

on't you just hate fungus gnats? What can be worse than gathering wild mushrooms, bringing them home, and preparing them for dinner only to find out that they are maggot nurseries? They are a serious and international threat to the commercial mushroom industry as well. Infestations are estimated to reduce yield up to 70% as larvae of Lycoriella ingenua (Sciaridae) eat the mycelia and compost while winged adults introduce spores of the destructive green mold, Trichoderma aggressivum (Dodson, 2016). It gets worse as the larvae of humpbacked flies (Megaselia: Phoridae) and cecid midges (*Heteropezina cathiestes*; Cecidomyiidae) invade and tunnel into pinhead and button stages making them unfit for sale (Singh and Sharma, 2016).

You have another reason to detest them if you grow plants indoors. Mycelia become established quickly when the growing medium is overwatered. Swarms of gnats emerge from containers on windowsills and home greenhouses. Place the words fungus, gnats, indoor, and plants in the YouTube search engine. Dozens of videos pop up about how to exterminate them from spritzing maggots with solutions of hydrogen peroxide or immobilizing flying adults on yellow sticky traps.

In fact, what we call a fungus gnat is really a blanket term for thousands of species (many still unnamed) representing members of at least eight families in the Order of true flies (Diptera). They include members of the Bolitophilidae, Cecidomyiidae, Diadocidiidae, Ditomyiidae, Drosophilidae, Keroplatidae, Mycetophilidae, and Phoridae. What they all have in common is that their lifecycles are tied to fungal growth. Not all of them lay their eggs in fruiting bodies. Many species oviposit in detritus or humus. Their larvae hatch out and search for mycelia. Including the fruit or vinegar flies (Drosophilidae) surprises some people, but it shouldn't. Many species in this family consume yeasts as adults and are attracted to mature mushrooms, as well as, natural sites of fermentation.

We must emphasize that, while many maggots feed on plant and animal substrates we find disgusting, some develop refined tastes as winged adults subsisting on the nectar and/or pollen of flowers. This includes both wild



vegetation (Raguso, 2020) and even some important crop plants. The best known are the tropical biting midges (Forcipomyia) that gave you that piece of chocolate you ate the other day. Pregnant females tracked pollen onto the pistil of a flower on a cacao bush (Theobroma cacao) allowing fertilization of those big seeds (Young, 1994). Do you like caraway seeds (Carum curvi) in rye bread or food fried in canola oil (Brassica napus)? Thank the polleneating hover flies in the Syrphidae (Jauker and Wolters, 2008; Toivonen et al., 2022). Consequently, many fungus gnats turn to food in flowers once their metamorphoses are complete.

Why do some flowers depend on fungus gnats?

Nevertheless, entrusting genes in your pollen grains to fungus gnats sounds like a poor choice. Regardless of family, and with important exceptions (Goldblatt et al., 2004), most fungus gnats are minute, less than 3 millimeters in length. Surely, such tiny insects are more likely to steal nectar without ever contacting the receptive tip (stigma) of the pistil, leaving pollen on its surface. Wouldn't bees, larger flies, butterflies, hawkmoths or even nectar-feeding birds make better sperm taxis?

As it so often happens, the answer



Female sciarid species with numerous pollinia on Acianthus pusillus.

must be considered in terms of real estate. It's all location, location, location. As more scientists study the ecology of fungus gnats, and the plants that need them, they note that natural selection favors flora with flowers modified to attract pollinators preferring gloomy and damp environments. Bees, butterflies, day moths and most nectar-feeding birds are sun lovers and may avoid flowers standing in shade much of the day. Readers with access to deciduous forests may have noticed that bumblebees stop visiting the spring flowers of the forest floor after the canopy leafs out. Some of the most efficient bees avoid nesting in wet sites as the wax that makes up their brood cells absorbs water vapor. Therefore, tropical forests at higher elevations receiving clouds and mist baths twice a day may be inhospitable to most bees. Then there are the wildflowers and shrubs living in gaps in conifer forests where tall pines and firs keep their needles all year long throwing long shadows. While these aren't the greatest places for bees and butterflies,



Copulating pair of Phthinia sp. (Mycetophilidae); female with pollinarium of Corybas diemenicus.

we know they encourage the growth and diversity of fungi. Where there are mushrooms, and humus loaded with mycelia, there are fungus gnats.

