ORCHIDS AND DIPTERA: SEX ON THE FLY

CAROL SIEGEL

THE FLY SWATTER IS EMBLEMATIC of how most people feel about flies. Denizens of dung, death, detritus, and dirt, flies are associated with filth and disease. People who swoon over butterflies and stand in admiration of bees feel positively righteous about squashing flies- or mosquitoes or pesky gnats. Despite the fact that flies are a unique and intriguing group, most of which have nothing to do with carrion and dung, nobody likes flies, except perhaps orchids. After the Hymenoptera (bees and wasps), the Diptera (true flies) are the most important pollinators of orchids. Van der Pijl and Dodson (1966) estimate that fifteen persent of all orchids are pollinated primarily by flies. According to Dorte Christensen (1994), that number is too conservative; he feels the number is closer to twenty-five percent.

For most people, orchids are beautiful flowers with a luscious smell, lovely colors, and arresting shapes. They wouldn't seem to attract flies at all. However, many orchids have surprisingly evolved disgusting smells, lurid colors, and weird shapes that imitate just the things that flies love the most. They fool the insects into thinking their stinky flowers are rotting corpses or feces or tasty aphids or fungi, just the things to lap up or give your larvae. Orchids provide (or pretend to offer) precisely the things that attract the Diptera to visit, linger, and, incidentally, pollinate.

Although many orchid genera have a few fly-pollinated species, four large groups have become predominantly myophilous (adapted to flies for pollination). Fly pollination is the rule in the tropical and almost exclusively epiphytic subtribes Pleurothallidinae in America and Bulbophyllinae in the Old World. Flies rule where it is cool and are particularly abundant at high altitudes and high latitudes where bees are not as common. For example, the Pleurothallidinae are very diverse in cool forests in the mountains where flies are found in greater numbers. Other important myophilous groups include most subtribes of Diurideae in Australia, especially Pterostylidinae and Acianthinae, and some of the pantropical and north temperate Cypripedioideae.

What Distinguishes Diptera?

The Diptera are commonly known as true flies and include many insects we are familiar with- mosquitoes, black flies, midges, fungus gnats, fruit flies, blow flies and house flies. Rather common, flies are found in numbers all over the world except Antarctica, and even that inhospitable place supports a few midges. Flies, like humans, are everywhere. About 160,000 species of flies have been described by scientists with named species increasing by about one percent a year; it is thought that there are between 400,000 and 800,000 fly species. Many more remain to be named, especially in the tropics. Researchers, in general, are more interested in studying shiny beetles and colorful butterflies than flies that are difficult to study and preserve which is why so many remain undiscovered and unnamed.

Over 3000 species of flies have been found in amber or other fossils. The earliest fossil flies are from the Upper Triassic, about 225 million year ago. Since then, flies have burst onto the insect scene to become a terrifically successful group. Although estimates vary, Stephen A. Marshall (2012) claims that between fifteen and twenty percent of all animal species are flies—amazingly, one in five or six! You can get an idea of how prevalent they are by looking at the splatters on your windshield when you have driven on the highway. In aquatic environments, they may be 35% of all animal species.

Greek philosopher Aristotle named Diptera more than 2000 years ago. "Di" means "two" and "ptera" means "wing." Most insects have four wings, but flies have one pair of functioning wings. The hind wings termed "halteres," are reduced to small stalked and club-like knobs that function as gyroscopes, bobbing up and down, to help with balance during flight. The halteres are responsible for the astonishing aerial agility of flies. Because of the reliance on only one set of wings, the bulging mesothorax is enlarged to contain the enormous flight muscles while the pro- and metathorax are reduced, resulting in the characteristic fly shape.

Flies taste with their feet! After tasting a sweet surface, a few pollen grains, or decaying matter, they regurgitate salivary enzymes onto the surface, liquefying the materials so they can flow by capillary action up the trough-like pseudo-trachea tubes toward the mouth. They feed primarily on liquid food, free water, soluble solids, and fluids of living and decaying plants and animals. Generally short-lived and freed of the burden of nursing or collecting food for their brood, they forage mainly for carbohydrates for their energy metabolism. Their bodies are not modified to carry pollen back to their offspring. They deposit their eggs on or near a food source for their larvae.

Brood Site Imitation or Come Lay Your Eggs on Me

Many orchids reward flies with nectar or soluble pollen masses in exchange for a pollination visit. However, orchids as a group have made a very successful living by cheating pollinators. Fully one-third attracts a pollinator by promising something they do not, and indeed cannot, deliver. Eleven percent of all orchids promise flies that they are a wonderful and appropriate place for them to lay eggs, a case of false advertising called "brood site imitation." Because many fly larvae do not move very far to find a food source, the female Diptera tries to make sure her eggs are placed on a

nourishing place to develop. Flowers tend to imitate desirable egg-laying sites such as mushrooms or the fruiting bodies of fungus (mycetophily), carrion (sapromyophily), or dung (copromyophily). This deceit occurs in many highly-evolved plant families including Aristolochiaceae, Asclepiadaceae, Araceae, Burmanniaceae, Hydnoraceae, Rafflesiaceae, Taccaceae, and, of course, Orchidaceae.

