or flagellated amoebae called swarm cells. The latter have two thread-like structures (one short and one long) called flagella that assist in locomotion. Each form is capable of converting to the other depending on conditions: they are flagellated swarm cells when it is wet and myxamoebae when it is dry.[5] The myxamoebae and flagellated swarm cells feed by engulfing other micro-organisms such as bacteria, yeasts and small protozoans.[6] They multiply by division and their populations can reach between 10 and 1000 and sometimes more than 10000 per gram of soil.[7] They require moisture to function but should the substrate become too dry they can change to a dormant stage called a microcyst, and revert to function normally when favourable conditions return.

Slime mould plasmodia

Two or more compatible myxamoebae combine to form the second trophic stage called a plasmodium. Plasmodia are a mass of protoplasm with numerous nuclei – sometimes numbering in the thousands. They have a fan-shaped feeding front edge ahead of a network of veins, and are constantly changing shape as they undergo rhythmic reversible streaming. Some plasmodia are enclosed in a slime sheath, a membrane believed to prevent desiccation. It is this plasmodial stage that periodically receives attention-grabbing headlines such as "scientists may use slime to design transport network"[8] or "slime mold uses an externalised spatial 'memory' to navigate in complex environments".[9] The research described is undertaken in the laboratory where that "lab rat" of slime moulds, *Physarum polycephalum*, moves about in a Petri dish searching for provided sustenance – usually pieces of oatmeal or a glucose solution. In natural situations plasmodia move through labyrinthine microhabitats in the soil and decaying organic material where they feed on various kinds of bacteria; fungal hyphae, fruiting bodies and spores; algae (which may remain alive and impart a greenish tinge to a plasmodium) and possibly lichens. They are also known to parasitise and predate plasmodia of other myxomycetes.[10] They are generally regarded as scavengers or predators, but some species are known to produce amylase and cellulase[11] that break down components in animal and plants respectively.

There are three main types of plasmodia found in the five myxomycete orders (Echinosteliales, Liceales, Trichiales, Stemonitales and Physarales). The most primitive and smallest, the protoplasmodia, characteristic of the orders Liceales and Echinosteliales, are tiny structures 100-300 microns in diameter that give rise to one or several minute fruiting bodies.

The most common type is the large and often conspicuous phaneroplasmodium whose external appearance belies a complex internal structure with pathways for ingestion, intracellular digestion and defecation vacuoles.[12] Phaneroplasmodia can attain sizes of up to one metre. They slowly advance over logs, tree trunks and leaf litter, sometimes travelling several metres within days;[13] a truly alarming sight for people unacquainted with slime moulds. They eventually produce several to several thousand tiny, usually stalked fruiting bodies, often dotted equidistantly along a log or other substrate. Phaneroplasmodia occur in the order Physarales and some Trichiales.

The third type of plasmodia, characteristic of the Stemonitales, is the large almost invisible aphanoplasmodia (aphano = invisible) whose thin strands can negotiate the micropores in rock-hard wood. Some aphanoplasmodia become pigmented when they are about to fruit. Hence, immature *Stemonitis* species can be yellow, pink or white when they first appear[14] and before they change to fluffy brown tufts. A type of plasmodium intermediate between aphanoplasmodia and phaneroplasmodia has been found in the Trichiales and it is likely that other intermediate forms may be found.[15] Like the first trophic stage, plasmodia can revert to a dormant structure called a sclerotium and reactivate when suitable conditions return.

Theoretically, if plasmodia are well fed and fruiting is inhibited they are immortal. However, like animals, some slime moulds cultured in the laboratory have a six month period of youthful vigour and luxuriant growth followed by two years of declining middle age and lastly a period of senescence and old age.[16]

Fruiting bodies

Eventually plasmodia transform into the spore-bearing stage, also known as fruiting bodies or fructifications. In the laboratory, changes in ambient conditions such as pH, moisture and temperature or exhaustion of the food supply have been proposed as triggers. In the field, the stimuli are more difficult to determine. My observations indicate that fruiting bodies of at least some species will appear as long as there has been enough precipitation to saturate the substrate.

Fruiting bodies take a number of different forms. The plasmodiocarp is the simplest and resembles the veins in the plasmodium. Sporangium (plural sporangia), the most common type found in approximately 75 percent of species, is stalked or sessile and usually between 0.5 millimetre and 3 millimetres tall (Figure 3). Its spore mass (sporotheca) is encased in a membrane, the peridium, which can be multilayered, iridescent, lime encrusted, wholly or partly persistent or evanescent depending on the genera or species.

Less common but more conspicuous are the large amorphous blobs (e.g. "dog's vomit") called either aethalium (plural aethalia) or pseudoaethalium. Their plasmodia migrate to the top of tree stumps or logs where their spores are mostly dispersed by water droplets or, inadvertently, by the several beetle species that become dusted with spores when they feed on this protein-rich food (Figure 4). (Spores from other plasmodia are mostly wind dispersed.) Pseudoaethalia resemble aethalia, but they are actually composed of individual closely packed sporangia.