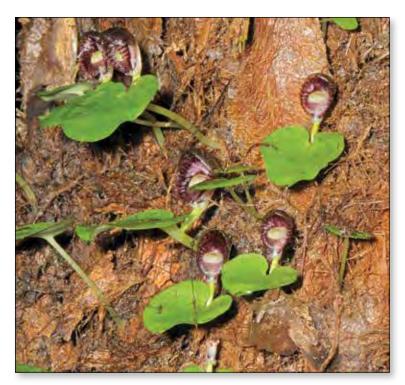
The number of plants dependent on fungus gnats for pollination may be rather extensive in some parts of the world, and the floral traits that best attract and enlist these insects may be shared by unrelated plants. Mochizuki and Kawakita (2017) examined the flowers of ten plant species, representing five different families, growing in Japanese forests, along stream sides and on cool, wet, subalpine meadows and bushlands. All produced small flowers accommodating the small dimensions of their gnats. Seven offered nectar but in very shallow cups. Their flowers wore drab colors. Two species offered greenish petals and the rest were dark burgundy or iodine red.

But what about orchids?

With over 20,000 species many members of the orchid family (Orchidaceae) grow in the same dreary

and/or wet habitats and enlist the same fungus gnats. We look at their flowers, collect their pollinators, and (when possible) analyze their scents. Many adopt the same adaptations as the woody plants and wildflowers of Japan. They produce small flowers that secrete nectar in shallow cups and wear dull red and green blotches or streaks. However, as orchids have a "flare for advertisement and fakery" we also see far greater variation in flower size and color. Some blossoms are dozens of times the size of their gnats. Some wear petals and sepals displaying creams, whites, browns, even purples so dark they appear black to our eyes.

But orchids have features uncommon or absent in most other plant families. About 80% of known species are epiphytes and colonize the branches of trees without parasitizing them. They don't grow under shady limbs. They grow on shady limbs. Most orchids don't release their pollen as loose grains. Each pollen-making anther attaches all the grains in the same anther chamber to



Helmet orchids, Corybas diemenicus.



Nodding Greenhood *Pterostylis nutans* with male *Mycomya* (Mycetophilidae) fungus gnats on labella.

each other, releasing a compound "lump" known as a pollinium. Depending on the orchid species, the solitary anther in most orchid flowers releases from two to eight pollen wads (pollinia) that ultimately attach themselves to the body of their pollinator by means of a sticky disc or glue drop known as the viscidium. The entire unit is known as a pollinarium. This means that, unlike the flowers in most plant families, the deposition of pollinia on a pollinator's body must be precise and repetitive. It explains why some orchid flowers are so huge compared to their pollinators. The insect must be beguiled, redirected, canalized, and corralled before it can leave the flower wearing pollinia restricted specifically to its tongue, or head, or thorax, or abdomen. Thousands of orchid flowers are frauds. Their shapes, colors, and smells look like they are offering good food or a sexual partner, but it's a lie. Depending on the orchid species, butterflies, moths, wasps, bees, and large flies are duped ... and so are some fungus gnats (Edens-Meier and Bernhardt, 2014).

It was long assumed that most orchids pollinated by fungus gnats worked on the basis of a form of pollination-by-deceit we call brood-mimesis. The flower "pretended to be a mushroom" luring pregnant gnats that pollinated the flower,

but left eggs that hatched into maggots. Of course, the larvae starved to death due to the absence of a proper host. We will see that this sweeping generalization is changing.

Speed dating in Dracula's ballroom

There can be no doubt, though, that some orchids pretend to be fungi. The more than 120 species in the genus *Dracula* are among the most convincing. Distributed through Central and South America most are epiphytes preferring the wet branches of trees in

upland cloud forests. While the flower often reminds people of the face of a monkey or a goblin, look at the lip petal (labellum). It resembles an upside down mushroom cap and its interior is sculpted and crinkled like gills. People who grow the "Dracs" comment that the flowers smell like mushrooms and this attracted the Swiss biochemist, Roman Kaiser. His team analyzed the odors of four species and they are rich in mushroom-like volatiles including oct-1-en-3-ol, oct-3-on3 and oct-3-ol. How close is this mimesis? In Ecuador, Kaiser compared the scent of *D. fleurii*





Pterostylis boormanii with male Orfelia sp. (Keroplatidae) on labellum.

to the parasols of *Filoboletus gracilis* (Mycenaceae) fruiting on dead wood while the orchid was in bloom. Both flower and mushroom tested positive for the same three molecules (Kaiser, 2011; Policha et al., 2016).

A team of American and Ecuadorian scientists, led by Dr. Bitty Roy at the University of Oregon did field and lab work on Dracula fleurii, and its close relation, *D. felix*. Both were pollinated by more than one species of drosophilid in the genus Zygothrica. That is, different species of fungus flies pollinated both orchid species but fly diversity was so great in this forest that the two orchids didn't share the same fly species too often (Policha et al., 2019). The flies, though, often passed their time moving back and forth between the lip petal of their preferred orchid and neighboring mushrooms representing at least ten genera in ten families, including Filoboletus (Endara et al., 2010).