This mimicry seems related to environmental conditions, especially temperature, so it becomes less common further north and south of the tropics. Although the syndrome is absent in Europe, it is strongly developed in the tropics and especially Sub-Saharan Africa and southeastern Asia, where pollinator flies are common, although examples do exist in some temperate species. The females are thought to be responding to olfactory chemical stimulation since olfactory stimuli are the most important in inducing egg-laying. Johannes Stokl and associates state, "With approximately eleven percent of orchid genera using brood-site mimicry, this is one of the most widespread deceptive mechanisms in the Orchidaceae."

Come Lay Your Eggs Amid My Aphids

Many Syrphidae, commonly called syrphid flies, flower flies, or hover flies, lay eggs near aphids. These important pollinators are the "beauties" of the fly world with bright attractive colors. Popular with photographers, they have readily observed behavior with 6000 or so named species. They range from just a few millimeters to a couple of centimeters in length, from non-descript black flies to stunningly beautiful mimics of bees and wasps. Flower constancy is highly developed in syrphid flies, making them a desirable and important pollinator of orchids.

The adult syrphids feed on nectar or pollen, but many of the larvae feed on aphids and their honeydew excretions (excess sugars secreted from the rear end of the aphid). The larvae are very efficient predators of aphids. The fly larvae, laid as eggs among aphids, feed voraciously, casting about with their blind, tapered heads, grasping the soft-bodied aphids using mouth hooks. Their helpless victims are held aloft until partially consumed and then cast aside in a wasteful manner. They feed on dozens of doomed aphids before pupariating (the process of larval-pupal transition) among their prey to transform into black and yellow flower flies. Orchids deceive syrphids into laying their eggs on what they think are aphids in what is called "prey imitation." Since no aphids are present, it is a case of false advertising, but the orchid gets pollinated (which is real).

Flies first diversified into their main lineages millions of years before nectar-rich flowering plants proliferated. The first flies probably picked up honeydew from leaf surfaces, Scale, aphids and other honeydew-producing homopterans were abundant long before flowering plants, and the honeydew was lapped up as fly fuel. Although flies now use nectar sugar, honeydew is still relevant to the group.

In my area in Las Vegas, *Epipactis gigantea*, the Chatterbox Orchid (for its movable lip), grows in many places along wet stream faces and seeps. On an orchid discovery walk, our club watched as syrphid flies, carrying bright yellow pollinia on their backs, flitted among the orchids to lay their eggs. Syrphid flies were documented in 1966 in the National Geographic with pollinia attached to their backs (130:6). This orchid species ranges from British Columbia to California, Arizona and New Mexico into southwestern South Dakota, growing along gravel shores of lakes and rivers, on sandbars in streams and seepage areas.

Syrphid flies also lay eggs in *Epipactis veratrifolia,* found throughout the Middle East, eastwards to the Himalayas, and south to Somalia and Ethiopia. This species, which is exclusively pollinated by five species of aphidophagous (aphid-eating) hoverflies, produces a scent that is similar to a number of aphid species. This generalized mimicry makes sense since its five pollinating hoverfly species feed on different aphid species. *Epipactis veratrifolia* shows just how complicated deception can get. The flowers present a real nectar reward in addition to the deceptive impression of an aphid reward. Small amounts of nectar are presented freely on the lip; adults lap this up. Males may defend the territory around the orchids and try to copulate with females approaching the flower. They contribute to pollination as nectar feeders. The females hover, land on the lip, lick the nectar and lay an egg on the lip or other parts of the flower. They may pollinate the flower during this process. Is this a deceptive orchid? It does present a small amount of actual nectar reward, but it is, on the other hand, advertising a different reward from that which is provided, which is indeed deception.

Epipactis veratrifolia misleads female hoverflies by bearing structures that look and smell like aphids. On the epichile of the lip, there are small, orange, drop-like lumps like honeydew. On the hypochile are some black warty bubbles that look very aphid-like or may even resemble a group of visiting flies. The flowers produce the same volatile compounds as are found in the alarm pheromone of some aphid species. The aphids not only produce this compound when under attack, but they also produce a small amount of it all the time; it is a reliable way of locating an aphid colony. The scent induces oviposition (egg-laying) in the female hoverflies.

The Japanese *Epipactis thunbergii* may exhibit a similar pollination strategy and is pollinated by several syrphids that also deposit eggs.

The large Asian genus *Paphiopedilum* attracts hoverflies to lay eggs on the staminode with its version of aphid mimicry. John T. Atwood, in 1985, studied the syrphid fly *Dideopsis aegrata*, a frequent pollinator of *Paphiopedilum rothschildianum* on Mt. Kinabalu. The flower emits a peppery smell and mimics brood sites of the female flies with the staminode and glandular

hairs looking like an aphid colony. Aphids are usually found on nectariferous plants in the same habitat. Atwood found as many as 76 eggs on one staminode. It is thought that egg-laying behavior is stimulated by promising smells and structures—lines, spots, warts, textures, and contrasting colors. The fly falls in the pouch of the orchid and takes about a minute to climb out the exit passage, pollinating the orchid after laying its doomed eggs.