Figure 3. *Metatrichia floriformis* has stalked sporangia approximately 2 mm tall.

Figure 4. Some beetles become dusted with spores as they feed on the protein-rich food.

Slime mould research

The dual life mode of myxomycetes not only makes them among the most unusual organisms on Earth, it also means they are extremely difficult to study under natural conditions. However, they are considered to be one of the most important regulators of bacteria and they contain a cocktail of compounds with anti-bacterial, anti-fungal and anti-cancer properties although there are yet to be practical applications for these chemicals.[17]

Although ever present and often abundant in terrestrial ecosystems, they are usually undetectable during their trophic stages so their ecological requirements and impact on other biota are almost impossible to discern. Most of what is known about slime moulds has been discovered through research on the relatively few species that survive in the laboratory on a limited diet of oatmeal or bacteria. It is likely that the hundreds of species that do not survive under laboratory conditions fill different ecological niches and have widely varying diets. Further difficulties in research arise because identification of the trophic stages is currently not possible, so assigning a species name depends entirely on the identification of their often tiny, ephemeral reproductive structures.

Because myxomycetes have a spore-bearing reproductive stage, surveys are usually undertaken by mycologists. Any study of a region involves at least one visit and, ideally, repeated visits over successive seasons to collect mature fruiting bodies. Unlike fungi, whose visible features such as size, shape and colour must be described soon after collection because they rapidly deteriorate, mature fruiting bodies of myxomycetes dry within hours and if stored properly retain indefinitely all features necessary for identification.

An adjunct to field surveys is the culturing of collected substrate (leaf litter, wood, bark of living trees and herbivore dung) placed on moistened tissue in a Petri dish or similar in the laboratory. This technique is especially useful for minute slime moulds that are likely to be overlooked in the field and it will often augment field collections by an additional 20–60 percent.[18] Although effective for certain families, some slime moulds may never complete their life cycle in moist chamber cultures.[19]

Distribution

Slime moulds are most abundant in temperate forests, but they are also found in tropical forests, deserts, heathlands and alpine areas; in fact anywhere where there is decaying organic material. There is a rich myxomycete flora associated with the bark of living trees and even one record on a living animal. Much to the surprise of a herpetologist who was collecting reptiles in eastern Honduras, a lizard (*Corytophanes cristatus*) with a "sit and wait" foraging strategy sat long enough for numerous sporangia of *Physarum pusillum* to appear on its body.[20]

In 1984 there were about 450 species known to occur worldwide.[21] In the past decades this number has risen to approximately 1000 species;[22] still a low number compared to the 1.5 million or so fungal species believed to exist.[23] Interestingly, the number of species recorded from any vegetation zone is remarkably constant with 50–60 species found in arctic regions, 30–60 in deserts, 60–100 in the boreal zone, 80–100 in the tropics and 120–180 in eastern temperate North America. Within each region there is an equally constant number of abundant species and 30–40 percent considered very rare – i.e. known from only one or two collections.[24]

Although tropical ecosystems are biodiversity hotspots for flora, fauna and fungi, they may not be rich in myxomycetes. The paucity is attributed to several factors including the rapid decay of potential habitat through the activities of termites and fungi; and the regular, usually daily, rainfall that either washes away the plasmodia or maturing fruiting bodies or creates humid conditions ideal for the proliferation of colonising fungi. In addition, they are food for the myriad invertebrates that inhabit the seething tropics.[25] However, recent surveys have found numerous myxomycetes on the vines and flowers in the upper strata – researchers may have been looking in the wrong places.

Once believed to be cosmopolitan in their distribution, it is now thought that there could be areas of endemism with certain species restricted to particular regions or forest types. For example, a recently described “new” species was found in *Nothofagus cunninghamii* (myrtle-beech) forest at two locations in Tasmania and a year later the same species was found in *N. moorei* forests at Barrington Tops in New South Wales. It could be the case that some species are restricted to *Nothofagus* forests in Australia; the species has not been found in more thoroughly surveyed *Nothofagus* forests in New Zealand. It will take many more surveys before this can be established.[26]

Scientific papers describing surveys of far flung regions of the world invariably discuss fruiting bodies with features that do not quite fit those of already described species. Because of the lack of comprehensive surveys in many places it is possible that they are new to science. However, in many cases it is more likely that they are variations of already described species. The plasticity of fruiting bodies is well documented. Environmental conditions at the time of the transformation of the plasmodia can affect their appearance. Even fruiting bodies presumably arising from the same plasmodium can be stalked or sessile depending on whether they appear on the under or the upper surface of the substrate.[27] Thus, it is suggested that newly described taxa should be known from several different locations and that all descriptions should be accompanied by scanning electron micrographs. Unfortunately, this takes much research beyond the realm of amateurs.