Male and female Zygothrica landed on the orchid's lip petal. Their behaviors were variable and complicated. Most of them lapped or probed the surface of the "gilled" lip petal, but the flowers did not secrete nectar. They do contain yeast colonies and they may nourish the pollinators. Some males defended the flower as if it was private property and they attempted to court females. Fly eggs were not found in the flower. The orchid can't transfer its pollinia to the fly until one crawls so far down the lip petal that its thorax is now under the flower's stalk of sexual organs stalk (the column). The insect is held in place and trapped briefly by the column organ known as the rostellum, which is the lobe that makes the pollinia's sticky attachment disc.

The sleazy lure of Lepanthes

Often sold as babyboot orchids, the 800-1,000 species in the genus Lepanthes have much the same tropical American distribution as Drac orchids,

but they are usually smaller plants often colonizing the slenderest outer twigs on a tree's canopy. Their flowers are tiny too, as the name *Lepanthes* means scale flower. The taxonomy of this genus is incomplete and confusing as flowers turn into black smudges when pressed. That's a big problem as the sculptures and hairs on the lip petal appear to be among the most important characters needed for identification. Preserving whole flowers in solutions of alcohol, like spiders or frogs, may be the best way to make sense of their natural variation.

Little was known about the pollination of these orchids until a publication by Blanco and Barboza (2005). They observed visits to the flowers of four babyboot species on display in an orchid garden in Monteverde, Costa Rica. None secreted nectar. While all four species were visited by fungus gnats, the two scientists focused most of their study on *L. glicensteinii*. The Zygothrica flies associated with Drac orchids never appeared. The pollinator of *L. glicensteinii* flowers was identified as *Bradysia floribunda*, a member of the dark-winged fungus gnats (Sciaridae). Once again, no eggs were laid in the flower, and for a very good reason. All the pollinators were males and the flower's pollinia was deposited on the gnat's butt, where he keeps his genitals.

The theory goes that the males of dark-wing gnats must be attracted to the babyboot because the flower is producing strong but fake pheromones. Certainly, that is the case in some other, unrelated orchids pollinated by male wasps and bees, in which their lip petals resemble the shape, eyes, hair and color of virgin females (Edens-Meier and Bernhardt, 2014). Blanco and Barboza observed that the dark-wing male definitely mistakes a structure attached to the lip petal as his "hot date." He grabs that lip petal appendage with the claspers on his abdomen, pivots and ejaculates. That twist is enough to deposit the whole pollinarium on his rear end. He, in turn, leaves a spermatophore globule on the appendage of the lip petal. This was a novel discovery, but not unique. In Australia, male ichneumon wasps do their best to copulate with several species of *Cryptostylis* or tongue orchids (Edens-Meier and Bernhardt, 2014) leaving their sperm behind.

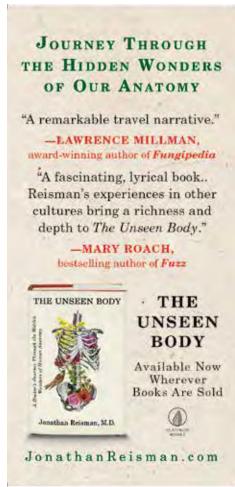


Male Sciaridae species, about 2 mm in body length, with pollinarium on thorax from *Pterostylis nana*.

Fungus gnats and winter orchids

In fact, southern Australia is exactly where we need to go to find hundreds of species of orchids pollinated exclusively by fungus gnats (Kuiter, 2016). Yes, it does seem like a contradiction as we think of Australia as a hot and dry continent, but forget the vast, central desert. Once you are south of the Tropic of Capricorn, the coastal regions of the continent, and the island

state of Tasmania, enjoy a temperate to Mediterranean climate. Freezes are rare, and the antipodal winter from June through August tends to be cloudy, cool, and wet. As usual, that's a great time for the growth of mushrooms and spread of mycelia. The orchids we seek bloom in eucalyptus woodlands and even in the shade produced by remaining pockets of temperate rainforests or "jungle gullies." In most cases. you are searching for small herbs growing from tubers in







Two tiny pollinator fungus gnats Mycetophila sp., looking minute next to flowers of Pterostylis grandiflora.

shallow soil, activated by winter showers. It's not unlike looking for mushrooms. The closest we have to an epiphyte that may entice fungus gnats is the mountain helmet orchid (Corybas grumulus). Sometimes it is found growing on the trunks of tree ferns.