Another example, *Paphiopedilum dianthum*, is also pollinated exclusively by egg-laying female hoverflies. *Paphiopedilum barbigerum,* pollinated by hoverflies, is a case where no eggs are deposited by the flies, and no floral odor can be detected. Perhaps the orchid is exploiting the innate color preference of the flies.

Some paphiopedilums attract hoverflies with generalized food deception, and usually have a bright yellow staminode. The syndromes of generalized food deception and brood site deception often overlap and are difficult to separate. In *Paphiopedilum villosum*, color contrast is the long-distance lure where hoverflies are attracted by the bright yellow staminode. The odor has been described as faintly like urine, which mimics the body fluids rich in salt that hoverflies like. Close-range attraction is thought to be the glittering staminode that may suggest honeydew. There is a slippery wart in the center that throws the fly into the pouch. When the hoverfly climbs out, the pollinium is attached to the thorax.

It is interesting to note that some *Paphiopedilums* and *Phragmipedium* species, both "slipper orchids," are pollinated by syrphid flies, but each genus has its fake infestations of aphids on different floral organs. Whereas the staminode is the aphid mimic on paphiopedilums, the staminode on phragmipediums is not exaggerated or vividly pigmented or ornate and may merge with the infolded margins at the base of the labellum. The infolded margins forming the rim and entrance to the dorsal opening of the labellum are the fly attractant and may show pigmentation patterns. In *Phragmipedium reticulatum*, *longifolium*, and *pearcei*, they are broad and intensely spotted. The gravid female visits before falling into the pouch.

Looking Like a Mushroom

Among the strangest orchids are the ones that look and smell like mushrooms and display the "fungus gnat syndrome." Mushroom- or toadstool-imitating orchids exploit the egg-laying or feeding behavior of fungus gnats and some other tiny Diptera. (Fungus gnats are part of a taxonomically controversial group that usually is thought to include the Mycetophilidae and Sciaridae). These mini-Diptera like to lay their eggs on fungi, which provide a food source for their larvae. They are attracted to anything mushroom-like, and many orchids oblige by doing a very convincing imitation of a mushroom. In Australia, New Zealand, and southern Asia, tiny plants of the genus *Corybas* have dark-colored flower heads borne upright near the ground level. The nectarless flowers in several species have reduced and rudimentary lateral sepals and petals to resemble mushrooms more closely. Growing in little groups on the forest floor, they resemble mushrooms growing in rotting leaf litter, a bizarre illusion to get pollinated. New Zealand, where the genus is prevalent, has few bees, and flies take their place as pollinators.

Similarly, *Cypripedium debile* of Japan and *Cyp. fasciculatum* of the coniferous forests of North America bear modified flowers that droop near the ground and have a pouched lip whose entrance bears a resemblance to small mushrooms. The dwarf species with a circular opening at the underside completes the illusion with a strong mushroom smell and many additional black-brown markings imitating gills. They deceive fungus-seeking flies like the Mycetophilidae.

In 1978, Vogel collected 125 examples of fungus-mimicry in the South American genus *Masdevallia*, now separated into the genus *Dracula*. The epichile of the lip of some draculas, such as *Dracula vampira*, even has a horseshoe-shape and radiating gill-like ridges on the side that face downward, just like the inverted cap of a mushroom. The scent is often like a supermarket mushroom. Fungus-gnat orchids dwell on the dark forest floor with flowers close to the ground (geophily) and are usually dark purple-brown with white or translucent patterns to complete the mushroom illusion. Gnats usually lay their eggs in the lamella or papery rib beneath a mushroom cap and, misled by the olfactory, visual, tactile, and humidity orchid stimuli, do so in these mushroom-mimics. Unable to eat the orchid tissue, the eggs and larvae perish, but the orchid often gets pollinated, the point of this elaborate deception.

One of the strangest orchids is *Cypripedium fargesii,* a critically-endangered species endemic to southwestern China, whose mottled leaves look like they are infected with Cladosporium fungus. The deceptive orchids attract the Platypezidae or "flat-footed flies," true fungus-eating flies, that like to drink up the wet exudates of leaves infected with Cladosporium by growing close to the ground in the leaf litter. Each short flowering stem bears rows of black spots on the upper surfaces, and the stem terminates in one small dark-red to dull-yellow flower with a faint unpleasant odor of rotting leaves. When Cladosporium infects leaves and fruits, it produces black mold spots. The black spots on *Cyp. fargesii*, along with the rotting leaf smell, fools these flies into thinking they are going to get a rotting leaf meal. Instead, they get nothing but a chance to pollinate this orchid. It is one of approximately five closely-related *Cypripedium* species in China which look like their leaves are infected with fungus.

According to Marc Hachadourian of the Bronx Botanical Gardens, it has been hypothesized that the jewel orchids with veins like the genus *Anoectochilus* and *Macodes*, hiding as they do among the rotting leaf litter, may also mimic fungal hyphae. No published studies confirm this.