Australia – the least studied region in the world

Australia’s myxomycetes are among the least studied in the world. In 1995, 105 species were documented from Australia, including only 29 species from Tasmania.[28] This is a surprisingly low number considering they are known to be abundant in temperate forests where at least 120 species usually occur. More recently, the number of species recorded from Australia has increased to approximately 290, but many regions of the country remain understudied.[29]

In 2010 I began to document and collect the myxomycetes from an area of approximately five hectares that encompasses several different vegetation communities, broadly categorised as wet sclerophyll forest. Forty metre high eucalypts are the dominant canopy trees with varying assemblages of understorey plants depending on aspect and drainage. Open areas have a diversity of small trees and shrubs with sedges, grasses and ferns covering the ground; tall thin paperbark (*Melaleuca ericifolia* and *M. squarrosa*) grow on swampy level ground that floods intermittently during winter. Steep, shaded hillsides and gullies with ephemeral creeks that flow only after periods of heavy rain grow dark-crowned blackwood (*Acacia melanoxylon*) with treeferns (*Dicksonia antarctica*) along the drainage lines. Dogwood (*Pomaderris apetala*), the dominant small tree in shady areas, is particularly vulnerable to strong winds. Once on the ground it quickly breaks down and its sodden spongy texture is a rich substrate for slime moulds. Copious quantities of its broad soft leaves accumulate to form a deep carpet of litter; wrist-thick clematis vines (*Clematis aristata*) snake through the canopy. Forestry activities in the 1950s, 60s and 90s left the forest floor strewn with fallen trees deemed unsuitable for mill logs, railway sleepers or telegraph poles probably because they were partially rotten. They are now in an advanced state of decay and covered with abundant mosses, leafy liverworts and lichens.

Because of my interest in the associations between different organisms, I began my study by documenting the invertebrates feeding on plasmodia or immature fruiting bodies. As it is extremely difficult to identify the food of small cryptic invertebrates, my series of photographs depicting this behaviour in at least five species of collembola (springtails) sent to researcher Penelope Greenslade lead her to conclude that slime moulds do indeed form an important food source for these animals (Figure 5).[30]

Figure 5. Collembola *Acanthanura* sp. feeding on immature slime mould.

Compiling a photographic record of plasmodia and mature fruiting bodies in the field, rather than collecting mature fruiting bodies, was my next focus. This was because I thought that slime moulds, like fungi, would reappear on the same substrate in subsequent years. When it became clear that this was not necessarily the case, I started collecting fruiting bodies. A request from Dr Tom May (Senior Mycologist at the National Herbarium of Victoria) to collect for the herbarium turned my rather sporadic collecting into, dare I say, an obsession.

It was the element of surprise and anticipation that really got me hooked. There are few people in the world interested in myxomycetes and even fewer who are fortunate enough to live in a place where they can make daily or if necessary hourly inspections of transforming plasmodia or immature fruiting bodies. This is really fun! Finding brightly coloured venous plasmodia pulsating over decaying vegetation or clusters of yellow, hot pink, bright orange or shiny white beads of immature fruiting bodies is easy; keeping track of their progress is the difficult part. As they mature their colour and shape gradually change and some turn invisibly dark in the damp shaded forest. Marking their location with brightly coloured tape eliminates the frustration of fruitless searching. Of course, not all slime moulds are noticed when they first appear because they are not all brightly coloured when young. Some are just dots on wood; specks of transparent jelly no larger than a pinhead. These are usually found when crawling around on the ground equipped with hand lens and headlamp.

Collecting slime moulds can be difficult and dangerous

It took a while to find the perfect tool for detaching small bits of wood with delicate fruiting bodies. Some are easy to collect: crumbly rotten wood falls apart at a touch and sodden substrate carves like clay. However, recently fallen logs, an unexpectedly rich substrate, are often coated in a slippery algal veneer that makes using sharp instruments dangerous. My tool of choice, a pocket knife with razor-sharp blade, is strong enough to take the force required to cut extremely hard wood. As this usually requires both hands and the weight of the body, gravity takes its toll and I watch in dismay as some get lost in the litter.

Timing is critical. Collect too early and the sporotheca (spore sacs) go rock hard and the spores do not mature. Leave them in the field and they risk getting washed away by rain or being covered in a fuzz of fungal filaments. Successfully collected specimens dry within hours and can be stored indefinitely by gluing substrate to card that, with folded up ends, fit snugly into the tray of a match box. Once mounted, the delicate structures are remarkably robust; they never need to be handled but can be inspected by manipulating the card. To date I have lodged over 250 collections representing approximately 80 species with the National Herbarium of Victoria (MEL) – the Tasmanian Herbarium does not have a myxomycete collection.