By July or August, it's not uncommon to find several species of fungus gnat orchid in bloom in the same patch of woodland. There is currently some debate on the classification of these plants, so we prefer to stick to an older, conservative taxonomy recognizing 12 species of mayfly orchids (Acianthus), 8 species of gnat orchids (Cyrtostylis), at least 300 species of greenhoods (Pterostylis), and 120 species of helmet orchids (Corybas). These genera are not restricted to Australia and a number of unique species are found in New Zealand, New Caledonia, and in tropical Asia as far north as the mountains of southwestern China (Jones, 2021).

Unlike more recent studies on

fungus gnat pollination in the orchids of the tropical Americas, attempts to understand reproduction in the winter orchids of Australia go back decades. They begin properly with the observations, drawings, and photos of gifted amateurs publishing in journals provided by local, natural history societies (Coleman, 1931; Jones, 1970). There are only a few Australian labs at universities and botanical gardens, at present, looking at fungus gnat pollination today.

Mayfly and mosquito orchids

It's possible that many different looking winter orchids bloom together in winter because they don't exploit the same family or even the same sex of fungus gnats. Mayfly and mosquito orchids appear to be honest producers of nectar on their lip petals, broadcasting their scents to fungus gnats as insects emerge from the detritus and look for mates. The flowers may broadcast strong

scents. In particular, Acianthus caudatus is well known by local naturalists as the dead horse orchid as its disagreeable smell reminds people variously of some form of rot or even the fur of a wet dog. The small mosquito orchid (Acianthus pusillus) is well visited by males and females of dark-wing fungus gnats in the genus Trichosia (Sciaridae). Photos taken by the second author show that fat and chunky females are big enough to hit the orchid's column as they feed on nectar and they carry away the pollen wads of the small mosquito orchid as they back out of the flower. In contrast, the males of the same species of Trichosia gnats are smaller and slenderer than their girlfriends. These boys also drink the nectar but are far too short to bump their backs against the orchid's column of sexual organs (Kuiter and Findlater-Smith, 2017).

In contrast, the common gnat orchid (Cyrtostylis reniformis) is more likely to attract pollinators in the genus Sciophila



Pterostylis revoluta are single flowered species which may form extensive colonies.

(Mycetophilidae). When the smaller, skinny males drink nectar at the base of the lip petal they literally get down on their knees. The back of their thoraces are now too low to reach the glue gun in the column. Once again, only the bigger females are likely to bonk the column on their way out of the gnat orchid's flower (Kuiter and Findlater-Smith, 2017). Although female gnats are the dominant pollinators in these orchids no one has found eggs in the flowers to date.

Kinky greenhoods

It's unlikely anyone will find fungus gnat eggs in the flowers of greenhood orchids either, as all the species studied to date are pollinated by male gnats in the family Mycetophilidae, or Keroplatidae, or Sciaridae. This, once again, may help explain why both of the authors have found so many different greenhood species flowering together in the same woodland. Different greenhood flowers probably appeal to males belonging to species in different families (Kuiter 2020). Biochemical work needs to continue, but at least one species, known as the coastal banded greenhood (P. orbiculata), produces three alkane compounds also produced by fertile females of Mycomya gnats (Hayashi et al., 2021).

At first glance, the pollination system of greenhoods shows some similarities with the babyboot orchid we've already discussed. Greenhood flowers don't secrete nectar either. Sculptures, hairs and pigments on the lip petals of greenhood flowers also appear to convince male gnats they are the bodies of females of easy virtue. Like the babyboot in Costa Rica, the swan greenhood (P. cycnocephala) also depends on pollination by a male Bradysia gnat (Sciaridae). However, like the Australian dead horse orchid and gnat orchids described above, the male Bradysia is far too short to contact the greenhood's column while it attempts to mate with the lip petal. This is a problem in all greenhoods. Even when propped up on its long, spindly legs, the male gnat's body stands far too low to reach the glue gun and pollen wads in the column. Then there's the weird, domed, and often elaborate hood each greenhood flower makes by fusing its inflated dorsal sepal fused to its two lateral petals. The hood completely hides the column from view. In some species the hood is so elaborate and inflated that the English botanist, George Caley (1770-1829) called the flowers "druid's caps." What is going on here?

Ah, there is a touch of the dominatrix in most of the greenhoods studied so far that is absent in babyboots and all the other orchids in this article. The mechanism has probably been known for over two centuries and has been captured on film. Recent videos



Pterostylis tunstalli, a tall greenhood with multiple flowers, usually occurs in loose colonies.

show clearly how the flower abuses its pollinator. You can watch what happens in most greenhood flowers by viewing any of several YouTube videos online.