Stinking Like a Herd of Dead Elephants

Not only do flies breed in fungus but some breed in (and also feed on) decaying organic matter (sapromyophily). These flies find smelly, dull greenish to purple-brown flowers with strong and unpleasant odors resembling decaying meat irresistible as places to lay eggs. With orchids that mimic dead things to attract flies, it is a false lure that causes the fly to waste eggs that die for lack of food. Nectar may or may not be present, but if it is, it is often remarkably rich in amino acids to help trapped flies survive until they visit their next flower. These are the stinky orchids that look and smell like death and decay and are frankly repulsive to us.

Orchids are not the only stinky plants to deceive flies in this way. Duped Dipterans can be found at many foul-smelling plants including the famously enormous *Rafflesia arnoldii* (the Stinking Corpse Lily) of Southeast Asia. The Corpse Flower (*Amorphophallus titanum*) is an Indonesian giant with flowers clustered in typical aroid fashion along a central heat-generating spadix up to eight feet tall (2.4 meters), rising from a vase-shaped spath as wide as 12 feet (3.7 meters). The enormous blossoms put out a powerful stink that attract flies even at a distance.

Olfaction (smelling) is an important sense for flies, and many important behavioral and developmental changes are directed by different kinds of pheromones. For example, males are attracted to females by volatile hormones, and females use olfaction to find suitable sites to lay eggs. The olfactory receptors are found mainly on the antennae and less often on the palpi (an appendage attached to an oral part and serving as an organ of sense in insects). Vision is thought more important in finding flowers, but smell is most important in locating decaying material.

The pantropical orchid subtribe Bulbophyllinae contains some of the worst smelling and most repulsive orchids in the world. They often have a nasty smell like decaying flesh, dirty diaper, or cat urine. To us, these are stinky, funny-looking flowers. To the flies, they must seem beautiful and desirable places to entrust their offspring. For flies, it appears that bad smells are good things.

For example, *Bulbophyllum fletcherianum* from New Guinea is pollinated by carrion flies, and when it is in bloom, it smells like a herd of dead elephants. You can buy it on EBay for as little as US$35, but nowhere do they tell you that this not a house plant. They call it the Tongue Orchid because its flowers look like big meaty red tongues sitting on seven-foot leaves. The seed pod is the size of a hand grenade, and each one has a cup of orange-yellow seed. With leaves five feet long, *Bulbophyllum phalaenopsis* is a true stinker. Pollinated by carrion flies, its flowers look and smell like rotten liver. *Bulbophyllum beccarii*, found in New Guinea and one of the largest of the bulbophyllums, has leaves that can be six feet long. Its flowers are said to smell like a rotting Borneo pygmy elephant, which I suspect is not a good thing. It has been called the worst smelling flower in the world, a dubious distinction. *Bulbophyllum echinolabium* from Sulawesi attracts flies with a fragrance that best resembles the odor from the toilet in the boys' bathroom. Fortunately, it smells most when the flower first opens, and the beautiful successively-opening flowers compensate for the relatively brief urine smell.

Bulbophyllinae is the Old World counterpart to the neotropical Pleurothallidinae with parallel evolution of adaptation to fly pollination. In the subtribe Pleurothallidinae, flies are often attracted by the smell of decay in several sapromyophilous orchids. They both often attract flies with their foul odors and resemblance to dead things. They both have spots, glands, slime, hairs, motile lips and appendages, and dull cream to yellowish green to purplish brown-colored flowers. Many trap their fly pollinators with ingenious devices to cause them to linger. Most pleurothallids are pollinated by small, nectar seeking flies like the Drosophila-like flies.

Many other orchids attract flies with foul odors. *Satyrium bracteatum* from South Africa has fleshy brown to black flowers and fits the sapromyophilous syndrome. It imitates the color and scent of rotting animals, feces, and putrid meat where carrion flies lay eggs. The pollinator lands near the plant and walks into the gaping mouth of the flower, where pollinia are deposited on the eyes of the flies. Sadly, these may gradually become blinded by the mass of the pollinia after several visits.

Rendezvous Flowers or Cruising for Females

Orchids often provide males a place to cruise for females. As we have noted with *Epipactis veratrifolia*, male flies have figured out that they might have a chance to mate by hanging around orchids where females stop to feed or lay their eggs. Some orchids exploit the sex drive of male flies during mate-seeking flights. Male flies defend their flowers and mate with females who are laying eggs, contributing to pollination.

For example, Johnson and Steiner (1994) observed pollination of *Disa obtusa* by nematoceran flies in Cape Province, South Africa. The flower only blooms in the first season after a fire, once in every five to forty years. Attracted by a strong scent from the nectarless flowers, the flies regularly mate on the flowers, with the males engaging in ritual fighting for females. Pollination success of 84% occurs, with both sexes carrying pollinia, and the only attraction seems to be that the orchids provide an attractive place to mate.

Draculas also provide shelters and rendezvous sites for flies during the prolonged rainy season. Even when rain violently disturbs the flowers, the spreading sepals act as a roof and protect the flowers' reproductive organs and their mating visitors.