Any field has its own vocabulary, and identifying these little-studied organisms requires specialised texts, none of which are directly applicable to Australian myxomycetes. *Myxomycetes, A Handbook of Slime Molds*[31] is an excellent book for beginners with a great introductory section covering biology, collecting, ecology, distribution and associated organisms. It also has descriptions with illustrations of a range of common and several rarer species “not likely to be encountered by the average collector”—whomever that may be.

When it became clear that the surrounding forest was rich in slime moulds, a more thorough coverage was required. *The Myxomycetes*[32], the most comprehensive tome at the time of its publication and the one credited with sparking much subsequent research, includes approximately 400 species. Its extensive introductory section outlines the many difficulties that arise when identifying species.

Les Myxomycètes[33] is a two-volume set: Volume 1 is devoted to keys and brief descriptions in both French and English. Volume 2 has colour photographs of 530 of the 853 taxa described in the keys and line drawings of the microscopic structures. These books are truly inspiring, not only because of the beautiful photographs, but also because the information is based mostly on the private collections of Jean Bozonnet and Marianne Meyer numbering 4,000 and 35,000 specimens respectively. Meyer’s collection, which is larger than many institutional herbaria, concentrates on the nivicolous (i.e., “snowbank”) species that are commonly found in the alpine mountains of Savoie where her work is concentrated. As my work is conducted in a very different habitat, it may be the case that “snowbank” species occur in the forests of Tasmania but with a different ecological niche.

Even the most comprehensive books do not overcome the problems confronting non-specialists. In many cases, it is relatively easy to identify the different genera. For example, *Cribraria* species have their spores enveloped in an intricate net of anastomosing threads and in the field even minuscule species barely 0.5 millimetre high can be recognised if one is equipped with a 10x hand lens. Similarly, the peridia of the genus *Lamproderma* are beautifully iridescent reflecting golden, silver, blue, green and/or purple hues. Within their spore mass is a structure called a columella, essentially an extension of the stalk. This can vary in length and shape even within the same species and the many intermediate forms make assigning a species name almost impossible without the right equipment. Unfortunately my online-purchased microscope – while adequate for appreciating the artistry in the decorations of spiral bands, cogs, spines and reticulations on the brightly coloured spores and fascinating capillitia of some species – is not up to the task required of it. Oh for a better microscope!

Other difficulties arise because of taxonomic revisions, name changes, the recognition of new families and removal of others, and the blurry lines that differentiate genera. Furthermore, descriptions of northern hemisphere substrate preferences do not necessarily apply here. For instance, *Cribraria* species are not "almost always associated with coniferous wood". In Tasmania enormous old eucalypt logs with a blanket of bryophytes and innards decayed to a mud-like consistency seem to be to their liking. The designations "very rare" or "tropical" are also misleading.

Most slime mould fruiting bodies require microscopic examination of spores and capillitia for identification. But surely the distinctive bicoloured fruiting bodies of one of the most commonly occurring species in 2010 would be easy to identify? Not so. It remained a mystery until colleague, Paul George, identified it as *Elaeomyxa cerifera*, a species described as "very rare [and whose] yellow waxy collar is known only from Japanese collections"[34] and "the very rare *Elaeomyxa cerifera* … [is] only known from terrestrial bryophytes".[35] My specimens have a distinctive yellow collar and although common and seen only on bryophytes in 2010, it has been less prevalent in subsequent years but has appeared on wood, not bryophytes.

Tubifera bombarda is the only slime mould with stiff bristles in its sporotheca. I had seen images of it when leafing through books and was keen to see this "tropical" species, unlikely as that seemed in temperate Tasmania. I was pretty excited when going through my early photographs to discover that I had recorded the species several times on tree trunks and bryophyte-covered logs (Figure 6). I have subsequently lodged several collections at MEL.

Figure 6. "Tropical" slime mould *Tubifera bombarda*

My study, now in its fourth year, has documented approximately 100 species. It is likely that this number will increase once I start culturing substrate in Petri dishes indoors. It is also likely that equivalent numbers will be found in other potentially rich sites elsewhere in Tasmania and on the Australian mainland. I have learnt so much – and not only about slime moulds. The study has reinforced for me the importance of rotting vegetation. My freshly collected slime moulds invariably come with an invertebrate or two; dead wood is full of life!

Birds are almost universally appreciated so no-one needs convincing of their worth. Fungi have in their favour a wonderful variety of beautiful colours and forms and their crucial ecological roles. But slime moulds are another matter entirely. Their common names "slime" and "mould" do not conjure up images of great beauty and one can only imagine the looks of indifference and boredom when attempting to define their proper name, myxomycetes. But show people some photographs, or a matchbox full of jewels, and they are almost invariably convinced.

Notes

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