The second author began studying greenhoods in 2010. Since then, he has devoted his winters to the fungus gnats visiting the greenhoods, rustyhoods, and other orchids in the Australian state of Victoria. His aim was to record the vectors of all the orchid species in Victoria publishing the results as a revised book (Orchid Pollinators of Victoria), now in its fourth edition. Observing fungus gnat pollinators on orchids requires patience and perseverance. In some cases, it took three seasons to learn when gnats were active in orchids to record their behaviors and capture their action in



Working its way through the column wings of Pterostylis smaragdyna, this Mycomya sp. male (Mycetophilidae) is about to hit the glue to collect a pair of pollinia sitting just above and in front.

images. Lengthy observations were always conducted in situ totaling as many as 20 hours for each orchid species. After all, when most insects visit one flower over the entire flowering time it stays less than a minute on any one

blossom. A naturalist and photographer must be at the right flower at the right time. The best strategy was to observe clusters of flowers in the same, discrete population and wait for incoming gnats. Finding orchid flowers maturing into

fruits, at these sites, was also extremely important as they indicated the presence of vectors at the site, a gnat "hot spot." The second author learned that fungus gnats fly at certain times of the day under certain weather conditions. In

most cases, greenhoods emit their scents by late morning and that's when the first fungus gnats are seen although some gnats visit their flowers until midafternoon, while others fly even later as the sun sets.

We now understand that a male fungus gnat is drawn to a greenhood flower by its scent and it lands on the lip petal. He pokes a part of the petal with his abdomen searching for the genital pore of the female gnat but, of course, there isn't one. This triggers a hinge that attaches the lip petal to the base of the column. The lip petal is suddenly catapulted upward slamming the unsuspecting gnat into the bubblelike dome or hood. The lip petal now closes the entrance to the flower like a door, trapping the insect. If the gnat was already carrying pollinia on his back, from another flower visited earlier that day, his thorax would contact the pollen-receptive stigma in the column transferring grains that, ultimately fertilize the flower. The male gnat stays trapped in the inflated hood for varying lengths of time.

Now a prisoner inside the hood, he looks for an exit. Guided by the winter light that beams through the translucent hood he must work his way through two wing-like brackets made by the style neck of the column. Pterostylis is Greek for winged style, after all. For a second time, the gnat is forced under the column but this time his thorax contacts the glue gun (rostellum) and he picks up fresh pollinia as the lip petal relaxes and he escapes. He wears a surprisingly long pollen wad now fixed back, in between his wings. Cross-pollination occurs when the same insect is lovesick enough to try again on another flower. Perhaps he does it out of frustration. The sadistic treatment of the flower did not allow him to ejaculate (Phillips et al., 2014).

You might ask, how long do greenhood flowers hold onto their johns and how often can the same flower play the same trick on unsuspecting gnats over its floral lifespan? It probably depends on the amount of light and warmth reaching the woodland floor where the plant grows. The first author studied the blunt leaf greenhood (*P. curta*) at a national park in New South Wales. Lip petals were tickled until they shut up then tagged. It took the flowers 9–24 hours to reset under cloudy, wintry

conditions. When the same species was grown in pots in an orchid house at the Missouri Botanical Garden the plants enjoyed controlled temperatures of 19–22 C. Tapping the lip petals with a dissecting needle triggered each flower, as usual, but most flowers reset only 2-3 hours later. Greenhouse pampering made the orchids even more excitable. If a flower reset 2–3 hours after it was triggered the first time, 60% of the little blossoms shut up again when tickled a second time. The remaining flowers waited a little longer to become sensitive but they could be induced to snap their lip petals several times over the week until they withered and dried (Bernhardt, 1995).

The second author notes that, in most other *Pterostylis* species, reset time is much shorter. Depending on environmental conditions the lip petal may reset after a few minutes, providing it's a warm day. When it's cooler it may take half an hour, or more. The little rustyhoods (*P. rufa*) are ready for a second go after a few minutes, but taller greenhoods can take one to two hours. The "sensitivity" of the catapult mechanism takes about the same lengths of time as long as the drawn reset-fluid is depleted.

Some years are bad for observations, especially during those long, confounding droughts, so typical of the Australian continent. Based on a decade of observation, the winter of 2014 proved to be the best for the second author observing and photographing the principal pollinators of greenhoods and rustyhoods, as well as mosquito orchids and helmet orchids (below). This must be done with additional patience and stealth. While real, female mosquitos are always "too friendly," fungus gnats are shy and touchy about letting you take their picture. They react to hand movements, so getting into position with a camera in time is often difficult. Wearing thin gloves helps in taking the closest images. These closeups are best taken while waiting for the insect to escape. The second author has now photographed an estimated 40 species of gnats in greenhoods and other winter orchids. Mycetophilids in the genera Allodia, Leia, Mycetophilia, Mycomya, and Phthinia visit greenhoods, while keroplatids in the genus Orfelia frequent rustyhoods.