Orchids sometimes supply flies with an attractant chemical that boosts their sex pheromone system to attract females. Some male fruit flies (*Bacterocera*) and some bactrocerophilous bulbophyllum have developed

a mutually beneficial system. Flowers of the *Bulbophyllum macranthum*, for example, release floral zingerone, the pungent essence of ginger to attract several fruit fly species. The zingerone is converted by the males to zingerole that acts as a sex pheromone to attract sexually mature female flies. The chemical is stored in the rectal gland and released as a sort of smoke during courting. Zingerone-fed males attract many more females than zingerone-deprived males. The *Bulbophyllum* species involved receive pollination service in exchange for this sexual success boost. Since fruit flies are often considered a pest, widespread eradication programs may threaten the reproduction of these wild orchids.

Having Sex with an Orchid

Not only do some male flies visit orchids to mate with a female fly, but some of them also visit orchids to mate with an ORCHID. Perhaps the most bizarre orchid deception involves flies that are so aroused by the scent, look and feel of an orchid that they try to mate with it. Called "pseudocopulation," or false copulation, it is only false for the insect. It is real for the orchid. The insect does not score, but the orchid does. In the course of the insect's frustrating amorous attempts, pollinia are picked up and delivered, and orchid sex is completed.

Sexual deception of insects has evolved at least six times in different lineages. It occurs with various insects in at least 18 orchid genera including many examples in the genus *Ophrys* in Europe, South African disas and, at least, nine genera of terrestrial orchids in Australia, altogether comprising about 400 species. However, Florian Schiestl says that this pollination syndrome is probably more widespread since new cases have been described in some genera of neotropical Maxillarinae and Pleurothallidinae. In the last group, sexual deception may be prevalent, Schiestl says, in the large genus *Lepanthes* with more than 800 species. Anecdotally, evidence exists for four other orchid genera, too.

Exploitation of fly mating behavior is important in the evolution of Telipogoninae (now Oncidiinae) and Pterostylidinae. Certain structures in flowers of *Trichoceros* species mimic the female of tachinid carrion flies. Van der Pijl and Dodson (1966) claim that the simulated insect in the lip "is commonly so life-like that it appears as though it could easily fly away." Males, attracted to the visual mimicry and receptive female smell, try to copulate with the flowers, which happily for the orchid, leads to pollination.

For example, *Trichoceros antennifer* is an amazing female fly mimic. It is found from Colombia to northern Peru at high elevations, growing among low-growing shrubs in relatively dry areas, usually on the bank of streams. These Compositae, primarily of the genus Mikania, attract numerous flies to its sweet fragrance and abundant nectar, especially Tachinidae. Female tachinid flies, when ready for copulation, land on a leaf in the sun and open and close their genital orifice for passing males. The flowers of *Trichoceros antennifer* simulate the female tachinid flies of *Paragymnomma* species in a remarkable way. The column and base of the orchid lip extend laterally to simulate extended wings. The stigma of the flower is located at the apex of the "false abdomen" of the flower and reflects sunlight like the female genital orifice. It has lots of bristles just like a fly. The male flies, stimulated by the signal from the genital orifice-like stigma, strikes the flower for a moment and picks up a pollinium.

The members of the genus *Telipogon* are similar, but the resemblance to a fly is not as pronounced. Bristles occur only on and around the column. The illusion is adequate to deceive male flies within their habitat, and seed pods are often found.

Pseudocopulation is also involved in the nectarless Australasian genus *Pterostylis*, the Green Hood orchids. The subtribe Pterostylidinae has only one genus, *Pterostylis* with 120-140 species, all terrestrial orchids with tubers. It is thought that all members of the group may be pollinated by pseudocopulation, attracted by a pheromone-like perfume combined with an insectiform labellum. Mosquitoes and mosquito-like fungus gnats are the most frequently reported visitor. Some male fungus gnats appear to be attracted sexually to the oddly insect-like small brown lip of *Pterostylis rufa*. The lip is an exquisitely sensitive trap, triggered by the tiny insect that weighs just one milligram. There is a specificity of odors in this genus, which leads to a strong specificity of visitors. A different species of fungus gnat is responsible for the pollination of each species of *Pterostylis*. It has been noted that insects visiting *Pterostylis* species appear to be intoxicated after several visits, perhaps a sort of reward.

Trapping the Little Bug(Ger) to Force Him to Stay

To operate the specialized pollination mechanism of orchids, many fly-pollinated deceiving orchids imprison or trap their pollinators for a short time. Only feeding insects can be made to orient themselves a certain way that is best for pollination. Most flies, excluding certain Syrphidae and Bombyliidae, are poor pollinators and require guidance to make them effective. They don't fly from flower to flower as bees do and are not designed for accurate guidance to a critical spot on the flower. They just fly back and forth in the neighborhood in steps, and land somewhere nearby. The flower adapts to this quality with an intricate guidance system that may include trap devices guiding non-adapted visitors or even catching and holding them with various mechanisms. The lip may be a see-saw affair that tips the fly into the sexual parts. There are often motile, club-like hairs vibrating in the wind, oscillators, to attract attention often with fine fringes or osmophores (odor-spreader) to allure the pollinator to approach. There may be peculiar slits or holes in the sides and transparent windows that guide flies to certain places in or out of the flower.

In the genus *Pterostylis*, flies are temporarily imprisoned in the orchid. The sepals form a hood, from one side of which the narrow lip may project before it is tripped by a visiting gnat. The lip is irritable, and when the fly touches the sensitive base, shuts upward, trapping the little visitor with its back against the column. If the insect is carrying pollinia, these are thrown into the stigma. The column has two wings near the tip, and the only way the insect can escape is by pushing between these wings with its back towards the column, picking up pollinia on the thorax. The gnats scramble about until they find the exit tunnel. You can imagine just how sensitive the trap is if you realize the tiny size of the gnat weighing only one milligram that is equivalent to 0.0000352 of an ounce!

In the *Bulbophyllum* complex, with over 2000 species, a balanced see-saw labellum hinged by a narrow springy claw tips over when the equilibrium is disturbed. The fly is thrown against the column so precisely that the poorly-directed flies can become efficient pollinators. Without this, pollination simply would not occur. *Bulb. macranthum* and *Bulb. gerlandianum* have non-resupinate flowers that rely on a sliding trap device that steers the fly down the oily vertical sepals onto the column. In *Bulb. gracillimum*, little dipterans on the pendant sepals climb to reach the balancing point on the lip and then are pitched into the column.

In many pleurothallids, there is a hinged motile lip for close range guidance where the fly's weight makes the lip turn at the balancing point to force the fly against the column. You find this in orchids in the genera *Dracula, Masdevallia, Pleurothallis, Dryadella, Zootrophion*, and *Scaphosepalum*. In *Acostaea* (now subsumed in *Specklinia*), Condylago (with two species now subsumed in the genus *Stellis*), and *Porroglossom*, there is a spring-loaded lip that works by changes in turgor, and a stimulus causes the lip to snap smartly and trap the intruder. In *Porroglossum muscosum,* it has been observed that the gentlest touch of a hair or by the foot of an insect will cause the lip to snap shut in less than two seconds.

Vogel suggested that flies in many Pleurothallidinae are guided by osmophores positioned on long appendages or inside the flower. The appendages are tail-like as in *Restrepia antennifera* (dorsal sepal), *Myoxanthus reymondii* (petals), *Dresslerella hirsutissima* (sepals), or form an area surface on the fused sepals inside the flowers as in *Scaphosepalum verrucosum.* In the genera *Masdevallia* and *Dracula*, elongated tips of the three sepals have osmophoric functions. They can smell like semen in *Myoxanthus reymondii*, musk in *Masdevallia caudata,* trimethylamine in *Diodonopsis erinacea*, or rancid butter in *Specklinia fuegi*. The appendages, moving in the breeze, are visually attractive.

The presence of strange transparent windows has also been reported and is present in orchids like *Paphiopedilum fairrieanum.* The window guides the fly and is thought to be related to the behavior of flies moving toward light in dark places. They are often mentioned as guidance for trapped insects inside the lip of Cypripedioideae. In this orchid, there are auxiliary transparent windows in the dorsal sepals.

A strange variation on a theme occurs in *Bulbophyllum gerlandianum* where the lip is very mobile, allowing the weakest breeze to keep it vibrating. The flies lick nectar from a groove in the lip, but the weight of the fly is not sufficient to pitch it into the column. The flower relies on wind assistance in its windy habitat to passively throw the fly. This is the first known case of wind-assisted pollination of an insect-pollinated plant. *Bulbophyllum weddellii* and *Bulbophyllum ipanemense* are also pollinated by wind-assistance. Small amounts of nectar keep the insects long enough on the flowers to allow the wind to gain sufficient velocity to do the job.

Disa Draconis Joins a Guild

There is marvelous kind of deception that involves flies that is called "guild mimicry." These include nectarless orchids that imitate a whole group of unrelated flowers that do have lots of nectar. They pretend to be in the same guild (a group of plants having a similar habit of growth and nutrition) to encourage pollinator visits.

The most outstanding example of guild mimicry occurs with the orchid *Disa draconis* in southern Africa and its pollinator, a tanglewing fly, the mega-nosed fly or "Pinocchio fly" (*Moegistorhynchus longirostris*). His proboscis, the longest mouthpart of any known fly, protrudes four inches from its head, five times the length of its bee-sized body. In flight, the prominent proboscis dangles between the insect's legs and trails behind its body. This weird organ enables it to reach deep pools of nectar inaccessible to less superbly endowed pollinators. Evolution has left this amazing pollinator and its guild of 20 long-spurred plant species dependent on one another, examples of extreme specialization. The plant guild of the mega-nosed fly includes a wide variety of plant families including Iridaceae, Orchidaceae, and Geraniaceae. Although unrelated, all these guild members are morphologically similar having cream or pink flower color, long, straight floral tubes or spurs, flowers that are open during the day at the same time, and no scent. Steve Johnson and Kim Steiner studied *Disa draconis* and found that, unlike the others in the guild, *draconis* has no nectar. The fly is deceived into visiting and pollinating the orchid because of its resemblance to other rewarding sympatric (originating in or occupying the same geographical area) flowers in the guild. This false advertising is all that is necessary for reproductive success.