When harvesting gnats from greenhoods how does the second author discriminate between a mycetophilid, sciarid or keroplatid? The arrangement of veins in their two functional wings lets you segregate them into families. Further variation in venation helps identify genera of mycetophilids and keroplatids but the dark-winged sciarids need extra work. They require stronger magnification to look for characters and sculptures on the 9th segment of the abdomen, found in all flies. This segment is called the hypopygium and that is where you find the organs modified for copulation.

Riddle of the Corybas orchids

The helmet orchids remain the least studied, but that is changing. There is a touch of ancient myth in their genus name, *Corybas*. In Greek mythology, the mother goddess, Rhea, created a battalion of helmeted priests, the corybantes, out of rain. Their noisy





Male Mycomya species (Mycetophilidae) on labellum of Pterostylis sanguinea in pseudocopulation position.



Pterostylis smaragdyna, with Mycomya sp. male (Mycetophilidae), on labellum.

rituals distracted Rhea's baby-eating husband, Kronos, from her last offspring, the infant Zeus (Bernhardt, 2008). Every winter, following rain, 33 species of helmet orchids appear in Australian woodlands and in jungle gullies. They are easy to miss as the flowers open almost flush with the humus and their petals and sepals are dark in color. Some naturalists would insist they are the most mushroom-like of all orchids. The dorsal sepal forms a smooth, cap-like dome over the column. The lip petal differs in outline from species to species. Sometimes its margins are beautifully scalloped and ribbed like mushroom gills. The center of the lip, when visible, features a raised, smooth, often whitish surface known as the boss.

Surely, these little flowers are mushroom-like enough to fool female, fungus gnats into laying their eggs in the flowers. Unfortunately, unless you are growing them in a pot on a shelf in a temperate orchid house they are not easy to observe. So close to the ground, wild populations must be viewed on your hands and knees and that is precisely what the second author did, studying eight Corybas species, and collecting the pollinators of five over several years. The only good thing about working on these plants in damp, shady, often messy conditions, was that their fungus gnats didn't become active until the afternoon visiting these flowers after lunch.

On good afternoons, gnat activity on the flowers of helmet orchids, in the Australian state of Victoria, was similar to the *Zygothrica* flies visiting *Dracula* orchids in Costa Rica. When male and female gnats found the flowers they often engaged in mating before or after they entered the helmets. The difference was that the helmet orchids appeared to offer a reward. Gnats were observed licking at the polished boss on the lip petal, although whole droplets could not be photographed. While all five species were pollinated by members of the Mycetophilidae, three depended only on gnats in the genus *Phthinia* while the remaining two exploited Mycetophila. When gnat specimens were identified the diagnosis was that each species of helmet orchid was pollinated by only one species of fungus gnat.

Differences among pollination systems didn't stop there. As in the dark-wing sciarids that pollinate mayfly and mosquito orchids, the sexes of mycetophilids occur in two sizes. The difference this time was that female mycetophilids were physically smaller than males. This limited the entrance space for gnats crawling down into their respective flowers placing their thoraces under the glue gun of the column. Only male Mycetophila gnats left the flowers carrying the pollen wads of the fringed helmet (*C. fimbriatus*) and slaty helmet (C. incurvus). Female Phthinia gnats carried pollinia of the cradle orchid (C. acontiflorus), stately helmet (C. diemenicus) and small helmet (C. unguiculatus). One size didn't fit all. Looking at the photos, one wonders how female Phthinia gnats endured the major load attached to their thoraces by the stately helmet, yet had enough strength to fly away to deposit eggs in the forest debris? A female may also wear pollinia while copulating with her mate.

After such close observation did the second author find that the flowers of the helmet orchids pollinated by females contained eggs? Yes ... but they hatched out as baby springtails (Collembola) and dark-wing sciarids, neither of which pollinated any of the helmet orchids (Kuiter, 2020). It's important to note that mycetophilids do not, as a rule, lay their eggs on fruiting mushrooms anyway. It is more likely that their females will try to dig into the humus to oviposit on, or near mycelia.