Such extreme specialization comes at a cost. The mega-nosed fly is threatened by the loss of wetland breeding habitat and by the loss of other insects they parasitize during their larval stage. Already, some flowers in the long-nosed guild produce no seeds because their exclusive pollinator is locally extinct.

It is interesting that the members of the guild are

greatly influenced by their shared fly pollinator. Most guilds are geographically localized to the habitat of the pollinator, so *Disa draconis* and its guild members are confined to a narrow strip of the Cape's west coast. The fly influences orchid flowering time as well, and the guild of plants pollinated by the fly (*Moegistorhynchus longirostris*) blooms when the fly is on the wing. Because the plants in the guild compete for pollination success, pollen and pollinia are deposited on different parts of the fly's body depending on the species of the flower. The appearance of the flowers, too, is influenced by fly morphological preference. Therefore, the fly affects not only orchid color and size, but flowering time, and pollinia placement as well.

South Africa has high levels of pollinator system specialization, and this is not the only plant guild there. Johnson (2014) points out that the long-proboscid fly pollination system consists of several distinct pollination guilds. To date, more than 20 different pollination guilds varying from five to over 100 plant species have been identified in the South African flora, and most guilds have orchid members. Not all are pollinated by flies. *Disa uniflora* is part of a guild of approximately 25 South Africa plant species specialized for pollination by the mountain pride butterfly *Aeroptes (Meneris) tulbaghia.*

Summary

Orchids have adapted to the Diptera by cleverly pretending to be the solution to some of their life cycle needs. Although orchids do sometimes offer real nectar rewards to encourage flies to stop by, they often fool this pollinator into becoming a pollen taxi by pretending to be a suitable place to lay eggs. Whether by imitating fungi or colonies of aphids or decaying matter, the orchid induces an otherwise-uninterested insect into visiting. Pretending to be a sexually willing female or a good place to mate, orchids have inserted themselves into the sex life of the fly. Manipulating and detaining flies with seesaws and traps further contribute to pollination success. Finally, by looking and smelling just like groups of flowers that do offer a nectar food reward, nectarless orchids have succeeded in luring an unlikely pollinator. The Diptera have become essential to the survival of many orchids, and flies and orchids have become tied together through evolution.

References

Christenson, Dorte. "Fly Pollination in the *Orchidaceae*," *in Orchid Biology Reviews and Perspectives VI,* edited by Joseph Arditti 415-454. New York: John Wiley & Sons. 1994.

Dressler, Robert L. *The Orchids Natural History and Classification*. Cambridge, Mass: Harvard University Press. 1981.

Edens-Meier, Retha, Yi-bo Lueo, Robert Pemberton, and Peter Bernhardt. "Pollination And Floral Evolution of Slipper Orchids (Subfamily Cypripedioideae)," in *Darwin's Orchids Then and Now,* edited by Retha Edens-Meier and Peter Bernhardt 265-287. Chicago and London: The University of Chicago Press. 2014.

Endra, Lorena, D. A. Grimaldi and B. A. Roy. Lord of the Flies: Pollination of *Dracula* Orchids. *Lankesteriana*.10(1): 1-11. 2010.

Johnson, Steven D. "Pollination of South African Orchids in the Context of Ecological Guilds And Evolutionary Syndromes," in *Darwin's Orchids Then and Now*, edited by Retha Edens-Meier and Peter Bernhardt 71-90. Chicago and London: The University Of Chicago Press. 2014.

Marshall, Stephen A. T*he Natural History and Diversity of Diptera*. Buffalo, New York: Firefly Books.2012.

Peakall, Rod. "Pollination by Sexual Deception in Australian Terrestrial Orchids," *Nature* (February 2007) http://www.anu.edu.au/BoZo/orchidpollination/ Accessed January 1, 2012.

Proctor, Michael, Peter Yeo, and Andrew Lack. *The Natural History of Pollination.* Portland, Oregon: Timber Press. 1996.

Schiestl, Florian P. "On the Success of a Swindle: Pollination by Deception in Orchids." Nurwissenschaften 92 (2005):255-264, doi10.1007/s00114-005-0636-y.

Sessions, Laura A. and Steven D. Johnson. "The Flower and the Fly." *Natural History* 114 (2) March 2005:58-63.

Stokl, Johannes, Jennifer Brodman, Amots Dafni, Manfred Ayasse and Bill S. Hansson. "Smells Like Aphids: Orchid Flowers Mimic Aphid Alarm Pheromones to Attract Hoverflies for Pollination," *Proceedings of the Royal Society* (October 2010), i10.1098/rspb.2010.1770.

Tan, K.H. "Fruit Fly Pests as Pollinators of Wild Orchids," *Orchid Digest* 73 (3) July, August, September 2009: 180-187.

Van der Cingel. *An Atlas of Orchid Pollination: America, Africa, Australia.* Rotterdam: AA Balkema. 2001.

Van der Pijl and Calaway Dodson. *Orchid Flowers: Their Pollination and Evolution*. Coral Gables, FL: University of Miami Press. 1969.