Female mycetophilids may not be interested in orchid flowers that smell like mushrooms anyway. Ongoing studies continue on Corybas geminigibbus and C. shanlinshiensis in the Heng Duan mountains of Yunnan, China by faculty and students at the Kunming Institute of Botany. The first species was pollinated by a female Phthinia while males and females of an Exechia species (also a mycetophilid) carried the pollen wads of the second. Both of these orchids bloomed in the presence of dozens of mushroom species. As wild mushrooms are so important as wild foods and traditional medicines to the people of Yunnan (Bernhardt and Ren, 2022) orchid scents were collected and compared to Suillus bovinus, and a Laccaria, and *Mycena* species fruiting in the same sites. The mushrooms released the usual octanone and octanol odors associated with Dracula orchids. The

Yunnan helmet orchids did not. They emitted combinations of three, different, molecules associated with the flowers of many other plants.

Orchids and fungi are linked

We now have to ask ourselves, has anyone ever found flies pollinating orchids after females left their eggs in the flower? The most convincing evidence comes from Brazil and the research of Eduardo Borba and Joao Semir (2001). They examined five native species of bonnet orchids (Pleurothallis), sold as "Pths" in the horticultural trade. Bonnet orchids are cousins of *Dracula* orchids. Female gnats pollinated and left their eggs in the flowers of two bonnet species that did not secrete nectar. It's possible these flowers are mimicking the place where the mother would normally leave her eggs, but these two flowers were definitely *not* pretending to be mushrooms. The insects that laid eggs in the bonnet orchids were all frit or eye flies in the family, Chloropidae. They aren't at all interested in fungi as adults or maggots.

We will keep looking, but does it really matter if we ever find a fungus gnat laying eggs in an orchid that looks like a mushroom? The relationship between fungus gnats and orchids in Australia and the American tropics looks tight because the relationship between orchids and basidiomycetes is so tight.

Think about it. Wild orchids do not provision their seeds with stored food. When they are ready to sprout, their embryos must be invaded by hyphae of appropriate fungi or the plantlet dies (Warcup, 1981). Outside the greenhouse, virtually all orchids keep fungal peletons in their roots or rhizomes during periods of active growth. They need to form mycorrhizae throughout their lives to obtain nitrogen and phosphorous the hyphae recycle from surrounding dead and decaying vegetation. Should it surprise us if pregnant gnats and orchid roots need the same or similar strains of Tulasnella, Russula, or Sebacina? Maybe we should ask the question, why hasn't fungus gnat pollination of orchids evolved more often?

The next time you find a fungus gnat on a mushroom, admire it. Consider the long, delicate legs, the two dainty wings, those pert compound eyes and how such a small, slender creature can bear the weight of mounds of pollen. Then ... squash it.

References Cited

- Bernhardt, P. 1995. Observations on the floral biology of *Pterostylis curta* (Orchidaceae). *Cunninghamia* 5: 1–8.
- —2008. Gods and Goddesses in the Garden; Greco-Roman Mythology and the Scientific Names of Plants. Rutgers University Press, New Jersey.
- —and Z.-X. Ren. 2022. Yunnan mushroom summers. *Fungi* 15(2): 20–26.
- Borba, E.L., and J. Semir. 2001. Pollinator specificity and convergence in fly-pollinated *Pleurothallis* (Orchidaceae) species: a multiple population approach. *Annals of Botany* 88: 75–88.
- Blanco, M.A., and G. Barboza. 2005. Pseudocopulatory pollination in *Lepanthes* (Orchidaceae: Pleurothallidinae) by fungus gnats. *Annals of Botany* 95: 763–772.
- Coleman, E. 1931. The pollination of *Corysanthes bicalcaratus* R. Br. *Victorian Naturalist* 48: 95.
- Dodson, B. 2016. Lord of the gnats. PennState Hotline, psu.edu/news/ research/story/lord-gnats/
- Edens-Meier, R., and P. Bernhardt, (editors). 2014. *Darwin's Orchids: Then and Now.* University of Chicago Press, Chicago.
- Endara, L., D.A. Grimaldi, and B.A. Roy. 2010. Lord of the flies: pollination of *Dracula* orchids. *Lankesteriana* 10: 1–11
- Goldblatt, P., P. Bernhardt, P. Vogan, and J.U.C. Manning. 2004. Pollination by fungus gnats (Diptera: Mycetophilidae) and self-recognition sites in *Tolmiea menziesii* (Saxifragaceae). *Plant Systematics and Evolution* 244: 55–67.
- Hayashi, T., B. Bohman, A. Scaffidi, R. Peakall, and G.R. Flematti. 2021. An unusual tricosatriene is crucial for male fungus gnat attraction and exploitation by sexually deceptive *Pterostylis* orchids. *Current Biology* 31: 1954–1961.
- Jauker, F., and F. Wolters. 2008. Hover flies are efficient pollinators of oilseed rape. *Oecologia* 156: 819–823.
- Jones, D.L. 1970. The pollination of *Corybas diemenicus* (H.M.R.) Rupp and W.H. Nicolls ex H.M.R. Rupp. *Victorian Naturalist* 87: 372–374. —2020. *A Complete Guide to Native*

- Orchids of Australia: a Botanical Obsession. Reed New Holland Publishers, Wahroonga, NSW, Australia.
- Kaiser, R. 2011. Scent of the Vanishing Flora. Verlag Helvetic Chimica Aca, Wiley-VCH, Zurich, Switzerland.
- Kuiter, R. 2016. Orchid Pollinators of *Victoria*, 4th edition. Production Printing Australia. Melbourne, Australia.
- —2020. Pollination by sexual deception of different fungus-gnat species, two (Mycetophilidae) in *Pterostylis* grandiflora and two (Sciaridae) in P. nana. The Victorian Naturalist 137: 41-47.
- -and M.J. Findlater-Smith. 2017. Initial observations on the pollination of Corybas (Orchidaceae). Aquatic Photographics 5: 1-19.
- Mochizuki, K., and A. Kawakita. 2017. Pollination by fungus gnats and associated floral characteristics in five families of the Japanese flora. *Annals* of Botany 121: 651–663.
- Phillips, R.D., D. Scaccabarozzi, B.A. Retter, C. Hayes, G.R. Brown, K.W. Dixon, and R. Peakall. 2014. Caught

- in the act: pollination of sexually deceptive trap-flowers by fungus gnats in Pterostylis (Orchidaceae). Annals of Botany 113: 629-641.
- Policha, T., A. Davis, M. Barnadas, B.T.M. Dentinger, R. Raguso, and B.A. Roy. 2016. Disentangling visual and olfactory signals in mushroommimicking *Dracula* orchids using realistic three-dimensional printed flowers. New Phytologist 210: 1058-1071; doi: 10.1111/nph.13855.
- -Grimaldi, D.A., R. Manobanda, A. Troya, A. Ludden, B.T.M. Dentinger, and B.A. Roy. 2019. Dracula orchids exploit guilds of fungus visiting flies: new perspective on a mushroom mimic. Ecological Entomology 44: 457-470; doi: 10.1111/een.12720.
- Raguso, R.A. 2020. Don't forget the flies: dipteran diversity and its consequences for floral ecology and evolution. Applied Entomology and *Zoology* 55: 1−7.
- Singh, A.U., and K. Sharma. 2016. Pests of mushroom. Advances in Crop Science Technology 4: 213. doi: 10.4172/2329-8863. 1000213

- Toivonen, M., A.-E. Karimaa, I. Herzon, and M. Kuussaari. 2022. Flies are important pollinators of massflowering caraway and respond to landscape and floral factors differently from honeybees. *Environment* 323: doi.org/10.1016/j.agee.2021.107698
- Warcup, J. 1981. The mycorrhizal relationships of Australian orchids. New Phytologist 87: 371–381.
- Young, A.M. 1994. The Chocolate Tree. Smithsonian Institution, Washington, D.C. T

Want to see and learn MORE about Australian orchids and their pollinators? Check out Rudie **Kuiter's book Orchid Pollinators** of Victoria, 4th edition (2016) from Production Printing, Melbourne, Australia. I have a copy and it's astounding! Chock full of concise information and more than 1,300 images. For information, drop Rudie a line at rudiekuiter@ optusnet.com.au. -Ed.

CHTHULUCENE

Could the much-vaunted state of consciousness that we as a species so prize — setting ourselves atop the pyramids. Surveying the universe as if star-struck, itki were ours. Could, in truth, this trick of signaling be no more an alpha leap than any pandemic coronavirus on a rip Than any fungi's mycorrhizal philosophies & hyphal praxis leading them to feedstock Consciousness may only be as mysterious as itki is common. Limited only by instinct's parameters All of us placelings, not just rubbing alien shoulders but horizontally transferring DNA in all directions

ART GOODTIMES

NOTA BENE:

"Ki" is a grammatical neologism Indigenous science writer Robin Wall Kimmerer advocates using in place of "it", "its", "it's" or "itself" to help correct English's objectification of the world. As a pre-school teacher I learned that we learn by going through the known to the unknown. So instead of substituting "ki", I've chosen to add the Indigenous neologism to our neutral English pronoun as a suffix, changing the way we speak of things in English from inanimate to animate, "itki." The neologist term is harvested from the last syllable of a longer word in Potawatomi for an "earth being." That syllable, "ki", is itkiself a Bodéwadmimwen suffix meaning "from the living earth."