Wiegeman, Brian M. and David K. Yeats. "Diptera the True Flies" Version 29. November 2007. In the Tree of Life Web Projects http://tolweb/org/8226/2007.11.29

Zoon, Xin Ren, De-Zhu Li, Peter Bernhardt and Hong Wang. "Flowers of *Cypripedium fargesii* (Orchidaceae) Fool Flat-Footed Flies (Platypezidae) By Faking Fungus-Infected Foliage" doi/10.1073/pnas.1103384108. March 1, 2011. Accessed August 11, 2012. www.pnas.org/cgi/

About the Author

Carol Siegel, a retired English teacher and medical offi ce manager, has been president and newsletter editor of the Greater Las Vegas Orchid Society for several years. She lectures on many subjects at societies, museums, and universities around the country and has written articles on Nevada's native orchids in addition to many for the Orchid Digest. Carol leads groups of Clark County school children on tours of the Springs Preserve, a museum and nature center complex. Carol Siegel E-mail: growlove@cox.net

Satyrium bracteatum
©Lourens Grobler

Bulb. macranthum releases floral zingerone to attract fruit flies and a sliding trap to steer the fly.
©Lourens Grobler

The smell attracts the flies to *Bulb. phalaenopsis.*
©Eric Hunt; Grower: Petite Plaisance

Bulb. Echinolabium attracts flies with its odor
©Eric Hunt; Grower: Petite Plaisance

The bristles of *Telipogon berthae* occur on and around the column, and deceive male flies.
©Lourens Grobler

Bulbophyllum fletcherianum pollinated by carrion flies.
©Ron Parsons; Grower: Zeon Zhou

Epipactis gigantea
©Ron Parsons

Paph. dianthum uses aphid mimicry.
©Ron Parsons; Grower: Zeon Zhou

Paph. barbigerum perhaps has a color that attracts the flies.
©Ron Parsons; Grower: Chris Mende

Dracula vampire attracts with the look and smell of a mushroom.
©Murray Cooper

Paph. rothschildianum uses aphid mimicry.
©Ron Parsons; Grower: Zeon Zhou

Cypripedium fargesii attracts fungus-eating flies.
©Ron Parsons

Pterostylis cheraphila traps flies in the sepal hood.
©Ron Parsons

These orchids mimic mushrooms. Left: *Cypripedium debile*; *Cypripedium fasciculatum*
©Ron Parsons

The spots on the wide, infolded margins of the labellums of these three species attract the flies.
Left: *Phrag. longifolium;* Center: *Phrag. pearsei*, Right: *Phrag. reticulatum*.
©Ron Parsons Growers: Left & Center: White Oak Orchids; Right: Howard Gunn

Dresslerella hirsutissima sepals have osmophores to guide the fly.
©Ron Parsons; Grower: Cindy Hill

Restrepia antennifera with osmophores on the dorsal sepal.
©Ron Parsons; Grower: Mary Gerritsen

Paph. villosum uses color contrast and odor to attract flies.
©Ron Parsons; Grower: Brad Cotten

18 Myoxanthus reymondii - grower_DanNewman_HangingGardens Ron Parsons...

Myoxanthus reymondii has osmophores on the petals.
©Ron Parsons; Grower: Hanging Gardens

Corybas diemenicus resembles a mushroom.
©Ron Parsons

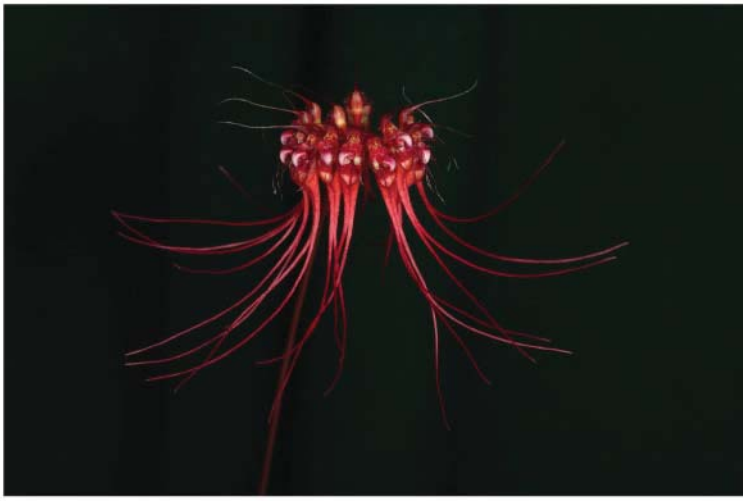
Epipactis veratrifolia lured a hoverfly by mimicking alarm pheromones usually emitted by aphids.
© MPI Chemical Ecology, Johannes Stökl

Masdevallia pollinated by tiny carrion flies.
Credit: ©Christian Ziegler/Minden Pictures

Masdevallia caloptera pollinated by Blue Bottle Flies.
©Christian Ziegler/Minden Pictures

Bulb. corolliferum and flies.
©Christian Ziegler/Minden Pictures

Trichoceros antennifer is a female fly mimic.
©Lourens Grobler



Bulb. gracillimum pitches the fly into the column.
©Eric Hunt